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COLEOPTEROUS PREDATORS OF LARCH SAWFLY COCOONS

by

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INTRODUCTION

A research group at the Winnipeg Laboratory is involved in a long-term study of the population dynamics of the larch sawfly including the identification of factors causing mortality and the evaluation of their impact on population fluctuations. Studies are being conducted in plots in southern Manitoba. Among the mortality factors affecting the cocoon stage, priority has been given to studies of parasitism, small mammal predation and flooding (Nairn et al 1961). The fact that certain Carabidae, Staphilinidae and larval Elateridae open larch sawfly cocoons and feed on the larvae has been known for some time but these predaceous Coleoptera have received only cursory attention because they have not been considered of major importance in the population dynamics of the prey.

Attempts to estimate the destruction of natural populations of larch sawfly cocoons by invertebrate predators have given figures of 1 to 8% (Buckner 1959), 9 to 18% (Turnock 1961) and about 2% (Turnock and Ives 1962). The first two of these estimates are based on all the cocoons found in soil samples and therefore represent the average predation over a period of time encompassing at least four sawfly generations. The last estimate, although derived from cocoons partially protected from invertebrate predation, gives some estimate of the annual destruction of cocoons by this factor. More accurate estimates would be difficult and time-consuming to obtain but some information on the predators and predator-prey relationships is being obtained from the the experimental testing of potential predators and from the routine sampling of bog insects conducted as part of the larch sawfly program.

The results of preliminary investigations of the ability of some coleopterous species to open larch sawfly cocoons, population estimates of potential predators, and some observations on their behavior and life history are given in this report. Limited testing of potential predators was first attempted in 1951 by R. Y. Zacharuk, then with Canada Dept. Agriculture, Saskatoon, using elaterid larvae and larch sawfly cocoons supplied by W. J. Turnock. More extensive testing was initiated by the latter in 1961 and continued by J. A. Garland in 1964 during his employment as a Technical Officer, Canada Department of Forestry, assigned to the Larch Sawfly Investigations at the Whiteshell Field Station, Whiteshell Provincial Park, Manitoba. Identifications of the insect species were made by E. C. Becker and R. de Ruette, Entomology Research Institute, Ottawa, and R. H. Burrage, Canada Agriculture Research Station, Saskatoon.

PREDACEOUS COLEOPTERA IN LARCH SAWFLY STUDY PLOTS

The emergence traps used to estimate populations of larch sawfly adults also sample predaceous Coleoptera. Each sampling unit consists of a conical screen cage covering 2 ft^2 of ground surface with a plastic trap at its apex (modified from the design described by Turnock 1957). Each of the study plots contains 100 of these sampling units randomly located with their bases set into the soil surface. Insects that move vertically away from the soil are caught in the traps where they are killed by an insecticide. The traps are exchanged at fortnightly intervals from late May to early September and the insects removed, pinned and identified.

All species of Carabidae, Elateridae and Staphilinidae recovered in these traps were included in a list of potential predators of larch sawfly cocoons as predation by some species in each of these families has been observed. The species of Salpingidae and Cleridae were added on the basis of published reports of the feeding habits of these families (Arnett 1960, Dillon and Dillon 1961). Table I shows the abundance of 26 species of Elateridae, 25 Carabidae, 5 Staphilinidae, and one species each of Salpingidae and Cleridae, expressed as individuals per acre. The number of individuals per acre for each species was extremely variable: many species occurred only occasionally and in low numbers but eight carabid and seven elaterid species had maximum populations of over 1000 per acre. The highest population estimated was 26,100 per acre in the Pine Falls plot in 1961 for Ctenicera triundulata Randall.

The sampling technique used in the study plot has provided satisfactory estimates of the populations of larch sawfly adults (Turnock 1960) and should provide equally satisfactory estimates for other species providing that the adult stage includes a period of either positive phototropism or negative geotropism. These conditions are met by the Elateridae whose adults emerge from the ground to feed and mate in the tree crowns. The behavior of adult carabids and staphilinids is more variable and less well known so that the differences in population estimates between species may be partially due to behavioral differences. The population figures for these two families must be accepted with caution pending further research.

Table I

Species and numbers per acre of potentially predaceous Coleoptera collected in emergence traps in larch sawfly study plots based on sampling in 1961, 1962, and 1963. Species were not collected in unlisted years.

Species	Year	Agassiz	Telford	Rennie	Pine Falls	Riverton
CARABIDAE						
Carabus serratus (Say)	62	0	0	0	218	0
Sphaeroderus lecontei Dejean	63	0	0	218	0	0
Scaphinotus bilobus Say	63	0	0	218	0	0
Blethisa quadricollis Haldeman	61	0	218	0	0	-
	62	218	218	0	0	0
	63	436	436	0	0	436
Elaphrus clairvillei Kirby	61	436	0	0	0	-
	62	871	0	218	0	1,742
	63	653	436	871	0	12,632
Nomius pygmaeus Dejean	61	0	0	218	0	-
Bembidion sp.	61	0	0	0	218	-
	62	653	2,178	0	436	0
	63	436	0	0	0	436
B. nudipenne Lindroth	62	1,089	4,356	0	0	0
B. quadrimaculatum (Linnaeus)	62	218	0	0	0	0
Patrobus foveocollis Eschscholtz	63	0	0	218	0	0
Pterostichus sp.	62	653	0	218	1,742	0
	63	436	0	436	436	218
P. pennsylvannicus LeConte	61	218	0	0	436	-
	62	218	0	218	871	218
	63	653	653	436	5,880	218
P. punctatissimus Randall	61	0	0	0	436	-
	62	218	0	436	653	0
	63	0	0	0	1,307	0
P. convexicollis (Say)	61	0	0	218	0	-
Synuchus impunctatus Say	63	0	218	0	0	0
Agnonum sp.	61	653	0	0	871	-
	62	3,267	1,307	871	0	2,831
	63	3,485	1,960	2,400	218	5,445

Table I cont'd

Species	Year	Agassiz	Telford	Rennie	Pine Falls	Riverton
A. quadripunctatum De Geer	61	0	0	218	0	-
	63	218	0	0	0	218
A. sinuatus Dejean	61	1,742	218	436	218	-
	62	4,356	0	871	218	1,525
	63	3,267	0	5,009	0	4,574
Amara sp.	63	0	218	0	0	0
Harpalus sp.	61	0	0	0	8,276	-
	62	218	0	436	3,267	0
	63	436	218	1,089	7,841	0
Bradycellus sp.	61	0	0	218	0	-
	63	0	0	0	0	218
Chlaenius sp.	62	0	0	0	0	218
	63	0	0	0	0	871
C. sericeus Forster	62	0	0	0	0	218
C. erarginatus Say	63	0	0	218	0	0
Dromius sp.	63	436	0	0	0	0
Number of species recorded		13	10	15	8	11
STAPHILINIDAE						
Staphilinus erythropterus Linnaeus	62	0	0	0	0	218
Philonthus sp.	61	0	218	436	436	0
P. politus (Linnaeus)	61	218	0	653	653	-
P. cyanipennis (Fabricius)	61	218	0	0	0	-
	62	436	0	0	0	0
Quedius sp.	61	2,831	653	0	0	-
Number of species recorded		3	2	2	2	1
ELATERIDAE						
Ctenicera resplendens (Eschscholtz)	63	0	0	218	0	0
C. nitidula (LeConte)	61	653	0	2,178	1,525	-
	62	218	0	0	1,307	1,307
C. arata (LeConte)	61	0	218	0	0	-

Table I cont'd

Species	Year	Agassiz	Telford	Rennie	Pine Falls	Riverton
C. destructor (Brown)	63	0	218	0	0	0
C. triundulata (Randall)	61	9,365	653	5,227	26,136	0
	62	4,357	0	4,356	16,117	0
	63	1,525	0	4,138	7,405	1,742
C. mediana (Germar)	61	0	218	218	218	-
C. propola (LeConte)	61	0	0	0	1,307	-
	62	0	0	436	0	0
	63	0	0	218	0	0
Hypolithus bicolor (Eschscholtz)	62	218	0	0	0	0
	63	0	0	0	218	0
Limonius pectoralis LeConte	61	871	0	0	0	-
L. aeger LeConte	61	218	0	218	218	-
	62	871	436	436	653	218
Drasterius debilis (LeConte)	61	218	0	0	0	-
	62	218	0	0	0	653
	63	218	0	0	218	0
Negastrius tumescens (LeConte)	62	218	0	218	218	218
	63	0	0	218	218	0
Melanotus sp.	62	0	0	218	0	0
Melanotus castanipes (Paykull)	62	0	0	218	0	0
Sericus incongruus (LeConte)	61	218	653	0	1,089	-
	63	0	218	218	1,526	0
Dalopius vagus Brown	62	436	0	0	0	0
Agriotes sp.	62	0	0	0	218	0
	63	0	0	218	0	0
A. limosus (LeConte)	61	0	218	0	0	-
	62	0	0	218	218	0
Megapenthes stigmosus (LeConte)	62	0	0	0	218	0
Ampedus melsheimeri (Leng)	61	0	0	0	218	-
	63	218	0	0	0	0

Table 1 cont'd

Species	Year	Agassiz	Telford	Rennie	Pine Falls	Riverton
A. pullus Germ	61	1,307	871	1,742	10,019	-
	62	436	0	0	6,970	0
	63	218	0	0	3,920	0
A. luctosus (LeConte)	61	0	0	218	0	-
	62	0	0	0	218	0
	63	0	218	436	871	0
A. subtilus (LeConte)	61	871	218	6,534	20,265	-
	62	653	0	5,445	6,534	0
	63	436	0	4,892	3,703	0
A. nigrinus (Herbst)	63	0	0	653	218	0
A. mixtus (Herbst)	61	218	0	218	0	-
A. rubicus Say	61	0	0	1,742	6,098	-
	62	0	0	1,960	2,614	0
	63	0	0	1,307	871	0
No. of species recorded		13	10	18	18	5
SALPINGIDAE						
Priognathus monilicornus Randall	61	0	0	0	436	-
	63	0	0	218	0	0
CLERIDAE						
Thanasimus undulatus Say	62	0	0	0	218	0

TESTS OF POTENTIAL PREDATORS OF LARCH SAWFLY COCOONS

The feeding habits of nearly all the species and most of the genera of potential predators listed in Table I are unknown. Among the Carabidae, Bembidion quadrimaculatum (Linnaeus) is reported to eat Hylemyia eggs (Lindroth 1963), and the crops of a related British species, B. lampros (Herbst), contained remains of Collenbola, insects, mites, other arthropods and earthworms (Mitchell 1963). The genera Sphaeroderus and Scaphinotus feed on snails while some Harpalus spp. feed on seeds, strawberries, cutworms and caterpillars (Arnett 1960, Dillon and Dillon 1961). The staphilinid genera listed in the table are vaguely reported to be found in fungus, carrion, dung or rubbish and reports on the Cleridae and Salpingidae merely noted that they are insectivorous (Arnett 1960, Dillon and Dillon 1961). These sources emphasize the phytophageous habits of the Elateridae but the larvae of many genera accept animal food (Zacharuk 1963) and several species are known to prey on larch sawfly cocoons: Ctenicera sp. and Ludius (Ctenicera) lutescens Fall. (Drooz 1961); Ctenicera triundulata, C. propola propola and C. resplendens aeraria (Turnock 1960). Some species of the genera Ctenicera, Agriotes and Ampedus were found to open cocoons of the European spruce sawfly in New Brunswick (Morris 1951).

Eight species of elaterid larva collected by W. J. Turnock in a tamarack bog near Prince Albert, Saskatchewan in October 1951 were tested as potential predators of larch sawfly cocoons by R. Y. Zacharuk at Saskatoon. Each larva was placed in a seamless tin with moss and sawfly cocoons and observed until death or up to five months. Three species gave evidence of the ability to prey on cocoons (Table II) but rearing difficulties prevented the use of the data to indicate the rate of feeding or to conclude that the remaining five species are incapable of opening cocoons.

Table II

Numbers of larch sawfly cocoons opened by elaterid larvae in tests conducted by R. Y. Zacharuk, Agriculture Research Station, Saskatoon, Saskatchewan, 1951.

Species	Number of elaterids tested	Number of elaterids opening cocoons	cocoons opened
Ctenicera triundulata (Randall)	5	1	3
C. propola propola (LeConte)	2	1	1
C. resplendens aeraria (Randall)	2	1	1
C. nitidulus (LeConte)	3	0	0
C. kendalli (Kirby)	2	0	0
C. cupresans (LeConte)	1	0	0
Eanus decoratus (Mannerheim)	2	0	0
Ampedus sp.	1	0	0

Subsequent tests were designed to determine which species feed on the contents of larch sawfly cocoons and to test their ability to discriminate between cocoons containing living and dead larvae. The testing universe was limited in size, a handful of sphagnum moss in a 6 oz jar, and animal food was limited to two cocoons containing living larvae and one cocoon containing a dead larva in each jar. The cocoons containing dead larvae usually had some fungal growth on their surface. The test jars may have contained some very small insects and microscopic animals but all larger potential animal food items were carefully excluded.

In 1961, adult beetles of the families Carabidae, Staphilinidae and Salpingidae and larval Elateridae were taken from samples of moss collected in a larch sawfly study plot near Rennie, Manitoba, and tests were begun in August and October. These potential predators were placed in individual jars at 62± 3F and examined once a month until 3 April 1962 unless the beetle died at an earlier date. At each examination, cocoons showing evidence of predator attack were replaced so that two living and one dead larva were available to each predator throughout the experiment. In this experiment 10 of the 12 species of potential predators opened larch sawfly cocoons and 8 of these opened cocoons containing living as well as dead larvae (Table III).

In 1964, the testing of potential predators of larch sawfly cocoons utilized specimens obtained in pitfall traps situated in a mixed tamarack-black spruce bog adjacent to the Whiteshell Field Station. Pitfall traps with or without bait have been used by many workers on Carabidae (Boer 1958, Gilbert 1958, Mitchell 1963, Williams 1958). For our work 30 one-quart oil tins were sunk to their rims into the soil in three lines to give an "F" shaped pattern. The distance between traps was 10 paces and the two parallel rows were 30 paces apart. For the first week, a weak sugar solution was poured into each trap to a depth of about 3 cm and a few leaves were floated on the surface. These were tedious to service and were replaced for the remainder of the trapping period with a modified bait container. This consisted of a plastic vial cap containing the bait attached to the top of a six-inch stick which was held upright by a piece of styrofoam plastic (Fig. 1). During a one-week test of the effectiveness of sugar solution and molasses as baits in paired traps, 17 beetles were

Table III

Dates of feeding and death of coleopterous species tested from 4 October 1961 to 3 April 1962

Species	Number and sex		Number of beetles feeding and number dead (in brackets) Oct.	Nov.	Dec.	Jan.	Feb.	March	Number of cocoons opened living	dead
Harpalus spp.	2	♀	1	0	1 (2)	-	-	-	0	2
Pterostichus spp.	1	♂	1	1	1	0 (1)	-	-	1	3
	4	♀	0	2 (1)	2	1 (1)	0 (2)	-	3	4
	2	?	0	1 (2)	-	-	-	-	0	1
P. pennsylvanicus	1	♀	1	0	1	1	1	0 (1)	6	1
P. punctatissimus	1	♀	1	1	1	1	1	1	17	1
Agonum spp.	1	♂	0	1	0 (1)	-	-	-	0	1
	5	♀	2 (1)	2 (1)	0	0 (1)	0	1 (1)	5	3
	2	♀	2	1	Experiment discontinued				3	1
	2	?	1	1	0 (1)	0 (1)	-	-	1	1
A. sinuatus	1	♂	0	0 (1)	-	-	-	-	0	0
	1	♀	1	1	1	1	0	1	8	2
Quedius spp.	32	?	2 (6)	2 (11)	1 (8)	1 (1)	0 (3)	1 (1)	1	5
Philonthus spp.	18	?	3 (12)	2 (5)	0	0 (1)	-	-	0	5
Ctenicera hieroglyphicus	1	?	1	0	0	1	1	1	5	2
Ampedus spp.	2	?	0	1	0	1	2	2	9	2
Priognathus monilicornis	1	?	0	0	0 (1)	-	-	-	0	0
Staphilinus erythropterus	1	?	0	0 (1)	-	-	-	-	0	0

Figure 1.- Pitfall trap for Carabidae consisting of a one-quart tin containing a vertical stick supported by a styrofoam plastic base and topped by a plastic vial cap of molasses.

caught with molasses and only 3 with sugar. Thereafter, only molasses were used. Screen bottoms were used for a few pitfall traps to prevent the accumulation of rain water but watertight bottoms had to be used in locations where the water table lay close to the ground surface. The traps were usually visited every second day to remove beetles, replenish the bait and repair the damage done by mice and squirrels which occasionally chewed the bait container. Trapping continued to the end of August.

Testing of the ability of the beetles to open larch sawfly cocoons began 3 July and continued until 2 September. During the first two tests, each of one week duration, each beetle was confined in a jar with sphagnum moss and four larch sawfly cocoons. No effort was made to distinguish between cocoons containing living or dead larvae. The remaining four tests lasted two weeks and presented each beetle with four cocoons containing two living and two dead larvae. In these experiments five of the six species of carabid beetles tested and the one staphilinid species showed the ability to open cocoons (Table IV). Individual chi-square tests were made to determine whether the number of cocoons containing living and dead larvae opened by each species was significantly different from the number expected on the basis of availability (Table V). The results of these analyses indicate four groups with different preferences in opening larch sawfly cocoons:

(1) Species that opened cocoons containing living in preference to those containing dead larvae: Pterostichus punctatissimus ♀.

(2) Species that opened cocoons containing living or dead larvae in relation to their availability: Pterostichus spp.; P. pennsylvannicus ♀; Carabus taedus Agassii♂; Agonum spp.; A. sinuatus♀; Staphilinus erythropterus ♀; Ampedus spp.; Ctenicera hieroglyphica.

Table IV

Dates of feeding and death of coleopterous species tested from 3 July to 2 September 1962

Species	Number and sex		Number of beetles feeding and number dead (in brackets) July 3-9	July 9-14	July 14-25	July 5-Aug. 4	Aug. 4-17	Aug. 17-Sept. 2	Number of cocoons opened living	dead	?
Pterostichus sp.	1	♂	-	-	-	-	-	1	1	0	0
	1	♀	-	-	-	0	0	0	0	0	0
P. pennsylvanicus	1	♂	1	1 (1)	-	-	-	-	0	0	7
	2	♀	2	2	2	1	discontinued		1	4	13
	1	♀	1	1	1	1	1	1	0	5	3
	1	♀	-	1	1	1	1	1	4	4	3
P. punctatissimus	4	♂	2	2 (2)	2	2	1 (2)	-	0	6	10
Sphaeroderus lecontei	1	♂	-	0	0	0	0	0	0	0	0
	1	♀	0	0 (1)	-	-	-	-	0	0	0
Scaphinotus bilobus	1	♀	-	-	0	0 (1)	-	-	0	0	0
Agonum spp.	4	♂	-	2	1	3	0	2 (1)	3	5	2
	3	♂	3	1	1	1	1	1	0	4	7
	8	♀	5	4	3 (1)	1	2	0	3	4	14
	4	♀	-	1	0 (1)	1	1	0	0	2	1
	1	♀	-	-	1	0	0	0	1	0	0
	3	♀	-	-	-	3	0	0 (1)	2	1	0
	1	♀	-	-	-	-	0	0	0	0	0
A. sinuatus	1	♀	1	1	1	0 (1)	-	-	0	2	5
Carabus taedus agassii	1	♂	-	-	-	1	1	0	2	0	0
	1	♂	-	-	-	-	-	0 (1)	0	0	0
	1	♀	-	-	0 (1)	-	-	-	0	0	0
Staphilinus erythropterus	1	♀	1	1 (1)	-	-	-	-	0	0	3
	1	♀	-	1	1	1	1	1	1	8	0
	1	♀	-	-	1 (1)	-	-	-	1	0	0

Table V

Numbers of cocoons containing living or dead larvae opened by coleopterous predators and the probability (chi-square tests) that living and dead cocoons were opened at random

	Sex	Number of predators	Ratio of living : dead cocoons Opened	Offered	Chi square	P
CARABIDAE						
Harpalus spp.	♀	1	0:2	2:1	3.97*	.05
Pterostichus spp.	♂	1	1:3	2:1	3.14	>.05
	♀	3	3:4	2:1	1.79	.10
	♀	1	1:0	1:1	1.00	.30
	unsexed	1	0:1	2:1	2.00	.15
P. pennsylvannicus	♀	1	10:2	2:1	1.50	.20
	♀	4	5:13	1:1	3.56	>.05
P. punctatissimus	♂	2	0:6	1:1	6.00*	.02
	♀	1	17:1	2:1	6.25*	.02
Agonum spp.	unsexed	1	1:1	2:1	0.25	.60
	♂	5	4:8	1:1	1.33	.25
	♀	1	0:1	2:1	0.50	.50
	♀	10	7:5	1:1	0.38	.60
	♀	5	4:4	2:1	0.99	.30
A. sinuatus	♀	1	0:2	1:1	2.00	.15
	♀	1	8:3	2:1	0.16	.70
Carabus taedus agassii	♂	1	2:0	1:1	2.00	.15
STAPHILINIDAE						
Staphilinus erythropterus	♀	2	2:8	1:1	3.60	>.05
Quedius spp.	unsexed	7	1:6	2:1	8.80**	.01
Philonthus spp.	unsexed	5	0:6	2:1	12.00**	.01
Ctenicera hieroglyphica	unsexed	1	5:2	2:1	0.06	.80
Ampedus spp.	unsexed	2	9:2	2:1	1.09	.30

(3) Species that opened cocoons containing dead larvae in preference to those containing living larvae: Quedius spp.

(4) Species that opened only cocoons containing dead larvae: Philonthus spp. Harpalus spp.; Pterostichus punctatissimus ♂.

In addition, Ctenicera triundulata, C. propola propola and C. resplendens aeraris opened cocoons in tests where the viability of the cocoons was not recorded and Agonum sinuatus ♂, Sphaeroderus lecontei, Schaphinotus bilobus ♀, Ctenicera nitidulus, C. kendalli, C. cupresescens, Eanus decoratus and Priognathus monilicornis did not open any cocoons. The difference in predatory behaviour noted between the sexes of P. punctatissimus, the variability between tests of the same species and sex and the possibility that clarification of the taxonomy of several genera may reveal several species of different predatory response indicates a need for further research. As material is difficult to obtain, testing can be expected to continue for several years.

It is significant that 15 of the 23 species tested to date have shown the ability to open sawfly cocoons and 11 of these opened cocoons containing living larvae. The rate of feeding for the species found to open larch sawfly cocoons varied from 0.2 to 1.7 living and from 0.2 to 4.0 dead cocoons per predator per month but these estimates are based on too few tests to provide a basis for calculating the potential predation by predaceous insects in the cocoon environment.

SEASONAL OCCURRENCE, LIFE HISTORY AND BEHAVIOR

Information on the seasonal occurrence of predaceous Coleoptera that are potential enemies of larch sawfly cocoons was collected from the annual emergence trap records and the 1964 pitfall traps. Some observations of the life history and behaviour of a few species were also made in 1964.

The seasonal distribution of captures of adult Carabidae and Elateridae was examined for indications of periods of activity that might influence their predation on larch sawfly cocoons. In the Carabidae, a capture indicates the presence of the predaceous stage while in the Elateridae it provides information on the period of adult emergence and thus, by inference, some clues to the period when the predaceous larval stage may have been active. The emergence trap capture records were tabulated on the basis of emergence dates to give frequency distributions for semi-monthly periods from late May to early September (Table VI). Species for which less than 10 captures were recorded were excluded from the tabulation.

Collection dates of adult Carabidae have been used by several workers to show basic life history patterns (Boer 1958, Gilbert 1958, Mitchell 1963). The Carabidae studied by these workers had life histories of two basic types, one overwintering as larvae and the other as adults. Those overwintering as larvae have a fall reproduction period and can be divided into groups of species on the basis of the number of adults which subsequently pass through the winter (Boer 1958). Species overwintering as adults oviposit the following spring or summer and the adults live up to a full year. Adults develop from eggs laid the same summer but they do not attain reproductive maturity until after the overwintering period. The sexually immature adults of some species remain in an inactive state and are not recorded in fall trapping while in others they are active. The

Table VI

Numbers of adult Carabidae and Elateridae collected in emergence traps in five plots 1961 to 1963

	May	June		July		Aug		Sept	Total
	L	E	L	E	L	E	L	E	
CARABIDAE									
Bembidion spp.	3	6	1	0	0	0	1	0	11
Elaphrus calairvillei	10	11	10	17	10	2	19	4	83
Blethisa quadricollis	1	2	2	3	0	0	2	0	10
Pterostichus spp.	3	2	2	2	2	2	5	3	21
P. pennsylvannicus	6	10	7	5	4	0	10	1	43
P. punctatissimus	0	5	2	2	2	2	1	0	14
Agonum spp.	12	22	19	16	14	10	13	2	108
A. sinuatus	10	22	20	24	3	2	18	3	102
Harpalus spp.	5	47	16	6	5	6	13	4	102
ELATERIDAE									
Ctenicera nitidula	0	11	11	7	3	0	0	0	29
C. triundulata	24	106	117	77	29	4	0	0	357
Limonius aeger	2	4	1	1	5	2	0	0	15
Sericus incongruus	5	8	3	1	0	0	0	0	17
Ampedus pullus	11	42	31	19	13	3	0	0	119
A. subtilus	39	100	49	30	4	2	0	0	224
A. rubricus	11	26	14	11	3	1	0	0	66

capture patterns given in Table VI give no indication of species with overwintering larvae. Among the spring and summer breeders, Bembidion spp. and Blethisa quadricollis show evidence of adult inactivity in the fall while in Elaphrus clairvillei, Pterostichus pennsylvannicus, P. punctatissimus, Agonium spp., A. sinulatus and Harpalus spp. the non-breeding adults appear to be active. Pterostichus spp. appear to reproduce in spring or summer but the absence of peaks in the capture records, possibly caused by the different habits of several species, prevents further classification of the life history. The pitfall captures in 1964 showed the same pattern of seasonal distribution of catches (Table VII).

Some additional information on the life history of the Carabidae can be obtained by considering the time of death of the experimental animals (Table VII). These data suggest that both sexes of some Pterostichus spp. overwinter but only the females of Pterostichus pennsylvanicus, P. punctatissimus, Agonum spp. and A. sinuatus. If the dates of male death are indicative, female reproductive diapause begins after mating, which apparently occurs in early July for three of these and somewhat later for Agonum spp. Thus, during the peak of cocoon availability, the populations of three of the most abundant carabids are composed only of females.

The evidence of these life history characteristics could best be confirmed by the collection of other stages in the life cycle but these are difficult to obtain. In 1964 a larva, later identified as a female Pterostichus sp., was collected on 8 August from a clump of sphagnum moss in the bog near the Field Station. The larva measured 12 x 2 mm at the time of capture. It was given an opportunity to prey on larch sawfly larvae and cocoons but did not do so before pupating on 17 August. The

Table VII

Numbers of adult Carabidae capture in pitfall traps in 1964

	June	July		August		Total
	L	E	L	E	L	
Agonum spp.	6	19	5	0	0	30
Agonum sinuatum	1	0	0	0	0	1
Pterostichus pennsylvannicus	3	2	0	0	0	5
Carabus taedatus agassii	[illegible]	0	2	0	1	3
P. punctatissimus	2	2	0	0	0	4
Sphaeroderus lecontii	0	2	0	0	0	2
Scaphinotus bilobus	0	1	0	0	0	1
Staphilinus erythropterus	0	4	0	0	0	4

pupal period lasted eight days with emergence on 25 August. A pupa of Elaphrus clairvillei was found in soil samples collected on 31 August and emerged later in September. These observations suggest that in these two species adult emergence occurs late in the summer and the duration of the period of predation on larch sawfly cocoons in the fall may be less than one month.

Captures of Staphylinidae were too few and the taxonomic picture too confused to justify tabulation of emergence records. Two pertinent observations were made in 1964: a small orange pupa of Philonthus spp. found inside an old larch sawfly cocoon in field-collected soil on 31 August, emerged as an adult later in September; and a pearly-coloured egg, measuring 3 x 2 mm was found associated with a female Staphilinus erythropterus on 14 August in a test jar. The egg color changed to brownish on 17 August and on 2 September the egg was flattened as if hatched or crushed. Careful examination failed to reveal a larva.

The captures of all species of adult Elateridae show a spring or early summer peak, consistent with reports of some species that pupation occurs in the fall and that the adults overwinter either in the pupal cell or emerge and winter in the soil (Becker 1956). The time of pupation can have an important bearing on the predation of larch sawfly cocoons by elaterid larvae: if pupation occurs in August, coincident with the peak abundance of cocoons, only small larvae of species with a life cycle of more than one year will be present and the level of predation will be substantially lower than if pupation occurs later in the fall and the cocoons are exposed to the attacks by the ultimate larval instar. No information on this is available since the instars of test larvae were not determined.

DISCUSSION AND CONCLUSIONS

The effects of soil-inhabiting predacious invertebrates on the population fluctuations of a forest defoliator which spends a portion of its life cycle in the ground are difficult to evaluate due to the problems of sampling both predator and prey, and to the paucity of information on the taxonomy, life history, and habits of the predators. In attempting to evaluate the effects of Coleopterous predators on larch sawfly cocoons some progress has been made in identifying the potential predators in the environment of the larch sawfly cocoon and in determining the ability of some species to open the cocoons. It appears that although the potential impact of an individual invertebrate predator in the soil is low, the presence in the bog environment of a large number of species and individuals may combine to give a high potential. The mortality caused by these predators may well have been underestimated due to sampling difficulties and the close resemblance of cocoons opened by Carabidae to those opened by mice. The results of these preliminary studies suggest that valuable information on a little-known factor in the natural control of forest insect populations is being obtained and these studies should be continued as time permits.

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