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Title DIURNAL AND SEASONAL FLIGHT PATTERNS OF BARK BEETLES (COLEOPTERA: SCOLYTIDAE) ASSOCIATED WITH DOUGLAS-FIR FORESTS OF WESTERN OREGON

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The study was undertaken to determine the seasonal and diurnal flight patterns of scolytid beetles inhabiting a second growth forest of Douglas-fir (Pseudotsuga menziesii (Mirb.)Franco) in western Oregon. Air temperatures, relative humidity, light intensity, and wind velocities were recorded for evaluation of their influence on flight activity.

The insects were trapped in flight by six mechanically powered rotary nets. These devices were arranged 110 - 140 feet apart in shaded and relatively exposed positions reaching from the base to the crest of a small ridge. Flights were in some cases related to patterns of emergence from caged logs.

The study was conducted during the spring and summer of 1963 and 1964, with some pertinent differences in seasonal flight activity noted. Due to an abundant host supply in 1963, greater numbers of many species were caught in 1964. Twenty-four scolytid species

were identified from net collections in 1964, whereas only 15 species were collected the previous year.

With the exception of a single species, *Scolytus unispinosus* LeConte, which overwinters in an immature stage, the initiation of seasonal flight depended on sufficiently high temperatures to induce flight. A wide range of air temperatures necessary to initiate flights of the respective species was observed. These differences in temperature thresholds resulted in a seasonal succession of species found in flight.

While changes in relative humidity caused no apparent effects on flight, light intensity was especially influential for certain species. Of 11 species in sufficient abundance for detailed study, six (*Pseudohylesinus nebulosus* (LeConte), *P. grandis* Swaine, *Trypodendron lineatum* (Olivier), *Phloeosinus sequoiae* Hopkins, *P. punctatus* LeConte, and *Scolytus unispinosus*) flew during the mid-day hours. The remaining five (*Hylastes nigrinus* (Mannerheim), *H. ruber* Swaine, *Gnathotrichus sulcatus* (LeConte), *G. retusus* (LeConte), and *Dryocoetes autographus* (Ratzeburg)) exhibited crepuscular flight patterns, flying in greatest numbers when light intensities were below 1000 foot candles.

DIURNAL AND SEASONAL FLIGHT PATTERNS OF BARK BEETLES (COLEOPTERA: SCOLYTIDAE) ASSOCIATED WITH DOUGLAS FIR FORESTS OF WESTERN OREGON

by

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INTRODUCTION

The bark and ambrosia beetles (Coleoptera: Scolytidae), with few exceptions, spend the majority of their life within the bark or wood tissues of the host tree, emerging for only brief periods to infest a new host. The importance of this brief dispersal period in the life cycle of this insect group is readily apparent. The vital objective of the insects during this period is to locate and invade suitable host material to ensure the establishment of a new generation. Survival of the population depends on success in locating new hosts, and requisite for this location are climatic conditions favorable for flight activity. This study seeks to enumerate these requirements as precisely as possible under field conditions for the complex of bark beetles associated with a typical Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forest of western Oregon. Emergence and flight temperature thresholds and seasonal and daily flight patterns as influenced by temperature, light, and wind fluctuations are emphasized. Such information is of value in predicting seasonal dispersal activity of potentially destructive forest pests, and of associated species which may function as interspecific competitors of the destructive species. With few exceptions, Gara and Vite' (24, p. 275-290), and Rudinsky (46, p. 27-37), flight studies dealing with bark beetles have not intensively measured daily and seasonal flight activity in relation to the environmental physical factors. Numerous studies have been conducted on specific habits and flight behavior in the laboratory (3; 4; 5; 28; 48), but field studies have been largely limited to observations of seasonal rhythms of the more destructive species.

Successful implementation of potential control programs utilizing the promising principle of chemical attractants will depend to some extent upon precise knowledge of seasonal flight rhythms and factors influencing the diurnal flight patterns. If control by insecticides directed against flying populations of bark beetles should ever prove feasible, this knowledge would again be essential. Also, timing of silvicultural and logging operations, such as thinning or salvage, could be aided by knowledge of seasonal flight activity. In addition, information concerning local dispersal patterns might be of significant value to related biological studies regarding the activities of predators or parasites of the various bark beetle species.

The study was conducted for the greater part of two flight seasons. The majority of information was acquired during the spring and summer of 1963, with supplementary data being obtained the following spring. Rotary traps provided a means of sampling the flying population, and various instruments were available for measurement of certain physical factors such as temperature, wind, humidity, and light intensity.

During the two seasons, a total of 24 species were found in the study area of which nine were present in sufficient numbers to permit detailed evaluations. These were *Pseudohylesinus nebulosus* (LeConte), *Pseudohylesinus grandis* Swaine, *Trypodendron lineatum* (Olivier), *Hylastes nigrinus* (Mannerheim), *Gnathotrichus sulcatus* (LeConte), *Gnathotrichus retusus* (LeConte), *Dryocoetes autographus* (Ratzeburg), *Hylastes ruber* Swaine, and *Scolytus unispinosus* LeConte. A tenth species, *Dendroctonus pseudotsugae* Hopkins, was also present in abundance, but was the subject of a separate study and therefore will not be specifically discussed in this work. This bark beetle is closely associated with many of the species covered in this investigation, however, and for this reason some comparisons and reference to *D. pseudotsugae* are made.

LITERATURE REVIEW

A survey of the literature revealed a multiplicity of factors that may affect insect flight activity. Until recently, little was known concerning the flight activities of bark beetles, although considerable work has been done with other groups of insects. However, in the past five years, some significant contributions have been made in the field of bark beetle flight behavior. Atkins (4, p. 943-953; 5) investigated the flight movements and capacity of the Douglas-fir beetle (Dendroctonus pseudotsugae); McMullen and Atkins (38, p. 1312-1324) and Rudinsky (46, p. 28-37) studied the effects of gross environmental factors, including the influence of attractants, under field conditions. Chapman and Kinghorn (11) discussed the seasonal flight rhythms of Trypodendron lineatum including notes on other genera, whereas Gara and Vite' (24, p. 278-288) investigated the diurnal as well as seasonal flight rhythms of various pine bark beetles in California. Henson (28) has recently contributed information from laboratory observations on the flight habits of the white pine cone beetle, Conopthorus coniperda Schwarz.

Uvarov (53, p. 87-99) listed temperature, humidity, light and radiation, atmospheric pressure, atmospheric electricity, and movement of the air as the physical factors that might affect the flight of an insect. Andrewartha and Birch (2, p. 129-332) emphasized the effects of temperature, moisture, and light as the main factors influencing insect activity. These factors were listed as the main environmental components which undergo a daily fluctuation (2, p. 321) and thus are particularly important in governing daily activity rhythms. In addition to the physical factors, various biotic factors and relationships can profoundly affect the flight behavior of certain species. For example, Chapman and Kinghorn (11) discussed the effect on the seasonal flight rhythm of Trypodendron lineatum caused by the late summer emergence flight, and Anderson (1) was the first to point out the concentrating effect of a naturally produced attractant on scolytid flight activity. Although all the factors known to influence insect flight could not be investigated in the present study, a thorough review of the literature was conducted in order to obtain an understanding of the complexity of factors involved. It was felt that such an understanding was necessary to permit accurate interpretation of flight patterns with the physical and biotic factors that were measured and observed.

Physical Factors

Temperature

As with other poikilothermic animals, the activity of bark beetles depends upon the temperature of the environment (45, p. 333). It appears that flight activity presents no exception to this generalization, although wide variations of temperature thresholds necessary for flight exist within the group. Rudinsky and Vite' (48) observed that the flight of the Douglas-fir beetle began at temperatures of 64.5-68.0^{o}F., although once begun, flight could be sustained at considerably lower temperatures. Rudinsky (46, p. 31) observed a mid-day flight depression to occur for this insect concomitant with higher temperatures. Gara and Vite' (24, p. 278) studying flight patterns of bark beetles in a western pine forest, concluded that temperature was the physical factor having the most limiting effects on bark beetle flight activity. These workers found that Ips confusus (LeConte) initiated flight at 66.2^{o} F., and demonstrated that a mid-day flight depression occurred concurrent with high temperatures (24, p. 284). Chapman and Kinghorn (11) however, found the flight threshold of Trypodendron lineatum to be 60^{o} F., a considerably lower temperature. In contrast to this, Henson (28) found that Conopthorus coniperda initiated spontaneous flight in the laboratory within the comparatively high range of 81.5-95.0^{o} F.

Although air temperature appears to be a relatively good indicator for predicting seasonal and diurnal insect flight, it is not a perfect measure and should not be considered as such. The above temperature thresholds for the various scolytid species refer to ambient air temperatures and thus cannot be completely accurate for purposes of estimating or predicting initial flights. Leigh and Smith (32, p. 612) investigating the flight activity of a butterfly, pointed out that flight is closely related to body temperature which can be modified by radiant energy, air temperature, and air movement. Uvarov (53, p. 94) would add humidity to this list of factors affecting insect body temperature. Digby (16, p. 279-288) stated that an insect in the sun has a higher temperature than the air, and that darker colored insects will have a higher absorption of radiant energy. Since most bark beetles are relatively dark in color, Digby's observations seem particularly applicable to this study. Atkins (4, p. 947-952), exposing a number of Douglas-fir beetles to the radiation of the sun, observed that flight could occur at air temperatures below the normal flight stimulating range. Such a radiation effect is considerably minimized on normal forest sites because of the shading effect of the forest canopy. However, Chapman and Kinghorn (11), in their field observations of Trypodendron lineatum, found that a few beetles are in flight at air temperatures below that normally necessary to initiate flight. This phenomenon could be induced by radiant energy received by the microhabitats of a small percentage of the species, and obviously such effects must be considered in a study of this type.

Another effect of temperature that is known to influence insect activity is the stimulating effect of falling temperature. Bently, Gunn, and Ewer (7, p. 190-192) found that falling temperatures stimulated activity of a spider beetle (Coleoptera: Ptinidae). Cloudsley-Thompson (13) observed a similar response with certain species of millipedes, and determined that falling temperature was a stimulus to orthokinetic locomotory activity with some of these arthropods. In addition to the above temperature effect, Johnson and Taylor (29, p. 220) found that flight of an aphid could be related to an accumulation of temperature and could be estimated. They observed that an increase in temperature over a period of time caused the teneral period to shorten and was followed by an increase in rate of flight.

Light

The effect of light on insect flight activity is surpassed in importance only by temperature. Rudinsky (45, p. 336) stated that during the dispersal flight the photopositive stimulus was the governing factor in many scolytids. Under controlled conditions in the laboratory, Atkins (3) found that the Douglas-fir beetle flew at light intensities of 2 to 500 foot candles, but the speed with which they reacted and the percentage that flew increased as light intensity increased. Graham (25) described the photopositive flight of Trypodendron lineatum as being necessary before orientation to olfactory stimuli could occur. Henson (28) found Conopthorus coniperda to be photopositive in its initial flight. Gara and Vite' (24, p. 281), however, noted the consistent late afternoon or evening flights exhibited by bark beetles of the genus Hylastes (Erichson). Apparently nocturnal or dusk activity for this family is not uncommon as a recent biological study of ambrosia beetles in West Africa revealed that each species had a distinct nocturnal, diurnal, or crepuscular rhythm of emergence and flight activity (21). Fisher, Thompson, and Webb (22), reviewing the biology and economic importance of the ambrosia beetle group related that the time of flight of the different species varies considerably within a day.

Decreasing light intensity appears to be the governing factor triggering activity in crepuscular insects. Curtis (14, p. 364-370) noted increased activity of mosquitoes in the Yukon with decreasing light intensity while other factors were stable and optimal. Stahler and Terzian (50) found that mating activity of a mosquito occurred at sunset and sunrise, and observed that these peaks were directly related to the time of sunset and sunrise. A study of blackflies (Diptera: Simuliidae) by Wolfe and Peterson (56) in eastern Canada revealed that they were most active during the evening with smaller peaks of activity occurring in the early morning. This periodicity was attributed to the level of light intensity, with no correlation established for atmospheric pressure, and only extremes of humidity (below 25 percent and above 95 percent) or temperature (below 45° F. or above 90°F.) had any effect on activity. However, the lower levels of morning activity were attributed to the lower temperatures prevailing during the earlier hours.

The interrelationship of light and temperature is well exemplified by Dyson-Hudson's (18) comparative field study of the flight patterns of _Drosophila obscura_ (Fallen) and _D. subobscura_ (Collin). High evening flight peaks and low morning peaks were observed for _D. subobscura_. Presumably, during the early morning hours when light intensity is at an optimum, temperature is too low, and after the temperature sufficiently increases, light is no longer optimal. In the morning, maximum activity occurred at a temperature of 58° F., while in the evening the greatest activity occurred at a temperature of 67° F. Dyson-Hudson concluded that at temperatures above 59° F. flight activity was determined by light intensity, and at temperatures below this threshold flight activity was primarily influenced by temperature with only the very low or high extremes of light intensity having any effect. A similar light and temperature interrelationship existed in the case of Drosophila pseudoobscura (Frowlowa) as shown by Mitchell and Epling in southern California (40, p. 708). This insect exhibited a distinct crepuscular periodicity during the warmer summer months, but during the cooler, early spring the activity periods were longer and peaks of activity less distinct. Variations in relative humidity were said to have little effect on this periodicity.

An additional role of light as a factor influencing a scolytid's flight activity can be discussed in terms of optic orientation. The amount and quality of light reflected by the surface of an object could potentially affect the response of bark beetles to the object, and thereby influence the local flight density. Entwistle (20) demonstrated a significantly higher catch by red traps than numerous other colors. Using collision type traps, Chapman and Kinghorn (11) found those colored brown captured more scolytids than green or yellow. This information is in accord with Henson's (28) findings for the white pine cone beetle, Conopthorus coniperda, which he observed to be initially photopositive in flight and to later orient on dark silhouettes. In contrast to the above, however, Schenk, Dosen, and Benjamin (49), using trap boards painted six different colors to trap various Ips DeGeer species, achieved their highest catch on those painted yellow.

Humidity

It is difficult to isolate the effects of humidity on insect flight activity from the influences of the other physical factors. Relative humidity generally is regarded as a secondary physical factor functioning indirectly and subsequent to changes of other physical factors such as temperature and pressure. It is evident, however, that this factor can be important to insect flight activity. Uvarov (53, p. 63) stated that the humidity of the air greatly affected body temperature, a factor that has already been discussed as being of primary importance in governing flight activity. Davies (15, p. 308) noted a fall in numbers of the black fly Simuleum venustum (Say) (Diptera: Simuliidae) in flight during mid-day and other periods when the evaporation rate was high. He found that the daily rhythm varied with temperature, saturation deficit, and wind, all of which affected the evaporation rate. Henson (28) noted, in studying Conopthorus coniperda, that preconditioning in high humidities reduced the amount of flight during testing cycles, whereas a drying period, not exceeding 12 hours, increased flight. Henson proposed from these results in the laboratory that one could expect that most field flight would occur on clear, warm days, providing excessive drying had not occurred previously. This concept might be an important factor governing density of early spring scolytid flights, particularly in areas prone to prolonged wet or dry periods of weather.

Wind

It is obvious that movement of the air should have a direct effect on the activity of flying insects. It has been shown that the effect may be inhibitory or activating depending upon the wind velocity (17, p. 794). Digby (17, p. 794), studying the flight of a blowfly (Diptera: Calliphoridae), found that velocities up to 2.28 feet per second activated flight while wind speeds above this figure were inhibitory. Uvarov (53, p. 98) stated that small insects such as the Simuliidae can fly only if the air is calm. Green and Pointing (26, p. 313) reported that the European pine shoot moth (*Rhyacionia buoliana* (Schiffenmuller)) (Lepidoptera: Olethreutidae) flew into the wind at velocities up to 3.5 miles per hour, cross-wind at velocities between 3.5 to 6 miles per hour, and downwind at velocities exceeding 6 miles per hour. Apparently scolytid flight is characteristically oriented against the wind. Chapman (12, p. 79) stated that the typical and characteristic flight of *Trypodendron lineatum* was against the wind. Rudinsky (46, p. 36) observed that the Douglas-fir beetle oriented against the wind in flight in response to attraction foci. The flight of this species terminated with steady winds of 5 miles per hour or greater, but flight was sustained with gusty winds of 4 to 9 miles per hour (46, p. 32).

Atmospheric Pressure

Another physical factor that may influence insect flight is atmospheric pressure. Davies (15, p. 311) found that falling pressures stimulated biting and flight activity of blackflies (Diptera: Simuliidae). Parman (42) however, noted a "depressant effect" of falling barometric pressures on the activity of certain muscid (Diptera: Muscidae) flies. Haufe (27, p. 524) conducted an extensive study on the flight responses of a mosquito (Diptera: Culicidae) to fluctuations in barometric pressures and concluded that these effects are of less importance than others such as temperature or saturation deficiency.

Static Electricity

Recent investigations by Maw (33; 34; 35) and Edwards (18, p. 899-912) indicate that static electricity is an additional physical factor that might influence insect flight activity. Edwards (19, p. 899-900) described the potential gradient or electrical field and a density or cloud of unipolar ions as the two aspects of atmospheric static electricity. Edwards stated that an electrical field is a line of force joining opposite electrical charges located on the earth's surface and extending somewhere in the atmosphere. The potential gradient refers to the charge in the intensity of the field with increasing height. Whitlock and Chalmers (55, p. 335) noted that during clear weather the changes in potential gradient are low; and Edwards (19, p. 909) stated that most insect response occurred with changing rather than static fields.

The second aspect of static electricity, referred to as "unipolar ions", is described by Edwards (19, p. 899-900) as molecules or condensation nuclei of a single charge. Such a cloud with more ions of one charge than the other results in a "space charge" which can be shifted about by wind currents.

Maw (33) also reported that insects can detect and will react to charges borne by plants and other objects. Maw (33; 34) stated that insects in flight are more sensitive to electrical fields, and mentioned some insects such as Aedes trichurus Dyar (Diptera: Culicidae) which tend to follow lines of certain intensities (presumably intensities of potential gradients). Edwards (19, p. 909-911), however, found considerable differences between species in their response to electrical fields. A 30 volt potential in static or alternating fields affected activity of a species of Drosophila (Diptera: Drosophilidae), but a potential of 1350 volts was necessary to cause even a slight reaction by a Calliphora (Diptera: Calliphoridae) species. The latter voltage figure is higher than potentials normally encountered in the field.

It appears that the effect of electrical fields on insect flight varys greatly with the species and could be expected to be influential in localized areas of an environment. More basic information is needed on the dynamics of this factor and methodology for its study in the field before it can be objectively applied in an investigation such as the one at hand.

Specific Factors Influencing Flight of the Scolytidae

The biotic factors influencing diurnal and seasonal flight rhythms of scolytids will be discussed as they apply to the various species. Life histories and known behavioral responses of the insects are considered insofar as they may result in a direct effect upon the insects' flight patterns. In some cases, reference will be made to the economic importance of a species, and its history as a forest pest.

Pseudohylesinus nebulosus (LeConte)

Walters and McMullen (54) reported *Pseudohylesinus nebulosus* as being the first bark beetle to infest Douglas-fir in the spring. Chamberlin (9, p. 200) recorded two generations per year for this insect, each with apparently one brood. A more recent study by Walters and McMullen (54) provided evidence that *P. nebulosus* has a one year life cycle with a single generation and one brood per year. In this study (54), heavy emergence of new adults from spring infested material was noted during late summer. These individuals did not begin a second generation at that time however. Although the new adults bored in fresh host material, the resultant galleries were irregular niches and described as feeding galleries in which some of the insects overwintered. Chamberlin (9, p. 199) stated that overwintering may occur in pupal cells and that mature adults hibernate in moss, the forest litter, or on tree trunks. A "sister brood" or second attack by re-emerged parent beetles is apparently not produced by this species since re-emerging adults soon die (54). From the above information, a major, early season attack flight can be expected with a subsequent summer flight of new adults to overwintering or perhaps feeding sites.

Chamberlin (10, p. 106-107) stated that this species is common and often destructive in the Willamette Valley of Oregon where it attacks and kills the tops of Douglas-fir. Walters and McMullen (54) noted that P. nebulosus is important as an interspecific competitor of the Douglas-fir beetle due to its early spring flight. Although this scolytid most commonly invades small diameter, thin barked host material, Walters and McMullen found heavy attack in logs up to 18 inches in diameter with a maximum bark thickness of 1.4 inches. These workers claimed that whole sections of logging slash may become unsuitable as host material for the Douglas-fir beetle due to gallery construction by P. nebulosus.

Pseudohylesinus grandis Swaine

This species differs from *P. nebulosus* in that a longer period of time is required for the insect to reach maturity. Thomas and Wright (52) provided evidence that the life cycle in the northwestern Washington area requires 24 months for completion. Egg galleries and brood are produced by overwintered adults in May or June. The developing brood overwinters the first season as larvae, not reaching maturity until mid-summer of the following year. At this time, the new adults emerge and make feeding or hibernation galleries in new hosts. During the second winter, hibernation of both *Pseudohylesinus grandis* and *P. granulatus* was observed in the base of trees and under bark scales. From this information, one might expect a seasonal flight rhythm similar to that of *P. nebulosus*, in that two peaks per season might be expected to occur; an initial attack flight for brood production would occur in the spring, and a subsequent flight of new adults (matured from the previous year's brood) to feeding or hibernation sites.

Trypodendron lineatum (Olivier)

The ambrosia beetles or wood boring members of the family Scolytidae do not present a menace to living trees in the Northern Hemisphere, but are well known in the Pacific Northwest and other areas due to their borings in cut sawlogs, windthrown trees, and other killed timber. McMullan (36, p. 36) stated that the annual loss due to ambrosia beetle damage in British Columbia amounts to at least hundreds of thousands of dollars and perhaps is in the millions of dollars. *Trypodendron lineatum* appears to be the most damaging of all species of ambrosia beetles in the area due to its habit of concentrating in dense numbers on host logs. Prebble and Graham (43, p. 105) reported gallery densities of 250 per square foot occurring in some Douglas-fir logs in British Columbia.

Chapman and Kinghorn (11) found that the spring flight of this insect occurred when air temperatures reached 60° F., although they also stated that small numbers will appear at temperatures below this figure. Novak (41, p. 17) stated that swarms of *T. lineatum* occur when the air temperature reaches 60.8° F. provided the soil temperature is 46.4° to 50.0° F. Chapman and Kinghorn (11) stated that although spring flights of *T. lineatum* are preceded by flights of *Pseudohylesinus nebulosus*, other scolytids do not generally occur as early in the season. Kinghorn and Chapman (31) attributed the early spring emergence and flight of this species to its habit of overwintering in the upper organic layers of the forest litter.

Chapman (12, p. 79) observed that in almost every instance beetles in flight flew against the wind, apparently exhibiting an anemotactic orientation. By utilizing a clever array of hidden logs and screening out potential sound and odor production from various controls, Chapman contributed substantial proof that flying T. lineatum are oriented and drawn toward suitable host logs due to attractive odors issuing therefrom. Chapman attributed the source of these attractive odors as being issued from the logs per se. However, from his description of experimental procedures used it can be seen that the attractive test logs were also infested with beetles. This beetle infestation introduces an additional factor, namely an attractive substance produced by the beetles themselves (47) in a manner similar to that shown for numerous other scolytids (1; 57, p. 82-94; 38, p. 1312-1324; 46, p. 28-37). Chapman (12, p. 81-82) elaborated considerably concerning the difference in attractiveness of apparently similar logs. Logs attractive early in the season later lost their attraction, whereas logs at first not attractive to the insects later became attractive. This factor must be considered when trapping quantitative numbers in flight for purposes of measuring seasonal flight patterns. Traps near attractive material would naturally catch more insects, but these catches would no longer be representative when the near-by logs lost their attraction.

Although T. lineatum has but one generation per year, at least one re-attack period can be expected later in the season (11). Chapman and Kinghorn (11) also stated that the numbers of insects involved in these late season re-attack flights are much less than in the initial spring flight. The late season or summer flights may also be composed of new brood adults flying to winter hibernation sites. Kinghorn and

Chapman (31) reported that a few new adults may overwinter beneath their brood logs, but that flight is possible for new emerging adults and typically occurs before the winter hibernation period. These workers found that movement to overwintering sites begins in early July and may continue as late as October.

Hylastes species

Relatively little information is available describing the biology or general life history of Hylastes nigrinus or H. ruber. Chamberlin (10, p. 116) stated that H. nigrinus attacks the roots of stumps or dying trees. It has recently been shown, however, that H. nigrinus, like the Douglas-fir beetle, infests fresh-cut or windthrown Douglas-fir logs.[1] Over 90 specimens of H. nigrinus were recorded emerging within a period of 2 days in 1962 from logs that had been invaded as fresh windthrow the previous year. Chamberlin (10, p. 116) concluded that the species is of no economic importance owing to its scarcity of numbers. Even less is known concerning the biology of H. ruber; Chamberlin (10, p. 117) reported its host to be weakened or dying Douglas-fir.

Information concerning the flight patterns of H. nigrinus is provided to a limited degree by Gara and Vite' (24, p. 281). Besides

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1/ Personal communication with J. A. Rudinsky, Professor of Forest Entomology, Oregon State University.

H. nigrinus, H. macer (LeConte) and H. minutus Blackman were present in the ponderosa pine (Pinus ponderosa (Laws.)) forest where this study took place. The three species were treated as a single entity under the generic name Hylastes. Seasonal flights began in early April in this northern California location, and terminated in May. In addition, it was reported that members of the genus had consistent diurnal flight patterns with peak activity occurring at about 1800 hours in the evening. The authors suggested (24, p. 281) that such consistent daily activity represents a circadian rhythm rather than a temperature dependent diurnal flight pattern.

Dendroctonus pseudotsugae Hopkins

Several intensive studies have been conducted on this species which have provided considerable information on flight habits, most of which has been previously mentioned. Atkins (3; 4; 5) has conducted extensive laboratory studies, whereas McMullen and Atkins (38, p. 1312-1324) and Rudinsky (46, p. 24-37) have contributed considerable information on field behavior. In addition, Bedard (6) provided valuable data concerning the seasonal activity of this insect.

Rudinsky (44; 46, p. 28-37) and McMullen and Atkins (38, p. 1312-1324) provided evidence of an attractant produced by the female of this species. This attractant, produced by the females boring in suitable host phloem tissues, serves to concentrate the beetle population on infested host trees and logs. Such a behavioral response would naturally have a profound effect on the density of beetles in a local area within the forest. Such an influence should be considered when measuring quantitative flight patterns on a seasonal basis to avoid a distorted picture of seasonal activity. Chapman and Kinghorn (11) explained the danger of forming conclusions on seasonal flight activity from trap catches located near attractive logs. Since the attractiveness of logs change during the season, an incomplete picture of the time and duration of flight activity may be derived. Because of such effects, attractants must continually be considered when sampling scolytids for determination of their flight patterns. Similar attractants have been found in other species. *Ips pini* Say (1) and *Ips confusus* (57, p. 83-95) both produce attractants which cause heavy, subsequent concentrations of beetles to the infested hosts. In contrast, *Ips typographus* Linne' has been found to respond to the attractive materials emitted by susceptible trees *per se* (39).

Gnathotrichus species

Less information is available on the biology and flight habits of ambrosia beetles of the genus *Gnathotrichus* than for *Trypodendron lineatum*. Chapman and Kinghorn (11), treating the two species as one, stated that the flight pattern of *Gnathotrichus retusus* and *G. sulcatus* is clearly different from that of *Trypodendron*. Graphic illustration by these workers showed a low density flight of the two species occurring throughout the summer with two distinct peaks of activity; the first peak occurred in late June and July and the second in September. Prebble and Graham (43, p. 93) reported that G. sulcatus is commonly in flight one or two weeks later in the spring than Trypodendron, with a second wave of attacks occurring in late summer or autumn.

Dryocoetes autographus (Ratzeburg)

In a recent revision of this group, Bright (8, p. 108-109) listed Dryocoetes americanus Hopkins, D. septentrionis LeConte, and D. pseudotsugae Swaine as synonymous with D. autographus. Bright stated that this species is commonly found in the base and roots of dying or injured standing trees, and in felled or windthrown trees. Chamberlin (10, p. 190-191), describing D. septentrionis, determined that it is of little or no economic importance since it seldom attacks living trees, and its short irregular galleries are often entirely within the bark. Although the species is probably not economically important as a forest pest, it may have some potential value as an interspecific competitor of the Douglas-fir beetle for gallery space within available host material.

Scolytus unispinosus LeConte

McMullen and Atkins (37) reported that weather conditions have a marked effect on the development and flight of *Scolytus unispinosus*. During three years of studying this species in British Columbia, they observed a wide variation in seasonal flight periods. In 1958, the peak activity occurred the latter part of May with most of the resulting progeny overwintering as fourth instar larvae. In 1959, the flight period was later, being held back by unsettled weather, and 11 percent of the progeny overwintered as third instars with the remainder as fourth instars. In 1960, May and June were unusually cold and wet, and activity was delayed until late June with 25 percent of the resulting larvae overwintering as third instars and the rest as fourth instars. This species was seldom caught when the temperature was below 68° to 70° F. (37).

Chamberlin (10, p. 47-48) related that *S. unispinosus* is not infrequently found killing young Douglas-fir trees. Stevens (51) reported an outbreak of *S. unispinosus* killing young Douglas-fir in stands in northwestern California. McMullen and Atkins (37) provided some interesting observations concerning the importance of this scolytid as an interspecific competitor of the Douglas-fir beetle. This species generally infests small diameter, thin barked material not usually invaded by the Douglas-fir beetle, although larger diameter hosts are sometimes invaded. Most important, *S. unispinosus* seasonal flight and establishment in host material occurs later in the season, giving the Douglas-fir beetle first opportunity to become established in the available hosts. It is concluded that this species could act as an interspecific competitor only with that portion of the Douglas-fir beetle population emerging or re-emerging late in the season.

Although McMullen and Atkins (37) recorded but one generation per year in British Columbia, Chamberlin (10, p. 48) stated that under most favorable conditions at low altitudes in western Oregon there are two generations per year.

MATERIALS AND METHODS

The research area was located about 20 miles west of Corvallis, Oregon, at an elevation of 1200 feet on the northeastern slope of Mary's Peak on the Siuslaw National Forest. The study was performed during the spring and summer of 1963, and also during the spring of 1964. A 180 to 200-year-old stand of site II, second growth Douglas-fir, comprised approximately 95 percent of the forest type. A small percentage of associated conifers were also present, namely, grand fir, *Abies grandis* (Dougl.) Lind., western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and western red cedar, *Thuja plicata* Donn.

The majority of apparatus and methods used in the study were for purposes of investigating emergence and flight activity of the various scolytids in relation to the physical factors of the environment. To a limited extent, methods were devised to observe the effect of olfactory responses on the flight of certain species.

Host condition

In the spring of 1963 a large amount of windthrown timber was present in the area due to the devastating windstorm of October 12, 1962. These large numbers of suitable host trees suffered widespread bark beetle infestations during the spring and summer of 1963. The amount of suitable host timber available in 1964 was reduced compared to 1963 since fewer trees had been predisposed to bark beetle attack by windstorm or similar damaging factors. Logging operations however, provided some fresh breeding material in certain areas of the forest in 1964.

It was significant that after bark beetle flights in 1963, logging operations for salvage of windthrow and felling of storm weakened timber served to expose much of the material infested in 1963 to direct solar radiation. Some exposure of infested material can also be attributed to the October 1962 windstorm's felling of large groups of trees which were then unshaded and subsequently infested. It is conceivable that higher temperatures sustained by bark beetles in these unshaded sites might affect their flight patterns.

Emergence

To compare emergence with diurnal and seasonal flight patterns, Douglas-fir logs infested during the previous season were placed within screened cages (4 feet x 6 feet x 6 feet) in an exposed, cut-over area and also within the stand (figure 1). Log sections varying in diameter from 6 inches to 26 inches, and with bark thickness varying from 0.25 inches to 2.5 inches, were used. It was felt that this variation in size would provide a good representation of the various species infesting the different portions of the stem. Not all species were expected to emerge from this material since several are known to emerge late in the summer and overwinter in the litter, in bark crevasses of living trees, within feeding galleries, etc. (31; 52; 54). The purpose of the two sites was to provide a comparison of emergence for the different species from shaded, forested areas and exposed, clearcut areas. This was considered especially important for this region, since clearcutting methods are commonly employed by logging concerns harvesting dense Douglas-fir stands west of the summit of the Cascade Mountains. If such logging activity occurs early enough in the season, the slash may be infested on the exposed site. Also, material infested in a forested area during the spring or early summer may later be exposed by late summer or fall and winter logging operations. Obviously, the exposed sites receive more radiation and higher temperatures may be expected to prevail. Thus, earlier emergence of scolytids can be expected from such areas. At each emergence site hygrothermographs were permanently housed in small shelters for a continuous seasonal record of temperature and humidity. Mercury thermometers placed inside the cages provided a rough comparison of air versus inner bark temperatures. As long as emergence activity lasted at least one daily collection was made, except when inclement weather obviously precluded any emergence or flight activity. On several days of optimum conditions, hourly collections were made to obtain an accurate comparison of emergence activity with flight and the prevailing physical factors.

As mentioned previously in the Literature Review, some of the

Figure 1. Emergence cage on exposed site with sheltered hygrothermograph.

Figure 2. Cage containing logs infested during current flight season to record re-emergence of parent beetles.

species are known to re-emerge after establishing a spring brood to infest additional logs and form a second brood. To relate re-emergence with flight it was necessary to cage material infested during the initial flights of the insects. During the first week of June, after the majority of flight activity for most of the species had occurred, log sections known to be infested earlier in the season were caged in a shaded area within the forest. For this purpose a nine-foot-square screened cage was utilized (Figure 2) to assure that a sufficient quantity of beetles would be obtained since it was not known what percentage would re-emerge.

Flight

Within the vicinity of the shaded emergence cage, six rotary nets were periodically run during the two seasons to measure the relative density of scolytid population in flight. In separate investigations comparing the efficiency of various types of insect traps, Gara (23, p. 15-85) and Juillet (30) both concluded that rotary traps are the more reliable. The single net assemblies used were modeled after those designed by Gara (23, p. 27-30). The size specifications for the materials used were identical to those which Gara found to be optimum for sampling bark beetle populations. The nets were of nylon mesh, 15 inches in diameter, 27.6 inches in depth, and mounted on steel hoops. These nets were mounted at the end of steel rods which, in turn, were attached at their fulcrum to a 0.25 horsepower electric motor. The radial length of rotation measured from the fulcrum to the end of the net was 71.3 inches. The electric motors drove the nets at a rate of 60 revolutions per minute. A single net, of the dimensions given, rotating at this speed sampled about 6558 cubic yards of air per hour. All net assemblies were operated at a standard height of six feet from the ground by shackling the electric motors to six-foot aluminum ladders (Figure 3). The power for driving the electric motors was supplied by three portable generators driven by gasoline engines (Figure 3).

The six nets were arranged in a curvilinear pattern 110 to 140 feet apart with each occupying a standard position throughout the season. The six positions varied in light conditions and somewhat in elevation. Nets 1 through 3 were located on a narrow logging spur along the crest of a small ridge running east and west. The forest canopy at these three sites will arbitrarily be referred to as semi-closed or partially shaded. Net 4 occupied a position at the base of this ridge which was relatively exposed, receiving direct sunlight throughout the day except for early morning and during the evening hours. Nets 5 and 6 were located to the south of the others and were generally within an area of deep shade. The forest canopy over these two sites will be referred to as a closed canopy. Net 1 occupied the highest topographical position, the remaining nets occupying positions of gradually decreasing elevation. Net 6 was located at the lowest point, being about 75 feet

Figure 3. Rotary net assembly including portable generator.

lower than Net 1. This arrangement of elevation and varied shade conditions was designed to provide a representative area for collecting scolytids in flight.

Seasonal Sampling

Because the methods and apparatus used required continued observation and maintenance, flight sampling was not continuous throughout the season. However, at the beginning of the season, when flight activity was at its peak for most species, net samples were taken hourly and totaled each day or every other day of favorable flight conditions. Later in the season (after mid-July) when the greater part of the seasonal activity was completed, net samples were taken every third to seventh day. These intervals were considered to be sufficient for providing a reasonably accurate picture of the seasonal activity patterns. As can be seen in Figures 6, 7, and 12 the seasonal activity pattern was frequently interrupted for as long as two or three weeks due to inclement weather. Such weather patterns are to be expected in the maritime climatic regions of the Pacific Northwest, and western Oregon is no exception in commonly experiencing intermittent cold and rainy periods during the spring and early summer months. The data presented on seasonal flight activity (Figures 6, 7, 9, 12, 17, 18, 23) represent total numbers of the respective species caught on a particular day of sampling. On the majority of days of sampling, the nets were run continuously from the beginning of flight activity in the morning until it ceased in the evening or earlier due to inclement weather. Naturally this results in considerable variation in quantities of insects caught, since favorable flight conditions occurred for only a few hours on certain days, and up to 12 and 14 hours on other occasions. On the limited occasions when the nets were not run for the duration of the favorable flight period the data were not included in construction of the seasonal flight patterns. This was because the numbers caught on these days were not considered comparable to totals caught when sampling throughout the day. Such occasions of incomplete sampling were so few as to be considered insignificant for purposes of reconstructing the seasonal patterns of flight.

Diurnal Sampling

Most of the information on diurnal flight activity was obtained during the spring when greater quantities of bark beetles were in flight. The net collections were made on an hourly basis, and the corresponding weather conditions recorded simultaneously. Besides a hygrothermograph recording temperature and humidity, mercury thermometers were placed at Net positions 1 and 5 for temperature checks. Wind meters accurate to 0.5 miles per hour were used to measure wind velocities when necessary.[2] Although no special equipment was

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2/ Made by the Dwyer Manufacturing Company of Michigan City, Indiana.

available to record light intensity during 1963, observations were made and recorded when gross changes occurred such as sudden overcasts or time of apparent sunset. In 1964, a Daylight Illuminometer used with a "Speedomax" Recorder was available during May for a period of about two weeks.[3] This apparatus provided an accurate measurement of light intensity during a critical period of the flight season. The illuminometer was situated at a height of about six feet in a relatively exposed, unshaded position in the forest. Ordinarily, net sampling was terminated in the evening with the cessation of scolytid flight, however, on certain occasions the nets were run in the darkness when temperature conditions remained favorable for nocturnal activity of bark beetles.

Effect of Attractants

Although it was not within the scope of this study to investigate the response of scolytids to attractants, this factor is intrinsically associated with flight behavior and thus could not be ignored. Net 1 was flanked by split sections of a 180-year-old Douglas-fir tree, windthrown during the windstorm on October 12, 1962. The sections were arranged seven yards from the net to the north and south. At the beginning of the season, these logs were observed closely to record the first attacks for comparison with the numbers of scolytids trapped in the near-by net.

3/ Manufactured by Leeds and Northrup Company, Philadelphia 44, Pennsylvania.

Such observations were expected to provide an indication of the host attraction *per se* compared to the attraction (if any) produced by the attacking species of bark beetles. In addition, the butt portion of a large, old growth (360-year-old) Douglas-fir, windthrown in the same windstorm, was lying parallel to and 10 and 5 yards respectively away from Nets 2 and 3. This material was also observed for bark beetle attacks and correlated with the nearby net samples. Since this log varied considerably in age, bark thickness, and possibly physiological condition, it was expected that it might be invaded by different species than the log sections adjacent to Net 1.

RESULTS AND DISCUSSION

Definite patterns of seasonal and daily flight activity occurred for each of the various species studied. Temperature was apparently the most important factor governing activity, although light intensity was of primary importance for certain species. The period of greatest seasonal activity for the majority of species was during the first few weeks of warm, clear weather in early spring (Figure 5). The diurnal pattern of flight for many species was similar to that of the Douglas-fir beetle, which increases flight activity with increasing light intensity and rising temperatures within the optimal limits. No scolytids were caught during the nocturnal period, but certain species, particularly of the genera *Hylastes* and *Gnathotrichus*, exhibited definite crepuscular patterns of flight activity.

Effects of Temperature

Some of the more obvious effects of temperature are presented as they commonly influenced the activity of the family Scolytidae as a whole. More specific findings concerning effects of physical factors and biotic influences on the individual species are discussed in later sections.

Emergence on Exposed and Shaded Sites

As expected, a wide variation in time of seasonal emergence occurred for the exposed and shaded plots. The variation in time was similar for all emerging species as that illustrated in Tables 1 and 2 and Figure 4 for the Douglas-fir beetle.[4] The earlier emergence in the clearcut area was obviously due to the predominantly higher temperatures that prevailed. In 1963, emergence from the exposed cage began March 19 and 20, whereas activity at the forested plot did not begin until April 28, a difference of 40 days. Since spring activity apparently begins when daily maximum temperatures exceed the activity threshold of the various species, such variations in clearcut and forested areas can be expected each season, although the magnitude of time difference may vary considerably. For example, during the 1964 season (Table 2), initial emergence in the clearcut area occurred on March 27 and in the forested area on April 19, a difference of only 23 days.

There is also an indication that a difference exists between the two plots involving the air temperatures necessary to initiate emergence. On various occasions in 1963 (Table 1) and 1964 (Table 2), beetles were recorded emerging in the exposed area at air temperatures lower than 60° F. It is probable that the emergence activity from the clearcut plot at the lower temperatures can be attributed to the radiant

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4/ Rudinsky, op. cit.

Table 1. Comparison of spring emergence of Dendroctonus pseudotsugae (Hopkins) from logs in clearcut and forested areas for 1963.

Date	Cleared Area		Forested Area	
	No. Beetles	Max. Temp. (°F.)	No. Beetles	Max. Temp. (°F.)
March 19, 1963	4	57	0	50
March 20, 1963	18	65	0	58
March 21, 1963	1	60	0	56
April 6, 1963	3	55	0	51
April 13, 1963	9	63	0	58
April 23, 1963	3	59	0	50
April 28, 1963	116	70	16	61
April 29, 1963	5	64	0	57
May 12, 1963	4	60	0	52
May 13, 1963	77	72	44	63
May 14, 1963	42	73	76	63
May 16, 1963	35	76	87	65
May 17, 1963	17	85	118	74
May 18, 1963	17	83	56	75
May 19, 1963	3	86	14	80
May 20, 1963	3	93	3	85
May 21, 1963	7	71	7	65
May 25, 1963	1	72	3	63
Mav 28, 1963	1	72	19	74

Table 2. Comparison of spring emergence of Dendroctonus pseudotsugae (Hopkins) in clearcut and forested areas for 1964.

Date	Cleared Area		Forested Area	
	No. Beetles	Max. Temp. (^{o}F.)	No. Beetles	Max. Temp. (^{o}F.)
March 27, 1964	7	60	0	53
March 28, 1964	10	68	0	59
March 29, 1964	96	72	0	64
March 30, 1964	39	65	0	60
April 7, 1964	38	65	0	56
April 8, 1964	11	61	0	47
April 13, 1964	17	60	0	56
April 14, 1964	55	62	0	57
April 17, 1964	1	55	0	49
April 18, 1964	13	61	0	55
April 19, 1964	52	69	52	61
April 20, 1964	1	55	0	50
April 21, 1964	8	59	0	52
April 28, 1964	70	71	45	62
May 6, 1964	1	56	0	50

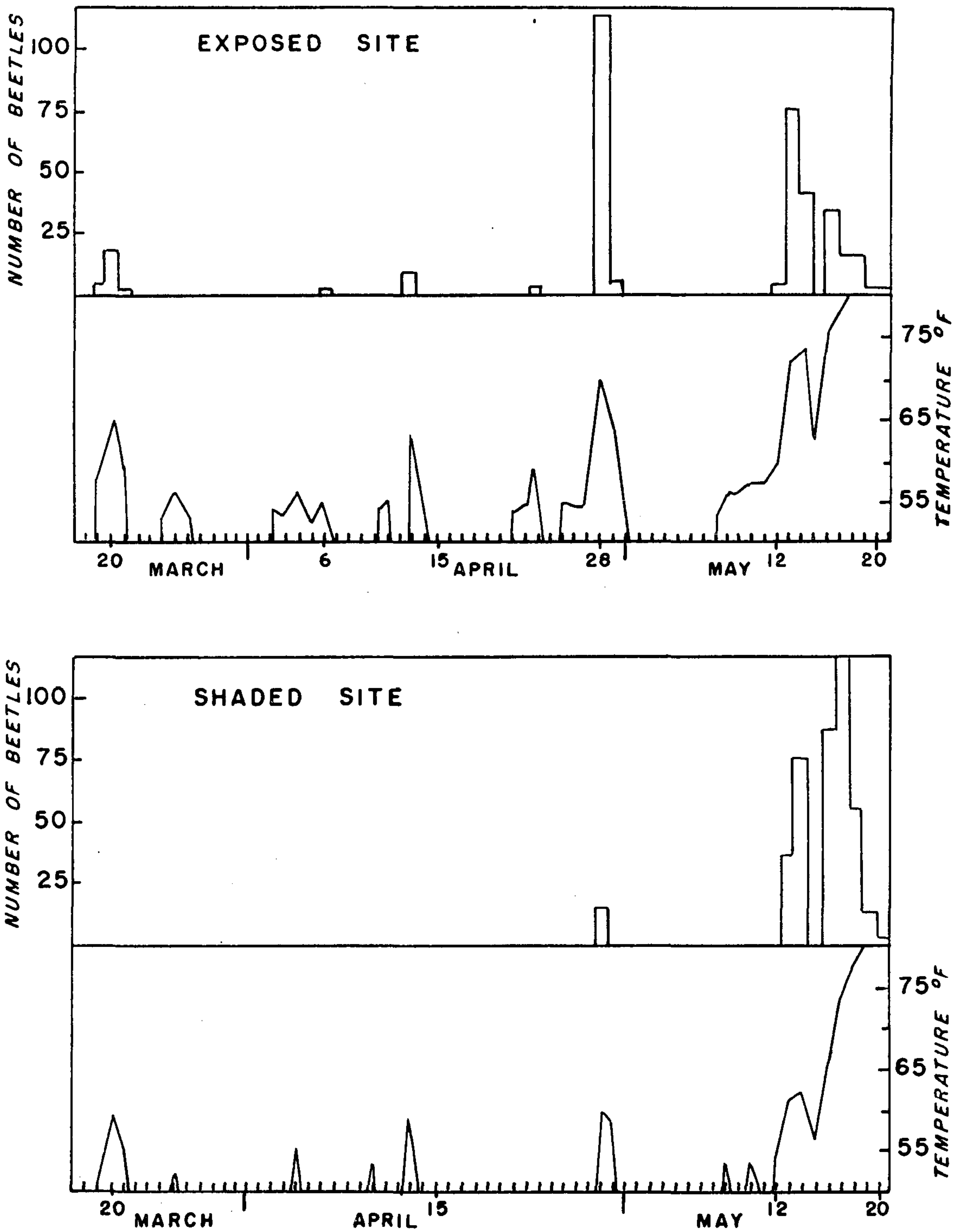


Figure 4. Emergence of Dendroctonus pseudotsugae from exposed and shaded sites in relation to maximum daily temperatures in 1963.

energy absorbed by the logs from the direct rays of the sun. Table 3 provides a comparison of air and sub-cortical temperatures of logs on the exposed and shaded emergence sites. It is apparent that the inner bark regions of logs exposed to direct sunlight become much warmer than those protected by the forest canopy.

Table 3. Comparison of air and bark temperatures in clearcut forested areas. May 13, 1963.

Hour of Day	Clearcut Plot		Forested Plot	
	Air Temperature (°F.)	Inner Bark Temperature (°F.)	Air Temperature (°F.)	Inner Bark Temperature (°F.)
0800	55	48.5	48	44.5
0900	58	61	51	47
1000	60	71.5	53	49
1100	63	75	56	50
1200	66	84	60	52
1300	67	87	60	54
1400	67	86	60	54
1500	68	86	61	54.5
1600	73	84	62	56
1700	69	79	61	55
1730	61	72	59	55

Flight

Temperature was also of primary importance in initiating flight activity. With the exception of Scolytus unispinosus, flights were initiated each season on the first occasion that temperatures equalled or exceeded flight thresholds of the respective species. A wide range of air temperatures was found necessary to initiate flight of the various scolytids and a definite sequence of seasonal flight patterns was the result, as evidenced in Figure 5. Figure 6 illustrates this close relationship of flight activity and maximum temperature for the family Scolytidae. It is apparent that very little activity occurred at temperatures below 57° F. in 1963. An exception was the flight of Pseudohylesinus nebulosus (Figure 7) which occurred earlier in the season at somewhat lower temperatures.

Pseudohylesinus Species

Pseudohylesinus nebulosus and P. grandis were the first bark beetles to fly in the spring of both 1963 and 1964. The spring dispersal flight of P. nebulosus slightly preceded that of P. grandis (Figure 5). This difference was apparently due to a higher temperature threshold required to initiate the flight of P. grandis. As can be seen in Figure 5, these species exhibited not only an early spring flight peak, but a smaller, late summer phase of activity as well. The diurnal activity

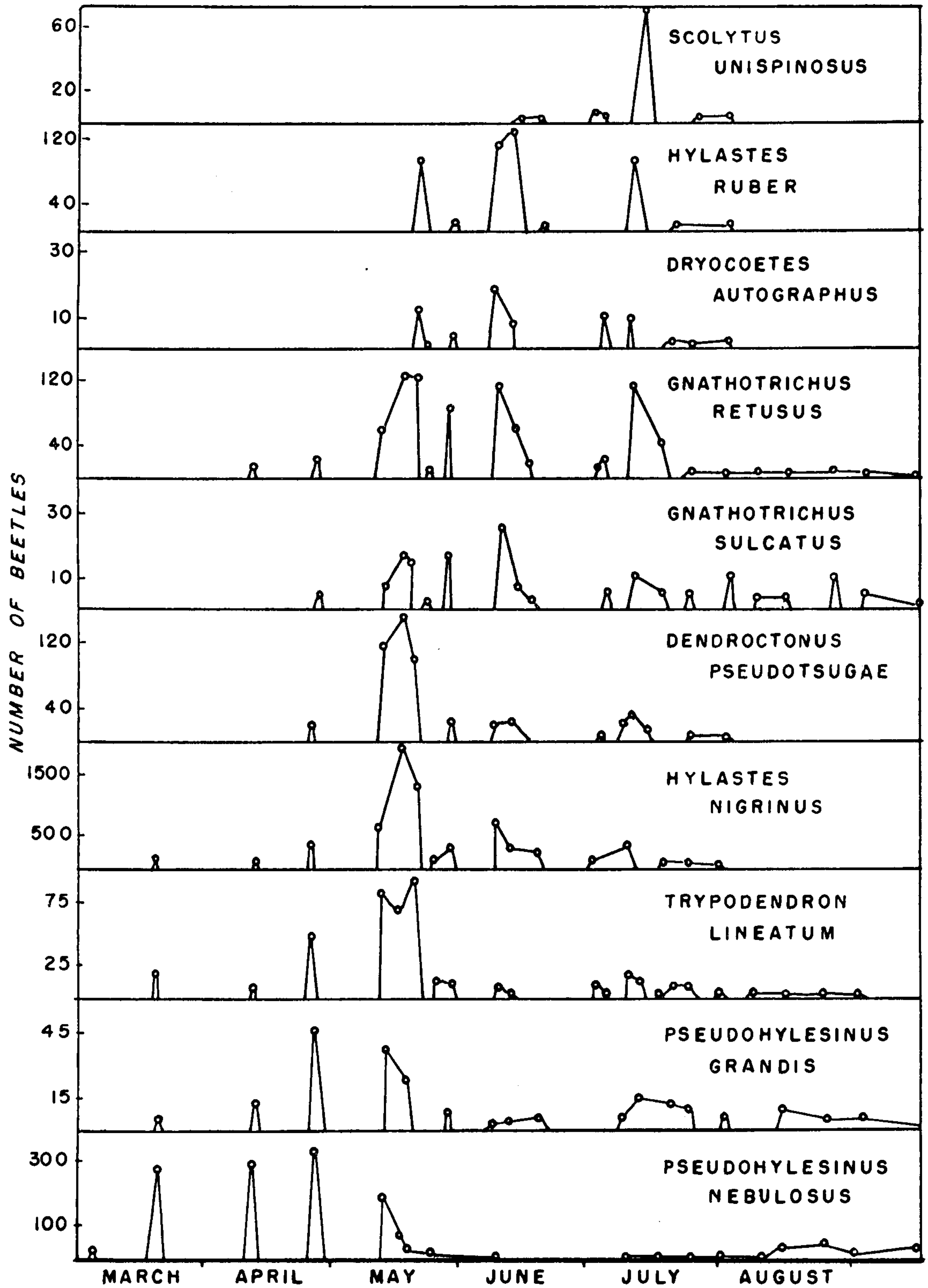
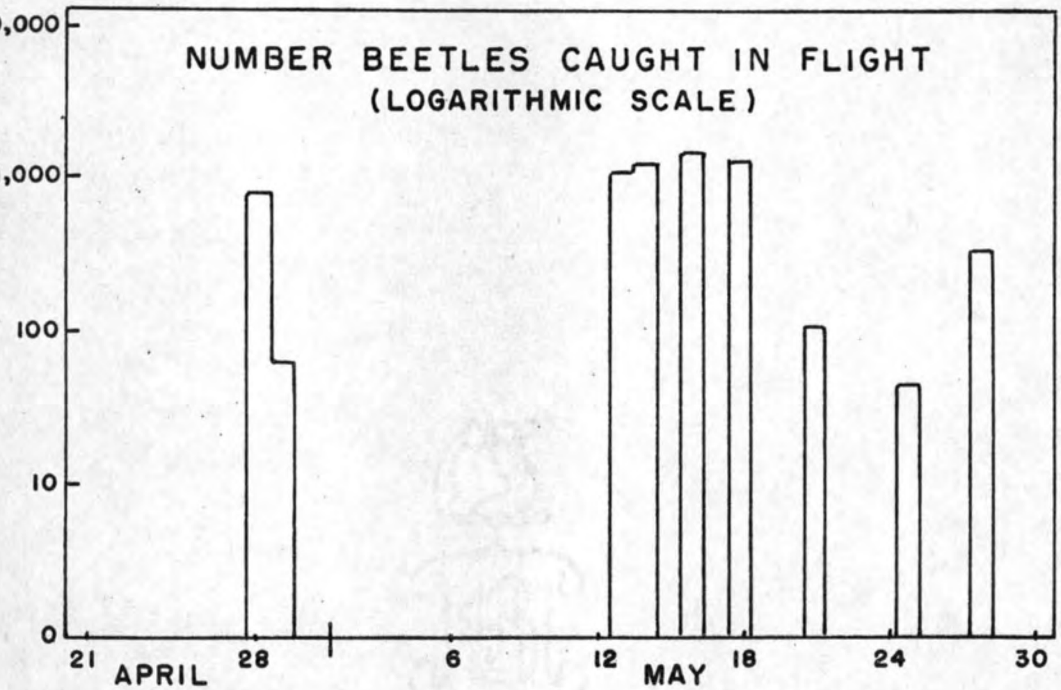


Figure 5. Seasonal flight sequence of scolytid species in 1963.



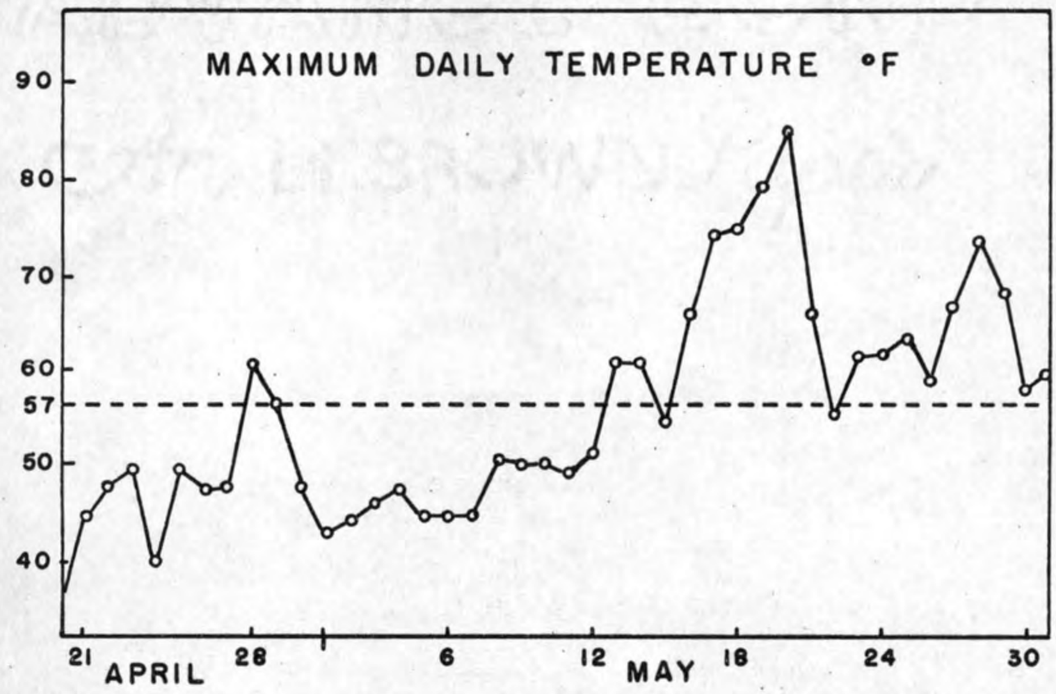


Figure 6. Daily maximum temperatures in relation to the 1963 spring flight pattern of Scolytidae.

pattern of these scolytids was similar to that found by Rudinsky (46, p. 31) for the Douglas-fir beetle. The emergence activity of P. nebulosus and P. grandis was not covered due to their habits of leaving the brood logs in late summer and overwintering in various scattered niches in bark crevasses, feeding galleries, moss, etc. (52; 54).

Seasonal Pattern

Pseudohylesinus nebulosus was the first bark beetle to infest windthrown and fresh-cut timber in both 1963 and 1964, substantiating Walter's and McMullen's (54) findings. In 1963, the initial flight of this insect took place on March 20 with peak activity occurring through April 28 (Figure 7). Activity was interrupted during the lengthy intervening periods by low temperatures and precipitation. In the 1964 season, the initial flight occurred about the same time, but the peak of flight activity was over by the end of March (Figure 7). In 1963, the highest phase of P. grandis flight activity occurred from the end of April to mid-May, whereas in the following season the peak activity began in March and continued to May 15, 1964 (Figure 9).

The comparatively higher proportion of flight activity of these scolytids in March of 1964 can be attributed to a longer period of favorable temperatures than occurred during that time the previous year. Another obvious difference regarding the P. nebulosus flight activity between the two seasons was the higher relative density of beetles in

1964 (Figure 7). The copious amounts of windthrown timber available in 1963 no doubt contributed to this increase in population. Although the difference in densities of P. grandis caught during the two seasons was not nearly as great as for P. nebulosus, the relative numbers of this species caught in 1964 was considerably higher than in 1963. Since this species requires two years to complete a single generation, this increase in numbers recorded in 1964 cannot be attributed to the large amounts of suitable host timber available the previous year. Mature P. grandis adults developing from this material could not be expected to occur in spring flight until 1965.

The low density flights of these scolytids, recorded late in the 1963 season (Figure 5), were new adults flying to winter hibernation quarters. The first P. nebulosus callow adults developing from the spring brood were found in the research area on July 26, and the peak of emergence from this material occurred during the latter half of August, thus corresponding to late season flight records (Figure 5). The new adults produced a few galleries when supplied with fresh Douglas-fir branches, but these galleries were distorted and no eggs were laid.

The late season phase of P. grandis flight occurred in July and August 1963, (Figure 6) which corresponds to the late summer emergence of new adults reported by Thomas and Wright (52). These individuals had just reached the adult stage after overwintering as larvae the first year of their development. Emergence of P. grandis from the caged logs infested in 1962 occurred from August 10, 1963 to September 6, 1963, corresponding roughly with the late summer flight illustrated in Figure 5. When a number of these emerging adults were provided with fresh Douglas-fir log sections most of them burrowed into the material, but no eggs were laid and the galleries were small and distorted indicating they were probably used for feeding purposes. This observation substantiates the findings of Thomas and Wright (52) that new adults of P. grandis emerging in late summer do not produce progeny, and bore into host material only for feeding or hibernation.

Diurnal Pattern

Temperature was found to be the most important single factor governing the diurnal activity of these bark beetles with light playing a secondary role. Flight density increased with increasing temperatures and normal daylight. However, it is significant that the flight numbers of both species also increased with time even though the temperature had leveled off or begun to slightly decrease (Figure 8).

In 1963, it was found that the ambient air temperature necessary to initiate flight of P. nebulosus was 54 - 55^{o} F. (Table 4), whereas in the 1964 season this species was caught in flight at the considerably lower temperatures of 50 - 51^{o} F. The temperature threshold necessary to permit flight of P. grandis was found to be somewhat higher.

Air temperatures of about 56 - 58° F. were necessary to permit flight in 1963 (Figure 8, Tables 5 and 6). Large numbers of this species were not found in flight at lower temperatures the following season as was the case with P. nebulosus. However, a few P. grandis were caught at temperatures as low as 52° F. in 1964.

These discrepancies in temperatures between seasons can most likely be attributed to the large amounts of infested windthrow from the October 1962 windstorm exposed to direct solar radiation in the 1964 season. It is probable that mature scolytids occupying hibernation sites in these areas were able to emerge and fly earlier than from cooler, shaded regions within the forest. Once flight has begun it can be sustained through cooler regions (5; 48), thus enabling the beetles to fly through shaded, forested areas at temperatures lower than that usually necessary for flight to occur. Thus, the 54 - 55° F. temperature threshold found for P. nebulosus in the 1963 season should be regarded as the air temperature necessary to initiate flight of this species in shaded areas.

It is important to note that a certain amount of daylight is required for flight to continue. It can be seen from Figure 8 that flight of P. nebulosus decreases sharply with the setting of the sun even though temperature remains favorable. On May 15, 1964, during a period of high flight density, the activity of P. grandis began to decrease by 1700 hours and had virtually ceased by 1900 hours although

Table 4. Flight activity of Pseudohylesinus nebulosus in relation to daily temperatures in 1963.

Date	Lowest temperature at which initial flight was recorded (^{O}F.)	Air temperature during hour of maximum flight activity (^{O}F.)
March 20, 1963	55	58
March 21, 1963	55	56
April 13, 1963	55	58
April 28, 1963	56	60
April 29, 1963	54	56
May 13, 1963	55	61
May 14, 1963	58	63

Table 5. Flight activity of Pseudohylesinus grandis in relation to daily temperatures in 1963.

Date	Lowest temperature at which initial flight was recorded (^{O}F.)	Air temperature during hour of maximum flight activity (^{O}F.)
April 13, 1963	58	58
April 28, 1963	57	63
April 29, 1963	57	58
May 13, 1963	56	62
May 14, 1963	60	64
May 16, 1963	59	66

sufficient temperatures to support flight prevailed for another two hours (Table 6).

Table 6. Diurnal flight of Pseudohylesinus grandis in relation to temperature and time of day.

Hour of day	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100
Temp. (°F.)	56	58	58	60	61	63	64	63	63	60	58	57
Beetles caught	0	17	28	68	86	93	91	82	41	30	0	0

No relationship was found between relative humidity and flight activity. Extremes of 39 - 65 percent minimum relative humidity were recorded in the study area on the various days when other conditions were optimal for flight. There is apparently no effect within these limits since flight fluctuated directly with varying temperature and light conditions. Since these limits of relative humidity are probably representative of the conditions normally recorded in the forests of this area in early spring it can be stated that this factor exerts little influence upon the flight activity of P. nebulosus or P. grandis.

Trypodendron lineatum (Olivier)

The seasonal flight pattern of the ambrosia beetle, Trypodendron lineatum, was marked by two distinct phases of activity; the first

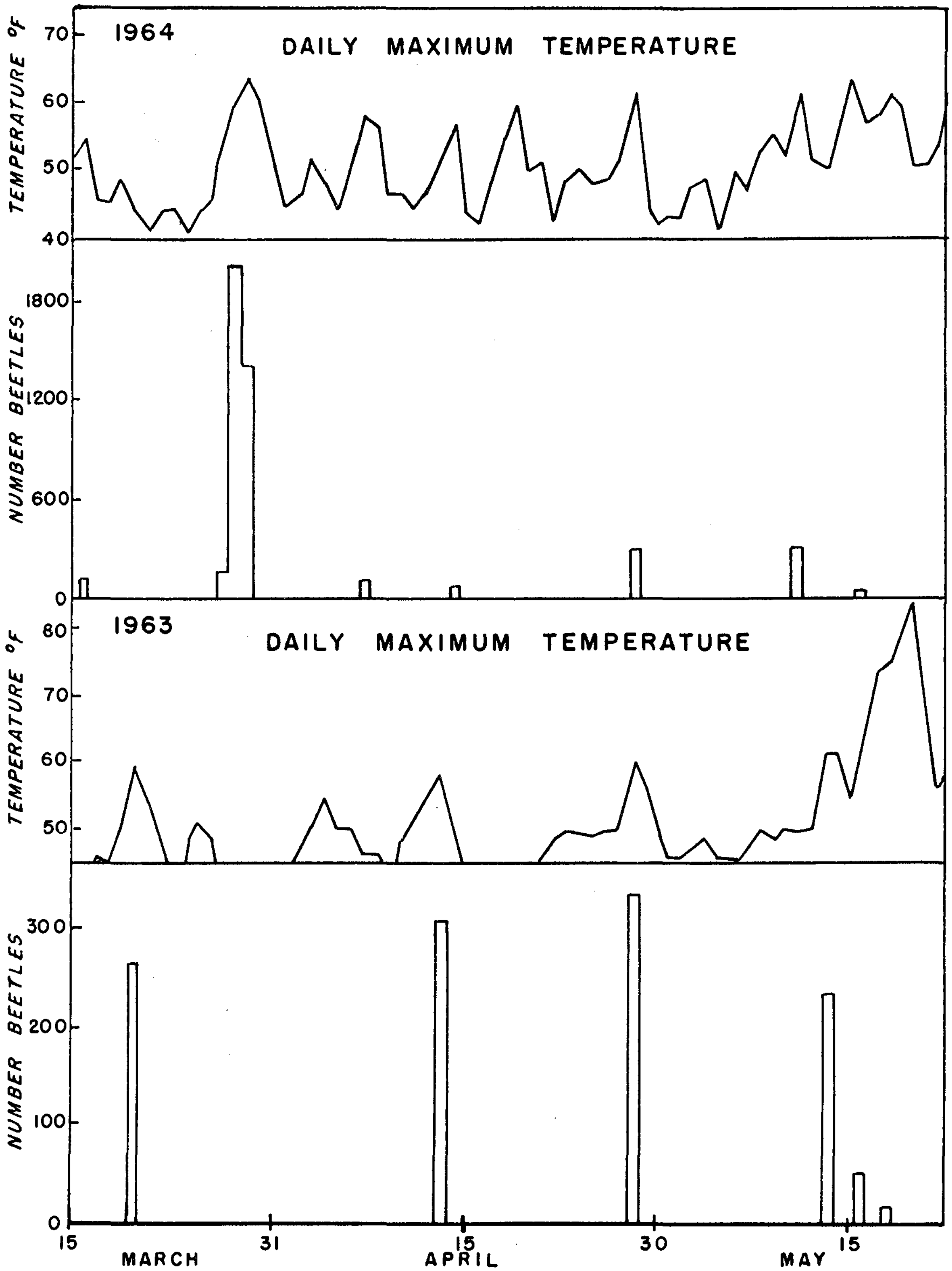


Figure 7. Seasonal flight patterns of Pseudohylesinus nebulosus In relation to temperature.

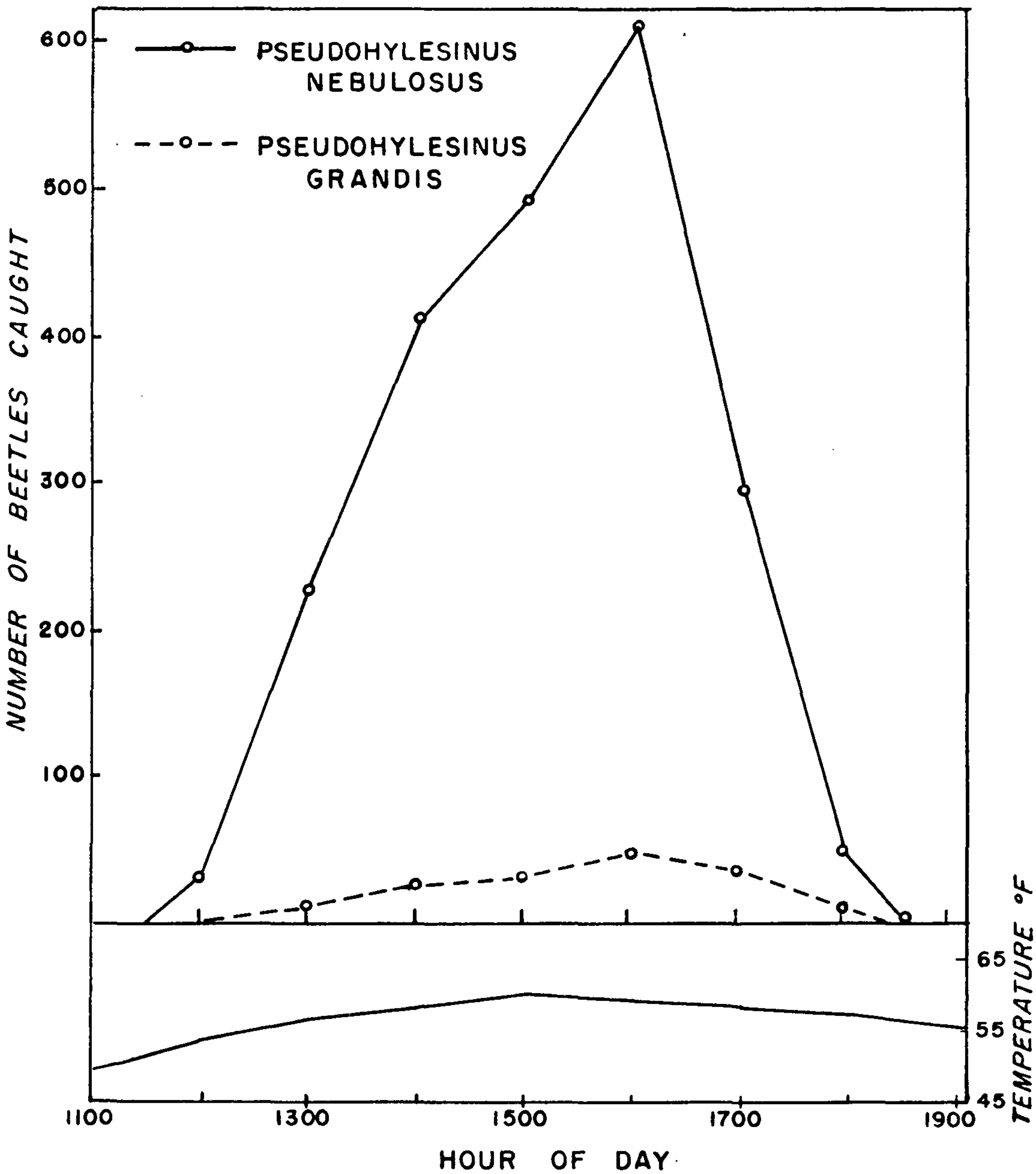


Figure 8. Diurnal flight patterns of Pseudohylesinus nebulosus and P. grandis.

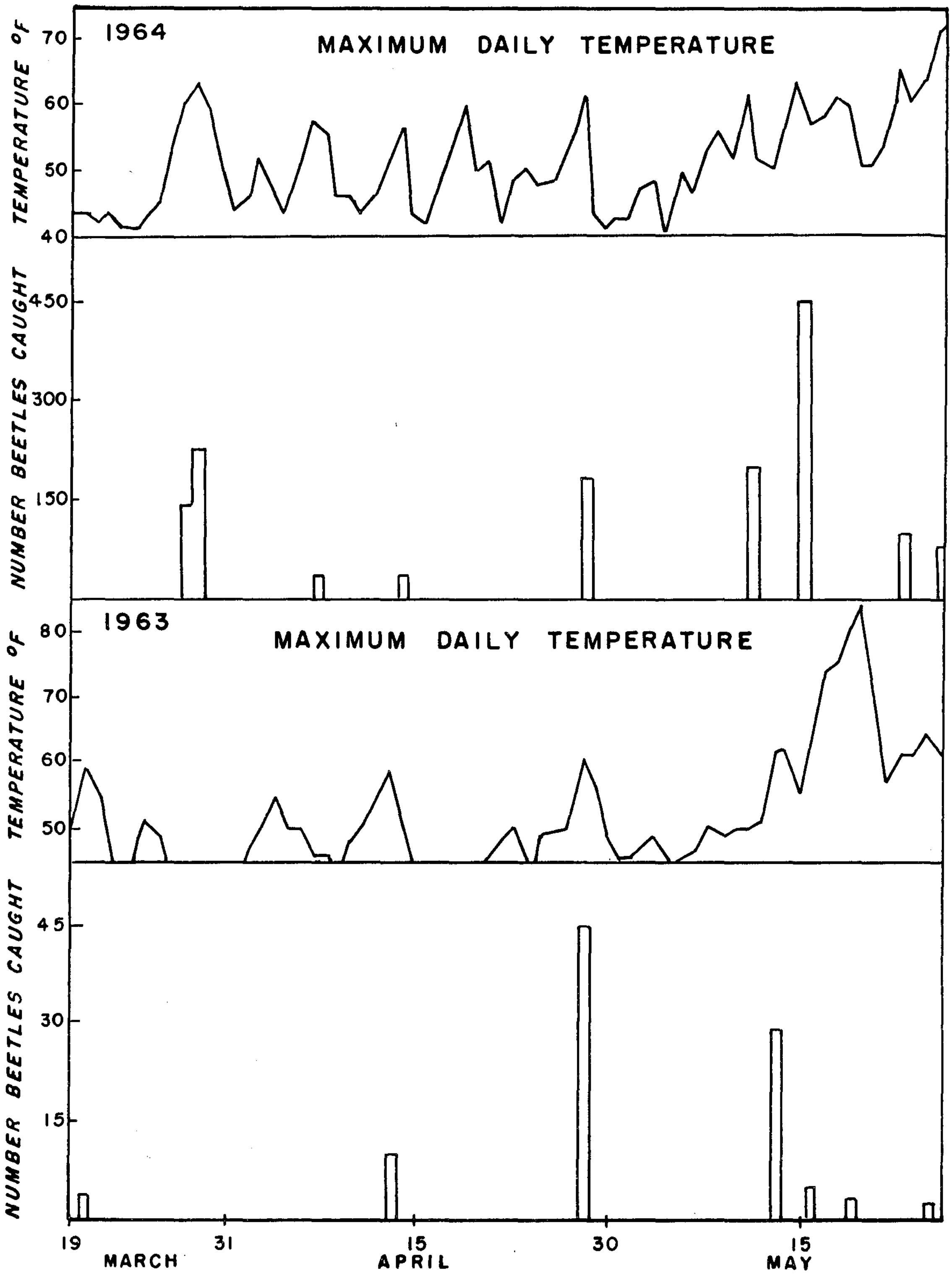


Figure 9. Seasonal flight patterns of Pseudohylesinus grandis in relation to temperature.

occurring during the early spring months, and the second during late summer. The diurnal pattern of activity was very similar to that described for the two species of Pseudohylesinus. In addition to the usual physical factors governing flight activity, a specific attractant produced by this insect (47) was found to greatly influence local flight density.

Seasonal Pattern

The spring flight period of this species was composed of higher population densities and was of shorter duration than the late summer flight. In 1963, spring flight began with the first favorable weather on March 20, and continued periodically until the last week in May at which time activity was terminated during a sustained period of warm weather (Figure 12). Although favorable temperatures for flight existed for a considerable number of days in June, very little flight occurred during that time (Figure 12) indicating that the spring emergence and flight of overwintered adults had ceased. In 1964, the spring flight pattern was similar, beginning on March 28, and terminating for the most part by the end of May. Beetles emerging from caged logs infested the previous season were low in number presumably because most T. lineatum emerge from brood logs the previous summer and overwinter in the forest litter. Spring emergence was not observed until April 13, 1963 (Figure 12), although this species had been caught in flight prior to this. This is not representative of the normal sequence of events, but was no doubt due, in part, to the low numbers present in the caged logs, and secondly, because overwintering sites in the forest litter may warm up sooner thus causing an earlier emergence than from the galleries of brood logs.

The late summer phase of flight activity in 1963 began July 3, and was still continuing at a low level when sampling was discontinued September 24 (Figure 12). The highest period of activity of this phase of flight was from July 3 - 18 and was probably composed of re-emerging parent beetles, whereas the remaining flight curve extending through September no doubt represents new adults in transit to hibernation quarters. On July 3, when numerous spring infested logs were examined, predominantly pupae and a few callow adults were found. This was an indication that it was still too early to expect new adults to be in flight. Emergence from spring infested material further substantiates the view that the first portion of the late summer flight was composed of re-emerged parent beetles. Figure 12 illustrates a small but distinct peak of emergence from these logs in July representing the re-emerging parents. This emergence also corresponds roughly with the July flight peak. Emergence then decreased until the middle of August when a sudden burst of activity occurred and was sustained during favorable weather until mid-September (Figure 12). This late season increase in numbers was apparently composed of matured progeny emerging to seek winter hibernation sites. It should be noted from Figure 12 that relatively few adults were caught in the nets during August and September in comparison to the large numbers emerging. This could possibly be due to a lack of sustained flight ability by the new adults. Novak (41, p. 32-43), for example, stated that most new adults emerge and hibernate beneath the brood log, but Kinghorn and Chapman (31) observed that flight of new adults at this time is typical.

Diurnal Pattern

As was the case with the two species of Pseudohylesinus, temperature was the primary factor governing the flight activity of the insect. Little or no flight occurred in 1963 at ambient air temperatures below 58 - 60° F. (Table 7), which closely corresponds with the flight threshold reported by Chapman and Kinghorn (11). The few insects caught in flight at temperatures less than this figure were no doubt flying from scattered areas in the forest receiving more radiant energy than the research plot. This particular aspect was exemplified in the 1964 season when beetles were caught on several occasions at temperatures less than the 58 - 60° F. threshold found in 1963. The cause of this was essentially the same as that postulated for Pseudohylesinus species in that extensive fall and winter logging activity exposed part of the overwintering population to direct solar radiation. During the 1964 season, T. lineatum was caught on several occasions at temperatures as low as 56° F. In regard to higher temperatures, a maximum of 74° F. was the highest recorded either season during the spring flight of this insect. Temperatures at this level seemed to have no adverse effect since numbers trapped in flight did not decrease under these conditions.

It was observed that daily emergence begins at somewhat lower temperatures than flight. Beetles were caught emerging at inner bark temperatures of 50 - 52° F., providing the air temperature was 56° F. or more. This finding differs somewhat with the 46.4 - 50.0° F. ground litter temperature reported as being necessary by Novak (41, p. 17). This difference could easily be due to the crude instrumentation used for measurement of inner bark temperatures in this study.

A decrease in flight was noted in the evening hours corresponding to the decreasing light intensity. This response is illustrated in Figure 11 where it can be seen that flight was terminated by 1800 hours, although temperature remained favorable for an additional hour. The minimum relative humidity recorded during the flight of this species was 30 percent, but no apparent effects were observed at this level or at higher percentages.

Olfactory Response

Trypodendron lineatum exhibited a definite olfactory response to certain infested logs causing a profound effect on local flight density.

During the first few days of flight in 1963 no particular difference was noticed among the six different sampling nets in regard to the numbers caught. Following the April 28 flight, it was observed that the windthrown logs in the proximity of Net 1 had been attacked. On subsequent days of flight activity a striking increase in numbers of T. lineatum caught by Net 1 was noted (Table 8). The cause of the concentration of this species in the vicinity of Net 1 was no doubt due to the production of an attractant by the invading beetles in the manner described by Rudinsky and Daterman (47). Since the duration of effectiveness of this attractant is not known, the numbers of T. lineatum caught in Net 1 were not used for purposes of reconstructing the seasonal flight pattern (Figure 12). Such an attractant could easily distort the seasonal picture of the insect's flight pattern if it did not remain uniform in its attractive power throughout the flight season. For this reason, a seasonal pattern based on the numbers caught in the remaining five nets was thought to be most representative of the insect's activity.

Table 8 also shows that somewhat higher numbers of T. lineatum were caught at Nets 2 and 3 which were located near uninfested host material, than at Nets 4, 5, and 6 which were not in the proximity of a suitable host. A tentative conclusion based on these figures might be that these insects are also attracted by the host per se. However, any differences in numbers caught in Nets 2 - 6 might be due to a multiplicity of factors other than host attraction. The degree of canopy shade, topographical position, density of the surrounding understory, and position in regard to prevailing air currents, are some other factors that could influence individual net efficiency. In view of these observations, knowledge of bark beetle flight behavior and proficiency in bark beetle flight sampling could be enhanced by future studies aimed toward critical evaluation of the effects of host attraction and sampling position in terms of sampling efficiency.

Effect of Wind

The olfactory studies of this species (47) enabled a more accurate observation of the effect of varied wind velocity on beetle flight. Net sampling proved to be less than successful for this purpose since only low numbers of scolytids were available in flight when comparative wind conditions were present for testing, and because steady winds of even low velocities caused very sharp decreases in numbers caught. The effect of varying wind velocities on numbers of _T. lineatum_ caught on an olfactory cage containing a female-infested log (47) is shown in Figure 10. Flight is sharply curtailed even by low velocities, as evidenced by the sharp increase in late afternoon when the wind suddenly ceased. While it is obvious that wind exerts an adverse condition on flight activity, it is also evident that flight is not terminated by the velocities shown in Figure 11. With winds of these velocities, flight apparently is more sporadic, and probably occurs at lower heights where wind speed is somewhat slowed by the forest undergrowth.

Table 7. Flight activity of Trypodendron lineatum in relation to daily temperatures in 1963.

Date	Lowest temperature at which initial flight was recorded ($^{O}F.$)	Air temperature during hour of maximum flight activity ($^{O}F.$)
March 20, 1963	59	59
April 13, 1963	58	59
April 28, 1963	59	62.5
May 13, 1963	60	64
May 14, 1963	61	65
May 16, 1963	60.5	66

Hylastes nigrinus (Mannerheim)

The spring flight of this scolytid began about the same time as Trypodendron lineatum. Although temperature was again an essential factor, light intensity was also found to be influential in governing the flight activity of this species. Hylastes nigrinus was the first of five species observed to have a crepuscular pattern of daily flight.

Seasonal Pattern

Like Trypodendron lineatum, the spring flight of H. nigrinus began with low densities in March. Unlike Trypodendron or

Table 8. Numbers of <u>Trypodendron lineatum</u> trapped at various net locations during 1963 in relation to the proximity of infested and uninfested host logs.

	7 yards from logs infested April 28, 1963	10 and 5 yards respectively from log uninfested in spring flight		25 yards or more away from suitable host logs		
Date	Net 1	Net 2	Net 3	Net 4	Net 5	Net 6
April 13	2	-	3	0	0	-
April 28	28	10	21	4	7	8
May 13	113	20	25	14	10	10
May 14	160	19	29	4	9	2
May 16	236	18	26	5	6	5
May 18	150	7	10	6	13	55*
May 19	21	2	3	0	1	3
May 21	8	1	1	0	1	1
May 28	7	0	4	0	0	1
Totals	725	77	122	33	47	85

* This comparatively large number may have been due to a possible attraction caused by a Douglas-fir tree felled May 17, 1963 and cut into sections on May 18, 1963.

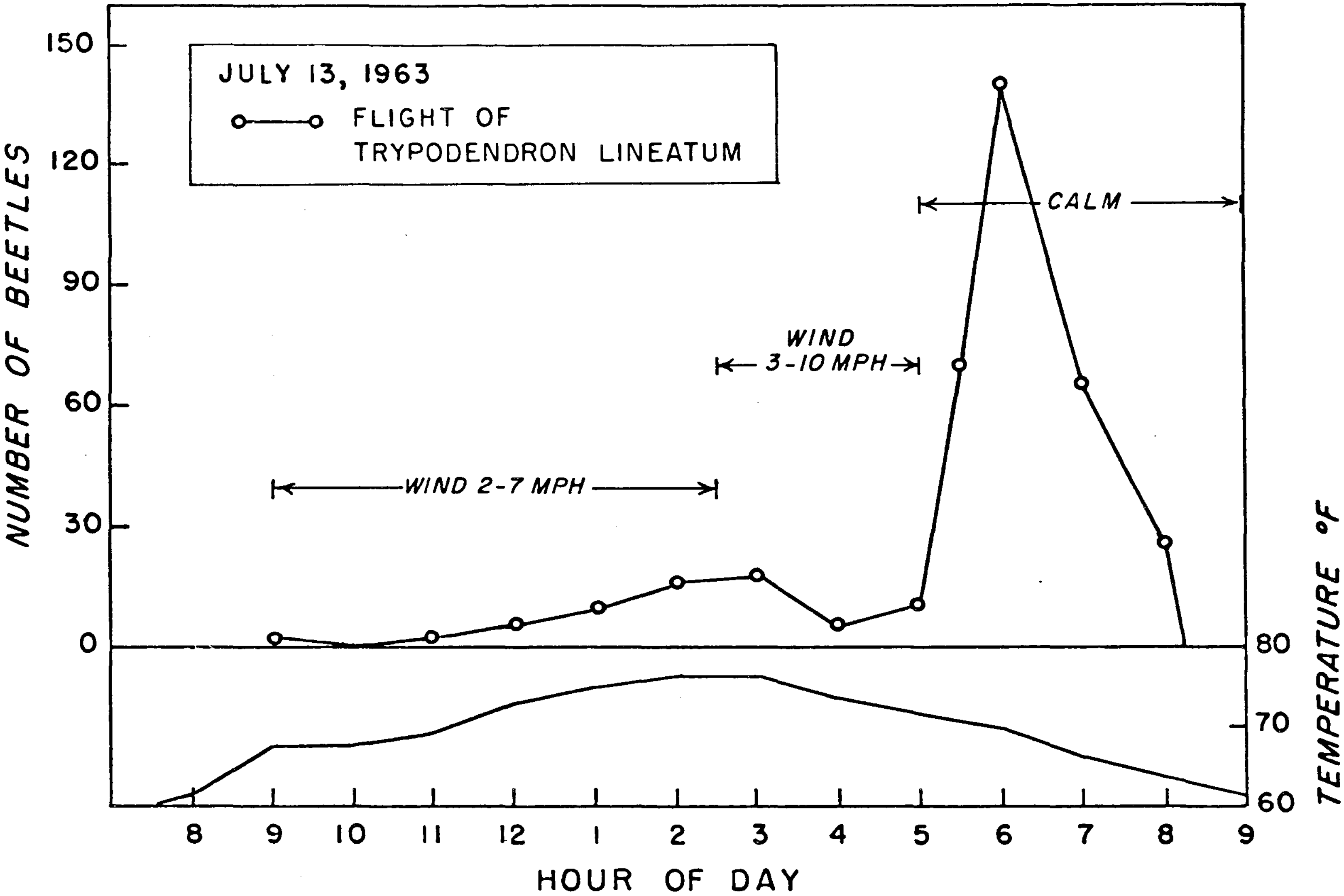


Figure 10. Effect of wind velocity on the flight of Trypodendron lineatum.

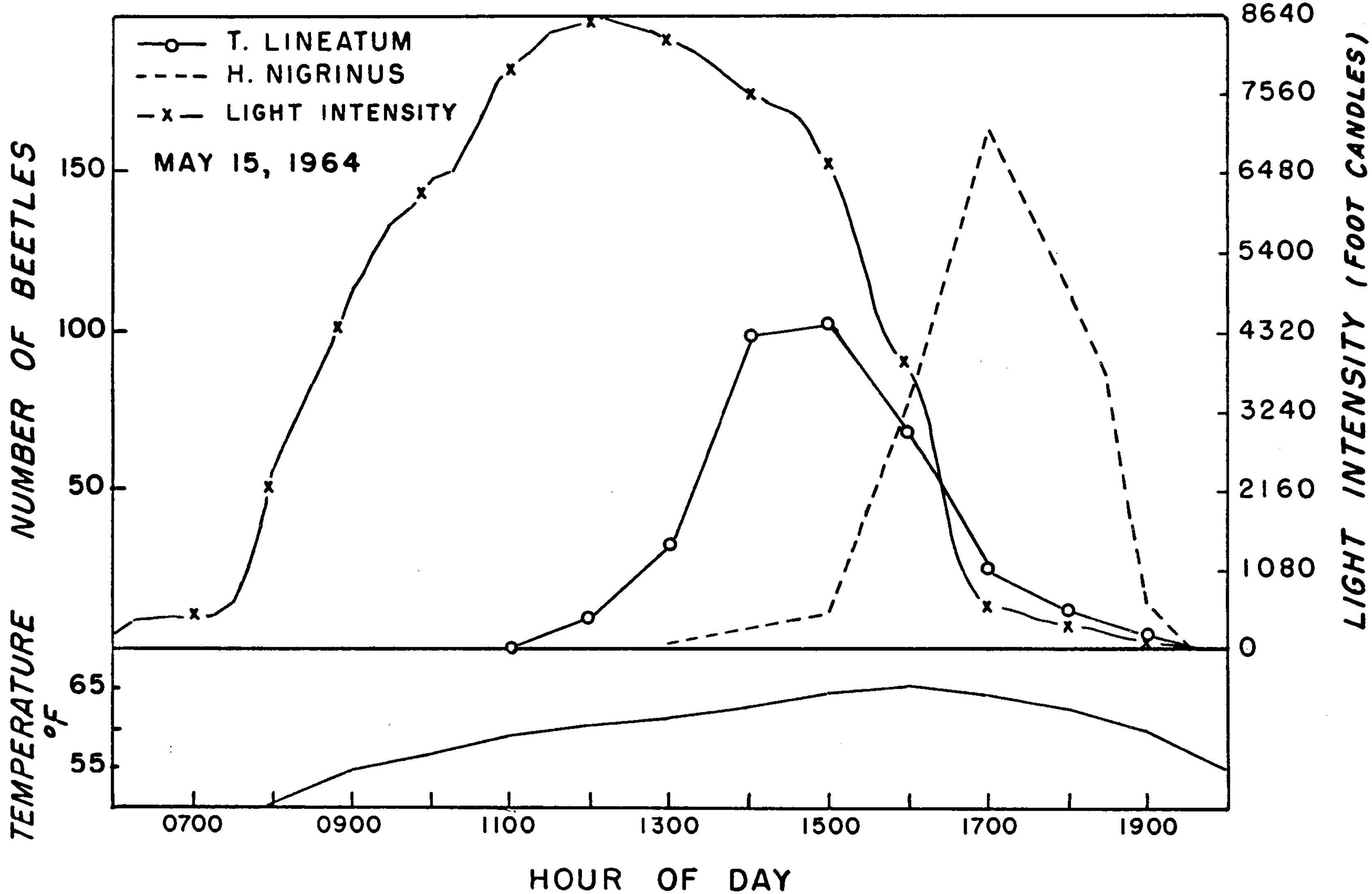


Figure 11. Diurnal flight of Trypodendron lineatum and Hylastes nigrinus in relation to light and temperature.

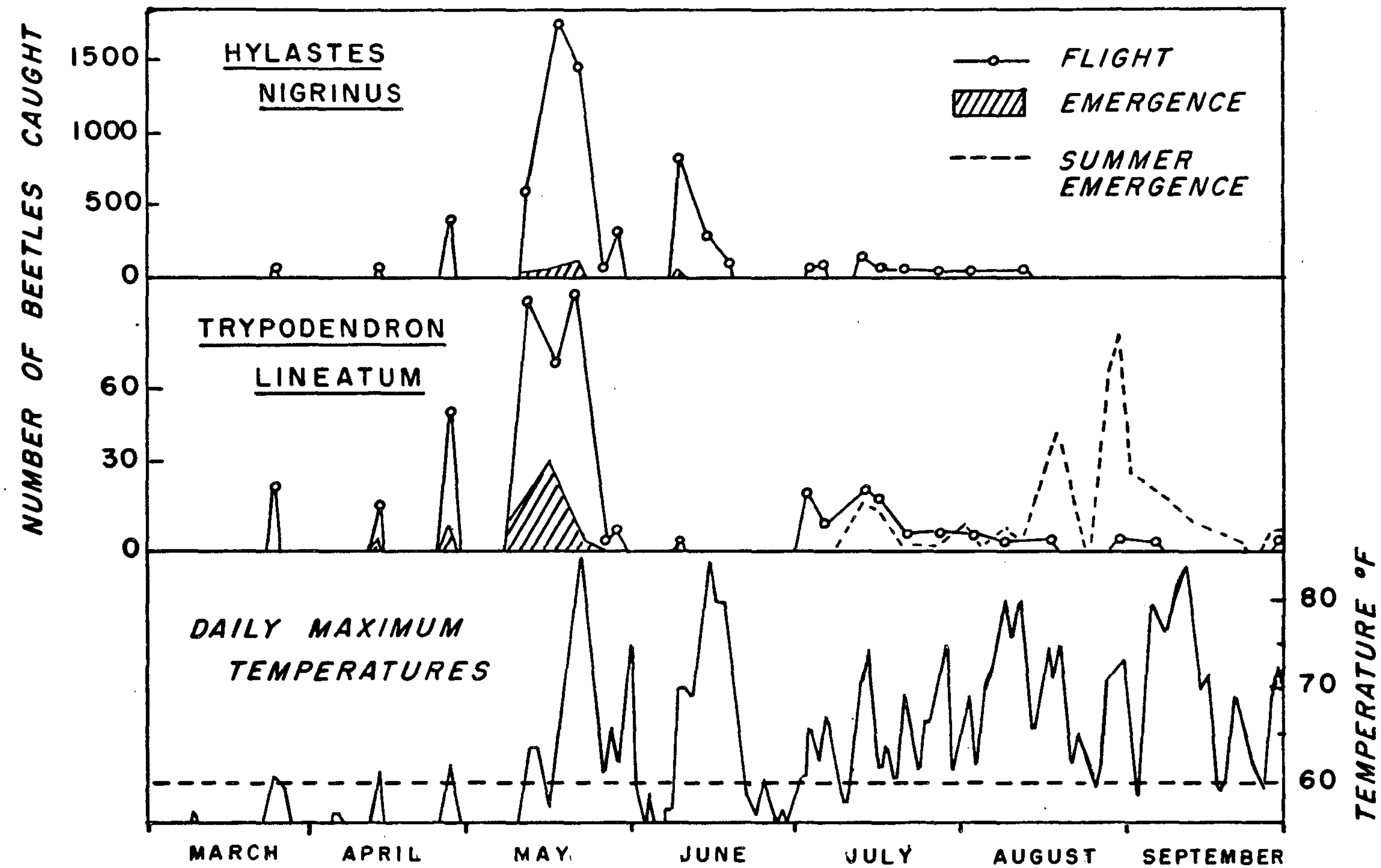


Figure 12. Seasonal pattern of emergence and flight of Trypodendron lineatum and Hylastes nigrinus.

Pseudohylesinus species, activity did not cease during the first extensive period of warm weather in May, but continued for a longer period of time (Figure 12). In 1963, for example, the peak period of activity was in May, but considerable numbers continued to fly during the month of June. The situation was essentially the same in 1964 with activity beginning in March and the maximum numbers in flight during May and June. Low numbers of this species were found emerging in April and May of 1963 from caged Douglas-fir windthrow infested the previous year (Figure 12). The numbers emerging were too few, however, to allow any observations regarding temperature or other factors.

Diurnal Pattern

Very few bark beetles of this species were caught in flight on days when ambient air temperatures did not exceed 58 - 60° F. (Table 9). While this temperature range is probably close to the threshold necessary to initiate flight, it was found that large densities of this species did not occur in flight except on days when maximum temperatures reached 64° F. or more (Figures 13 and 14). Such behavior differs from that observed for the species previously discussed. *Pseudohylesinus nebulosus*, for example, flys in increasingly higher numbers once the temperature has reached or exceeded the flight threshold. This difference exhibited by *H. nigrinus* is apparently due to a strong influence exercised by light intensity.

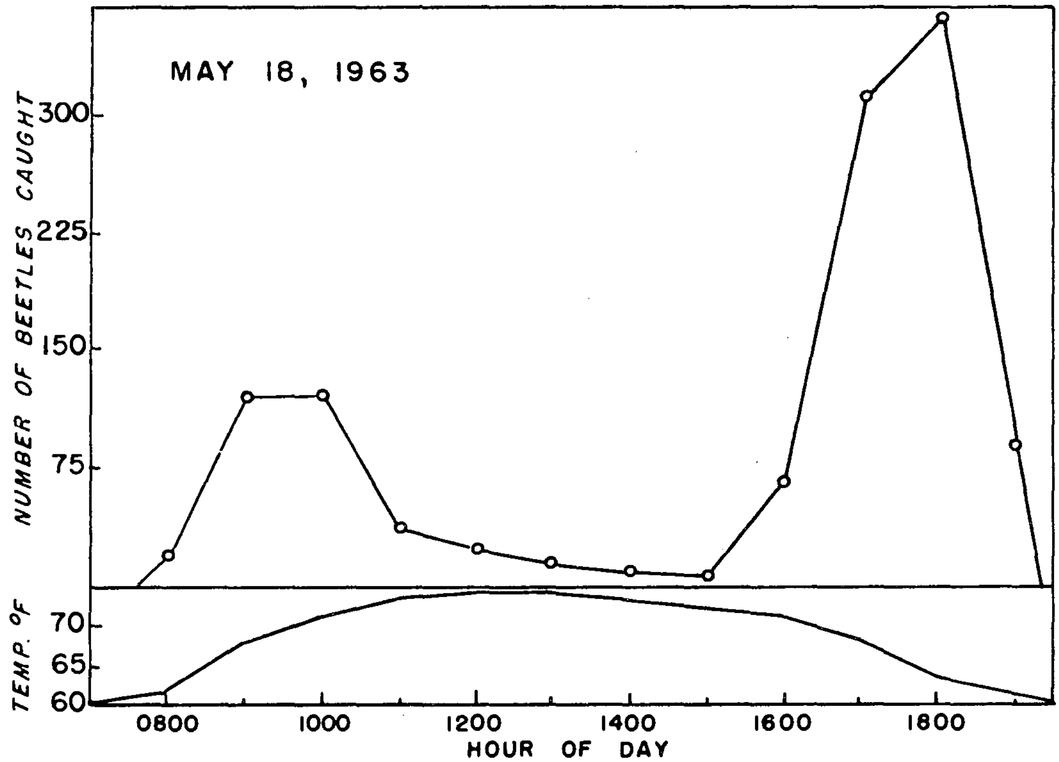


Table 13. Flight of Hylastes nigrinus with high temperatures.

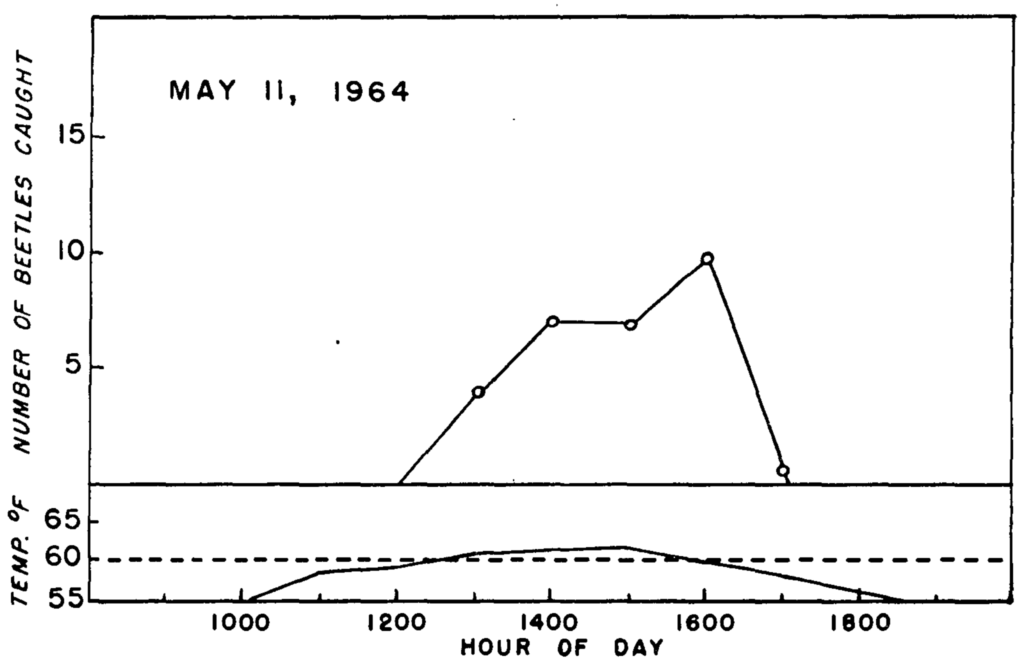


Figure 14. Flight of Hylastes nigrinus with marginal temperatures.

This bark beetle can be classified as crepuscular in its daily flight rhythm since its activity was predominantly found to occur during the late afternoon or early evening hours. This, of course, was true only when favorable temperatures prevailed. Figure 11 and Table 9 present the time of flight characteristic of this species. It can be seen that little flight occurs during the mid-day hours even though favorable temperature may exist (Figures 11, 13, 14) (Table 9). This serves to explain why so few of these insects are found in flight on days when the temperature just equals or barely exceeds the purported threshold of 58 - 60° F. Since it is normal for air temperature to drop in the late afternoon when sunlight is decreasing, the temperature on marginal days thus will be below the flight threshold when light conditions become favorable. The result is that low numbers fly when the temperature is sufficiently high due to high light intensity, and secondly because temperature has decreased when light has become favorable (Figure 14).

The strong influence of light intensity upon the flight activity of this species is exemplified by the diurnal activity pattern on May 14, 1963 (Table 9). A cloud formation resulting in a completely overcast sky by 1215 hours caused a distinct decrease of light intensity in the forest. Subsequent net collections at 1300 hours revealed a sharp increase in numbers of *H. nigrinus* in flight. At 1200 hours, 99 specimens were collected, whereas 832 were trapped in the nets during the following hour. It is significant to note that air temperature remained stable

Table 9. Flight activity of <u>Hylastes nigrinus</u> in relation to various physical factors in 1963.

Date	Time maximum flight occurred	Temp. (°F.)	Percent of relative humidity	Apparent condition of light intensity	Temperature condition the following hour	Temperature at which initial flight occurred (°F.)
April 28	1700	60.5	58	Decreasing	Below threshold	58
May 13	1600	62	43	Decreasing	Below threshold	60
May 14	1300	64	60	low (overcast)	Below threshold	61
May 16	1730	63	52	Decreasing	Optimal	62
May 18	1730	66	38	Decreasing	Optimal	62.5
May 19	1900	75	32	Very low	Optimal	-
May 21	1600	64	66	Decreasing	Below threshold	60
May 28	1730	65	46	Decreasing	Optimal	64
June 10	1730	66	60	Decreasing	Optimal	65
June 13	1830	70	53	Decreasing	Optimal	-
June 17	1830	69	58	Decreasing	Optimal	-

at 64°F. from 1100 hours until 1305 hours. On May 18, 1963 when favorable temperatures prevailed throughout the entire day, a morning flight period was observed in addition to the usual late afternoon activity (Figure 13). This observation further accentuated the importance of light intensity, as a factor determining the time of daily flight activity.

It can be seen in Table 9, that on the occasions when maximum flight occurred before 1700 hours, the subsequent decrease in activity was due to temperatures falling below the minimum necessary to support flight. When temperatures remained optimal until the later evening hours, maximum activity occurred at a later hour. This appears to be a reliable indication that light intensity is more favorable at these later periods. More exact information was obtained in 1964 through use of the illuminometer for measurement of light intensity. Figure 11 depicts the daily curve of light intensity in relation to the flights of Trypodendron lineatum and H. nigrinus. Light intensities below 1000 foot candles are apparently more favorable for H. nigrinus flight activity. However, flight began increasing at somewhat higher light intensity values. During intermittent overcast periods, the illuminometer recorded light intensities as low as 1500 - 850 foot candles. These figures are sufficiently low to explain the marked increase in flight of H. nigrinus during heavy overcast periods such as May 14, 1963 (Table 9).

Relative humidity was also considered as a possible factor influencing the flight of this species. However, the range of values listed in Table 9 had no noticeable effect on flight. Changing relative humidity was also thought to be a factor which might cause a crepuscular pattern of insect flight activity. Since relative humidity normally increased in the late afternoon or evening it was felt that it could be an initiating factor. However, on May 18, 1963 when H. nigrinus exhibited its usual evening flight peak (Figure 13), relative humidity remained stable at 38-40 percent from 1530 to 2100 hours. This observation appears to substantiate the view that the crepuscular flight pattern of this species functions relative to fluctuations in light intensity and not relative humidity.

Therefore, it can be stated that with favorable temperatures the maximum daily flight activity of H. nigrinus during the spring months will occur between 1700 and 1900 hours. It is somewhat more difficult to predict early morning periods of activity. It is clear, however, that at least minimal temperatures must be present at this time for any activity to occur.

It might also be significant to note from Table 9 that peak flight activity occurred considerably later on May 19, and June 13 and 17, 1963, than on the other occasions listed. On these dates prevailing temperatures were also considerably higher, especially on May 19 when maximum activity was delayed until 1900 hours. On this date, maximum activity occurred at a temperature of 75° F., and temperatures of 79 - 77° F. prevailed until 1800 hours. This observation presents the possibility of another type of temperature and light interaction in that activity might be further delayed in the evening due to unusually high temperatures.

In view of these observations, it is apparent that laboratory studies supplementing these field results would benefit the pool of information concerning the effects of the physical factors on scolytid flight behavior. Under controlled experimental conditions the comparative influences of temperature and moisture, and the optimal range of light intensity could be more accurately evaluated.

Gnathotrichus species

No appreciable differences were noted between the diurnal or seasonal flight patterns of *Gnathotrichus retusus* and *G. sulcatus*. One distinction between the two populations was the consistently higher numbers of *G. retusus* caught during both seasons. Both species exhibited a crepuscular flight pattern similar to that of *Hylastes nigrinus*.

Seasonal Pattern

Gnathotrichus species began seasonal activity at about the same time as the Douglas-fir beetle. Considerable numbers of these ambrosia beetles continued to fly throughout the duration of the summer

(Figure 15). Low densities were recorded flying in April, with maximum activity occurring in May and June. Considerable flight also occurred in July, with lower densities of both species trapped in flight through September (Figure 15).

Since much of the life history of these insects is unknown, it is impossible to evaluate the seasonal flight pattern in terms of the origin of groups of beetles participating in flight as the season progressed. Trypodendron lineatum, for example, is known to re-emerge after establishing initial brood galleries and make a second flight to an additional host to form a second brood. Such behavior has not been described for Gnathotrichus species thus making it difficult to evaluate their late season flights. Although Gnathotrichus emerging from logs infested the previous year were low in number, all had emerged by the second week in June. This is perhaps an indication that dispersal of overwintered adults had ceased by this time, and subsequent activity was due to re-emerged parent beetles. No re-emergence of Gnathotrichus from logs infested by scolytids earlier in the season occurred, however, and therefore this view is questionable.

Diurnal Pattern

Temperature was found to be of importance in governing flight, but light intensity was also of primary influence in the timing of daily maximum activity. Temperature preferenda for the two species apparently differ little, since both were usually caught in the same relative densities under identical weather conditions. It is difficult to ascribe a minimum, threshold air temperature necessary for the flight of these particular insects, due to their habit of flying predominantly during the evening hours. Unlike Hylastes nigrinus, which flew in lower densities during mid-day (Figures 13, 14), Gnathotrichus were largely restricted to the evening hours. The typical daily flight performance of these two species was consistently like the pattern illustrated in Figure 16. During clear weather, low numbers were first caught in mid-afternoon with maximum activity occurring about 1800 hours. Sporadic flight was recorded earlier on intermittently cloudy days such as May 14, 1963 (Table 10), and at low densities through the duration of heavily overcast days providing temperatures were favorable (Figure 17).

Although it was difficult to determine threshold flight temperatures for these species since they initiate flight late in the day when temperature is either at the maximum or just starting to decline, it is nevertheless evident from Table 10, that maximum activity was recorded on days when air temperature reached 65^{o} F. or higher. Only low densities of beetles were caught in flight when temperatures did not exceed $61-63^{o}$ F. These latter temperatures can be regarded as being close to the flight threshold. Fewer beetles are caught when maximum temperatures go no higher than $61-63^{o}$ F. since the light factor does not

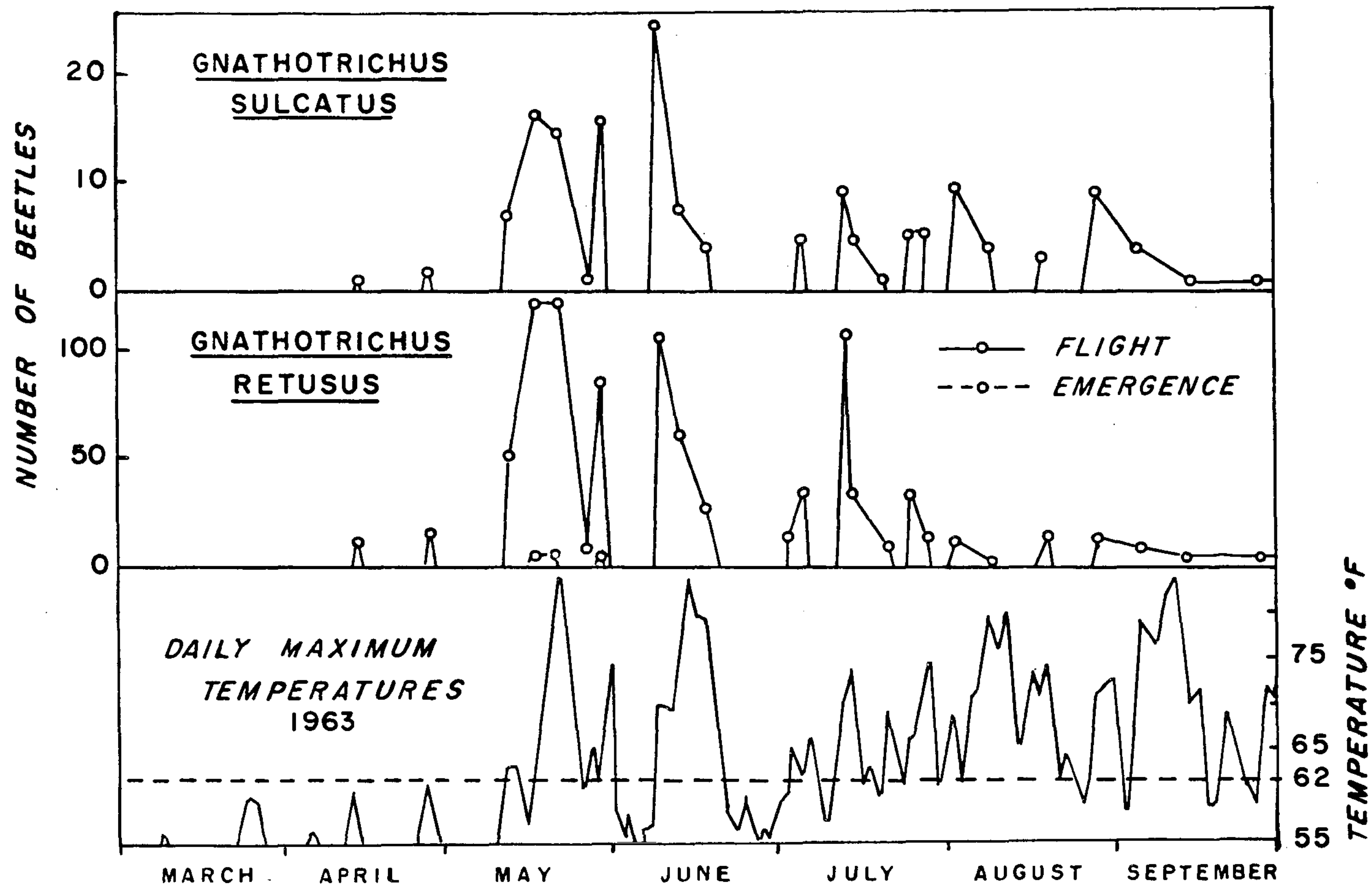


Figure 15. Seasonal flight patterns of Gnathotrichus sulcatus and G. retusus in 1963.

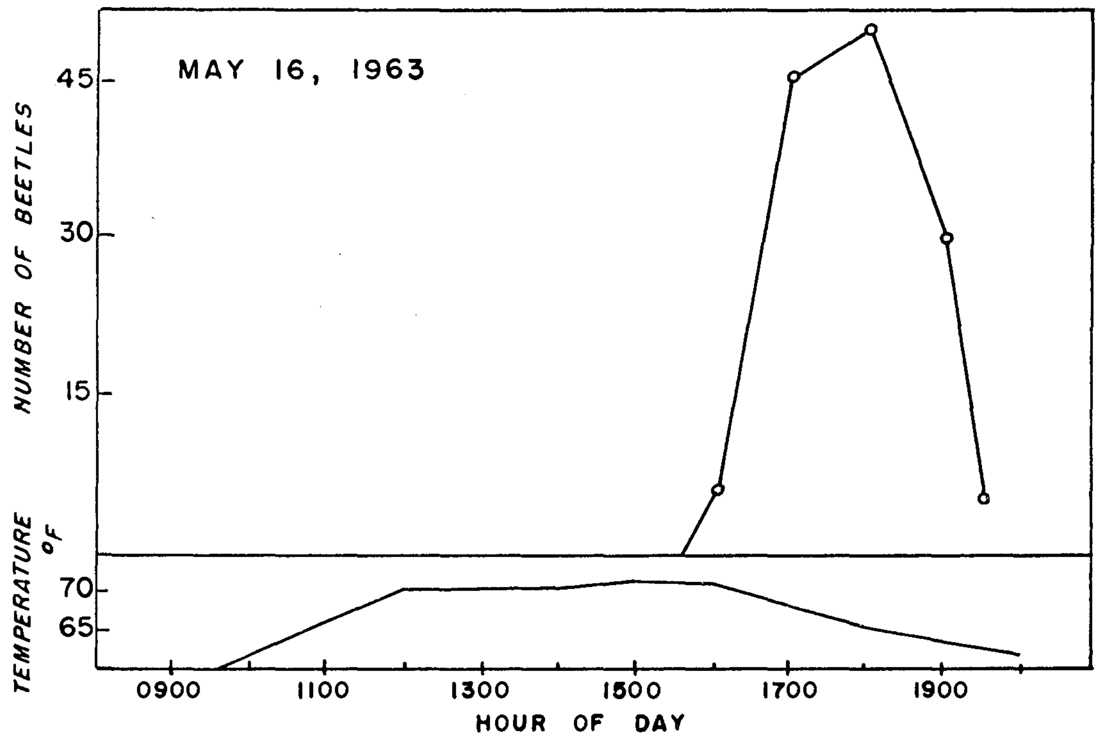


Figure 16. Flight of Gnathotrichus species in clear weather.

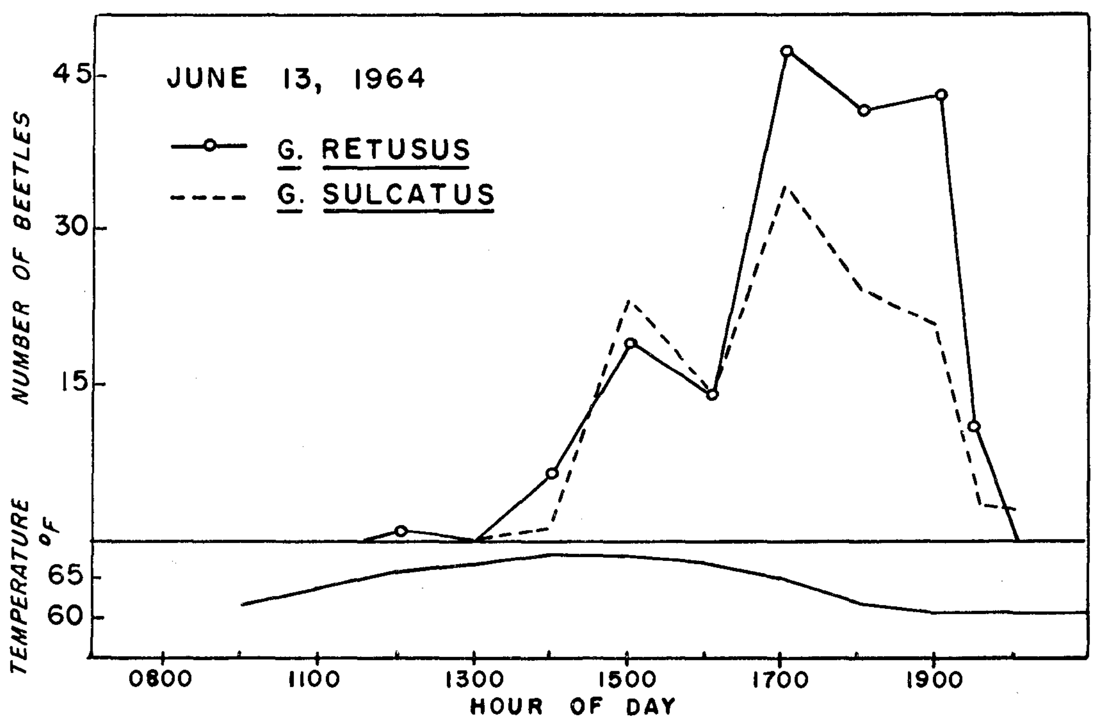


Figure 17. Flight of Gnathotrichus retusus and G. sulcatus in overcast weather.

Table 10. Flight of *Gnathotrichus* species in relation to temperature and the time of day for 1963.

Date	Hour of day maximum flight occurred	Temp. (°F.)	Temperature condition the following hour	Condition of light intensity	Temperature (° F.) at which initial flight occurred
May 13	1600	63	Below threshold	Decreasing	61
May 14	1330	62	Below threshold	low (overcast)	64
May 16	1730	63	Marginal	Decreasing	65
May 18	1800	65	Optimal	Decreasing	72
May 19	1830	77	Optimal	Decreasing	-
May 25	1600	63	Below threshold	Decreasing	63
May 28	1730	65	Below threshold	Decreasing	63
June 10	1730	66	Optimal	Decreasing	68
June 13	1830	70	Optimal	Decreasing	72
June 17	1800	71	Optimal	Decreasing	-
July 12	1800	70	Optimal	Decreasing	-
July 13	1800	70	Optimal	Decreasing	64
July 25	1800	65	Optimal	Decreasing	63

become favorable until later in the day after temperature has decreased.

Too few specimens of this genus emerged from caged material to establish any definite air or bark temperatures required for emergence. Relative humidity was also considered as a factor influencing flight activity, but no relationship was evident within the same range of values listed in Table 9 for Hylastes nigrinus.

The influence of light intensity on the flight activity of Gnathotrichus species was generally similar but somewhat more restrictive than that observed for Hylastes nigrinus. Gnathotrichus species were more restricted to the evening hours whereas Hylastes nigrinus flew in low numbers early in the day with a higher evening phase of activity. An interrelation of light and temperature, similar to that found for Hylastes nigrinus, was noted for these ambrosia beetles concerning the timing of their maximum daily activity. It can be observed from Table 10 that on occasions when maximum flight occurred before 1730 hours, activity was depressed due to temperatures below the minimal level. On occasions when the temperature factor remained above this value, flight peaks occurred between 1730 and 1830 hours. Since the time of maximum evening activity was predominantly later for Gnathotrichus species than for Hylastes nigrinus, it is apparent that a lower range of light intensity is more favorable for flights of these scolytids. In view of this comparison and the daily light intensity curve illustrated in Figure 11, it is probable that light intensities below

600 foot candles are more favorable for flights of these ambrosia beetles.

Higher temperatures persisting in the evening hours did not appear to appreciably delay or prolong activity. Maximum flight occurred no later than 1830 hours at temperatures up to 77° F., and similar timing occurred at a temperature as low as 65° F. (Table 10).

In contrast to *Hylastes nigrinus*, no early morning flight of *Gnathotrichus* was recorded, but this is not to say that such a phenomenon could not occur. Indeed, flights recorded on overcast days (Table 10, Figure 17) are evidence that such activity could occur providing air temperatures of at least 61 - 63° F. prevailed.

Dryocoetes autographus (Ratzeburg)

This insect was found to fly later in the season than those species discussed above, and about the same time as *Hylastes ruber* (Figure 18).

Seasonal Pattern

Higher temperatures than those found necessary for the species previously discussed are apparently essential for the dispersal activity of this insect. As illustrated in Figure 18, all phases of the seasonal pattern correspond with the periods of higher temperatures which occurred sporadically during 1963. The possibility that this late season pattern exhibited by *Dryocoetes autographus* is due to its overwintering in an immature stage does not seem logical. Portions of emergence logs used in the 1963 season were previously examined in January and found to contain overwintering adults of this species. The presence of overwintering adults in these logs plus the occurrence of flight with periods of high temperatures implicated temperature as the factor necessary to induce flight. Neither emergence nor flight activity occurred before mid-May (Figure 18). Emergence was initially recorded on May 16, with the first flight of the season also being registered on that date. In 1963, maximum flight took place in May and June, with some interruptions due to cool weather. Low densities of this species also flew in July and August. These late flyers may have been re-emerged adults, but probably represented an extension of the initial dispersal flight that was delayed by a prolonged period of low temperatures in late June and part of July.

Diurnal Pattern

D. autographus was found to have a crepuscular flight pattern, similar to that described for Gnathotrichus species and Hylastes nigrinus. The daily onset of flight was consistently just before or during the twilight hours when temperatures and other conditions were favorable. On various sampling days from May 16 to July 13, 1963, maximum flight occurred between 1700 and 1900 hours (Table 11). This represents a somewhat wider range of favorable twilight hours than that

Table 11. Flight of *Dryocoetes autographus* in relation to temperature and the time of day in 1963.

Date	Hour of day maximum flight occurred	Temp. (°F.)	Temperature condition the following hour	Condition of light intensity	Temperature (°F.) at which initial flight occurred
May 16	1700	65	Below threshold	Decreasing	68
May 18	1700	68	Optimal	Decreasing	71
May 19	1830	77	Optimal	Decreasing	78
June 10	1730	65	Below threshold	Decreasing	68
June 13	1800	71	Optimal	Decreasing	75
July 5	1700	63	Below threshold	Decreasing	66
July 11	1700	64	Below threshold	Decreasing	66
July 12	1830	70	Optimal	Decreasing	71.5
July 13	1900	68	Optimal	Decreasing	68

observed for Gnathotrichus species, suggesting perhaps, that this insect's flight responses are somewhat less dependent on a particular range of light intensity than Gnathotrichus. However, in view of the time of day that maximum flights occurred it can be stated that light intensities of less than 1000 foot candles are more favorable for flights of D. autographus.

Like other crepuscular species, such as Gnathotrichus retusus and G. sulcatus, Dryocoetes also flew earlier during the day when the light intensity was decreased by overcast weather conditions. Figure 20 illustrates the longer period of daily activity usually occurring with overcast skies, whereas Figure 19 depicts the more typical crepuscular rhythm associated with clear weather.

Due to this insect's evening flight habits and the low densities caught in flight, it was difficult to establish the temperature thresholds of emergence and flight activity. However, some indication of temperature preferenda for flight activity is obtainable from the data summarized in Table 11. Initial flight did not occur at air temperatures below 65^{o} F. However, some flight was recorded in the evening when the air temperature was as low as 63^{o} F. These instances occurred later in the evening on days when much warmer temperatures had initiated the activity. Flight was apparently inhibited at lower temperatures and ceased soon after the air temperature had dropped below 63^{o} F. In view of the information summarized in Table 11 and observations in

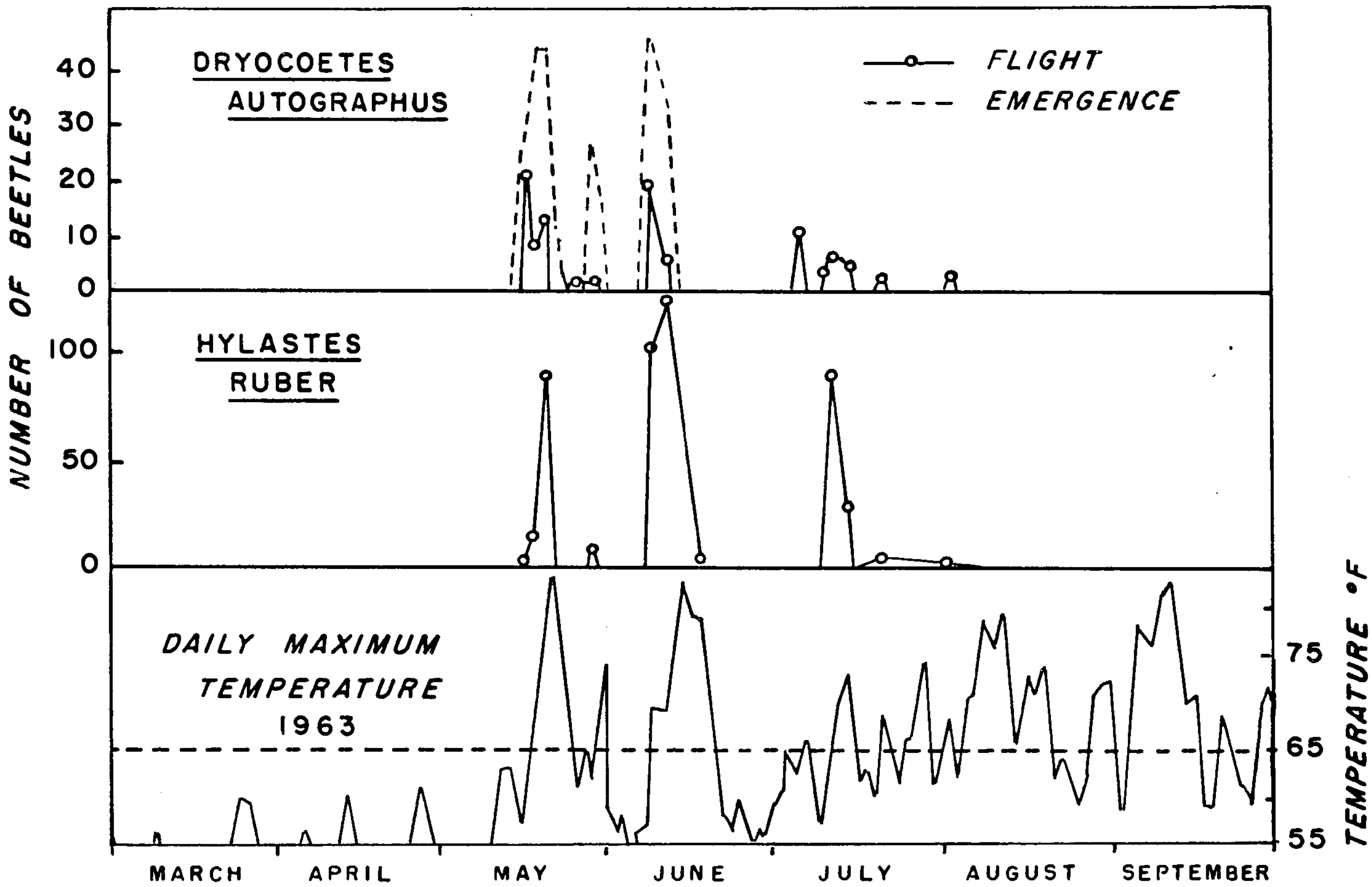


Figure 18. Seasonal activity patterns of Dryocoetes autographus and Hylastes ruber in 1963.

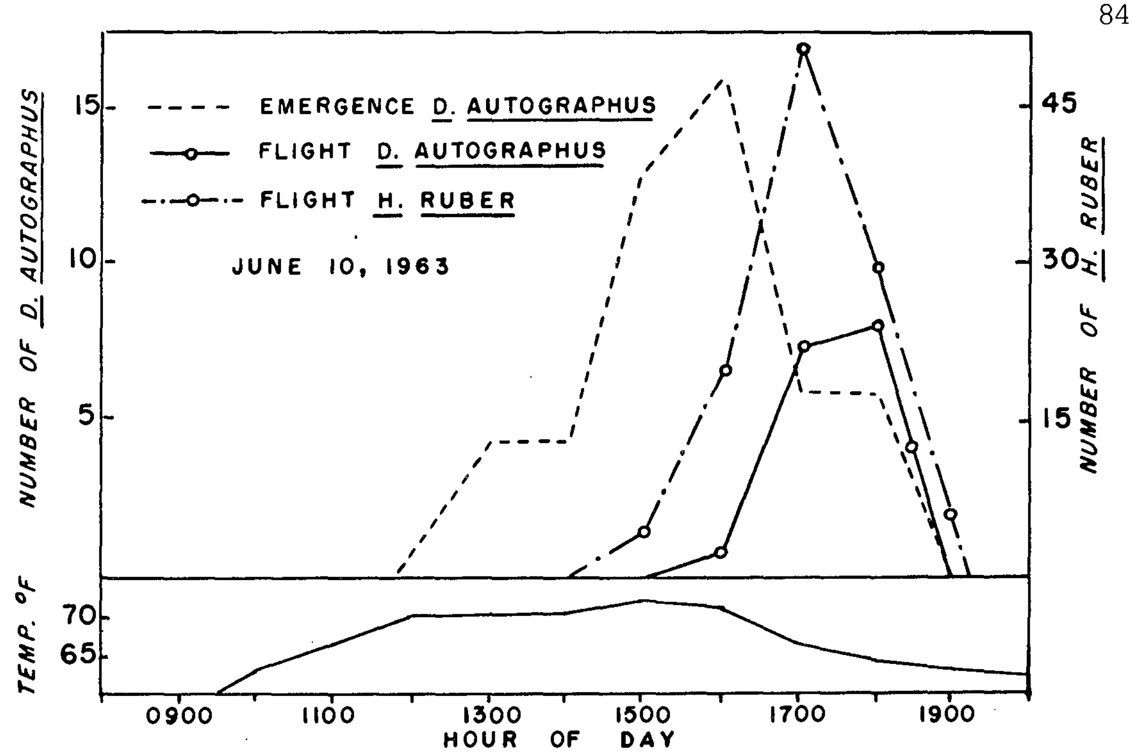


Figure 19. Flight of Dryocoetes autographus and Hylastes ruber in clear weather.

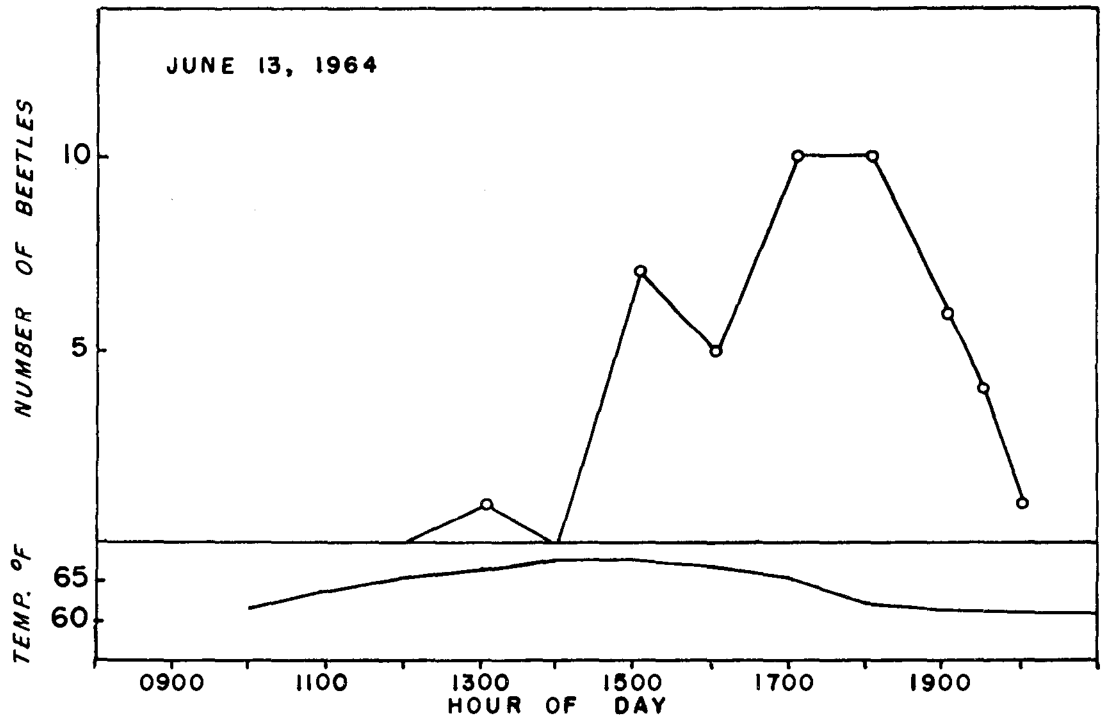


Figure 20. Flight of Dryocoetes autographus in overcast weather.

the field, it is probable that the air temperature necessary to initiate flight activity of D. autographus lies between 65 - 68° F. However, once flight has begun, it can be sustained at temperatures as low as 63° F.

This species differed somewhat from Trypodendron lineatum and some other species studied in that emergence did not occur at temperatures lower than those necessary to support flight activity. On 12 days when emergence was recorded from the shaded cage, no emergence activity took place when air temperatures were below 66° F.

Hylastes ruber Swaine

As with Dryocoetes autographus, Hylastes ruber demonstrated a dependency on higher temperatures for implementation of dispersal activity. This was the fifth scolytid species found to have a crepuscular flight rhythm.

Seasonal Pattern

In 1963, the seasonal activity of this barkbeetle began May 18, coinciding with the beginning of Dryocoetes autographus flight. A relatively greater amount of activity by this species took place in June and July however, as compared with Dryocoetes (Figure 18). Due to the lack of information available on the life history of this species, it is questionable whether the occurrence of initial seasonal activity depended entirely on a temperature threshold. It is significant that no seasonal flight by this insect was recorded prior to the first period of fair weather and higher temperatures in mid-May. This close relationship of flight activity with the sporadic periods of high temperatures (Figure 18), seems to indicate that temperature is the primary factor regulating the flight of this species. In view of these observations, flight could conceivably occur earlier or later in the season, depending on the occurrence of favorable temperatures.

Diurnal Pattern

The comparatively few days on which a substantial flight of this scolytid took place makes determination of conclusions difficult concerning the effects of the physical factors on dispersal activity. However, some general statements can be made after consideration of the data presented in Table 12 and Figures 18 and 19.

It is evident from Table 12 and Figure 19 that considerably higher temperatures than the thresholds found for species discussed formerly are necessary to initiate the flight activity of H. ruber. Air temperatures of at least 68° F. are apparently necessary to induce flight of this scolytid, although temperatures of 70° F. or more are evidently more favorable (Table 12). In some instances (Table 12) maximum evening flight occurred at temperatures as low as 67° F.,

Table 12. Flight of <u>Hylastes ruber</u> in relation to temperature and the time of day in 1963.

Date	Hour of day maximum flight occurred	Temp. (°F.)	Temperature condition the following hour	Condition of light intensity	Temperature (°F.) at which initial flight occurred
May 18	1730	67	Below threshold	Decreasing	68
May 19	1830	77	Optimal	Decreasing	78
June 10	1700	67	Below threshold	Decreasing	70
June 13	1800	72	Optimal	Decreasing	73
July 12	1730	71	Optimal	Decreasing	73
July 13	1800	71	Optimal	Decreasing	74

indicating that flight can be sustained at air temperatures lower than those required to initiate flight.

Maximum daily flight consistently occurred between 1700 and 1830 hours (Table 12), indicating that light intensity is most favorable within that period during the time of year sampling was conducted. In view of this observation, it is probable that the light intensities recorded as being most favorable for other crepuscular species would also be optimal for this scolytid. Although no morning flight of this species was ever observed it is probable that it would occur if favorable temperatures occurred concomitantly with low light intensity during that period of the day. While an early morning pattern of flight was not uncommon with Hylastes nigrinus, it is unlikely to occur with H. ruber in this area due to the predominance of cool wet weather and the higher temperatures necessary to support the flight of this species. Figure 19 illustrates a typical example of the daily, crepuscular pattern of this scolytid with favorable temperatures and clear weather.

Scolytus unispinosus LeConte

Seasonal Pattern

The seasonal flight of Scolytus unispinosus was of short duration and composed of relatively low numbers. These factors caused some difficulty in the assessment of the effects of the various physical factors.

This beetle represents the single exception of all the scolytids treated in detail in that it did not begin seasonal flight with the initial occurrence of favorable temperatures. This was not surprising however, since it was demonstrated by McMullen and Atkins (37) that this insect overwinters in the third and fourth larval stages. Thus, during spring, a sufficient period of favorable temperature must occur for completion of brood maturation. After development to the adult stage, dispersal flights were found to take place with the periodic occurrence of favorable temperature.

Emergence from caged host material infested by this insect did not occur in the shaded area until June 1963 (Figure 23), indicating the beetles had not reached the adult stage prior to this time. Maximum emergence from the shaded plot did not occur until mid-July. These logs had been examined the second week of April and found to contain only late instar larvae. Emergence of this species from the cage exposed in the clearcut area of the forest occurred considerably earlier (Figure 23). Since the infested material had been obtained from the same source, this accelerated development can obviously be attributed to the predominantly higher temperatures sustained in the unshaded cage. Peak activity at the two positions occurred about one month apart, being recorded at the exposed position about June 10, and at the shaded plot on July 12, 1963 (Figure 23).

In 1963, no flight of this scolytid was recorded in May and little in June even though considerable periods of favorable weather occurred within this time (Figure 23). In July, however, these insects had matured and were obviously ready to fly with the first occurrence of favorable conditions. In 1964, large numbers of this scolytid were recorded in flight as early as June 22. Thus, depending upon the prevalence of cool or warm weather during a given season, the time of dispersal flights may vary somewhat. The effect of predominantly higher temperatures was emphasized by the earlier emergence noted from the cage exposed to direct sunlight. On the basis of events recorded in 1963 and 1964, it appears that late June and early July is the most likely period for flights of this bark beetle.

Diurnal Pattern

Scolytus unispinosus exhibited a mid-day or early afternoon diurnal flight rhythm like that of *Pseudohylesinus* species, Trypodendron lineatum, and Dendroctonus pseudotsugae (46, p. 31). Considerably higher temperatures were required to support the flight of this species than were found necessary for the former species. It is evident from Table 13 that air temperatures in excess of 70° F. are most favorable for the dispersal activity of this species. In view of the temperatures listed in Table 13, it is probable that the threshold air temperature necessary to initiate the flight of this scolytid is within the range of 68 - 72° F. Emergence was found to begin at somewhat lower temperatures than those necessary for flight. On at least two occasions daily emergence began at air temperatures as low as 65 - 66° F. Figure 22 typifies the daily pattern of emergence and flight activity of this insect.

The flying population was observed to decrease sharply in the late afternoon even though temperature remained favorable. This behavior was exemplified on July 13, 1963 (Figure 22), when activity decreased sharply at 1600 hours although temperature remained above 70° F. until past 1800 hours. This depression effect might be due to the normal decrease in light intensity. Exact determination of the cause of such responses, however, requires study under more controlled conditions.

Table 13. Flight activity of Scolytus unispinosus in relation to daily temperatures in 1963.

Date	Lowest temperature which initial flight was recorded (°F.)	Air temperature at hour of maximum flight activity (° F.)
June 17, 1963	72	78
July 3, 1963	69	69
July 12, 1963	71	74
July 13, 1963	75	78
July 25, 1963	68	69
August 2, 1963	75	75

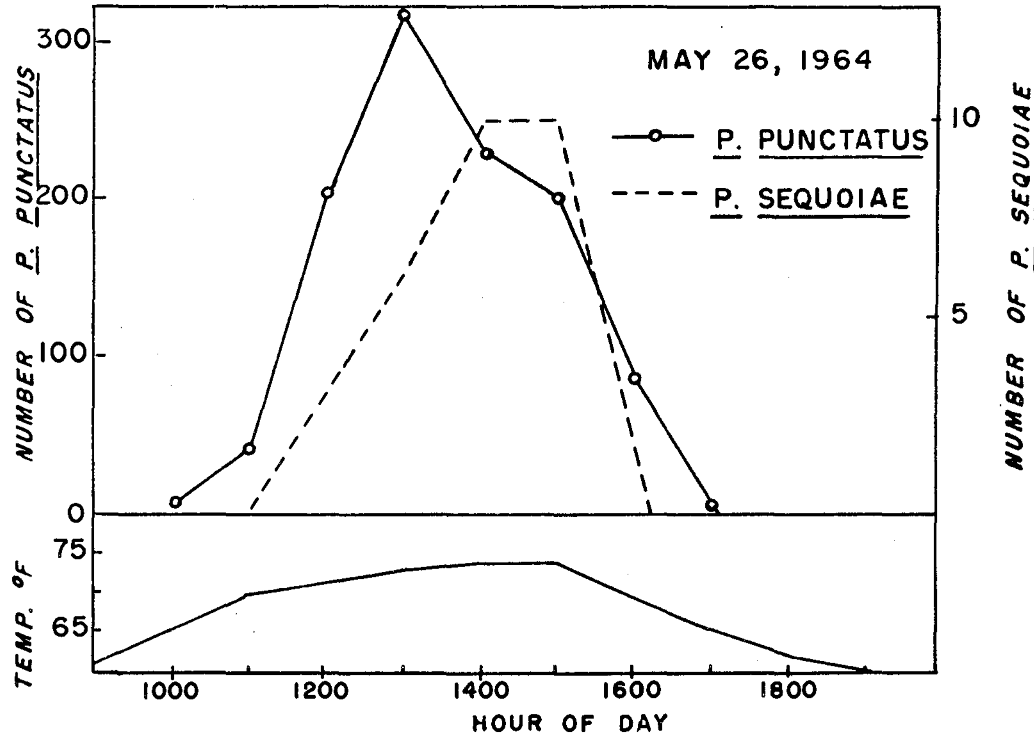


Figure 21. Daily flight patterns of Phloeosinus species.

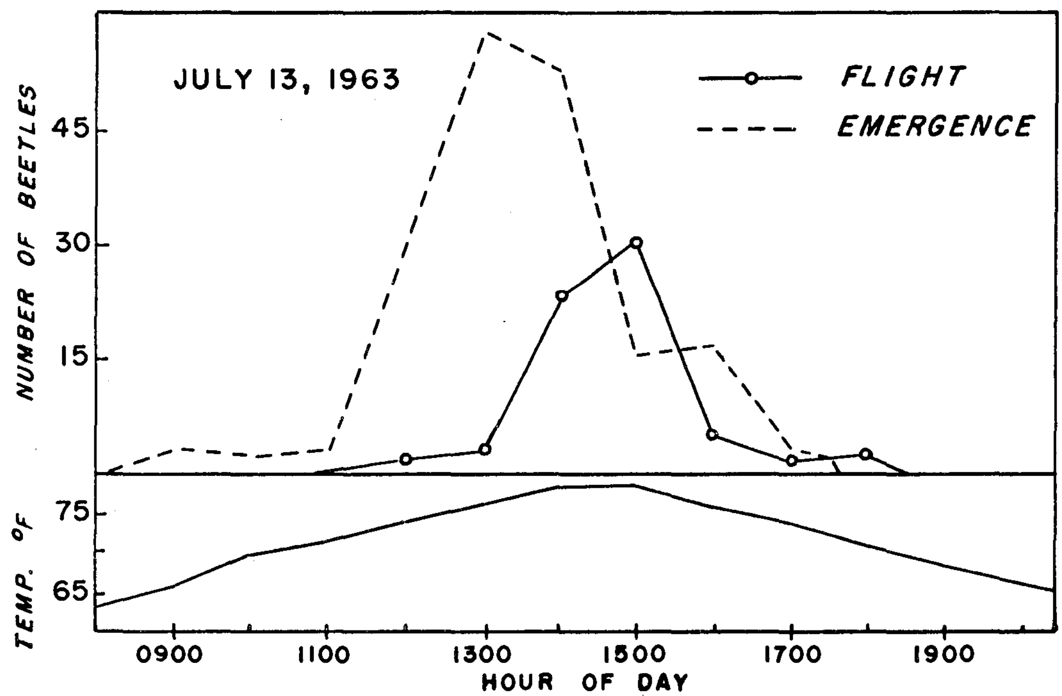


Figure 22. Daily emergence and flight activity of Scolytus unispinosus.

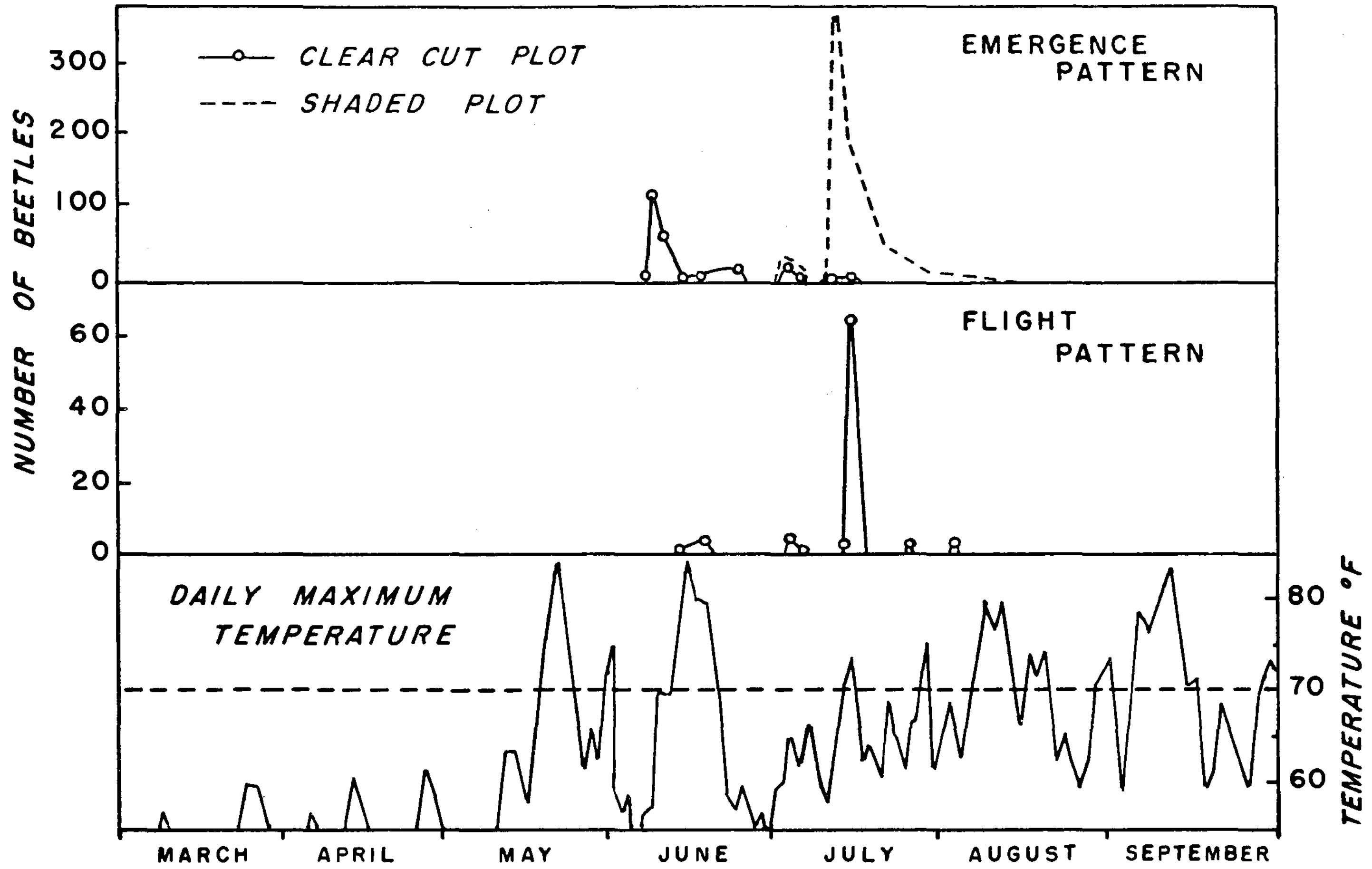


Figure 23. Seasonal emergence and flight activity of Scolytus unispinosus in 1963.

Miscellaneous Species

In both 1963 and 1964, a number of other bark beetle species were caught in addition to those discussed above. Most of these were present in too few numbers to permit reliable interpretation of the effects of the physical factors on flight activity. In 1964, some of these more obscure species were caught in relatively greater numbers providing some indication of their patterns of dispersal flight. Table 14 lists the less abundant species in the sequence they were caught during the season.

Table 14. Miscellaneous species of Scolytidae trapped in 1963 and 1964.

Species	Date caught	Temperature at time of catch (°F.)
Hylurgops rugipennis (Mannerheim)	March-April	54-60
Taenioglyptes pubescens (Hopkins)	April-May	61-65
Pseudohylesinus granulatus (LeConte)	April-May	63-65
Phloeosinus punctatus LeConte	May	64-75
Pseudohylesinus nobilis Swaine	May-June	63-65
Anisandrus pyri (Peck)	May-June	65-76
Ips concinnus (Mannerheim)	May	65-66
Carphoborus vandykei Bruck	May	65
Monarthrum scutellare (LeConte)	May	66-73
Pseudohylesinus tsugae Swaine	May-June	66-74
Phloeosinus sequoiae Hopkins	May-June	68-74
Leperisinus californicus Swaine	May	72
Alniphagus aspericollis (LeConte)	May	73
Scolytus tsugae (Swaine)	July-August	72-77

Little more can be stated concerning the flight activity of most of these species other than the date captured and prevailing temperatures as listed in Table 14. Higher densities of Phloeosinus species were caught in 1964 however, permitting more extensive analysis of their flight activity.

Phloeosinus Species

A sharp increase in the population of these bark beetles was evidenced in the 1964 net samples, especially of the smaller species, Phloeosinus punctatus. Over 1000 individuals of this species were collected in the net samples during a single day in 1964. Seasonal dispersal activity was of short duration however, since large numbers of this species were caught only on May 15 and May 26. Thereafter only a few isolated specimens were found in the net samples. P. sequoiae did not increase in numbers so dramatically during the two seasons, but a distinct difference was noted. This scolytid was present in flight from May 26 to June 22, 1964.

Figure 21 depicts the typical diurnal flight patterns of these bark beetles. Both apparently reach their maximum daily flight densities during the mid-day or early afternoon hours. There was a definite indication that P. punctatus had a lower temperature threshold for flight activity than P. sequoiae. On may 26 (Figure 21) and other occasions when this species was caught, flight began at air temperatures of

64 - 66° F. In contrast, *P. sequoiae* was not caught when the air temperature was less than 68° F.

Seasonal Differences

Some significant seasonal differences were found in the sampling records taken in 1963 and 1964. Many of these differences concern the time of dispersal of the various species which vary considerably due to the difference of threshold temperatures. Initial occurrence and duration of flight depended on the periodic occurrence of favorable weather, which is normally sporadic and unpredictable for the area. Thus, while knowledge of temperature thresholds provide some indication of when flights will occur, it is difficult to make accurate predictions due to the variable, highly fluctuating weather patterns. The seasonal flight of *Pseudohylesinus nebulosus*, for example, was prolonged until the first week of May in 1963, whereas the peak flight of this species was completed by the end of March in 1964. Large numbers of *Scolytus unispinosus* were not caught until mid-July in 1963, whereas peak flight activity was in progress by the third week of June in 1964.

After considering the differences in seasonal flight rhythms of the various species for the two seasons, some generalizations can be made regarding the months of the year most favorable for flight. With the exception of *Pseudohylesinus nebulosus*, which may fly in considerable numbers in March, the most critical period for most of the species appeared to be April, May, and June. However, May through July was the period most critical for species requiring higher temperatures, such as Hylastes ruber, Dryocoetes autographus, and Scolytus unispinosus. Since S. unispinosus requires a certain period in the spring to complete development to the adult stage, a temperature accumulation or "day degree" study might be of considerable aid in predicting seasonal flights of this species.

Other seasonal differences were undoubtedly linked with host availability and location during the two seasons. The copious volume of windthrown timber available in 1963 provided the potential for an extensive population increase of scolytids. Population increases were expressed for several species in 1964 by greater numbers trapped in the rotary nets. This was particularly evident for Pseudohylesinus nebulosus, Trypodendron lineatum, Dryocoetes autographus, and Phloeosinus species. There was also a marked increase in the number of different species caught in 1964. As mentioned previously, a total of 15 species were identified from the 1963 net catches, whereas 24 species were caught in 1964. Most of the species not found in 1963 were probably present in too low densities for detection by the sampling techniques used. The plentiful host supply in 1963 no doubt led to an increase in numbers of these less abundant species which then resulted in capture of a few specimens by the rotary traps.

There is also the possibility that the less abundant host supply in 1964 may have led to a greater number of species caught during that season. The location of suitable host material by bark beetles in 1964 could understandably be more difficult than in 1963 when freshly felled trees were common in most areas of the forest. It is conceivable that in 1964 scolytids might have been forced to fly farther and for longer periods of time to locate the less plentiful host material. Such flights would automatically enhance the insects' chances of being caught in flight traps by making them vulnerable to capture for longer periods of time.

The location of host material as effected by recent logging activities or storm damage was also believed to exert an influence on the time of dispersal flights. Certain species such as Pseudohylesinus nebulosus, P. grandis, and Trypodendron lineatum, were caught in flight at considerably lower temperatures in 1964 than the previous year. The chief factor instrumental in causing flights at lower temperatures in 1964 concerns the disposition of brood logs infested in 1963. As discussed previously, large groups of infested logs, felled by windstorm or logging operations, were exposed to direct solar radiation in the spring of 1964. Due to higher temperatures received at these sites, scolytids were no doubt able to initiate flight sooner than from shaded sites. The ultimate result of this situation was that once flight had begun in these warmer regions it could be continued into cooler areas, such as the experimental plot, where the beetles were trapped in flight at lower air temperatures than thought necessary to initiate flight activity.

In view of these differences, it can be stated that the variations in host availability and the disposition of the brood logs infested the previous year can have profound influences on scolytid flight activity. Such factors should be considered when studying flight activity of bark beetles in relation to the physical factors and when surveying the region for a particular species.

SUMMARY AND CONCLUSIONS

Six rotary nets were run at standard positions in a western Oregon Douglas-fir forest for purposes of sampling flight populations of bark beetles. The flight traps were run at prescribed intervals during the spring and summer months of 1963 and 1964 in an effort to ascertain the diurnal and seasonal flight patterns of the various scolytid species. Air temperatures, relative humidity, and to some extent light intensity and wind velocities, were measured for evaluation of their effects on flight activity.

Temperature was found to be the primary factor governing flight activity. With the exception of Scolytus unispinosus, the initiation of seasonal flight depended on the occurrence of sufficiently high temperatures to induce flight of the various species. Since S. unispinosus overwintered in the larval stage, a period of time was required for completion of development before flight could occur the following season. A wide range of air temperatures necessary to initiate flight of the various species was observed. These differences in temperature thresholds (Table 15) resulted in a definite sequence in temporal distribution of scolytid species in flight throughout the season.

Light intensity was also found to be influential in governing the flight activity of several bark beetles. For example, many of the day flying species such as Pseudohylesinus nebulosus, P. grandis, and Trypodendron lineatum sharply decreased flight activity in late afternoon and ceased activity at darkness even when temperatures remained optimal. In contrast, five species were found to have crepuscular patterns of daily flight activity. Hylastes nigrinus, H. ruber, Gnathotrichus sulcatus, G. retusus, and Dryocoetes autographus were found to fly in greatest numbers in the evening between 1700 and 1900 hours. Light intensity recordings by an illuminometer indicated that intensities of less than 1000 foot candles were most favorable for flight activity of these species.

Table 15. Threshold air temperatures necessary to initiate flight activity of various scolytid species.

Species	Flight threshold (° F.)
Pseudohylesinus nebulosus	54-55°
Pseudohylesinus grandis	56-58°
Trypodendron lineatum	58-60°
Hylastes nigrinus	58-60°
Gnathotrichus sulcatus	61-63°
Gnathotrichus retusus	61-63°
Dryocoetes autographus	65-68°
Hylastes ruber	68-70°
Scolytus unispinosus	68-72°

Relative humidity within the range of values which occurred during the two seasons had no apparent effect on flight activity.

Winds were usually of a "gusty" or intermittent nature in the area. Recurrent breezes of velocities as low as 3 - 4 miles per hour curtailed flight activity of Trypodendron lineatum. However, activity of this species was not completely terminated with gusts as high as 3 - 10 miles per hour.

Besides the effects of the various physical factors, olfactory response to an attractant was found to be highly influential in governing flight activity. T. lineatum, a species known to produce a natural attractant (47), concentrated in high flight densities in local areas known to contain attractive material. This behavior noticeably affected net catches, depending on the proximity of the attractive material. It is recommended that this factor should be further investigated for other species as well as T. lineatum. There was also the possibility that host logs per se might be attractive to these insects and this factor should also receive attention in the future.

Certain noteworthy seasonal differences in scolytid flight were observed during the 1963 and 1964 seasons. In 1964, certain species were captured in flight at temperatures somewhat lower than had been found necessary the previous year. It is probable that flight was recorded at lower air temperatures in 1964 due to the extensive amount of brood logs exposed on unshaded sites. The temperatures listed in

Table 15 are representative of the values necessary to induce flight of the respective species from shaded sites in the forest. The effect of the predominantly higher temperatures received by exposed, unshaded sites was exemplified by comparing emergence of beetles from shaded logs and from logs placed in clearcut areas of the forest. Emergence from the clearcut areas preceded that of the shaded sites by as much as five weeks.

Greater densities of certain bark beetles as well as a larger number of species were caught in the traps in 1964 as compared to 1963.

In the opinion of the writer, the pool of information on scolytid flight behavior would be enhanced by future studies related or supplementary to this work. As mentioned previously, for example, the existence and effects of various attractant materials should be investigated. Also, the interrelationships of temperature, moisture, and light intensity in regard to scolytid flight should be more critically evaluated by conducting studies under controlled laboratory conditions. More explicit values of favorable light intensities could also be determined for the crepuscular species. Additional field studies could be conducted evaluating the effects of such factors as canopy shade, elevation, and prevailing air currents on flight sampling efficiency. Critical evaluation of such factors could lead to increased proficiency and economy in use of rotary nets for sampling flight populations of bark beetles.

BIBLIOGRAPHY

1. Anderson, Roger F. Host selection by the pine engraver. Journal of Economic Entomology 41:596-602. 1948.

2. Andrewartha, H. G. and L. C. Birch. The distribution and abundance of animals. Chicago, The University of Chicago Press, 1954. 782 p.

3. Atkins, M. D. A study of the flight of the Douglas-fir beetle Dendroctonus pseudotsugae Hopk (Coleoptera: Scolytidae) I. Flight preparation and response. The Canadian Entomologist 91:283-290. 1959.

4. Atkins, M. D. A study of the flight of the Douglas-fir beetle Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) II. Flight movements. The Canadian Entomologist 92:941-954. 1960.

5. Atkins, M. D. A study of the flight of the Douglas-fir beetle Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) III. Flight capacity. The Canadian Entomologist 93:467-474. 1961.

6. Bedard, W. D. The Douglas-fir beetle. 1950. 10 p. (U. S. Department of Agriculture. Forest Service. Circular 817)

7. Bentley, E. W., D. L. Gunn and D. W. Ewer. Biology and behavior of Ptinus tectus Boie. (Coleoptera: Ptinidae) I. The daily rhythm of locomotory activity, especially in relation to light and temperature. Journal of Experimental Biology 18:182-195. 1941.

8. Bright, Donald E. Jr. Bark beetles of the genus Dryocoetes (Coleoptera: Scolytidae) in North America. Annals of the Entomological Society of America 56:103-115. 1963.

9. Chamberlin, W. J. The bark and timber beetles of North America north of Mexico. Corvallis, Oregon State College Cooperative Association, 1939. 513 p.

10. Chamberlin, W. J. The Scolytoidea of the Northwest. Corvallis, Oregon State College, 1958. 208 p.

11. Chapman, J. A. and J. M. Kinghorn. Studies of flight and attack activity of the ambrosia beetle, Trypodendron lineatum (Oliv.) and other scolytids. The Canadian Entomologist 90:362-371. 1958.

12. Chapman, J. A. Field studies on attack flight and log selection by the ambrosia beetle Trypodendron lineatum (Oliv.) (Coleoptera: Scolytidae). The Canadian Entomologist 94:74-92. 1962.

13. Cloudsley-Thompson, J. L. Diurnal rhythms. In: Transactions of the 9th International Congress of Entomology, Amsterdam, 1951. p. 305-310.

14. Curtis, C. L. Observations on mosquitoes at Whitehorse, Yukon Territory (Diptera: Culicidae). The Canadian Entomologist 85:353-370. 1953.

15. Davies, Douglas M. The population and activity of adult female black flies in the vicinity of a stream in Algonquin Park, Ontario. The Canadian Journal of Zoology 30:287-312. 1952.

16. Digby, Peter S. B. Factors affecting the temperature excess of insects in sunshine. Journal of Experimental Biology 32:279-298. 1955.

17. Digby, Peter S. B. Flight activity in the blowfly, Calliphora erythrocephala, in relation to wind speed, with special reference to adaptation. Journal of Experimental Biology 35:776-795. 1958.

18. Dyson-Hudson, V. R. D. The daily activity rhythm of Drosophila subobscura and D. obscura. Ecology 37:562-567. 1956.

19. Edwards, D. K. Effects of artificially produced atmospheric electrical fields upon the activity of some adult diptera. The Canadian Journal of Zoology 38:899-912. 1960.

20. Entwistle, P. F. Some evidence for a color sensitive phase in the flight period of Scolytidae and Platypodidae. Entomologia Experimentalis et Applicata 6:143-148. 1963.

21. Flight period and life-cycles of ambrosia beetles in West Africa. Colonial Research 48. 1957. (Abstracted in Forestry Abstracts 19:3239. 1957)

22. Fisher, R. C., G. H. Thompson and W. E. Webb. Ambrosia beetles in forest and sawmill. Their biology, economic importance, and control. I. Biology and economic importance. Forestry Abstracts 14:381-389. 1953.

23. Gara, Robert I. Flight behavior of bark beetle populations. Master's thesis. Corvallis, Oregon State University, 1962. 93 numb. leaves.

24. Gara, Robert I. and J. P. Vite'. Studies on the flight patterns of bark beetles (Coleoptera: Scolytidae) in second growth ponderosa pine forests. Contributions of the Boyce Thompson Institute 21:275-290. 1962.

25. Graham, Kenneth. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature 184:283-284. 1959.

26. Green, G. W. and P. J. Pointing. Flight and dispersal of the European pine shoot moth, Rhyacionia buoliana (Schiff.) II. Natural dispersal of egg-laden females. The Canadian Entomologist 94:299-314. 1962.

27. Haufe, W. O. The effects of atmospheric pressure on the flight responses of Aedes aegypti (L.). Bulletin of Entomological Research 45:507-526. 1954.

28. Henson, W. R. Laboratory studies on the adult behavior of Conopthorus coniperda (Coleoptera: Scolytidae) III. Flight. Annals of the Entomological Society of America 55:524-530. 1962.

29. Johnson, C. G. and L. R. Taylor. Periodism and energy summation with special reference to flight rhythms in aphids. Journal of Experimental Biology 34:209-221. 1957.

30. Juillet, J. A. A comparison of four types of traps used for capturing flying insects. The Canadian Journal of Zoology 41:219-223. 1963.

31. Kinghorn, J. M. and J. A. Chapman. The overwintering of the ambrosia beetle Trypodendron lineatum (Oliv.). Forest Science 5:82-92. Mar. 1959.

32. Leigh, Thomas F. and Ray F. Smith. Flight activity of Colias philodice eurytheme (Boisduval) in response to its physical environment. Hilgardia 28:569-624. 1959.

33. Maw, M. G. Effects of atmospheric electricity on behavior. In: Research report of the Belleville, Ontario, Entomological Research Institute for Biological Control, 1960 and 1961. p. 17.

34. Maw, M. G. Behavior of an insect on electrically charged surface. The Canadian Entomologist 93:391-393. 1961.

35. Maw, M. G. Suppression of oviposition rate of Scambus buolinae (Htg.) in fluctuating electrical fields. The Canadian Entomologist 93:602-604. 1961.

36. McMullan, D. L. Ambrosia beetles and their control in British Columbia. Forestry Chronicle 32:31-43. 1956.

37. McMullen, L. H. and M. D. Atkins. The life history and habits of Scolytus unispinosus LeConte (Coleoptera: Scolytidae) in the interior of British Columbia. The Canadian Entomologist 94:17-25. 1962.

38. McMullen, L. H. and M. D. Atkins. On the flight and host selection of the Douglas-fir beetle (Dendroctonus pseudotsugae). The Canadian Entomologist 94:1309-1325. 1962.

39. Merker, E. Lockstoffe and Nahrstoffe in Wirtspflanzen einiger Waldschadlinge. (Attractants and nutrients in the host plants of some forest insect pests.) Allgemeine Forst-und Jagdzeitung 124:138-144. 1957. (Abstracted in Forestry Abstracts 14:3831. 1954)

40. Mitchell, Donald F. and Carl Epling. The diurnal periodicity of Drosophila pseudoobscura in southern California. Ecology 32:696-708. 1951.

41. Novák, V. Drevokaz čárkovaný a boj proti nemu. Prague, Státni Zemědělské Nakladatelstvi, 1960. 131 p.

42. Parman, D. C. Observations on the effect of storm phenomena on insect activity. Journal of Economic Entomology 13:339-343. 1920.

43. Prebble, M. L. and K. Graham. Studies of attack by ambrosia beetles in softwood logs on Vancouver Island, British Columbia. Forest Science 3:90-112. 1957.

44. Rudinsky, J. A. Developments in forest pest research at Oregon State University. In: Proceedings of the Annual Meeting of the Western Forest Pest Committee. Portland, 1961. p. 14-15.

45. Rudinsky, J. A. Ecology of Scolytidae. Annual Review of Entomology 7:327-348. 1962.

46. Rudinsky, J. A. Response of Dendroctonus pseudotsugae (Hopkins) to volatile attractants. Contributions from Boyce Thompson Institute 22:23-38. 1963.

47. Rudinsky, J. A. and G. E. Daterman. Field studies of flight patterns and olfactory responses of ambrosia beetles in Douglas-fir forests of Western Oregon. The Canadian Entomologist. (In Press) 1964.

48. Rudinsky, J. A. and J. P. Vite'. Effects of temperature upon the activity and the behavior of the Douglas-fir beetle. Forest Science 2:258-267. 1956.

49. Schenk, J. A., R. C. Dosen and D. M. Benjamin. Non-commercial thinning of stagnated jack pine stands and losses attributable to bark beetles. Journal of Forestry 55:838-841. 1957.

50. Stahler, Nathan and Levon A. Terzian. Some studies on the influence of light on the mating activity of Anopheles quadrimaculatus Say. Annals of the Entomological Society of America 49:429-435. 1956.

51. Stevens, R. E. What's wrong with my trees? Douglas-fir damaged by engraver beetles. 1959. 2 p. (U. S. Department of Agriculture. Miscellaneous paper no. 30)

52. Thomas, Gerard M. and K. H. Wright. Silver fir beetles. 1961. 7 p. (U. S. Department of Agriculture. Forest Pest Leaflet no. 60)

53. Uvarov, B. P. Insects and climate. Transactions of the Entomological Society of London 79:1-247. 1931.

54. Walters, J. and L. H. McMullen. Life history and habits of Pseudohylesinus nebulosus (LeConte) (Coleoptera: Scolytidae) in the interior of British Columbia. The Canadian Entomologist 88:197-202. 1956.

55. Whitlock, W. S. and J. Alan Chalmers. Short-period variation in the atmospheric electric potential gradient. Quarterly Journal of the Royal Meteorlogical Society 82:325-336. 1956.

56. Wolfe, L. S. and D. G. Peterson. Diurnal behavior and biting habits of black flies (Diptera: Simuliidae) in the forests of Quebec. The Canadian Journal of Zoology 38:489-497. 1960.

57. Wood, David L. and J. P. Vite'. Studies on the host selection behavior of Ips confusus LeConte (Coleoptera: Scolytidae) attacking Pinus ponderosa. Contributions from Boyce Thompson Institute 21:79-95. 1961.