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Predators of the Douglas-Fir Beetle

In Western Oregon

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Predators of the Douglas-Fir Beetle In Western Oregon

B. D. Cowan and W. P. Nagel

Introduction

The forests of Oregon constitute the state's most valuable natural resource, contributing more than a billion dollars annually to its income. More than 50% of the timber volume is in the Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, forests in the western half of the state. The most serious threat to these forests is the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), which is continually present in endemic numbers, breeding in windthrown trees. However, this insect has become epidemic in the past, killing millions of board-feet of standing timber, and it maintains this potential, especially following an extensive disaster, i.e., windstorm or fire.

Although the origin of a Douglas-fir beetle epidemic in western Oregon depends primarily on the amount of available windthrown trees, the decline of Douglas-fir beetle populations is probably caused by a combination of host resistance, competition, parasitism, and predation. These factors are usually studied separately to understand their individual effects on the population before they are evaluated in combination.

Most of the previous research on the natural enemies of the Douglas-fir beetle has been descriptive with little reference to the effectiveness of these agents in control (Blackman, 1931; DeLeon, 1934; Doane et al., 1936; Keen, 1929; Person, 1940). Many of the studies have been made either on different bark beetle hosts of the predators concerned, or within the Douglas-fir forests of the interior regions. Douglas-fir trees and bark beetles in these areas exhibit different growth and behavior patterns than in the coastal forests, and undoubtedly the associated predator populations would also differ.

Six species of Cleridae are found on Douglas-fir in western Oregon: *Enoclerus sphegeus* Fabricius, *E. lecontei* Wolcott, *E. schaefferi* (Barr), *E. eximius* Mannerheim, *Thanasimus undatulus* Say, and an undescribed species of *Enoclerus* (Plate I). Of these species *E. sphegeus* is the most prevalent. Kline and Rudinsky (1964) described the immature stages of *E. sphegeus, E. lecontei,* and *T. undatulus,*

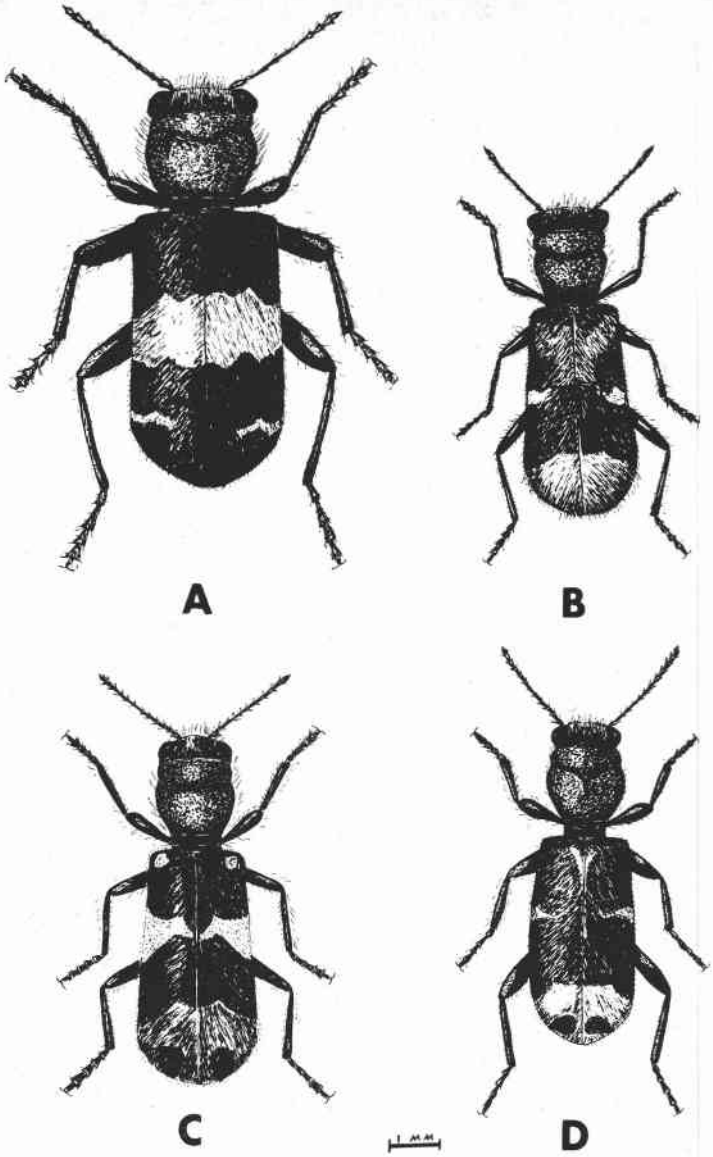

PLATE I. Adult Cleridae: A, *Enoclerus sphegeus;* B, *Enoclerus lecontei;* C, *Enoclerus* sp.; D, *Thanasimus undatulus.*

including detailed descriptions of three larval instars for each species. Böving and Champlain (1920) described the seasonal history of *E. sphegeus* and gave some data for *E. lecontei, E. schaefferi,* and *T. undatulus.* The biology and habits of *E. sphegeus* associated with *Ips* spp. (Coleoptera: Scolytidae) in Alberta, Canada, were reported by Reid (1957). Struble (1942b) reared *E. sphegeus* through three instars in the laboratory and described its life history in California, and Furniss (1957) studied its seasonal history in Idaho. Person (1940) studied the life history of *E. lecontei* and tested its effectiveness in controlling the western pine bettle, *Dendroctonus brevicomis* LeConte, in California. Bedard (1933) followed the seasonal history of *T. undatulus* in Idaho, while Gauss (1954) made a detailed study of the biology of *T. formicarius* Latreille, a closely related European clerid.

The objectives undertaken in this study were to delineate the life histories of the six species of Cleridae found on Douglas-fir in western Oregon; to determine which species, if any, were primarily associated with the Douglas-fir beetle; and to investigate their effectiveness in reducing Douglas-fir beetle populations.

Experimental Procedure

Field studies emphasized the measurement of population densities of the Douglas-fir beetle and its predators in windthrown Douglas-firs on the Marys Peak Watershed, Siuslaw National Forest, 14 miles west of Corvallis, Oregon. The forest type consisted of nearly pure stands of 150- to 200-year-old Douglas-fir on slopes with a northeasterly aspect, at elevations from 1,100 to 2,000 feet. Large numbers of trees in the area had been blown down in a violent windstorm in October 1962. This study began with the emergence of Cleridae which developed in 1962, continued with the invasion and seasonal development of the Douglas-fir beetle and its predators in 1963 in the blowdown resulting from the storm, and concluded after obtaining data on the clerids and Douglas-fir beetles developing in less extensive windthrows in 1964. Trees for study included concentrated as well as scattered windthrown trees in exposed and shaded areas.

Studies of adult Cleridae

A number of laboratory and field studies were conducted to determine emergence patterns, seasonal occurrence, and longevity of adult clerids, as well as feeding, mating, and oviposition behavior. Laboratory studies were timed to coincide with the life of adult clerids in the field, whenever possible. Major emphasis was placed upon studies of *E. sphegeus.*

Sex determination. Struble and Carpelan (1941) stated that the only constant external sex difference found on *E. sphegeus* is the fifth abdominal sternite, where the posterior margin is more concave in the male than in the female. This character proved difficult to observe, and a more accurate method of sex determination was required for detailed studies of mating and oviposition. Close observations of specimens under 15X magnification revealed that the sixth abdominal sternite of females of all species extended to the apex of the abdomen, while the sixth sternite of males was slightly shorter and exposed the tip of the copulatory organ, which could be seen moving against a fleshy pad (Plate II). For viewing under a dissecting microscope, the clerids were held ventral side up with the abdomen pointed toward the light. The character was consistent, although somewhat difficult to see on the smaller species. Its reliability was proven by the mating behavior and/or oviposition records of more than 60 clerids sexed by this method.

Emergence. Four screen cages, each measuring 4 feet square and 5 feet high, were used for studies of adult emergence. Two cages were in a shaded area at 1,400 feet, one in a clear-cut area at 1,400 feet, and one near a shaded ridge crest at 2,000 feet elevation. Logs infested by Douglas-fir beetles in 1962 were placed in three of the cages, while Douglas-fir branches infested with *Scolytus unispinosus* LeConte were kept in the fourth. The cages were inspected daily from March to September 1963, and periodically until November 1963, to determine emergence patterns of the associated Cleridae.

Further seasonal emergence data was obtained by cutting bark in August 1963, which contained clerid larvae and pupae from a large windthrown tree infested by Douglas-fir beetles in the spring of 1962, and by keeping a record of the emerging clerids. Sections of bark were cut from four sides of the trunk of the windthrow and placed individually in metal boxes with wooden tops. The boxes were kept in dense shade at 1,400 feet elevation and were checked periodically through November 1963.

Overwintering. Sixteen laboratory-reared adult clerids were marked with red nail polish and placed in outdoor cages in the watershed in November 1963, to determine whether they were capable of overwintering. Logs, loose bark, and litter were placed in the cages to provide shelter. The contents of the cages were inspected in December 1963, and in January and March 1964.

Another group of adult clerids were fed varying amounts of Douglas-fir beetle adults and then were refrigerated at 40° F for six months. Some clerids were placed in the refrigerator without food immediately following eclosion, while others were fed from one to

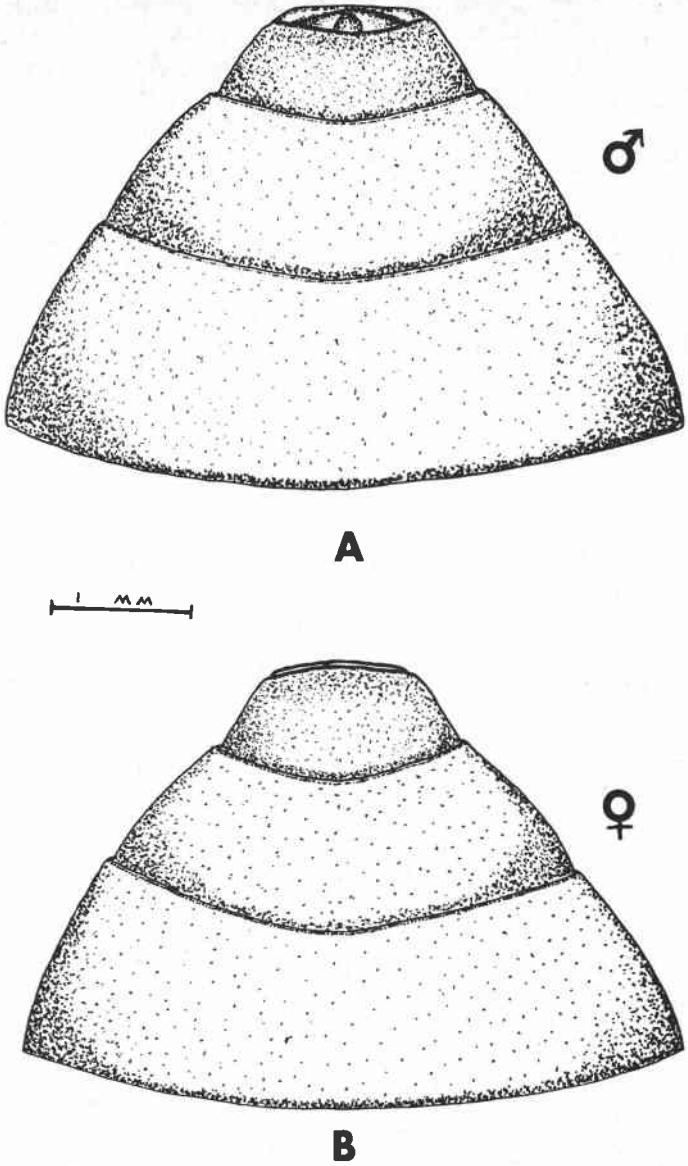

PLATE II. Ventral view of the abdomen of *Enoclerus sphegeus*, showing external sex differences: A, male; B, female.

five Douglas-fir beetles. Records were kept of clerid survival in relation to the quantity of food eaten.

Feeding. Eighteen adult clerids were given a continual supply of live Douglas-fir beetle adults for 30 days to determine maximum daily feeding potential. The predators were kept individually in plastic petri dishes at 75° F with a minimum of five live Douglas-fir beetle adults supplied daily. Dead bark beetles were not considered killed by clerids unless the ventral membrane between the mesothoracic and metathoracic coxae was torn open. The petri dishes were checked two or three times a day, and prey were added to maintain a nearly constant supply of five Douglas-fir beetles with each clerid, regardless of the number destroyed.

Mating and oviposition. The longevity and fecundity of 30 recently eclosed adult clerids were assessed in the laboratory. The clerids were maintained without food at 40° F from November to March. During the remainder of the year, they were kept at 70° to 75° F and provided with one Douglas-fir beetle adult per day.

Clerids were mated at various intervals to determine the length of time fertile eggs could be laid following a single copulation. As soon as a pair had mated, the female was isolated from the male until nothing but infertile eggs were laid for three days, after which she was again mated and the process repeated. Female clerids were supplied with a triangular piece of paper rolled into a spiral to serve as an oviposition site, but most females preferred to lay their eggs on the bottom and sides of the petri dish, usually under the blotting paper. Adult females were transferred to clean petri dishes at frequent intervals.

Fertile eggs could be detected three or four days after oviposition by the appearance of white streaks in the eggs; infertile eggs remained a clear orange color and eventually shriveled. Fertile eggs were often detected the day they were laid, as they were usually in neat clusters or rows on the bottom of the petri dish; while infertile eggs were often scattered indiscriminately around the sides of the dish or on the lid, indicating that egg fertility affected oviposition behavior. Egg fertility estimates were obtained by incubating the eggs at 75° F.

Density. Methods of observation were developed to: 1) obtain densities of active adult Cleridae on defined areas of bark surface; 2) estimate the relative seasonal abundance of clerids on fallen timber; and 3) relate predator abundance to densities of Douglas-fir beetle adults and beetle entrance holes. Two windthrown trees, about 200 feet long, were marked for observation into numbered sections 6 feet long. The order in which sections were observed was determined randomly. The observer seated himself as quietly as possible on the

ground about 3 feet from a section and observed an area of approximately 10 square feet of bark surface. Next, the number of Douglas-fir-beetle attacks on the visible area was estimated by counting the piles of boring dust at the entrance holes. The observer then made note of all Douglas-fir beetles and clerids which appeared in the measured area within a 5-minute period. Nearly eight hours were spent observing sections, from April to August 1964, on warm afternoons when the clerids or Douglas-fir beetles were most active and easily seen.

A more practical and less time-consuming method than actual clerid density observations was needed to estimate the total number of adult clerids on a tree. A procedure similar to that described by Lincoln (1930) made it possible to include motionless clerids which were undoubtedly overlooked in the observations. A ratio of unmarked to marked clerids was obtained by marking clerids on the pronotum with red nail polish, releasing them on a windthrown tree, and later making a series of observations on the tree. The ratio of unmarked to marked individuals established the index, which, when applied to the number of marked releases, gave an estimate of the total population (Graham, 1963). Refined calculations to allow for emigration, immigration, and mortality were not made, as only a relative estimate of the population was desired. Sampling was first done on the day following release in order to minimize the number of marked clerids which might disperse to other trees before a ratio could be obtained. Twenty-seven clerids were released on the tree, and of those released 25 remained on the tree over night. The number of marked releases applied to the formula, then, was 25.

Studies of larval development

The larvae of five species of Cleridae were reared in the laboratory to determine the number of instars for each species, to study feeding behavior, and to record their development at different temperatures. Results of laboratory rearings were correlated as much as possible with observations and collections of clerid larvae in the field. All larvae and pupae collected were recorded, and those which were not readily identified were reared to the adult stage.

Instar determination and growth rates. Larvae which emerged from eggs laid in the laboratory were placed individually in 0.75- by 0.75- by 0.75-inch, clear plastic boxes. Eggs were incubated at 75° F, and the larvae were reared in unlit controlled-temperature chambers set at 50°, 70°, 80°, and 90° F and in a chamber which oscillated between 60° and 80° F every 12 hours.

Clerid larvae were reared in plastic containers with woodshavings and moistened bark beetle frass. Addition of two drops of distilled

water every two or three days provided sufficient moisture to allow Douglas-fir beetle larvae to survive for 24 hours, and gave the clerid larvae a more natural environment with a long-lasting food supply. The larvae were first reared on different feeding schedules. However, since they would feed only for certain periods of time during each instar, these schedules were abandoned and the larvae were fed one bark beetle larva per day until they refused to eat for five consecutive days. They were then provided with one Douglas-fir beetle larva a week, unless they resumed feeding, in which case they were again given one Douglas-fir beetle larva per day.

The containers were checked daily for evidence of molting, which was easily detected by the presence of a cast skin, the lighter color of a newly molted larva, and an obvious increase in the size of the head capsule. Changes in behavior and appearance were noted throughout the development of each insect. The widths of the head capsule, the prothoracic shield, and the basal plate were measured; however, the widths of the latter two were not as consistent for a given instar as the head capsule, since they flattened as the larva grew and their widths expanded. Larvae were placed on a small block of ice under the microscope and measurements were taken with a calibrated ocular micrometer.

Density and effectiveness. More than 1,000 square-foot bark samples were taken from 19 windthrown Douglas-fir trees in the watershed throughout 1963 and 1964: (1) To study the development of clerid larvae in the field; (2) to compare Douglas-fir beetle and predator larval densities; and (3) to estimate the reduction of bark beetle broods by predators. Trees for sampling were chosen to give a thorough coverage of tree sizes, degrees of infestation, elevation, and exposure within the areas of windthrow. Each tree was marked into three equal sections from the base to the top. Sampling was done every two or three weeks throughout the spring, summer, and early fall and once during the winter. Samples were taken from the top, sides, and occasionally from the bottom of each section. Bark was removed by first sawing two rings around the circumference of the tree with a hand saw, and then making longitudinal cuts by striking the head of an ax with a sledge hammer. When the sample was completely cut, it was removed by prying it from the tree with a screwdriver.

As soon as the sample was removed, all stages of Douglas-fir beetles and predators which could be seen were counted. The sample was then numbered, placed in a plastic bag, and taken to the laboratory where Douglas-fir beetle galleries were counted and measured. Samples in which some Douglas-fir beetle larvae had reached the fourth instar or pupated were scraped with a chisel to locate those which had tunneled into the bark and were hidden from view.

Results and Discussion

The life histories of *Enoclerus sphegeus, E. lecontei,* and *Thanasimus undatulus* were found to be similar in many respects to those reported previously. New information was gained regarding the seasonal emergence and life span of adult clerids, the development of immature stages, and the effectiveness of clerids as predators of the Douglas-fir beetle.

Enoclerus sphegeus

Although *E. sphegeus* adults were most abundant on windthrown trees in May and June 1963, none appeared in emergence cages until August. Prepupal larvae were found in the outer bark of 1962-infested trees throughout the spring of 1963, but no pupae were discovered until July 9. *E. sphegeus* began emerging in cages containing Douglas-fir beetle infested logs (Table 1) on August 2, about three weeks after the first pupae were discovered. Emergence continued until October 18, with the peak around mid-August (Fig. 1). There was no evidence of emergence in the spring, as was reported by Kline and Rudinsky (1964).

E. sphegeus adults remained inactive in their pupal cells for about four days following eclosion. They emerged on the fifth day, fully colored and ready to feed and mate. Adults were rarely found on trees infested with Douglas-fir beetles during late summer and early fall, and since few Douglas-fir beetle adults were available at this time, the newly emerged clerids probably fed on a variety of other insects (Table 2).

E. sphegeus adults found during April, May, and June in 1963 and 1964, had apparently emerged the previous August or September, and had overwintered as adults. Evidence of overwintering was obtained when 16 young *E. sphegeus* adults were marked and left in two cages in the watershed from November 1963 to March 1964. The cages were checked in December and again in January, and on both

Table 1. Emergence of Different Species of Cleridae From Material Containing Douglas-fir Beetle and *Scolytus unispinosus* in 1963

Species	Number emerged	
	Material with Douglas-fir beetles	Material with *Scolytus unispinosus*
Enoclerus sphegeus	61	0
Enoclerus lecontei	1	38
Thanasimus undatulus	2	6
Enoclerus schaefferi	0	7

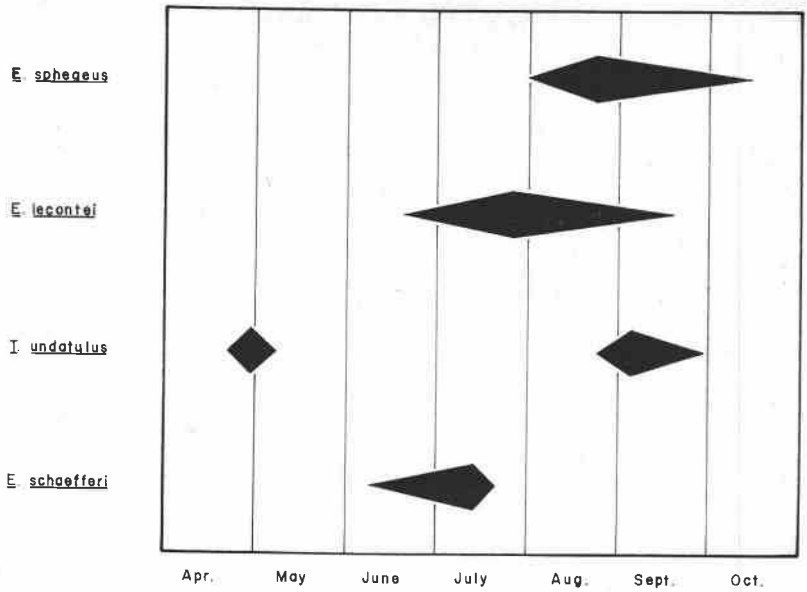

Figure 1. Emergence of adult Cleridae in 1963, from logs infested with Douglas-fir beetles and *Scolytus unispinosus*.

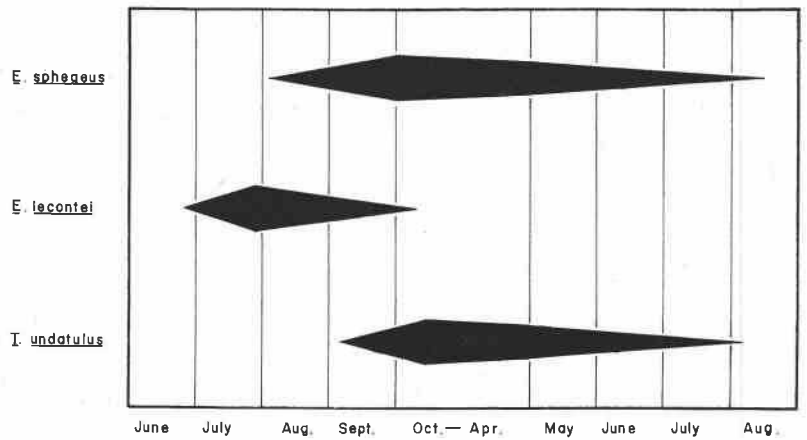

Figure 2. Adult life span of three species of Cleridae in the field.

Table 2. ADULT INSECTS EATEN, ATTACKED, OR IGNORED BY ADULT *Enoclerus sphegeus* IN THE FIELD OR LABORATORY

List of insects		Observation	
Family	Species	Field	Laboratory
Scolytidae	*Dendroctonus pseudotsugae*	E*	E
	Pseudohylesinus spp.	E	E
	Trypodendron lineatum	E	E
	Gnathotrichus sulcatus		E
	Gnathotrichus retusus		E
	Scolytus unispinosus	E	E
Cerambycidae			E
Coccinellidae			E
Chrysomelidae			E
Bruchidae	*Bruchus brachialis*		E
Curculionidae	*Pissodes* spp.	E	A
Cicadellidae			E
Muscidae	*Musca domestica*		E
Dolichopodidae	*Medetera aldrichii*	E	
Ichneumonidae			E
Ostomatidae	*Temnochila virescens*		A
Cantharidae			A
Vespidae		A	A
Tenebrionidae	*Tribolium castaneum*		I
Forficulidae			I
Formicidae		I	I

*E—Eaten.
A—Attacked, but not eaten.
I—Ignored.

occasions marked *E. sphegeus* were found hidden under the edge of a removable top of one cage and hear the door hinge of the other. Four of the clerids were observed again under the removable top on March 19, indicating that *E. sphegeus* adults probably hibernate in protected places above the ground, most likely in bark crevices as reported by Struble (1942a). Logs, loose bark, and litter placed in the cages to provide shelter were carefully inspected, but no clerids were found in any of this material.

Approximately 90% of *E. sphegeus* adults kept in a refrigerator for six months at 40° F survived when previously fed five or more Douglas-fir beetle adults. Survival was only about 10% with those which had been fed one Douglas-fir beetle, and zero when the clerids were not fed. Some *E. sphegeus* adults survived up to 17 months in the laboratory—6 months overwintering at 40° F, and the remainder at 70° to 75° F—while adults lived about 12 months in the field (Fig. 2).

E. sphegeus adults appeared on attacked trees toward the end of April 1964, simultaneously with the Douglas-fir beetles. They were found on the attacked trees until the end of July, nearly a month after most Douglas-fir beetle adults had entered the bark (Fig. 3). *E. sphegeus* seemed to be attracted to the trees by oleoresin fumes released through bark beetle entrance holes (W. G. Harwood, Oregon State University, personal communication) and appeared in greatest numbers on the bark surface where the Douglas-fir beetle attack densities were high (Table 3).

Four of 25 marked *E. sphegeus* released on a windthrown tree on June 12, 1964, were observed on the tree the next day along with other *E. sphegeus,* in a ratio of 6 unmarked to 1 marked clerid. The

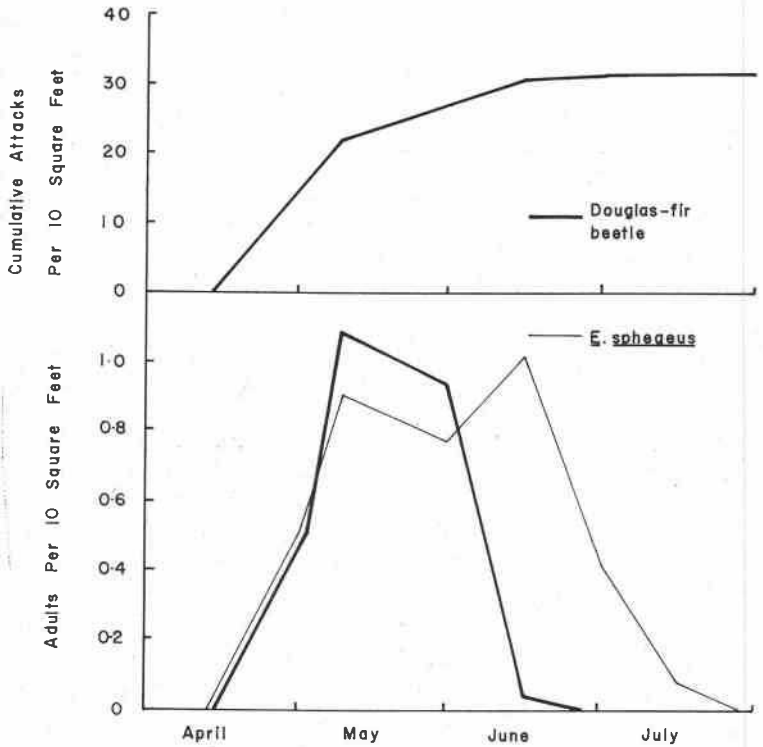

Figure 3. Seasonal prevalence of *Enoclerus sphegeus* and Douglas-fir beetle adults, as observed in five-minute intervals on the bark surface of two trees, compared with cumulative Douglas-fir beetle attacks.

Table 3. Densities of *Enoclerus sphegeus* Adults Observed on the Bark Surface of Two Windthrown Trees, Related to Douglas-fir Beetle Attack Densities; May 10 to June 30, 1964

Douglas-fir beetle attacks per 10 square feet	Number of observations	*E. sphegeus* observed per 10 square feet		
		Mean	*Standard error*	*Range*
0	2	0.00	.....	.....
1-10	13	0.12	± 0.03	0.00-0.82
11-20	10	0.91	± 1.15	0.00-3.30
21-30	18	0.92	± 1.01	0.00-2.60
31-40	5	1.38	± 0.99	0.00-2.50
41-50	3	1.73	± 0.02	1.60-2.00
51-60	0	.....	.....	.....
61-70	3	2.16	± 0.99	1.60-3.30

total number of *E. sphegeus* adults on the tree was estimated to be 175, using the Lincoln Index formula (Graham 1963):

$$\frac{4}{25} = \frac{4 + 24}{175}$$

where 175 = total population being sampled;

25 = total number of marked clerids released;

24 = number of unmarked clerids observed later;

4 = number of marked clerids observed later.

Another observation on the same tree on June 29, 1964, revealed a ratio of five unmarked to one marked clerid, indicating there had been little influx of clerids during the two-week interval. Although *E. sphegeus* adults were often seen flying on and off infested trees during the early part of the season, they were seldom observed in flight after June 1. *E. sphegeus* adults began to disappear from infested trees by the end of July (Fig. 3), because of: 1) Lack of Douglas-fir beetle adults on which to feed; 2) mortality resulting from cannibalism or other insect predators; 3) the possibility that the infested trees no longer attracted clerids; or 4) natural mortality.

E. sphegeus adults were observed mating in the laboratory 5 days after eclosion (as soon as they became active), although they did not begin to oviposit for about 30 days. Some eggs are laid before overwintering because two newly emerged larvae were collected in the field in October 1964. However, in the laboratory the majority of eggs were laid after overwintering (Table 4). Fecundity of *E. sphegeus* females in the laboratory was extremely variable; the

number of eggs laid ranged from 0 to 289 in a period of 6 months following overwintering (Table 5).

Table 4. Average Number of Eggs Laid by *Enoclerus sphegeus* in the Laboratory at 75° F Throughout Each Month of Active Adult Life

Month	Equivalent in field	Number of females	Eggs laid	
			Mean	*Standard error*
1	August	6	1	± 2.00
2	September	5	9	± 7.45
3–8	Oct.-March		(Overwintering)	
9	April	16	6	± 8.64
10	May	11	23	± 32.70
11	June	9	23	± 27.40
12	July	9	16	± 21.00
13	August	9	6	± 8.44
14	September	8	6	± 8.08
15	October	5	0	.....

Table 5. Maximum Number of Eggs Laid by One Female in the Laboratory at 75° F

Species	Months active	Number of eggs laid		
		Mean per month	*Standard deviation*	*Total*
Thanasimus undatulus	7	56.42	± 38.95	395
Enoclerus sphegeus	6	48.16	± 32.86	289
Enoclerus lecontei	2	57.50	± 4.53	115
Enoclerus schaefferi	2	5.00	± 5.00	10
Enoclerus sp.	4	1.25	± 2.17	5

Reid (1957) observed oviposition by *E. sphegeus* on a lodgepole pine four to five minutes after copulation had taken place. Mating in our studies, however, did not appear to influence the rate or time of oviposition of *E. sphegeus* females in the laboratory. Fertile eggs were laid by nine females for an average of 30.0 ± 15.3 (SE) days following each mating, after which infertile eggs were laid until the clerids were remated. One *E. sphegeus* female was repeatedly mated with *T. undatulus* males and laid eggs, but none were fertile.

Gravid *E. sphegeus* females were often observed running over the bark surface of windthrown trees, stopping every few inches and inserting the ovipositor under a bark scale, as though searching for a suitable oviposition site. Although *E. sphegeus* adults occurred most frequently where Douglas-fir beetle attack density was high, female

clerids were not observed to orient to Douglas-fir beetle entrance holes when searching for oviposition sites. Only once was oviposition of *E. sphegeus* actually observed in the field; six eggs were laid in a cluster under a bark scale, about 0.2 inch beneath the surface, and 6 inches from the nearest Douglas-fir beetle entrance hole.

E. sphegeus larvae normally pupated after the second instar, and developed into normal-sized adults which mated and laid fertile eggs, even though *E. sphegeus* had been described as having three and four instars (Kline and Rudinsky, 1964; Reid, 1957; Struble, 1942a). *E. sphegeus* larvae showed no overlap of head capsule size in the first- and second-instar (Table 6), but the head capsules of most second-instar larvae were as large as those of the third-instar as described by Kline and Rudinsky (1964). Large, mature, first-instar larvae (Plate III, Fig. C) collected in the field molted into second-instar larvae with a head capsule width up to 1.80 mm, slightly greater than that of any larvae reared in the laboratory. Third-instar *E. sphegeus* larvae occasionally developed from small second-instar larvae, which were undersized as a result of starvation during the first instar.

The immature stages of *E. sphegeus* developed more rapidly as the temperature increased from 50° to 80° F, with the optimum for survival at 70° F. Larvae and pupae developed faster at temperatures oscillating between 60° and 80° F than at a constant 70° F, although eggs hatched sooner at 70° F. (Table 7). No larvae completed development at 50° and none survived at 90° F.

Table 6. Head Capsule Widths of Cleridae Larvae in Millimeters

Species	Instar	Number measured	Mean width	Standard error
Enoclerus sphegeus	1	42	0.74	± 0.06
	2	82	1.45	± 0.21
Enoclerus lecontei	1	9	0.26	0.00
	2	19	0.43	± 0.06
	3	11	0.75	± 0.05
Enoclerus schaefferi	1	4	0.30	0.00
	2	6	0.47	± 0.04
	3	4	0.82	± 0.06
Enoclerus sp.	1	2	0.42	± 0.07
	2	1	0.77	.....
	3	1	1.00	.....
Thanasimus undatulus	1	20	0.35	± 0.01
	2	17	0.55	± 0.04
	3	25	1.08	± 0.03

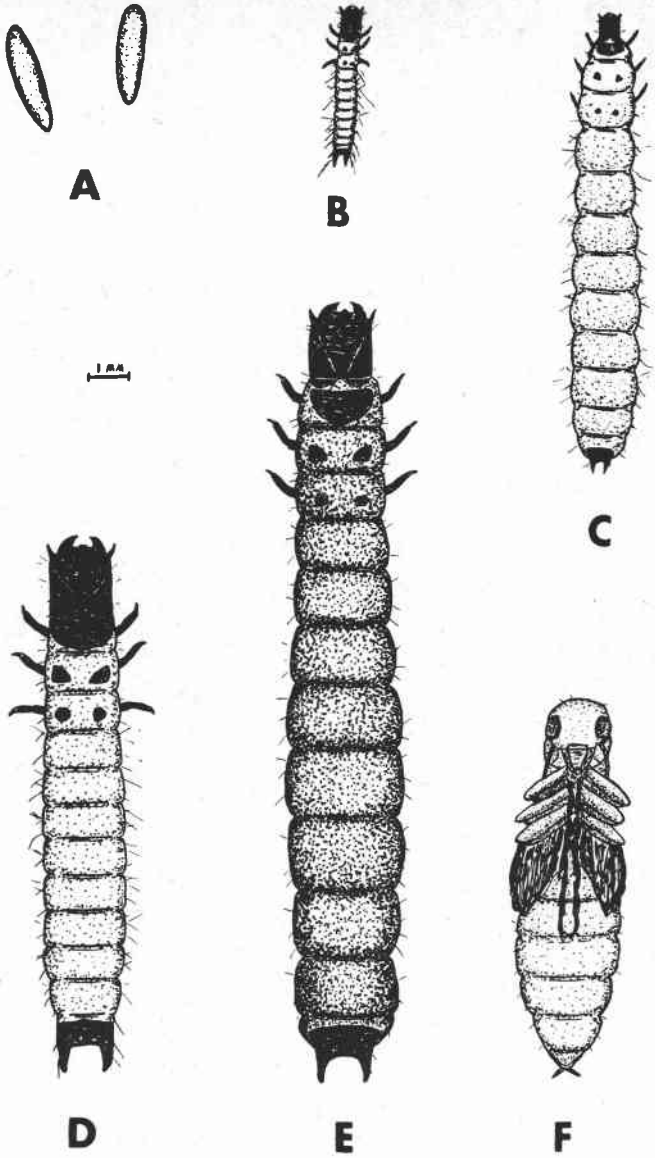

PLATE III. Immature stages of *Enoclerus sphegeus:* A, eggs; B, first-instar larva, newly emerged; C, first-instar larva, pre-molt form; D, second-instar larva, orange, feeding form; E, second-instar larva, lilac, migrating form; and F, pupa.

Table 7. Duration of the Immature Stages of *Enoclerus sphegeus* at Different Temperatures

Stage	Temperature °F	Number	Mean days	Standard error	Percentage mortality
Eggs	50	4	80	0.00	*
	70	14	10	± 1.75	*
	80	35	7	± 0.37	*
	90	1	6	.....	*
	60–80	8	12	± 0.29	*
First-instar larvae	50	4	83	± 24.20	25
	70	15	22	± 3.20	6
	80	14	14	± 4.05	14
	90	5	9	0.00	40
	60–80	6	15	± 2.44	16
Second-instar larvae	50	7	**	.....	40
	70	9	115	± 32.10	22
	80	17	58	± 14.46	61
	90	11	.....	.....	100
	60–80	7	103	± 18.00	28
Pupae	50	1	109	.....	0
	70	8	22	± 1.18	12
	80	16	12	± 0.84	6
	90	1	.....	.....	100
	60–80	7	17	± 1.18	14

* No count was made.
** None pupated or molted.

The incubation period of *E. sphegeus* eggs ranged from six days to two and a half months in the laboratory, depending on the temperature (Table 7). First-instar larvae were bright orange, becoming paler as they grew. Newly hatched first-instar larvae (Plate III, Fig. B) are reported to enter bark beetle galleries through bark beetle entrance holes (Kline and Rudinsky, 1964; Reid, 1957). However, most larvae had great difficulty penetrating through the boring dust when placed in or near an entrance hole and usually crawled or tumbled out along with loose particles of boring dust. Only 26 of 110 first-instar *E. sphegeus* larvae placed on seven logs, each log averaging two Douglas-fir beetle attacks per square foot, were later recovered underneath the bark. One first-instar larva was found in a tunnel it had apparently made itself, which extended from the bark surface to the cambium, three weeks after being released on the bark surface.

First-instar *E. sphegeus* larvae were found in Douglas-fir beetle galleries from about June 15 to the first week of October (Fig. 4). The first-instar stadium lasted at least a month in the field, with the larvae developing most rapidly where the bark surface was exposed to the sun. First-instar *E. sphegeus* larvae tripled their length after

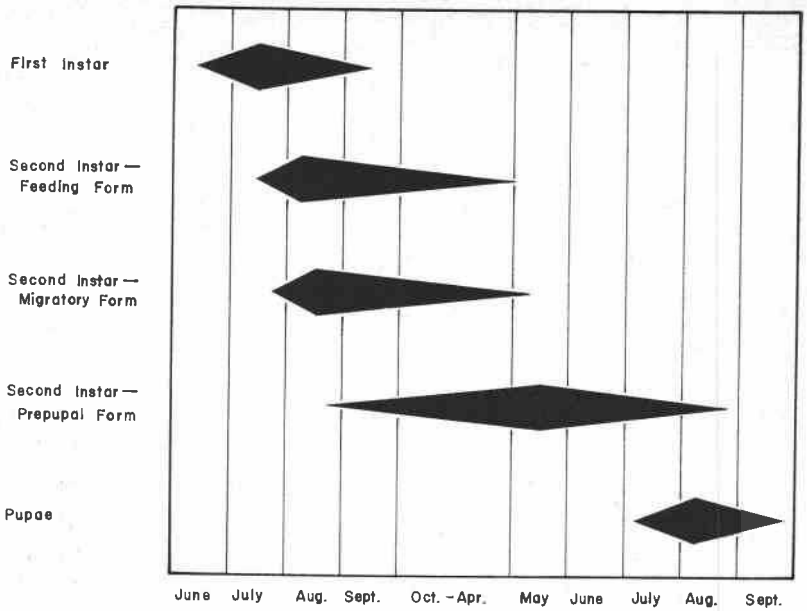

Figure 4. Seasonal duration of the immature stages of *Enoclerus sphegeus*.

feeding on an undetermined number of Douglas-fir beetle eggs or larvae, and then remained dormant for about three days before molting (Plate III, Fig. C). The second-instar head capsule could be seen forming within the prothorax of the first-instar larva, with only the mouthparts and clypeus extending into the head capsule. Reid (1957) described a similar condition, which, he said, took place in mature second-instar larvae before molting to the third instar. First-instar larvae in this premolt condition were very readily preyed upon by other clerid larvae and mites.

Young, orange-colored, second-instar *E. sphegeus* larvae (Plate III, Fig. D) began feeding one day after molting and consumed approximately 10 Douglas-fir beetles, mostly consisting of third- and fourth-instar larvae, pupae, or callow adults. Second-instar larvae attained their full size and their color changed from orange to a deep lilac (Plate III, Fig. E). Thereafter, they seldom fed but became more active and those in the laboratory attempted to pry their way out of the plastic containers. They gradually assumed a state of relative inactivity and began secreting exudatium for lining their pupal cells. Mature, lilac-colored, second-instar larvae in the field began leaving Douglas-fir beetle galleries after August 15 (Fig. 5), and

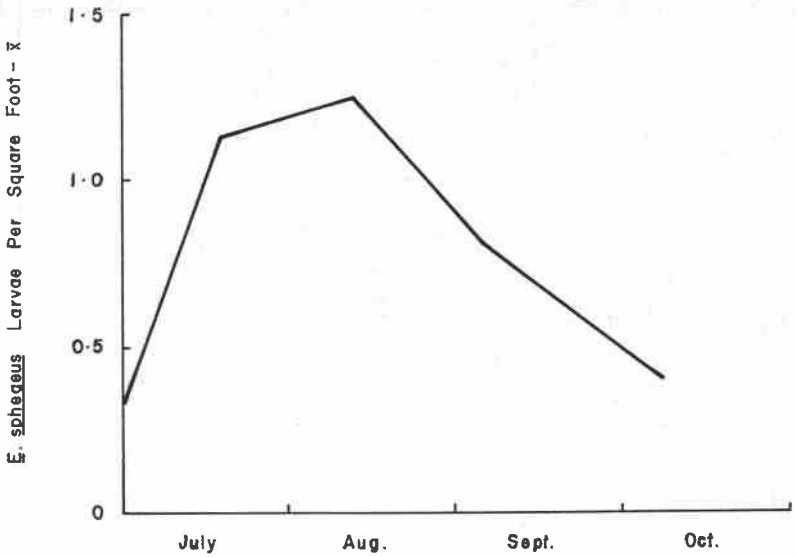

Figure 5. Average densities of *Enoclerus sphegeus* larvae in Douglas-fir beetle galleries during 1964.

tunneled to the surface of the bark. They then tunneled back to a depth of 0.50 inch in trees where the bark thickness was at least 0.75 inch, and pupated. Clerid larvae disappeared almost entirely by November from windthrows where the bark was less than 0.75 inch thick, and probably dropped to the ground. Prepupal larvae from a standing, infested snag were found in May, inside pieces of partly decayed bark previously placed in a collar at the base of the snag. *E. sphegeus* evidently spends nearly a year as prepupal second-instar larvae before pupating in July or August (Fig. 4).

The rate of development of second-instar *E. sphegeus* larvae in the laboratory varied from one to five months, and could theoretically have been completed by some individuals in the field by the end of their first summer, as reported by Furniss (1957) and Struble (1942a). However, no evidence was found of *E. sphegeus* pupating in the field during their first summer.

Both first- and second-instar *E. sphegeus* larvae were observed feeding on larvae, pupae, and callow adults of the Douglas-fir beetle. First-instar *E. sphegeus* larvae were seen feeding on Douglas-fir beetle eggs. They occurred mainly with Douglas-fir beetle brood ranging from the egg to the second-instar, while second-instar clerids were associated with third-instar to callow adult Douglas-fir beetles.

E. sphegeus larvae in the laboratory fed on the larvae of a parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae), and on parasitized Douglas-fir beetle larvae. *E. sphegeus* readily attacked the larvae of *E. lecontei* and *T. undatulus*, and occasionally ate predaceous larvae of *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae) when supplied with no other food. They were usually killed when placed with the more aggressive larvae of *Temnochila virescens* var. *chlorodia* (Mannerheim) (Coleoptera: Ostomatidae). One *E. sphegeus* larva survived six months and molted to the third instar when fed dead, dry Douglas-fir beetle larvae moistened with a drop of water; another was reared to an adult on buprestid and cerambycid larvae. No clerid larvae grew or survived, however, when supplied with only moistened frass or moistened dog food pellets.

E. sphegeus adults consumed more Douglas-fir beetle adults per predator per day than did other species of clerids (Table 8). Other species apparently had some difficulty capturing Douglas-fir beetle adults and showed a decided preference for *Scolytus unispinosus* or *Trypodendron* spp. when these smaller scolytids were present with Douglas-fir beetles. Further evidence that *E. sphegeus* was associated more with the Douglas-fir beetle than other species of Cleridae is seen in Table 1, where it is shown that *E. sphegeus* emerged in cages containing logs infested with the Douglas-fir beetle, while the four other species of clerids emerged more commonly from Douglas-fir branches infested with *Scolytus unispinosus*. Larvae of *E. sphegeus* were the only clerid predators of sufficient abundance in Douglas-fir beetle galleries to be of any importance. The numbers of immature forms of different species collected in more than 1,000 square feet of bark in 1963 and 1964 were: *Enoclerus sphegeus*, 602; *Enoclerus lecontei*, 21; *Thanasimus undatulus*, 4; *Enoclerus* sp., 2; *Enoclerus schaefferi*, 0; *Enoclerus eximius*, 0. *E. sphegeus*, therefore, was the only clerid given consideration as a possible effective predator of the Douglas-fir beetle.

Table 8. Douglas-fir Beetle Adults Killed or Eaten per Predator per Day at 75° F by Adult Cleridae Continually Supplied With Living Prey for 30 Days

Species	Number	Prey killed		
		Mean	Standard error	Range
Enoclerus sphegeus	8	1.67	± 0.47	0–14
Thanasimus undatulus	6	1.02	± 0.32	0– 6
Enoclerus lecontei	1	0.56	.....	.....
Enoclerus sp.	1	0.38	.....	.....
Enoclerus schaefferi	1	0.33	.....	.....
Enoclerus eximius	1	0.16	.....	.....

The Douglas-fir beetle population in 1963 occupied approximately 50% of the bark area sampled on infested windthrown trees. The effect of predation by clerids on the Douglas-fir beetle population could not have been great because densities of both adults and larvae of *E. sphegeus* were extremely low. Adult clerids were rarely seen on the trees, and clerid larvae were found in only 10% of the sampled bark area which contained Douglas-fir beetle galleries (Table 9).

Table 9. Frequency Distribution of *Enoclerus sphegeus* Larvae in Square-foot Bark Samples Collected From July to September, in 1963 and 1964

	1963		1964	
E. sphegeus per square foot	Number of samples	Percentage	Number of samples	Percentage
0	137	90.8	182	65.0
1	12	8.0	42	14.9
2	1	0.6	26	9.2
3	1	0.6	7	2.5
4	0	0.0	9	3.2
5	0	0.0	6	2.1
6	0	0.0	3	1.0
7	0	0.0	4	1.4
8	0	0.0	2	0.7
Total	151	100.0	281	100.0

Windthrown trees were fewer in 1964 and contained considerably higher densities of Douglas-fir beetle and *E. sphegeus* larvae (Table 9). However, it was not known whether the absolute clerid population increased or decreased in 1964.

The number of Douglas-fir beetle adults eaten per day by each of 8 *E. sphegeus* adults in the laboratory was usually between zero and three, although as many as 14 were killed in a day by one individual. An *E. sphegeus* adult, surviving eight months after overwintering, and eating an average of 1.67 Douglas-fir beetle adults per day (Table 8), could theoretically consume 400 Douglas-fir beetles in its lifetime. Availability of Douglas-fir beetle adults in the field, however, was limited to about two months in 1964 (Fig. 3). Densities of Douglas-fir beetle adults on the bark surface at any given time were never much above those of the clerids, even at the peak of bark beetle attack, and they were exceeded by clerid densities after the first week of June (Fig. 3). Since the field of effective vision of clerids is limited from 1 to 2 inches (Gauss 1954), the chance of a clerid contacting one Douglas-fir beetle would be low even at the highest bark-beetle densities. *E. sphegeus* adults on several occasions were observed

passing within an inch or two of Douglas-fir beetle adults and none were able to locate their prey. The actual number of Douglas-fir beetles eaten per adult clerid in the field, then, is probably much smaller than the potential number as determined from laboratory experiments.

The effect of *E. sphegeus* larvae on Douglas-fir beetle brood populations in 1964 was determined from numerical comparisons of Douglas-fir beetle brood in square-foot samples containing various densities of *E. sphegeus* larvae. The number of Douglas-fir beetle brood per inch of parent gallery in each sample was used as the unit of measurement. Clerid counts were not taken from samples later than August 15, since the average number of clerid larvae per square foot began to decrease after August 15 due to larval migration (Fig. 5). Samples were taken in three, two-week periods between July 1 and August 15, 1964, from nine trees. Each sample was only compared with other samples taken within the same two-week period to minimize differences of Douglas-fir beetle brood development. Samples in each two-week period were grouped according to *E. sphegeus* larval densities: zero, one to two, and three to seven per square foot. Although there was a reduction in prey densities as predator densities increased, an analysis of variance showed no significant differences in Douglas-fir beetle survival at the 5% level of probability (Table 10). In addition, the number of *E. sphegeus* larvae per square foot was independent of the number of inches of Douglas-fir beetle gallery per square foot (Fig. 6), indicating that the differences in brood survival were probably related to gallery

Table 10. Douglas-fir Beetle Brood Survival Related to Different Densities of *Enoclerus sphegeus* Larvae in Nine Trees During the Summer of 1964

Date	*E. sphegeus* per square foot	Number of samples	Douglas-fir beetle brood per inch of parent gallery	Pooled variance	D.F.	F
July 1 to July 15	0	59	4.16 ± 2.20 (SE)	4.90	2/69	0.70
	1–2	11	3.50 ± 2.41			
	3–7	2	2.83 ± 1.17			
July 16 to July 31	0	26	3.27 ± 3.04	6.30	2/53	1.86
	1–2	19	2.63 ± 2.24			
	3–7	11	1.54 ± 1.07			
August 1 to August 15	0	30	2.11 ± 2.17	2.75	2/59	2.76
	1–2	19	1.43 ± 1.01			
	3–7	13	0.88 ± 0.73			

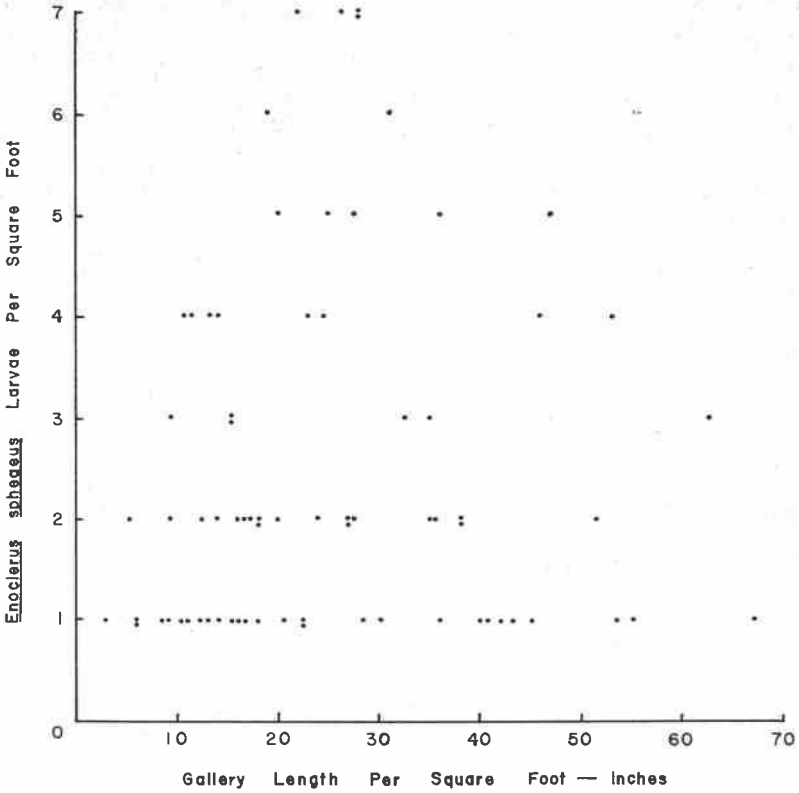

Figure 6. Scatter diagram of the relationship between *Enoclerus sphegeus* larval densities and inches of Douglas-fir beetle parent galleries per square foot; samples from nine trees, July 1 to August 15, 1964.

density or other factors than predation by *E. sphegeus*. McMullen and Atkins (1961) found that as Douglas-fir beetle adult gallery lengths per square foot increased, the number of surviving progeny decreased. Reid (1963) similarly observed that the survival of mountain pine beetle brood per inch of parent gallery decreased with increasing gallery density, as a result of competition. The conclusion, then, is that Douglas-fir beetle survival, at the prey- and predator-density levels studied, depended to a large extent on gallery and progeny density, and was relatively unaffected by the presence of *E. sphegeus* larvae.

Enoclerus lecontei

E. lecontei (Plate I, Fig. 3) has a range from British Columbia east to Michigan and south to Guatemala (Papp, 1960). Doane and others (1936) and Keen (1928) reported it to be an active predator of the western pine beetle, *D. brevicomis* LeConte. Person (1940) claimed that each adult killed at least 25 western pine beetles during a life of six to eight weeks, and that the larvae of *E. lecontei* caused up to 42% mortality of the brood. Bedard (1933) and Kline and Rudinsky (1964) felt that although the insect is found on Douglas-fir, it is of no great importance in controlling the Douglas-fir beetle. Kline and Rudinsky (1964) found *E. lecontei* ". . . to be more abundant in association with smaller bark beetles, such as *Scolytus unispinosus* Lec. and various species of the genus *Pseudohylesinus* . . ." in western Oregon.

E. lecontei emerged from June 15 to September 21, 1963, with the peak of emergence about July 27 (Fig. 1). Adults were found in the field only from June 15 to the end of September (Fig. 2); they survived a maximum of two months in the laboratory and gave no evidence of overwintering in the adult stage. *E. lecontei* emerged mainly from Douglas-fir branches infested with *Scolytus unispinosus*

Table 11. Duration of the Immature Stages of *Enoclerus lecontei* at Different Temperatures

Stage	Temperature F	Number	Mean days	Standard error	Percentage mortality
Eggs	70	11	12	± 0.32	*
	80	15	6	0.00	*
	90	8	5	0.00	*
	60–80	12	9	± 0.42	*
First-instar larvae	70	13	25	± 4.76	30
	80	11	14	± 1.52	63
	90	8	16	± 1.58	62
	60–80	12	23	± 7.05	16
Second-instar larvae	70	8	15	± 4.10	12
	80	4	10	± 0.81	0
	90	3	8	± 1.00	33
	60–80	9	13	± 2.12	0
Third-instar larvae	70	7	176	± 6.14	55
	80	4	26	.....	75
	90	1	.....	.....	100
	60–80	10	64	± 1.73	67
Pupae	70	1	17	.....	0
	60–80	3	11	0.00	0

* No count was made.

(Table 1), and the adults of *E. lecontei* were most abundant in the field several weeks after the main Douglas-fir beetle flight, which further reduced their value as potential predators of the Douglas-fir beetle. Larvae of *E. lecontei*, although occasionally found in Douglas-fir beetle galleries, were more often found associated with the larvae of *Melanophila drummondi* Kirby (Coleoptera: Buprestidae).

E. lecontei females laid up to 115 eggs, with oviposition beginning about 21 days after adult emergence. The immature stages developed more rapidly as the temperature increased to 80° F, although the optimum for survival was at temperatures oscillating between 60° and 80° F. All immature stages developed faster at temperatures fluctuating between 60° and 80° F than at a constant temperature of 70° F. No eggs hatched at 50° F and no larvae survived at 90° F (Table 11).

Predator larvae fed Douglas-fir beetle larvae required at least three instars to complete development; a few that molted to the fourth instar all died. In the field, the larvae grew through the first and second instars during July, August, and September, then overwintered as third instar larvae (Fig. 7) in the outer bark or in host galleries, where they later pupated.

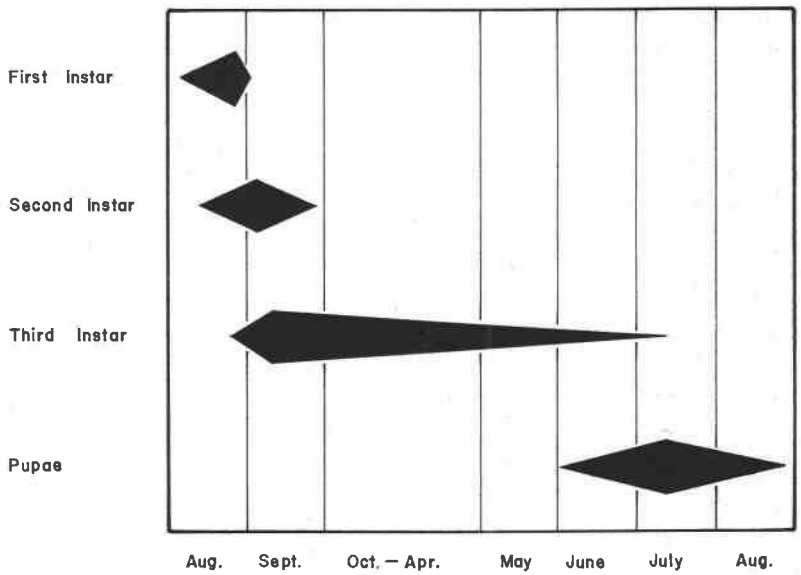

Figure 7. Seasonal duration of the immature stages of *Enoclerus lecontei*.

Thanasimus undatulus

T. undatulus (Plate I, Fig. D) was found on Douglas-fir, but appeared to be associated with small scolytids such as *Scolytus unispinosus,* since only four larvae were found in more than 1,000 square feet of bark containing Douglas-fir beetle galleries in 1963 and 1964.

Two adults were collected in an emergence cage on April 28, 1963, but no more emerged until the end of August, suggesting two periods of emergence (Fig. 1). Adults overwintered in the laboratory for 6 months at 40° F and survived up to 13 months. *T. undatulus* adults occurred on infested trees during April, May, and June, and appeared to live about 12 months in the field (Fig. 2).

Observations in the laboratory indicated that *T. undatulus* females produced an attractant that elicited prompt male responses. Pairs readily mated when placed together, with the male rushing toward the female and mounting her almost immediately. *T. undatulus* males placed in petri dishes with *E. sphegeus* females showed little tendency to mate, except when both insects were in a petri dish recently occupied by a *T. undatulus* female, in which case they usually mated immediately. Some type of attractant produced by *T. undatulus* females had contaminated the petri dish and stimulated *T. undatulus* males sufficiently to cause them to mate with a different species. The effect of the stimulus was observed to an even greater degree after placing *T. undatulus* males and Douglas-fir beetle adults in a petri dish which had recently contained a *T. undatulus* female; the *T. undatulus* males were then observed attempting to copulate with the Douglas-fir beetles. *E. sphegeus* males and *T. undatulus* females were similarly placed together in petri dishes which had been occupied by *E. sphegeus* females, but were not observed to mate because *E. sphegeus* males were unable to catch the faster *T. undatulus* females. Inter-specific mating of clerids was not observed in the field, although normal mating may have been influenced by species-specific pheromones produced by females of all the species of Cleridae.

Little was learned concerning the seasonal history of the immature stages of *T. undatulus* in the field because of their scarcity in Douglas-fir beetle galleries. One first-instar larva was found on May 8, 1964, where it was feeding on Douglas-fir beetle eggs.

T. undatulus was the most prolific of the clerids in the laboratory, laying as many as 395 eggs in 7 months (Table 5). *T. undatulus* had three larval instars in the laboratory, developing more rapidly as the temperature increased from 50° to 80° F (Table 12). No larvae completed development at 50° and none survived beyond the first instar at 90° F. Larvae and pupae developed faster at temperatures oscillating between 60° and 80° F than at a constant temperature of 70° F, although eggs hatched sooner at 70° F. Temperature oscilla-

tion apparently caused much greater variation in the rate of development of third-instar *T. undatulus* larvae (Table 12), probably allowing some larvae to complete development during the first summer. Bedard (1933) stated that a few larvae reached the adult stage by August and September, while the majority overwintered as larvae and emerged in May and June. Pupae have been found underneath the bark (Reid, 1963), or in the outer bark and on the ground (Bedard, 1933).

Table 12. Duration of the Immature Stages of *Thanasimus undatulus* at Different Temperatures

Stage	Temperature F	Number	Mean days	Standard error	Percentage mortality
Eggs	50	9	85	± 26.00	*
	70	28	9	± 0.84	*
	80	13	7	± 0.00	*
	90	18	6	± 0.51	*
	60–80	20	11	± 0.52	*
First-instar larvae	50	11	106	± 11.10	27
	70	16	29	± 2.68	25
	80	14	23	± 5.00	36
	90	18	.....	.....	100
	60–80	15	18	± 3.29	0
Second-instar larvae	50	9	215	± 50.50	11
	70	11	22	± 3.56	0
	80	7	43	± 35.30	0
	60–80	13	20	± 4.00	0
Third-instar larvae	50	7	**	.....	30
	70	8	323	± 1.81	37
	80	8	23	.....	87
	60–80	10	177	±101.70	40
Pupae	70	5	*	.....	20
	80	1	13	.....	0
	60–80	5	17	± 2.58	0

* No count was made.
** None pupated or molted.

Enoclerus schaefferi

This species closely resembles *E. lecontei,* but differs by the presence of two small red humeral spots on the elytra. *E. schaefferi* has been reared from insect-infested cones of Douglas-fir in Oregon and California (Böving and Champlain, 1920; Essig, 1942). The adults occasionally killed and ate Douglas-fir beetle adults in the laboratory, although the species is not listed as a predator of the

Douglas-fir beetle. Larvae were fed Douglas-fir beetle larvae and molted to the fourth instar in the laboratory at 70° F, but they all died (Table 13).

Table 13. DURATION OF THE IMMATURE STAGES OF *Enoclerus schaefferi* AND *Enoclerus* SP. AT 70° F

Species	Stage	Number	Mean days	Standard error	Percentage mortality
E. schaefferi	Eggs	9	12	± 0.61	*
	First-instar larvae	8	12	± 0.89	25
	Second-instar larvae	6	12	± 1.00	0
	Third-instar larvae	6	12	± 7.80	67
	Fourth-instar larvae	2	.....	.....	100
Enoclerus sp.	Eggs	1	16	.....	0
	First-instar larvae	1	28	.....	0
	Second-instar larva	1	21	.....	0
	Third-instar larvae	1	166	.....	0
	Pupa	1	31	.....	0

* No count was made.

Enoclerus eximius

Although two specimens were collected on Douglas-fir in western Oregon, this species has not been listed as a predator of the Douglas-fir beetle. One specimen consumed a few Douglas-fir beetle adults in the laboratory. Essig (1942) stated that it preys on ptinid beetles infesting trees such as California bay, alder, willow, and similar trees from California to British Columbia. No immature forms were discovered in the field or reared in the laboratory.

Enoclerus sp.

Four adults of a new species of *Enoclerus* (Plate I, Fig. C) were collected on or near Douglas-fir trees, and a larva and pupa of the species were found in Douglas-fir beetle-infested bark. Adults were seven to eight mm long, black with a red abdomen, and had two pink, triangular markings on the medial margins of the elytra. W. F. Barr (University of Idaho, personal communication) stated: "I am now of the opinion that it represents an undescribed species or subspecies, most closely related to *E. eximius*." Adults occasionally ate Douglas-fir beetle adults, and a larva was reared through three instars, feeding on Douglas-fir beetle larvae and completing development (Table 13).

A mature larva of *Enoclerus* sp. found in April 1963, in the outer bark of a windthrow infested the previous spring, indicated that this species was capable of overwintering in the larval stage. One pupa of *Enoclerus* sp. was found on August 24, 1963, in the outer bark of a windthrown tree infested with Douglas-fir beetles in 1963. Adults of *Enoclerus* sp. were found from May 11 to July 27, and survived up to 12 months in the laboratory, but relatively few eggs were laid (Table 5).

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