SCOLYTID FLIGHT RESPONSE TO OLFACTORY STIMULI, WITH SPECIAL REFERENCE TO *Dendroctonus pseudotsugae* HOPKINS (COLEOPTERA: SCOLYTIDAE)

by

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ABSTRACT

An automatically recording flight mill was developed to analyze the response of flying insects to insect-produced and host volatiles. With this apparatus, the flight and arrestment responses of striped ambrosia beetle, Trypodendron lineatum, males and Douglas-fir beetle, Dendroctonus pseudotsugae, males and females were analyzed. Analysis of males of both species showed that pretest flight exercise was necessary before an arrestment response to female frass occurred. Analysis of the amount of flight exercise showed that freshly emerged T. lineatum required 30 minutes and D. pseudotsugae required 90 minutes of flight before arrestment occurred. Before flight, D. pseudotsugae swallowed large amounts of air. The resulting ventricular air bubble might be used by the beetle to detect adverse weather conditions via barometric pressure fluctuations.

Female D. pseudotsugae were not arrested to frass even after pretest flight exercise. Therefore, they may be able to detect some insect-produced "masking" compound in the frass, since both males and females are arrested to Douglas-fir, Pseudotsuga menziesii, phloem tissue.

Studies of lipid metabolism and gaseous exchange showed D. pseudotsugae to be predominantly a fat utilizer. Infrared measurements of CO_2 production and manometric measurements of O_2 consumption in flight and at rest indicated RQ values of 0.7 and 0.8, respectively. Lipid extraction and gas-liquid

chromatographic separation showed some selective oxidation of monounsaturated fatty acids. This was hypothesized as a means of releasing the ability to respond to olfactory stimuli.

ACKNOWLEDGEMENTS

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Time constant is 14 seconds; count range per minute (CPM) is 500. Solid bars represent one minute exposure to odor of 3 g of attractive female frass or ground host phloem tissue. Recordings read from right to left. Pretest flight experience and significant flight and response characteristics are: Fig. 23a, b, not preflown, no response to 5 repeated frass stimuli (Fig. 23a) and 3 phloem stimuli (Fig. 23b); Fig. 24, not preflown, erratic behavior in early flight; Fig. 25, preflown 9 hours, typical fatigue flight pattern;

INTRODUCTION

BIOLOGY AND ECONOMIC IMPORTANCE OF CERTAIN SCOLYTIDS

Dendroctonus pseudotsugae

The Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., is by far the most destructive insect pest of marketable sized Douglas-fir. Severe infestations have resulted in heavy losses of timber throughout the recorded ranges of the host tree, Pseudotsuga menziesii (Mirb.) Franco. In British Columbia it was established that trees containing some 66 million board-feet of timber were killed from 1952 to 1956 in the Nimpkish Valley on Vancouver Island and 75 million board-feet from 1953 to 1955 in the Lac LaHache area in the Interior (Cottrell and Fiddick 1962). From 1961 to 1965, inclusively, over 111.6 million board-feet of marketable Douglas-fir was killed by the Douglas-fir beetle in B.C.

Outbreaks in the interior region are more severe and persist longer than those in the coastal regions primarily because of the reduced vigor of the interior Douglas-fir. The limiting factor of inland outbreaks seems to be the availability of host trees, with a minimum of approximately 10 inches in diameter at breastheight (DBH) (Rudinsky 1962). The shorter outbreaks of D. pseudotsugae in coastal regions usually follow logging operations which leave slash or damaged trees on the margins (e.g. from unchecked slash burning) in

which beetle populations can build up. Otherwise beetle populations remain endemic in scattered unburned slash (e.g from road building), blow-down, fire-weakened or diseased trees (Furniss 1936; Lejeune, McMullen and Atkins 1961; Johnson and Belluschi 1969). During outbreaks on the coast the host trees are able to resist attack (possibly by lethal resinosis as in pine) (Walters 1955; Reid, Whitney and Watson 1967) and large volumes of timber are killed rapidly only at first; then the beetle population declines to its endemic level. Termination of the Nimpkish Valley outbreak may have occurred at least partly through a microsporidian epizootic (K. Graham, personal comm.).[1] Some serious epidemics have occurred in the Rocky Mountain regions, particularly in trees weakened by drought, fire and defoliation; or in trees close to logging operations harboring endemic beetle populations in the slash (Walters 1956; Wright and Lejeune 1967).

D. pseudotsugae causes continuous scattered mortality even when not in outbreak conditions (Ross 1957; Cottrell and Fiddick 1962, 1968). In the commercial coastal areas mortality from Douglas-fir beetle attack is not as apparent, although often the killing of groups of mature trees in second growth stands may occur (Rudinsky 1962).

Douglas-fir beetle attack is characterized by small holes

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in the bark of the tree below which a reddish-brown frass is produced. It collects around the base of the tree or in bark crevices (Skovsgaard 1968). No pitch tubes are formed (Rudinsky 1961, 1966a; Belluschi, Johnson and Heikkenen 1965) as frequently occurs with other bark beetle species. On fallen trees the attack is usually concentrated on the shaded underside. The adult beetles (Hopkins 1909; Wood 1963) are reddish to dark brown, often black, about 0.5 cm long and covered with long conspicuous hairs which are probably used to gauge tunnel diameter (Walters 1955). Although the male remains in or near the gallery entrance, the female mines egg galleries parallel to the long axis of the tree (Furniss 1962, 1964) in the inner bark. The egg galleries usually range in length from about 20 to 35 cm, although some have been observed up to 100 cm in length (Walters 1955). The eggs are laid along the main gallery, the larval mines diverge from the main gallery and extend along the inner bark, completely disrupting phloem translocation in the host tree. The tunnels are extended and widened as the larvae mature, producing fan-shaped patterns of tunnels at the end of which larvae pupate. The callow adults and some larvae (Walters 1955) overwinter in diapause in the bark (Beal 1934; Ryan 1959; Johnson 1967) and in spring, mature adults bore their way out through the bark, fly to new nost material and begin another generation (Walters 1955). In B.C., the overwintering adults emerge in April or May when the average daily temperature reaches about 20°C (Rudinsky 1963).

The overwintering larvae metamorphose and emerge in June and July along with some adults that have re-emerged and are attacking a second tree (Walters 1955). It is also possible that some of the young overwintering larvae do not have time to develop fully before the cold weather overtakes them in the fall (Vité and Rudinsky 1957), and consequently spend another winter in the same host tree. Except for these two principal peaks of emergence, the entire emergence pattern is somewhat obscured by overlapping of the different broods and variation in times of development. This complicates some control programs as the emergence patterns are quite imprecise, making predictions unreliable (Daterman, Rudinsky and Nagel 1965).

Detection is difficult during the early stages of beetle infestation (Furniss 1962) on standing trees as there are no pitch tubes and only the frass may indicate the presence of beetles in the bark. Moreover, foliage color changes do not usually occur until late in the season, and sometimes the following spring. The foliage color changes from green to pale yellow-green to red, the rate of change being dependent on temperature and humidity (St. George 1930; Belluschi and Johnson 1969), and this alteration can be easily observed from high vantage points or from the air (Cottrell and Fiddick 1968). However, control is hindered since the host trees cannot be detected sufficiently early in the attack (Furniss 1964) except by costly ground survey crews. Death of the tree does not usually occur for several months, until the girdling of the tree

by larval mining completely disrupts phloem translocation. Possibly aerial survey techniques using infrared films and automatic scanners (Colwell 1970) will be able to detect early alterations in the host metabolism, enabling more adequate controls (e.g. salvage logging) to be applied before the dispersal flight take place the following season.

Douglas-fir beetle activity can be confirmed by removing the bark (which is usually quite loose due to larval undermining) and observing the egg galleries with their typical alternating groups of egg niches on either side of the egg galleries. The galleries of species of Pseudohylesinus and Scolytus may also be present as they are frequently found associated with the Douglas-fir beetle (Chapman 1964; Rudinsky 1966b). Typical galleries of these two genera are narrower and shorter, and often are confined to the crown and branches of the trees. These beetles are secondary pests and are not necessarily very damaging by themselves in coastal Douglas-fir (Chapman 1964; Bright 1969).

Because healthy, vigorous trees are much less susceptible to attack, the primary control measures against the Douglas-fir beetle consists of careful forest management (Walters 1956). In suppressing beetle outbreaks, few methods have proved more practicable than proper management in coastal or inland regions, simply because of the inaccessability of the stand and the size of the trees. However, the immediate economic cost of "careful logging practices" or sanitation logging, as suggested by

Walters (1956) and Lejeune, McMullen and Atkins (1962), poses a problem to the budget-minded logging industry. Moreover, endemic populations are often so scattered and inaccessable that managerial practices do not decrease beetle numbers.

Trypodendron lineatum

The life cycle, particularly the spring emergence flights and attack patterns, of Trypodendron lineatum Oliver are similar to that of D. pseudotsugae. Notable differences in behavior from D. pseudotsugae are its xylem mining habit on dead coniferous trees or logs (Dyer and Chapman 1965) and its mutualistic association with a fungus which it inoculates into the tree and upon which it relies for food (Chapman 1958). A further behavioral difference is that the broods emerge from infested logs and fly to nearby standing forest where they overwinter in the bark of standing trees, in rotting stumps or in the litter on the forest floor (Chapman 1955a,b, 1962, 1963; Dyer and Chapman 1965).

T. lineatum is an important forest products pest of holarctic distribution (Dyer and Wright 1967). The galleries cause severe devaluation of lumber and plywood (Graham, Kinghorn and Webb 1950; McBride 1950). In British Columbia, log booms in the water are sprayed yearly with chemical insecticides to prevent T. lineatum attack; there is no economical means to prevent attack on logs left in the forest (Richmond 1968).

INSECT AND HOST VOLATILES AND THEIR POSSIBILITIES FOR USE IN CONTROL

Graham and Knight (1965) suggested methods by which integrated control of insects might be obtained in the complex forest environment, including silviculture, systemic pesticides, electromagnetic stimulation, radiation or chemical sterilization, repellants, anti-feedants, parasites and pheromones. Typically, all of these techniques are more or less species specific and efficient and, in theory, do not disrupt the ecosystem nearly as much as burning, for example. Generally these methods manipulate host tree physiology or scolytid behavior or both. However, most of them have not yet reached a sufficient state of development to be of practical use.

Such is the case with bark beetle pheromones (Atkins 1968). An aggregating pheromone attractive to both sexes (Jacobson 1965) in produced by the female T. lineatum (Rudinsky and Daterman 1964a,b) and by the female D. pseudotsugae (McMullen and Atkins 1962; Rudinsky 1963) as they bore into the host tree. During construction of the main galleries, pheromone production is maintained. As the male is attracted by it, the volatile principle is at least in part utilized by the female beetles as a sex pheromone to guide and orient the male to the tunnel entrance. The substance or substances in the Douglas-fir beetle pheromone are not only very powerful in that they can be detected in minute quantities by the male, but also are species specific, although there is some indication of cross attraction

with the spruce beetle, Dendroctonus obesus Hopk. (Chapman and Dyer 1969). In addition, frontalin (1,5-dimethyl-6-8-dioxabicyclo(3.2.1)octane), a principal pheromone component (Renwick and Vité 1968, 1969; Kinzer and Fentiman 1969; Pitman and Vité 1970), is shared by other scolytid species (Renwick 1967). Therefore, specificity must be maintained by other compounds, e.g. camphene (Pitman and Vité 1970). Species specificity of pheromone is important in species specific control. Specific control can utilize the natural conditions in which "reproductive isolation between closely related species would be most efficiently achieved by isolating mechanisms operating at the sensory and behavioral levels, preventing the two sexes of the related species from approaching each other for mating" (Shorey and Gaston 1967).

Assuming that the difficult task of producing, purifying, identifying and synthesizing a sex pheromone (Silverstein, Rodin and Wood 1967) for D. pseudotsugae or T. lineatum can be accomplished, its application in a control program in the natural habitat of the beetles would still pose problems. A thorough knowledge of the physiological (Rudinsky and Vité 1956) and environmental conditions (Chapman 1967) that initiate the dispersal patterns in the field is essential for pheromone control (Jacobson 1965). The pheromone could be used in two principal manners: either by causing a disorientation through the broadcasting of super-threshold amounts of the pheromone into the environment (Gaston, Shorey and Saario 1967) or by initiating

an orientation towards some point of additional control.

Although scolytid pheromones are specifically produced by one sex of one species, many parasites, predators and competitors of the target species may also be attracted (Rudinsky and Daterman 1964a,b; Pitman, Vité and Renwick 1966; Rice 1967; Bedard, Silverstein and Wood 1970; Wood and Silverstein 1970), thus initiating the decline of biotic factors already contributing to the control of the pest. The effective range of synthetic attractants and their ability to compete with naturally occurring pheromones has not yet been determined. In the natural environment, the micrometerology within and outside the forest stand adds a further unknown to the dispersive pattern of the pheromone (Chapman 1967). Atkins (1968) indicated a pheromone control program must be efficient or else the upset in the population gradient from escaped insects soon negates any possible beneficial effects of the control procedures. Some species of insects must attack en masse to overcome host resistance, whereas in others this is not required. Thus, an evaluation must first be made of the attack pattern (Atkins 1959) and of the response to specific volatiles (Borden and Bennett 1969) at different periods in the dispersal phase.

In addition to aggregating pheromones, at least two other types of volatile materials affect the flight and orientation of D. pseudotsugae. The host volatiles in Douglas-fir (i.e. the host oleoresin volatiles and especially the terpene constituents) can attract both T. lineatum and D. pseudotsugae (Rudinsky 1966a).

This supports Heikkenen and Hrutfiord (1965) who suggested that the tree oils containing terpenes constituted the primary host attractant. Another type of volatile material was suggested by Rudkinsky (1968, 1969), who hypothesized that the female D. pseudotsugae produces a "masking" pheromone or substance which inhibits the aggregation response of the male beetles. He also suggested that the presence of stridulating males near the female stimulates the production of the "mask" in the female. There is evidence that a similar masking pheromone occurs in T. lineatum (Nijholt 1970). Thus, it is evident that many types of volatiles could be affecting the behavior of scolytid beetles in their dispersal flight orientation.

In observing flying insects it is especially important to understand the effect of any volatile material on flight behavior. A walking bioassay is usually acceptable to obtain recognition responses for some behavioral work and for isolation of unknown compounds, but if population manipulation of flying insects is contemplated then the variability of flight responses must be understood. By far the most precise way to determine such variability is by laboratory flight experiments. Verification of lab results in the field is then necessary, but the primary method for isolation, simplification and categorization of behavioral responses is to bioassay in the controlled conditions of the laboratory. An understanding of the intricacies of flight response may greatly enhance the use of pheromones and other volatiles to control naturally flying populations.

INSECT FLIGHT AND PHYSIOLOGY

To measure insect flight parameters, several methods have been employed, such as the use of a stroboscope to determine wing-beat frequency to an accuracy of ± 1% (Chadwick 1939), and the use of a microphone to record the wing-beat frequency on a frequency meter (Vité, Gara and Klieforth 1963). Glover et al. (1966) used radar to observe speed, duration, height and direction of free flight in several species of insects. These studies were observational and exploratory with respect to the behavior of insects in normal flight.

Hocking (1953) devised a rotary flight mill that allowed the suspended insects to fly in a circle, thereby allowing measurement of flight speed, distance and duration. With such an apparatus Atkins (1961) found that the flight capacity of the Douglas-fir beetle, D. pseudotsugae, varied under different environmental conditions. He also measured the flight time over four and eight hour periods and attempted to establish a "normal" flight capacity for the beetle.

Both Hocking (1953) and Smith and Furniss (1966) used photocells and electric counters to produce recordings of the individual revolutions of insects on rotary flight mills. Hocking (1953) used kymograph drums to record each revolution, but Smith and Furniss (1966) recorded the summed number of revolutions per unit time on a non-reset electric counter. Data were recorded manually, although the authors suggested that they

could be recorded more conveniently by time-lapse photography. In general, the frequency of sampling was low, and any immediate changes in flight behavior could not be detected.

Rowley, Graham and Williams (1968) produced a flight mill apparatus for mosquitoes that used a photoresistor counting system which continuously recorded flight range, flight distance and flight speed. Standardized mounting procedures were used to ensure uniformity for flight speeds. With this apparatus it was possible to investigate the flight potentials of female mosquitoes in relation to age (Rowly and Graham 1968), relative humidity and temperature (Rowley, Graham and Williams 1968).

The utilization of lipid as a major source of energy during flight was reported by Fulton and Romney (1940) in Euttetix tenellus and extensively documented by Weis-Fogh (1952) for Schistocerca gregaria. Weis-Fogh reports that lipid is an ideal substrate for flying, because the more hydrated glycogen would make isocaloric quantities eight times heavier than lipid. Meyer, Preiss and Bauer (1960) later demonstrated that S. gregaria flight muscle was able to oxidize 8 to 18 carbon chain fatty acids, and Domroese and Gilbert (1964) demonstrated oxidation of ^{14}C-1-palmitate by flight muscles of Hyalophora cecropia.

Atkins (1966a,b, 1967) demonstrated a positive correlation between the fat content of D. pseudotsugae and inclination to fly. Moreover, beetles that had flown contained significantly less lipid than control beetles (Atkins 1969).

OBJECTIVES

In this study my objectives were: (1) to develop a means of automatically recording the flight parameters of scolytid beetles in tethered flight, (2) to determine the effects of host and insect-produced volatiles and certain other factors on the flight of beetles with varied pretest flight exercise, and (3) to determine the nature of lipid metabolism in flying D. pseudotsugae and its relationship to in-flight behavioral responses.

Male beetles are predominant in the mass response to secondary attraction (Chapman 1966; Atkins 1966c), and are the most likely potential targets for olfactory manipulation in nature. Therefore, the majority of experiments were performed with males.

METHODS AND MATERIALS

COLLECTION OF BEETLES

In the early spring scolytid beetles in a pre-dispersal condition (Rudinsky and Vité 1956) were collected in the lower mainland and on Vancouver Island. Overwintering populations of D. pseudotsugae were collected from fallen Douglas-fir logs by removing the infested bark and piling it in screened cages at room temperature. The beetles emerged at this temperature and were collected off the cage walls. Forest litter containing overwintering striped ambrosia beetle, T. lineatum, were collected from the forest margins near logging clearings (Chapman and Dyer 1969). Adults were obtained by using warming pans on a hot plate to drive the insects from the litter. Both species of insects were sexed and stored at 4°C in moist paper towelling.

PREPARATION OF NATURAL STIMULI

Frass collections were made from both species by introducing virgin females into logs approximately 60 cm long. As tunneling progressed, the frass was collected periodically throughout the day and stored in sealed jars at -40°C. Before flight tests, samples of D. pseudotsugae frass were bioassayed using male beetles as described by Borden, Silverstein and Brownlee (1968).

As in Ips confusus (Wood et al. 1966), wood borings and fecal pellets are more attractive than only fecal pellets to D. pseudotsugae (Zether-Moller and Rudinsky 1967). An average response of 50% was considered to be the minimum requirement for the frass to be used as a stimulus in flight bioassays. Similar bioassay techniques (Borden, Brownlee and Silverstein 1968) were used to ascertain the attractancy of T. lineatum frass.

Phloem was prepared from fresh Douglas-fir logs by grinding it with a cheese grater to the consistency of frass. The phloem was then exposed to air for approximately the same time as the frass before being collected and stored at -40°C.

CONSTRUCTION AND USE OF THE FLIGHT MILL

An apparatus was constructed to test the effect of a volatile substance on flight behavior which has the advantages of a relatively short time lag, continuous recording, reliability and mobility (Fig. 1). It consisted of a rotary flight mill, flight chamber and recording apparatus which were mounted together on an angle-iron frame to which castors were attached.

The construction of the flight mill (Fig. 2) was based on Hocking's (1953) design. A 2.5 cm piece of 0.3 cm glass tubing was sealed at one end, then cemented to a 15.3 cm piece of capillary tubing, through which a piece of fine wire was secured by thermally tapering the glass at both end. The wire protruded about 5 cm from both ends of the tubing, forming a "T" upon which

Fig. 1: Rotary flight mill and recording apparatus mounted on a mobile frame.

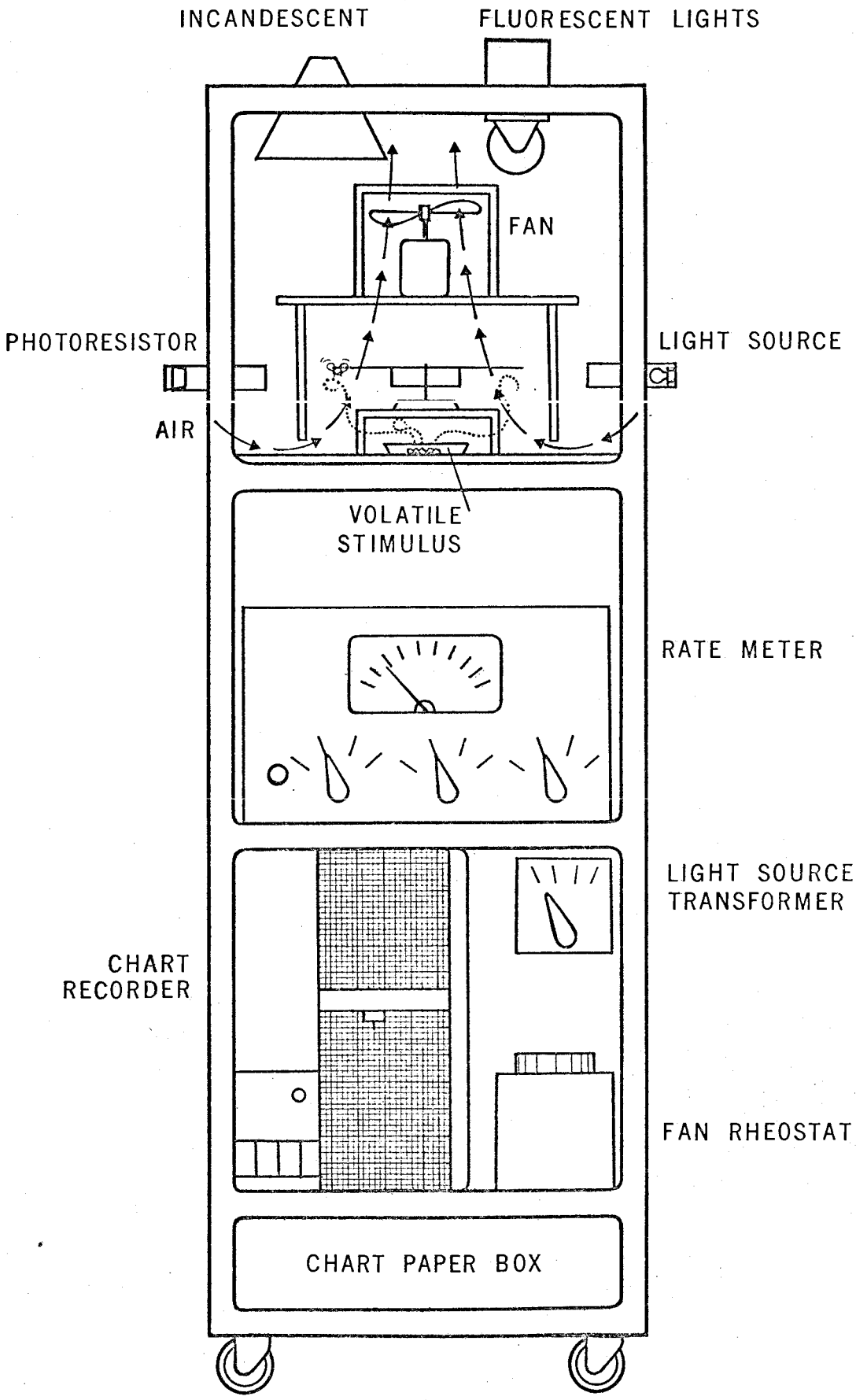
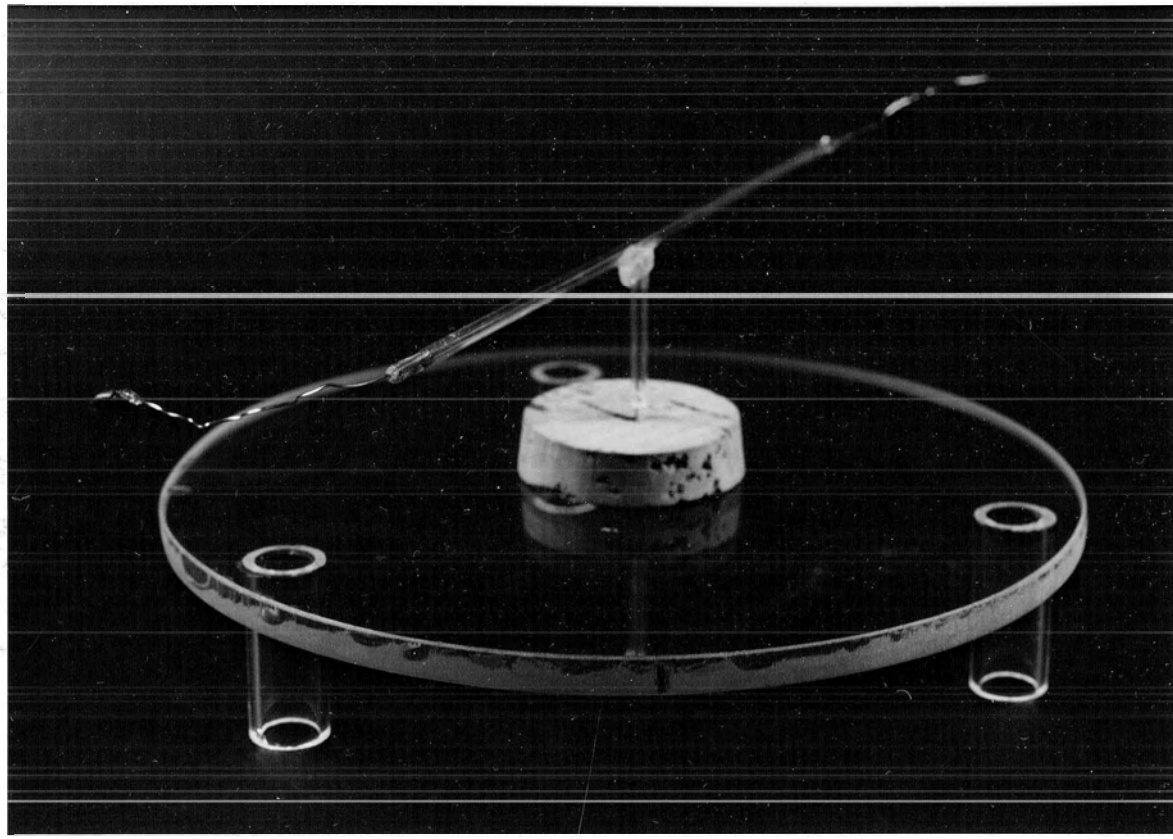

INCANDESCENT
FLUORESCENT LIGHTS
FAN
PHOTORESISTOR
LIGHT SOURCE
AIR
VOLATILE
STIMULUS
RATE METER
LIGHT SOURCE
TRANSFORMER
CHART
RECORDER
FAN RHEOSTAT
CHART PAPER BOX

Fig. 2: Flight mill resting on raised platform, showing space for stimulus in petri dish to be put underneath.



the beetles could be mounted. A base was constructed of a No. 18 cork cut 1.3 cm from the base and a No. 2 insect pin pushed through the center of the cork at a right angle. The experimental insects were attached to one end of the flight mill by the pronotum, using a fast-drying silicone glue.

A rectangular chamber (Fig. 1) was devised in which the release of volatile substances into the air surrounding the flying insects could be controlled. It was constructed out of 4 glass sheets, each 32.5 x 15.3 x 0.6 cm. A piece, 2.5 cm wide and 32.5 cm long, was cut from one of the glass sheets and hinged to it with a tape to form a trap-door at the bottom of one side. This opening allowed volatile stimuli to be placed into or removed from the chamber. The sides were glued together with silicone glue and 4 pieces of glass were glued to the bottom corners, producing a 0.6 cm air intake slot around the base. This was placed on a 32.5 x 32.5 cm sheet of glass 0.6 cm thick and a lid, also 32.5 x 32.5 x 0.6 cm, with a 7.6 cm diameter hole in the center, was placed on top. A 15.3 cm length of plexiglass tube, 10.2 cm in diameter, containing a small electric fan to evacuate air from the chamber, was inserted in this hole. The velocity of the air flow was controlled by a rheostat so as to maintain a flow of about 2 litres/sec.

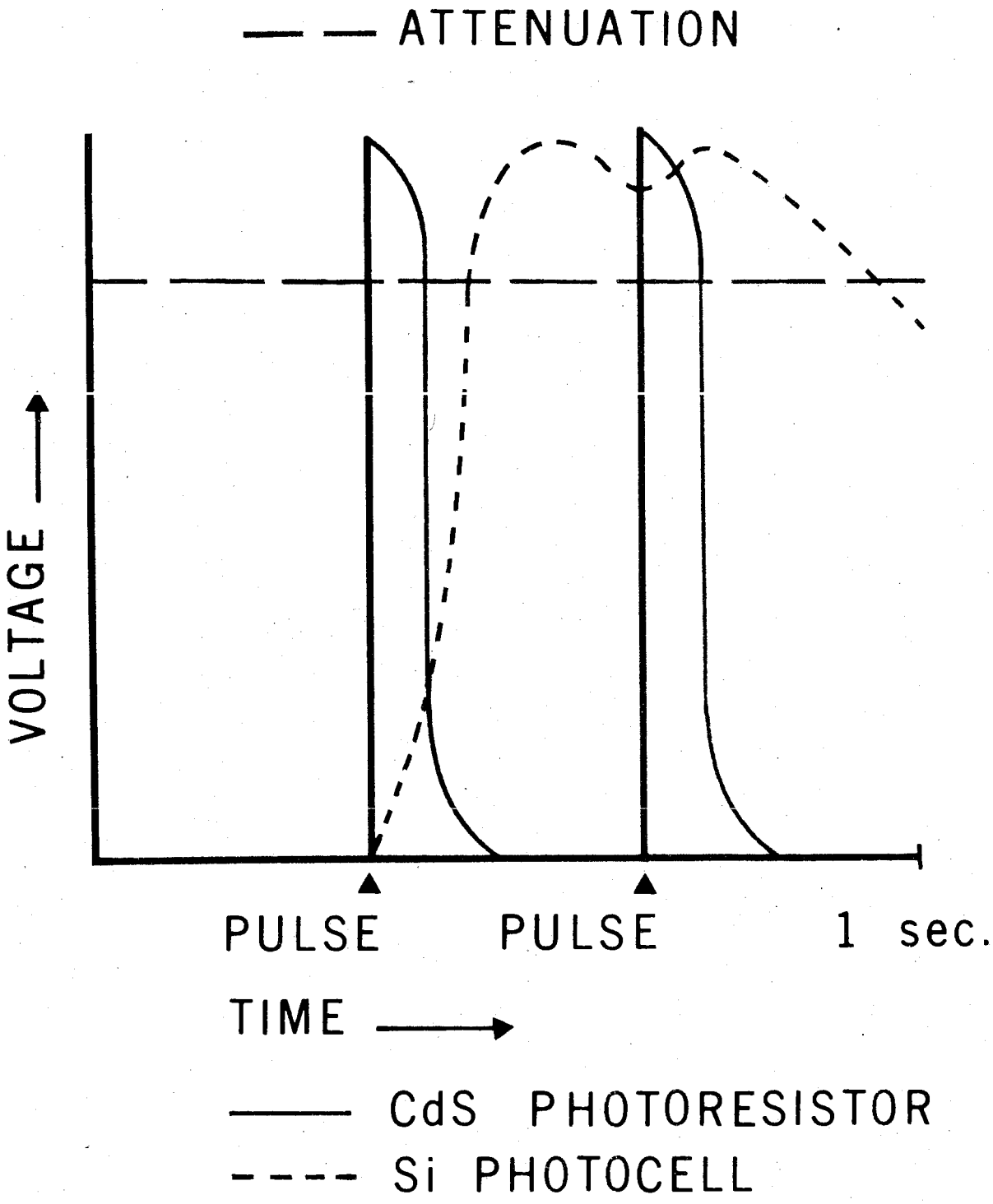
The flight mill was placed upon a 15.3 cm diameter glass platform raised from the center of the chamber by three 2.5 cm glass legs. One 60 watt incandescent bulb and one 61 cm

fluorescent tube were suspended above the flight chamber. These illuminated the flight mill area with an intensity of approximately 400 footcandles. This proved adequate to overcome the phototactic threshold of all test insects. A black-bulb thermometer was taped inside the chamber to measure the air temperature within the chamber.

A standard microscope lamp was mounted outside the glass chamber on a level with the vertical bar of the flight mill. A 5.1 x 5.1 cm piece of aluminum foil was folded over the horizontal bar at the pivot point, thus forming a light barrier. A cadmium sulfide photoresistor was attached to the end of a No. 16 cork and mounted within a piece of plexiglass tubing, 7.6 cm long and 2.5 cm in diameter. The plexiglass surface was sprayed with black enamel to prevent extraneous light from affecting the photoresistor's operation. This entire piece of apparatus was aligned with the light source on the opposite side of the flight chamber. The flight mill was arranged so that the aluminum foil broke the light beam twice each revolution and thus doubled the sensitivity of the recording. During construction of the apparatus it was anticipated that the flight speeds of insects would vary greatly, possibly up to 5 revolutions/sec. A cadmium sulfide photoresistor which has a very rapid decay time was chosen instead of a silicon photocell which has a slow decay time and which could resolve only those counts slower than one revolution/sec. (Fig. 3).

When light falls on the photoresistor, its resistance

Fig. 3: Pulse decay curves of silicone photocell and cadmium sulfide photoresistor. Horizontal dashed line indicates the threshold voltage required to pass by the attenuator.


— — ATTENUATION
VOLTAGE
PULSE
PULSE
1 sec.
TIME
—— CdS PHOTORESISTOR
---- Si PHOTOCELL

decreases, thus permitting an increase in the flow of current from a 22.5 volt battery through a simple telephone relay. The relay activates a modified ratemeter (Fig. 4) consisting of a triode attenuator, pulseformer and integrating circuit. In response to a pulse input, the ratemeter emits a pulse with an exponential decay (Fig. 5). A rapid sequence of pulses such as occurs when the flight mill is rotating produces a DC signal proportional to the frequency of the pulses (rotating velocity of the flight mill). The rate counting circuit was calibrated with a pulse generator through all the counting ranges.

The attenuator (pulse height discriminator) is a method for eliminating background noise induced in the circuit by magnetic and electronic fluses; e.g. radio waves. The attenuator is adjusted by increasing the threshold voltage until pulses are no longer registered and then decreasing it until the pulses just register; at this level most miscellaneous "noise" is eliminated (Fig. 3).

The pulses entering the integrating circuit must have a constant amplitude and duration in order that its output will be proportional to the number of input pulses, so a pulse former triggered by the relay was used. The integrating circuit was a resistance-capacitance time constant circuit. Settings on the instrument allowed 3.5, 14 and 56 seconds for time constants, however only the 14 second setting was usually used. Similarly, the count ranges used were 100, 250, 500 and

Fig. 4: Block diagram showing modified ratemeter circuitry. The broken line encloses the counting integration circuit. Although not included in the actual apparatus, the digital voltmeter and tape punch connected by a broken line to the counting circuit output indicates possible adaptation for computerization of data.

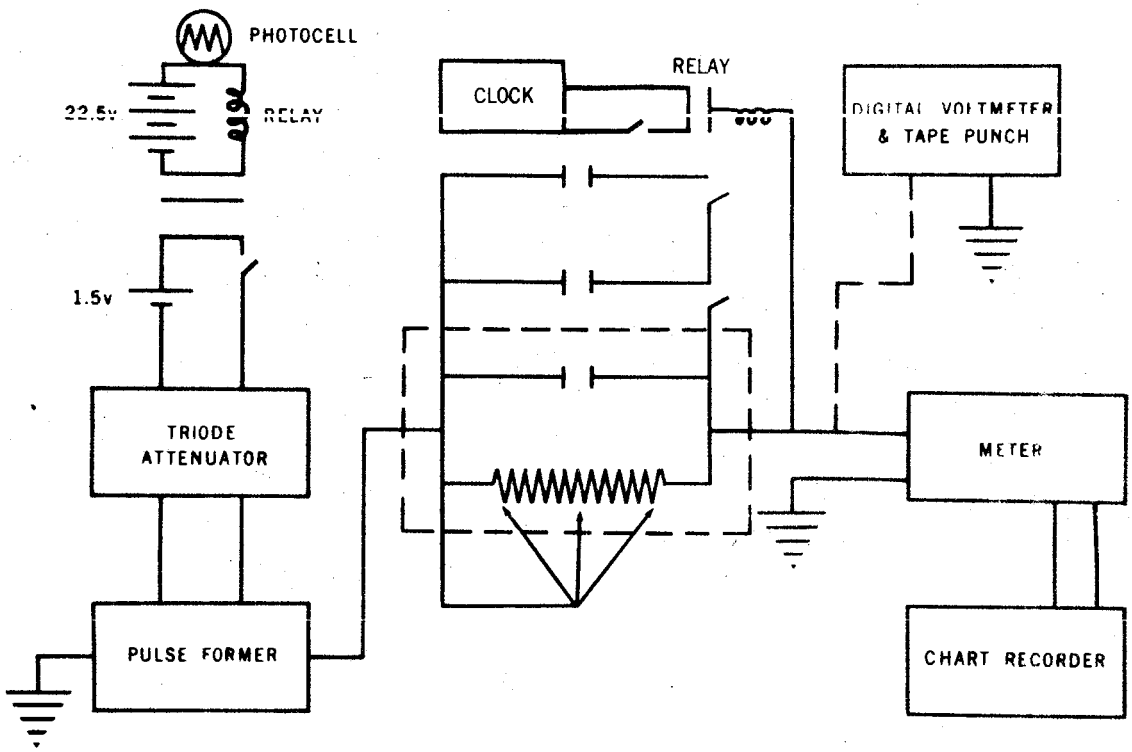
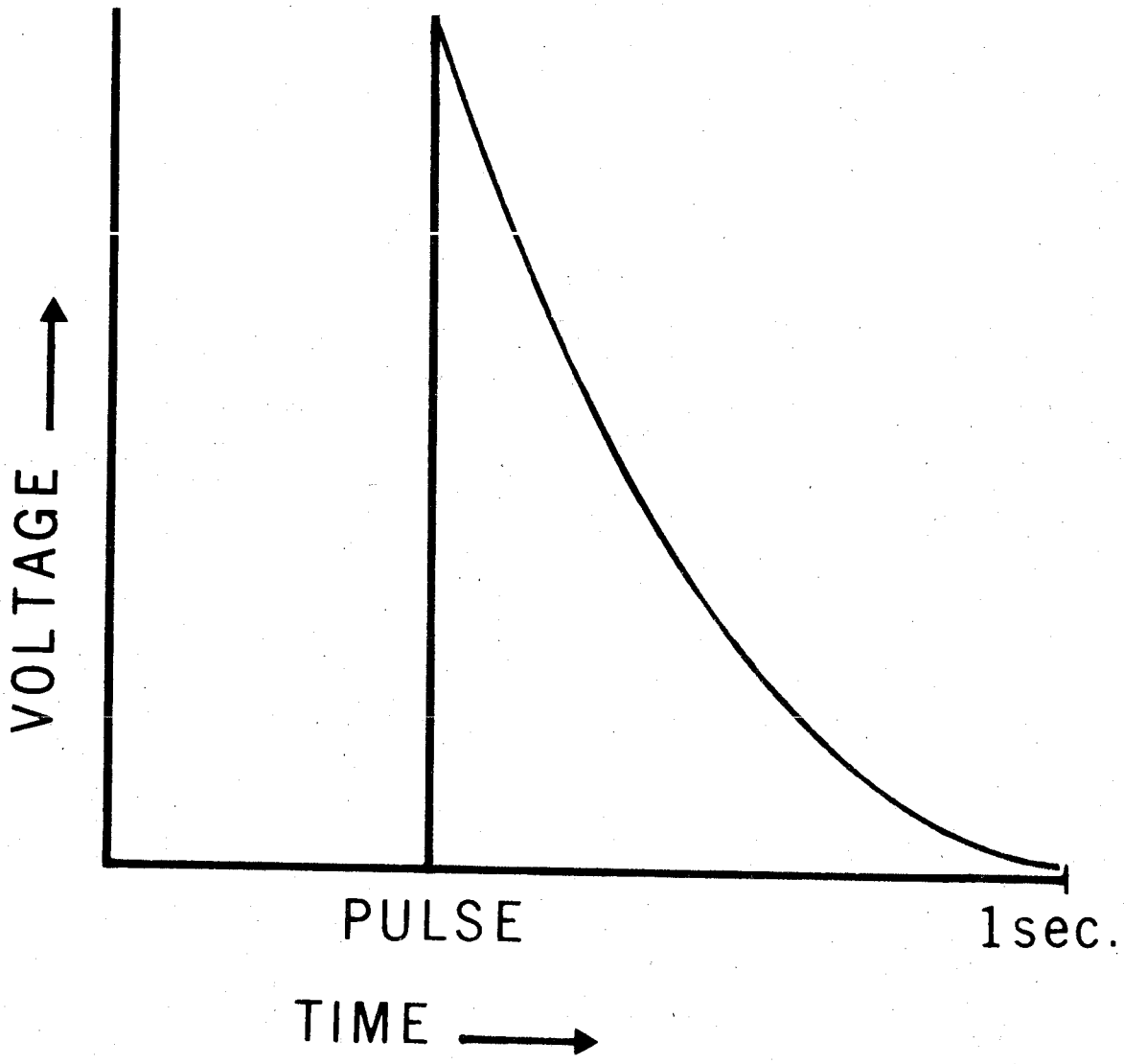

PHOTOCELL
22.5v
RELAY
1.5v
TRIODE ATTENUATOR
PULSE FORMER
CLOCK
RELAY
DIGITAL VOLTMETER & TAPE PUNCH
METER
CHART RECORDER

Fig. 5: Output of ratemeter in response to single input pulse.


VOLTAGE
PULSE
1sec.
TIME

1000 counts/min. (CPM), but usually the 250 and 500 ranges were used for T. lineatum and D. pseudotsugae, respectively. This permitted recording of small flight velocity changes and allowed easier reading of the graphs. If the time constant was 56 seconds, then small fluctuations in the flight velocity were lost because of the slow reaction time of the ratemeter, even though the total flight characteristics were still recorded. The count range was preadjusted according to the previous known maximum flight speed of the species used, so as to maintain the approximate full range of flight velocities of the insect within the meter scale of zero to 100. Thus the recording indicates the flight speed relative to the maximum for the species tested. Whenever the ratemeter recording insect flights exceeded 20% of the full-scale, a relay closed allowing an electric clock to run. This gave an easy means of tabulating total flight time and pretest flight periods.

Permanent recordings were made with a 10 millivolt potentiometric recorder at a chart speed of 2.5 cm/min. To convert the current produced by the resistance-capacitance circuit (which the meter reads) into a voltage, a fixed resistor was put across the meter. The potentiometric recorder was connected to measure the voltage across the resistor.

FLIGHT TESTS

Beetles were tested on the flight mill for their response

to insect and host olfactory stimuli after varying periods of pretest flight experience. In all tests, the receptacle containing the volatile to be tested was placed underneath the flight platform so that the odor path and the arc of the flying insect coincided (Figs. 1 and 2). As a standard stimulus, the insect was exposed to the odor from 3 g of material (e.g. attractive female frass or ground host phloem tissue) for one minute. Occasionally longer stimulus durations were used. Repetitive stimuli were usually administered after a 2 minute flushing period in which the beetle flew through odor-free air.

Data recorded on each chart were: species, sex, prestimulus flight time, count range, time constant, chart speed, stimulus, time of day, temperature, relative humidity, barometric pressure and test insect emergence date and locality. When a test was over or when a beetle ceased flying, the chart recording was filed for later analysis.

ANALYSIS OF D. PSEUDOTSUGAE LIPID METABOLISM AND GAS EXCHANGE[2]

In order to investigate the lipid metabolism of D. pseudotsugae during flight, three separate groups of 30 freshly emerged male beetles were flown on auto-recording flight mills for 1, 2 and 5 hours as previously described. After flight the insects were

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[2] This work was done in collaboration with S.N. Thompson, Graduate Student, Department of Biological Sciences, S.F.U.

preserved by deep freezing. Three non-flown control groups were individually frozen before, during and after the experimental period.

After initial wet and dry weight determinations, the insects were homogenized in a tissue grinder, the total lipid extracted (Bligh and Dyer 1959), saponified (Lepper 1950) and esterfied with diazomethane (Schlenk and Gellerman 1960). Fatty acid analysis was carried out on a Carlo-Erba gas-liquid chromatograph with hot wire detector. Two meter glass columns (4 mm I.D.) were packed with 15% diethylene glycol succinate on Chromosorb W(AW), mesh 60/80. The carrier gas was helium. Methylated fatty acid standards containing myristic (C14:0), palmitic (C16:0), palmitoleic (C16:1), stearic (C18:0), oleic (C18:1), linoleic (C18:2) and linolenic (C18:3) acids were run with each sample for identification purposes. The unsaturated fatty acids used in the standard mixture, palmitoleic, oleic, linoleic and linoleic acids, are specific isomers, each of which belongs to a group of isomers represented as C16:1, C18:1, C18:2 and C18:3 respectively. However, since the chromatographic technique used only separates the mixture according to chain length and degree of saturation, any one of the isomers in a group may serve as a standard for that group. The unsaturated acids were not degraded to determine which isomers were present.

In contrast to previous manometric techniques (Chadwick 1949, Weis-Fogh 1967, Williams et al. 1969), the CO_2 expired by flying

male beetles was measured with an infrared gas analyzer in a modified open system similar to that described by Hamilton (1964). Gilson manometric techniques (Gilson 1963) were used to measure O_2 consumption. The rates of change in concentration of these gases were then compared and respiratory quotients (RQ) calculated for non-flying and flying insects.

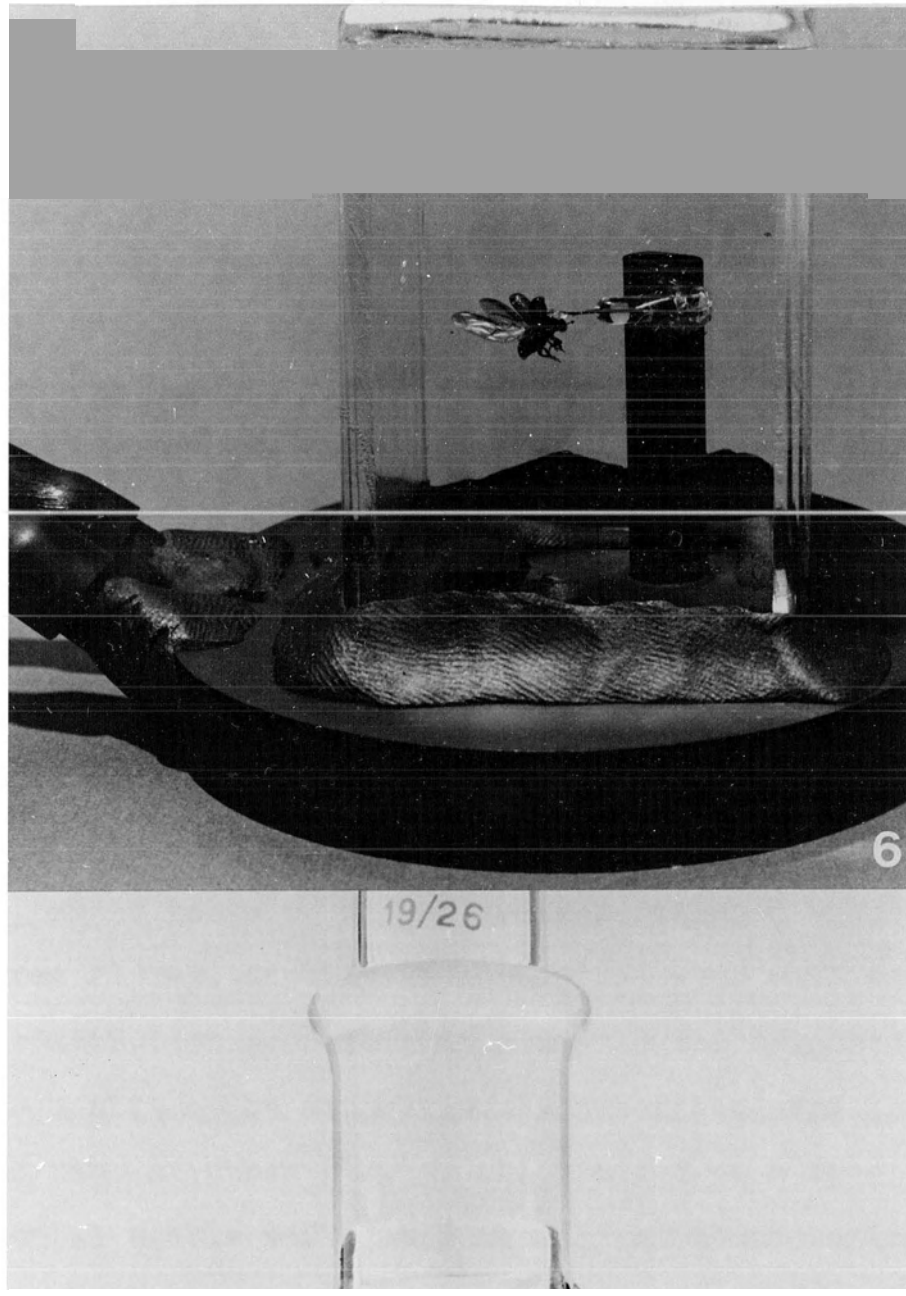
Measurements of CO_2 concentration were made in a small plexiglass flight chamber (5.08 x 5.08 x 7.62 cm outside diameter) with a rubber base (Fig. 6), a diaphragm pump and the IR gas analyzer which were interconnected with plastic tubing. The system had a total volume of 231 cc and a flow rate of 410 cc/min. The analyzer was calibrated by adjusting the gain control with a known concentration of prepared gas (250 ppm CO_2 in N_2) so that a deflection of 50% to 60% on the recorder meter represented a change in concentration of 85 ppm. Because of the rather small size of the Douglas-fir beetle, a closed circulation method was used to give accumulated concentrations rather than an open circulation system as used by Hamilton (1964).

The test insects were suspended inside the plexiglass chamber by a mount consisting of a short piece of wire partially heat sealed into a piece of glass, which in turn was glued onto the exhaust port and extended 3 cm into the chamber from the base. To this firm base the prothorax of a beetle was attached with a soft silicone glue (Fig. 6).

After a beetle was attached, the chamber was sealed with plasticine and allowed to reach equilibrium with the system open.

Fig. 6: Flight chamber used in conjunction with an IR gas analyzer for the isolation and quantitative measurement of CO_2 expiration of D. pseudotsugae males.

Fig. 7: Flight chamber used in conjunction with a Gilson respirometer to measure O_2 consumption of D. pseudotsugae males.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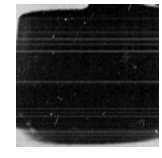

At atmospheric CO_2 concentration the instrument read below 50% of full scale. When a test sequence began, the system was closed and the concentration within the plexiglass cell was measured with the gas analyzer and recorded on a strip chart recorder. Measurement of the CO_2 output of non-flying beetles were made by keeping the light intensity fairly low, because as soon as it was increased for any length of time the insects usually started flying steadily. To keep the temperature constant at 26°C, a water bath was used to cool the light source. Individual insects were tested either in the non-flying group or in the flying group, but not in both, and if an insect stopped flying during the flight test period the recordings were not included in the calculations. Groups consisted of 20 to 25 insects each. Tests of beetles were finished when the recorder readings were greater than 60% on the meter scale, while tests of flying beetles finished whenever the insect stopped flying, usually when readings were well past 60%.

In O_2 consumption measurements a beetle was attached by the prothorax to a wire mount as previously described, and the wire was inserted into a rubber stopper which acted as a base (Fig. 7). The mounted beetle was placed in a 25 ml round bottom flask, which was then attacked to the respirometer and allowed to equilibrate for 15 minutes at 26°C. Usually 10 insects were run simultaneously on a 14 station respirometer, leaving 4 stations as control thermal barometers. When the system had equilibrated, the flasks were closed and readings began. Non-flying values were obtained with one group of insects by leaving the water.

bath tank lights off. Flight was induced in another group of insects by turning on these lights. Again the insects were continually observed and if any stopped flying during the test period readings were discarded. Readings for groups of flying and non-flying insects were taken every 5 minutes for 2 hours.

RESULTS AND DISCUSSION

FLIGHT PREPARATION: AIR SWALLOWING

When beetles were taken from cold storage, their inclination to fly varied. Flight testing usually started in the morning with 10 beetles being mounted on flight mills at a time. Often after being mounted on the flight mills, the beetles moved their legs very rapidly and flexed their abdomens up and down before any flight took place. Typically, freshly mounted beetles did not begin to fly unless they had been allowed to warm up for at least 10 minutes, presumably the time necessary for the flight muscles to warm up to operating temperatures (Chapman 1955b; Chapman and Kinghorn 1955; Atkins 1959, 1966b).

Although all the beetles tested should have been in the dispersal phase as they had been cooled and stored right after emergence, about 80% to 90% of the test population reacted similarly and either flew or did not fly, apparently depending on factors other than those controlled in the laboratory. The only observable phenomenon that could be correlated to the proportion of beetles that would fly was the outside cloud cover. When there was any cloud cover at all, the beetles flew very erratically and for only short periods, but when the sky was clear the majority would fly strongly and continuously soon after they were mounted on flight mills. The laboratory had no windows, was at a relatively constant temperature and the lighting was

constant. However, the barometric pressure and relative humidity associated with cloudy weather could influence flight initiation and presistence in the laboratory.

Chapman (1955b) observed that in both T. lineatum and D. pseudotsugae dissected immediately after flight, there was a large gas bubble in their ventriculus, greatly distending it. Lesser amounts of gas were also observed in the proventriculus and oesophagus, but the rest of the digestive system was almost empty. Although Chapman did not suggest the purpose of this bubble, both Wellington (1948) and Graham (1961) observed that reversal of phototactic reactions occurred in spruce budworm larvae and in adult T. lineatum respectively. Photic reversal could be induced in budworm larvae by increasing the internal pressure of the insects by air injection, food ingestion and ligation, or in ambrosia beetles by allowing air swallowing. Graham (1961) proposed that as the beetle obtained more flight exercise it swallowed more and more air until the internal pressure possibly activated stretch receptors which inhibited photopositive responses. He also found that when the ventricular gas bubble was punctured and deflated, the beetles reverted to their photopositive behavior.

To determine whether this air swallowing mechanism could be related to initiation of flight in newly emerged insects, the ventriculus was observed in D. pseudotsugae dissected before warming up, after warming up for 10 minutes and after one hour of flight. In all cases where the beetles were allowed to warm

up (N=10) or fly (N=10), the ventriculus contained similar sized gas bubbles. However, before warming up (N=5), beetles had no air bubble in their ventriculus. As soon as they were allowed to move about and warm up, air swallowing began (Fig. 8). In three of the insects allowed to warm up for 10 minutes, small gas bubbles could be observed entering the ventriculus and adhering to other bubbles as if covered by a viscous coating. Gradually as more bubbles entered, the smaller bubbles coalesced (Fig. 9) until finally only one large bubble remained (Fig. 10). Although exact measurements were not made, the air bubbles in insects that had warmed up were approximately the same size as in insects that had flown. Although I did not look for ventricular air bubbles in T. lineatum, C.E. Slater (personal comm.)[3] has noted their frequent occurrence in T. lineatum adults held for various periods after emergence without flight at room temperature.

At variance with Graham's (1961) hypothesis that air swallowing by T. lineatum during flight eventually causes a reversal of photopositive response, it appears that in D. pseudotsugae air is ingested before flight and little or none is ingested during the first hour of flight. The release of chemotropic response following flight exercise (Graham 1959, 1960) must be controlled by other factors such as lipid metabolism (Atkins 1969).

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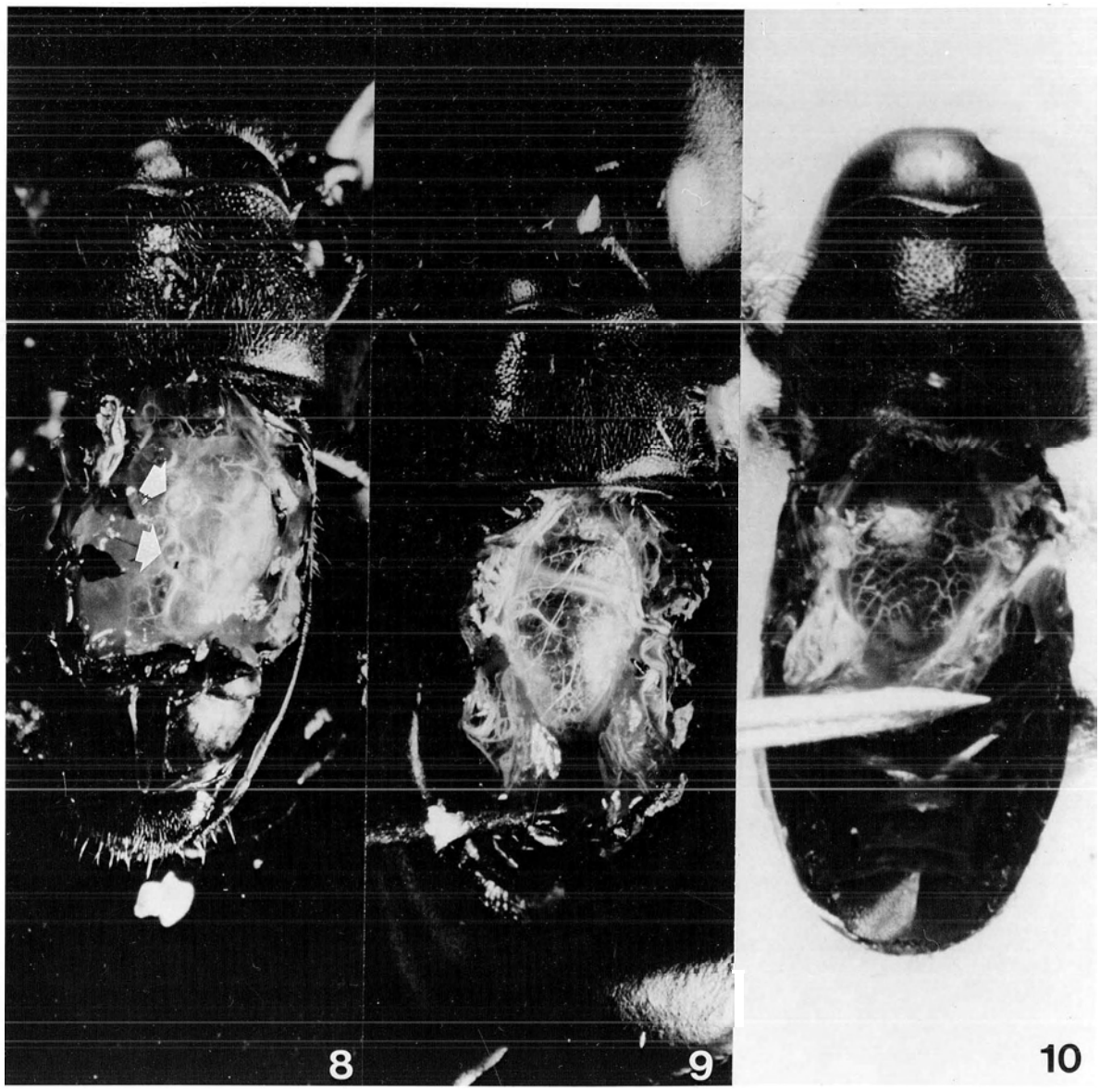
[3] Graduate Student, Department of Biological Sciences, S.F.U.

Fig. 8: Small air bubbles (arrows) in the ventriculus of D. pseudotsugae male, dissected immediately after removal from 4°C.

Fig. 9: Two large air bubbles in the ventriculus of D. pseudotsugae male, dissected after warming up for 10 minutes.

Fig. 10: Single air bubble in the ventriculus of D. pseudotsugae male, dissected after warming up and flying for 60 minutes.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The insects may be using these gas bubbles as an internal barometer, not to detect high or low barometric periods but rather short term changes during unstable periods of low pressure. Generally (Critchfield 1966), and locally (R.B. Sagar, personal comm.)[4], during low pressure periods, the barometric pressure is quite unstable and the micro-barometric changes are much more pronounced than in fair weather. Fluctuations of this type tend to occur within short time periods of one to 5 minutes per cycle and thus could be much more readily detected by the insect than the slower overall barometric pressure changes. Also, during low pressure and transitional pressure periods, mean wind speeds are generally much higher than in stable high pressure conditions (Middleton and Spilhaus 1953). Surface friction in forest boundary micro-habitats from these winds might then cause minute and relatively rapid (within one second or so) fluctuations in barometric pressure (Geiger 1966) which also might be detected by means of the gas bubbles in the ventriculus. A mechanism for detecting short term air pressure variations could enable dispersing insects to remain flightless or terminate flight during unstable weather.

BEETLES IN FLIGHT: STOPPING POSTURES

Both *T. lineatum* and *D. pseudotsugae* show similar arrestment

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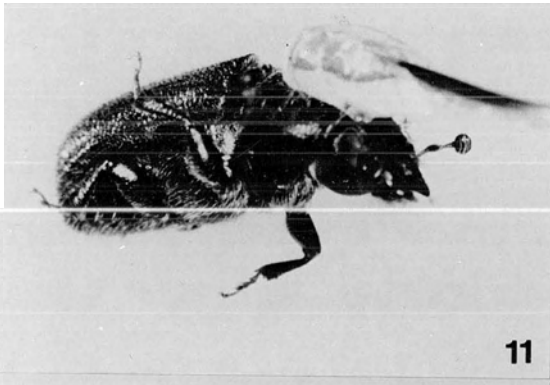
[4] Assistant Professor and Head of Department of Geography, S.F.U.

reactions to frass and phloem volatiles on the flight mill. These reactions can be classified into three principal types: wings completely folded (Fig. 11), wings out (Fig. 12) and wings folded down and back (Figs. 13 and 14). Although it is difficult to be sure that reactions of insects on the flight mill are similar to those which would occur in free flight, certain arrestment responses consistently occur with specific stimuli and after similar durations of flight. Therefore, these arrestment patterns might be useful as an indicator in bioassay techniques.

The first type of arrestment response, with wings completely folded, is a charactertistic response to frass and phloem stimuli, although just what volatile portion or portions of these stimuli elicits this response is not known. Usually within a few seconds after encountering the stimulus, the beetle folds its wings very quickly and completely closes the elytra, meanwhile "clawing" the air with its tarsi - presumably grasping for a substrate (Fig. 11). This is quite a rapid stopping response and could also be characterized descriptively as a "drop-stop".

The second type of arrestment response is distinguished by both the elytra and the wings being fully extended either horizontally or inclined upwards (Fig. 12). This posture is typified by three different modes of use. One is simply a glide with no beating, flexing or planing of the wings until the flight mill stops; then the wings are folded and the elytra closed. The second is similar to the first, except that the insect vibrates its wings through a small arc (about 10 degrees) for a few

Figs. 11-14: Flight arrestment postures for D. pseudotsugae.
Fig. 11, "drop-stop" with wings completely folded;
Fig. 12, "hover-glide" with wings extended horizontally and elytra raised; Fig. 13, "wings-back glide" with elytra in normal flight position; Fig. 14, "wings-back glide" with elytra almost closed.



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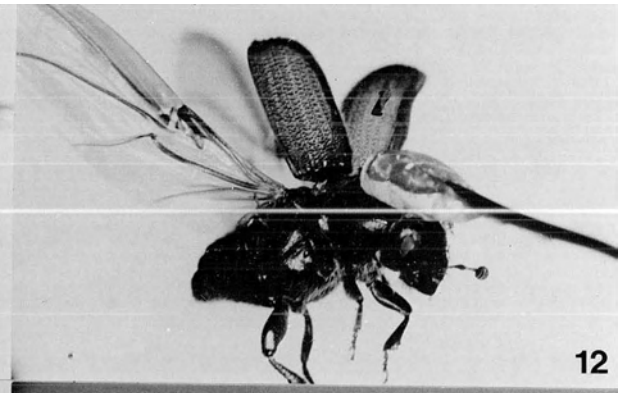

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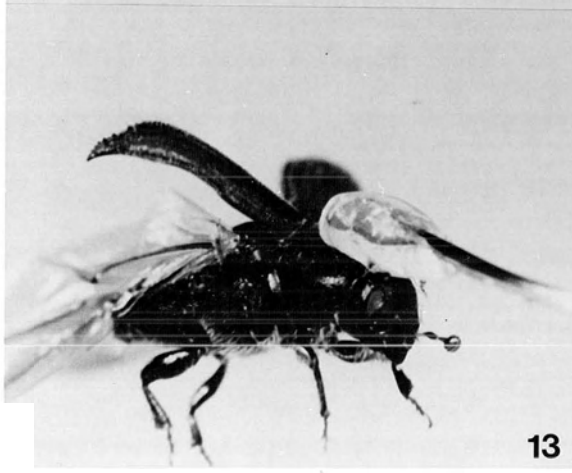

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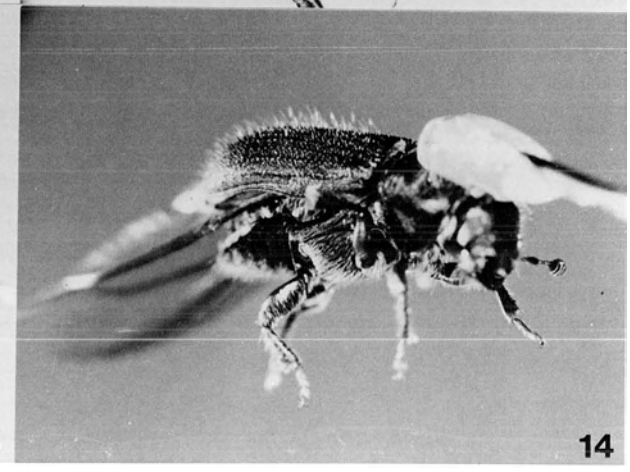

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seconds, then glides and then repeats the wing vibration. This sequence usually continues until the flight mill stops or the stimulus changes. A third variation of this response occurs when the insect vibrates its inboard wing continuously in the same small arc, while planing with its outboard wing held straight down - as if an attempt to turn out of the imposed arc of the flight mill.

The third type of stopping response, a glide, is usually elicited soon after the insect encounters an arresting volatile. Typically, the wings are folded down at each side and held back while the elytra are left either in their normal flight position (Fig. 13) or are folded back in their resting position but left slightly open (Fig. 14). When the circular motion of the flight mill has ceased, the insects usually remain in this glide posture for approximately 20 seconds, and then slowly fold up their wings and completely close their elytra.

TYPICAL FLIGHT AND ARRESTMENT RECORDINGS

Many and varied chart recordings were obtained of the flight of *T. lineatum* and *D. pseudotsugae*. In many cases arrestment was recorded in response to such stimuli as attractive female frass and freshly ground phloem tissue. In addition, factors such as weather, prolonged flight and prestimulus flight exercise influenced the recordings. As the body angle of the hand-mounted insects is variable and critical to their maximum flight speed,

all recordings were treated as relative.

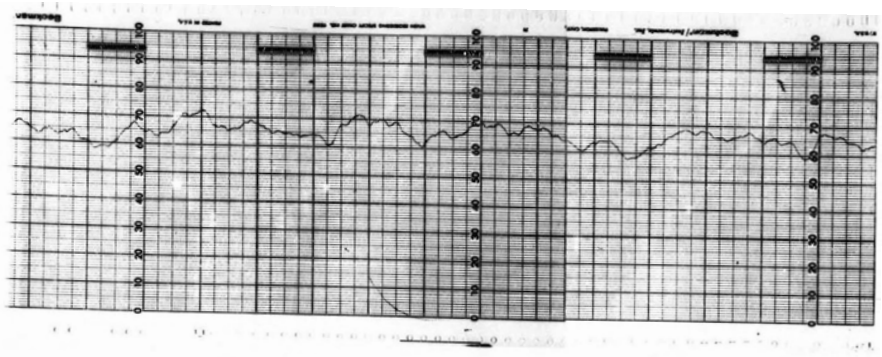
Trypodendron lineatum

Figs. 15 to 22 show typical flight chart recordings of male ambrosia beetles, T. lineatum. Flights of this insect were recorded on a counting range of 100 or 250 CPM and a time constant of 14 seconds. At this range and sensitivity both the fastest flight speeds (which were actually one-half of the counting range because each revolution of the flight mill generates two counts) and slight fluctuations in speed could easily be recorded.

In a typical non-arrestment response of a beetle that was not preflown (Fig. 15), there is no arrestment to any of the stimuli and the flight continues as before. Although no arrestment occurred, the flight was quite erratic and rapid changes in flight speed continuously took place. This is typical of freshly mounted specimens. In addition, freshly mounted insects are more susceptible to external influences (e.g. vibration, light intensity changes, wind changes or movement near the flight mill) and may stop flying. The flight of a beetle which was preflown for 30 minutes becomes much more regular (Fig. 16). After 10 minutes of continuous flight, the tendency to respond to external conditions is not apparent.

In a typical flight arrestment response (Fig. 16), a preflown male beetle stopped flying completely approximately 10 seconds after exposure to the frass stimulus. The tracing

Figs. 15-22: Flight chart recordings from T. lineatum males. Time constant is 14 seconds; count range per minute (CPM) is 250 (Figs. 15, 19-21) and 100 (Figs. 16-18). Solid bars represent one minute exposure to odor of 3 g of attractive female frass. Recordings read from right to left. Pretest flight experience and significant flight and response characteristics are: Fig. 15, not preflown, no arrestment response; Fig. 16, preflown 30 minutes, arrested by stimulus; Fig. 17, preflown 30 minutes, response to repeated stimulus; Fig. 18, preflown 30 minutes, "hover-glide" response; Fig. 19, preflown 30 minutes, "hover-glide" plus arrestment response; Fig. 20, preflown 30 minutes, arrested on second stimulus; Fig. 21, preflown 15 minutes, arrested on second stimulus; Fig. 22, not preflown, erratic response including planing of outboard wing until flight stopped.



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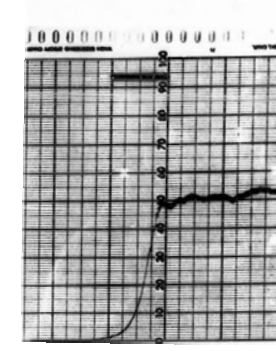

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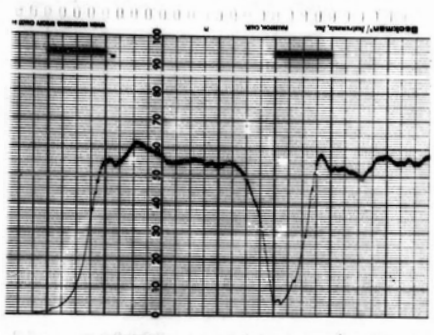

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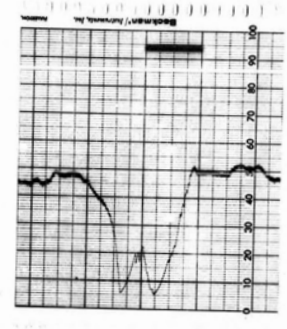

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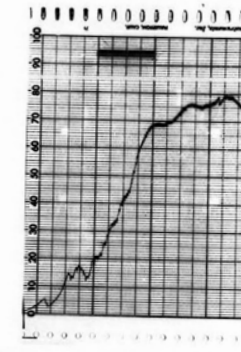

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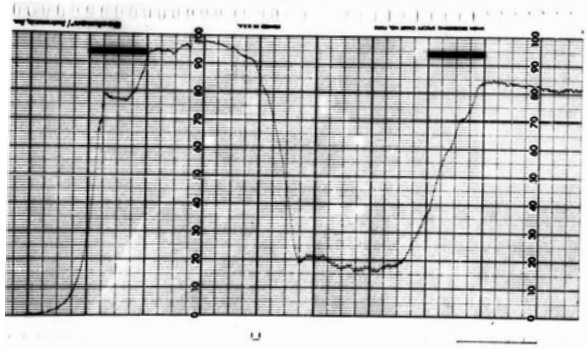

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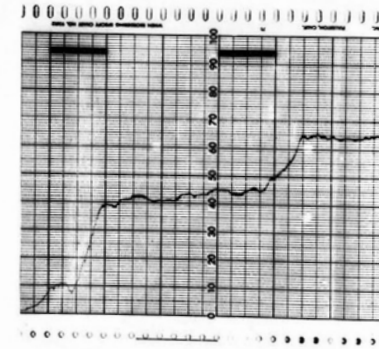

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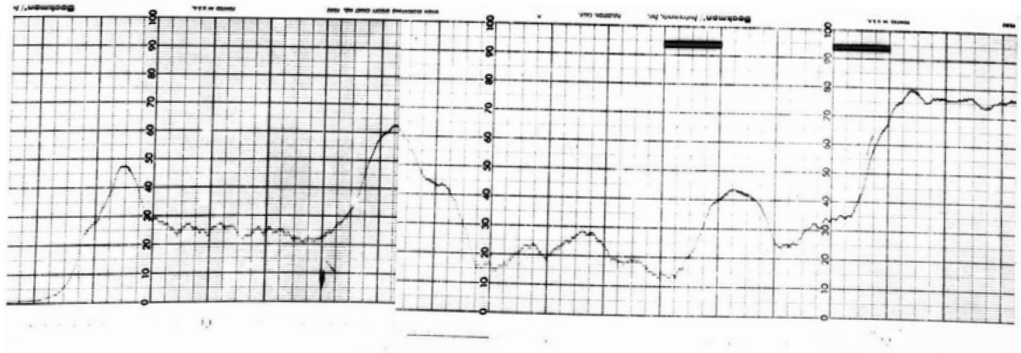

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shows the typical decay curve of the apparatus. The curve breaks sharply from the main flight line (at 50 on the relative scale) and decays fairly smoothly down to zero, indicating a "drop-stop" with no further flight by the insect.

Fig. 17 indicates the response of another insect that had also been preflown for at least 30 minutes and the stimuli introduced at 4 minute intervals. As often is the case, the insect increased its flight speed slightly, as soon as it encountered the stimulus and before its flight was arrested. Immediately after the first stimulus was removed, the beetle resumed flight until it encountered the second stimulus, whereupon it abruptly ceased flying and glided to a stop.

In another characteristic response of a preflown beetle (Fig. 18), the insect adopted an open-winged hover-glide posture for the first 40 seconds of the stimulus, vibrated its wings in a small arc for the rest of the stimulus duration, glided for about 20 seconds after the frass had been removed, and then resumed full flight. This type of response was frequently observed in freshly preflown insects and possibly indicates an attempt to search for and hover over the source of the arrestment stimulus.

Fig. 19 also depicts a hover-glide response, but in this case the slight vibration of the extended wings began about half-way through the stimulus duration (after 30 seconds) and continued for 30 seconds after the stimulus had been removed. Only then did the insect glide to a stop. The responses shown

in both Figs. 17 and 18 were considered as arrestments because their relative flight speeds fell below 10% of that at the introduction of the stimulus.

Fig. 20 shows an arrestment response initiated by the second stimulus. On introduction of the first stimulus, the preflown insect immediately started to glide until about 30 seconds after the frass had been removed, at which time the beetle vibrated its wings in a small arc and propelled itself forward at a slow rate. After approximately 100 seconds of this behavior, it resumed rapid flight but at a higher speed than before stimulation. On encountering the subsequent stimulus, the insect reduced its flight speed by about 20% and after 40 seconds of stimulus abruptly stopped flying. Again the chart recording shows that, although flight speed changes suddenly during transitions from high to low flight speeds and vice versa, flights at either high or low rates are characteristically regular and stable - as is usual when insects have extensive flight experience.

In a similar arrestment response on the second stimulus (Fig. 21), the pretest flight experience was only 15 minutes. Inexplicably, a significant reduction in flight speed occurred prior to the first stimulus. However, the stimulus induced a change in flight pattern in which the insect alternately vibrated its fully extended wings and then glided every few seconds for the full 3 minutes until the second stimulus was introduced. At this time, the insect immediately glided to a stop. Such behavior indicates the need for visual observation to supplement chart

recordings to produce a more meaningful bioassay.

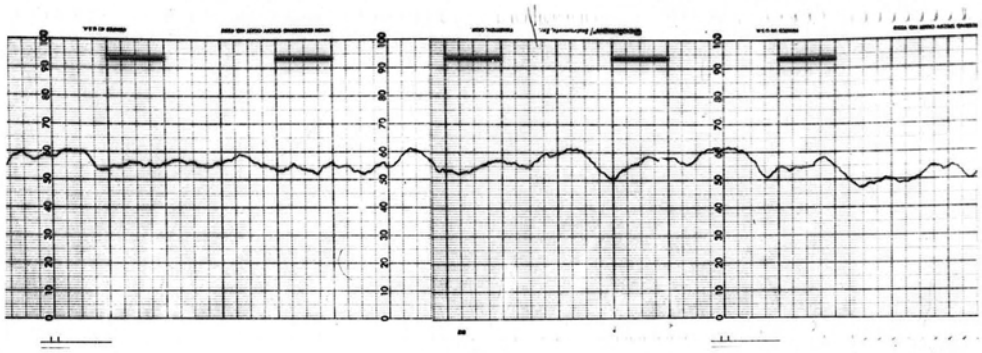
One beetle, which had not been preflown, was not arrested, but at each introduction of the frass stimulus immediately began to glide, then vibrated its wings, then glided again; this cycle of behavior produced a very erratic flight pattern (Fig. 22). After the frass was removed for the second time the beetle began a type of turning response (arrow), beating its inboard wing while planing its outer wing as if attempting to turn out of the imposed arc of the flight mill. This response is similar to one in D. pseudotsugae. With one wing propelling the insect and the other planing, the insect continued flying at erratic speeds until it abruptly stopped. Such flight behavior, although not a typical response, was observed in several tests with non-preflown T. lineatum males.

Dendroctonus pseudotsugae

Since D. pseudotsugae is larger and flew faster than T. lineatum, a greater counting range was needed on the ratemeter, usually 500 or 1000 on the relative scale. In addition, a time constant of 14 provided the required capacity for the higher counts and the sensitivity allowed small fluctuations in flight speed ($\pm$ 1%) to be detected.

An unresponsive male beetle, partially preflown, was not arrested by five consecutive frass stimuli (Fig. 23a) followed by three of freshly ground phloem tissue (Fig. 23b). This insect had completed only 60 of the required 120 minutes pretest flight

Figs. 23-27: Flight chart recordings from D. pseudotsugae males. Time constant is 14 seconds; count range per minute (CPM) is 500. Solid bars represent one minute exposure to odor of 3 g of attractive female frass or ground host phloem tissue. Recordings read from right to left. Pretest flight experience and significant flight and response characteristics are: Fig. 23a,b, not preflown, no response to 5 repeated frass stimuli (Fig. 23a) and 3 phloem stimuli (Fig. 23b); Fig. 24, not preflown, erratic behavior in early flight; Fig. 25, preflown 9 hours, typical fatigue flight pattern; Fig. 26, preflown 2 hours, arrestment to repeated frass stimuli; Fig. 27, preflown 2 hours, no arrestment to frass stimulus.



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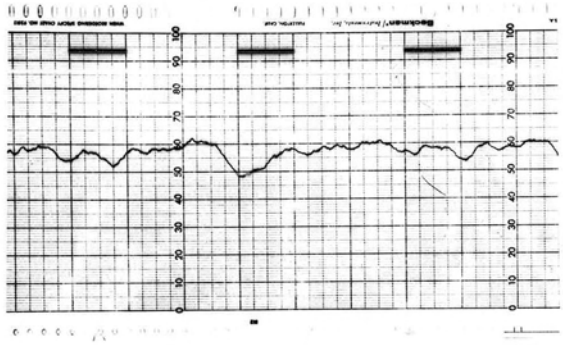

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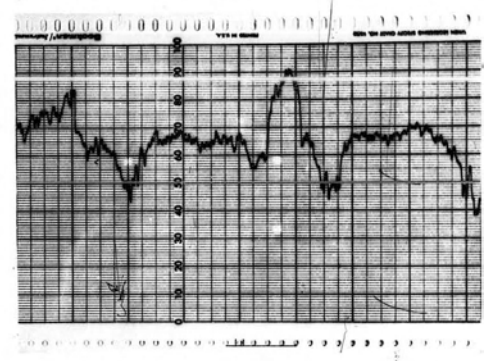

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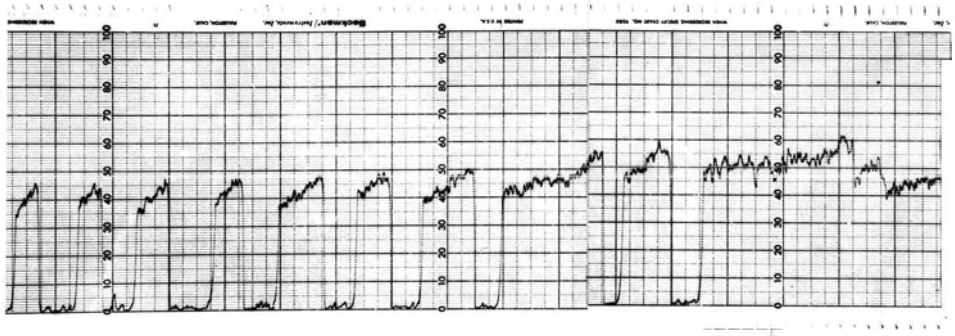

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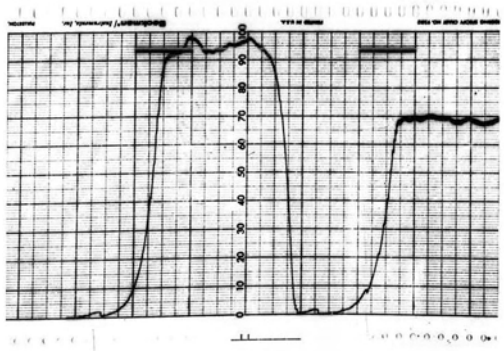

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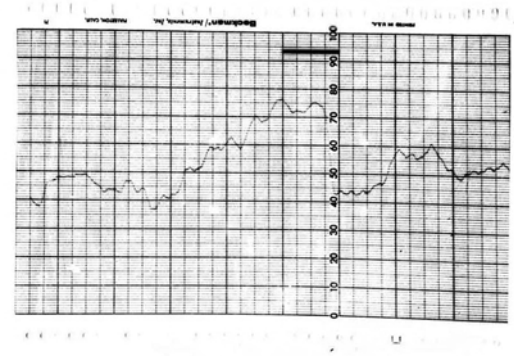


27

period and showed only minor effects such as a slight increase in flight speed with the removal of the stimuli. The flight is slightly erratic and irregular, although not as erratic as it would probably be earlier in the flight period. As in T. lineatum, the frequency of fluctuations in speed during non-test periods generally decreases as the amount of pretest flight time lengthens.

Fig. 24 shows a control flight recording of a male beetle that had no pretest flight experience. The chart recording indicates, first, the very erratic nature of the flight in a freshly mounted insect and, second, the possible unstabling effect of an overcast day on the flight pattern. As with T. lineatum, D. pseudotsugae just after commencing flight is very sensitive to vibrations, wind speed changes or gusts, light intensity changes, movement near the flight mill and the numerous odors that occur in the laboratory. Any of these factors can terminate flight in the early stages. However, after some pretest flight experience has been obtained, these factors, if transitory, usually will not deter flight. In addition, during overcast days the nature of the flight was generally so erratic and the periods of flight so short that no meaningful bioassays could be conducted. Even if the insects were allowed to remain on flight mills all day during overcast days, they rarely began to fly at regular speeds and remained very sensitive to the previously mentioned factors, stopping flight at the slighest disturbance. The beetle usually used the "drop-stop" type of arrestment behavior (Fig. 11) under these circumstances but often did not resume flight even after artificial

stimulation (Chapman 1955b) with puffs of air.

Fig. 25 is a control recording of a male beetle that has flown continuously for 9 hours without any bioassay testing. The flight pattern is common in insects which have flown for long periods. Usually the insect either flies with its wings fully extended (Atkins 1960), using a wingstroke about 2/3 normal or else it stops flying, leaving its wings fully extended horizontally until it begins to fly again. The flight periods gradually become shorter and shorter until they are only about half a minute, whereupon the insect stops flying, folds its wings and closes its elytra for several hours. When (and if) flight is finally resumed, the time required until it again begins these short flights and stops with wings extended is much reduced.

In a typical arrestment response of a preflown male beetle to the frass stimulus (Fig. 26), the insect folded its wings down and back and partially closed its elytra (Fig. 14). After about 90 seconds it resumed flight at a higher flight speed than previously, a very common characteristic. Usually if no further stimulation occurred, the beetle would gradually reduce its flight speed and within about 10 minutes would again be maintaining the previous flight speed. On the second stimulation the arrestment response occurred, with the wings folded down and back but the elytra closed. The wings were gradually pulled in and tucked under the elytra. Usually if the wings were folded soon after stopping, it indicated that the insect would soon fly again. Conversely, if the wings were left extended for any length

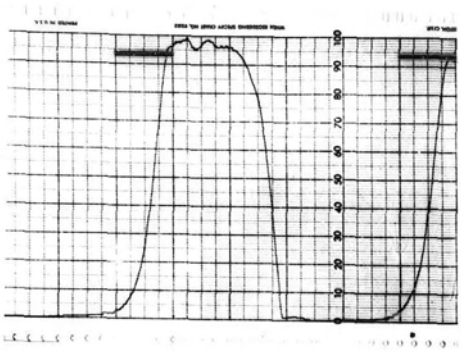
of time after the flight mill stopped, then the insect generally did not fly again very soon afterwards.

Occasionally male D. pseudotsugae that are fresh and vigorous, when they have flown for the prescribed pretest period, are not arrested by a frass stimulus. They may increase their flight speed (Fig. 27) and, after the stimulus has been removed, gradually reduce their speed to the prestimulus level. In addition, the flight speed is usually erratic in nature for about 5 minutes after the stimulus is removed.

The arrestment response of male D. pseudotsugae to freshly ground phloem tissue (Fig. 28) is similar to the frass response. On exposure to the first stimulus, the insect immediately folded its wings and closed its elytra in the typical "drop-stop" manner, and remained in that posture until well past the duration of the stimulus. When it again began to fly, the insect started to vibrate its inside wing and plane the outboard one, a type of flight also observed in T. lineatum. Using this flight pattern it regained prestimulus flight speed. When it encountered the phloem stimulus the second time, it glided with wings fully extended until the flight mill stopped and then folded its wings and closed its elytra.

Preflown female beetles are also arrested by a phloem stimulus (Fig. 29). In response it at first continued to fly, but beat its wings more slowly and decreased its flight speed. After 30 seconds, it glided to a stop with its wings fully extended, immediately folded them up and closed its elytra.

Figs. 28-31: Flight chart recordings from D. pseudotsugae males (Figs. 28, 30, 31) and female (Fig. 29) exposed (solid bar) to odor of 3 g of ground host phloem tissue for one (Figs. 28, 29) or 2 (Figs. 30, 31) minutes. Time constant is 14 seconds; count range per minute (CPM) is 500. Recordings read from right to left. Pretest flight experience and significant flight and response characteristics are: Fig. 28, preflown 2 hours, arrested to 2 repeated stimuli; Fig. 29, female, preflown 2 hours, arrested to stimulus; Fig. 30, preflown 2 hours, not arrested to prolonged stimulus but ceased flying after stimulus removed; Fig. 31, preflown 2 hours, erratic flight in overcast weather, arrested to 2 minute stimulus in"on-off-on" hover-glide response.



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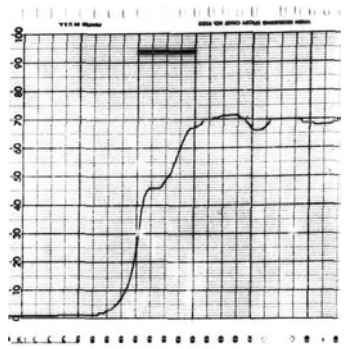

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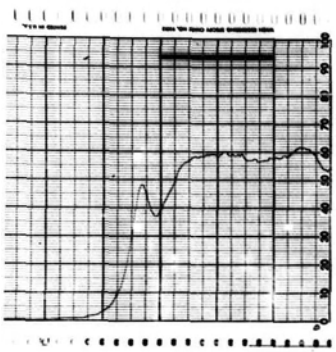

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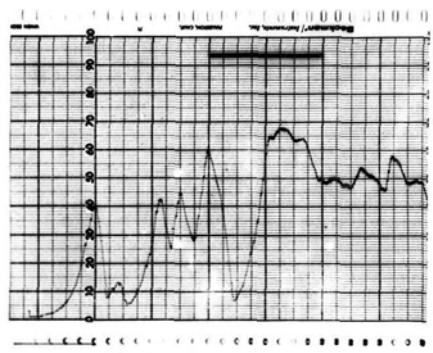


31

Fig. 30 demonstrates the effect of prolonged (2 minute) exposure to phloem stimulus on a male D. pseudotsugae that had been preflown. Although the insect flew at fairly even flight speeds, it was unresponsive to the stimulus until near the end of the stimulus duration when it started to glide with wings fully extended. However, when the stimulus was removed the beetle immediately started to fly, increasing its flight speed until it stopped after 15 seconds and began to glide with wings fully extended until the flight mill stopped. Typically this beetle would not normally have flown again for at least 30 minutes. However, when stimulated by a puff of air, it flew erratically for short periods.

During overcast weather periods, the flight of a preflown male D. pseudotsugae is characteristically erratic and varied (Fig. 31). At the introduction of a prolonged (2 minute) phloem stimulus, the beetle increased its flight speed for about 15 seconds, more or less leveled off for 45 seconds, then glided with the wings fully extended. Just before the flight mill came to a stop, the insect vibrated its wings rapidly in a small arc and propelled itself forward. Then it alternately glided and vibrated its wings for 2 minutes, after which it glided with the wings still extended until it stopped. This type of flight could be characterized as "on-off-on" arrestment behavior and typifies the response during cloudly periods or on days when the temperature is above the 30°C optimum (Atkins 1959).

AVERAGE RESPONSE DURING STIMULUS

Single chart recordings, although indicative of a particular beetle's physiological conditioning and response to a stimulus, do not indicate just what is the average response of the population (Atkins 1966c) to a given stimulus under similar conditions. Fig. 32 is a bar graph of the relative mean RPM flight values for 24 T. lineatum males that had been preflown for 30 minutes and exposed to a single stimulus of 3 g of female frass for one minute. Values were taken from the chart recordings zero, 15, 30, 45 and 60 seconds after introduction of the stimulus and one minute after its removal. The average response of the beetles to the stimulus was definitely arrestment since during the duration of the stimulus the population flight speed decreases significantly and continuously. One minute after the stimulus had been removed some of the beetles started to fly again or to increase their speed, thus increasing the average mean RPM at 120 seconds.

Similarly, Fig. 33 shows the mean RPM flight values for 34 preflown male and 23 preflown female D. pseudotsugae to female frass in a single stimulation. The females showed no arrestment response. In fact, the average flight speed actually increased slightly during exposure to the stimulus. However, they continued flying at slightly lower mean RPM values after the stimulus was removed (at 120 seconds). In subsequent tests, of 17 preflown females given repetitive stimuli, only 3 were arrested, 2 on the second and one on the fourth stimulus. The other 14 did not

Fig. 32: Mean percent RPM flight values for preflown male *T. lineatum* to a 3 g single female frass stimulation. Arrows indicate one minute of stimulus duration.

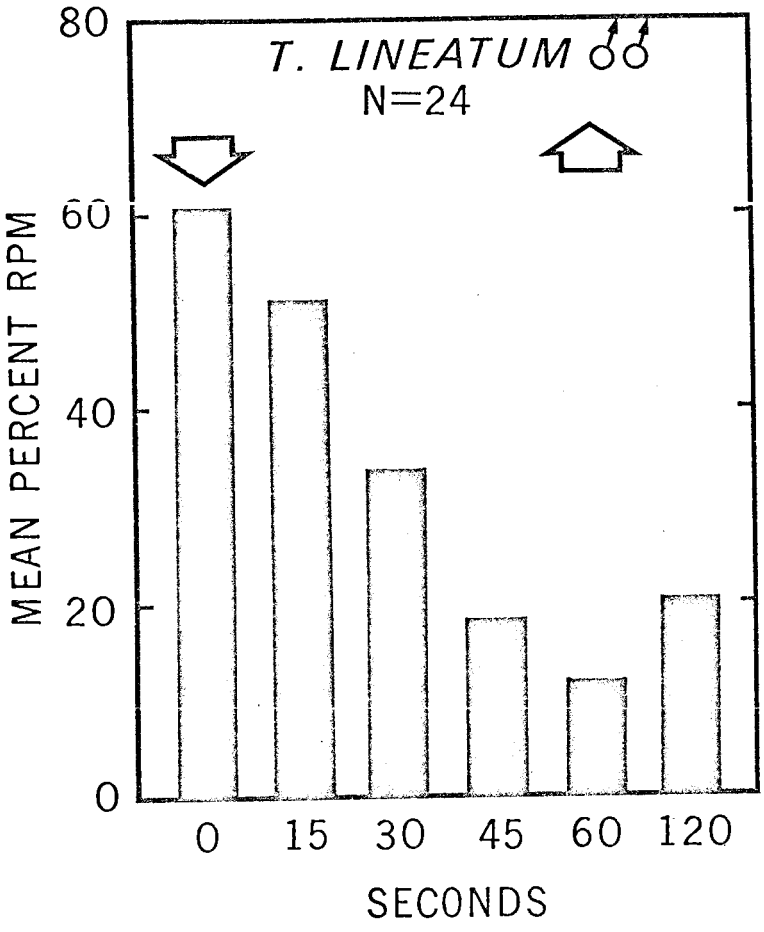
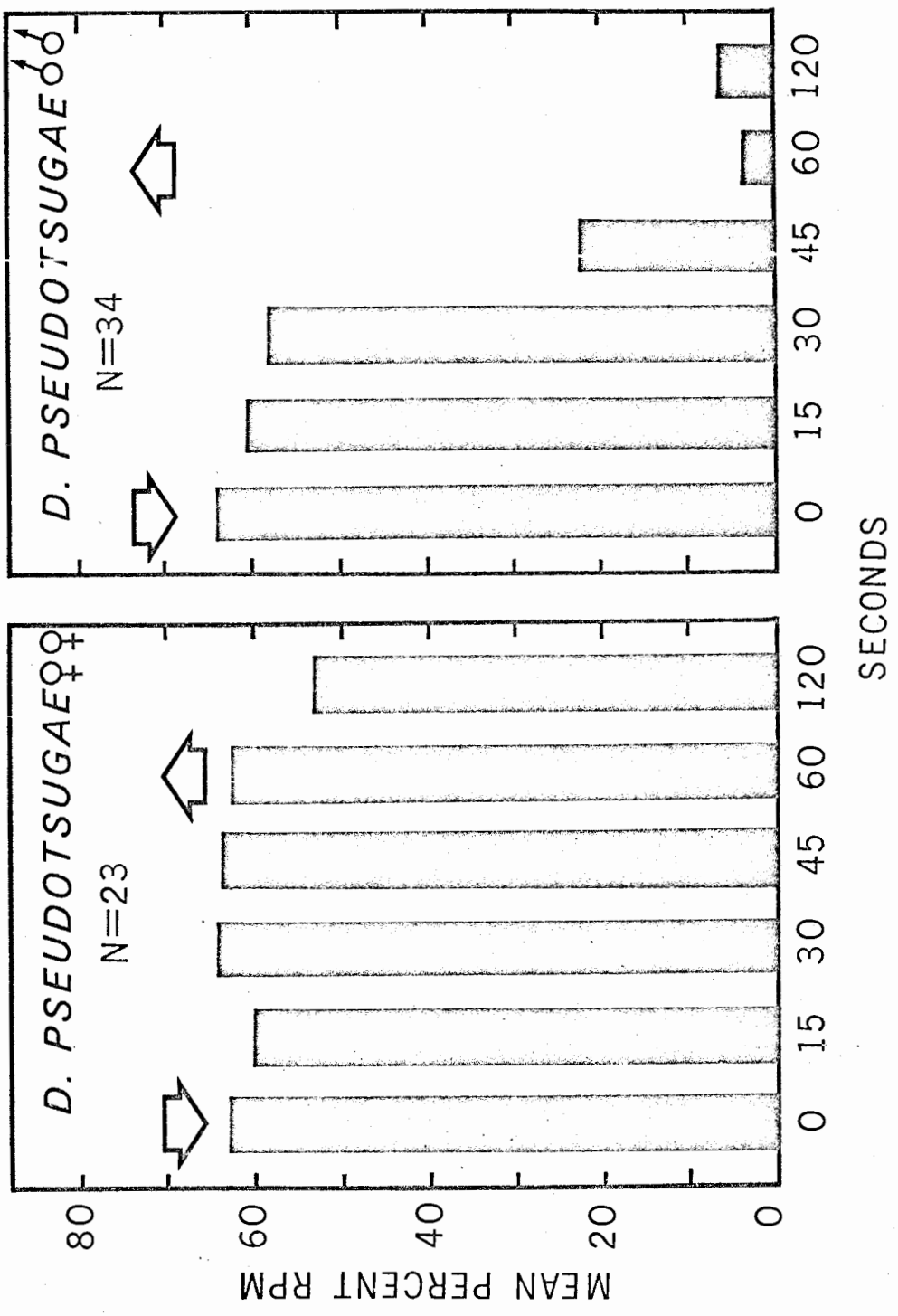

T. LINEATUM ♂♂
N=24
MEAN PERCENT RPM
80
60
40
20
0
0
15
30
45
60
120
SECONDS

Fig. 33: Mean percent RPM flight values for preflown male and female D. pseudotsugae to a 3 g single female frass stimulation. Arrows indicate one minute of stimulus duration.


D. PSEUDOTSUGAE ♀♀
N=23
D. PSEUDOTSUGAE ♂♂
N=34
MEAN PERCENT RPM
0
20
40
60
80
0
15
30
45
60
120
SECONDS

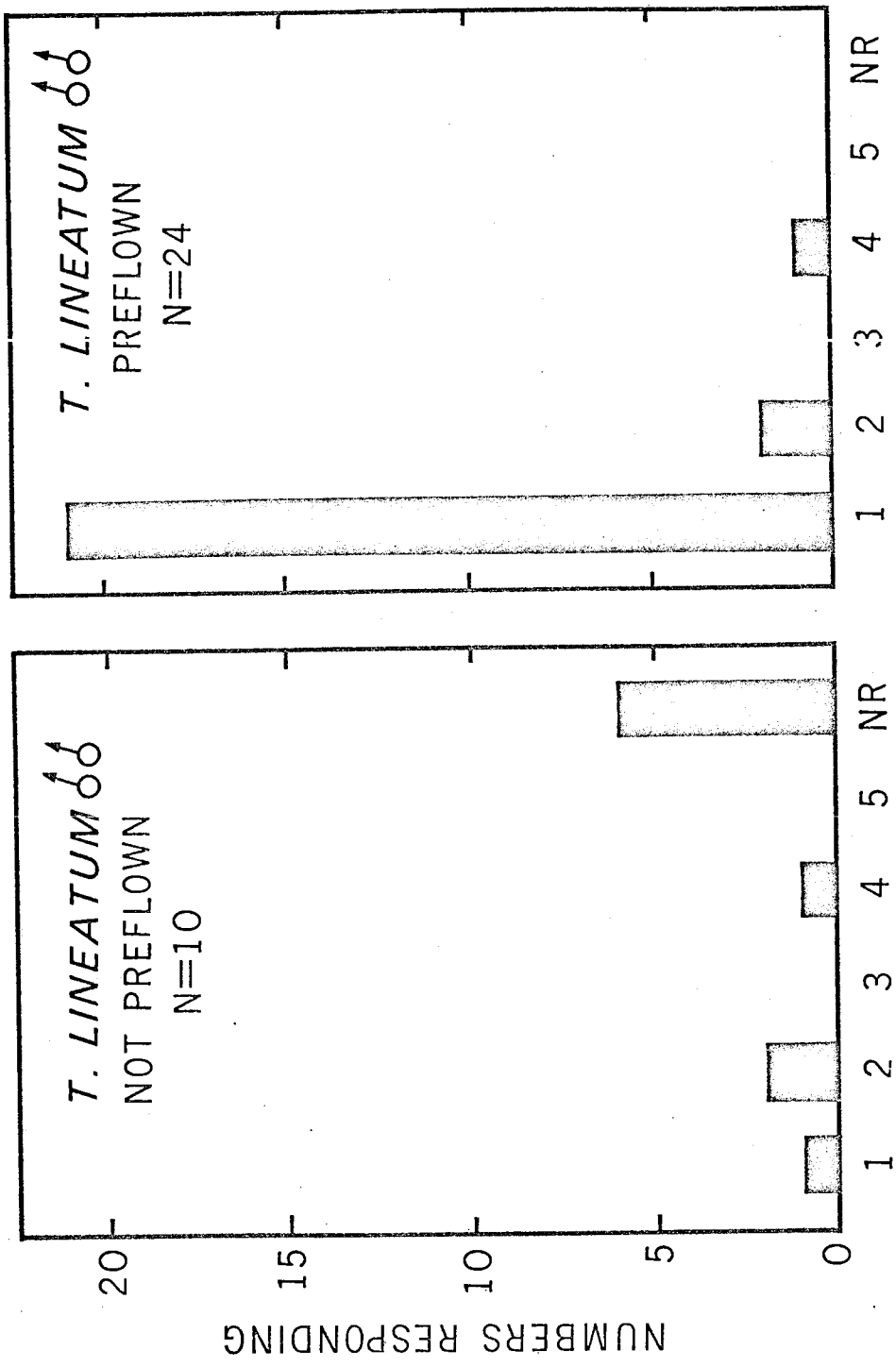
respond to 10 successive stimuli. Therefore, it is concluded that females rarely (if ever) stop flying in response to a stimulus of female frass.

The overall male response (Fig. 33) showed that the average RPM decreased drastically during the stimulus exposure due to the arrestment effect of the frass. However, prior to the 15 second mark, 25 of the 34 beetles actually increased their flight speed to an average of 69 RPM, resulting in a slight overall increased flight speed right after the stimulus introduction. This type of arrestment response pattern can be seen in the first stimulus of Fig. 17. However, as can be seen by the length of the bar, after 60 seconds most of the beetles had ceased flying and few had resumed flight within 120 seconds. Thus, in males of both species the frass stopped flight for at least one minute after the stimulus was removed.

PRETEST FLIGHT EXPERIENCE IN RELATION TO ARRESTMENT RESPONSE TO FRASS

In flight arrestment tests, male scolytids generally responded erratically until they had gained some flight experience. In Fig. 34 the response of two groups of male T. lineatum are compared: one group tested to five frass stimuli without allowing any previous flight experience and the other preflown a minimum of 30 minutes before the arrestment tests were made. Only one insect that was not preflown was arrested by the first stimulus, two on

Fig. 34: Response (less than 10% RPM at introduction of stimulus) to repeated one minute stimuli of female frass odor by unflown and preflown (30 minutes minimum) T. lineatum males. Arrested beetles not re-exposed to stimulus. NR = no response.


T. LINEATUM ♂♂
NOT PREFLOWN
N=10
T. LINEATUM ♂♂
PREFLOWN
N=24
NUMBERS RESPONDING
0
5
10
15
20
1
2
3
4
5
NR
STIMULUS AT WHICH RESPONSE OCCURS

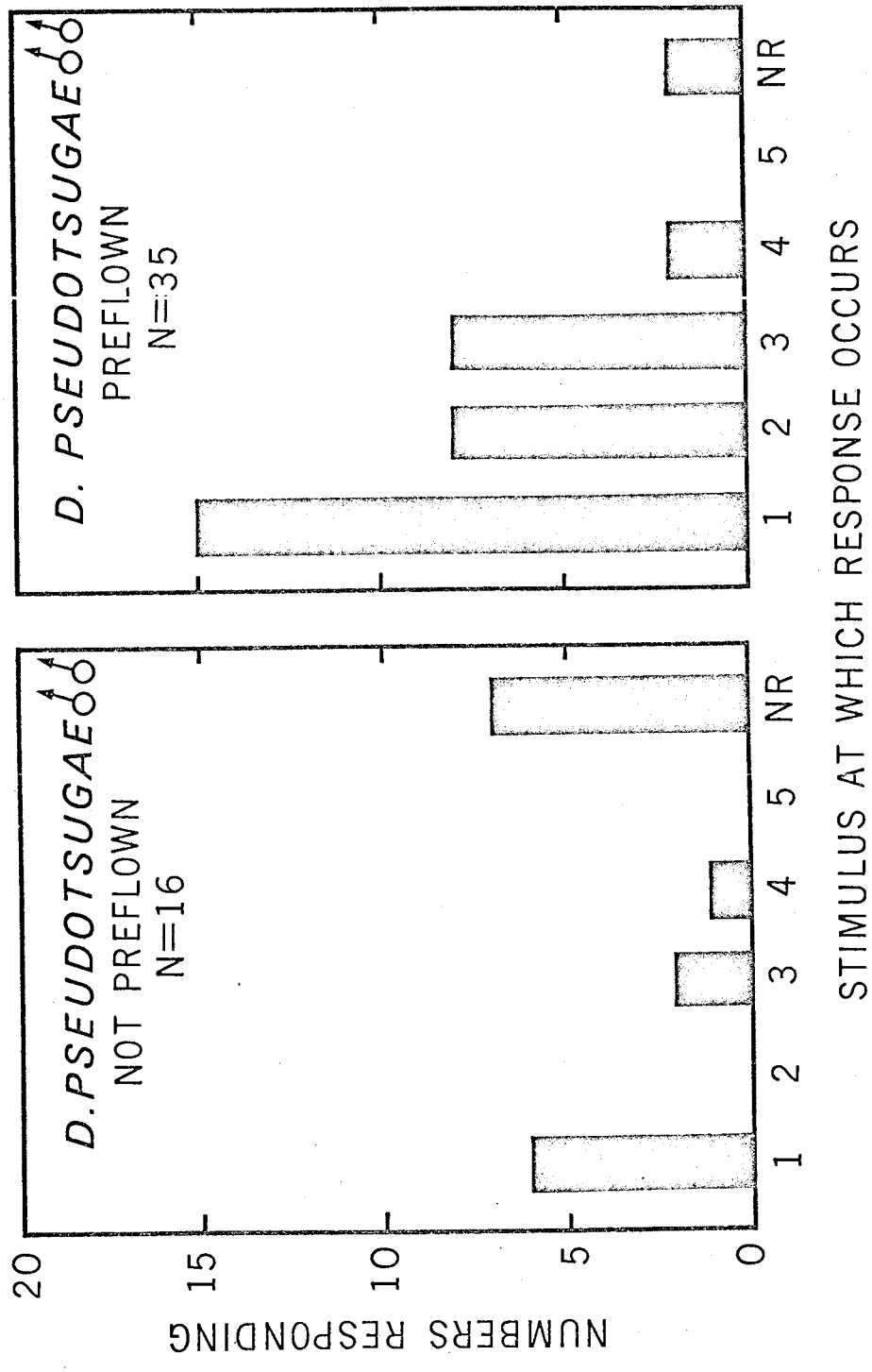
the second, one on the fourth and no response was found in 6 of the 10 insects tested even after five stimuli. Responders were arrested in an erratic hover-glide response and resumed flying when the stimulus was removed. Conversely, of the 24 insects that had been preflown, 21 responded on the first stimulus, two on the second, and after four stimuli, all had responded.

A similar type of response was also observed in D. pseudotsugae. Of the 16 beetles tested without being preflown, 6 were arrested on the first stimulus and 7 were not arrested at all (Fig. 35). Two stopped on the third and one on the fourth stimulus. As in T. lineatum, the arrestment response was a very erratic hover-glide type and was usually followed by a resumption of flight.

A sample of 35 Douglas-fir beetles preflown for a minimum of 60 minutes were more responsive to the frass stimulus (Fig. 35). Fifteen stopped on the first stimulus and all but 3 had stopped by the fourth stimulus. The arrestment response was most often of the abrupt "drop-stop" variety. Arrestment was usually followed by a period of no flight activity.

Additional documentation of the effect of pretest flight experience was obtained by testing groups of D. pseudotsugae males preflown for periods of zero to 180 minutes to frass stimuli. Control insects were flown for up to 180 minutes with no exposure to the frass stimulus. If they stopped flying spontaneously through "natural" causes (i.e. other than frass stimulation) during the same period that a frass test was made,

Fig. 35: Response to repeated one minute stimuli of female frass odor by unflown and preflown (60 minutes minimum) D. pseudotsugae males. Arrested beetles not re-exposed to stimulus.


D. PSEUDOTSUGAE ♂♂
NOT PREFLOWN
N=16
D. PSEUDOTSUGAE ♂♂
PREFLOWN
N=35
NUMBERS RESPONDING
0
5
10
15
20
1
2
3
4
5
NR
STIMULUS AT WHICH RESPONSE OCCURS

this response was recorded as a control response. After varying periods of control flight, some control insects were tested for frass response, and thus became experimental insects from that time on.

In pretest flight periods of less than 90 minutes, there was no significant difference in response to the first frass stimulus in the treated groups from the random flight arrestment of the control insects (Fig. 36). However, after 91 to 120 minutes of pretest flight, the percent of the insects responding to the first frass stimulation immediately increased to a significant 75% arrestment. The response of groups tested even later, although somewhat less, is still highly significant when compared to the control group which shows no real change in the percent of arrestment responses even after 180 minutes of flight.

A similar pattern occurs in insects which stopped for the first time on the second frass stimulus (Fig. 37). Test groups of insects in the flight groups of up to 90 minutes continued to produce no significant response during the second test. However, the 91 to 120 minutes group again exhibited significant flight arrestment response in comparison with the control group. Only the 151 to 180 minutes test group (in which one of five insects responded) failed to show a significant arrestment response.

It is clear that flight experience of approximately 90 minutes affects the behavioral response of the insects, possibly by relieving an inhibitory influence on their chemotropic arrestment response. Thus Graham's (1959, 1960) conclusion

Fig. 36: Response on first one minute stimulus of female frass by D. pseudotsugae males preflown for various periods. All responses after 90 minutes preflight are significantly different from the controls (X^2 test, P = 0.01). Numbers in each of the test periods from zero to 30 through greater than 180 minutes, respectively, are: controls, 105, 75, 63, 49, 39, 25, 15; experimentals, 29, 12, 10, 12, 12, 7, 5,

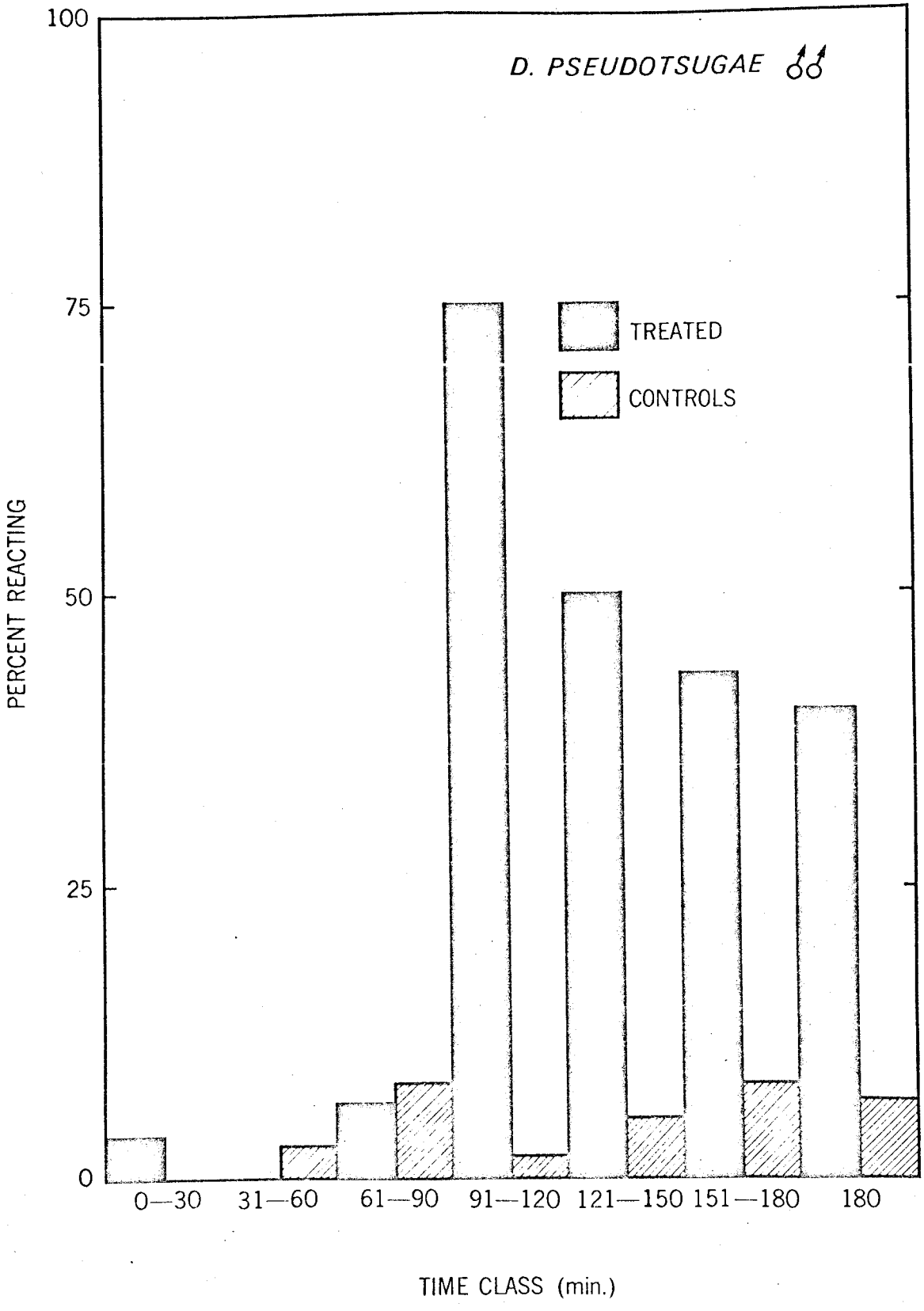
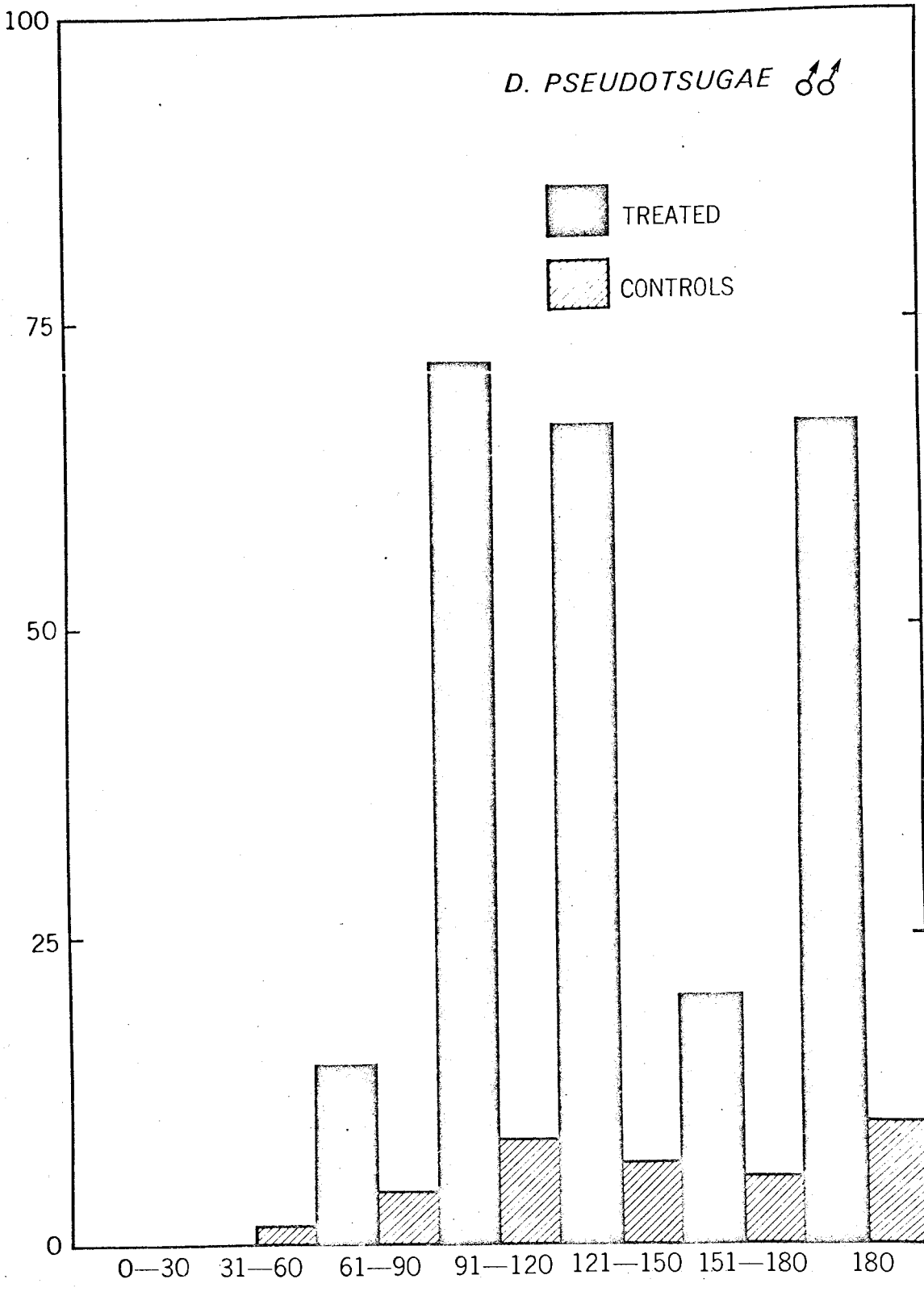

D. PSEUDOTSUGAE ♂♂
TREATED
CONTROLS
100
75
50
25
0
PERCENT REACTING
0—30
31—60
61—90
91—120
121—150
151—180
180
TIME CLASS (min.)

Fig. 37: Response on second one minute stimulus of female frass by D. pseudotsugae males preflown for various periods. All responses after 90 minutes preflight (except in the 151 to 180 minutes time class) are significantly different from the controls (X^2 test, P = 0.01). Numbers in each of the test periods from zero to 30 through greater than 180 minutes, respectively, are: controls: 105, 74, 63, 46, 31, 18, 10; experimentals, 4, 1, 7, 7, 6, 5, 3.


100
75
50
25
0
D. PSEUDOTSUGAE ♂♂
TREATED
CONTROLS
0—30
31—60
61—90
91—120
121—150
151—180
180
TIME CLASS (min.)

that flight exercise releases a chemotropic response in T. lineatum is further supported and extended to include D. pseudotsugae. Although Graham allowed his insects to fly and then tested their chemotropic response in a walking bioassay. Figs. 15 to 31 clearly demonstrate that the chemotropic response can occur during flight. Other investigations have not found such a phenomenon in other scolytids, e.g. Ips confusus (Gara 1963; Borden 1967) and even T. lineatum will respond to chemical stimuli without being preflown in some experimental situations, e.g. in darkness (Francia and Graham 1967; Borden, Silverstein and Brownlee 1968). Nevertheless, in an appropriate experimental setting, Graham's (1959, 1960) conclusions are supported. Therefore, it is quite possible that obligatory flight prior to olfactory response is a widespread phenomenon in nature.

The behavior of populations of insects can not often be determined from a small number of tests because of individual variation (Guenther 1965). Individual variation is important, however, since it is the type of diversity which allows populations to adapt and respond to new and random stimuli. Therefore, a response, other than flight arrestment, to an olfactory stimulus may indicate a positive response by the insect but not a positive response within the framework of the experiment. An example of the diversity of responses of flying male and female D. pseudotsugae is indicated in Table I, in which other possible flight reactions are shown: increase, decrease and no change in flight speed, as well as the arrestment response to a frass stimulation. Usually

Table I: Variation in percent response (±5%) to a stimulus of female frass odor by male and female D. pseudotsugae after zero or 60 minutes minimum pretest flight experience.

	Males		Females	
Flight Response	Nonflown N = 8	Flown 60 min. minimum N = 45	Nonflown N = 12	Flown 60 min. minimum N = 11
Increase speed	12.5	26.7	16.7	45.5
Decrease speed	12.5	2.2	0	0
No change in speed	75.0	20.0	83.3	54.5
Arrested	0	51.1	0	0

a non-responsive, non-preflown male beetle showed no arrestment and little or no change in flight speed. Of the male beetles that were preflown for 60 minutes, many were arrested on the first stimulus test. However, a relatively large number increased their flight speed on encountering the frass and several showed no response at all. This demonstrates that the response of partially preflown males (60 minutes) is not as predictable as those insects which had flown for the entire obligatory preresponse flight period (90 minutes). Evidently, the behavioral response of a population to a stimulus is quite diverse and composed of at least four separate responses.

An interesting pattern can be seen in the response of females to the frass stimulus. Although small numbers of females were tested, there was no arrestment response to the frass stimulus. About half of the preflown beetles, however, substantially increased their flight speed on encountering the frass stimulus. This indicates that, although the females are not arrested by frass, they do react but in a manner different from the males.

RESPONSE OF D. PSEUDOTSUGAE TO P. MENZIESII PHLOEM

The bulk constituent of the frass that was used during the previous arrestment tests was particulate host phloem tissue. Although the insect-produced volatiles in the excreta were considered the most likely source of arrestment stimuli, it also appeared important to determine the arrestment effect of the host

phloem volatiles.

Both male and female D. pseudotsugae were strongly arrested to host phloem odor (Table II). The female response is notably different from their lack of response to frass (Fig. 33). This indicates that they have the ability to recognize or detect fresh female-produced frass and distinguish some volatile or volatiles in it as being different from the host volatiles. This constituent (possibly one or more pheromone compounds) might have a "masking" effect that overrides the arrestment signal of the host tree, and either stimulates another, non-arrestment response or else just signals no host response. Thus, the increased speed (possibly an avoidance reaction) by females exposed to female frass (Table I) may occur in response to beetle-produced constituents in the frass.

The arrestment response of males to both female frass and ground host phloem tissue suggests that arrestment is induced by host tree volatiles, but is not inhibited by beetle-produced substances. Such a mechanism would permit males to respond to female-produced pheromones and to alight whenever the host volatile stimulus was sufficiently high. Females, however, could orient upwind to an aggregating pheromone, but would be inhibited from alighting in the immediate proximity of an occupied gallery. Therefore, a non-random gallery distribution pattern, such as noted in Scolytus ventralis (Berryman 1968) would be promoted, and overcrowding would be prevented.

Table II: Arrestment response (percent) of male and female *D. pseudotsugae* preflown for 2 hours, to ground Douglas-fir phloem.

Response	Males N = 31	Females N = 34
Arrested	97	91
Not arrested	3	9

ANALYSIS OF D. PSEUDOTSUGAE LIPID METABOLISM AND GAS EXCHANGE

Zebe (1959) and Beenakkers (1969) have categorized three physiological types of flight muscle: the carbohydrate utilizers, the dipterous insects (Chadwick 1949); the lipid utilizers, the lepidopterous insects (Zebe 1954); and the combination utilizers, the orthopterous insects (Krogh and Weis-Fogh 1951). During non-flying periods, D. pseudotsugae maintained a RQ of 0.7 (Table III) indicating oxidation of fat with no substrate interconversion. D. pseudotsugae, therefore, is predominantly a fat utilizer.

Absolute and relative changes in wet, dry, lipid and fatty acid weights during flight of D. pseudotsugae males are evident (Figs. 38 and 39). All decreased after flight. The loss of water was greatest during the first hour of flight as is indicated by the large increase in the dry weight as a percent of wet weight.

The flight RQ of 0.8 determined for the first few hours of flight indicates that carbohydrate is being partially utilized with lipids during this early period (Table III). Similar results were obtained by Krogh and Weis-Fogh (1951) who demonstrated that S. gregaria is dependent on fat as the main source of energy during flight, but on carbohydrates during the early flight stages. Meyer, Preiss and Bauer (1960) suggested that the locust uses carbohydrates during the early period of flight until the body temperature reaches a level at which fat can be efficiently oxidized.

Table III: Uptake of O_2 and evolution of CO_2 by flown and non-flown male D. pseudotsugae.

	Flying	Non-flying
Carbon dioxide evolution:		
ppm/minute/beetle	5.31	1.26
µg/minute/beetle	2.40	0.57
Oxygen uptake:		
µl/minute/beetle	2.10 ± 0.21	0.57 ± 0.03
µg/minute/beetle	3.00	0.82
Respiratory quotient	RQ = 0.80	RQ = 0.70

Fig. 38: Changes in wet, dry, fat and fatty acid weights during flight of D. pseudotsugae males.

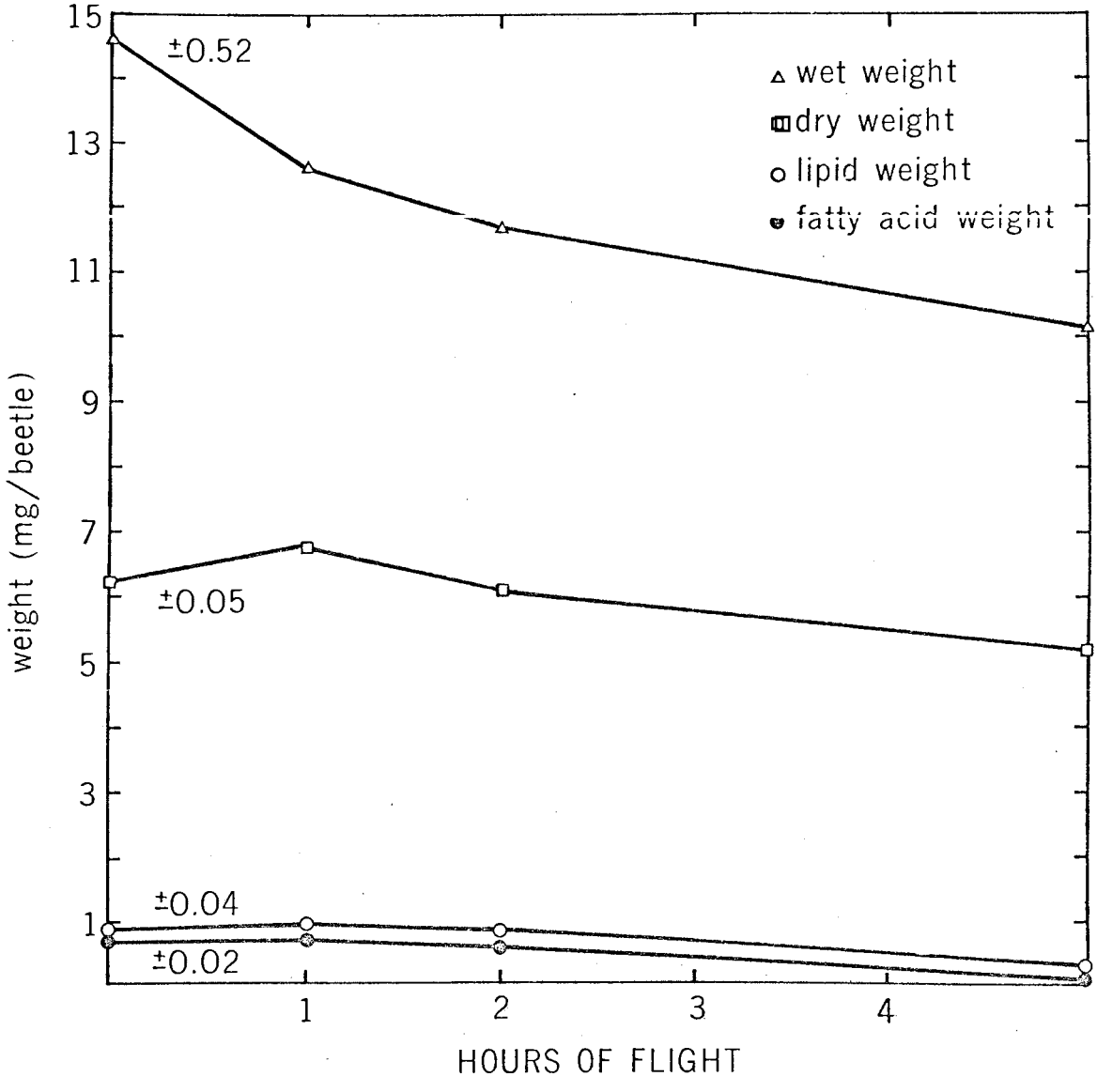
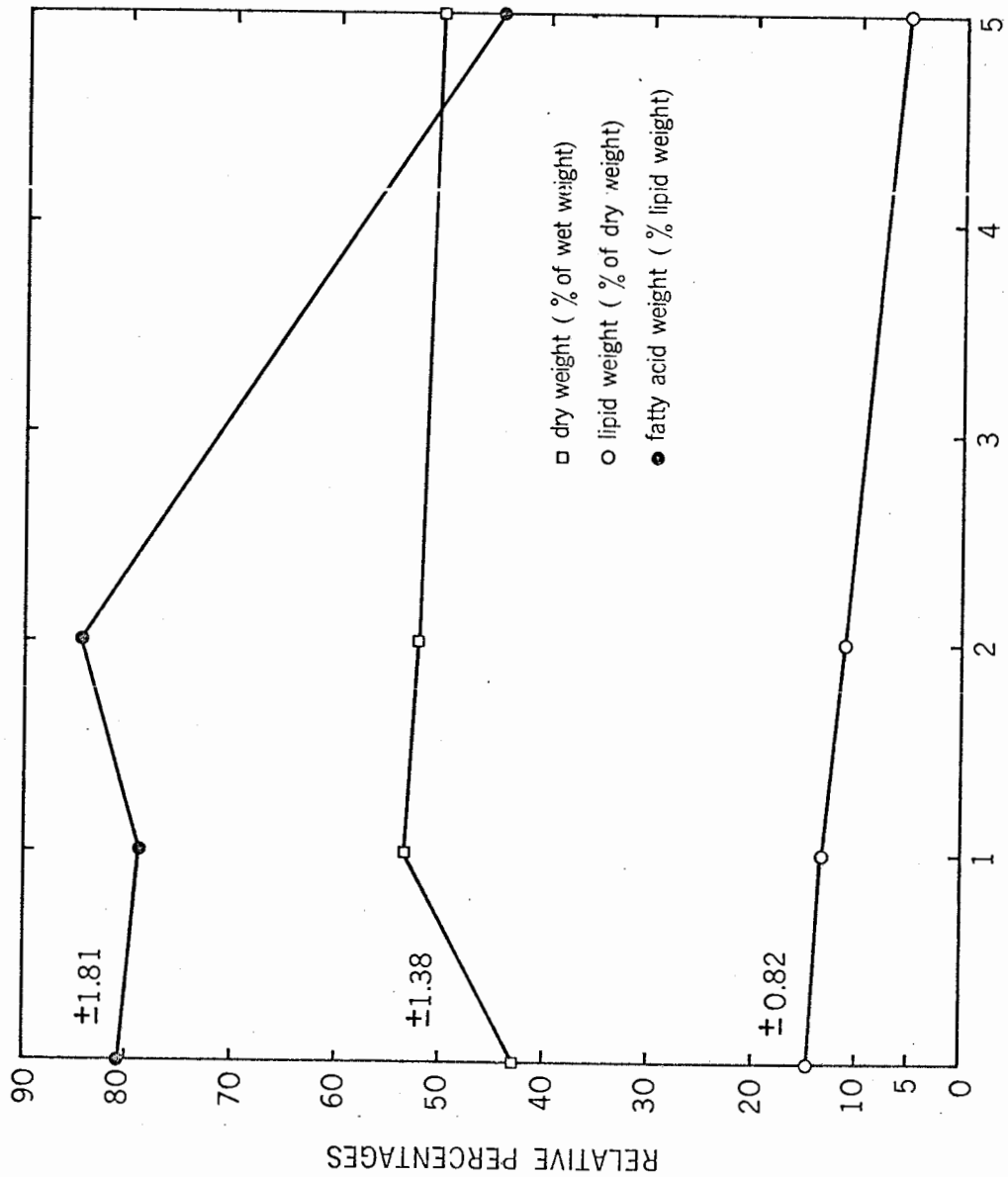

15
13
11
9
7
5
3
1
±0.52
±0.05
±0.04
±0.02
wet weight
dry weight
lipid weight
fatty acid weight
weight (mg/beetle)
1
2
3
4
HOURS OF FLIGHT

Fig. 39: Percent (± standard error) changes in wet, dry, fat and fatty acid weights after flight of D. pseudotsugae males.


RELATIVE PERCENTAGES
HOURS OF FLIGHT
dry weight (% of wet weight)
lipid weight (% of dry weight)
fatty acid weight (% lipid weight)
±1.81
±1.38
±0.82
0
5
10
20
30
40
50
60
70
80
90
1
2
3
4
5

The relative rates of CO_2 production in the test apparatus (Fig. 40) remained constant for resting insects. Flying insects, however, decreased their CO_2 production rate slightly after 40 minutes in those cases where insects flew for at least 80 minutes before stopping. Flight cessation was attributed to too high a CO_2 concentration, since after the apparatus was "flushed" with atmospheric air, flight usually resumed immediately. It is possible to use a semi-open system of detection whereby the CO_2 concentration is kept constant by addition of a measured amount of atmospheric air and, using this method, longer periods of flight could be monitored without the CO_2 concentration becoming too high. The CO_2 production rate would then be proportional to the amount of air added to the system. It would be important to see if any metabolic changes occur after 2 hours of flight as male D. pseudotsugae appear to react to host and insect-produced attractants much more strongly after this time.

The fatty acid pattern (Fig. 41) and percent composition (Table III) are, in general, consistent with that previously reported for coleopterous insects (Barlow 1964). However, the high C16:1 content is unique, and is generally characteristic of dipterous insects (Barlow 1964) and a few lepidopterous insects (Bracken and Harris 1969). Changes in percent composition and absolute weight of individual fatty acids during flight are shown in Table IV and Fig. 42. In general, the weight of all fatty acids decreased during flight. Some selective oxidation is evident. The monounsaturates, C16:1 and C18:1 fatty

Fig. 40: Expiration of CO_2 by flying and non-flying D. pseudotsugae males. Reading relative to meter scale (50-60% = 85 ppm).

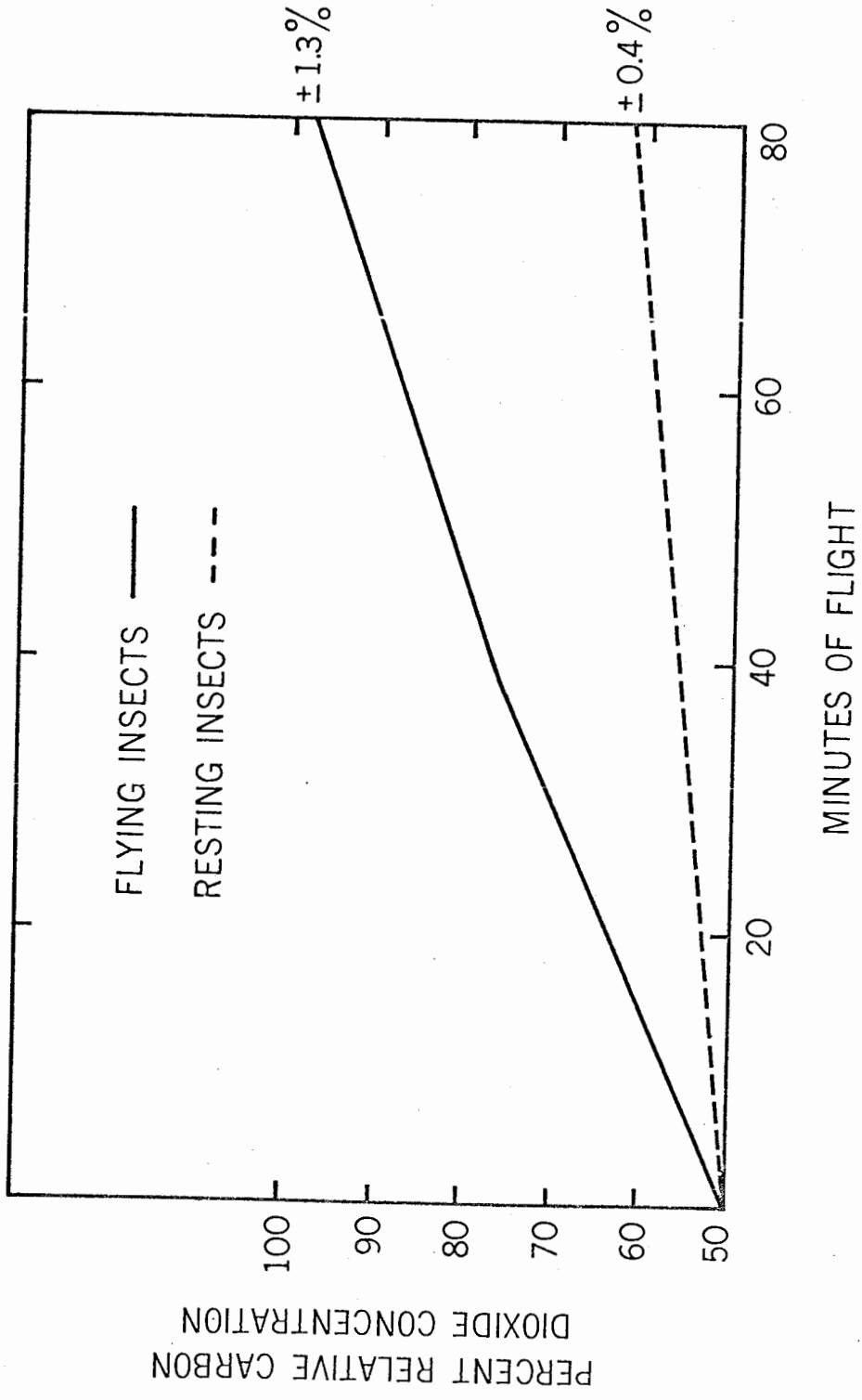

PERCENT RELATIVE CARBON DIOXIDE CONCENTRATION
100
90
80
70
60
50
20
40
60
80
MINUTES OF FLIGHT
FLYING INSECTS
RESTING INSECTS
± 1.3%
± 0.4%

Fig. 41: The fatty acid pattern of non-flown D. pseudotsugae males.

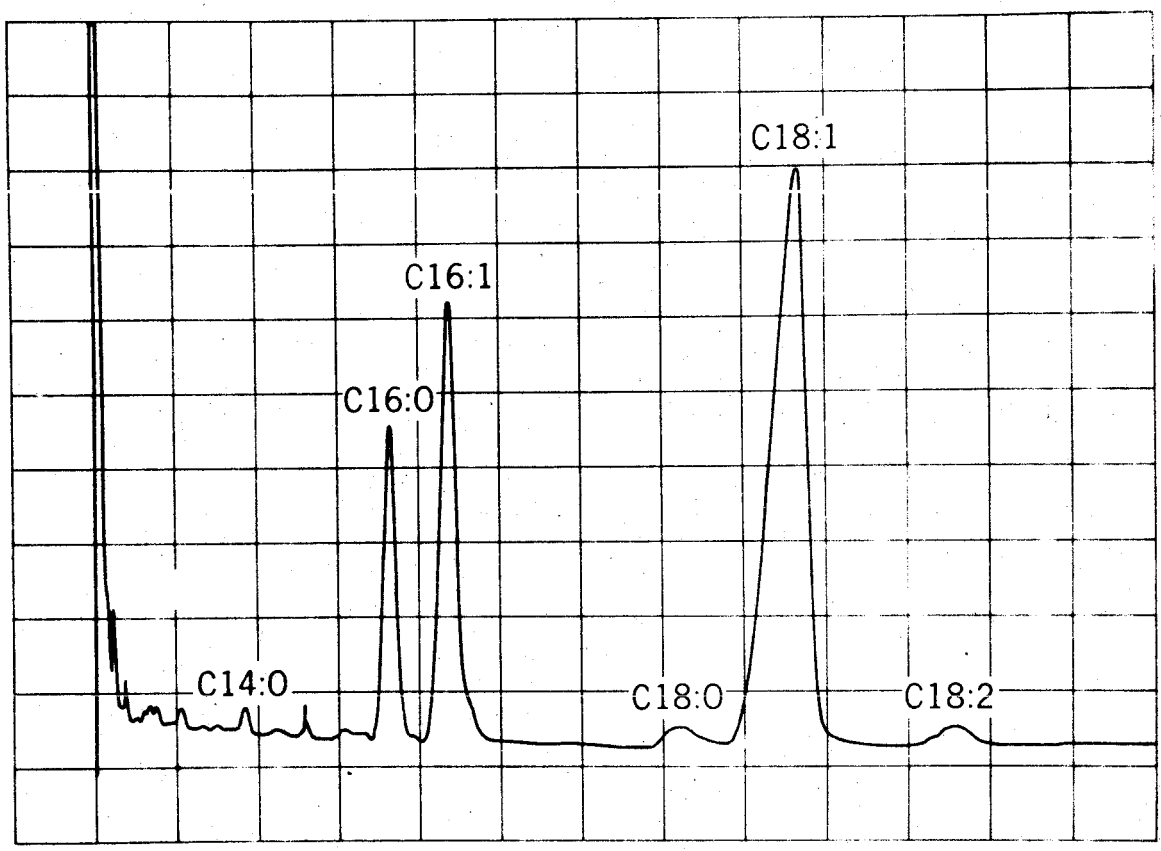
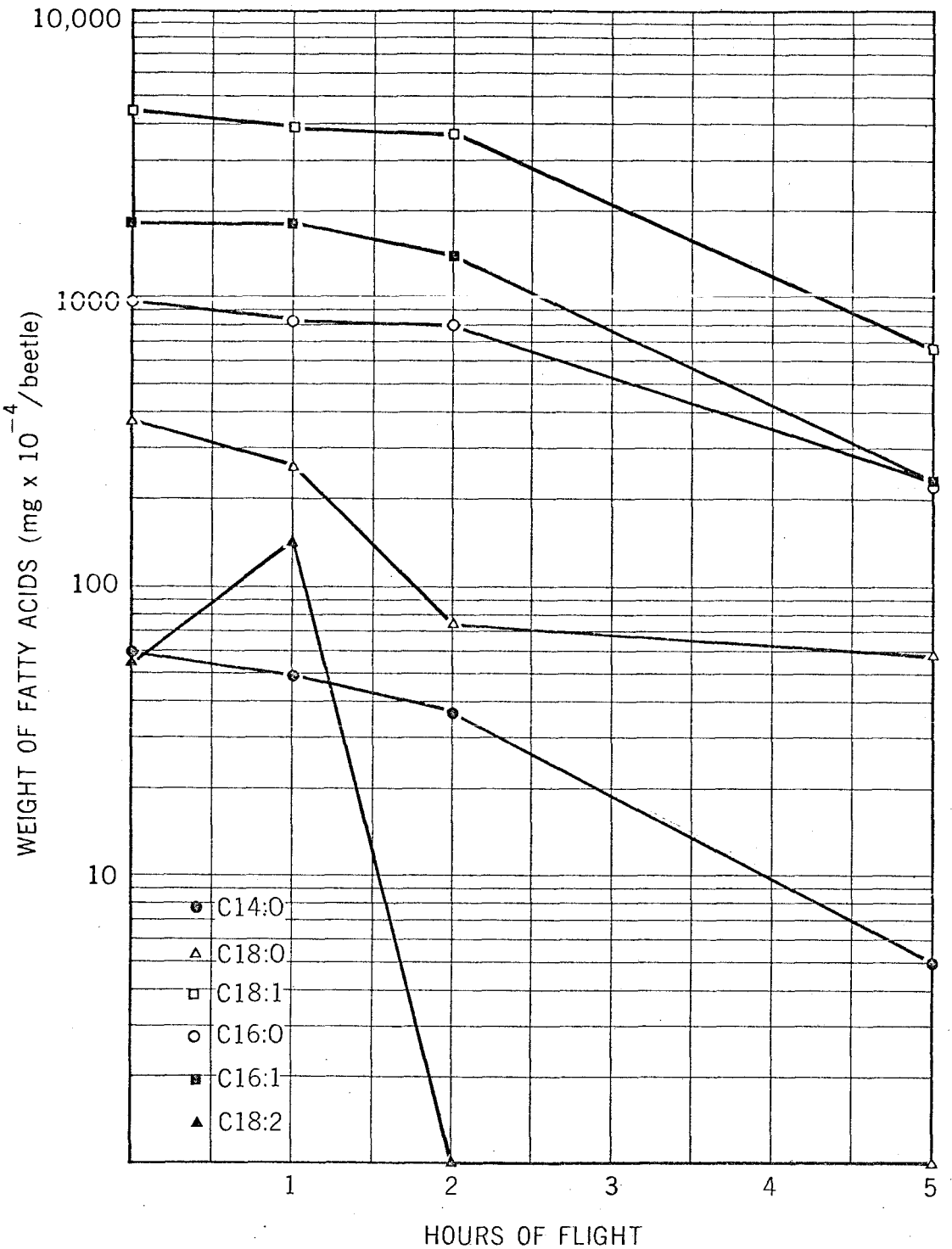

C18:1
C16:1
C16:0
C14:0
C18:0
C18:2

Table IV: Percent composition and weight of individual fatty acids of D. pseudotsugae before and after flight.

	Control		Flown					
	Non-flown		1 hour		2 hours		3 hours	
Acid	%	wt.(mg x 10^{-4})	%	wt.	%	wt.	%	wt.
C14:0	0.77 ± 0.16	59 ± 14	0.7	49	0.6	37	0.4	5
16:0	13.23 ± 0.58	994 ± 40	11.9	833	13.4	817	19.7	236
16:1	23.67 ± 0.65	1983 ± 85	26.3	1841	13.5	1434	19.7	236
18:0	1.83 ± 0.14	137 ± 12	1.8	126	1.2	73	4.8	58
18:1	59.80 ± 0.24	4506 ± 193	57.2	4004	61.3	3739	55.3	664
18:2	1.10 ± 0.21	58 ± 16	2.1	147	0	0	0	0

Fig. 42: Change in weight of individual fatty acids of *D. pseudotsugae* males during flight.


10,000
1000
100
10
WEIGHT OF FATTY ACIDS (mg x 10^{-4}/beetle)
C14:0
C18:0
C18:1
C16:0
C16:1
C18:2
1
2
3
4
5
HOURS OF FLIGHT

acids respectively, are oxidized at the greatest rate, followed by the saturates palmitic (C16:0), stearic (C18:0) and myristic (C14:0) acids respectively (Fig. 42). These results are contrary to the contention of Beenakkers (1965) that palmitate and oleate are preferentially oxidized.

During the analyses some oxidation of C18:2 fatty acids occurred (Fig. 42). The values obtained for C18:2 (Table IV) are, therefore, questionable as this acid was found only in very small or trace amounts in this species.

Atkins (1966b) reported that young female adults of D. pseudotsugae which initially responded negatively to host material, showed a positive response to the same material after varying amounts of flight exercise. Beetles with more than 20% of their dry weight composed of fat usually rejected suitable host material and displayed a strong inclination to fly and disperse; those with less than 10% fat usually failed to fly for more than a few minutes. On the other hand, beetles with between 10 and 20% fat content, although capable of sustained flight, usually responded readily to host material. In the experiments, the fat of freshly emerged male control beetles was 14.79 $\pm$ 0.82% of the dry weight (Fig. 39). This decreased during flight until after 5 hours the fat was only 5.21% of the dry weight. Most of the beetles flew continuously as described in the methods section until they were stopped and frozen. Male beetles, therefore, appear to lack the relationship between lipid content and inclination to fly.

Atkins (1969) concludes that behavioral changes may not be due to total fat combustion alone but that accumulation of metabolic by-products or selective combustion of different types of lipids may be responsible. The results in Fig. 42 support the latter hypothesis, since there appears to be selective oxidation of monosaturated fatty acids. Also, males appear to have less lipid than females. In general, this supports the findings of various workers for a great variety of insects as reviewed by Gilbert (1967). Female bark beetles, Ips paraconfusus, have been shown to accumulate and utilize fat for oogenesis (Penner 1970). Also, D. pseudotsugae females probably require more lipid for flight than males, since they are the "pioneers", while the males usually follow directly to the new host. Although unlikely, it is possible that some dimorphic differences in fatty acid metabolism occur, since previous workers have demonstrated distinct behavioral sex differences in scolytid beetles.

CONCLUDING DISCUSSION

Data from this study contribute to knowledge in three important, interrelated areas of scolytid biology: the response of flying beetles to volatile stimuli, the behavioral changes produced by flight experience in which flight positive beetles become responsive to olfactory stimuli, and the physiological mechanisms underlying such behavioral changes.

Most studies of olfactory responses of scolytids have encorporated the use of walking bioassays to determine the attractive strength of volatiles. While this type of bioassay is of value, it does not assess the type of response that would occur in nature, i.e. a flight response. Beetles that are in the dispersal phase are flight positive and, therefore, encounter most of their initial arrestment volatiles while flying. As a result, many factors that are associated with the metabolism of flight, flight dynamics and external stimuli encountered while flying are neglected in walking bioassays. While many field investigations have demonstrated orientation of flying beetles to olfactory sources, this is the first study using scolytids that has demonstrated a specific flight arrestment response to phloem and frass volatiles.

This response is undoubtedly a key step in the sequence of behavioral events involved in scolytid host selection and secondary attraction. It provides a transitional mechanism whereby the orientation response to suitable hosts or mates

(or both) is terminated, and gallery construction or reproduction (or both) is initiated. Of considerable interest is the fact that males are arrested to both female frass and host phloem tissue while females are arrested only to phloem, revealing a possible mechanism which would inhibit females from alighting near occupied galleries, and thus decrease chances of intraspecific competition. Once a beetle is in a suitable location flight must be inhibited. Although inhibitory mechanisms are unknown in most scolytids, Ips paraconfusus will not take off in the presence of attractive frass (Borden 1967). Within one to two days, the flight muscles degenerate (Chapman 1956; Atkins and Farris 1962; Borden and Slater 1969) through lysosomal activation (Bhakthan, Borden and Nair 1970) and the insect is rendered physically unable to leave a proven host.

My results support Graham's (1959) hypothesis that flight exercise releases a chemotropic response from photopositive domination. If freshly emerged beetles have an internal mechanism which inhibits an arrestment response soon after flight has begun, then such a mechanism would have considerable ecological significance. It would greatly increase the chances of the scolytids dispersing to find new host material. When the beetles emerge they typically fly straight up until they reach the tree crown layer and then fly horizontally above the tree tops (J.A. Chapman, personal comm.).[5] This type of flight response

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[5] Research Entomologist, Canadian Forestry Service, Victoria, B.C.

would enhance the opportunity of getting into strong air currents. If an added mechanism required the beetle to be airborne for some time (approximately 90 minutes in the case of D. pseudotsugae), then the insects would be even more likely to locate host material far from the emergence site. Such a mechanism would increase the chances of insects from distant broods encountering each other in a sexually responsive condition.

Experiments involving the release of chemotropic response by flight exercise have largely been neglected in other scolytids and the physiological preconditioning by flight has been untested, mainly due to the extensive use of walking bioassays in the laboratory or field trapping of naturally flying insects. This might not matter in isolation and identification studies of attractive pheromones, but when these compounds are used with respect to the flight response as in manipulation of population movements in the field, a walking response may be very different from the flying one.

Although the mechanisms releasing olfactory behavior after flight exercise are unknown, my data contradict Graham's (1961) hypothesis that air swallowing is the principal mechanism triggering this response. Because beetles swallow air before they fly, this mechanism apparently neither inhibits flight nor enhances arrestment response. However, the involvement of lipids (Atkins 1969) is supported since D. pseudotsugae selectively oxidized monounsaturated lipids C16:1 and C18:1 and the saturated lipids C16:0 (palmitic), C18:0 (stearic) and C14:0 (myristic).

This might be an evolutionary advantage for the beetle to rely on an internal process of this type because, firstly, it is internal and effectively independent of external factors and, secondly, it is a good indicator of the physiological condition of the beetle. Since fat is the primary energy source for flight in insects (Weis-Fogh 1952), it would be advantageous for the beetle to have a flight arrestment mechanism that included an estimate of physiological energy reserves, so that the length of the dispersal flights could be regulated depending on the condition of the insect.

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