

INCIDENCE OF PARASITIDS ATTACKING ENDEMIC SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE) POPULATIONS IN NEW BRUNSWICK

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Abstract

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Annual population estimates of spruce budworm, *Choristoneura fumiferana* (Clem.), larvae and the incidence of larval parasitism were monitored in northern New Brunswick following the collapse of the 1949–1959 epidemic in the region. The most common parasitoid among the very sparse hosts was *Synetaeris tenuifemur*, although it had been rarely found during the epidemic. Larval parasitism sometimes exceeded 50% but it could not be shown as a key factor associated with changing host abundance.

Résumé

Dans le nord du Nouveau-Brunswick, après que l'épidémie de Tordeuses des bourgeons de l'Épinette eut fortement diminué, les auteurs suivirent de près la population annuelle des larves de la Tordeuse et le taux de parasitisme des mêmes larves. Le parasitoïde le plus commun sur les hôtes devenus rares était *Synetaeris tenuifemur*, bien qu'auparavant, durant l'épidémie, on l'ait alors trouvé rarement comme parasite des larves. Parfois plus de 50% des larves étaient parasitées mais on ne put prouver qu'il s'agissait d'un facteur principal affectant l'abondance des hôtes.

Introduction

Several studies have been carried out on the abundance and diversity of parasitoids attacking epidemic populations of the eastern spruce budworm, *Choristoneura fumiferana* (Clem.), (Dowden *et al.* 1948; Wilkes *et al.* 1948; McGugan and Blais 1959; Blais 1960; Miller 1963). One conclusion arising from these studies in different regions of eastern North America is that many species of parasitoids attack outbreak populations but only about 15 could be classed as prevalent in a region and common to all regions. Of these 15, five could be classed as univoltine and, by implication, relatively specific to the spruce budworm. Even with this complex, parasitoids are not strong regulating agents over a wide range in host densities and are most prevalent in the declining phase of an outbreak after other factors have initiated the decline (Blais 1960; Miller 1963).

The observations above generally apply to epidemic populations and only limited data have been obtained at endemic or sparse population levels. Blais (1959) and Fye (1963, 1965) investigated endemic populations in the Gaspé and Ontario, respectively. We annually observed some aspects of parasitism in endemic populations in northern New Brunswick from 1960 to 1971 after the collapse of the 1949–1959 outbreak and our findings are the subject of this paper. The study was part of a program to detect factors that influence the abundance of endemic budworm populations.

The study area encompassed three watersheds in northern New Brunswick: Green River (referred to as area 1), Tobique (area 2), and Iroquois (area 3), although observations did not begin in area 3 until 1969. The three watersheds had two characteristics in common, a predominantly balsam fir, *Abies balsamea* (L.) Mill., cover type and budworm populations that followed somewhat similar density trends from 1950.

Methods

A total of nine plots were established in the three study areas and, within each, single mid-crown branches from 100 to 1000 trees were examined each spring to obtain a fix on budworm abundance. At that time, the bulk of the population was in the third and fourth larval instars. All larvae were collected from the branches and living larvae were reared individually in vials on fresh fir foliage. In these rearings, dead and dying

larvae were examined for disease, issuing parasitoids were identified, and surviving adults were used in oviposition studies. When circumstances permitted, a second collection was made during the sixth instar, from trees felled during pulpwood cutting operations. These collections were limited because of the major effort required to find larvae. No pupae were collected from endemic populations because, on the average, there was only one pupa on every 100 mid-crown branches. The first pupal collections were made in area 3 in 1969 when populations had reached a level of one pupa per two branches. Thus our parasitoid story is incomplete because it mainly includes those parasitoids that attack overwintering larvae and young larvae in the spring; parasites that attack later stages were not studied.

Lepidopterous larvae associated with the spruce budworm (excluding the rare Geometridae) were also collected from foliage samples and reared for parasitoid recoveries. The defoliator complex included: *Acleris variana* Fern. (blackheaded budworm), *Pulicalvaria* spp., *Griselda radicana* Walsh., *Eucordylea atrupictella* Dietz, and *Parapandemis borealis* Free. All stages (eggs to pupae) of the black-headed budworm were collected and reared as part of a special bird predation study (Gage *et al.* 1970).

Results

The densities of third-instar budworm larvae in study areas 1 and 2 from 1960 to the early 1970's are listed in Table I. A budworm epidemic covering both areas began in the mid-1940's and reached an epidemic density of about 350 third-instar larvae/m² of foliage in the early 1950's. Density declined rapidly in the late 1950's to an endemic level of about 0.05 in the mid-1960's which is equivalent to 3–5 feeding larvae per middle-aged fir tree. From 1968 to 1971 density increased in association with warm, dry weather and again reached epidemic levels in area 2 and some parts of area 1. Although the *trend* in density was similar in areas 1 and 2 the mean endemic densities, 0.06/m² in area 1 and 0.35/m² in area 2, in the mid-1960's were quite different (Table I). Furthermore, the change in density from the endemic (0.35/m²) to epidemic level (366/m²) in 1972 was 1000 times in area 2 but much less during the same time in area 1 (Table I). These points are discussed later in the text.

During the period of low budworm density in the 1960's about 4000 larvae were collected and a total of 18 parasitoid species was recovered (Table II). Table II also lists time of attack, some alternative hosts, and abundance relative to particular budworm population phases. The list applies to endemic populations and does not contain those species recorded during earlier studies of outbreak populations (Miller 1963). About 8000 other lepidopterous larvae associated with the budworm were reared and 21 parasitoid species were recovered (Table III). Surprisingly, 33 of the 39 parasitic species recorded in the study were relatively specific to one host even though most species searched current shoots containing a variety of prey. More species were reared from the spruce budworm and the blackheaded budworm simply because of our research interest and extra field collections of these two defoliators.

The number of budworm larvae reared each year and estimates of apparent parasitism by species are listed in Tables I and IV. The data are separated by areas and by plots in area 3 for two reasons:

- (1) The density in area 2 was consistently higher than in area 1 (Table I). The cause is not known although recent data on adult dispersal (Greenbank 1973) lead us to suspect that egg-carrying females from a persistent outbreak to the south of area 2 supplemented the native population. Whatever the cause it is possible that the different budworm densities had an effect on the incidence of some parasitoids.

- (2) Budworm densities increased in all three areas in 1968 and generally continued to increase over the next 4 years (Tables I and IV). But the rates of increase were quite

Table 1. Budworm density, number of larvae reared, and percentage parasitism by species, areas 1 and 2

	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972 ^c
	Area 1												
Budworm density ^a :	.25	.95	.29	.22	.06	.07	.06	.05	.41	2.44	1.50	3.34	10.9
Budworms reared													
Early collection	44	220	74	108	27	37	13	35	254	293	80	42	
Late collection	60	113	7	23	0	0	0	8	26	50	57	0	
Parasitoid													
<i>A. fumiferanae</i>	2	4	4	2	19	0	0	17	2	1	1	7	
<i>Apanteles</i> spp.	2	19	3	13	4	11	0	3	5	18	0	0	
<i>G. fumiferanae</i>	0	0.1	0	0	0	0	0	0	0	0	0	0	
<i>T. arenicola</i>	0	5	14	4	0	0	0	0	4	0	9	2	
<i>S. tenuifemur</i>	31	10	10	18	0	3	15	17	1	4	9	55	
<i>M. trachynotus</i>	18	6	– ^b	4	–	–	–	–	–	0	4	–	
<i>E. nigripalpis tectulum</i>	0	0	–	2	–	–	–	–	–	2	4	–	
<i>A. interrupta</i>	0	0	–	0	–	–	–	–	–	4	0	–	
	Area 2												
Budworm density:	.48	.31	3.99	1.16	.41	.40	.32	.25	.50	3.57	18.3	168	366
Budworms reared													
Early collection	30	12	263	112	37	41	38	24	46	122	96	247	
Late collection	29	90	251	186	190	27	10	11	0	0	0	123	
Parasitoid													
<i>A. fumiferanae</i>	7	6	11	12	5	20	16	4	4	2	11	18	
<i>Apanteles</i> spp.	0	8	1	6	8	2	0	0	0	6	0	0	
<i>G. fumiferanae</i>	3	0	2	1	1	0	0	0	0	0	1	0	
<i>T. arenicola</i>	3	10	2	5	3	4	0	0	0	0	0	0	
<i>S. tenuifemur</i>	53	4	2	17	49	44	23	14	2	8	3	5	
<i>M. trachynotus</i>	0	18	6	3	4	0	0	0	–	–	–	0	
<i>E. nigripalpis tectulum</i>	0	0	0	0	0	0	0	0	–	–	–	0	
<i>A. interrupta</i>	0	0	0	0	0	0	0	0	–	–	–	0	

^aDensity of third-instar larvae per m² of foliage.

^bDash = no data.

^cPopulation count only.

different — in area 2 and parts of area 3 (plot B) there was a sharp and continuing rise in density, while in area 1 and plot A area 3, density stabilized in 1969, 1970, and 1971 following a minor increase. There is little doubt that this difference had an effect on the numerical response of some parasitoids.

In addition to area differences, it must be noted that the endemic period under study (1960–1967) was extremely short compared with past budworm cycles in eastern Canada and this also could have had some effect on host and parasitoid abundance.

Notes on Parasitoids Attacking Larvae and Pupae

Synetaeris tenuifemur (Wly.). *S. tenuifemur* was the most common parasitoid reared from endemic populations. It is univoltine, overwinters as a cocoon, and attacks small budworm larvae in June (Miller and Renault 1963). It was first recovered in area 1 in the declining phase of the 1949–1959 outbreak and we cannot explain our failure to find it at any earlier date at the peak of the epidemic.

The incidence of *S. tenuifemur* in relation to budworm density is shown in Tables I and IV. The maximum attack rate under the most favourable conditions of host and parasitoid density was 55% in area 1, 53% in area 2, and 42% in area 3. These data show the capability of *S. tenuifemur* to kill a high proportion of an endemic budworm population.

Table II. Parasitoids reared from endemic spruce budworm populations on balsam fir, 1960–1971

Spruce budworm parasitoids	Budworm stage ^a		Budworm population phase ^b			Alternative hosts
	Attack	Kill	R	D	E	
<i>Apanteles fumiferanae</i>	I–II	IV	X	X	X	
<i>A. petrovae</i>	L	L	X	XS	X	
<i>A. morrisoni</i>	L	L	S	X	S	<i>P. borealis</i>
<i>A. absonus</i>	L	L	X	S	X	<i>G. radicana</i>
<i>A. milleri</i>	L	L	S	S	S	<i>P. borealis</i> <i>Pulicalvaria</i> spp.
<i>A. renaulti</i>	L	L	S	0	S	<i>Pulicalvaria</i> spp. <i>G. radicana</i>
<i>Glypta fumiferanae</i>	II	VI	X	X	X	
<i>Tranosema arenicola</i>	I–II	V	S	X	X	
<i>Diadegma conodor</i> (Vier.)	IV	V	X	X	S	<i>A. variana</i> <i>E. autrupictella</i> <i>G. radicana</i>
<i>Synetaeris tenuifemur</i>	III–IV	V	S	S	X	
<i>Eubadizon</i> sp.	L	L	0	0	S	<i>Pulicalvaria</i> spp. <i>G. radicana</i> <i>A. variana</i> <i>E. autrupictella</i>
<i>Meteorus trachynotus</i>	V	VI	X	X	X	
<i>Exochus nigripalpis</i> <i>tectulum</i>	V–VI	P	S	0	S	
<i>Campoplex</i> sp.	L	L	S	S	S	<i>A. variana</i> <i>Pulicalvaria</i> spp.
<i>Actia interrupta</i>	V–VI	P	X	X	X	
<i>Elachertus cacociae</i> How.	L	L	0	0	X	
<i>Amblymerus verditer</i>	P	P	S	S	S	
<i>Trichogramma minutum</i> (Riley)	E	E	X	X	X	

^aI, II, III, IV, V, VI — larval instars; L — larvae, unknown instar; P — pupae; E — egg.

^bAbundance of parasitoid: X — common; S — scarce; 0 — none. Population phase: R — release; D — decline; E — endemic.

Table III. Specific parasitoids of *A. variana* and *Pulicalvaria* spp., defoliators of balsam fir associated with spruce budworm

<i>A. variana</i>			
ICHNEUMONIDAE		TACHINIDAE	BRACONIDAE
<i>Glypta</i> sp.		<i>Acta diffidens</i> Curt.	<i>Ascogaster</i> sp.
<i>Itopectis vesca</i> Tow.			<i>Ascogaster</i> nr. <i>argentifrons</i>
<i>Exochus peroniae</i> Tow. & Tow.			<i>Microgaster peroneae</i> Wly.
<i>Exochus decoratus scitulus</i> Prov.			<i>Meteorus argyrotaeniae</i> Johansen
<i>Phytodietus vulgaris</i> Cress.			
<i>Pulicalvaria</i> spp.			
ICHNEUMONIDAE	TACHINIDAE	BRACONIDAE	CHALCIDIDAE
<i>Diadegma</i> sp.	<i>Schizactia vitinervis</i>	<i>Meteorus pinifolii</i> Mason	<i>Copidosoma deceptor</i> Miller
<i>Campoplex</i> sp.	Thompson	<i>Eubadizon gracile</i> Prov.	<i>Perilampus fulvicornis</i>
<i>Pimploterus</i> sp.		<i>Agathis binominata</i> Mues.	prothoracicus Smul.
		<i>Orgilus</i> sp.	
		<i>Chelonus</i> sp.	

Two patterns of host-parasitoid interaction emerge from our data on *S. tenuifemur*. During the 1963–1967 low density period in area 1 the average parasitism was 13% (32 parasitoids from 243 hosts) dropping to 1% during the first year of budworm increase in 1968, but then climbing to 55% in 1971. We attribute this response to a host population that increased in 1968 and 1969, and then stabilized at a density of 2–3 larvae/m² in 1970 and 1971 (Table I). The same sequence of events may have occurred in plot A area 3. In this plot, budworm density stabilized at about 10 larvae/m² in 1970–1971 and parasitism reached the 42% level (Table IV).

In area 2 and in plot B Area 3, the response of *S. tenuifemur* was drastically different. In area 2, in the 1963–1967 low period of budworm density, the mean attack rate was 32% (209 parasitoids from 661 hosts). But as host density increased rapidly over the next 3 years, apparent parasitism dropped to 5% (Table I). It was still at 5% in 1971 by which time host density had increased rapidly and reached a level of 168/m² (Table I). A similar trend was recorded in plot B

Table IV. Budworm density, number of larvae reared, and percentage parasitism by species in two plots in area 3

	Plot A				Plot B		
	1969	1970	1971	1972	1970	1971	1972 ^c
Budworm density/m ² :	11.3	8.5	10.5	145	76.8	140	232
Budworms reared							
Early collection	297	192	52		187	156	
Late collection	315	109	— ^a		293	S ^b	
Parasitoid							
<i>A. fumiferanae</i>	1	1	8		7	10	
<i>Apanteles</i> spp.	6	0	0		0	0	
<i>G. fumiferanae</i>	0	1	4		1	3	
<i>T. arenicola</i>	0	0	0		0	0	
<i>S. tenuifemur</i>	17	24	42		1	3	
<i>M. trachynotus</i>	6	2	—		2	S	
<i>E. nigripalpis tectulum</i>	0	0	—		0	S	
<i>A. interrupta</i>	2	5	—		0	S	
<i>P. hariolus</i>	0	6	—		3	S	
<i>I. conquisitor</i>	1	5	—		8	S	
<i>A. ontario</i>	8	4	—		9	S	
Diptera	1	0	—		10	S	

^aNo data.^bS indicates sprayed.^cPopulation counts only.

area 3 where the attack rate by *S. tenuifemur* was drastically diluted to 3% as host density increased sharply to over 140 larvae/m² (Table IV).

It is concluded from these data that *S. tenuifemur* can respond in a delayed manner to relatively low rates of increase in budworm density but cannot respond to explosive increases. Furthermore the maximum rate of attack occurs at a host density of 5.0 to 10.0 larvae/m² of foliage. Thus, unlike the behavior of the 'classical' parasitoid, some factor(s) limits the response of *S. tenuifemur* so that the attack rate varies inversely with increasing host densities.

We attempted to derive a simple equation to describe the attack response of *S. tenuifemur*. Using the Watt (1959) model, parasitoid density was calculated on the assumption that the number of hosts attacked in one generation was equal to the number of attacking parasitoids in the next generation, an assumption of constant survival. In fitting the Watt model using iterative procedures, the values of $K = 75$, $a = 0.0041$, and $b = 1.7090$ gave the best fit to the observed number of attacked hosts.

Simulation runs with this model were not successful. In one run it was assumed that a released budworm population multiplied from a density of 0.05 to 200 in 5 years — a phenomenon observed in exploding epidemics. The model generated an attack rate of 6% in the second year increasing to 72% in year 6. However, no such attack rate was noted in the field and, in fact, the opposite trend was recorded in area 2. Next, it was assumed that budworm density increased at a much slower rate, as observed in area 1, but the model failed to reflect field observations. Royama (1971) has pointed out some inconsistencies in the Watt model.

***Apanteles* spp.** A complex of *Apanteles* attacks the spruce budworm and a recent taxonomic revision by Mason (1974) lists six species: *A. fumiferanae* Vier., *petrovae* Wall., *absonus* Mues., and the new species *milleri*, *renaulti*, and *morrissi*. Of these, only two are specific to the spruce budworm, *A. fumiferanae* and *A. petrovae*. *A. fumiferanae* is the more common. It was one of the most common species found in the declining phase of the 1949–1959 outbreak in areas 1 and 2, with an apparent parasitism ranging from 20 to 30% (Miller 1963). In the endemic phase, the incidence of *A. fumiferanae* in area 1 ranged from 0 to 19% (Table I) but the high values of 19% in 1964 and 17% in 1967 must be interpreted carefully because of the low number of hosts reared in those years. Instead, if the data for the low budworm density years of 1963 to 1967 are combined, they show that 13 *A. fumiferanae* were reared from 220 hosts giving an apparent parasitism of 6%. We conclude from these data that the general level of parasitism caused by *A. fumiferanae* was about 6% during the endemic phase in area 1. The species was more common in area 2. In the same period a total of 30 parasitoids was recovered from 252 hosts giving an apparent parasitism by *A. fumiferanae* of 12%. One obvious explanation for the difference is the higher endemic density in area 2.

As budworm density began to increase in 1968 and 1969, the incidence of *A. fumiferanae* dropped to 1% in area 1, 3% in area 2, and was still only at the 10% level in 1971 in an exploding outbreak in area 3 (Table IV, plot B). Thus, there is good evidence of a lagging response by *A. fumiferanae* to sharp increases in budworm density and, consequently, a failure to damp the release phase of an outbreak.

Little is known of *A. petrovae* because few were recovered from outbreak populations. During the endemic phase, its incidence was low in areas 1 and 2, although it was found in most years. It was not reared from defoliators associated with the budworm.

Of the remaining *Apanteles* spp. — *absonus*, *morrissi*, *renaulti*, and *milleri* — all have alternative hosts and all, except *milleri*, probably attack the budworm in June. Thus, their abundance would be determined by both alternate and alternative hosts. Except in 1961 and 1969, their level of attack was generally low. The high levels in 1961 and 1969 in area 1 can be traced to *A. absonus* (Table I). In both years, more than 200 budworms were reared; therefore the data on apparent parasitism by *A. absonus* are relatively reliable, yet the reasons for the sudden rise and fall of this species are unknown. One possible reason is the fortuitous appearance of an alternate or alternative host.

***Glypta fumiferanae* Vier.** This specific budworm parasitoid caused 10 to 15% apparent parasitism at the peak of the 1949–1959 outbreak in area 1, then declined to a very low level as the outbreak collapsed. This decline continued into the endemic phase to the point where only one or two specimens were found from 1963 to 1970 in area 1 (Table I). Neither Blais (1959) nor Fye (1963) recovered it during their endemic studies in Quebec and Ontario. We reared a few specimens from area 2 (Table I). *G. fumiferanae* obviously reaches a very low level when under

the stress of low budworm abundance. Furthermore it failed to show a rapid response to increases in host density. For example, in 1971, the incidence of *G. fumiferanae* reached only 3% in area 3, plot B after 4 years of budworm increase. Our conclusion is that *G. fumiferanae* is an 'epidemic' parasitoid having little or no effect on endemic populations.

***Tranosema arenicola* (Thom.).** *T. arenicola* is more common among endemic than epidemic populations. In the early 1960's, in area 1 and area 2, it caused up to 14% parasitism. However, very few were reared as budworm populations began to increase in the late 1960's and none was reared in area 3 as budworm density reached the epidemic level. This parasitoid could be classified as part of the 'endemic' complex.

***Meteorus trachynotus* Vier.** *M. trachynotus* attacks late-instar larvae and caused up to 40% apparent parasitism in the final collapse of the 1949–1959 outbreak in area 1. A high incidence of this species among collapsing budworm populations has also been recorded in Quebec (Blais 1960) and Ontario (McGugan and Blais 1959). In the post-epidemic period, 1960 to 1963, 21 specimens were reared from 203 hosts equalling 10% apparent parasitism. In the same period in area 2, the incidence was 44 parasitoids from 560 hosts, or 8%. None was reared from small samples collected in area 2 during the 1965 to 1967 period of low budworm density (Table I) and it is suspected that *M. trachynotus* was also scarce in area 1. *M. trachynotus* did not respond to the late 1960 increase in budworm abundance. An apparent parasitism of 4% was found in area 1, 2% in area 3, but none was recorded in area 2. There is little doubt that *M. trachynotus* reaches maximum effectiveness in the final collapse of a budworm outbreak and fails to respond to released populations.

Other Parasitoids attacking late-instar larvae. One hymenopteran, *Exochus nigripalpis tectulum* Tow. & Tow., and a complex of five dipterous species — *Actia interrupta* Curr., *Phryxe pecosensis* Tns., *Aplomya caesar* (Ald.), *Lypha setifacies* (West.), and *Madremyia saundersii* (Will.) — have been recovered from epidemic budworm populations but only *Exochus* and *A. interrupta* were reared from endemic populations. This could have been a function of inadequate sampling of late-instar larvae. Larger collections were made as populations increased in area 3 in the late 1960's and three species — *A. interrupta*, *P. pecosensis*, and *A. caesar* — were recovered although the total apparent parasitism was only 10% (Table IV).

Parasitoids attacking pupae. No pupae were collected from endemic populations. The first collections were made in area 3 when density reached 0.5 pupa per mid-crown branch and four parasitoids were recovered — *Apecthis ontario* (Cress.), *Itopectis conquisitor* (Say), *Phaogenes hariolus* (Cress.), and the chalcid, *Amblymerus verditer* Nort. — with a combined parasitism of 20% (Table IV). Even during the 1949–1959 outbreak, pupal parasitism never reached more than 25%, largely because most pupal parasitoids (with the possible exception of *P. hariolus*) have alternate and alternative hosts. It is doubtful whether pupal parasitoids have a regulating effect on the budworm although they attack when host density for the generation is reaching its minimum level. In theory, a small pupal-parasitoid complex would only have to attack a relatively few individuals in order to have a significant effect on the host but there is no evidence of this happening to the spruce budworm.

Summary

Major differences occur in the abundance and diversity of parasitoids attacking epidemic and endemic populations of the spruce budworm in northeastern New Brunswick and much of the difference can be traced to a few species: *A. fumiferanae*, *M. trachynotus*, and *S. tenuifemur* (Table V).

A. fumiferanae and *M. trachynotus* are common during the collapse phase of an outbreak but both decline as host density reaches the endemic phase. In contrast, *S. tenuifemur* is common during the endemic phase but fails to respond to sharp increases in budworm density that occur during a population release. Beyond this broad statement we are unable to give a direct and quantitative answer to the question "Did parasitoids play a significant role in determining changes in endemic budworm density?" because a continuous story in one area was not obtained on the presence of all species. However, the somewhat fragmented data failed to clearly show that increases in parasitism were associated with decreases in budworm density. There is little doubt that parasitoids and

Table V. An index of abundance (% parasitism) of the common budworm parasitoids in area 1 in relation to budworm population phases

Parasitoids	Population phases			
	Endemic	Release	Decline	Post-outbreak ^a
<i>A. fumiferanae</i>	6	7	18	
<i>Apanteles</i> spp.	9	<1	<1	
<i>G. fumiferanae</i>	<1	1	1	
<i>T. arenicola</i>	3	<1	<1	
<i>Diadegma</i> sp.	<1	<1	3	
<i>S. tenuifemur</i>	13	1	2	30
<i>M. trachynotus</i>	5	2	44	10
Diptera complex	<1	10	2	
Pupal parasitoid complex	— ^b	20	25	

^aOr the first 2 years of the endemic phase.^bUnknown.

particularly *S. tenuifemur* accounted for the death of a significant proportion of sparse larval populations, particularly in area 2 in the 1960's, but it failed to respond to the host release in the late 1960's. Furthermore, a regression analysis of budworm density in year $t+1$ over density in year t for declining populations in areas 1 and 2 gave a regression equation with $b = 1.02$ ($N = 22$; explained \ln variance = 95%). The slope of 1.02 'suggests' that factors which caused population declines in particular years were not density related and that other factors including weather play a significant role in the dynamics of endemic budworm populations.

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