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The Flight and Olfactory Behavior of Checkered Beetles (Coleoptera: Cleridae) Predatory on the Douglas-fir Beetle



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CONTENTS

	<i>Page</i>
INTRODUCTION	3
LITERATURE REVIEW	4
<i>Enoclerus sphegeus</i>	5
<i>Enoclerus lecontei</i>	6
<i>Thanasimus undatulus</i>	7
Flight Behavior of <i>Dendroctonus pseudotsugae</i>	8
Composition of Oleoresins	9
MATERIALS AND METHODS	12
Study Area	12
The Use of Nets	12
The Use of Olfactometers	13
Attraction Cages	20
Observation Logs	20
Meteorological Records	20
RESULTS AND DISCUSSION	21
Diurnal Flight Patterns	21
Seasonal Flight Patterns	25
Olfactory Behavior	29
SUMMARY	33
REFERENCES CITED	34

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The Flight and Olfactory Behavior of Checkered Beetles (Coleoptera: Cleridae) Predatory on the Douglas-fir Beetle

W. G. HARWOOD and J. A. RUDINSKY

INTRODUCTION

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is probably the most destructive insect of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, throughout the natural range of this economically important tree. The volume of green timber killed by this insect during the 1951-1954 epidemic amounted to over three billion board feet in Oregon and Washington alone. Another epidemic started in 1964, and losses for that year and 1965 have been estimated at some 2½ billion board feet of green timber.

The main regulatory factor of the Douglas-fir beetle population is apparently the amount of suitable brood material available in wind-thrown trees. Other factors such as weather, competition, host resistance, and biological agents certainly play a more or less important role from time to time. It is through a knowledge of these individual factors that a safe, effective, and economical method of integrated control may be achieved. Entomophagous insects have often been considered important factors in reducing or preventing the development of high populations of destructive forest insects.

Three species of checkered beetles (Coleoptera: Cleridae) which may exert regulative pressures on the Douglas-fir beetle population in western Oregon are *Enoclerus sphegeus* Fabricius, *Thanasimus undatulus* Say, and *E. lecontei* Wolcott. The close association of these clerids with the Douglas-fir beetle has prompted past investigations into their biologies and estimates of their effectiveness, but the flight periods and the means by which these predators locate their prey have not been investigated. Therefore, the study reported here was instigated with the following objectives: (1) to determine the flight patterns of these insects in relation to the flight of the Douglas-fir beetle; and (2) to determine the mechanisms by which these predators locate their prey.

Knowledge of the flight of these clerids may be of value to workers attempting to control the Douglas-fir beetle and other scolytids by: (1) providing a means of estimating population levels of the clerids in a given area through trapping; (2) determining the associations between uncertain predators and bark beetles through comparisons of

their flight schedules and tree hosts; and (3) developing a method of trapping large numbers of Cleridae for release in other areas where scolytids are epidemic.

LITERATURE REVIEW

The family Cleridae is composed of approximately 3,300 species of which about 317 species are represented in North America north of Mexico (27).¹ With very few exceptions, the members of this family are closely associated with bark- and wood-boring insects, mainly Scolytidae, as predators in both the larval and adult stages (5, 1, 20).

Balduf (1) considers the clerids in general to be more specialized as predators than most Carabidae and Cicindelidae because they have limited their prey to a group of insects with more or less uniform habits and development. This limitation is said to be indicated by the predator and prey life cycles which appear to be correlated seasonally and numerically. He also considers the development of these predators to be parallel to that of their prey, which is evidenced by the fact that the clerid larvae feed on the immature stages of the prey and the clerid adults upon the prey adults. These points agree at least in part with the information available on *E. sphegeus*, *E. lecontei*, and *T. undatulus*.

Evaluations of the effectiveness of these three species as predators have ranged from little or no value to highly beneficial, depending on the location and/or the prey insect (18, 35, 3, 19, 8).

It is at least of historical interest that the first insect to be introduced into the United States to combat a forest insect pest was a clerid, *Thanasimus formicarius* Lec. (7, 10). This introduction was made by Hopkins in 1892 against the southern pine beetle, *Dendroctonus frontalis* Zimm., in West Virginia (14). The species apparently did not become established, at least in part because the host population collapsed shortly after the release (10).

Although some workers have found these predators to be of little apparent value in several areas of the western United States, possible future benefits from these insects should not be overlooked. In light of the increasing use of silvicultural operations as our forests are converted from virgin stands to intensively managed ones, the ability to manipulate environmental conditions in favor of the predators becomes more feasible. Böving and Champlain (5) and Person (28) foresaw this possibility and suggested that cutting of bark beetle-infested trees be timed to coincide with periods when the immature stages of the predators were not beneath the bark. The latter author felt that many earlier cut-and-burn operations of beetle-

¹ Italic numbers in parentheses refer to Literature Cited, p. 34.

infested trees were unsuccessful because their poor timing reduced the predator populations to levels below those needed for adequate subsequent predation.

Although the life histories of these three species have been investigated by various workers, attention here is given mainly to the adults. Particular emphasis is placed on the flight and olfactory behavior of each species and the volatile materials produced by associated tree species which may be chiefly responsible for the olfactory responses exhibited by the predators.

Enoclerus sphegeus

Enoclerus sphegeus was first described by Fabricius in 1787 (22, 27) and was more thoroughly described recently by Brown (29). Larval instars have been described by Struble (35), Reid (29), Kline and Rudinsky (19), and Cowan and Nagel (8). *E. sphegeus* is distributed from Alberta, Canada, southward along the Pacific coast states into Mexico and eastward into Colorado, Arizona, and New Mexico (29, 38, 27).

The period of adult flight activity appears to occur at various times of the year in different parts of the range of the species. In the central Sierra Nevada Mountains of California at elevations of 4,500 to 6,500 feet, *E. sphegeus* adults appeared in greatest numbers from September to November (35). These adults apparently overwintered in bark crevices and reappeared the following spring. Furniss (12) reported that adults were most numerous in Idaho between mid-May and early July. *E. sphegeus* adults in western Oregon were reported to emerge with the Douglas-fir beetle in April and May by Kline and Rudinsky, but Cowan and Nagel concluded that this species on Marys Peak in western Oregon had a two-year life span with the adults emerging in late summer, overwintering in bark crevices and litter, and reappearing the following spring with the emergence of the Douglas-fir beetle. Although these adults could be found from the last part of April through July, they were seldom seen in flight after June 1 in 1964. After a release of 25 marked beetles on a log June 12, 1964, Cowan and Nagel found that the relative numbers of marked to unmarked beetles changed little during the following two weeks. They concluded that few additional beetles had flown to the log.

E. sphegeus has been reported to occur on most of the common coniferous trees in the west. Champlain summarized the observations on file with the United States National Museum and wrote, "It is found in most of the western pines, spruce, and fir; also *Pseudotsuga taxifolia* and *Larix occidentalis*" (5). It has also apparently been

found on *Tsuga heterophylla* (Raf.) Sarg., western hemlock, by McGhehey (25).

Although *E. sphegeus* has been studied in numerous areas by several workers, information is lacking on the mechanism by which it finds concentrations of prey insects. Without any explanation, Furniss reported that the greatest number of adults were found on the stumps of felled trees, and Böving and Champlain stated that *E. sphegeus* were attracted to trees containing *D. ponderosae*. Reid (29) was able to find *E. sphegeus* on a log only after it had been attacked the previous day by *Ips* sp. The predators were not on the log approximately one week after the *Ips* had entered the bark. Vité and Gara (1962) were able to attract *E. sphegeus* to ponderosa pine logs infested with species of *Dendroctonus* and *Ips* and also to uninfested logs. They concluded that attraction was greatest to infested logs, but did not elaborate on the causes of this attraction.

In summation for *E. sphegeus* adults, information is available on the general seasonal appearance of the beetle in several areas, but no mention is made of diurnal activities or the factors affecting flight. Concerning oriented flight, concentrations of these predators have been noted on scolytid-infested logs and on uninfested fresh logs, and attraction has been found to infested and uninfested ponderosa pine logs, but in neither case have explanations been given.

Enoclerus lecontei

The nomenclature of *Enoclerus lecontei* has been confused by changes of both the generic and specific names. The adult *E. lecontei* was first described by Le Conte in 1861 as *Clerus nigriventris*. Wolcott renamed the species *Clerus lecontei* in 1910, but this name was later changed to *Enoclerus lecontei* Wolc. (22, 5, 42). Since this last revision, the name *Thanasimus nigriventris* has been used by Balduf (1) and Blackwelder (19), and *Thanasimus lecontei* (Wolc.) by Person (28). Descriptions of the larvae have been made by Böving (6) and Kline and Rudinsky. The range of *E. lecontei* extends from British Columbia east to Michigan and south to Guatemala (27, 42), but it is apparently most abundant in Washington, Oregon, and California (28).

The time of flight activity for *E. lecontei* appears to differ only slightly throughout its range. The beetles were reported to be present from April to October by Böving and Champlain, while Bedard (2) found them to be most numerous from the latter part of July through August in Idaho. Person concluded from his studies in California that newly emerged adults appeared twice each year, from May 15 to June 20 and also late each summer. This second emergence group was com-

posed of 80 to 95% of the brood from the spring-emerged adults. The remaining 5 to 20% overwintered as mature larvae and made up the spring emergence group. Recent studies on Marys Peak by Cowan and Nagel revealed *E. lecontei* adults to be present from about June 15 through September.

This insect is best known as a predator of *D. brevicomis* Lec. attacking ponderosa pine (18, 11, 28), but it has also been found associated with *Ips confusus* (Lec.) on ponderosa pine (36), *D. monticolae* Hopk. on lodgepole pine and western white pine (9), *D. obesus* Mann. (= *engelmanni* Hopk.) on engelmann spruce (23), and *D. pseudotsugae*, *Scolytus unispinosus* Lec., and *Pseudohylesinus* sp. attacking Douglas-fir (2, 3, 19).

Vité and Gara (39) concluded from field olfactory tests that *E. lecontei* were attracted to sections of ponderosa pine logs which contained various species of *Ips* and *Dendroctonus* in early and advanced stages of infestation, as well as being attracted to uninfested sections.

In brief, the information available on the flight and olfactory behavior of *E. lecontei* is limited to statements of the seasonal appearance of adults in several areas and attraction to scolytid-infested and uninfested log sections of ponderosa pine. No explanation was given for this attraction.

Thanasimus undatulus

The adult *Thanasimus undatulus* was first described by Say in 1835 under the name *Clerus undatulus* (32). Because of revisions of the generic nomenclature, it was placed in the genus *Thanasimus* (22), but through a typographical error the specific name was listed as *undulatus* (19, 42). This error was carried forward by Chamberlin (7) and Papp (27). Kline and Rudinsky (19) state that Bedard mistakenly identified *T. undatulus* as *T. dubius* (Fab.) in 1933. This identification was also used by Bedard in 1950.

At least three subspecies or forms have been recognized by Chamberlin and Papp, while five varieties have been listed by Wolcott. Barr preferred to call all the forms *T. undatulus* (19). If all the varieties or forms are considered as a single species, this insect is distributed from Alaska to eastern Canada and south into New Mexico (7, 27, 42).

Few studies have been conducted on *T. undatulus*, but the adults appear to be active during most of the summer months throughout the species' range. Beetles were reported to fly from May to September by Böving and Champlain (5). Bedard (2) found them to be most abundant in Idaho in late May and June, while Kline and Rudinsky found them in April and May in western Oregon. On Marys Peak in

western Oregon, most adults were found to emerge in September, overwinter, reappear in the spring, and remain active until mid-August (8).

Although several hardwood species occur within the range of *T. undatulus*, it has been reported associated only with bark beetles attacking coniferous species. Referring to observations made by Hopkins, Burke, Fiske, and Champlain, Böving and Champlain state, "It is a predator of *Dendroctonus* and other bark beetles in coniferous trees, *Pinus*, *Picea*, *Pseudotsuga*, *Larix*, *Abies*, and cedar . . ."

Although no information is available on the mechanism by which this species finds concentrations of prey insects, Cowan and Nagel found evidence of the production of an olfactory sex stimulus by the females. They were able to produce interspecific matings between *T. undatulus* males and *E. sphaeus* females when the two insects were placed in a container occupied by a *T. undatulus* female just prior to the test. The test was repeated with *T. undatulus* males and Douglas-fir beetles, and it was found that the clerid males would also attempt to mate with them.

In conclusion, no information is available concerning factors affecting the seasonal flight of *T. undatulus*, no mention is made of the diurnal patterns of flight, and no mechanism has been found by which this species finds its insect prey.

Flight Behavior of *Dendroctonus pseudotsugae*

Although the Douglas-fir beetle normally attacks unhealthy or recently downed trees, epidemic populations and primary tree killing usually occur following extensive windthrows and fires which provide abundant suitable food material for good survival of developing broods. These broods mature in the functional phloem and cambium of the tree host throughout the summer and overwinter there, mainly as callow adults, while their obligatory low-temperature requirement is being met. The adults emerge in the spring with the first sufficiently warm temperatures and attack new suitable host material. During the periods of high population levels, when there is an insufficient quantity of fresh fallen timber to absorb the beetles, healthy trees may be overcome and killed by large numbers of invading beetles. Such mass attacks are accomplished with the help of a pheromone produced by feeding virgin female beetles. This pheromone attracts both males and additional females to the area of initial attack. This account of the life history, flight, and olfactory behavior has been summarized from the reported investigations of Hopkins (15), Bedard (2, 3), Walters (41), Furniss (12), Vité and Rudinsky (40), McCowan and Rudin-

sky (24), Rudinsky (30, 31), Hendrickson (13), and Jantz and Rudinsky (16).

The diurnal and seasonal flight patterns of the Douglas-fir beetle on Marys Peak have been investigated during the last four years by Rudinsky (31) and the diurnal and seasonal patterns of response have been reported by Rudinsky (30), Hendrickson (13), and Jantz and Rudinsky (16). The most important physical factors affecting the flight of this beetle are considered to be temperature, light, and wind.

Diurnal flight was found to occur essentially from 10 a.m. until 7 to 8 p.m. standard time, or until darkness, with the greatest number of individuals flying about 2 p.m. Exceptions to this pattern were found when temperatures exceeded approximately 75° F. Two-peaked flight curves were obtained on these days, due to a mid-day depression of flight activity. The beetles also rarely were found to fly below 58° F., although flight activity was noted to occur occasionally at lower temperatures.

The seasonal flight of the Douglas-fir beetle was found to occur from April through July with the main period of primary flight activity occurring during May. Secondary peaks of flight were found to occur in July; these flights were considered to be made up predominantly of reemerged beetles. A gradual decline in flight activity was reported to occur after July.

Composition of Oleoresins

Because oleoresins and their fractions were found to be important to the finding of bark beetle prey by the checkered beetles in this study, this section is included here to provide information concerning the physical and chemical natures of these substances.

Many investigations have been made on the physical and chemical properties of the oleoresins of the pines, but information is lacking for most other species. Oleoresin is defined by the American Society for Testing Materials as follows:

the nonaqueous secretion of resin acids dissolved in a hydrocarbon oil which is (1) produced in or exuded from the intercellular resin ducts of a living tree, (2) accumulated, together with oxidation products, in the dead wood of weathered limbs and stumps (26, p. 157).

Mirov adds to this statement that the resin acids may also be dissolved in paraffin hydrocarbons or even benzene derivations.

Oleoresin may be separated physically into rosin, a mixture of various nonvolatile materials, and turpentine which is the composite of completely volatile substances. These volatile substances are predominantly cyclic hydrocarbons, terpenes with the formula $C_{10}H_{16}$, most often in mixtures with sesquiterpenes, $C_{15}H_{24}$, but occasionally with nonterpene substances (26). Kurth states that volatile materials

from wood include essential oils and volatile acids, but that the distinction between the two groups is arbitrary since the essential oils may contain acids. He says that the chief substances in essential oils are terpenes, sesquiterpenes, and the oxygenated derivatives of alcohols, aldehydes, or ketones and that phenols, phenolic ethers, esters, oxides, and acids may also be present.

The composition of terpenines is a genetically fixed character of each tree and changes but little during the growing season (26). Composition differences may be great between genera of the same family and even species of the same genus (21, 26), and considerable differences may be found among different parts of the same tree (26). This variation is shown by Kurth (page 565) who summarized the findings of Johnson and Cain (17), Schorger (33), and Benson and McCarthy (4) on the various oleoresins of Douglas-fir:

VOLATILE OILS FROM DOUGLAS-FIR	
Source	Known constituents
Wood	1-a-pinene, 30%; 1-camphene, 6%; 1-limonene, 14%; 1-a-terpineol, 32%
Bark	1-a-pinene, 27%; 1-B-pinene, 24%; 1-camphene, 7%; dipentene, 8%; geraniol, 6%; and azulenogenic sesquiterpenes
Leaves and twigs	1-B-pinene, 33%; dipentene, 18%; 1-a-pinene, 12%; 1-camphene, 7%; geraniol (caprate or acetate), 12%; phenols (salicylic acid) 0.07%; and capric acid.
Oleoresin caused by injuries	1-a- and B-pinene and small amounts of 1-limonene and 1-terpineol.

Such differences among various tree parts most likely occur also in other species and are important determinants of the quality of vapors released from fallen trees. Unfortunately, such complete information is unavailable for most tree species. The fact that most of the bark beetles preyed upon by these clerids penetrate the bark of the stem and larger limbs, causing volatilization of resin from only these parts, contributes some uniformity to the oleoresin quality.

Table 1 presents the compositions, when known, of the oleoresins produced by the more common species of conifers in western United States and also by those species with which *E. sphaegeus*, *E. lecontei*, and *T. undatulus* have been associated. *Larix decidua* is listed in place of *L. occidentalis* because no information is available on the latter species. It should be noted that the fractions alpha-pinene, beta-pinene, and limonene are present in most of the pines (*Pinus*), true firs (*Abies*), Douglas-fir (*Pseudotsuga*), the larch (*Larix*), and at

Table 1. THE COMPOSITION OF THE OLEORESINS OF SOME CONIFEROUS SPECIES

Tree species	Constituents ^a										Source of information
	camphene	delta-carene	geraniol	limonene	myrcene	beta-phallandrene	alpha-pinene	beta-pinene	alpha-terpineol	others ^b	
<i>Abies amabilis</i>				+		+	+	+			Kurth, 1952
<i>Abies balsamea</i>						+	+	+			Kurth, 1952
<i>Abies grandis</i>	19					5	20	15		41	Trupp and Fischer, 1939
<i>Chamaecyparis lawsoniana</i>				3			46			51	Kurth, 1952
<i>Larix decidua</i>							+				Kurth, 1952
<i>Picea glauca</i>							50				Kurth, 1952
<i>Pinus contorta</i>						P	+				Mirov, 1961
<i>Pinus lambertiana</i>						2-3	70-75	5		12-15	Mirov, 1961
<i>Pinus monticola</i>				7			32	45		16	Mirov, 1961
<i>Pinus ponderosa</i>		25-64		0-15	0-5		1-45	0-50		0-10	Mirov, 1961
<i>Pseudotsuga menziesii</i> wood	6			14			30		32	18	Kurth, 1952
<i>Pseudotsuga menziesii</i> bark	7		6				28	24		35	Kurth, 1952
<i>Tsuga canadensis</i>	12			6	2		18	3		50	Shaw, 1951

^a Numerals represent the percent of total weight; + represents presence without a determination of percentage; P represents the predominating constituent.

^b Includes other volatile fractions, unknown fractions, and nonvolatile materials.

least one spruce (*Picea*). Another fraction, beta-phallandrene, is present in lodgepole pine and some of the true firs. Also to be noted in this table is the absence of the fractions geraniol, alpha-terpineol, and myrcene in most of the species. The chemical nature of these fractions will be presented in the following section.

MATERIALS AND METHODS

The investigations reported here were conducted during the spring and summer months of 1963, 1964, and 1965 with the major data coming from the latter two years. All the field studies were on the northeast slope of Marys Peak, 14 miles west of Corvallis, Oregon. Metal olfactometers and screened cages containing various baits were used to trap insects in flight responding to the attractive substances, while electrically driven insect nets were run to collect those insects in undirected or random flight. Several laboratory tests were also conducted to confirm the results obtained in the field and to study close-range olfactory behavior.

Study Area

The main study area is along a ridge extending west to east at an elevation of 1,100 feet in the Marys Peak watershed of the Siuslaw National Forest. The stand density varies from moderate along the ridge crest to high along the flanks of the ridge, while several clearcuts occur nearby. The overstory is predominantly 180- to 200-year-old second growth Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, but with scattered trees of western red cedar, *Thuja plicata* Donn; western hemlock, *Tsuga heterophylla* (Raf.) Sarg.; and grand fir, *Abies grandis* Lindl. The common understory woody plants include vine maple, *Acer circinatum* Pursh.; salal, *Gautheria shallon* Pursh.; and Oregon grape, *Berberis nervosa* Pursh.

The Use of Nets

Six electrically driven rotary insect nets were run periodically during the spring and summer of all three years to sample the flying populations of Cleridae and Scolytidae. These nets were spaced approximately 100 feet apart at standard positions in a curved line which extended along the flank and crest of the ridge. These traps were identical to those described by Vité and Gara which were found the most suitable for sampling bark beetle populations. Each net assembly consisted of a net bag mounted on a shaft which was rotated horizontally by an electric motor equipped with a reduction gear box and 90° coupling. The motors hung by brackets from the top of 6-foot step lad-

ders. Three portable electric generators driven by gasoline engines supplied the 110-volt current needed for the motors.

Information on the seasonal flight patterns of the insects was obtained by running the nets approximately one day each week of the spring and summer for three years. Deviations from this schedule occurred when climatic conditions were not conducive to flight and in the late summer when insect flight levels were low. The total number of days on which nets were run for the three years 1963 through 1965 was 31, 20, and 18, respectively.

Diurnal flight patterns were obtained throughout the three flight periods, but only those gathered early each season during the periods of high flight activity contained sufficient numbers of insects to be reliable. On each of the collection days, the nets were started before flight activity began and were emptied each one or one-half hour until the insects being studied ceased to be collected.

The Use of Olfactometers

The metal olfactometers (Figure 1) were the chief source of data on both flight and olfactory response. They were located 100 feet apart in a straight line along the ridge crest with each location as nearly like the others in respect to exposure as was possible under natural conditions.

These olfactometers were patterned after those used and described by Vité and Gara to study olfactory behavior of forest insects in California. They are essentially sheet metal tubes standing approximately 6 feet high. Midway inside each olfactometer is an electric fan which draws air from the base, containing the olfactory materials being tested, and forces it out the opening in the top. Above the fan is a wire screen funnel pointing downwards and ending in a removable glass jar which receives the attracted insects. Transparent plexiglas baffles are centered atop each olfactometer to stop the insects following the scent stream to the source. The insects were collected from the olfactometers at one-half or one-hour intervals.

Most of the tests were made using a different olfactory material in each of five olfactometers with the sixth one containing either ethanol, benzene, or nothing as a control. Table 2 lists the materials tested during 1964 and 1965 and the total number of hours each one was tested. All the solutions were tested at known, standardized concentrations in identical bottles to assure that evaporation rates were comparable, exclusive of variations in vapor pressure of the various substances. A 2½% solution of Douglas-fir oleoresin with 95% ethanol was exposed during most tests as a standard attractant source for determining the seasonal flight pattern and also for comparing the at-

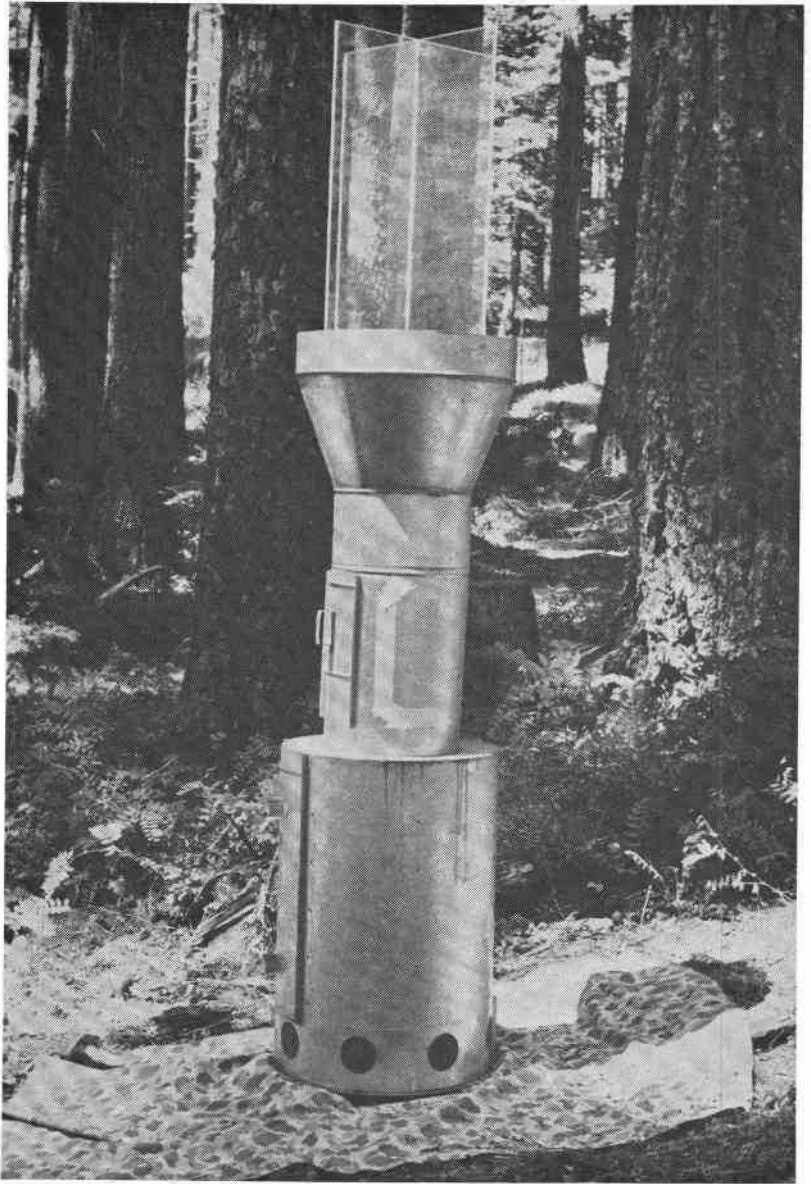


Figure 1. A sheet metal olfactometer used for attraction studies.

tractive qualities of materials that were tested on different days. Tests early in the 1964 season indicated this concentration to be the most attractive. All the solutions were diluted in 95% ethanol to the concentrations shown in Table 2, except for the fraction myrcene and grand fir oleoresin which were diluted in benzene because they were not completely soluble in ethanol.

Table 2. THE MATERIALS TESTED AND THEIR TOTAL HOURS OF EXPOSURE IN SHEET METAL OLFACTOMETERS IN 1964 AND 1965^a

Materials tested	Total hours of exposure
½% Douglas-fir oleoresin	11½
1% Douglas-fir oleoresin	11½
2½% Douglas-fir oleoresin	166
5% Douglas-fir oleoresin	27
10% Douglas-fir oleoresin	11½
15% Douglas-fir oleoresin	2½
20% Douglas-fir oleoresin	11½
50% Douglas-fir oleoresin	6
100% Douglas-fir oleoresin	8½
2½% Ponderosa pine oleoresin	71½
2½% Grand fir oleoresin	24½
1% α-pinene	84
1% β-pinene	84
1% Camphene	50½
1% Geraniol	54
1% Limonene	73
1% Myrcene	29½
1% α-terpineol	32½
Uninfested Douglas-fir log	9½
Douglas-fir log infested with Scolytidae	39½
Empty control	87
Ethanol control	30
Benzene control	8

^a Grand fir oleoresin and myrcene were diluted in benzene. All other solutions were with 95% ethanol.

The various substances tested were obtained from several sources. The Douglas-fir and ponderosa pine oleoresins were collected from living trees approximately five miles north of Corvallis, Oregon, while the grand fir oleoresin was collected from trees in the watershed. The oleoresin of grand fir was collected from small pockets in the outer bark of green trees, while the other two oleoresins were collected from the xylem. The trees were tapped by boring a hole through the bark and cambium and driving a short iron tube into it. A rubber balloon was fitted over the end of the tube to collect the oleoresin exuded over a period of three to seven days. The fresh oleoresin was diluted 50%

with ethanol and stored in glass bottles at 40° F. The dilution was necessary to prevent crystallization of the oleoresin. The oleoresin was further diluted to the desired concentration just prior to testing.

The oleoresin fractions were obtained as commercial preparations from two companies. The fractions D-alpha-pinene, beta-pinene, D-camphene, myrcene, DL-limonene, and geraniol were obtained from K & K Laboratories, Inc. Plainview, New York, and a sample of alpha-terpineol was donated by the Hercules Powder Company, Incorporated, Wilmington, Delaware. These materials were stored full strength in air-tight brown glass bottles until just prior to testing when they were diluted to a 1% concentration with 95% ethanol.

The fractions of oleoresin tested for attractiveness in this study may be separated into five groups based on their chemical properties and structure. Limonene (Figure 2) is the sole representative of the monocyclic terpenes while myrcene (Figure 3) is the only olefinic open-chain terpene tested. Two terpene alcohols were tested, alpha-terpineol (Figure 4) and geraniol (Figure 5). Three fractions are members of the bicyclic terpene group—alpha-pinene (Figure 6), beta-pinene (Figure 7), and camphene (Figure 8).

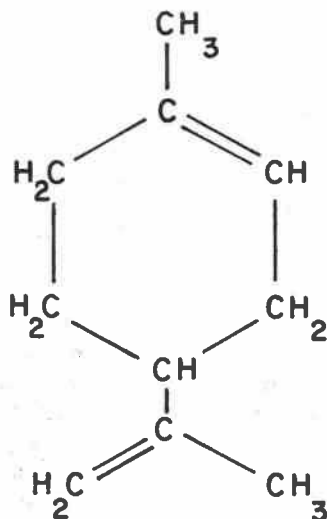


Figure 2. The structural formula of limonene.

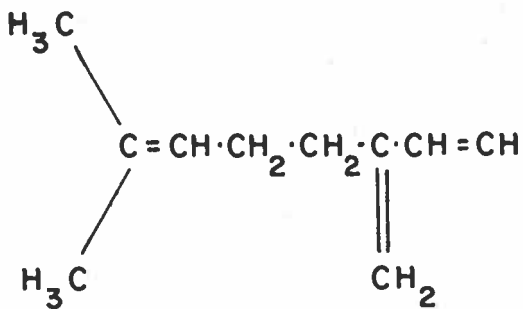


Figure 3. The structural formula of myrcene.

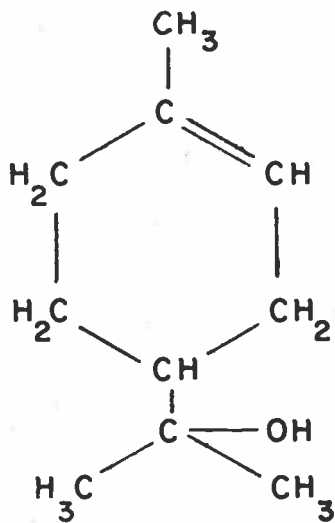


Figure 4. The structural formula of alpha-terpineol.

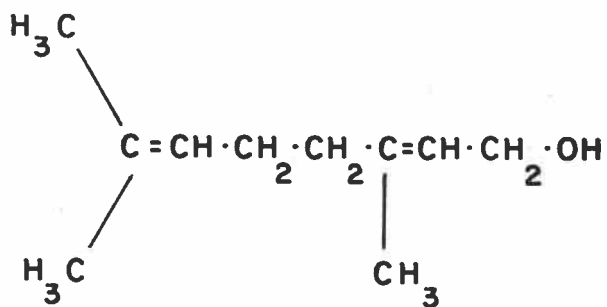


Figure 5. The structural formula of geraniol.

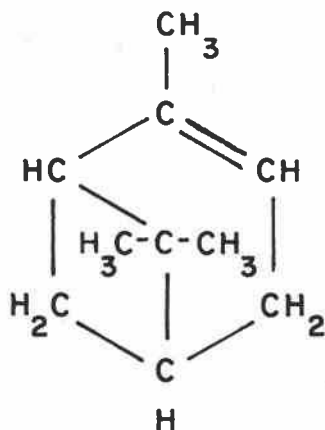


Figure 6. The structural formula of alpha-pinene.

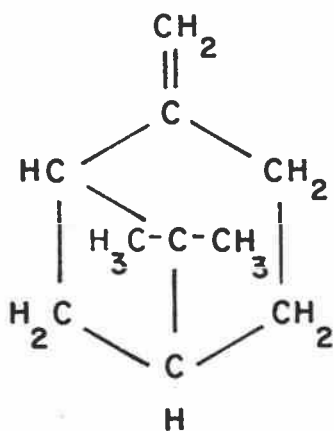


Figure 7. The structural formula of beta-pinene.

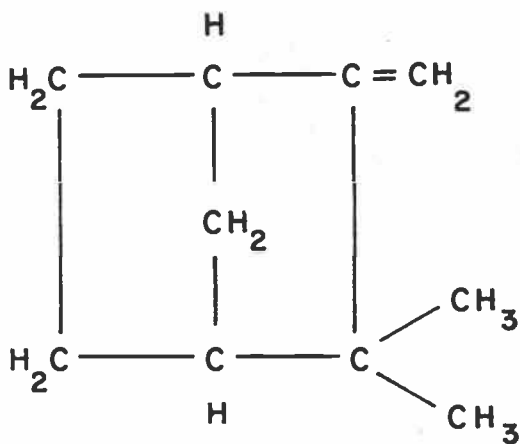


Figure 8. The structural formula of camphene.

Attraction Cages

Screened cages measuring 2 feet by 2 feet by 5 feet were used in the study area all three years. The number of cages used varied from 3 to 12. These cages usually contained Douglas-fir log bolts infested with 40 virgin Douglas-fir beetle females, but other materials used as baits were logs of ponderosa pine, white pine, and grand fir with and without female beetles, and Douglas-fir logs with freshly punched holes or male Douglas-fir beetles. No solutions were tested with these cages because they were not comparable to the metal olfactometers with forced air systems.

Observation Logs

After the results of the flight studies suggested that *E. sphegeus* adults may remain for extended periods on a log once it is found, releases of marked beetles and periodic counts afterwards were undertaken. Three logs were selected at different locations in the watershed. One log was windthrown during the winter of 1964-1965, while the other two were cut on May 18, 1965. The diameters at breast height of these trees were 13, 15, and 26 inches. The number of Douglas-fir beetle attacks on the logs averaged nine per square foot on the windthrown log and one and one-half on the other two.

The insects to be released were marked with different colors of nail polish or paint to distinguish the two sexes and the logs they were released on. The first releases were unsuccessful because the insects immediately flew away. These attempts used beetles collected in the olfactometers and stored at 40° F. until release. A more successful method was to spread the beetles along the log while they were still cold from being kept in cooler-chests with salted ice. Fewer beetles flew away as they warmed up than in the first release attempts, but the results were still not satisfactory. The most dependable method found was to mark naturally occurring beetles on the logs where they were found. Any sudden movement would excite the beetles to the point of flying away or falling from the log, so extreme caution was necessary. The logs were then inspected approximately each week, and the numbers of marked and unmarked beetles were recorded.

Meteorological Records

Measurements and records were taken of temperature, humidity, wind, and sky-overcast during the three seasons. Two hygrothermographs² were run continuously during the flight seasons. One instru-

² Manufactured by the Foxboro Company, Foxboro, Massachusetts.

ment was permanently located in the study area under a dense tree canopy, while the second instrument was located in a clearcut near the study area. Both hygrothermographs were protected from direct sunlight by open enclosures approximately four feet above the ground. Additional temperature measurements were taken from mercury thermometers at half of the net and olfactometer sites. When air movements were noted, the direction was recorded and velocity was measured with a hand-held wind meter.³ Whenever clouds were present, their extent was recorded as the percent of sky covered.

RESULTS AND DISCUSSION

Although the flight and olfactory behavior of three species of Cleridae were investigated, the amount of information obtained varied for each species. *E. sphegeus* was the most abundant of the three species near the study plot on Marys Peak and the information gathered on this species was the most complete. *T. undatulus* was the second most numerous and the amount of information obtained was intermediate to that collected on the other two species. Little information was obtained concerning *E. lecontei* because specimens were seldom encountered in the area.

Diurnal Flight Patterns

Enoclerus sphegeus

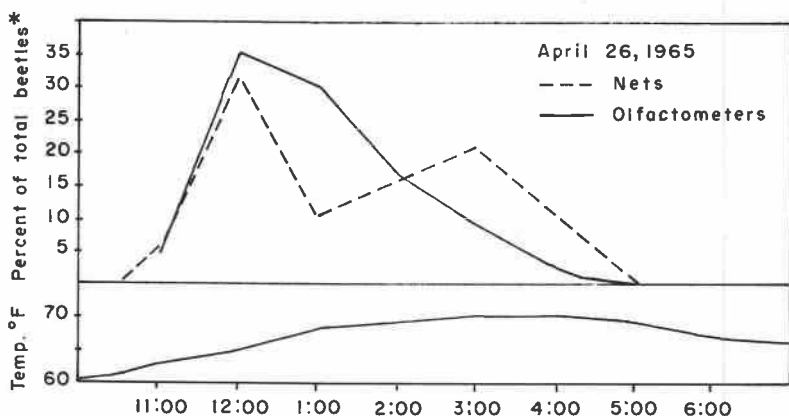
Although the nets and olfactometers were run periodically throughout the seasons of flight of the predators, sufficient numbers of *E. sphegeus* were caught on only one or two days each season to provide reliable information concerning diurnal flight patterns.

The lowest temperature at which *E. sphegeus* was found flying was 55° F. Olfactometers containing attractive oleoresins from Douglas-fir and ponderosa pine were run while the ambient air temperature was near the suspected temperature threshold for the species' flight. *E. sphegeus* were caught at the olfactometers only after the air temperature within the stand had reached 55° F.

The highest temperature within the stand at which *E. sphegeus* was found flying was 80° F. on July 23, 1965. It can not be concluded from the data that this temperature is the limit for the species' flight activity because insufficient numbers were caught for reliable evidence from mid-summer on, when temperatures are more often above 80° F. within the stand.

³ Manufactured by the F. W. Dwyer Manufacturing Company, Michigan City, Indiana.

Although some individuals of this species were found to fly at 55° F., flight activity generally did not begin until the temperature was approximately 60° F. In late April and May during the main seasonal flight period, the typical diurnal flight pattern exhibited by *E. sphegeus* (Figure 9) is such that flight is usually initiated from 10 to 11 a.m. standard time and is terminated by 5 p.m. This restricted period of flight occurred although the air temperature was sufficiently high for flight activity before and after this six- or seven-hour interval and suggests that light intensity and/or humidity influence the diurnal flight pattern of *E. sphegeus*.

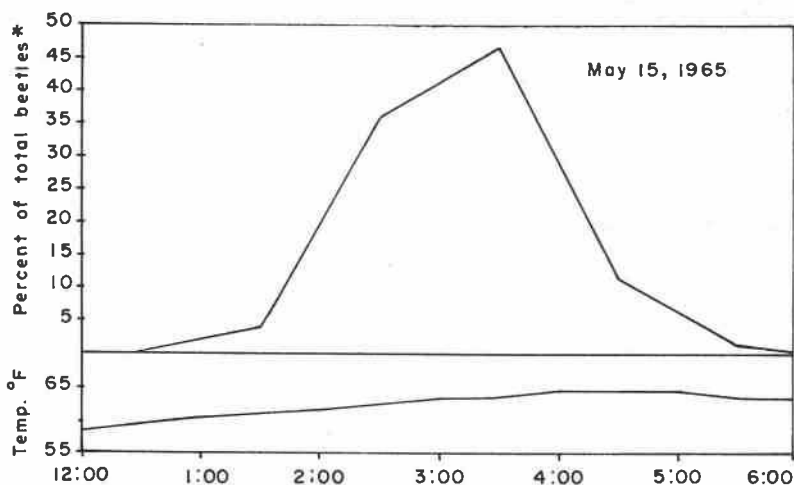


* The total number of beetles caught at olfactometers was 316 and the number caught in nets was 19.

Figure 9. A typical diurnal pattern of flight activity of *E. sphegeus*.

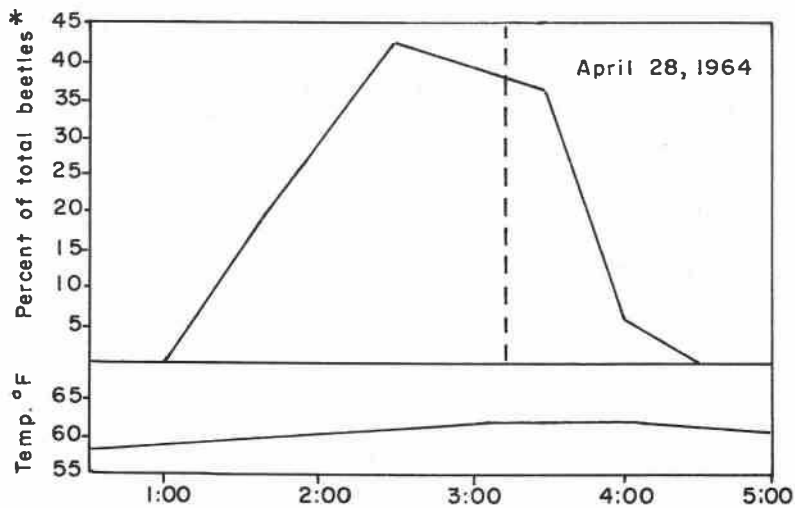
Consistency of the hour of flight termination is shown by the flight patterns on those days when flight was delayed by morning low temperatures (Figure 10). Although the insects did not begin flying until 12:30 to 1:30 p.m. standard time, the flight did not extend more than one-half hour beyond 5 p.m. Throughout the 1964 and 1965 seasons, only two specimens of *E. sphegeus* were collected after 5 p.m. standard time. These collections were made on May 15, 1964, from 4:30 to 5:30 p.m. and on July 23, 1965, between 7 and 8 p.m.

Another environmental factor found to affect the diurnal flight of *E. sphegeus* was the air movement with velocities above approximately five miles per hour within the stand. When continuous winds occurred above this velocity, the numbers of *E. sphegeus* trapped rapidly diminished to zero (Figure 11). Winds above the forest canopy and short gusts within the stand of velocities greater than about five



* The total number of beetles caught was 101.

Figure 10. A diurnal pattern of flight activity of *E. sphegeus* which was delayed because of low temperatures.



* The total number of beetles caught was 83.

Figure 11. The reduction of flight activity of *E. sphegeus* with the initiation of a five mile per hour wind at 3:15 p.m.

miles per hour appeared to have little effect on the beetle flight as measured with the olfactometers and nets.

Thanasimus undatulus

The lowest air temperature within the stand at which *T. undatulus* were caught in the nets and olfactometers was 61° F. Trapping of this species at this temperature occurred on three days in 1964: April 19, May 11, and May 15. The warmest air temperature within the stand when this species was caught in flight was 77° F. on June 22, 1964. Although this species is apparently attracted to oleoresins as is *E. spegeus*, sufficient numbers were never trapped to distinguish accurately the periods of low levels of flight activity from those of non-activity.

The maximum number of *T. undatulus* trapped in one day was 12 with the olfactometers on April 26, 1965, so no reliable diurnal flight pattern can be made. In general, specimens of *T. undatulus* were trapped during the same time of day as were *E. spegeus*, and no specimens were collected before 10 a.m. or after 5 p.m. standard time.

Enoclerus lecontei

A total of four specimens of *E. lecontei* were caught by the nets during the three seasons of flight. Two insects were collected on August 2, 1963, between 12 and 3 p.m. standard time while the air temperature within the stand increased from 68° to 74° F. A third specimen was collected from 1 to 2 p.m. standard time on June 19, 1965, at a temperature of 62° to 64° F. within the stand, and the fourth specimen from 1 to 2 p.m. standard time on July 3, 1965, while the temperature was 72° to 73° F.

Discussion

A comparison of the diurnal flight patterns of *E. spegeus*, *E. lecontei*, and *T. undatulus* with that of the Douglas-fir beetle found on Marys Peak indicates considerable similarity among the predators and the prey. The most noteworthy difference between the flight patterns of *E. spegeus* and *T. undatulus* and that of the Douglas-fir beetle is the time of flight cessation. Whereas the predators had discontinued flight by 5 p.m. standard time regardless of the temperature each day except for two occasions, the Douglas-fir beetles were found to fly throughout the evening until darkness when the temperature was permissive. The apparent absence of mid-day flight depressions is probably due to the early occurrence of *E. spegeus* and *T. undatulus* each season. The highest temperature recorded within the stand during the period of high flight activity in 1964 and 1965 was 72° F.

Higher temperatures were not reached until mid-summer when the number of predators in flight was too low to distinguish the presence of such depressions.

Seasonal Flight Patterns

The information obtained concerning the seasonal flight patterns of the three species varies as it did for the diurnal flight. Numbers of insects of each of the species trapped by the nets were too low for determining differences of flight activity within each season. The information presented here is based on the insects trapped in the olfactometers using a standard attractant source of 2½% Douglas-fir oleoresin unless stated otherwise.

Enoclerus sphegeus

Variations between the seasonal records of flight for *E. sphegeus* in 1964 and 1965 (Figures 12, 13) can be explained by considering the temperature differences of the two years. Flight for each season apparently began with the first occurrence of temperatures sufficiently high for flight activity (55° to 60° F.) and continued at high levels until about June 1 on scattered days whenever temperatures were not restrictive. Two days of high flight activity occurred in 1964 on April 28 and May 15 while three periods of lower activity occurred in 1965 on April 26, May 10, and June 2.

After May 23 in 1964 and June 2 in 1965, the flight activity, based on olfactory responses, decreased sharply and then continued at low levels through the remainder of each season. In order to explain this pattern, *E. sphegeus* found on windthrown trees were marked with paint on May 27 and June 1, 1965. Subsequent insect counts yielded insufficient numbers of marked beetles to provide significant evidence for explanation of the rapid decrease in catches to the olfactometers, but the numbers of naturally occurring beetles (Table 3) suggests that this species was most abundant on logs about June 1 and gradually declined in numbers thereafter.

Thanasimus undatulus

None of the methods used to measure the level of flight activity of these predators trapped sufficient numbers of *T. undatulus* to establish reliable seasonal flight curves for the species. The first and last days of each season on which *T. undatulus* were recorded flying (Table 4) are similar to those found for *E. sphegeus* (Figures 9, 10). Periods of maximum flight activity also appear to coincide in 1964 and 1965, although sufficient evidence was not obtained to fully support this coincidence.

Enoclerus lecontei

The information obtained concerning the flight activity of *E. lecontei* consists of the trapping of two specimens on August 2, 1963, one specimen on June 19, 1965, and another one on July 3, 1965. Each of these four insects were trapped in nets.

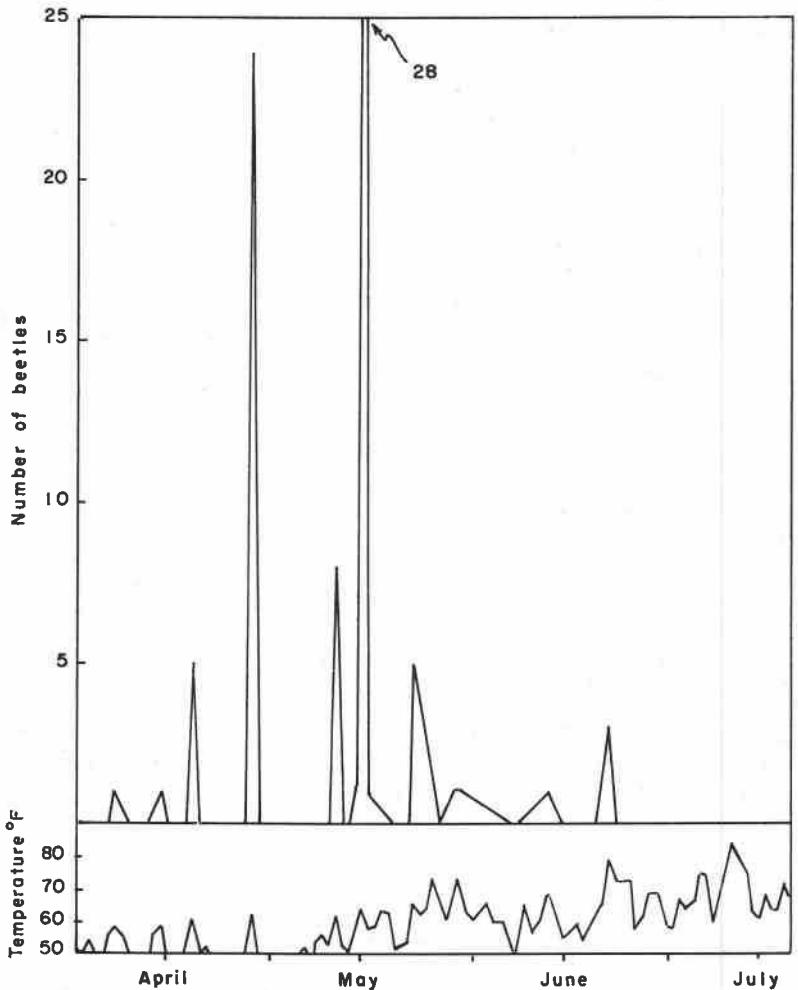


Figure 12. The seasonal pattern of flight activity of *E. sphegeus* in 1964, based on the highest number of beetles caught per day in a single hour using one olfactometer containing 2½% Douglas-fir oleoresin.

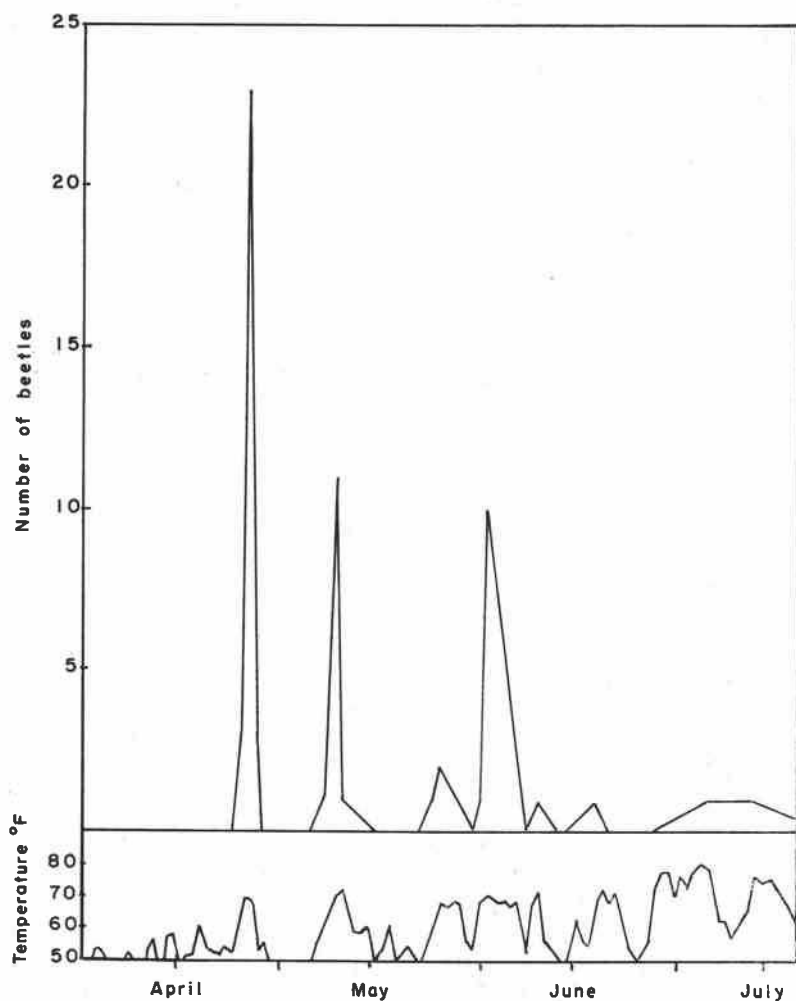


Figure 13. The seasonal pattern of flight activity of *E. sphegeus* in 1965, based on the highest number of beetles caught per day in a single hour using one olfactometer containing 2% Douglas-fir oleoresin.

Table 3. THE NUMBERS OF *E. sphegeus* ADULTS COUNTED ON A LOG DURING THE LAST PERIOD OF MAJOR FLIGHT ACTIVITY IN 1965

Date	Number of <i>E. sphegeus</i>
May 25	37
June 1	85
June 10	33
June 16	40
June 28	18
July 6	0
July 13	0

Table 4. THE FIRST AND LAST DAY OF 1963, 1964, AND 1965 ON WHICH THE FLIGHT OF *T. undatulus* WAS NOTED BY TRAPPING WITH METAL OLFACTOMETERS, ATTRACTION CAGES, OR NETS

Year	First day of flight	Last day of flight
1963	April 28	June 13
1964	March 29	June 22
1965	April 26	June 3

Discussion

The periods of flight activity of *E. sphegeus* and *T. undatulus* found in this study are similar to that found for the Douglas-fir beetle by Rudinsky (31) and Jantz and Rudinsky (16). While peaks of emergence and flight of the Douglas-fir beetle occur in May, the two species of predators were found to fly during 1964 and 1965 primarily from late April to early June. This synchronization of the predator and prey flight periods tends to favor a higher occurrence of predation by increasing the probability that members of the two insect groups would occur at the same time on the tree. This simultaneous occurrence of Douglas-fir beetles and *E. sphegeus* adults on logs was reported by Cowan and Nagel in 1965, based on five-minute observation periods made throughout the 1964 season. The trapping of specimens of *E. lecontei* only from mid-June through the first week of August suggests that this predator is not associated with the Douglas-fir beetle as closely as the other two species of predators and that this species may be predatory mainly on another species of Scolytidae.

The periods of flight activity found in this study also conform with the seasonal schedule of adult occurrence reported by Cowan

and Nagel, except for the emergence of new adults of *E. sphegeus* and *T. undatulus* during August and September. No increase was found in the number of *E. sphegeus* or *T. undatulus* trapped by either the nets or olfactometers during this time of year. Possible reasons for the failure to obtain evidence of these emergence periods include (1) the newly emerged adults were not attracted to the oleoresins used as bait in the olfactometers; (2) the nets used were not efficient enough for sampling insects with such low population levels; and (3) the newly emerged beetles may remain near the site of emergence and not search for prey on recently downed logs.

Olfactory Behavior

Evidence of the occurrence of oriented flight of *E. sphegeus* and *E. lecontei* was reported by Vité and Gara (39). They reported the two species of predators to be attracted to ponderosa pine logs infested with two species of Scolytidae as well as to uninfested logs of ponderosa pine. Similar evidence was found in preliminary studies in 1963. Small numbers of *E. sphegeus* and *T. undatulus* were collected from cages containing Douglas-fir logs infested with *D. pseudotsugae* and uninfested Douglas-fir logs, while no predators were found on empty cages.

Considerable variation in the numbers of predators trapped occurred from one day of testing to another as well as among different hours of the same day. This variation limits the usefulness of the data obtained to assigning general qualitative characteristics to the substances tested and has prohibited most attempts to determine the relative attractiveness of the substances. Because of this limitation, it was necessary to obtain evidence that volatile substances escaping from the tree were attractive per se to the predators and that the presence of the prey was not necessary. The results of three separate tests (Tables 5 and 6) show that oleoresin collected from living trees of Douglas-fir, ponderosa pine, and grand fir are attractive to *E. sphegeus* and, to a lesser extent, to *T. undatulus* adults.

An empty olfactometer was not used as a control on April 26, 1965, when the highest numbers of predators were caught to the oleoresins. As can be seen in Table 2, olfactometers containing nothing, 95% ethanol, and benzene were run a total of 87, 30, and 8 hours, respectively, during the 1964 and 1965 seasons. One or more of these controls were used on most of the days when high numbers of predators were trapped. After May 9, 1964, at which time the six olfactometers were relocated to provide 100 feet between each one, one *E. sphegeus* and two *T. undatulus* adults were the only clerids trapped

Table 5. RESPONSE OF *Enoclerus spegeus* TO 2.5% SOLUTION OF OLEORESIN OF DOUGLAS-FIR, GRAND FIR, AND PONDEROSA PINE IN THREE-HOUR TESTS

Date	Number of <i>Enoclerus spegeus</i> attracted to			
	Douglas-fir	Grand fir	Ponderosa pine	Empty check
May 23, 1964	8	10	--	0
May 26, 1964	3	2	1	0
April 26, 1965	32	--	98	--

Table 6. RESPONSE OF *Thanasimus undatulus* TO 2.5% SOLUTION OF OLEORESIN OF DOUGLAS-FIR, GRAND FIR, AND PONDEROSA PINE IN THREE-HOUR TESTS

Date	Number of <i>Thanasimus undatulus</i> attracted to			
	Douglas-fir	Grand fir	Ponderosa pine	Empty check
May 23, 1964	1	0	--	0
May 26, 1964	3	2	0	0
April 26, 1965	1	--	2	--

at an empty, ethanol, or benzene control olfactometer during the two years of study.

The concentration of 2½% used for the oleoresins was selected after preliminary tests appeared to indicate that this was the most attractive concentration (Table 7).

Additional tests were conducted with the olfactometers to determine which of the various fractions of Douglas-fir, ponderosa pine, and grand fir oleoresins were attractive to the two species of predators. The one percent concentration used for all the fractions was selected only because it was less than that used for the oleoresins and not because this concentration was found to be most attractive. The results of some of these tests are presented in Tables 8 and 9. Although much variability is present among the tests, some of the fractions which consistently attracted *E. spegeus*, and to a much lesser extent *T. undatulus*, were alpha-pinene, beta-pinene, limonene, and camphene, while the fractions myrcene, geraniol, and alpha-terpineol usually attracted few or no predators.

It is of interest that alpha-pinene, beta-pinene, and limonene, which are three of the four fractions that appear to be most attractive to *E. spegeus* and possibly *T. undatulus*, are present in the oleoresins

Table 7. RESPONSE OF *Enoclerus sphegeus* TO DIFFERENT CONCENTRATIONS OF OLEORESIN FROM DOUGLAS-FIR IN THREE-HOUR OLFACROMETER TESTS

Date	Number of <i>Enoclerus sphegeus</i> attracted to concentrations of oleoresin				Empty check
	½%	2½%	5%	50%	
April 26, 1964	--	37	--	11	-
May 11, 1964	0	17	2	--	0

of most of the tree species with which these predators have been reported to be associated (Table 1). Also of interest is that the three fractions myrcene, geraniol, and alpha-terpineol which are of questionable attractiveness to the predators, have been found to occur in the oleoresin of only one or two of the tree species the predators have been reported to be associated with. These two relationships suggest that *E. sphegeus* and *T. undatulus* adults locate concentrations of prey insects by being attracted directly to the volatile materials escaping from the tree host of the prey insects. It is also suggested that the predators *E. sphegeus* and *T. undatulus* would be effective controlling agents only on those insects that are associated with tree species that produce oleoresins containing specific fractions attractive to these predators.

The complete absence of the third species, *E. lecontei*, at the olfactometers is contradictory to the attraction reported by Vité and Gara (39). In view of the fact that only four specimens were trapped in the nets during three years of sampling, it appears that either the population level of *E. lecontei* is very low in the vicinity of the study area, or else conditions within the stand surrounding the area are unfavorable to the species. In either case, not enough specimens were collected in the nets to conclude that *E. lecontei* was present but unresponsive in the area.

Table 8. RESPONSE OF *Enoclerus sphegeus* TO VARIOUS OLEORESIN FRACTIONS IN THREE-HOUR TESTS

Date	Number of <i>Enoclerus sphegeus</i> trapped								
	2½% Douglas- fir oleoresin	1% alpha- pinene	1% beta- pinene	1% camphene	1% limonene	1% myrcene	1% geraniol	1% alpha- terpineol	Empty check
May 15, 1964	27	37	...	10	0	0
April 26, 1965	45	47	61	18	46
April 26, 1965	22	11	14	..	5	0	..
April 27, 1965	5	0	2	..	1	4	0
May 10, 1965	16	4	0	..

Table 9. RESPONSE OF *Thanasimus undatulus* TO VARIOUS OLEORESIN FRACTIONS IN THREE-HOUR TESTS

Date	Number of <i>Thanasimus undatulus</i> trapped								
	2½% Douglas- fir oleoresin	1% alpha- pinene	1% beta- pinene	1% camphene	1% limonene	1% myrcene	1% geraniol	1% alpha- terpineol	Empty check
May 15, 1964	..	1	1	..	1	0	0
April 26, 1965	1	5	1	1	2
April 26, 1965	0	0	1	..	0	0	..
April 27, 1965	0	2	0	..	0	1	1
May 10, 1965	1	1	0	..

SUMMARY

The diurnal flight pattern of *E. sphegeus* was found to be similar to that of the Douglas-fir beetle. Adults of *E. sphegeus* were found to fly only when ambient air temperatures within the stand were 55° F. or higher. Flight was observed at 80° F., but no maximum temperature limit of flight activity was determined. Flight activity was found to be restricted by continuous winds of velocities greater than approximately five miles per hour within the stand, while no effect by winds above the forest canopy or gusts within the stand was detected. Flight occurred almost exclusively between 10 a.m. and 5 p.m. standard time, although air temperatures before and after this seven-hour interval were high enough for flight activity.

The diurnal flight pattern exhibited by *T. undatulus* was found to be similar to that of *E. sphegeus*. The minimum and maximum air temperatures occurring within the stand while *T. undatulus* adults were trapped in flight were 61° and 77° F., respectively, but no temperature limits of flight activity were determined.

E. lecontei were trapped while in flight during mid-day while the air temperatures within the stand were between 62° and 74° F., but the lower and upper temperature limits of flight activity were not determined.

The seasonal flight patterns of *E. sphegeus* and *T. undatulus* were found to closely resemble that of the Douglas-fir beetle. *E. lecontei* were observed in flight only after mid-June which is after the main flight period of the Douglas-fir beetle.

Adults of *E. sphegeus* and *T. undatulus* were found to be attracted to vapors of the oleoresins from Douglas-fir, ponderosa pine, and grand fir as well as to alpha-pinene, beta-pinene, camphene, and limonene which are constituents of these oleoresins. No definite attraction was found to the oleoresin fractions geraniol, myrcene, or alpha-terpineol. It is concluded from the attraction studies that *E. sphegeus* and *T. undatulus* adults locate concentrations of prey insects by being attracted directly to volatile materials escaping from the tree host of the prey insects. It is also suggested that the predators *E. sphegeus* and *T. undatulus* would be effective controlling agents only on those insects that are associated with tree species that produce oleoresins containing specific fractions attractive to these predators.

Attraction of *E. lecontei* was not found to any of the materials tested, but this may have been due to a low absolute population of this species in the area.

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