

AN ABSTRACT OF THE THESIS OF

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Title Studies on the Flight Behavior of Ips confusus
(Lec.) (Coleoptera:Scolytidae) in Response to Attractants

Abstract approved [REDACTED]
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The flight behavior of Ips confusus (Lec.) was primarily studied under field conditions, but augmented with complementary laboratory studies whenever feasible. The experiments were mostly conducted in areas of endemic population levels, but also under epidemic and prairie conditions.

The techniques and devices used in marking, releasing, attracting, and trapping of the test beetles in the field are described in detail. The flight behavior of Ips confusus under laboratory conditions were studied by means of flight bars, standardized flight mills, and a laboratory olfactometer that incorporated flying scolytids. Flight behavior was also observed under restricted flying conditions as found in a large flight arena and in a 27 cubic meter screened cage.

By attracting Ips confusus to baited field olfactometers over short distances, it was possible to observe the entire flight from take-off to subsequent response and landing. From these studies the following conclusions can be made: Beetles take-off with the wind and respond against it. The responses to attractants occur immediately, indicating that flight exercise is not a prerequisite in the response of this species.

When Ips confusus are attracted over longer distances (i.e., 500 meters) they clearly respond against the wind. The distance over which the beetles responded directly and in appreciable proportions was between 500 and 1000 meters.

The relative attractiveness of the test material depend on the intensity of attack and on the age of the material. Responding beetles aggregate in greater numbers on the strongest attractive source. Beetles released from either end of an attractant gradient respond in greater proportions to the strongest attractant, regardless of wind direction.

By measuring the wind at various heights it was noted that Ips confusus response flights were densest in the regions of the least wind. When relatively high winds

prevail, the flights are restricted practically to ground level.

Light conditions seem to have little influence on response flights except that direct solar radiation seems to be avoided. Both released beetles and the field population exhibit diurnal response patterns that apparently are temperature dependent.

The ability to respond to attractants was found to vary from beetle to beetle, with sex, within a brood, and from population to population. Beetles which had responded once (termed responding beetles) repeatedly responded better than unselected, freshly emerged beetles (termed emerging beetles). This heterogeneity in response was due to the response ability of individuals rather than to their flight capacity.

Females and responding beetles are superior in response over distances greater than 25 meters, but males and emerging beetles respond in larger proportions over distances up to 25 meters.

Within the same brood, the ability to respond decreases from the first developing beetles to the later emerging individuals. There also seem to be large differences in the response ability among various populations.

These findings suggest that the differences are due to physiological condition of beetles and populations rather than to inherited abilities.

Further studies are suggested on the possible influence of various host materials on beetle development. The relative ability of beetles to respond to attractants can be used as a criterion of their physiological performances.

STUDIES ON THE FLIGHT BEHAVIOR OF IPS CONFUSUS
(LEC.) (COLEOPTERA:SCOLYTIDAE) IN
RESPONSE TO ATTRACTANTS

by

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STUDIES ON THE FLIGHT BEHAVIOR OF IPS CONFUSUS
(LEC.) (COLEOPTERA: SCOLYTIDAE) IN
RESPONSE TO ATTRACTANTS

INTRODUCTION

Bark beetles (Scolytidae) complete their entire life cycle inside their host plant with the exception of a short flight period. The flight period becomes particularly important to species which are able to colonize living tissue by first overcoming the resistance of their host tree through mass attack. Accordingly, the flight of these species has a twofold purpose: first, to disperse the population; second, to find and concentrate on suitable breeding material.

The fact that certain bark beetles are able to congregate on their host material has been recognized for almost two centuries. Only in recent decades, however, has it been possible to show that bark beetles respond to volatile materials that either emanate from the host per se or are produced by random attacking beetles.

The literature indicates that various mechanisms exist by which scolytids are attracted to their hosts. According to Schwerdtfeger (81), latent populations of Ips

typographus Linne' depend upon a few suitable hosts, sometimes found over considerable distances, for their survival. The host finding may occur at random but more likely through the aid of an attractant which is assumed to emanate from the suitable host material (81, p. 91). Schwedtfeger (81, p. 92) concludes that the most efficient host finding stimuli are temperature and scent. "Durch Sinnesreize, unter denen am wirksamsten die Temperatur und der Duft sein dürften, wird also der in geringer Zahl vorhandene Käfer an die brutfähigen liegenden oder kränkelnden Bäume gebracht." Even though many European investigators have assumed the existence of an olfactory stimulus, none have been entirely successful in proving such a phenomenon.

The presence of olfactory responses was suggested as early as 1910 (103). A handbook by Nüsslin-Rhumbler (61, p. 260) also mentions that a "delicate sense of smell" guides the bark beetles in their choice of breeding material. The source and nature of such olfactory attractants, however, was not investigated until the late 1940's. Schimitschek (78) found in the phloem of trap trees certain products of fermentation such as amines, ammonias, and terpenes which are formed as the cambium

deteriorates. He proposed that these fermentation products are important as volatile attractants. Merker (56), by means of laboratory tests, showed that Ips typographus and other subcortical feeding insects preferred the sap pressed from the phloem tissue of their respective hosts over other test materials and that the actual attractants are not associated with resinous material: "Die eigentlichen Lockstoffe der Rinden haben mit den Harzen nichts zu tun" (56, p. 140). European workers succeeded in isolating methylesters of fatty oleic acids, linoleic acids, and linolenic acids which proved, under laboratory conditions, to be the most attractive extracts of the phloem sap to Ips typographus and other subcortical feeding insects (1) (2, p. 431-432). However, the attractive power of synthetic methylesters of linoleic and linolenic acids were of little value in attracting bark beetles under field conditions.

More recently, Chararas (21) concluded on the basis of laboratory experiments with olfactometers of various designs and limited field observations, that terpenes extracted from raw oleoresin are, in various concentrations and combinations, the actual attractants for many of the more important European scolytids, including Ips

typographus, Cryphalus picea Ratzeburg, Pityogenes chalcographus Linné and others. Similarly, Dässler and Henker (22) found in laboratory studies that certain fractions of terpentine separated from the raw resin of scotch pine (Pinus sylvestris Linné), especially Dipenten and Camphan, were highly attractive to Ips sexdentatus Boerner. Additionally, aliphatic aldehydes such as propionaldehyd and acetone were found to have some attractive properties for this species. Esters of fatty acids, among them methylesters of oleic and linoleic acids, were of little attractiveness to Ips sexdentatus. Perttunen (64) found, while testing the attractiveness of the terpene pinene on two scolytid species, that the concentration of the test material may be crucial. He suggested that varying concentrations of attractants may either repel or attract the test species.

A more complete review of European studies on attractants to bark beetles was recently compiled by Francke-Grosmann (33).

Little information and no reports on experiments exist regarding the distances over which Ips typographus and other European scolytids may respond to attractants (69, 73, 102). A German study proposed that bark

beetles respond against the wind in response to attractants that had drifted over several hundred meters (102). Bombosch (7, p. 269) observed that Ips typographus flew up to a distance of one kilometer in its response to volatile materials.

Studies in North America indicated that Trypodendron lineatum (Olivier) are attracted to Douglas-fir (Pseudotsugae menziesii (Mirb.) Franco) logs and slash (16, 17 18, 20). A recent flight study by Chapman (17, p. 84) confirmed that Trypodendron does respond to olfactory substances emanating from logs. He showed that beetles gathered over attractive logs regardless of the location or visibility. Trypodendron failed to congregate when the same logs were covered by a thin plastic sheet that could easily conduct sound. The attractiveness of Douglas-fir logs was found to vary with the season and age of the material (17, p. 74-92; 20, p. 365). There is, however, no reference as to the nature of the attractants.

A study made by Werner and Graham (97) on T. lineatum revealed that two major constituents of gas-distilled extracts from both attractive and non-attractive wood possess retention volumes identical to those of alpha- and

beta-pinene, in a ratio of 12 to 1. Subsequent tests were conducted to determine the attractiveness of either one or both pinenes; the tests proved negative.

The flight patterns of responding Trypodendron were also observed. Their flight pattern was normally found to be oriented against the wind. The most dense flights occurred between 1.7 mph and 3.4 mph. At wind speeds of approximately 4 mph, the beetles showed zero ground speed; this being their maximum flight velocity (17, p. 80).

Although laboratory tests have shown that the ambrosia beetle has a flight capacity of long distances (15, p. 375-376), there have been little field data to support the assumption. In an experiment by Dyer (27), 7,000 beetles were marked on the pronotum with fluorescent paint and released on a day when a dense natural flight of Trypodendron was expected. The results of this study seemed to be rather inconclusive since only four beetles were recovered in a distance of 110 feet, 3 to 6 days after release. As Dyer states (28, p. 4), "The low numbers of marked beetles recovered, and the short distance from which the marked beetles came, suggest that a combination of large numbers of marked beetles, log material

known to be highly attractive, and efficient recovery techniques will be necessary before a clear indication of beetle movements at this period of the year can be obtained by this method." The same author, some 16 months later, reported finding an additional marked beetle hibernating in the litter 2-1/2 miles from the release point: "This field observation further supports the belief that Trypodendron may in some circumstances fly several miles to attack logs" (27, p. 4). The long time which elapsed from release to subsequent finding seems to make this observation practically obsolete for determining the distance of response. Since flight-distance experiments are reliable only when the distance achieved and the elapsed time to respond correspond closely enough for accurate correlations, there seems to be neither proof nor probability that the beetle actually directed its flight over this distance. It is more likely that the beetle was also blown and shifted by the winds.

The removal of Douglas-fir logs infested with Dendroctonus pseudotsugae Hopkins has long been recommended as a control practice (6, 43, 44, 48). Only recently, however, has it been reported that the freshly felled material is perhaps more hazardous in increasing

the beetle population in a given area (46, 75, 76). As Johnson and Pettinger (46, p. 1) found, after two years of observation, "freshly felled Douglas-fir attracts Douglas-fir beetles which, once in the area, will attack nearby living trees, as well as the down material." When freshly cut log sections were placed next to standing trees, attacks began to appear on both the log and tree (46, p. 5).

In laboratory studies, the Douglas-fir beetle was attracted to associated yeasts rather than to material from galleried and fresh bark. Isolation of yeasts associated with the beetle revealed four isolates:

Saccharomyces pastoria, Hansenula capsulata, Candida parapsilosis, and Candida mycorderma. Subsequent laboratory tests with a modified Y-type olfactometer showed that all cultures containing a combination of the four yeast species were significantly attractive to the beetles (53, p. 338). Additional tests (53, p. 339) using individual yeast species indicated that Saccharomyces pastoria was most attractive to the beetle, while tests using the other yeasts either gave insignificant results or were entirely rejected. However, substances proving attractive to walking beetles in laboratory olfactometers may

not apply at all under field conditions where the beetles only select their hosts in flight.

In contrast to the idea of yeast produced attractants, it was found that the attractive substance responsible for mass invasion by the Douglas-fir beetle was a pheromone (as defined in (47)) produced by virgin females (76, p. 23; 77). The attractive principle was produced only after the unmated females fed on suitable phloem of the Douglas-fir. In addition, it was found that old Douglas-fir logs and even other tree species may be invaded when beetles are in the areas of attraction (77).

Flight-capacity studies have shown that the Douglas-fir beetle is capable of flying several hours (5, p. 943). Even though Douglas-fir beetles have the capacity for long flights, there have been little field data to support the existence of long flights. Walters (94, 95) made two attempts to establish the beetle's flight range by releasing 6843 and 4800 specimens by marking them with nail polish or by clipping their tarsi. The results of these experiments were negative although a search was made of the surrounding trap logs which were placed up to a mile from the release point. More recent studies (46, 76, 77) using natural sources of attractants and observing

subsequent attacks, may indicate that the Douglas-fir beetle is at least responsive over short distances (1 - 16 ft.); the existence of longer response distances is most probable but as yet not ascertained.

The flight patterns of D. pseudotsugae responding to attractants have been investigated (74, 75). Flying populations concentrating on attractants were found to exhibit distinct diurnal and seasonal response rhythms. These patterns were influenced by such environmental factors as temperature, wind, and daylight.

The mechanisms influencing the host selection of pine bark beetles are thought to be different from those of other conifer inhabiting Scolytidae (33, 73). In general, pines are adapted to the more adverse sites and characteristically possess more specialized survival features as found in their resistance to drought (6, 77, 88, 93) and insect attack. Therefore, unlike the relationship between bark beetles and other conifers, several of the scolytids attacking pine have acquired survival mechanisms that increase the probability of successful attack (3, 33, 73). Since the primary defense of pine trees against insect attack is the oleoresin, invading scolytids must either withstand the resin or curtail its

production. Consequently, certain bark beetles (Dendroctonus valens Leconte and Dendroctonus terebrans (Olivier)) have a high tolerance to oleoresin flow while other scolytids overcome the host's resistance through directed mass attacks (3, 33, 35, 73, 80, 91, 92, 108).

Although the attractiveness of the host material itself, especially oleoresin, has been substantiated for several pine-inhabiting coleopterous species (9, p. 114-128; 35, p. 284; 57; 61; 80; 103), this may not apply to the more aggressive species as suggested by past workers (43, 44, 48, 57). As early as 1931, Person (62) hypothesized that fermentation products in the inner bark of ponderosa pine (Pinus ponderosa Lawson) may initially attract Dendroctonus brevicomis Leconte. He further stipulated (62, p. 697), "But after a few attacks are made a second, stronger attraction is started by the yeast introduced by the attacking beetles, finding the inner bark a favorable medium for its growth. This secondary attraction is probably strong enough to attract beetles for a considerable distance." Person's statement that strong attractants are produced after initial attack may be essentially correct; however, the role that yeasts play in this process is doubtful. Early work by Holst (42) and

the more recent work of Shifrine and Phaff (82) indicates that the yeasts from bark beetles have only a weak capacity to ferment monosaccharides. Also because the attraction is often exhibited a few hours after the beetle invasion, it is improbable that attractants are produced by this process (8; 82, p. 45). Similarly, other works, published and unpublished (57, 91, 97), have failed to encourage any beliefs in the hypothesis that materials attractive to scolytids attacking ponderosa pine originate through a fermentation process.

Although Anderson (3) did not advance a theory on why Ips pini (Say) initially attacks its host, he did convincingly prove that the subsequent attraction of beetles is more dependent on the activity of the first attacking beetles ("pioneer beetles") than on the attractiveness of the host per se. Additional results (3, p. 597) indicated that, "only the males when working alone on the bark attract other beetles -- both males and females." Moreover, as would be expected, the intensity of attraction was dependent on the number of fresh attacks. Similar observations were made for Ips confusus Leconte attacking ponderosa pine; it was experimentally shown that initial attacks by male Ips attracted both sexes (90, 91, 106, 108).

Callaham (in 54, p. 154), working with D. brevicomis, advanced the plausible host selection theory that initial boring attempts are made at random. On resistant trees, the attempts fail because of copious resin flow; while on susceptible trees, the beetles succeed. Once the initial attacks are started, other beetles are drawn to the scene en masse. Vité and Wood (108) observed that both D. brevicomis and Dendroctonus monticolae Hopkins, under epidemic conditions, invaded their host species at random without preference for weakened or resistant trees. If the initial attack was successful, a mass invasion usually followed.

Investigations conducted at the Boyce Thompson Institute Forest Research Laboratory (90, 91, 108) revealed that the attractants responsible for mass attack of ponderosa pine by Ips confusus, Ips ponderosae (Swaine), and Dendroctonus brevicomis are species specific. The attractants originate in both Ips species from initial attacks by the mature males, but in D. brevicomis, from initial attacks of mature females.

Earlier studies on flight distances of ponderosa pine beetles have been performed mainly with D. brevicomis (57). The flight distances were usually determined from the

OBJECTIVES

The studies presented here are primarily restricted to Ips confusus attacking second growth ponderosa pine. The basis for these studies was the working hypothesis that the flight period of Ips confusus consists of two phases: a dispersal flight in which the gallery initiating sex, the male, selects the host at random; and a subsequent concentration phase in which both sexes respond to attractants produced by the pioneer beetles. The objectives of this work were, first, to determine if the test species can be experimentally concentrated by using such attractants under various environmental conditions. Consequently, a major effort was made to develop and standardize methods to study the behavior of I. confusus during its concentration flights. The second objective was to investigate which individuals of a given population respond to attractants, to establish under what conditions this response occurs, and over what distances beetles respond.

MATERIALS AND METHODS

Test Species

The most commonly used test animal was the California five-spined engraver, Ips confusus. The general life cycle of this insect has been frequently described (14, 26, 48, 86), therefore, only a brief sketch of its biology is presented.

Ips confusus is found from southern Oregon, south along the Sierras to the Laguna Mountains in southern California (86). The beetle is known to attack all pines within its range, but the only host considered in this study was Pinus ponderosa.

The number of generations of I. confusus varies from two per year in the north of its range to five per year in the south part. Throughout most of its range, the average number of generations is three to four; one generation more or less than the average may occur for a given locality as a result of seasonal variations in temperature. Broods may overwinter as callow or mature adults, pupae, or full grown larvae; during this dormant period they remain under the bark of slash or standing trees.

In the central portion of its range (where this study took place), the initial spring attacks by overwintering adults begin early in April. Attacks occur constantly until early November -- the densest flights coinciding with peak emergence and favorable weather conditions (35, 86). Each attack is initiated by a male beetle; as it enlarges its nuptial chamber, it secretes a species specific pheromone (91, p. 266). The pheromone marshals a mass attack on the host rendering it more suitable breeding material. I. confusus primarily breed in fresh pine slash throughout the spring and mid-summer; occasionally, however, they attack standing pine in late summer and fall. Even though attacks on green stems have produced loss to growing stock, infestations are generally sporadic and short lived. Sizeable spots or group kills usually occur in pulpwood or pole-sized stands, less often in more mature stands.

Ips confusus is an excellent test animal: it flies in large numbers throughout the season; it is easily reared in insectaries; and it withstands considerable manipulation, i.e., tethering to flight mills, painting with dyes, storing at low temperatures, and transporting to test sites.

The beetles used in this study were gathered from two main sources. The majority were obtained from infested logs stored in the insectaries. As the insects emerged from the logs, they were collected from the screens of the insectaries by means of aspirators. The aspirators were constructed as suggested by Peterson (66) and powered by small vacuum cleaners ("Pixie" by Hoover). A constant supply of emerging beetles was assured by placing infested logs in a large thermostatically controlled insectary. This insectary was divided into four large cages; each cage was approximately 50 sq. ft. This partitioning was designed to segregate logs with infestations of different ages. Thus, it was possible to stagger the emergence by adjusting the temperature of the insectary and by maintaining broods in different stages of development. In addition, an outside insectary that was protected from the weather by a tin roof was available. This cage proved useful in approximating the natural emergence patterns as they occurred in the experimental forest.

The second main source of Ips confusus were those captured in specially constructed bait traps. As the beetles responded to the male pheromone, they were trapped in mason jars. This collection method will be more

extensively discussed in the section on olfactometer techniques.

Other scolytids were also used in some comparative studies. These bark beetles were Dendroctonus brevicomis, Dendroctonus valens, and Dendroctonus pseudotsugae.

Test Areas

Flights of I. confusus responding to attractants were primarily studied in an area where the beetles occurred in endemic proportions. For comparison, tests were also performed under epidemic conditions and on a prairie. Boyce Thompson Institute Experimental Forest. The response studies were performed in the Boyce Thompson Institute Experimental Forest near Grass Valley, California, unless stated otherwise. The forest, which lies just south of the city limits, covers approximately 800 acres; it is rectangular in shape, approximately 1.5 miles long, and .75 miles wide. The elevations range from 2400 feet in the north to gently sloping, 2120-foot creek bottoms in the east and south. The forest is rather uniformly stocked with 60-95-year-old ponderosa pine except for an 80-acre meadow running east and west through the middle of the property.

Because of the complete depredation of the former ponderosa pine and sugar pine virgin growth through gold mining activities in the mid-nineteenth century, the dominating stand appears as rather uniform second growth ponderosa pine. The better south sites sustain many 90-year-old ponderosa pines that reach an average dominant height of 152 feet, while on the northern plateau, similar age stands only reach 116 feet.

The normally endemic, economically important scolytids occurring on the ponderosa pine are Dendroctonus valens, D. brevicomis, Ips confusus, and Orthotomicus latidens (Leconte). Although outbreaks do not occur each season, these insects infest one to five per thousand stems each year.

Nevada City Airport. Tests with I. confusus under epidemic conditions were performed on the Nevada City Airport. This abandoned airdrome was situated on a plateau of approximately 200 acres five miles southeast of Nevada City, California. The plateau and the surrounding hills were moderately covered by second growth ponderosa pine. For the most part, these stands were growing on very thin and rocky soil; the soil's condition was a result of hydraulic gold mining in the last century. The lower slopes

around the air port were being cleared in patches for housing developments. Because of this accumulation of favorable breeding material and weakened hosts, bark beetle populations thrived in this area. Since 1959 there have been reports of large Ips and Dendroctonus spot kills; Manzanita (Arctostaphylos manzanita Parry) and California black oak (Quercus kelloggii Newberg) have become dominant thus thwarting all hopes of pine regeneration. Even a cursory surveillance from the airport revealed fading, red-topped pine in all directions; and a walk in the stands readily disclosed recently infested brood trees.

Using the abandoned runways to set up experiments was advantageous since the runways ran in cardinal directions. In this way, one was constantly aware of the prevailing wind direction, the location of equipment, the location of release points, as well as the position of all personnel.

Sierraville Prairie. Tests with Ips confusus under prairie conditions were carried out near Loyalton, California. The Sierraville prairie, 5500 feet elevation, encompasses approximately 400 sq. miles of range and farm land between the southeastern corner of the Plumas

National Forest and the northeastern segment of the Tahoe National Forest. The largest settlement in the area is Loyalton, although there are farm and ranch homes scattered throughout the prairie. Most of the prairie can be characterized as strictly range land supporting Artemesia tridentata as the dominant forb with Sitonia sp. and Poa secunda as main grasses. A large portion of the prairie is also farmed; rye and wheat are the main crops.

The experiments were performed in the center of the prairie, seven miles south or north from the nearest pine stands. East and west from the center, the pine cover was over 14 miles away. Since the mornings were too cold for flight, and the afternoons were generally too windy, experiments were restricted to approximately a two-hour period between 11:00 a.m. and 1:00 p.m.

Development of Techniques to Study Flight-Response Behavior

The first requirement of this study was to develop techniques that would measure the beetles' response to attractants under laboratory and field conditions.

In laboratory approaches, behavior influenced by chemoreception was observed only with flying insects. Traditional approaches of crawling beetles responding in

olfactometers were discarded. Conclusions drawn from such approaches mostly proved inadequate when applied to field conditions. Rudinsky (74, 75) and others (50, 87, 91, 92, 108), have demonstrated that olfactory responses under natural conditions are more intimately related to flight activity. Moreover, an apparent positive response demonstrated by beetles walking to a particular test material may largely be an arrestive phenomenon. As Dethier points out (23, 24, 25), arrestive reactions may be governed by geotactic, phototactic, thigmotactic, or chemotactic reactions -- not necessarily a singular olfactory response.

To minimize artifacts introduced by laboratory conditions, field-techniques were emphasized in this study.

Techniques of marking beetles. When investigating the response of I. confusus under field conditions, it became important to distinguish the test insects from the natural population.

Keen (57, p. 51) as early as 1917 marked large quantities of D. brevicornis in hopes of later finding them in infested trees. His method was to dissolve rosolic acid in 95 percent ethanol and to spray the solution on test

insects. Beetles so marked could be identified by a color reaction when dropped into a solution of NaOH, even though they had received only a few droplets of the dye solution. Such an approach would have merit if the beetles were not to be flown again or if the mere presence of marked beetles in the host was all the data desired.

Walters, studying the dispersal of Dendroctonus pseudotsugae, released beetles with clipped tarsi or marked with nail polish was found to be inadequate. The beetles so marked showed a substantial decrease in flight ability; if the nail polish were applied in smaller quantities, it readily rubbed off.

Speers (85) used radioisotopes in tracing the attack patterns of Dendroctonus frontalis Zimmerman from release to subsequent attack. An approach of this type would be of little use in determining exactly which or how many beetles were tagged out of a given sample. Furthermore, Speers points out that tagged beetles showed a decrease in flight capacity (85, p. 139-140).

The use of fluorescent dyes proved to be the most propitious means of marking the test beetles (28). Beetles marked in this manner could instantly be identified from a large sample by means of a small ultra-violet hand

lamp. The smallest residual trace of dye on an insect could readily be spotted. This method was also advantageous in that the dyes were available in many colors, thus beetles marked with different colors could be simultaneously released. The marking was best done on the pronotum with a small amount of dye applied by a pin-pointed brush. Marking the elytrae seemed to influence the beetle's capacity to fly.

It was advisable to mark a larger number of beetles than needed in an experiment, because only about 70 percent of the treated beetles took off readily when stimulated to fly.

Marking beetles with fluorescent dyes, however, had its disadvantages. The greatest problem was the time and effort consumed in the procedure, since each beetle had to be individually marked. Undoubtedly, the additional handling also had some effect on the percentage of beetles able to fly.

Selection of beetles. Before releasing the beetles, it was important to determine what effects mutilation, storage, and marking would have on the test beetles in respect to their flight capacity and responsiveness to

attractants.

Most of the experiments involved large numbers of marked beetles. To assure that marked beetles were on hand, sufficient quantities of them were marked and stored. Test insects were stored in a walk-in cooler that was maintained at 5° - 7°C. The insects were kept in Petri dishes, with no more than 200 beetles per dish. As long as the beetles were cooled, the only mutilation evident was the slight amount due to handling. Upon removing the animals from the cooler, however, they revived and began to masticate the appendages of their neighbors.

An experiment was conducted to determine the effects of mutilation on flight capacity and response ability of Ips confusus. Each day, for two days, 500 freshly emerged insects underwent the following treatments: 100 were left intact, 100 had a tarsus removed from a front and hind leg respectively, 100 had all tarsi removed, 100 had one antenna removed, and 100 had both antennae amputated. Each of these groups, so identified, was released within a circle of field olfactometers and the number able to fly and to respond was counted.

The data (Table 1) indicate that the removal of extremities did not greatly affect the flight ability of

Table 1. The ability of I. confusus with amputated appendages to fly and respond to attractants. Beetles released five meters from the baited olfactometers.

Treatment of Beetles	Flight Positive %	Attracted %
Intact Beetles	81.2	26.2
2 Tarsi removed	80.0	23.8
4 Tarsi removed	71.0	12.8
1 antenna removed	69.8	11.2
Both antenna removed	72.3	0.0

the test animals, but mutilation did decrease their ability to respond. As a result of this experiment, it became necessary to eliminate damaged beetles from the test material because it was important that both antennae, the receptive organs for olfactory stimuli (24, 40, 55, 58, 71, 79), remained intact.

Early in the course of this study, it appeared evident that storing in the cooler and possibly prior marking affected the flight and the response of the test beetles. To establish the extent of these effects, 2000 painted and 2000 unpainted beetles were put in the cooler. At the same time each day, for 20 days, 100 of the painted and 100 of the unpainted beetles were removed from the cooler and flown within a five-meter radius of olfactometers. At the moment, 100 beetles which had freshly emerged from the

insectary were also released as a control. The results of these tests (Figure 1) clearly show that storage has a pronounced effect on both the ability of the insects to fly as well as to respond. Beetles marked with fluorescent dye prior to storage showed a parallel decrease in ability to fly and in ability to respond. However, statistical analysis indicated that in comparison to the stored and unpainted beetles, the ones that were previously marked and stored did not exhibit a significant decrease in ability to fly and respond to attractants. This analysis measured the interval estimate of the difference between intercepts at the 95 percent level of significance.

To minimize the effects of prior marking and storage on response ability of the test animals all efforts were made to fly the insects within three days after marking and storing. Whenever possible either freshly gathered insects or beetles marked and stored overnight were used during the study.

Release for free flight techniques. The development of an efficient method to induce the test insects to fly was essential before field studies on response behavior could begin.

Eraenkel (30, p. 372) was one of the first to outline

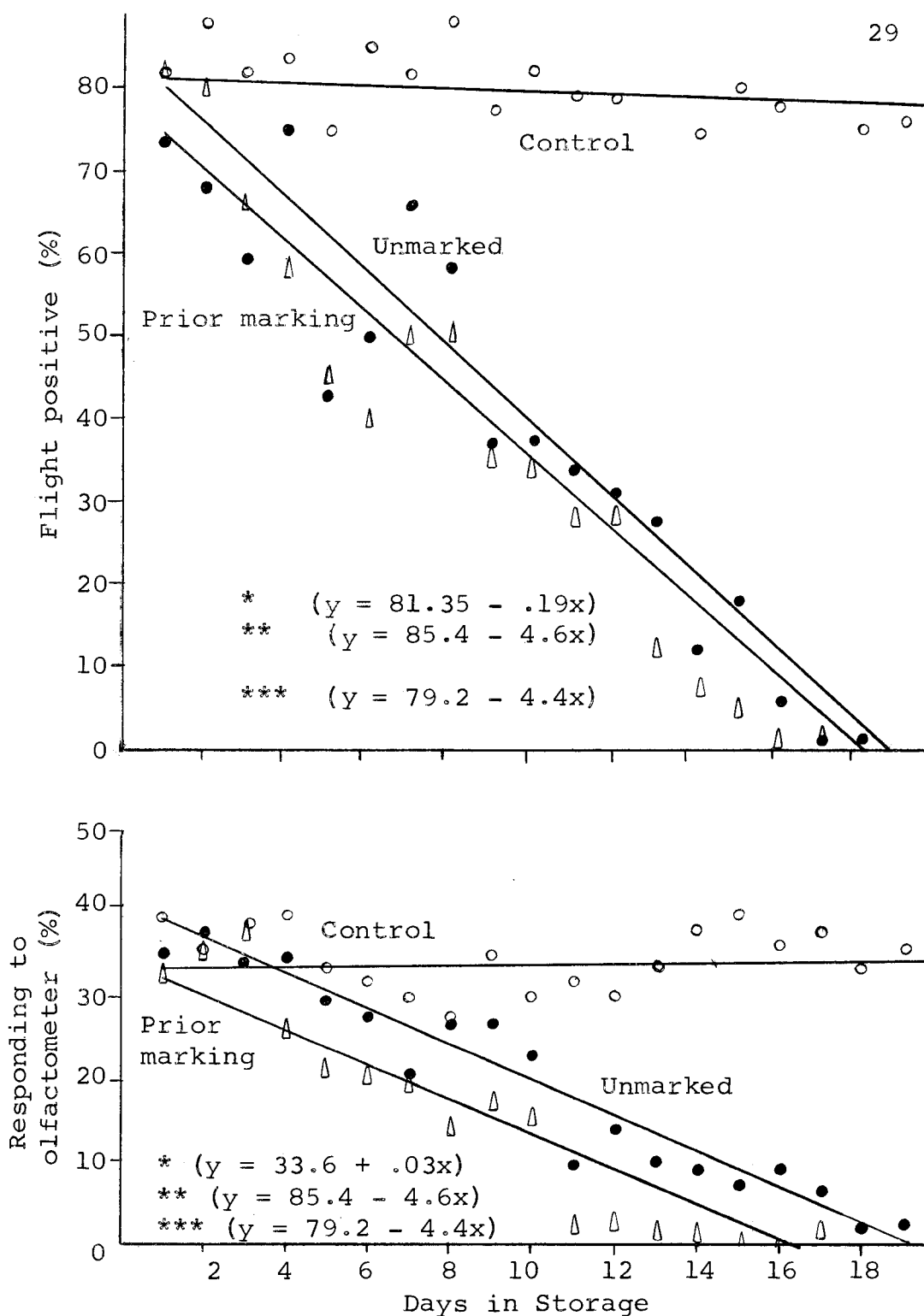


Figure 1. Effects of storage in cooler and prior marking with fluorescent dye on the flight ability and response ability of Ips confusus.

*Control-o **Unmarked-● ***Prior marking-Δ

the reflexes responsible for the initiation of flight. One of the most important stimuli is the removal of the insect from contact with the substratum (34). This stimulus constitutes the now well-known "tarsal reflex" as termed by Fraenkel (30). Roeder (72, p. 649) points out that this stimulus apparently is shared by all insects with wings, even by some mutant forms that are unable to fly.

The use of the tarsal reflex principle has been shown to be effective in initiating flight in various species of Scolytidae (27, 28, 57, 75, 91, 92). Rudinsky (75), however, has found that the Douglas-fir beetles fly more readily and in greater numbers when exposed to sunlight and allowed to take off without additional stimulation.

Ips confusus could be made to fly by exposing them to direct sunlight for a short period and then lifting them on a large blanket into the air by gently swinging the blanket (91). Even though this method was quite successful in promoting flight, it was too gross, in that many of the insects that did not fly were scattered on the ground and could not be counted.

In working with percentages of beetles attracted to the pheromone, it was important to determine exactly how many test animals actually flew. Since hurling beetles

into the air by a blanket was unacceptable, different approaches were tried. One technique involved a method whereby tarsal reflex could be quickly induced to a mass of beetles, and yet the ones not flying could be accurately counted (Figure 2). A metal cylinder, 15 cm. in diameter (I.D.) and 10 cm. long was attached lengthwise to the blunt end of a 1.5 meter wooden stake. When the stake was inserted into the ground, one opening of the cylinder was pointed downward and parallel to the earth. This opening was provided with a magnetic lid that was hinged to the cylinder. In operation, a white sheet was placed directly under the cylinder and test beetles placed inside the container. By pulling a lanyard attached to the lid, the beetles were deprived of their substrate and dumped in the direction of the sheet. This apparatus worked rather well in inducing beetle-flight; an average of 60-65 percent of the beetles took wing on initial release. This technique was not employed generally because of the time involved in gathering the beetles from the sheet and reinserting them into the cylinder in attempts to improve the percentage of flying insects. In addition, the insects massed together in the confines of the cylinder tended to quickly mutilate themselves.

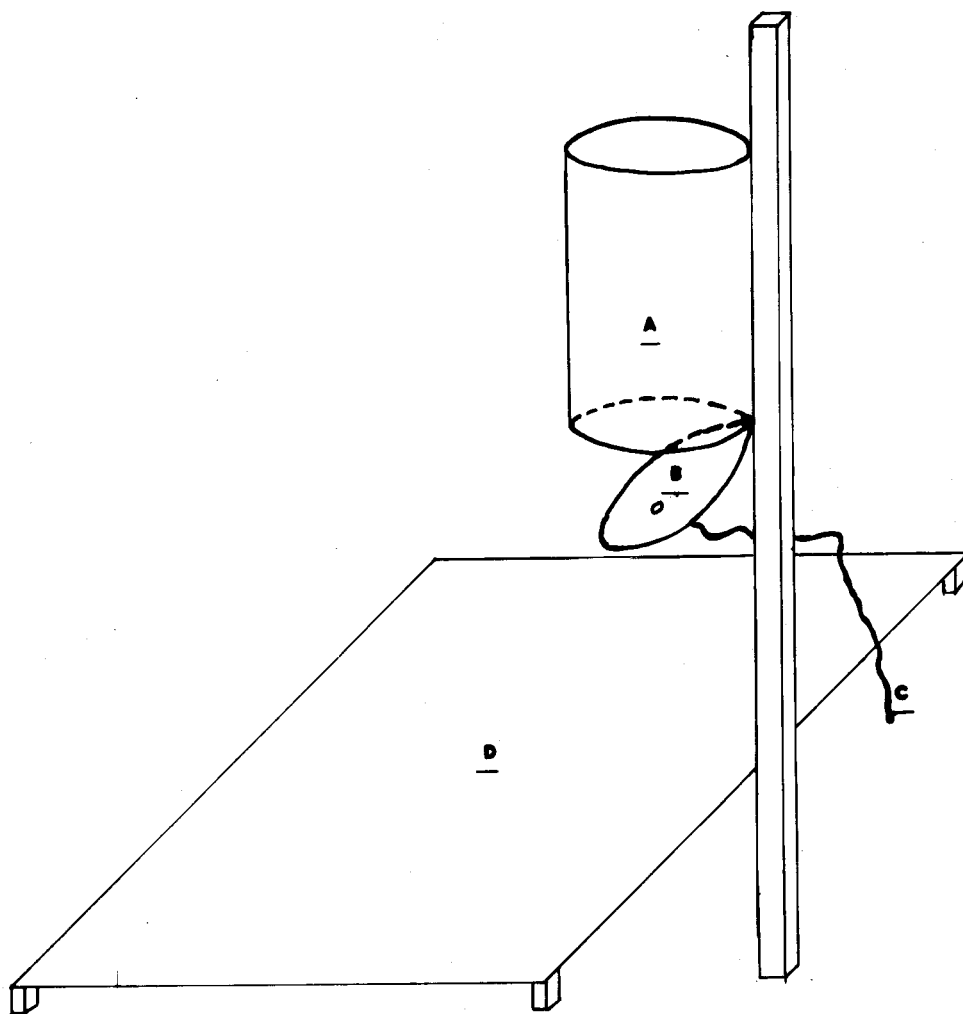


Figure 2. Beetle releasing device. Beetles placed in metal cylinder (A), when lanyard (C) is pulled, magnetized lid (B) opens and the non-flying insects are collected on sheet (D).

The technique that was finally evolved and used, not only worked on the tarsal reflex principle but also provided a "leap" stimulus. Chadwick and Dethier (12) point out that most insects customarily begin flight by leaping which insures loss of tarsal contact. In effect the leap may be an important sequence in initiating flight.

The device (Figure 3) used through this study -- termed a "beetle-launcher" -- was constructed in the following manner. A large, square frame, 1.5 meters on a side, was assembled from 1/4 inch pipe. The frame was held 1.5 meters above the ground by means of collapsible legs attached to each corner. A sheet of bleached muslin was fastened to the perimeter of the frame so that the loose folds fell inside the square. A smaller wooden frame was stapled to the bottom of the loose sheet, and screen door springs were attached from each corner of the wooden frame to the inside corners of the outer frame. The beetle-launcher operated by placing test insects on the inner frame, then, by pulling the small frame downward the springs were distended. Releasing the tension caused the beetles to leap into the air; invariably a large percentage (up to 90 percent) flew on the first trial. Subsequent repetitions of the procedure soon



Figure 3. (Foreground) Beetle launcher: inner frame attached to outer frame by springs from each corner. Beetles placed on inner frame are hurled into flight upon depression and subsequent release of inner frame. (Background) Standard olfactometer used throughout study.

separated the beetles capable of flying from the non flyers. One could easily collect and count the non-flyers with the aid of a simple aspirator.

Later, the beetle-launcher was simplified even more. A small wooden frame was constructed with muslin tightly stretched across it. The beetles were placed on the cloth, and by snapping the underside of the muslin with one finger, the beetles were projected into the air. This procedure was performed directly over the larger frame so that the non-flyers could be easily recovered.

Olfactometer techniques. Most of the flight behavior studies of Ips confusus responding to attractants were conducted in the field. It was felt that investigating their behavior under natural conditions would lessen possible artifacts encountered in laboratory studies (91, p. 41).

In developing bait-traps for field studies, certain criteria were established. First, it was important that the equipment per se would not be overly repulsive or attractive to the beetles. Only the volatile pheromone could be attractive to the beetles. Second, bait-traps provided with attractants would have to collect responding

beetles in an efficient and standardized manner. Third, all beetles would be easily recovered without undue effort or loss of time.

Because of these desired requirements, many of the previously described bait traps were not employed (57). Trap trees and trap logs suggested in various studies (43, 44, 48, 57, 61, 80) give only a relative concentration figure. Although beetles are attracted to trees and logs, all do not necessarily attack; on the other hand ideally designed bait traps retain most of the attracted population. Trap trees and logs also include the tedium of excising beetles whereas spraying insecticides on the substrate may add a questionable variable (35).

Chapman and Kinghorn (19, 20) developed a simple bait trap that was suitable for their purposes. This trap (termed a "window trap") was made from a piece of 2 x 2 feet window glass set in a three-sided frame from which a sheet metal trough hung. As insects collided with the glass barrier, they fell into the trough which contained a killing liquid. By placing window traps six feet above logging slash, they noted that the logging debris served as an excellent attractant for scolytids normally infesting cut material. Rudinsky (74, 75) found that portable

cages positioned over logs freshly infested by female Douglas-fir beetles served as an excellent bait trap. In this case, the criteria for a good field olfactometric technique were satisfied in that D. pseudotsugae, when in the presence of its pheromone, is not only attracted but is also arrested for a long time on the outside of the cage.

The bait trap or field olfactometer used in this study was previously designed during investigations on the flight behavior of several scolytid species (91). In this previous work the olfactometers proved to have the following advantages: (1) released as well as field populations were readily attracted, (2) attracted beetles were trapped and easily collected, (3) the apparatus could be standardized for the most efficient operation, and (4) it was collapsible and easily transported.

The field olfactometer (Figure 4) consisted of three parts: a cylindrical box, 60 centimeters in diameter; a funnel, 100 centimeters deep and 60 centimeters in diameter; a pipe section with a fan, 30 centimeters in diameter and 54 centimeters in length, which connected the box to the funnel. Air was drawn from the box, which in operation contained highly attractive material, and

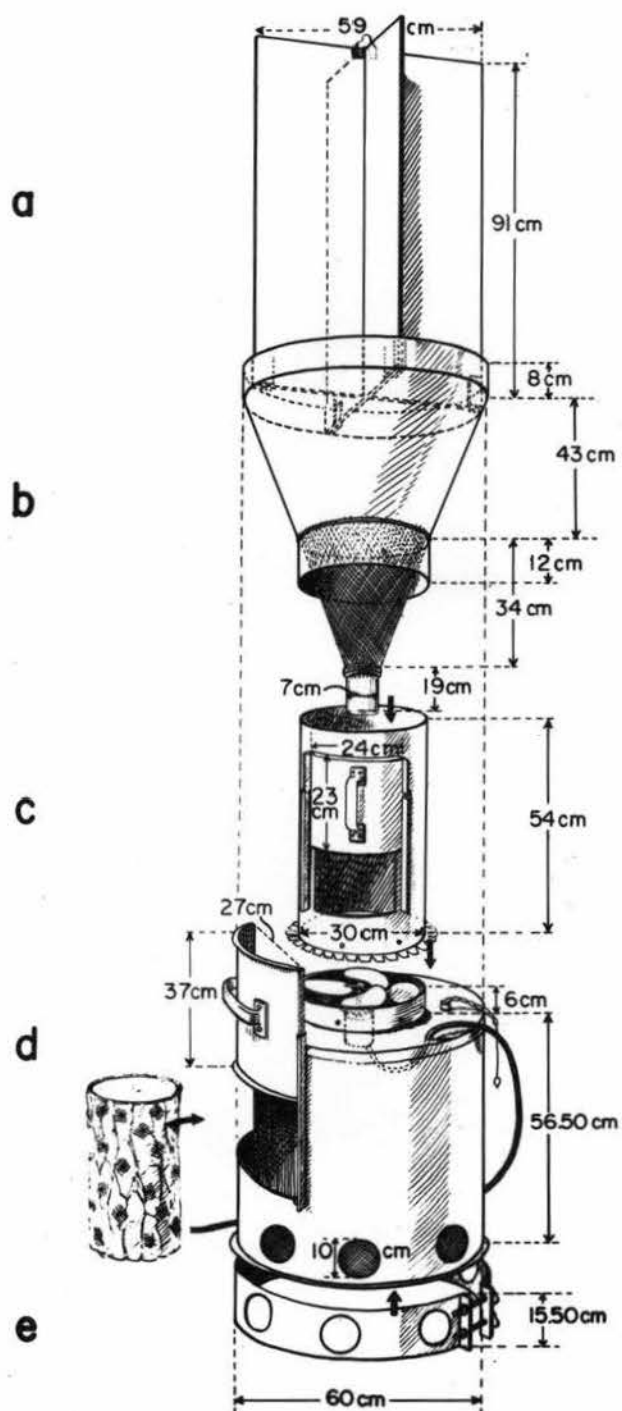


Figure 4. Field olfactometer used throughout study: (A) flight barrier, (B) metal funnel with screen cone and collection jar, (C) connecting tube with sliding door, (D) bait box with fan, (E) air stream regulator.

blown through the lower third of the funnel which was made from metal screening. Glass or wooden plates set across the top of the funnel served for better distribution of the air saturated with attractant as well as a barrier to flying insects.

The pipe section connecting the box and the funnel contained a 1/40 horsepower electric fan of 1500 revolutions per minute. The fan produced a maximal air current of approximately 25 cubic meters per minute with an air speed of 120 meters per minute. Air speed and volume were regulated by an air stream regulator at the base of the olfactometer; the air speed could be reduced to a minimum of 30 meters per minute.

The upper two-thirds of the funnel was made from sheet metal, while the lower third (covered by the pipe section) was from metal screening that pointed, with a four centimeter wide opening, into a glass collecting vessel (Mason jar). A sliding panel in the pipe section facilitated the removal of the jar affixed to the screen portion of the funnel by means of a screw ring.

In operation, the attracted insects flew against the glass (or fibre-board) barrier, or voluntarily entered the funnel by falling or crawling into the collecting jar.

From previous developmental tests (91) it was found that the primary limiting factor in trapping insects was the speed of the air stream produced by the fan. In general, the stronger the air stream the better was the attraction; however, with an increasing air velocity more insects, especially the smaller ones, were prevented from entering the funnel. With Ips confusus, best results were obtained when the air flowed at a rate between 60 and 90 meters per second. During the course of this study, the field olfactometers were standardized to produce an air flow of approximately 80 meters per minute.

Random trapping technique. In contrast to bait traps which attract and capture insects by means of a luring stimuli, random traps catch insects by chance encounter and without the use of attractants. The random trapping technique used in this study was the aerial net trap (13, 90). This technique was previously standardized and used to determine the relative density of flying scolytid populations (90). The aerial net trap assembly consisted of a single deep nylon net 38 cm. in diameter and 70 cm. deep which was affixed to the center of rotation by a radial arm 235 cm. in length. The center of rotation was

connected, by a shaft-coupler, to a 1/4 horsepower electric motor of 60 r.p.m. which enabled the net to travel at a speed of 53 km/hr., while sampling air at the rate of 6,000 cu. meters per hour. The entire assembly was supported on a two-meter aluminum ladder. Thus, the aerial net traps could be moved easily from one sampling area to another. A typical aerial net assembly is seen in Figure 5.

Preparation of Attractive Material

The attractants for the field olfactometers were obtained from male Ips confusus inserted into fresh ponderosa pine log sections. The beetles were inserted in the following manner: Logs approximately two feet by eight inch diameter were used with the rough and loose portion of the bark scraped away. About 1/4 inch holes were driven into the bark by a blunted nail. One male I. confusus was gently placed head first into each hole and his exit was quickly covered by stapling a piece of 18 mesh metal screen over the hole. Plastic screen proved unacceptable since the beetles readily chewed through it.

To determine the sex of live beetles, the stridulation organ of the female -- as recently described by Wood

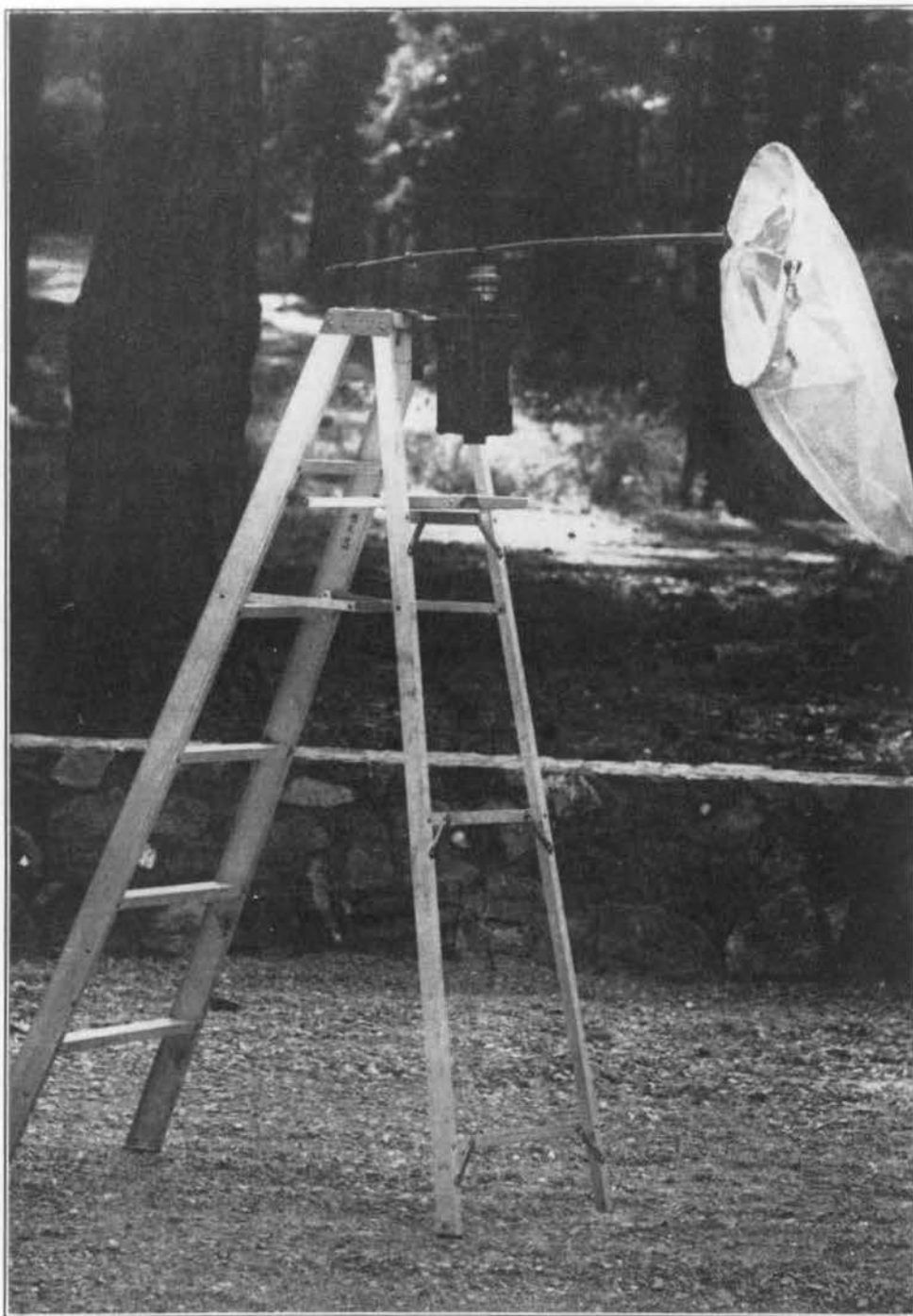


Figure 5. Aerial net trap assembly used for random trapping of insects.

(104) -- was used.

In earlier research (91, p. 266), it was demonstrated that as the beetles chew toward the cambium, there is a coincidence between the beginning of attraction and the construction of the nuptial chamber. As the beetles ingest the cambial tissue during this construction, the attractive substance is passed out with the feces; Pitman and Vité (67) located specialized secretory cells in the hind gut that may add the attractive principle to the fecal material. In any case, 24 hours after males are inserted into logs, the attraction produced is comparable to those infested for several days and useful as test material (Figure 6).

The attractant containing material used in this study, if not stated otherwise, consisted of three logs per field olfactometer, each log with 25 male Ips confusus. The logs used for each experiment were cut from the same tree in order to forestall any variation in attraction that might originate from the host material itself. To assure approximately equal attractiveness through the tests, the bait was renewed each week.

To test differences in the vertical response of Ips confusus, field olfactometers were positioned in trees.

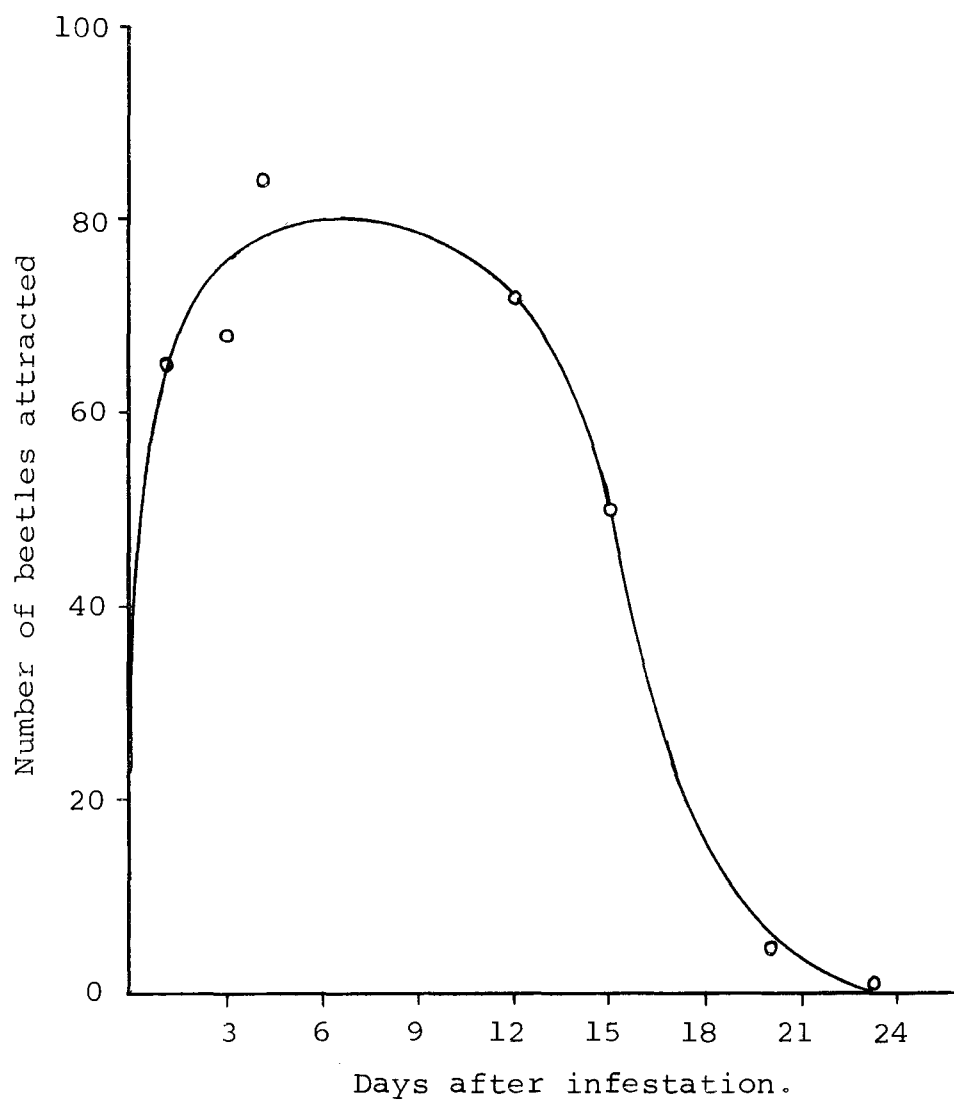


Figure 6. Attractiveness of log sections infested with Ips confusus in relation to the age of infestation.

However, such a set up required the building of platforms and ladders in order to check them. To alleviate this problem a series of small olfactometers (tree olfactometers) were designed that could be hoisted up and down between two trees (Figure 7). The olfactometers basically consisted of an outer and inner funnel arrangement. The outer-funnel was 60 centimeters in diameter tapering down for 50 cm. to a 10 cm. diameter opening. The smaller end of this funnel was attached to the exhaust end of a small vacuum cleaner ("Pixie" vacuum cleaner by Hoover). A smaller inner funnel of 52 cm. diameter was positioned inside the larger funnel. The smaller funnel was held in place by soldering a 4 centimeter wide strip of 18 mesh screen to the peripheral lips of the inner funnel and the outer funnel respectively. The inner funnel tapered for 27 centimeters to a 3 centimeter opening. This opening was soldered to a 3 centimeter diameter pipe which obliquely extended through the wall of the outer funnel, protruding outside approximately 12 centimeters. This pipe was securely soldered to the wall of the outer funnel. One end of the flexible vacuum cleaner hose was attached to the pipe, the other end to the middle portion of a pressure reducing chamber. The upper end of this

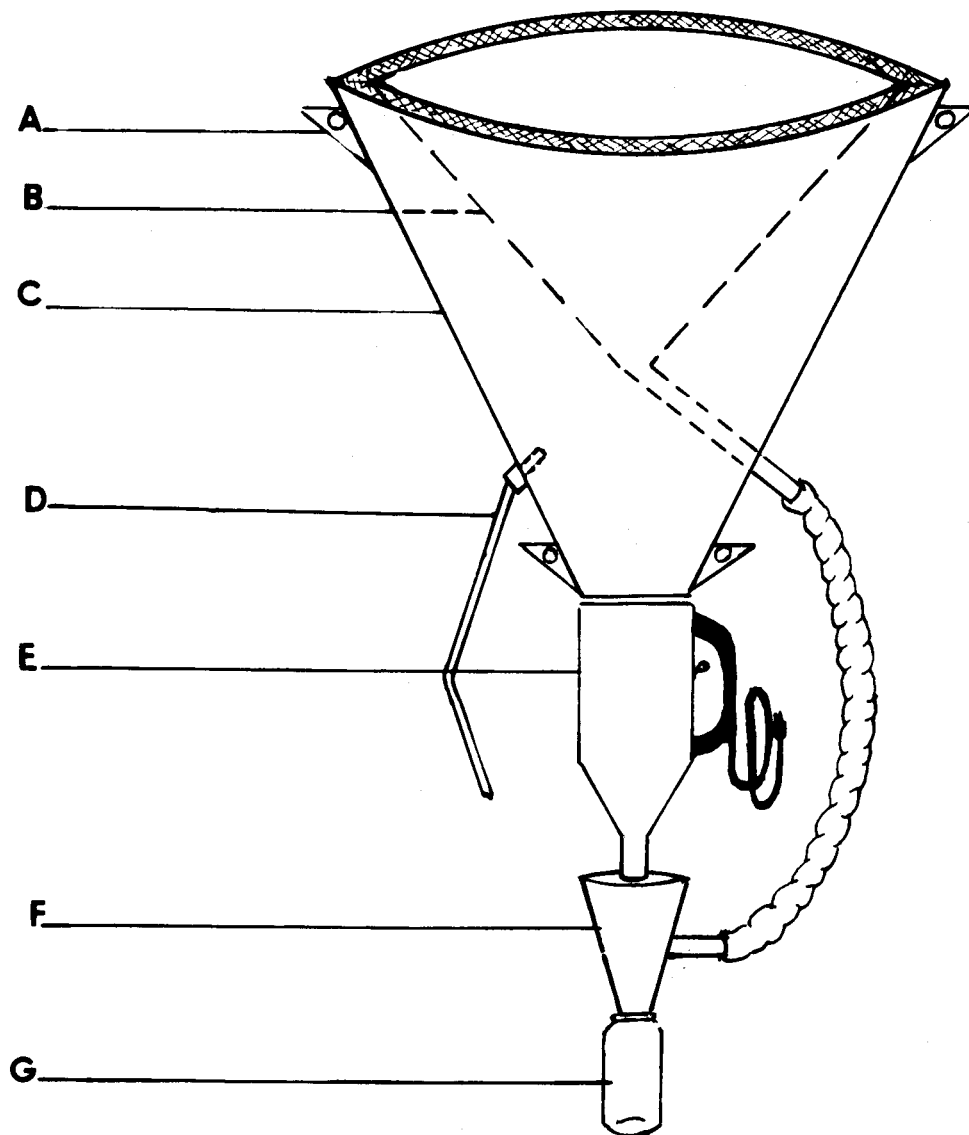


Figure 7. Olfactometer designed to be hoisted up a tree:
(A) eye for attaching assembly to hoisting rope, (B) inner funnel for receiving attracted beetles, (C) outer funnel for dispersing attractants, (D) hose carrying attractants, (E) vacuum cleaner, (F) pressure reducing chamber, (G) collecting jar.

chamber was slipped over the suction end of the vacuum cleaner and the other end held a collecting jar.

In operation, attractants were supplied to the outer-funnel by means of a plastic hose which transported attractant laden air from a box containing infested logs and a compressor. The attractants were thus carried upward and out by the exhaust of the vacuum cleaner. Responding beetles fell into the inner funnel and were suctioned into the pressure-reducing chamber where they fell into the collection jar. To enhance trapping, a glass plate was usually placed across the two funnels.

To haul these olfactometers into the air, the corresponding ends of two boards were nailed at the top of a tree. The other ends were nailed to the top of a neighboring tree. Two pulleys, 60 centimeters apart, were fastened on the central portion of this platform and ropes that doubled to the ground were run through the pulleys. Each end of an 80 centimeter beam was attached to one end of each rope; the beam itself substended two additional ropes. The olfactometers were spaced between the beam-ropes by means of four snap fasteners. Two of the fasteners were attached opposite each other on the rim of the outer funnel and the other two were similarly

placed, but on the lower aspects of the funnel. This type of fastening assured that the olfactometers would ride level as they were hauled up the tree.

In practice usually four tree olfactometers were hauled up and down the trees -- one at ground level, and the others at elevations of 10, 20 and 30 meters respectively (Figure 8).

Restricted flight techniques. During the experimentation, the term restricted flight was applied to tests in which the flight of test animals was in some way limited, either through tethering to flight devices or through unhindered flight in confined spaces.

Flight bars. Ips confusus as well as other scolytids could be flown in place without actual locomotion. This was accomplished by attaching a 0.4 millimeter glass capillary tube to their pronotum by means of a wax droplet. The free end of the tube was then inserted through a horizontal balsa-wood arm. By rotating the tube between thumb and index finger, the beetle could be induced to fly. Such a device was useful in determining the beetle's wing beat frequency by means of a sooty Petri dish (76) that rotated at a known speed, or with a frequency meter



Figure 8. Series of olfactometers hoisted between two trees to attain heights of 10, 20, and 30 meters above ground.

technique (see page 54).

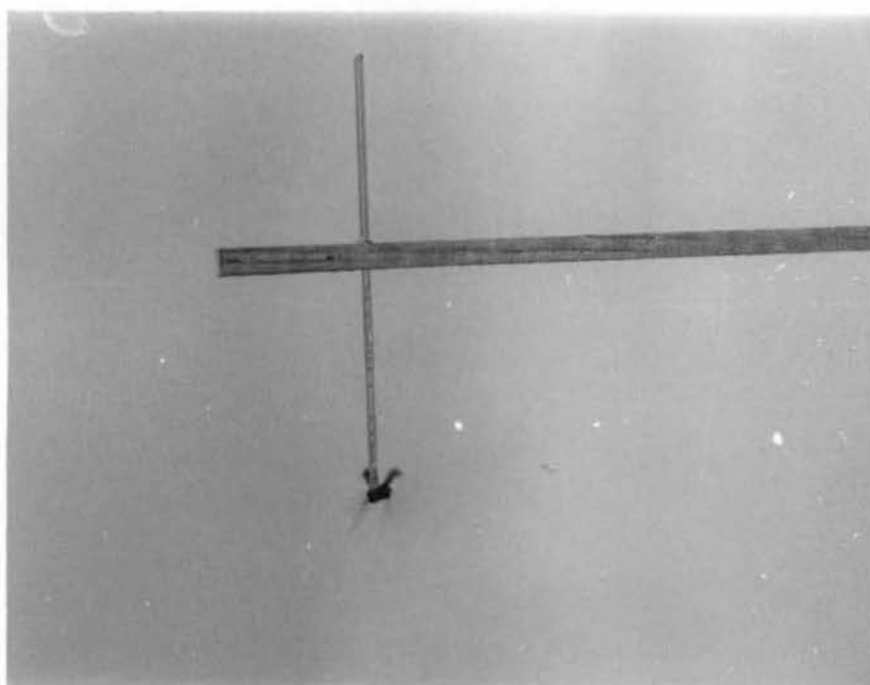
Flight mill. A balsa-wood flight mill (Figure 9) was developed to test the flight capacity of test insects. The principle of flight mills to study flight in respect to the physiological effects of flight as well as flight capacity is well represented in the literature (5, 9, 11, 39, 41, 52, 72, 98). The device developed in this study was similar to Chapman's (15, p. 375) technique. It consisted of a longitudinally positioned balsa-wood arm which rotated by means of a pin inserted through a glass bead bearing. The part of the pin which penetrated the glass bead fitted inside a brass tube of a slightly greater diameter than the pin. The brass tube was positioned on top of a vertical balsa arm which was attached to a broad wooden base.

One end of the horizontal arm was pierced by a 0.4 millimeter glass capillary tube that extended downward about 3 centimeters. The test beetle was attached at its pronotum to the capillary tube by a drop of wax. The other end of the balsa arm was counterbalanced to insure level flight.

In practice, there appeared to be an optimum radius of rotation for the horizontal arm. With shorter arms,



A



B

Figure 9. Balsa wood flight mill: (A) entire assembly, (B) I. confusus attached to horizontal arm of flight mill.

the rotation was too fast for accurate observation, while longer arms induced rapid exhaustion of the test animal. To standardize the flight mill, a series of tests were conducted by flying three species of beetles attached to arms of varying lengths. The beetle species used were D. valens, D. brevicomis, and I. confusus. In each test series, five beetles of each species were flown on horizontal arms that were lengthened after each test. The arms varied from a minimum of 10 centimeters (the shortest practical length) to a maximum radius which the beetles were unable to rotate. In each individual test, the beetle was allowed to complete five revolutions. The average time for one revolution was determined, then expressed as a rate in meters per second. Thus, for each arm length the speed recorded represented the average speed of five beetles.

The results of these tests (Figure 10) indicated that 20-25 centimeters would be an ideal radius of rotation for I. confusus and D. brevicomis; 20 centimeters was adopted as a standard length. However, in comparison to the smaller test species, D. valens could easily rotate flight mill arms of longer lengths (Figure 10). Sixty centimeters was used as a standard for this species.

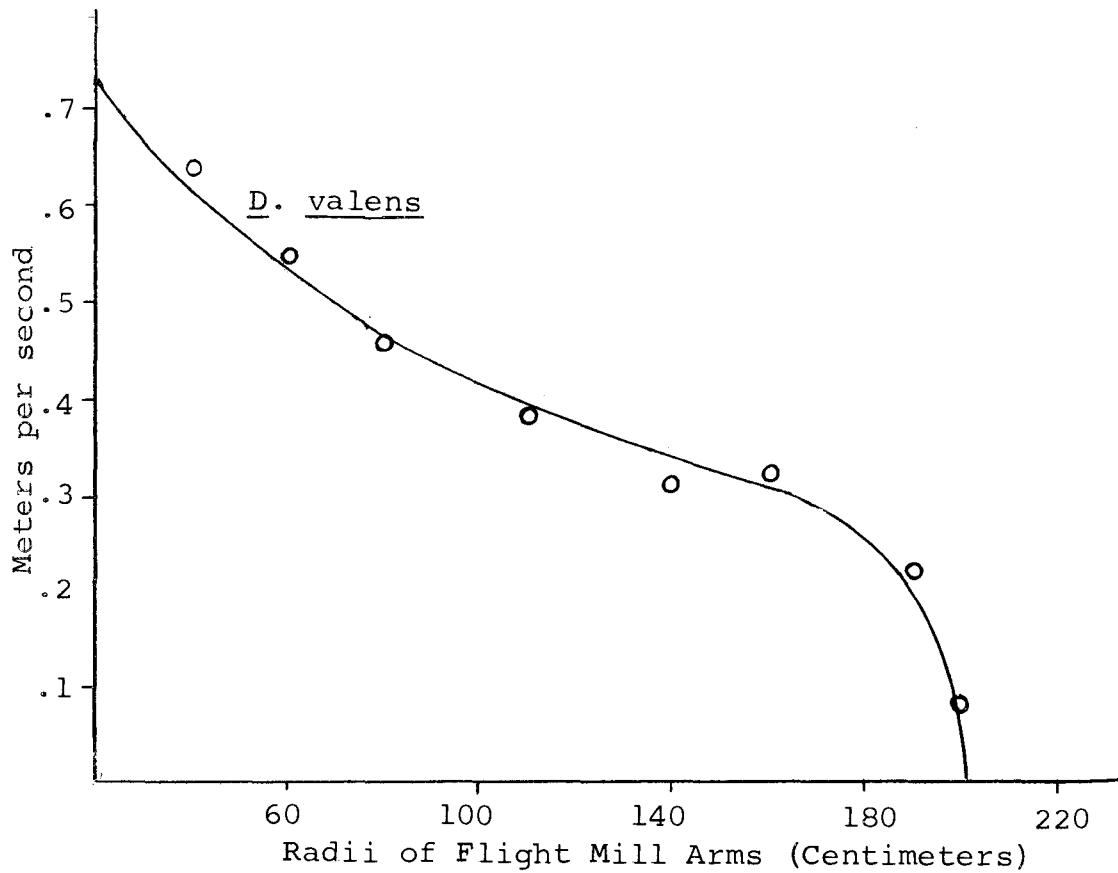
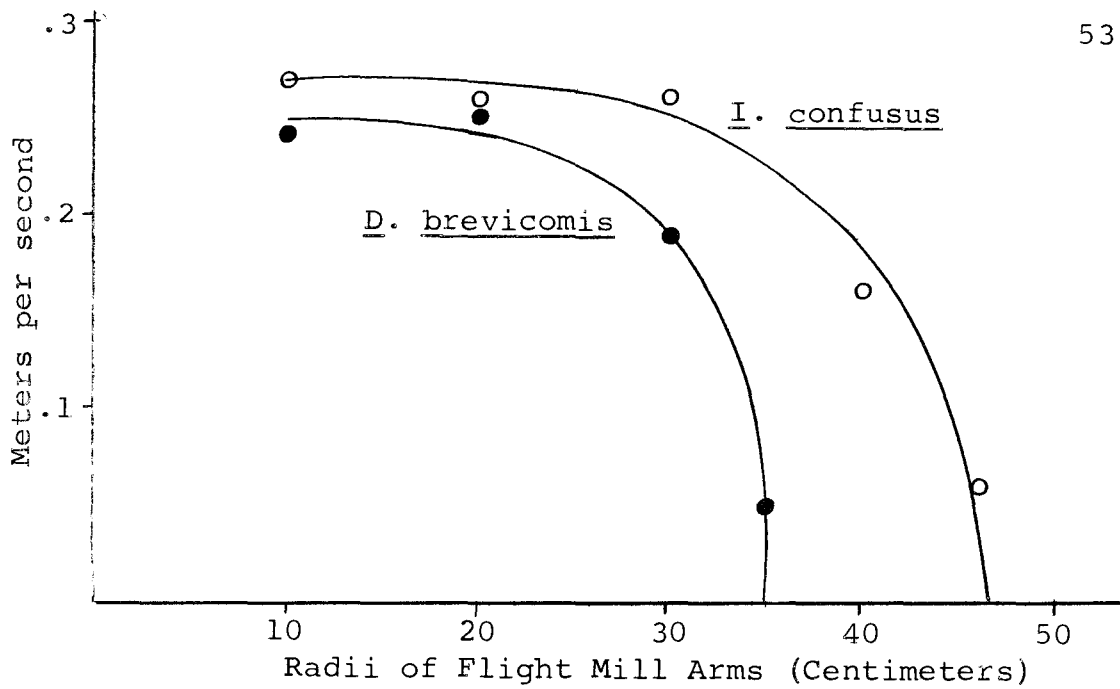


Figure 10. Rotation speed of flight mill for horizontal arms of different lengths and for three species of scolytids.

Laboratory olfactometer. As a supplement to observations noted in the field, a laboratory flying olfactometer was developed. The device was based on the principle that a flying bark beetle in the presence of an attractant (either sex or feeding attractant) will alter its wing beat frequency. It was anticipated that insect's wings might beat faster if the insect was excited or perhaps slower if landing reactions ensued.

The study of wing beat frequencies in relation to several physical and biological factors has been a subject for investigation for over three-quarters of a century (54; 72, p. 578). Early investigators determined wing beat frequencies by audient and kymographic techniques (83; 84; 72, p. 588-592). More recently, Rudinsky and Vité (76) used a kymographic method in determining the effects of temperature on the wing beat frequency of D. pseudotsugae. Objections raised against kymographic recording are that the insects must be fastened and that wing movement and frequency may be distorted by friction. However, most of the results reported have been in reasonable agreement with those obtained by more refined methods.

More modern and sensitive innovations employed such devices as high speed cameras (54), stroboscopic lights

(5, 10, 100), and electronic instrumentations (29; 39; 41; 70; 71; 72, p. 588-592; 88). Williams and Galambos (101, p. 301) used the technique of measuring the audial frequencies produced by the wing beats of Drosophila funebris by means of a microphone, amplifier, and oscillograph. Essentially, this is the method developed for this study, differing only in the use of a frequency meter instead of an oscillograph. The use of the frequency meter had an advantage over all other previous methods by allowing observations of instantaneous changes in the wing beat. It was felt that the slightest inflection in the basic wing beat frequency of a test scolytid might be significant as a behavioral response to volatile test materials.

The audio determination of wing beat frequency was accomplished by using a Barker and Williamson frequency meter (model 300) driven by a Fisher PR-6, 4 watt pre-amplifier with a response of 20-30,000 cycles per second. The input to the preamp was a dynamic microphone (Lafayette model PA-29) with a rated response of 50-1,000 cycles per second. The apparatus was calibrated audially by means of a tuning fork ($C = 523.3$ cycles per second) and electronically with an audio oscillator and oscilloscope.

Exploratory experiments involving the audio

measurements of wing beat frequency were conducted with D. pseudotsugae. Sources of Ips confusus were not available during the development of the technique.

The basic wing beat frequencies of the Douglas-fir beetle were obtained by mounting the specimen on a flight bar near the head of the microphone pickup. The beetle and the microphone were enclosed in a box of acoustical tile ("flight chamber") to reduce background noise. This was an especially important precaution since the wing beat frequencies obtained were close to the line frequency. During the tests, temperature and flight conditions were kept constant to avoid undue variations (4; 5, p. 11; 10; 11; 12; 29; 34; 39; 52; 71; 77). Test chemicals were presented to the flying insect by placing a drop of the substance on a glass rod and inserting the rod into the flight chamber. An aperture in front of the chamber accommodated the rod. The complete set up is shown in Figure 11.

Although this olfactometric technique was not completely perfected, its future use as a bioassay tool for isolation of attractive substances is indicated. A limited series of exploratory tests showed that there was a reduction of the basic wing beat frequency of D. pseudotsugae when flying beetles were confronted with female

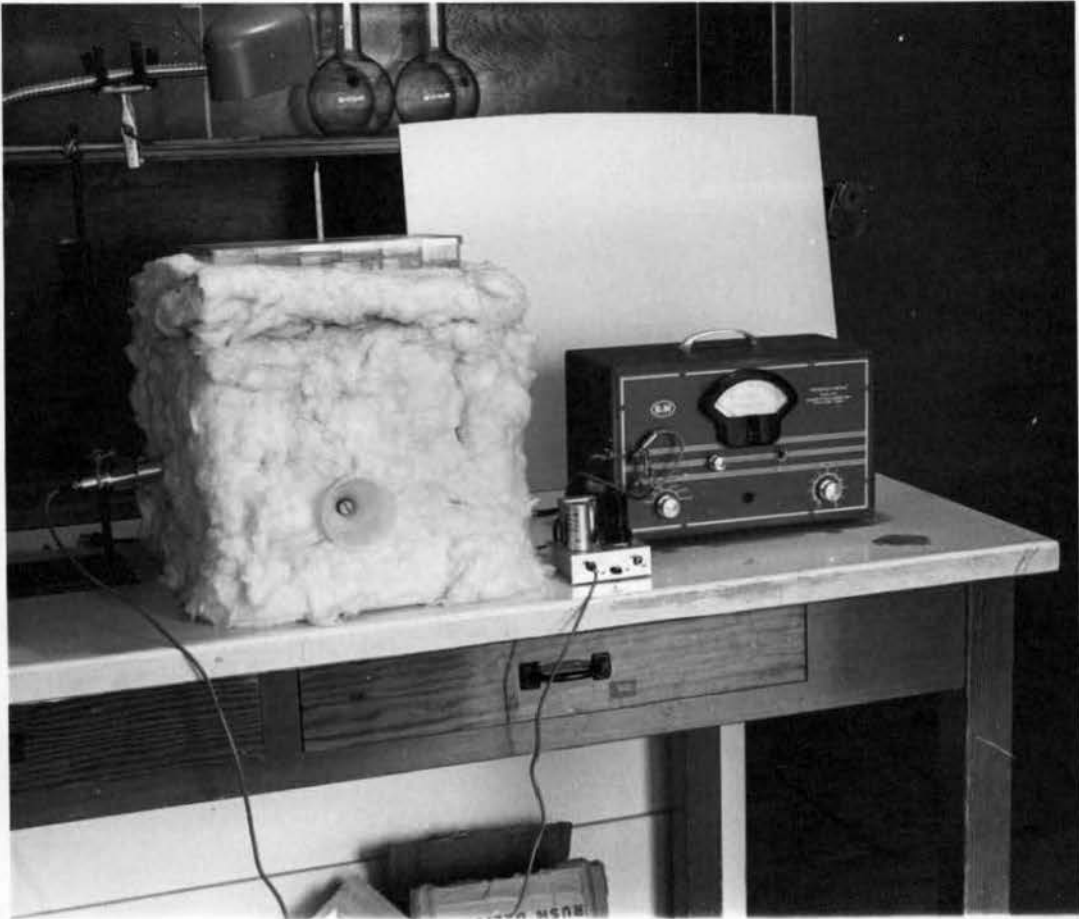


Figure 11. Laboratory olfactometer. From left to right: microphone inserted in soundproof flight chamber; output of microphone enters 4 watt preamplifier which leads into frequency meter. Top of flight chamber contains a window to admit light; water in plastic tray aids in maintaining constant temperature within chamber.

boring dust -- the substance known to be attractive to Douglas-fir beetles (74). The results of these tests are presented in Table 2.

Flight arena. A large hall, 27 meters long, 6.5 meters wide and 3 meters high, once a wash room for gold miners, was converted into a flight arena. All of the plumbing facilities were removed except those pertaining to the heating system. Several temperature and humidity regimes could be maintained, and wind movement was controlled by two large fans installed at one end of the hall and sliding panels installed at the other end. Lighting was controlled by plastering over the windows and white-washing the entire interior. Fluorescent lights in two continuous bars along the ceiling were then the only source of light.

Table 2. The average range of wing beat frequencies of four D. pseudotsugae in response to various test materials at a constant temperature of 22°C.

Test Material	Wing Beat Frequency (Cycles per Second)
Water	98 - 100
♀♀ Boring dust and water	84 - 95
♂♂ Boring dust and water	100 - 105
Oleoresin	100 - 102
Control	100 - 105

By positioning freshly baited field olfactometers in the hall, it was hoped the flight behavior of responding I. confusus could be observed.

Ips confusus, regardless of origin or previous conditioning, released under such conditions did not respond in any way to material known to be attractive. However, they did respond quickly and positively to any light source. This photic reaction was useful in determining the flight speed of I. confusus; a factor to be used in the field studies.

The free flight velocity was determined by darkening the hall except for a single light located at one end. Beetles were released, and their flight was timed over a measured course to the light source. To prevent the initial velocity (which is slower due to inclination of the insect's body (5)), from reducing the level flight velocity, the I. confusus were not timed until they had flown one or two meters. To prevent variation of velocity induced by inclined or zig-zagged flight, only those beetles flying straight and level to the light were measured. Fifty of the beetles flying the straightest course accomplished a 6.5 meter distance in an average time of 4.68 seconds or 1.3 meters per second. This is a velocity of

2.9 miles per hour; a speed considerably slower than velocities calculated for other scolytids (5; 17, p. 80; 57). This flight speed for I. confusus was also verified in the laboratory. A beetle was tethered to a flight mill, and an air stream was directed against it as it flew. It was found that head winds of approximately 1.3 to 1.5 meters per second, or 2.9 to 3.3 miles per hour would result in ground speeds of the insect approaching zero. With wind speeds greater than 1.5 meters per second, the beetles continued to fly but were blown backwards.

Captive beetles on balloons. Insects, the size of scolytids, flying over a meter per second are difficult to observe. It was thought that bark beetles could be observed more accurately as they responded to attractants if their presence were made more obvious and if their flight speed were decreased. As a matter of speaking, it was hoped that their flight behavior could be "observed in slow motion." To accomplish these ends, beetles were tethered to small helium-filled balloons. The balloons were filled with just enough gas that they floated only if the tethered beetle was flying. At first, the beetles were fastened to the balloons by a short length of nylon "fly tying" line. However, since the beetles merely flew in tiny circles

beneath the ascending balloon, this proved unsatisfactory. This problem was solved by gluing a small piece of balsa wood on the balloon and inserting a three-centimeter long capillary tube in the wood with the beetle attached to this rigid "harness;" the beetle could then fly in the direction in which it was stimulated to travel.

This method was initially tried in the flight arena with a group of D. valens, each attached to its own balloon. An olfactometer baited with fresh resin (attractant for D. valens) was placed in the arena and the "squadron" was released. The position and direction taken by each beetle was easily observed; each, however, navigated its balloon to the nearest light source.

The balloon technique was subsequently attempted in the field, but the most imperceptible wind destroyed the operation.

Attaching beetles the size of Ips confusus to balloons was totally unsuccessful, in that these insects could not pull the balloons against the air resistance.

Flight cage. Since I. confusus only responded to light sources in the flight arena, it was hoped that additional response patterns could be investigated by flying the insects in an outdoor flight cage. The flight cage

was made by screening a 3 x 3 x 3 meter frame with 18 mesh screen. The bottom of the cage was a concrete slab.

For response tests, the cage was equipped with a field olfactometer which blew air containing the attractants toward the ceiling of the cage. A small version of the beetle launcher from which the beetles were released was located in one corner of the cage (Figure 12). Beetles thus released inside the cage flew against the screen before they could respond to the olfactometer. Those on the ceiling began crawling to the brightest corner without any further inclination of flying to the olfactometer. Some of the beetles on the walls of the cage continued to fly but soon were similarly sitting in a bright corner.

Instrumentation techniques for measuring environmental factors. Wherever possible, flight behavior studies were conducted with a knowledge of the prevailing light, temperature, wind, and moisture conditions. Even though attractants were found to be the dominating stimulus guiding concentration flights of I. confusus (35), other environmental factors were important in initiating, maintaining, and routing these flights.

Temperature and relative humidity. Temperature and



Figure 12. Flight cage with olfactometer in center.

relative humidity were recorded daily in the experimental forest by two spring-wound hygrothermographs, made by the Foxboro Company. These instruments traced the hourly temperature (degrees centigrade) and relative humidity on circular charts. Each chart represented a week's recording. One hygrothermograph was located near the outdoor insectary in order to predict emergence and flight conditions. The other apparatus was positioned in the field.

Immediate temperature conditions were recorded by a Taylor minimum-maximum mercury thermometer.

Wind direction and velocity. Wind velocity and direction in the Grass Valley area were periodically obtained from two rotary-anemometers -- one recording 14 feet elevation winds, the other 100 feet elevation winds. Wind direction was also frequently estimated by observing the direction smoke drifted from an ignited smoke candle or by the position of a wind vane.

For instantaneous and extremely accurate wind speed measurements, a thermal anemometer was used (Figure 13). This was a portable, battery powered instrument with the sensing element connected to the indicator by a wire of



Figure 13. Thermal anemometer showing sensing wand attached to main chassis by means of 30 meter cord. Meter is calibrated to read air movement of 0.02 to 3 meters per second.

any desired length. With this arrangement, the sensing element could be elevated to measure wind velocities in the crowns of trees -- up to 30 meters. The device could detect air movement from 0.02 to 3 meters per second.

RESULTS OF STUDIES ON RESPONSE TO ATTRACTANTS

Investigations on Response Behavior

The small size of bark beetles has made observations of their response flight difficult for more than 100 feet (57, p. 47). As a result, previous field investigations depended on observations of flight immediately after emergence or upon beetles flying toward an infested host (57). The activity of beetles between these two points has merely been speculated upon by lack of more concrete observations. However, with techniques developed for this and other studies (16, 17, 18, 19, 20, 21, 35, 74, 90, 91), more direct approaches can be taken in the investigation of scolytid flight behavior.

Preliminary investigations. Before investigating some of the major environmental factors affecting response flights, a series of experiments was conducted to get a general impression of the take-off and subsequent response of Ips confusus. In addition, it was essential to know if locating attractive material in various parts of the forest would greatly increase the beetle population at these points, and thus endanger the surrounding stand.

Take off and landing. By attracting I. confusus to

field olfactometers over short distances such as three to eight meters, it was possible to observe the total flight of individual beetles from take-off through the subsequent response-flight and to the landing in or at the olfactometers.

These tests were performed by placing three olfactometers in three separate circles of 3.5, 5, or 8 meters radius respectively. Beetles were released from the center of each of these circles. There was no need to mark the beetles since their entire flight and landing could be observed.

Under wind conditions of less than 0.3 meters per second, the beetles took off in all directions and rose to a height of about 10 meters. At that time, in the five meter radius circle, many of the insects literally dove into the nearest olfactometer funnel. In circles of olfactometers of other radii, the beetles tended to circle the funnels before diving into them. With winds of 0.3 to 1.0 meters per second, the beetles took off predominantly with the wind, and they rose to a height of about 10 - 15 meters. However, in all test circles, the beetles sooner or later turned, oriented themselves against the wind and then flew back toward the sources of attraction. With

higher winds of 0.8 to 1.5 meters per second prevailing, it was noted that the beetles took-off lower, many almost hugging the ground, in the direction of the wind. After a few moments, low flying beetles were seen returning in the direction of the olfactometers. Most of the beetles did not enter the funnels but hit the sides and base and fell to the ground or lay on the flat surfaces of the olfactometers.

The role of take-off height in respect to orientation and subsequent response to attractants was also demonstrated with the flight cage. One hundred marked I. confusus were released inside the cage which contained a field olfactometer blowing attractants toward the top of the enclosure. The wind, at the time of release, was about 0.1 meters per second. The flight carried most beetles to the ceiling of the cage where they crawled about with no further flight attempts. These beetles were carefully collected and re-released outside the cage, five meters from the field olfactometer. Within 3 minutes, 27 percent of the beetles which did not respond within the cage were found sitting on the outside of the screen, directly over the field olfactometer. In addition, members of the field population readily aggregated to the same area.

Pattern of concentration. From field observations it is well known that recently infested trees, whether cut or standing, are frequently responsible for the subsequent attack of neighboring trees as a result of an increased population level due to mass attraction (26, 43, 44, 48, 57). It is not entirely understood, however, whether this phenomenon is a result of the limited brood material represented by the originally infested tree, or of a host selection habit of bark beetles. In view of the possible danger to the surrounding stand, it was determined whether or not the attraction of I. confusus led to an increase of the population level throughout the area in which the testing took place.

This experiment was carried out by first finding a 12 inch (Dbh) tree that had been recently infested with I. confusus and was thus highly attractive. This tree was cut into about 30, 10-inch blocks and placed in an upright, sheet metal cylinder which contained a 1/4 horsepower exhaust fan in its upper opening. The air blown from this fan was directed towards an aerial net rotating directly above the cylinder containing the infested log sections. Three concentric circles were measured around the attractive center, each having radii of 15, 30, and 45 meters

respectively. Four aerial nets were positioned in cardinal directions around the periphery of each circle in order to sample the beetles responding to the center. After six hours of operation, it was clear that attacking I. confusus concentrated their flight directly toward the attractive source (Figure 14). Of the 1,244 beetles caught, 1,065 were trapped in center, 134 in the inner circle, 45 in the 30-meter circle, and 0 in the outer circle.

This experiment points out that I. confusus focus their flights directly on a source of attraction. They produced little increase in the population 30-45 meters away from the source.

Factors affecting response behavior.

Intensity of attraction. While working with attractive materials at two different locations (500 meters apart) in the experimental forest, the effects of competing attractive sources were noted. When more I. confusus attractants were used in one station than the other, the most highly attractive station attracted more beetles. But even more interesting, the number of beetles caught dropped markedly at the station with the weaker attraction. In order to obtain more quantitative data on this

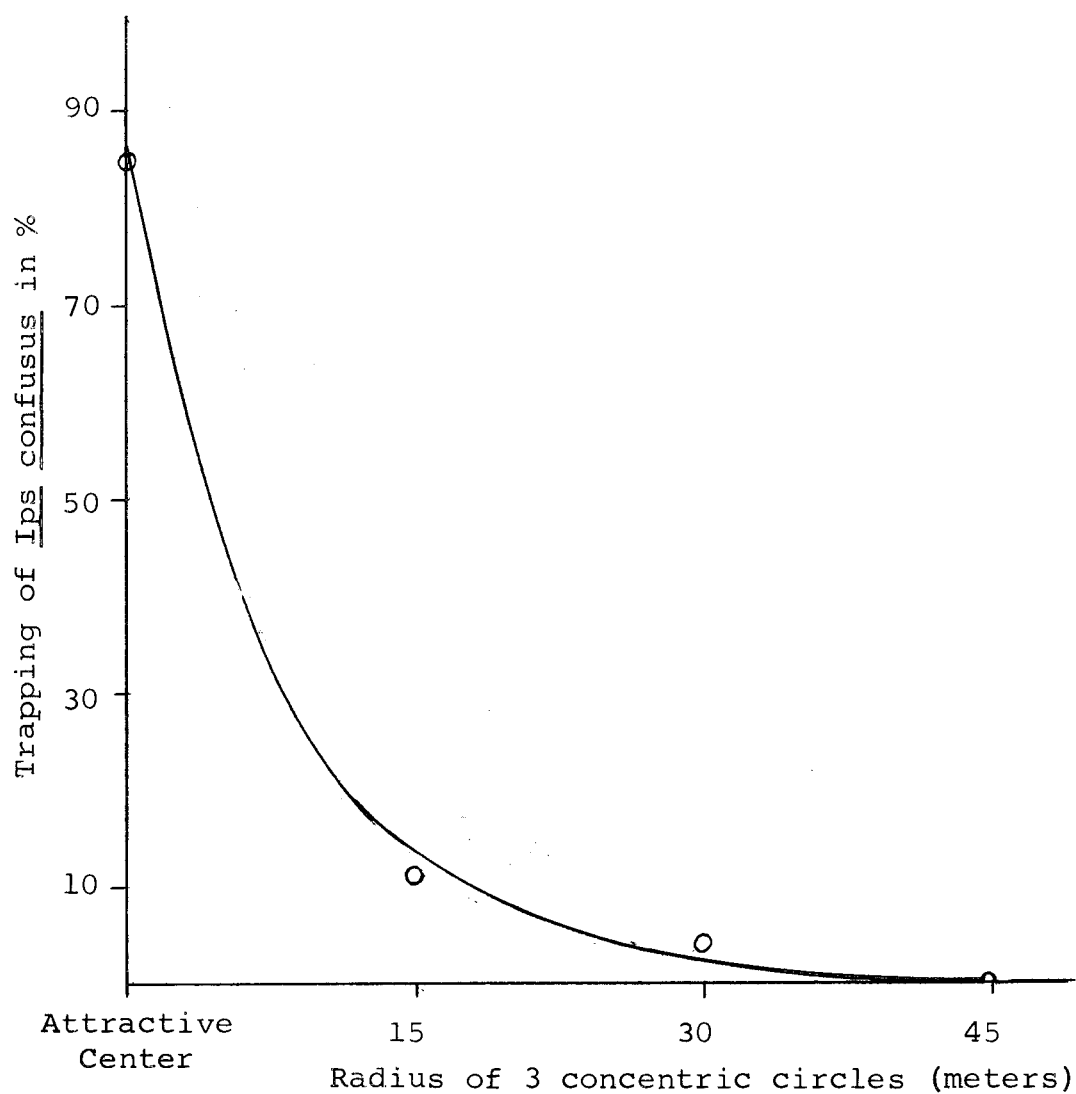


Figure 14. Distribution of *Ips confusus* caught by a rotary net located above an attractive center and in rotary nets placed in three concentric circles from the center -- four nets per circle.

phenomenon, five field olfactometers were set up at each location. Two small, freshly-infested trees were cut and divided into 40, 10-inch sections. This material was alternated between the two stations by placing 30 sections, for a 2-hour period, in the olfactometers at the first station and 10 sections in the olfactometers of the second. This switching of the material from one station to the other was done for 10 hours, with a 1-hour pause to transfer the materials between each test. To minimize the effects of different cover conditions and the accompanying variations in environment, both locations were chosen in the same stand of second growth ponderosa pine. The results (Table 3) indicate that the flying population concentrates in greater numbers to the strongest source of attraction.

The relationships between the actual number of I. confusus attacking ponderosa pine and the intensity of attraction was studied in additional tests. Fresh log sections of 9- to 12-inch diameter and 2-feet long were cut from the same tree. The sections were infested with various numbers of mature male beetles -- ranging from 1 beetle in a log to 100. The logs were then placed in 6 olfactometers, 1-6 beetles in one series and 6-100 in

Table 3. Number of Ips confusus caught in field olfactometers at two stations, 500 meters apart.

Time	No. of Freshly Infested Logs		No. of Beetles Caught	
	Station	Station	Station	Station
	1	2	1	2
0800-1000	30	10	98	33
1100-1300	10	30	18	44
1400-1600	30	10	81	29
1700-1900	10	30	295	440
2000-2200	30	10	310	220

another series. Each series was run four hours, and the results are presented in Figure 15. These results indicate a rapid increase in attractive power when the number of attacks by male Ips was greater than two. In the intensity of attack from 6-100 beetles, a similar rapid increase in concentration was noted, however in this case on a higher level; this indicates that the more highly attractive sources drew beetles from a larger area.

To study the influence of natural sources of attraction on a known population, tests were conducted in the Boyce Thompson Experimental Forest (endemic area), at the Nevada City Airport (epidemic area), and on the Sierraville prairie. The tests were designed to evaluate the extent to which natural infestations influence the response of

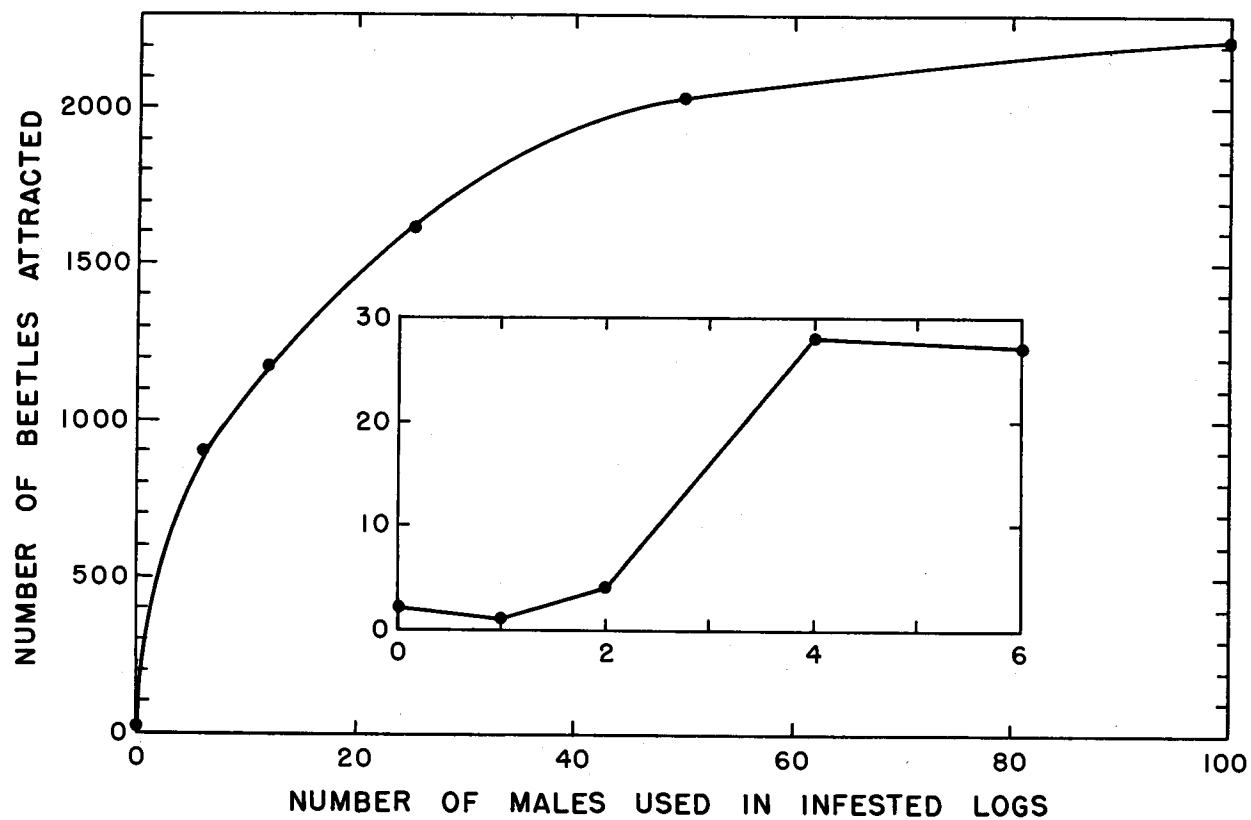


Figure 15. Influence of the number of Ips confusus males inserted on the attractive power of artificially infested logs.

released Ips confusus flying over long distances. For this purpose, freshly baited field olfactometers were located at 100, 500 (450 in epidemic area), and 1000 meters upwind from the point where marked beetles were released. The test beetles were I. confusus that had been previously gathered from olfactometers.

Even though these experiments were conducted on different days with different weather conditions, the results (Table 4), nevertheless, indicated that the smallest percentages were recovered in the epidemic area.

Intensity gradient. Previous studies have shown that beetles accumulate in the largest numbers at sources with the strongest attractants. It has also been suggested that marked beetles released in areas with high amounts of natural attraction are not readily re-captured in olfactometers. However, the actual mechanism of selecting an attractive source was still in doubt. Do beetles respond to the closest attractive source, or do they actually follow an attraction gradient to the most intense source?

In order to establish whether I. confusus follows an olfactory gradient during host selection, the following experiment was performed. Nine olfactometers were set on

Table 4. Response of Ips confusus when released in areas with different degrees of infestation.

Site of Test		Distance Travelled to Olfactometers, Meters	Number of Beetles		Recovery %
Location	Infestation		Released	Recovered	
Nevada City Airport	High	100	692	55	8.1
		450	722	15	2.1
		1000	522	0	0
B. T. I. Exp. Forest	Low	100	454	54	12.0
		500	1430	157	11.0
		1000	708	9	1.3
Sierraville Prairie	None	100	510	52	10.2
		500	413	39	9.5
		1000	400	8	2.0

a line parallel to the prevailing wind direction at intervals of eight meters. Log sections placed in the central olfactometer were infested with 250 male beetles while those to either side contained 100, 37, 25 and 8 beetles. Beetles marked with different colors of dye were released simultaneously at each end of the line. Each release was 15 meters from the nearest olfactometer. Once the test beetles were flying, the olfactometers were checked in three-minute intervals for 18 minutes, and, as the marked insects responded, their time of arrival was noted. In addition, the presence of the unmarked beetles was noted. The results (Table 5) indicate that the beetles released downwind responded against the wind along an olfactory gradient. Even though most of the beetles responded to the strongest source of attraction in the centrally located olfactometer, some overlapped into the upwind end of the line.

While the beetles released upwind responded in a similar pattern to those released downwind, they arrived at the olfactometers somewhat later. This suggests that in spite of having a tailwind, they, too, must have responded against the wind. The pattern of beetles responding from the field population was similar to the marked beetles,

Table 5. Recovery of responding Ips confusus when simultaneously released at the upwind and downwind ends of an attractant gradient. Also shows flight flight time of test beetles and distribution of responding field beetles.

Olfactometer Stations		Recovery of Beetles Released, %		Average Time of Recovery after Release, Minutes		Capture of unmarked Beetles, % of Total (field population)
Location	No. of Beetles in Log	Marked Blue Upwind	Marked Yellow Downwind	Upwind	Downwind	
1 (upwind)	8	0	0	-	-	4.3
2	25	3.3	1.6	12.0	12.0	21.0
3	37	5.0	3.2	12.0	9.0	15.9
4	100	0	0	-	-	10.3
5	250	16.4	17.5	13.5	9.0	21.0
6	100	1.7	1.6	-	-	14.7
7	37	0	0	-	-	4.4
8	25	0	0	-	-	1.7
9 (downwind)	8	0	0	-	-	.8

indicating response against the wind toward the strongest attraction.

Wind direction and velocity. The effect of wind on the response behavior of I. confusus has been observed in preliminary experiments in which beetles responded over short distances. Further experiments were conducted to establish whether or not the beetles continued to respond against the wind, even when the attractants were placed at longer distance from the release point. In one series of tests, six olfactometers were placed throughout a ponderosa pine stand at equal distances along the perimeter of a circle which had a radius of 500 meters (Figure 16A). Marked beetles were released from the center of this circle whenever rather constant winds prevailed. However, the only winds tended from the west and the south blowing at .10 - .75 meters per second (.2 - 1.7 miles per hour). Beetles released in a westerly wind indicated a preference for the olfactometer situated west of the release point. With the wind from the south, the beetles preferred the most southerly olfactometer. In addition, in both releases, the marked beetles also responded to olfactometers in all other directions (Table 6). The subtle shifting of low velocity winds as well as the flight habit of I. confusus

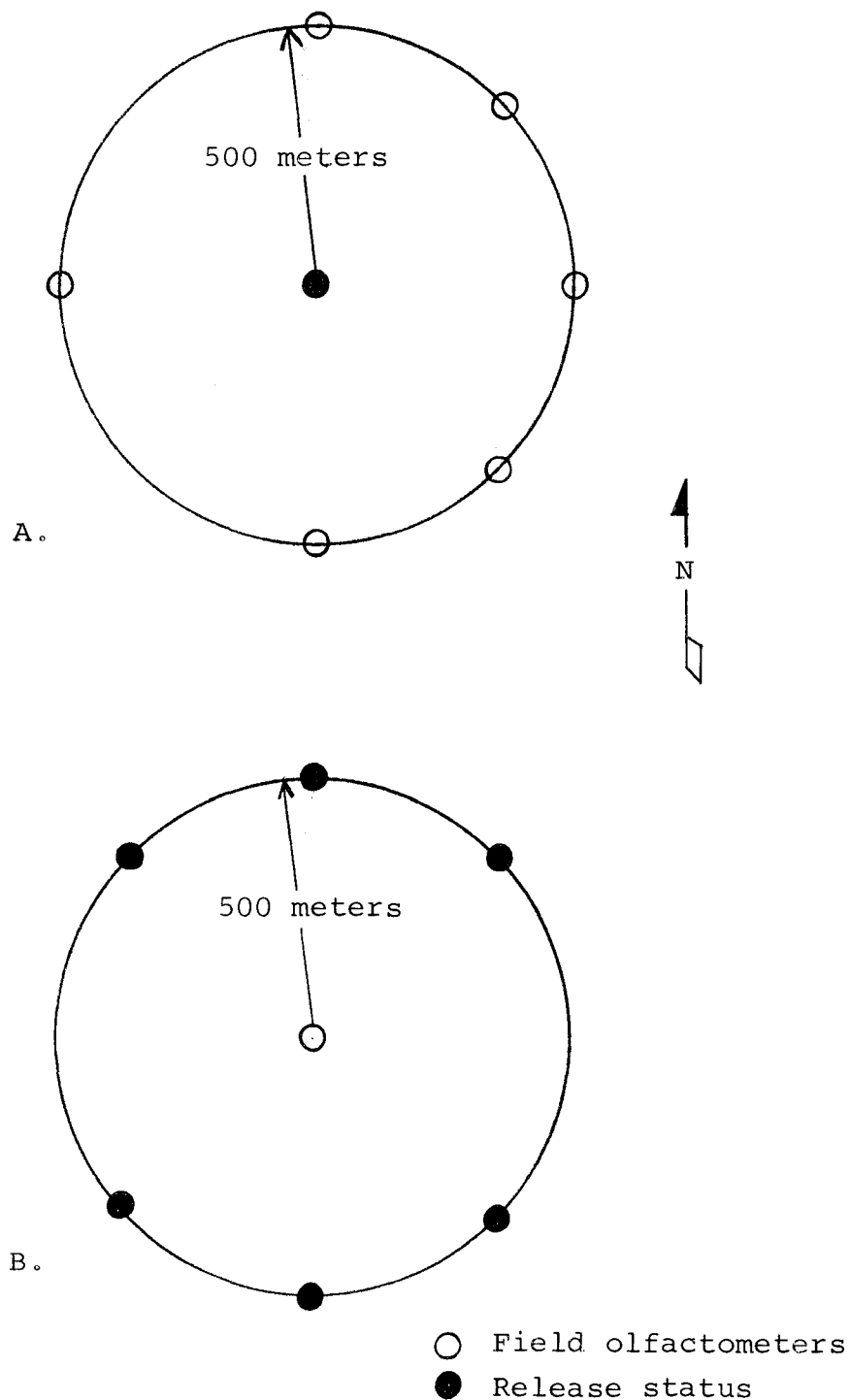


Figure 16. Diagram of two release and attraction set-ups: (A) release point in center of circle with six olfactometers around periphery; (B) six release points around periphery of circle with olfactometers grouped in center.

Table 6. Recovery of marked Ips confusus released at the center of a 500-meter radius circle of olfactometers.

Wind Direction	Location of Olfactometer from Point of Release	Marked Beetles Recovered	
		Number	Percent
West	North	24	15
	Northeast	17	11
	South	22	14
	Southeast	29	19
	East	19	12
	West	46	29
South	North	8	06
	Northeast	7	05
	South	51	41
	Southeast	30	24
	East	12	10
	West	18	14

to take off after release in all directions, but preferably with the wind, may explain this observation.

Another experiment was arranged with six release stations around a circle of 500-meter radius that contained an attraction center consisting of three closely spaced olfactometers (Figure 16B). At the time of the experiment, a wind of about .8 - 1.0 meters per second prevailed from the southeast. The results of the releases (Table 7) again revealed that insects responded best against the wind

Table 7. Recovery of marked I. confusus released from the periphery of a 500-meter radius circle. Response was to three olfactometers in center of circle.

Location of Release Point from Source of Attraction	Marked Beetles Recovered	
	Number	Percent
North	4	23.5
Northeast	1	6.0
Northwest	8	47.0
South	0	0
Southeast	0	0
Southwest	4	23.5

direction. The ones released with the wind probably flew past the attraction center and subsequently responded up-wind. The total beetle recovery in this test was low due to gusts of strong winds and to the fact that peripheral releases are less effective than releases within an olfactometer circle.

Additional tests were made in the Sierraville prairie where strong but constant west winds prevailed. In these tests three olfactometers were set up as a "T", each being 500 meters from the center. One olfactometer was directly south of the center, the other two were due east and west from the center. Unmarked beetles were released from the center of the "T" in wind speeds that seldom were less than one meter per second (two miles per hour). Frequently, the

wind approached or surpassed the flight speed of the insects (1.3 meters per second) .

Upon release, the insects took off with the wind and flew only a few feet from the ground. When responding, the beetles actually did not enter the funnel of the olfactometer but rather hit the basal portions and were either gathered from the ground or from the top of the bait box.

The results of these tests (Table 8) show that most of the beetles responded to the most eastern olfactometer, but occasionally to the western one when lower wind speeds prevailed. Even though the beetles responded in greater numbers to the eastern olfactometer, the time differential from release to response indicated a response against the wind. If the insects would have responded with the wind, then they would have arrived at the eastern olfactometer within a time period relative to the existing tail wind plus their flight speed. Because the beetles took up to 50 minutes in apparently traversing only 500 meters indicates that they were blown past the attractant source and responded back against the wind. Since there were intermittent periods of decreased wind speeds, those beetles with the most endurance finally reached the attractive source.

Table 8. Recovery of I. confusus released in the Sierra-ville prairie. Released from center of three olfactometers positioned 500 meters east, west, and south of release point.

Time of Release	Beetles Responding to East, West, or South Olfactometer	Speed of West Wind Meters/Sec.	Time of Response
1210	--	1.0 - 1.9	--
	2 (East)	1.2 - 1.9	1227
1250	--	1.0 - 1.3	--
	3 (East)	1.0 - 1.3	1304
	4 (East)	1.0 - 1.3	1305
	3 (East)	1.0 - 1.3	1311
	3 (West)	1.0 - 1.3	1314
	8 (East)	1.0 - 1.3	1315
	5 (East)	.9 - 1.0	1323
	2 (West)	.9 - 1.0	1340
	2 (East)	.9 - 1.0	1350
1935	--	1.5 - 1.7	--
	1 (East)	1.3	1947
	8 (East)	1.2 - 1.5	1948
	1 (East)	1.2 - 1.4	1950
	1 (East)	1.5 - 1.6	1952
	2 (East)	1.2 - 1.3	1956

The influence of wind velocity on vertical distributions of I. confusus was studied in more detail by means of three olfactometers. These small olfactometers were hoisted between two trees to different heights ranging from ground level to 30 meters. The wind velocity was measured

every half-hour at the level of each olfactometer with the thermal anemometer. Every hour, the olfactometers were lowered, and the number of responding beetles was determined for each elevation. The results of five days' observations are presented in Table 9.

Frequently the ground level, as well as the highest crown region, exhibited the lowest winds and the beetle densities were correspondingly higher in these areas. When relatively high winds prevailed (1 to 1.5 meters per second), the response was restricted practically to ground level.

Time of day. It was previously established that I. confusus respond to attractants in a definite diurnal pattern (35, p. 284). This is also the case of D. pseudotsugae (74, p. 31). However, all of these studies were performed in early summer.

To prove whether or not the diurnal rhythm of I. confusus varies as the season progresses, the diurnal response was ascertained for mid-August. This was accomplished by recording the hourly catches of five olfactometers from dawn to dusk. As shown in Figure 17, the August diurnal response pattern was similar to the one in July and, likewise, appeared to be temperature dependent.

Table 9. Response of Ips confusus to attractants at different elevations above ground line.

Range of Wind Speed, Meters per Second	Average Wind Speeds (Meters/Second) and No. Beetles Caught per Hour at Four Elevations							
	Ground Level		10 Meters		20 Meters		30 Meters	
	Wind	Beetles	Wind	Beetles	Wind	Beetles	Wind	Beetles
0.1 - 0.3	0.1	84.5	0.3	12.0	0.2	6.7	0.1	13.7
0.4 - 0.6	0.4	27.3	0.6	7.0	0.5	17.3	0.4	26.0
0.7 - 0.9	0.7	21.0	0.8	4.3	0.7	5.7	0.7	7.0
1.0 - 1.2	1.0	18.0	1.1	3.0	1.0	4.0	1.1	3.0
1.3 - 1.5	1.3	24.0	1.5	2.5	1.5	0.5	1.4	0.5

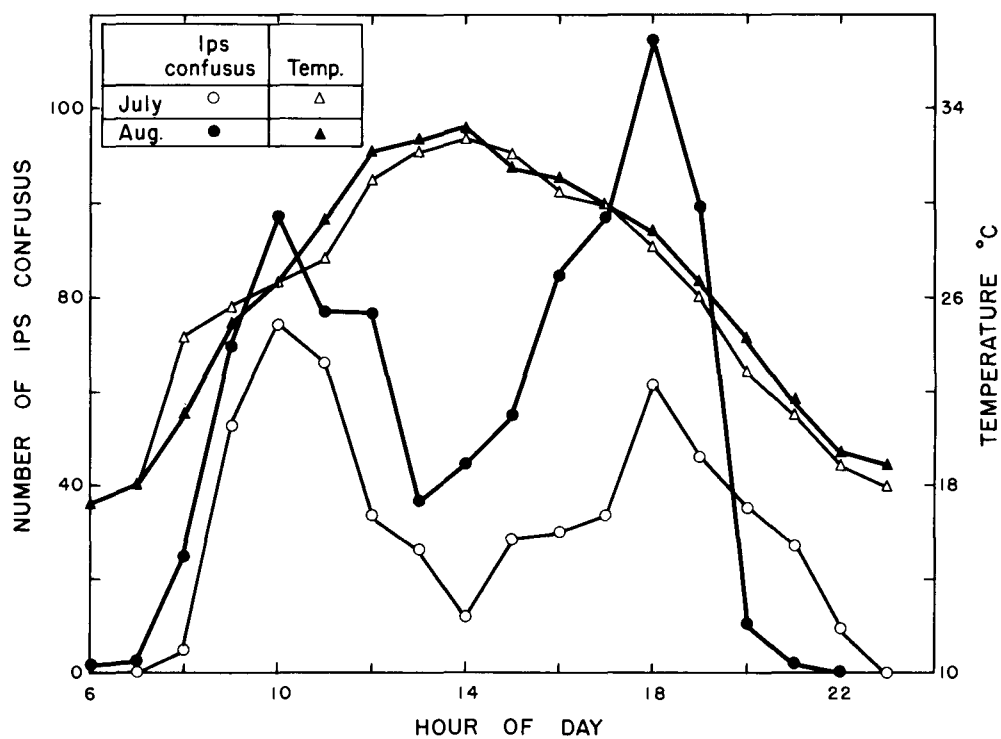


Figure 17. Diurnal response of Ips confusus to attractants on two different dates.

Ips confusus initiated flight in the morning at 19°C but drastically interrupted its response to baited olfactometers as soon as the early afternoon temperature rose above 28°C, but again responded in the evening with the declining temperatures.

The existence of a diurnal response rhythm was also demonstrated by releasing marked beetles. Beetles were gathered hourly from the insectary, marked with fluorescent dye, and released within a circle of olfactometers of five meter radius. These beetles presented a diurnal response pattern similar to the field population: the response was best in the morning and the evening; but even during the mid-day hours, the beetles responded in appreciable numbers to the olfactometers (Figure 18).

Light and temperature. Field and laboratory studies have clearly pointed to the importance of light and temperature in initiating, sustaining, and ending scolytid flights (4, 5, 17, 18, 20, 35, 57, 60, 73, 74, 75, 76, 80, 91). It has been shown that flights of I. confusus occurred only when the temperature averaged over 15°C, while later in the season, the flights were limited by temperatures over 20°C (35).

Through the placement of aerial net traps in various

○ Ips confusus
● Temperature

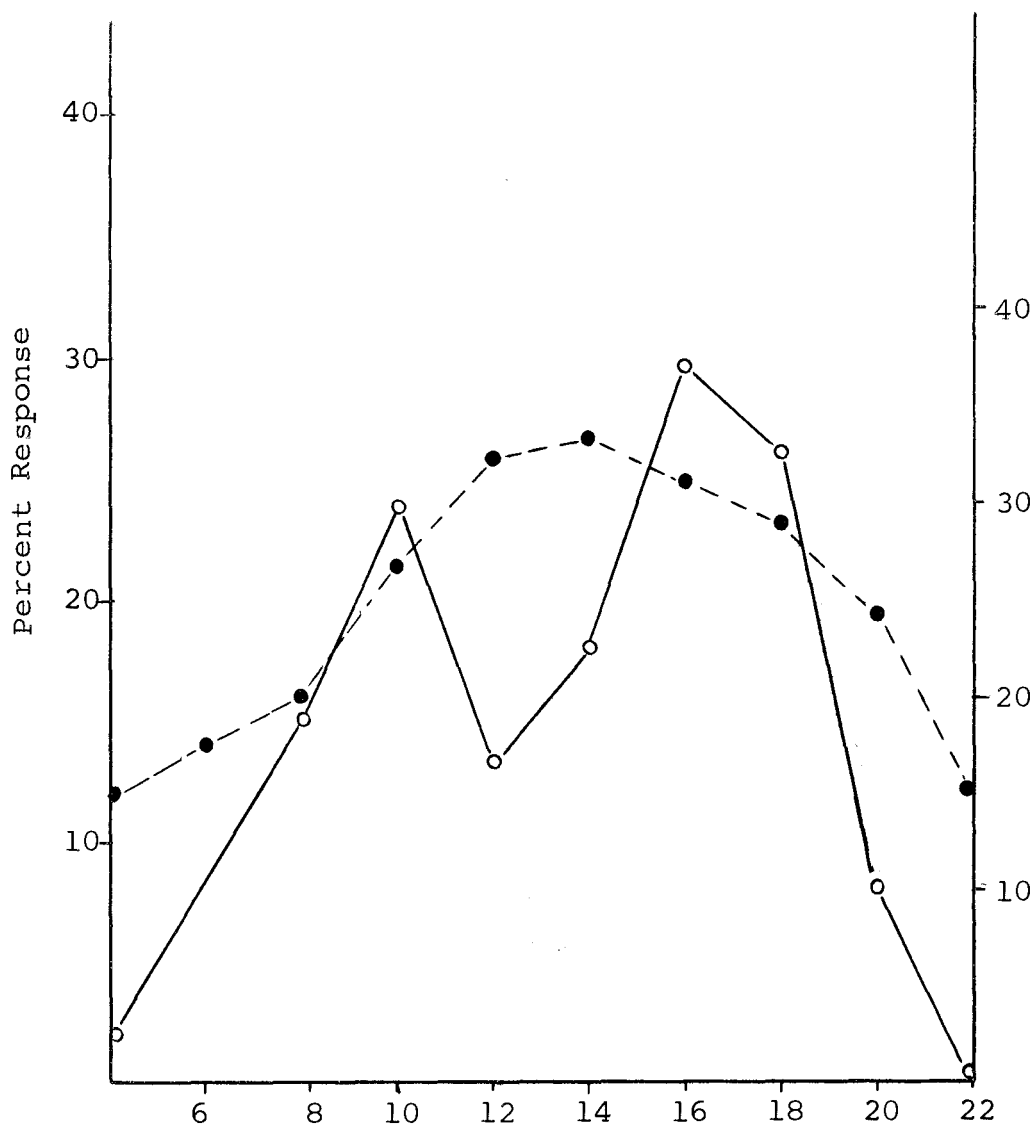


Figure 18. Diurnal response pattern of Ips confusus released from center of circle of olfactometers with a 5-meter radius.

localities in the forest, it was evident that I. confusus preferred to fly in shady places. Small openings seemed to be avoided as few beetles were caught, while the highest number of beetles were caught just inside the stands at the borderline of openings. The preference of beetles to fly just inside the edge of a stand has also been expressed for Ips typographus (73, 81).

Although light and temperature have been shown to determine the flight season and dominate the diurnal flight pattern to a large degree, these two factors together with all other orienting stimuli seemed to become suppressed as soon as attraction was encountered. Both I. confusus and D. brevicornis were found to respond to olfactometers in places where flight did not normally occur (35). This behavior was reaffirmed by releasing I. confusus under prairie conditions where they were exposed to direct sunlight and yet they responded in numbers comparable to responses under endemic forest conditions (see Table 4).

An even more conclusive experiment on the completely overpowering attraction power of the male pheromone occurred when I. confusus were attracted to their death. A

series of olfactometers were placed on an exposed rock dump consisting of highly refractive material that produced such high temperatures that collection of the responding beetles was almost prohibitive. Indeed, the insects continued to be attracted even though contact with the metal surfaces of the olfactometers immediately killed them.

Investigations on Response Ability

Background. Recent reviews of man's knowledge of the food-plant perception of insects have been provided by several authors (23, 24, 50, 72, 87). These accounts have highlighted studies showing the apparent intimate association between olfactory response and flight activity of phytophagous insects. Kennedy (50), working with alate aphids, proposed the hypothesis that, during the dispersal flight, the thresholds of stimuli generated or reflected by the host plant are lowered to a level at which the insect becomes responsive to these chemotactic signals.

Early observations on bark beetles also established a concept of alternation of events during host selection. Keen (57), observing D. brevicornis, revealed that the emerging beetles tended to move away from the vicinity of

parental host trees. It was even suggested that the western pine beetle may delay 3 to 26 days from emergence to re-attack; presumably the insects were flying and resting during the interim (57). Apparently, this driving dispersal tendency was above the threshold of attraction provided by adjacent susceptible breeding material. Such observations are in accord with the theory that the first flight activity is in response to light and temperature stimuli, regardless of neighboring chemotactic stimuli (37, 57, 87).

Graham (37, 38) demonstrated that freshly emerged Trypodendron lineatum are extremely photopositive and have a compulsion to fly to the nearest light source. He found that only through "flight-exercise" was the over-ruling response to light abolished, and only then would the insects favorably respond to their host material. Graham (38, p. 519) points out the ecological significance of this behavior by stating: "Evidently the photopositive response which initially compels it, advantageously, to dispersive flight indirectly sponsors termination of flight and unmask a latent responsiveness to host factors, allowing it to settle down." The mechanism for photic reversal of T. lineatum through "flight-exercise" was found to be

the intake of air into the ventriculus (38). In support of this conclusion, it was demonstrated with stored beetles: "that the unflown beetles are strongly photopositive; that through prolonged flight, but not without it, they become indifferent or negative to light; that accumulation of gas in the gut accompanies the change, and the change is always associated with the gas; that deflation restores the photopositive response; and that artificial inflation is effective in abolishing the photopositive response (38, p. 520)." Photic reversal through physiological preconditioning, followed by feeding, has also been discussed regarding other insects (17, 45, 50, 64, 65, 72).

Factors affecting response ability.

Physiological condition of the insect. With ample background work on the sequence of events necessary to predispose insects to respond to their hosts, it was of interest to see how different physiological conditioning would affect the ability of I. confusus to respond to attractants.

In a preliminary series of tests, the relative ability to respond to attractants of freshly emerged beetles was compared to those already in flight that had been

collected as they responded to bait traps. These two groups will henceforth be referred to as emerging and responding beetles, respectively. These comparative tests were conducted by releasing differently marked emerging and responding beetles from the center of a circle of olfactometers. These devices were set up equal distances apart along the periphery of a circle of 50-meter radius.

This experiment was replicated four times. The results showed that out of 469 emerging beetles that flew, 28 responded for a 6.0 percent return. However, from the 952 responding beetles released, 156 were recovered for a 16.4 percent return. These results were perhaps anticipated since the responding beetles had already experienced a period of flight exercise while the emerging beetles were fresh from the cages.

In an effort to investigate further the ability of I. confusus in various physiological conditions to respond to attractants, five olfactometers were set up around a circle of five meter radius. For this series of experiments, the test insects were divided into six groups: the first were emerging beetles collected from cages; the second, responding beetles collected from field olfactometers; and the third portion consisted of beetles gathered from cages

several days after their emergence. The latter group appeared to be photonegative since they preferred to bore into bark crevices and other debris rather than to fly to the light-exposed screen of the cages. In addition, three other groups of emerging beetles underwent various treatments. The first treatment consisted of dehydrating the insects for six hours in an air-tight box by means of silica gel. Dehydration was suggested as a photo reversal mechanism by Finnish workers (64). In another treatment, the insects were flown on a flight mill for two hours; in the last treatment, the insects were rotated in an aerial net for half an hour. Fifty beetles were selected from each of these six groups. Each group of beetles was marked with a different fluorescent dye shortly before they were simultaneously released from the center of the test circle. This experiment was performed only twice because of the large amount of time and labor involved in obtaining 50 beetles capable of flying 2 hours on the flight mill. It was also difficult to get 50 intact beetles after they had rotated half an hour in the aerial net. The results are presented in Table 10.

It appears that at relatively short distance of five meters emerging and responding beetles respond in similar

Table 10. Response of six groups of Ips confusus, each representing different physiological preconditioning. Beetles were released from center of olfactometer circle of five meter radius.

Preconditioning of Group	Flight Positive %	Flight Negative %	Recovery of Beetles Rel. %
<u>Emerging</u>	83	17	26.0
<u>Responding</u>	94	06	23.0
Photonegative	62	38	19.0
Dehydration	78	22	12.5
Preflown on flight mill	84	16	19.0
Rotated in net	77	23	26.0

proportions. Rotating in the net did not seem to hamper response although their ability to fly was reduced; most likely the wind pressure against the net imperceptably damaged many of the beetles. Possibly, the effects of fatigue can be seen in the group preflown on the flight mill as well as the photonegative group since only 19 percent of each group responded. However, the greatest effects of exhaustion were seen in the dehydrated group.

Distance of attraction. Emerging and responding beetles revealed marked differences in their response to olfactometers. As was already noted, responding beetles respond in larger numbers over distances of 50 meters than

emerging beetles, while at 5 meters both their responses were similar. This investigation was pursued further in order to determine to what extent the degree of response changed in relation to distance between the point of release and the bait trap. For this purpose, five field olfactometers were alternately set up in circles of 3 to 2,000 meters in radius. Again, the emerging and responding beetles were marked with different colors of fluorescent dye to differentiate them from each other and the field population. The beetles were subsequently released from the center of each olfactometer circle. After each series of releases the radius of the circle of olfactometers was increased.

The results presented in Table 11 indicate that the beetles which had responded previously responded again in greater proportion, when attracted at a distance of over 25 meters, than freshly emerged beetles. Little differences existed, however, in the response of emerging and responding insects over shorter distances; in a test circle of 5-meter radius, the emerging beetles even responded slightly better than the responding insects.

Heterogeneity of response behavior. The variability between individual beetles to respond to attractants, as

Table 11. Recovery of emerging and responding Ips confusus in olfactometers placed in a circle around release point. Radius of circle was increased after each release.

Distance of Olfactometers From Release Point, Meters	<u>Emerging</u> Beetles		<u>Responding</u> Beetles		Recovery, %	
	Number Released	Number Recovered	Number Released	Number Recovered	<u>Emerging</u> Beetles	<u>Responding</u> Beetles
3	985	183	987	188	18.6	19.0
5	1015	286	1362	364	28.2	26.5
10	907	187	324	84	26.0	20.6
25	1868	294	2464	418	15.7	17.0
50	469	28	952	156	6.0	16.4
100	173	4	227	27	2.3	12.0
500	484	7	1430	157	1.4	11.0
1000	287	2	708	9	0.7	1.3
2000	800	0	764	1	0	0.13

exemplified by the superior response of beetles previously selected for this trait, was investigated in additional experiments. Both emerging and responding I. confusus were marked and released within a circle of olfactometers of 25-meter radius. Both groups of beetles were then collected carefully from the olfactometers and released again. This process was repeated three more times. As shown in Figure 19 (representing averages of 3 separate tests), the initial response of the newly emerged beetles was approximately equal to that of the responding beetles. After that, continued release and recapture demonstrated that after each release, proportionally fewer recently emerged beetles were captured than responding beetles. This indicates that the emerging beetles contained a greater percentage of individuals with a lower capability to respond than the group of responding insects. From the results, one could also postulate that if the better responding beetles of the emerging population were separated, they should perform as well as responding beetles.

For this purpose, 1,000 marked emerging beetles were released and re-released within a 25-meter circle of olfactometers. This process was continued until 50 percent of the residual population responded. These remaining

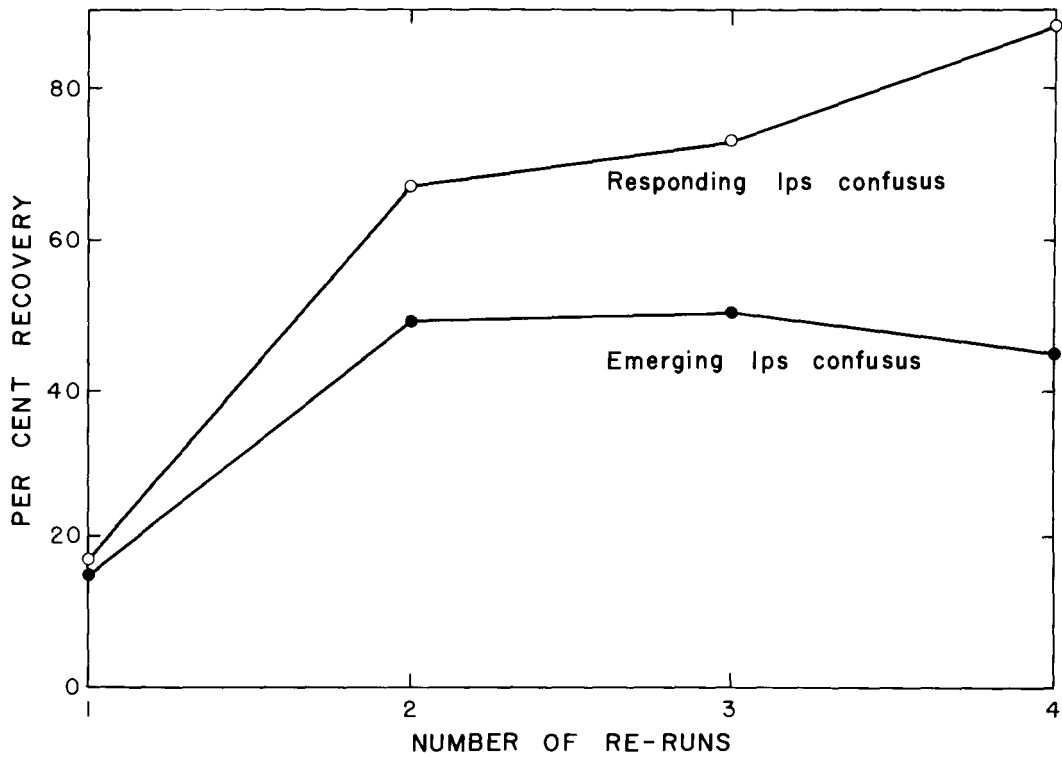


Figure 19. Gain in ability to respond to attractants in two lots of beetles when chosen by repeated release and recovery in olfactometers to eliminate non-responding members.

beetles were then flown over a 50-meter course together with a similar number of beetles freshly caught from the field population which were then marked with a different color. Minutes after release, 35 percent of the beetles selected from the emerging population were recaptured, while only 17 percent of the beetles freshly caught from the field population responded to olfactometers. Again, reference is made to Table 11 which shows that only six percent of unselected, emerging beetles normally are expected to respond over 50 meters.

Response ability vs. flight capacity. The heterogeneous capability of I. confusus to locate its attractant may be due to variability in flight capacity or in response ability. "Flight capacity," as used here, refers to the insects' endurance for flights of sufficient duration to reach a source of attraction. On the other hand, "response ability" refers to the relative efficiency of the beetles' chemoreception mechanism that orients or guides flights toward the source of olfactory stimulus.

The relative flight capacity of emerging and responding beetles was tested on standardized flight mills. Test insects from the emergence cages as well as beetles fresh from the olfactometers were tethered to flight mills. The

different flight capacities were determined by the beetle's ability to turn the mill. Their performances were divided into five categories: a) beetles not flying at all; b) beetles achieving one revolution; c) beetles performing through five revolutions; d) beetles performing ten revolutions; and e) beetles performing more than ten revolutions. Approximately 200 of each kind of test insect were used. These beetles represented the number of beetles that could be tested by two people working for two days. As shown in Table 12, there was no difference in the performance in the emerging and responding beetles.

By virtue of a previous test, Table 1, it was shown that beetles with both antennae amputated could fly, but did not respond. Similarly, removal of one antennae decreased the response ability 50 percent but not the flight

Table 12. Relative flight capacities of emerging and responding Ips confusus as measured by ability to turn flight mill.

<u>Ips</u> <u>confusus</u>	Non- flyers	1 Revolution	5 Revolutions	10 Revolutions	Supe- rior
<u>Responding</u>	58	99	19	11	14
<u>Emerging</u>	64	93	18	11	15

capacity. In this experiment, then, differential response ability was artificially induced; however, the use of intact beetles to demonstrate the existence of differences in response ability posed a problem. A direct approach using intact beetles would have required the capture of beetles that did not respond for possible re-testing, but such an approach was impossible. As a more indirect approach 2,000 freshly emerged I. confusus were marked and released within a 5-meter circle of olfactometers. Those that responded were again released and subsequently caught through five repetitions. Another group of emerging beetles, marked differently, was released and recaptured only once over a 25-meter course. Both residual groups, as well as marked emerging and responding beetles were released in a 25-meter circle of olfactometers. The results are presented in Table 13. The beetles which had been selected one time over 25 meters proved to respond in much higher proportion than those selected five times over five meters.

Sex. In experiments where I. confusus was released and attracted over various distances, the proportion of males to females varied with the distance. Although the ability of a population to respond seems to vary with the individuals, there nevertheless exist well delineated

Table 13. Response of Ips confusus selected according to prior behavior when released at the center of a 25-meter radius circle of olfactometers.

Prior Behavior of Test Beetles	No. of Beetles		Recovery %
	Released	Recovered	
Beetles which responded once at a 25-meter distance	22	15	68
Beetles which responded 5 times at a 5-meter distance	33	16	48
Responding beetles from field population	63	12	19
Newly emerged beetles	97	6	6.2

differences in the distances over which the males and females respond (Figure 20). It seems evident that males of I. confusus respond best over distances less than 50 meters, with no response at 1,000 meters. In contrast, the females respond about 2 percent less than the males under 50 meters; but at greater distances, the females respond over 50 percent better than the males.

On two occasions, during the peak of the second I. confusus flight (May 30 to June 29, 1962), daily catches of the natural population responding to the olfactometers as well as the beetles emerging from caged logs were separated according to sex and counted. It was found that

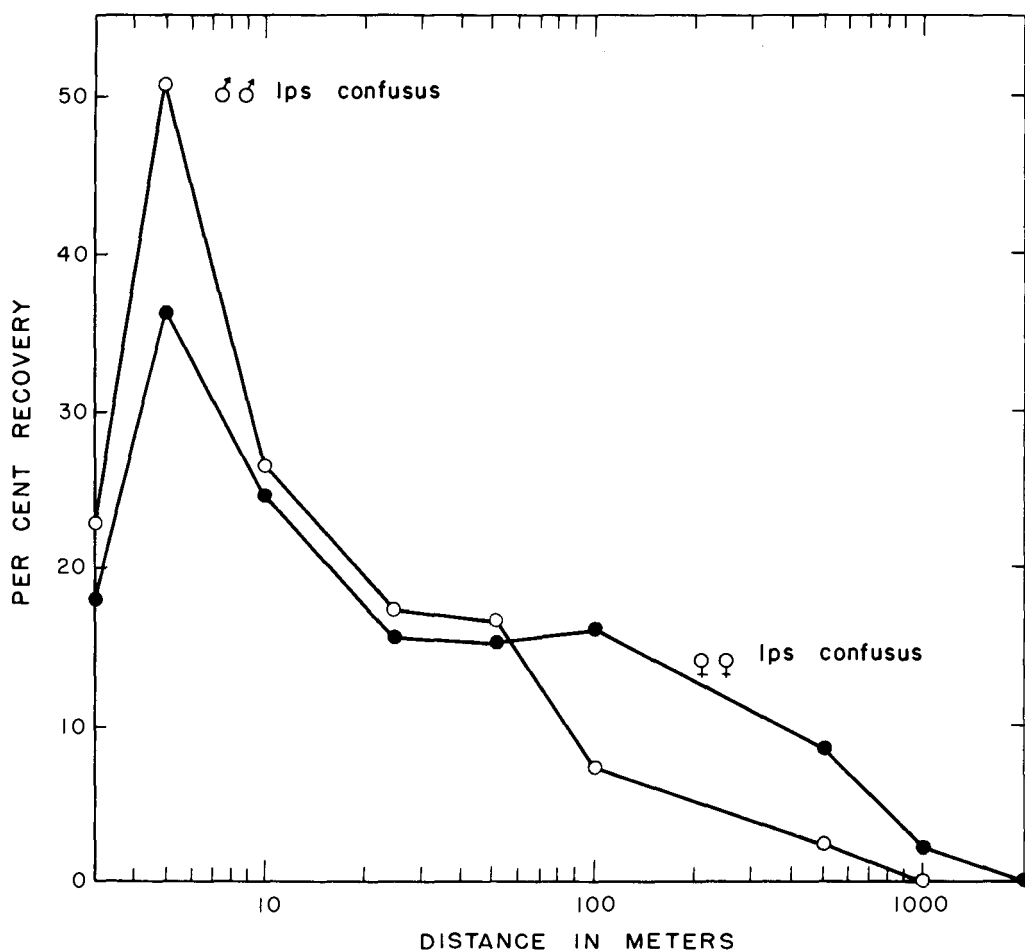


Figure 20. Relative ability of male and female *Ips confusus* to respond to attractants at different distances from the point of their release.

1,650 females to 938 males responded to the olfactometers, while the beetles in the cages emerged in a ratio of 1.18 females to 1 male. The fact that only about 36 percent of the attracted beetles were males indicates that most of the beetles may have been attracted more than 50 meters. Actually the nearest known emergence sources were approximately 200 meters from the olfactometers.

Physiological make-up of population. During the course of experimentation, it was noticed that the frequency in response of emerging, as well as responding beetles varied through a wide range even when the beetles were consistently flown over the same distances. Therefore, investigations were made to ascertain the variations that might exist within the same brood and among the various populations.

Brood differences. A cut ponderosa pine was exposed to the attack of the field population and placed in a cage as soon as the infestation was completed. As the brood began to emerge, the beetles were collected daily and a sample of 100 insects was marked and flown in a five-meter circle at the same time each day. The results are presented in Figure 21. The data indicate that the beetles which emerged first had higher response abilities and

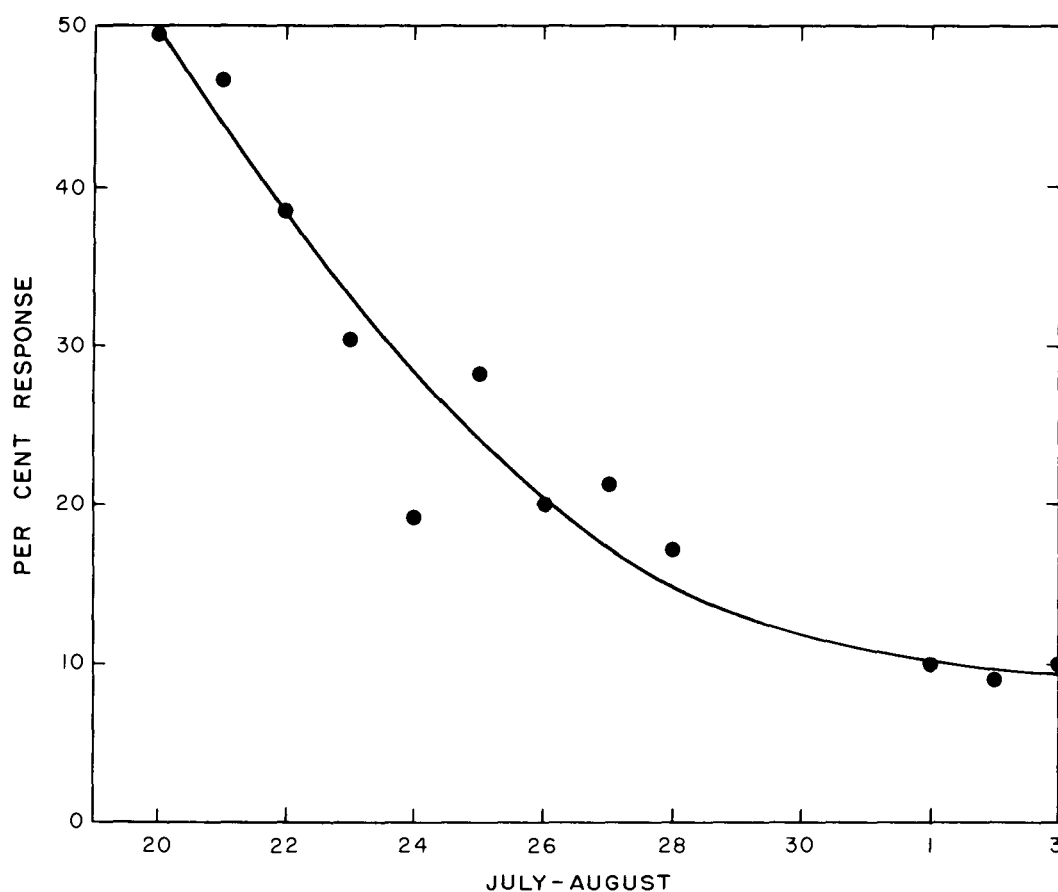


Figure 21. Relative responsiveness of early and late emerging members of a brood of Ips confusus from a single tree to attractants at a distance of 5 meters.

that the responses decreased as the time needed for emergence increased.

Population differences. To test whether or not noticeable differences in response occur between beetles from different populations, olfactometers were set up in three different localities. One olfactometer was placed adjacent to a large, well shaded, concentration of ponderosa pine logging slash which was heavily infested with I. confusus. Struble and Hall (86, p. 11) reported that such accumulations of fresh slash are the most favorable breeding material and consequently are most heavily attacked. The attack densities on the larger tops were estimated at 12 - 18 per square foot. Even though no study was conducted to determine brood survival, other investigations with D. brevicornis (57), D. pseudotsugae (59), and Dendroctonus engelmanni Hopkins (51) have indicated that comparable densities significantly lower brood vigor and survival.

Another olfactometer was set up in an area that contained a small infestation of I. confusus. All of the attacks were well distributed on a few large trees that had been cut for road construction.

The third olfactometer was placed in an area away

from any known infestation.

Beetles collected from the three bait traps were kept separated and differently marked. Subsequently, these insects were released in groups of a hundred, each group from the center of a 25-meter radius circle containing five olfactometers. The test animals were released each day at the same time for three days. The results of this test (Figure 22) indicated that there existed substantial differences in response between the population bred under crowded conditions and the group reared in ample breeding material. The response of the group from the unknown source was the best since these were beetles with an a priori ability to respond.

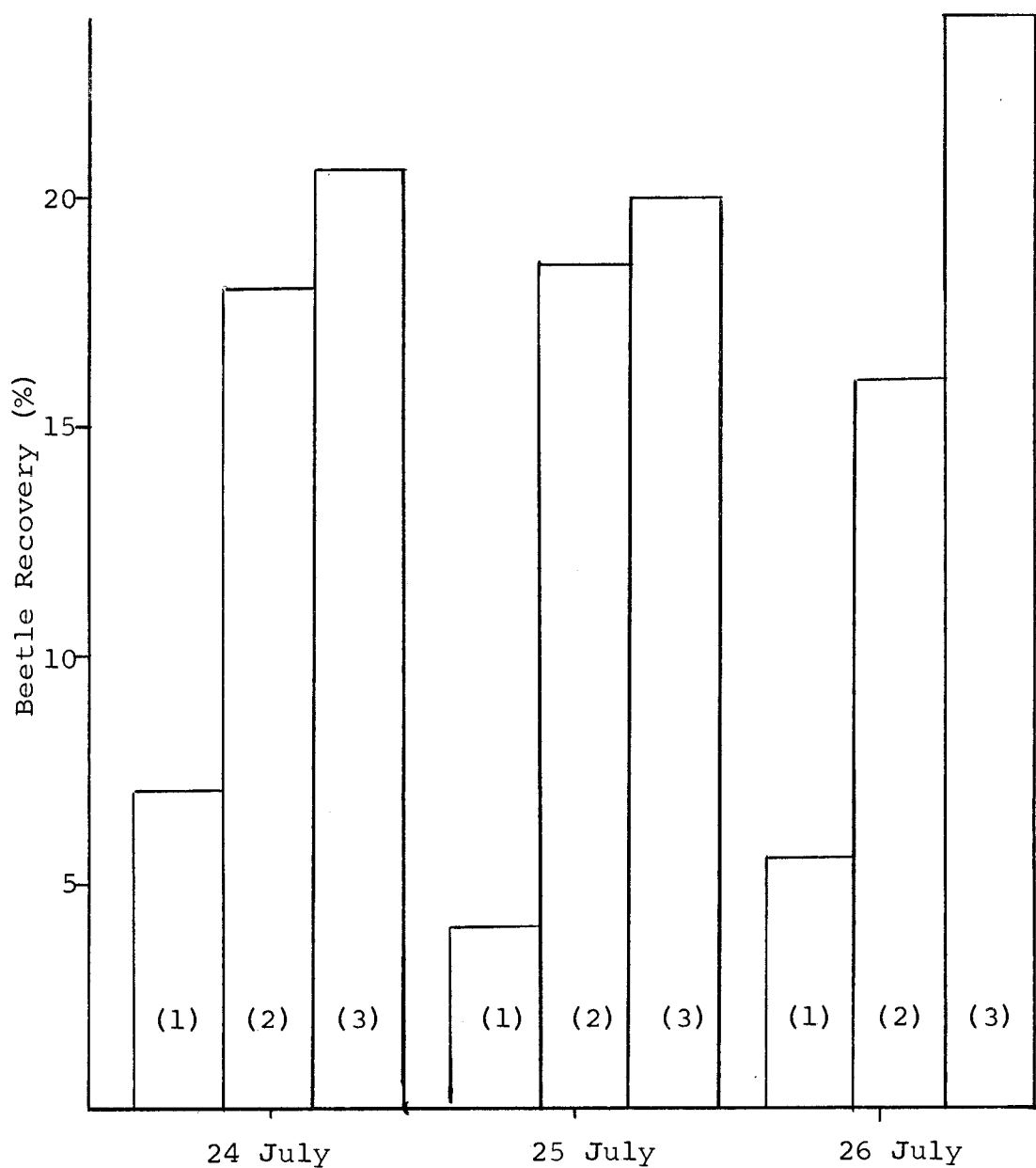


Figure 22. Relative response of *I. confusus* collected from three breeding sites: (1) dense slash pile, (2) scattered logs, (3) field population from unknown source.

DISCUSSION AND CONCLUSIONS

The use of attractants made it possible to observe I. confusus flights from take-off to landing. The take-off phase seemed important in the insects' initial orientation to attractants. This was shown when beetles were readily attracted to the outside of the flight cage by attractants emanating from the cage; yet the same beetles, when collected and put into flight inside the cage, failed to respond to the same stimuli. Apparently, the screen interrupted the initial flight phase before olfactory responses became dominant. As a result the beetles scattered, stimulated mainly by phototactic and geotactic stimuli, while a large number of the outside population continued to focus toward the source of attractants.

The need for a take-off phase before responding to attractants may indicate that the insects are employing most of their metabolic resources and muscular coordination to the formidable task of getting off the ground (72, p. 623-647). Studies have shown that, at the beginning of flight, wing-beat frequencies and stroke amplitudes are at their highest values within a few cycles (72, p. 607). This immediate, maximal effort is essential

in overcoming their starting inertia and attaining sufficient flight velocity to maintain themselves in the air. Hollick (41, p. 605) was able to show that the stroke amplitude of a dipterous insect decreased once its normal flight speed was attained.

Evidently in winds under 0.3 meters per second, I. confusus reached its normal flight velocity at a height of about 10 meters. At this time, with the exigencies of take-off over, the insects became receptive to olfactory stimulation and could coordinate their flight activity toward the attractive source.

The extremely positive response behavior of beetles released in the five-meter circle (under wind conditions of less than 0.3 meters per second) indicates the existence of an optimum orientation distance to attractants. At the five-meter distance, I. confusus dive directly toward the attractive source, while at three or eight meters, the beetles circle the olfactometers before entering the funnels. Accordingly, fewer beetles are caught at these distances which indicates that I. confusus accomplish a period of reorientation for distances other than five meters. The optimal five-meter distance may be based on a ratio of vertical height attained on take-off to the

horizontal distance from the attractants. This ideal relationship is altered when higher winds prevail as the beetles fly closer to the ground -- a stratum of decreased wind velocity.

In 1957, Dethier (24) reviewed studies on the behavior of several insect species as they responded to olfactory stimulation. He pointed out that odors seem to have a stimulating effect which is associated with a positive anemotaxes (as termed by Fraenkel and Gunn(32)) or flight against the wind. Furthermore, if an insect is stimulated to fly against the wind in response to a persisting odor, it is capable of approaching the source. Then a random search or a response to a more local diffusion gradient could readily lead to its discovery.

Dethier (24, 25) suggests that if such a mechanism prevails, the process of simple diffusion and dispersion of molecules are sufficient in explaining known facts of insect orientation to sources of attractants. Nevertheless, Chapman (17, p. 89) as shown in his studies with T. lineatum, feels that even though the ambrosia beetle responds to its breeding material against the wind, "... there is no reason to believe that beetles can distinguish between a faint stimulus, due to a strong source of

attractants some distance away, from one arising at a closer weak source."

It appears, however, that I. confusus exhibits a mechanism in locating its host as suggested by Dethier. By releasing beetles long distances (i.e., 500 meters) from sources of attractants, it was apparent that the insects found the odor sources while responding against the wind. However, as the insects approached the area where the attractant was located, they responded to the strongest source. This behavior was clearly shown by releasing beetles at either end of an attraction gradient wherein the strongest source attracted the most beetles. Similarly, when beetles were released in the epidemic area, fewer were recovered than in the endemic and prairie releases; and by increasing the number of fresh infestations in attraction centers, beetles were attracted in greater numbers and apparently over a greater area.

It seems apparent that wind velocity does not influence the basic mechanism by which I. confusus find their pheromone, but rather it affects their pattern of response. Accordingly, the densest response flights occurred in localities and elevations where the lowest winds prevailed. When winds of 1 - 1.5 meters per second predominated, the

insects flew close to the ground. Low level response flights in high winds have likewise been reported for other scolytids (17; 74, p. 32).

Releases of test insects in the Sierraville prairie indicated that not only did beetles fly in winds approaching or exceeding their air speed, but the ones that finally responded, did so against the wind. It is not likely that the insects landed and awaited winds of lower speeds before responding, because: (1) laboratory tests showed that beetles continued to fly in head winds that equalled or exceeded their flight speed (see page 60); (2) with no arboreal cover on the prairie, high solar radiation would continue to induce flight; and (3) beetles in the presence of their pheromone were observed to exhibit an overwhelming compulsion for response, regardless of environmental conditions. In addition, earlier studies noted that scolytids may be blown by high winds for several miles, even from areas containing fresh infestations (57).

In consolidating the results of experiments on response flights of I. confusus, possible clues on their anemo-tactic behavior emerge. As an underlying principle, it is first proposed that flying insects (in fact most flying organisms) primarily detect the direction and rate

of movement of the air mass in which they are flying by optical reference to stationary objects. Thus, an insect that is stimulated to fly upwind can only perceive that it is correctly oriented by the rate and direction of objects moving in its field of vision. The role of the optical sense in anemo-taxis has been demonstrated by Kennedy (49). By testing mosquitoes in a wind, or with a moving background, he found that the insects would not tolerate movement of ground configurations that exceeded a certain slow rate. These insects would also keep oriented so that ground objects passed from front to back, and landed when head winds exceeded their air speed and objects passed from back to front. However, Kennedy noted this upwind flight occurred regardless of the presence of host odors or repellents. Other studies have proposed different optical orientation mechanisms (31, 72, 99).

In review, it was shown that I. confusus responded against the wind while in the presence of the slightest trace of its pheromone. Moreover, flying in stands of its host, I. confusus preferred to fly at elevations where the lowest wind prevailed and flew near the ground in high winds.

In explaining the response behavior of I. confusus,

it may be that the pheromone actually induces an upwind flight which will eventually lead to the source of attraction. In the presence of the attractant, the beetle may perceive it is flying upwind only when objects pass by its field of vision at a certain threshold rate. This rate of background movement is slower than the rate expressed by the beetle's air speed alone. If the insect is flying at an elevation where the wind speed is too high, the insect may be stimulated to fly lower until it perceives that lateral configurations speed up to a certain threshold. When winds of 1 - 1.5 meters per second prevail, the insect flies close the ground where slower winds are found (36).

In the absence of attractants, experiments show that the insects disperse with the wind (35, 91). Perhaps the perception of some critical value for movement of background objects is not initiated until the insect encounters its pheromone. Such a mechanism would have additional survival values since there would be fewer behavioral limitations on efficient dispersal.

The experiments and observations confirm the concept that freshly emerged I. confusus may immediately respond to sources of attraction, flying no more than a few meters

with a flying time of less than a minute. This would indicate that the consummation of a dispersal flight is not necessary in predisposing beetles to respond to attractants. Flight exercise in the sense of physiological conditioning, therefore, is not prerequisite to concentration on host material.

In other studies where host selection was shown to occur only after photic reversal, the test insects were subjected to rather harsh physiological stresses (37, 38, 64, 65). Moreover, such studies used walking insects which performed in laboratory olfactometers of various designs. It is conceivable that these insects were responding to a "shelter reaction" in locating their host; with host recognition taking place primarily through mechanoreception rather than chemoreception. Thorsteinson further points out, with studies on the sweet clover weevil (87), that the influence of attractants cannot be demonstrated in the laboratory because, apparently, the insect is responsive to host odors only while flying; this is in harmony with the results presented here.

The studies presented here demonstrated that the ability to respond to sources of attraction varied from beetle to beetle, between the sexes, within a brood, and from

population to population. These differences were tested by determining the ability of beetles to find the sources of attractants over various distances as well as their ability to find such sources repeatedly.

The heterogeneity in response behavior between emerging and responding beetles is a reflection of individual abilities. At distances of five meters, both groups were able to respond equally well, indicating that a large portion of the population readily responds over short distances. At distances over 25 meters, I. confusus which had responded to attractants before responded in greater numbers than freshly emerged beetles. In contrast to beetles from the insectary, the test animals collected from the olfactometers had undergone natural selection by means of the bait traps and thus already demonstrated an ability to respond. These beetles were more likely to find sources of attractants than beetles from an unselected population.

The heterogeneity evident in the response ability of I. confusus populations may have an important dispersal value.

The distance over which the beetles may respond, directly and in appreciable proportions, in colonizing new

host material can be estimated at between 500 and 1000 meters. Beyond this distance, the colonizing of new host material must depend to a large degree on populations in dispersal.

It is of interest to note that female I. confusus were attracted over longer distances than males. This indicates that even though the male-produced attractant is species-specific, it may have a sex-bound evolutionary history. Furthermore, this high degree of sensory specialization in the females may explain some of the peculiarities in the biology of I. confusus. Emerging in a sex ratio of 1 male to 1.18 females, the actual ratio of attacking populations is usually 1 male to 3 females, or at a very low population level, 1 male to 5 females. In this manner, the pheromone can attract females from a larger area, thus accounting for the group's high efficiency in concentration. It may be assumed, however, that a portion of the male population is lost in locating new hosts. In turn, the somewhat superior ability of males to respond over short distances makes new attacks near recent infestation more severe. This behavior may have importance in survival. The flight period of bark beetles is short, fraught with hazards not encountered under the bark; it is

a time when the insect is most vulnerable to environmental decimation. The enlargement of established infestations by emerging males would assure a continuing source of attraction thereby serving to concentrate the dispersing population in a minimum of flight time. This proposal is in opposition to Wood's (1977, p. 1076) recent findings. He observed the response behavior of I. confusus as they walked in a laboratory olfactometer and stated that males were less responsive to attractants at short distances than females. Wood extrapolated these observations to field conditions, proposing that this behavior was instrumental in dispersing the population by assuring that all of the males of a population would not concentrate on the first successfully attacked tree. This proposal seems doubtful, because: first, actual field experiments showed that the response of males is higher at shorter distances than females (see Figure 20); second, the principal role of the male beetle in host selection is to concentrate the population on suitable breeding material wherever it may be located. This is certainly evidenced by the male pheromone or "aggregant," (as termed by Thorsen and Steinson (1977, p. 198)), which is capable of concentrating beetles from distances of 3 - 2000 meters as well as focusing them to a small

olfactometer placed in a 100 square mile prairie. In fact, Pitman and Vité (67) have recently identified the specialized structures in the hind gut of the male responsible for production of the pheromone -- evidence that the male is morphologically specialized for concentrating the population.

It must be reiterated, that artificial conditions produced by laboratory olfactometers often influence the context of insect behavior to a point where it is difficult to interpret the actual behavior of the populations in the field (33, 45, 50, 87, 91, 92). This is especially applicable to investigations on host selection behavior of bark beetles since only during flight do scolytids allocate their host material.

Within a brood, the first beetles to emerge demonstrated a superior ability in finding host material than the later developing brood. This indicates that the first larvae to emerge from the eggs experienced more optimal nutritional conditions than later larvae. Indeed, Pitman (68) found the relative proportions of carbohydrates drastically change as the phloem tissues age. It is thus plausible that the last eggs were laid in a medium that was only marginal for normal physiological maturation.

Furthermore, the breeding material, in time, gradually supports more inter- and intra-specific competitors to the developing Ips confusus broods. This would tend to limit the vigor of the later developing progeny even more.

There are also indications that one population might possess a lower ability to respond than another population. This too was shown to be a possible effect of crowding resulting from competition for food and space.

Many of these findings indicate the differences in response to attractants are due to physiological condition of beetles and populations rather than to inherited abilities. As has been suggested for I. typographus by Bombosch (7), this would explain why certain populations may appear aggressive due to their ability to concentrate on new host material in large numbers and over long distances, while populations with small proportions of physiologically fit individuals are prone to decline.

SUMMARY

1. Most of the studies were performed in the field and were restricted to Ips confusus with Pinus ponderosa as host material. The experiments and observations were primarily carried out in the Boyce Thompson Institute Experimental Forest near Grass Valley, California, where I. confusus occur as endemic populations. Additional tests were performed in an epidemic area near Nevada City, California, and under prairie conditions in the Sierraville prairie close to Loyalton, California.
2. Investigations of the response flights of Ips confusus under field conditions required marking techniques to distinguish test beetles from the field population. Marking beetles on the pronotum with fluorescent dyes proved to be the most satisfactory technique.
3. The condition of the insects used in the tests was important and their responsiveness to attractive sources had to be established. Unmarked beetles stored in a cooler gradually lost their ability to fly and to respond to olfactory stimulation. Beetles marked prior to storage showed a parallel reduction in ability to

fly and to respond. It was necessary to remove mutilated beetles from the test material since even the loss of one antenna resulted in a 50 percent decrease in response to attractants as compared with intact beetles.

4. A simple device (beetle launcher) was developed to hurl beetles into flight and to collect those that did not fly.
5. Funnel-shaped bait traps (field olfactometers) were used to attract test beetles or the field populations to attractants. These devices were standardized for efficient performance. A series of smaller olfactometers was also developed to test differences in the vertical response of Ips confusus.
6. Attractive material was obtained by infesting log sections with male I. confusus; 25 to a log was used as a standard.
7. Aerial net traps were used in this study to randomly determine the relative density of flying Ips confusus. These traps were standardized in a previous study.
8. Various techniques were developed to study the flight behavior of I. confusus under restricted flying conditions. By means of flight bars the beetles could be

flown in place without actual locomotion. In this position the wing-beat frequency could be measured by flying the insect close to a microphone. The wing-beat frequency was determined by means of an amplifier and a frequency meter. The results of these studies, which were solely exploratory, indicated that the wing-beat frequency may possibly be an indicator for olfactory responses.

9. A flight mill was designed to test the flight capacity of test insects. With insects the size of I. confusus and D. brevicomis, the most ideal radius of rotation was 20 centimeters. This length was standardized in a series of tests with arms of different lengths.
10. A large, empty hall, 27 meters long, 6.5 meters wide, and 3 meters high was prepared as a flight arena. Light, temperature, humidity and air movement were controlled. I. confusus released in this arena did not respond in any way to material known to be attractive but only responded to the light sources.
11. By attaching beetles to helium filled balloons it was hoped their flight could be more easily observed. This technique proved to be unsuccessful.
12. A screened cage, 3 x 3 x 3 meters was erected outdoors

to observe response patterns under more natural but yet limited flying conditions. Even with attractants present, the test insects flew to the brightest corner of the cage.

13. Temperature and relative humidity were determined during the study with a spring wound hygrothermograph. Wind speeds were precisely measured with a thermal anemometer.
14. By attracting I. confusus to field olfactometers over short distances (3 - 8 meters), it was possible to observe the total flight of individual beetles from take-off to subsequent response and landing in or at the olfactometers. Beetles were found to take-off with the wind and respond against it. When the distance from the point of release to the olfactometers was five meters, the test insects immediately dove into the funnels after once air borne -- indicating that flight exercise is not a prerequisite to response.
15. I. confusus concentrate narrowly toward sources of attraction without a noticeable increase of the population level in the general area.
16. The relative attractiveness of the infested material depended on the number of male attacks and on the age

of the material.

17. By releasing beetles either with or against the wind in an attraction gradient, it was evident that the strongest attractive source collected the most beetles.
18. By measuring the wind at various heights, it was seen that I. confusus response flights were densest in the regions of the least wind. When relatively high winds prevailed (1 to 1.5 meters per second), the response was restricted practically to ground level.
19. Light conditions seemed to have little influence on response flights except that direct solar radiation seemed to be avoided.
20. Both released beetles and beetles of the field population exhibited a diurnal response pattern that seemed to be temperature dependent.
21. The ability to respond to attractants was found to vary from beetle to beetle, with sex, within a brood, and from population to population.
22. Beetles which had responded once repeatedly responded better than unselected, freshly emerged beetles. This heterogeneity in response seemed to be due to the response ability of individuals rather than to their flight capacity.

23. Female and responding beetles were superior in response over distances greater than 25 meters, but males and emerging beetles responded in larger proportions over distances up to 25 meters.
24. Within the same brood, the ability to respond decreases from the first developing beetles to the later emerging individuals. There also seemed to be large differences in the response ability among various populations. These findings suggested that the differences are due to physiological condition of beetles and populations rather than to inherited abilities.
25. The distance over which I. confusus populations responded directly and in appreciable proportions seemed to be between 500 and 1000 meters.
26. All of the findings suggest a closer investigation of the possible causes of the heterogeneity of populations in their response to attractants.

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