

A STUDY ON THE FLIGHT OF THE DOUGLAS-FIR BEETLE
DENDROCTONUS PSEUDOTSUGAE HOPK. (SCOLYTIDAE)

by

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B.A., University of British Columbia, 1956

A thesis submitted in partial fulfilment of

the requirements for the degree of

Master of Arts

in the Department

of

ZOOLOGY

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ABSTRACT

This paper presents a study of three phases of the flight of the Douglas-fir beetle, viz: flight preparation and response, flight attitude and movements, and flight capacity. A room equipped with temperature and humidity controls was used for some of the experiments. The wing movements were studied with a stroboscope and flash photography. Flight mills were used in the studies involving flight duration and velocity. The only effect of nematode and mite associates was reduction of the duration of the initial flight caused by internal nematodes. Temperature played an important role in all phases of flight studied.

Temperatures from 72° to 89° F. were optimum for spontaneous flight, while 68° F. seemed to be the lower limit of flight in the absence of additional stimuli. In sunlight, spontaneous flights occurred at 63° F. Increasing temperature caused a rapid increase in the wing-beat frequency up to the threshold for spontaneous flight, then increased only slightly to the level of heat prostration. Lower temperatures greatly reduced the duration of the initial flight and caused a broken flight pattern, but failed to influence the over-all flight duration. The effects of relative humidity followed a similar pattern to those of temperature inasmuch as evaporational cooling of the insect occurred at low relative humidities not at high relative humidities. Increased light intensity increased the speed of the flight response and caused slight increases in the wing-beat frequency; both results being attributed to increased nervous stimulation. Studies on the effect of the change in the beetles' activity from dispersal to gallery construction to re-emergence, on the response to flight stimulation, showed that once gallery construction had begun the females became flight refractory, some regaining their inclination to fly after

15 days. On the other hand, the males could be expected to be either flight positive or refractory throughout the duration of gallery construction. The number of individuals responding positively to flight stimulation by tossing increased greatly following the first toss, then diminished until no further change occurred after six tosses.

Wing mutilation and loading produced changes in the wing-beat frequency similar to those found by other workers, and indicated that the changes were probably due to altering the inertia of the oscillating system. Fatigue caused a gradual reduction in the wing-beat frequency over a four hour period although the final per cent decrease attributable to fatigue was much lower than that reported for other insects.

The flight velocity was of the order of 90 to 115 metres per minute or 3.3 to 4.2 miles per hour, changes in the flight velocity seemingly being related directly to changes in wing-beat frequency. It is concluded from these studies that the Douglas-fir beetle is a strong uniform flier despite the complexity of components affecting several phases of flight. The various thresholds for spontaneous flight were consistently above the levels required for continuation of the activity. The flight of the Douglas-fir beetle can be expected to vary greatly from year to year and from season to season depending on the environmental factors. Of the flight movements it is the wing-beat frequency which is affected the most by environmental changes, thus varying the strength, velocity and magnitude of the flight. The Douglas-fir beetle is capable of an average flight of up to 10 miles immediately following take-off and from between 15 to 20 miles a day for several days; favourable air currents would increase these figures substantially.

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ACKNOWLEDGMENTS

I wish to thank Dr. W.G. Wellington, Mr. R.R. Lejeune and Dr. L.H. McMullen, Forest Biology Laboratory, Victoria, for their generous assistance in the design of the experiments, analysis of the data and the preparation of this paper. I am also indebted to Dr. K. Graham, Dr. G. Scudder and Dr. P. Dehnel, Department of Zoology, University of British Columbia for their guidance and criticism.

Thanks are extended to Dr. M.A. Khan, Entomology Division, Lethbridge, and Dr. C.V. Morgan, Entomology Division, Summerland, for identification of the nematodes and mites respectively.

The data presented in this thesis were collected while in the employ of the Forest Biology Division, Research Branch, Canada Department of Agriculture. Permission to use these data for thesis purposes has been granted by the Director, Forest Biology Division, to whom I am especially grateful.

I also extend thanks to Miss E. White, Forest Biology Laboratory, Victoria, for her unyielding patience in the typing of this thesis.

INTRODUCTION

The study of insect flight has received the attention of naturalists and research workers for many years, but only in the past half century have some of the intriguing features been described in detail. However, although much has been accomplished by workers such as Hollick (1940) and Jensen (1956) on kinematics, Sotavalta (1947, 1952, 1953) and Chadwick (1940, 1951, 1953) on wing beat frequency and amplitude, Weis-Fogh (1949, 1956) on aerodynamics, and Boettiger (1951, 1955, 1957) on flight muscles, the Coleoptera have largely been neglected as experimental material. The work on the flight of Coleoptera has mainly involved water beetles (Jackson, 1952, 1956) and lamellicorns (Stellwaag, 1914 and Schneider, 1952). Information on the flight of forest Coleoptera, especially such important groups as the Scolytidae and Curculionidae, is confined almost entirely to unpublished reports.

The flight of bark beetles, particularly of the genus Dendroctonus, has been considered important for many years. This has necessitated the acquisition of a thorough understanding of the basic biology and behaviour of this important member of our forest Coleoptera. In an epidemiological sense, a thorough knowledge of the insects' dispersion capabilities is necessary in order to determine the minimum safety zone that may be established through sanitation salvage. In addition it is necessary that we understand the flight behaviour and capacity in order to anticipate the direction and magnitude of the dispersion and thus know where to look for new areas of population growth.

Although bark beetles generally fly for only one or two brief periods during their comparatively long life, these times of flight are of major importance. These are the periods when the adults disperse to new host material when they are subjected to new external stimuli and a new

complement of untempered climatic conditions. These periods of winged activity are the times affording an opportunity to study a most important aspect of the beetles' behaviour and to discover the cues of orientation which guide them to new sites of infestation. Also, we should understand what effect varying physical factors have on the beetles' flight in order to estimate the potential threat of the species under different seasonal conditions.

Miller and Keen (1945) brought together a large amount of information from unpublished reports on the biology and control of the western pine beetle, Dendroctonus brevicomis Lec., from which the following review of flight studies was extracted. In 1916, Keen concluded from a long series of observations and experiments on the western pine beetles' habits that they flew down wind, but not blindly. In another study he released 8,000 marked beetles. Two weeks following the release, 4,000 beetles were removed from newly attacked trees one quarter of a mile from the release point: 181 of the 4,000 beetles proved to be marked. Patterson (1920) removed all the infested material for a quarter of a mile around a series of trap logs which were later attacked. Similar experimentation between 1924 and 1934 showed that the beetles were capable of flying from infested trees one-half to two miles away. The last in this series of experiments, to determine the distance that D. brevicomis could fly, resulted in attacks occurring 12 to 30 miles from the nearest known infested pine and it was concluded that the eradication in the experimental area had not been complete. However, Miller (1928), upon finding new centres of attack in areas where there was previously little evidence of beetle activity, stated, "Although the heaviest killings were found close to the largest bodies of wind-thrown trees, groups of beetle-killed trees were found 6 to 8 miles distant from any mass of windfalls. Apparently this was the

result of a flight of part of the beetles emerging from the down logs." More recently Walters (1954, 1955) in two attempts to establish the flight range of the Douglas-fir beetle released 6,843 and 4,800 specimens marked with nail polish or by clipping the tarsi. None were recovered from the surrounding trap logs at a distance of up to one mile from the release point, but all of the beetles were observed to fly down wind.

Pearson (1927) ascertained from the flight behaviour of the western pine beetle under different temperature conditions that the optimum was between 70° and 80° F. Gordon (1933) found that light was necessary for flight. Rudinsky and Vité (1956) showed that temperature has little effect on the flight capacity of the Douglas-fir beetle, but that it delimits the zone of flight activity. They showed that flight attempts did not occur below 20° C. (68° F.) unless some additional form of stimulation was present, and that flight activity was reduced at 33° to 35° C. (91° - 95° F.) as the beetles became photo negative. They also indicated that the flight velocity and wing beat frequency increased only slightly with temperature increase and when the optimum for flight was reached (68° - 72° F.) there was almost no further change.

Chapman (1954, 1955) showed that the two-lined ambrosia beetle, Trypodendron lineatum (Oliv.) and the Douglas-fir beetle would fly readily on flight mills, flights of several hours being not uncommon. One Douglas-fir beetle flew continuously for nine hours, then after eight hours rest flew an additional six hours. He also indicated that the flight response to the stimulus of being tossed varied according to the stage of the adults' life.

The evidence from the literature shows that insect flight can be divided into four basic components which lend themselves to independent study but which are all inter-related. These are: (1) flight preparation

and response; (2) flight movements and their resultant forces; (3) flight capacity, and (4) flight orientation. Although many authors have dealt with these various phases of flight, and studies have been made on a wide variety of insect species, very few complete studies of flight have been made for a single species. An outstanding exception is the work on locust flight by Weis-Fogh and Jensen (1956).

The objective of this project was to increase our fundamental knowledge of the flight of bark beetles, especially the genus Dendroctonus and specifically the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. This is attempted through a study that takes into consideration 1) the effect of nemic and mite associates, 2) the stage of adult life and external environmental factors such as temperature, relative humidity and light intensity on the flight response, 3) flight movements, and 4) flight capacity of the beetle. The methods used were mostly basic techniques and involved a room with temperature and moisture controls, flight mills, a stroboscope and flash photography.

The studies were carried out at the Canada Department of Agriculture, Forest Biology field stations near Lumby and Lac la Hache, B.C., and the Victoria and Vernon Forest Biology Laboratories.

FLIGHT PREPARATION

The Douglas fir beetle, like many other insects, passes through a series of preflight movements. In the still air of the laboratory at 73° F., the beetles usually walked towards the light. Under conditions of nearly even lighting they wandered seemingly at random over a flat surface, although many individuals walked up an inclined surface. In gently moving air most of the beetles walked into the flow. The amount of walking without a flight attempt varied widely from a few seconds to

long periods.

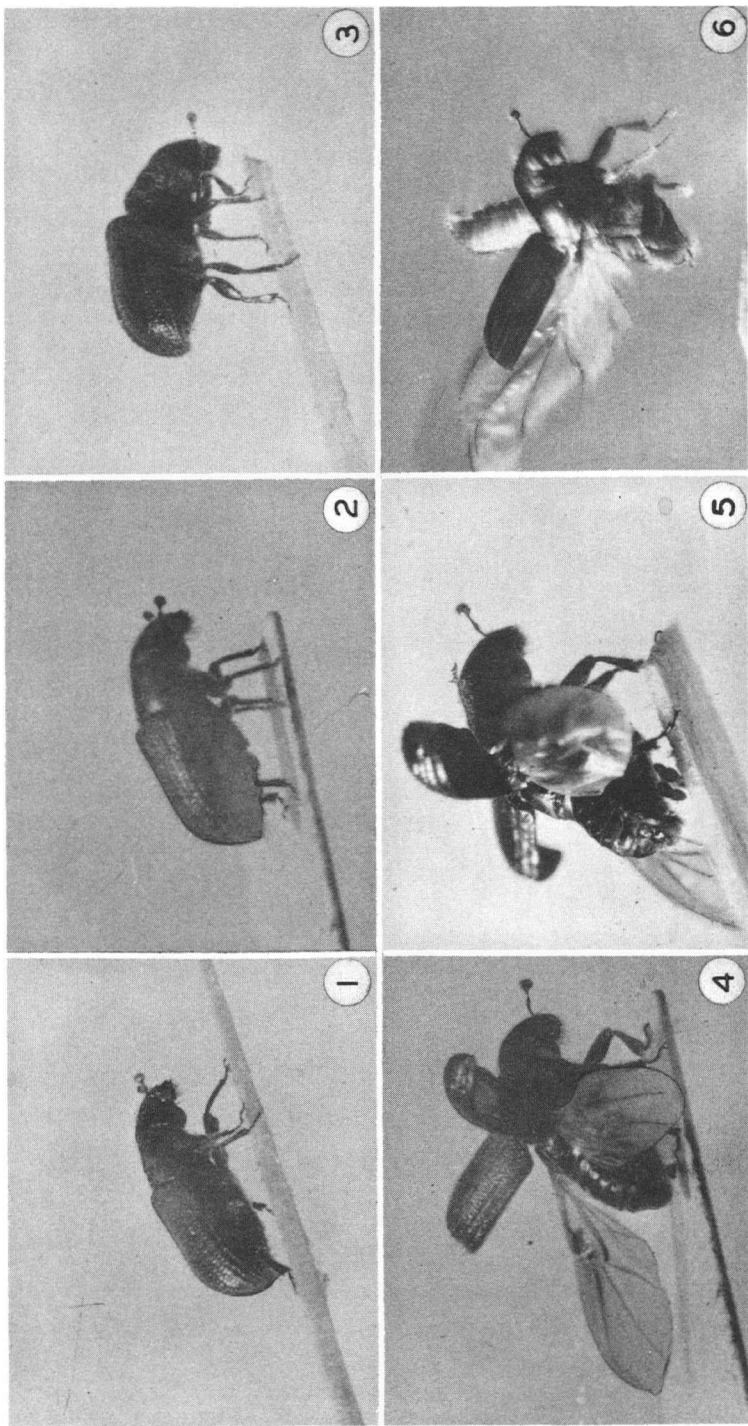
Just prior to taking flight, the beetles stopped walking (Fig. 1) and slowly waved their antennae. The legs were then raised and lowered in turn, as if to plant the tarsi firmly on the substrate, after which the pro- and mesothoracic legs were arched and the hind legs were bent towards the rear, tilting the body backwards (Fig. 2). This position was maintained for varying lengths of time during which there was noticeable pumping of the abdomen. Eventually, either the body was quickly rocked forward and the elytra partially opened (Fig. 3) or walking was resumed. The loosening of the elytra over the wings was immediately followed by a backward tilt of approximately 45 degrees ending with the wings fully extended (Fig. 4). Another brief pause occurred in this position during which the mesothoracic legs were lifted to their flight position below the posterior margin of the elytra (Fig. 5). This was followed by a straightening of the hind legs producing a jump which initiated flight (Fig. 6). The photographs were taken using the method described by Atkins (1959).

FLIGHT RESPONSE

A. INTRODUCTION

The response phase of insect flight is important because it is the initial function that changes the insect's position in its environment and brings an entirely new complement of forces into action. Since an individual will not respond positively under unsuitable conditions, a study of the stimuli prompting flight should reveal the optimum conditions for it while at the same time disclosing any stimuli which may enable the insect to fly under sub- or extra-optimal conditions. This is particularly important in insects such as the Douglas-fir beetle, as the basic factor of temperature may be sub-optimal while the humidity might be supra-optimal during the spring flight period.

Figures 1-6. The preflight movements and take-off of the
Douglas-fir beetle.



B. METHODS AND RESULTS

THE EFFECT OF ASSOCIATES ON THE FLIGHT RESPONSE

Two hundred young adults which emerged in May and July from overwintered logs were collected daily in samples of 20 or 30 and placed in petri dishes containing moist paper. When the room temperature reached 72° to 74° F., each individual was stimulated to fly by tossing. As for many other insects (Roeder, 1953), tossing produces a strong flight stimulus for the Douglas-fir beetle. After three tosses each beetle was classified as to response according to the following categories.

1. GOOD - The flight was strong following a rapid response.
2. POOR - The response was slower and the flight was weak.
3. FLUTTER - The beetle dropped with wings vibrating insufficiently for organized flight.
4. REFRACTORY - Either there was no visible positive response or the wings were extended but not vibrated.

Following the determination of the response of each beetle, dissections were made to determine the sex, gut condition (material present or absent), and the presence or absence of mites and nematodes.

Since the number of possible combinations in these data is great and the range of the degree of associate infestation was wide, the results are not amenable to simple analysis. Therefore the data are condensed in Table 1, omitting sex and gut condition which obviously had no effect. From these results it appears that the presence of mites and nematodes had little or no effect on the insects' flight response, at least when a strong stimulus was applied.

TABLE I

Flight response following stimulation and results of dissection of 200 Douglas-fir beetles

Response	Total	Associates absent	Nematodes			Mites only	Mites and nematodes
			Internal only	External only	Internal & external		
Good	150	26	8	32	6	17	61
Poor	13	0	1	3	0	1	8
Flutter	15	2	2	1	1	2	7
Refractory	22	4	0	6	2	2	8
Total	200	32	11	42	9	22	84

The influence of associates on the normal flight reflex was ascertained from 50 beetles placed on a flat surface at 73° F. and 50 foot candles in still air and allowed to move at will. As the beetles flew, they were captured and noted as having a positive response. Those which did not fly within a period of 15 minutes were considered refractory. Dissections were made to observe the previously mentioned features. The results summarized in Table 2 show that the associates did not have any effect on spontaneous flight.

To date identifications indicate that there are at least 18 species of nematodes, belonging to 10 genera, associated with the Douglas-fir beetle. This, as well as the complexity of nematode life histories, the lack of knowledge on their host relations and the difficulty with which they are identified, makes it impossible to determine if any one species had an effect. Even if the adults could be identified easily it would not necessarily mean that accompanying larvae were of the same species.

THE EFFECT OF TEMPERATURE ON THE FLIGHT RESPONSE

Four samples of 25 young adults each were placed in open but shaded petri dishes containing moist paper at the prevailing temperature and allowed to walk at will and make voluntary flight attempts. Ten minutes later each beetle was tossed three times and classified according to response. Upon completion of the test the beetles were placed in closed petri dishes until the temperature increased a few degrees, at which time they were retested. This test was conducted at six or seven different temperatures with each sample of beetles.

TABLE II

Spontaneous flight response and results of dissection of 50 Douglas-fir beetles

Response	Total	Associates absent	Nematodes			Mites only	Mites and nematodes
			Internal only	External only	Internal & external		
Positive	41	16	18	4	3	0	0
Refractory	9	4	2	2	1	0	0
Total	50	20	20	6	4	0	0

At 57° to 59° F. the beetles walked around the dishes and in a few cases extended their wings. At 64° to 66° F., several unsuccessful flight attempts were observed while at 68° F. three of 50 beetles made successful flights to a window a few feet away. If the petri dishes were moved into direct sunlight many beetles made successful flight attempts at air temperatures from 63° to 68° F. From 72° to 90° F., almost all of the beetles made successful voluntary flights in the shade. At temperatures ranging from 90° to 97° F., only a few flights occurred; the majority of the beetles crawled around the edges of the dishes or under the paper, demonstrating a change in phototaxis. These findings vary only slightly from those of Rudinsky and Vite (1956).

On the other hand, when the same beetles were tossed throughout the range of temperature used (57° to 97° F.) there was little variation in the response. At 57° to 59° F. only 20 per cent of the beetles were flight negative and at temperatures above 86° F., only 16 per cent showed a negative response. In addition, at temperatures from 64° to 86° F., there was a consistent 5 to 10 per cent of the beetles which were flight negative.

THE EFFECT OF RELATIVE HUMIDITY ON THE FLIGHT RESPONSE

Six samples of 20 spring-emerged beetles that showed a strong positive response to a toss stimulus were used. The relative humidity was increased (by a humidifier) from 25 to 95 per cent and then decreased (by refrigeration) to 25 per cent at 68°, 75° and 85° F., with stops at 25, 50, 75 and 95 per cent. Two samples of beetles were used at each temperature, one as the humidity increased and one as it decreased. The test beetles were kept in petri dishes of moist "vermiculite" (expanded mica) during changes from one humidity to another. The time required for each beetle to take flight was recorded with a maximum of 20 minutes.

The average reaction time required for the first half of the sample to fly was taken as the value for the sample under the test conditions. The results presented in Table III show that high RH increases the possibility of spontaneous flight at sub-optimal temperatures, and decreases it at high temperatures. At optimal temperatures RH has little effect on the flight response.

THE EFFECT OF LIGHT INTENSITY ON THE FLIGHT RESPONSE

A number of newly emerged adults that showed a strong positive response to a toss stimulus were released on a gently inclined surface with an illumination of 10 foot candles (1 foot candle = 10.764 lux). As individuals made voluntary flights they were removed from the test area and placed in numbered vials. The beetles (25 per cent) which had not flown after 10 minutes were considered negative. The test was repeated at 0.5, 2, 15, 35, 65, 300 and 500 foot candles within a temperature range of 73° to 77° F.

No beetles flew at 0.5 foot candles. At two foot candles the reaction was slow and during the ten minute trial only 45 per cent of the beetles flew. At 15 and 35 foot candles, 25 per cent failed to fly, while at the remaining light intensities all but one beetle (the same individual in each case) flew. However, the speed of reaction appeared to increase with the light intensity.

TABLE III

The speed of flight response of the Douglas-fir beetle in relation to relative humidity at different temperatures

Temperature in ° F.	Relative humidity in per cent	Average reaction time in seconds	Percentage of sample that responded
68	25	no reaction	0
	50	" "	0
	75	" "	0
	95	472	10
75	25	316	100
	50	324	100
	75	309	100
	95	278	95
85	25	172	100
	50	143	100
	75	148	85
	95	116	55

In order to establish whether or not the light intensity had any effect on the speed with which the beetles made spontaneous flights an additional test was conducted. Each of 5 samples of 20 flight positive beetles was released at 5 light intensities (2, 15, 35, 65 and 250 foot candles) within the same temperature range as above, with a short rest period in darkness between trials. The time required for each beetle to take flight was recorded. The average reaction time of the first 10 beetles in each case was considered to be the value for the corresponding light intensity. The tests were conducted with both increasing and decreasing light intensity in order to reduce the error that may arise from adaptation or fatigue. The results are presented in Table IV.

THE EFFECT OF GALLERY EXTENSION ON THE FLIGHT RESPONSE

Douglas-fir beetle galleries were tagged on the day of initiation and opened at various stages of development from 1 to 40 days later. When a gallery was examined the parents were numbered for transport to the laboratory, and the length of the gallery and the number of eggs deposited therein were recorded. In the laboratory the parent beetles were sexed according to the methods described by Chapman (1955) and then tossed three times. The flight response was recorded as either positive, opened elytra, or negative.

In the summary of the results shown in Table V, the numbers of beetles which responded by opening their elytra have been omitted since this response cannot satisfactorily be classed as either positive or negative.

TABLE IV

The speed of flight reaction of the Douglas fir beetle
in relation to light intensity

Light intensity in foot candles	Average reaction time in seconds	Percentage of sample that reacted
0.5	no reaction	-
2.0	284	45
15.0	142	75
35.0	122	95
65.0	117	95
250.0	53	95

TABLE V

Summary of the effect of gallery age from 1 to 40 days
on the flight response of the Douglas-fir beetle

Gallery age in days	No. of galleries examined	Average length of galleries in inches	Average no. of eggs per gallery	Response in per cent of total of each sex ^{1/}			
				Positive		Refractive	
				F	M	F	M
1	25	Through outer bark	none	14.3	36.8	38.1	15.8
2-3	15	.50	.4	0.0	44.4	80.0	22.3
4	10	.85	.8	0.0	60.0	70.0	0.0
5	10	1.12	2.3	0.0	40.0	50.0	20.0
7	24	1.47	6.5	0.0	17.6	56.5	41.2
10	12	2.18	8.5	0.0	12.5	91.7	50.0
12	12	2.70	10.0	0.0	0.0	100.0	62.5
13	9	2.77	9.6	0.0	0.0	100.0	0.0
15	12	4.15	13.5	8.3	16.6	41.5	33.6
18	20	6.21	19.7	15.0	20.0	55.0	40.0
21	13	7.13	31.0	7.2	14.3	78.5	28.6
25	15	7.83	47.7	6.7	20.0	86.6	20.0
28	13	4.2 ^{2/}	25.6	0.0	0.0	71.4	33.3
31	9	4.9 ^{2/}	25.7	0.0	0.0	100.0	100.0
34	10	5.6 ^{2/}	37.7	0.0	0.0	100.0	60.0
40	15	5.5 ^{2/}	39.0	0.0	0.0	91.7	25.0

^{1/} Values for opened elytra response equal residual.

^{2/} Galleries taken from a different source.

It is evident that some females would fly during the first 24 hours of gallery construction, but once egg laying either had begun or was about to begin all of the females tested showed a negative response for the following 14 days. The remaining flight-positive females were taken from galleries 15 to 25 days old. On the other hand, some males in the samples taken during the first ten days of gallery extension were flight positive, as were some throughout the reoccurrence of flight positive females. In addition, the sex ratio of adult beetles in the galleries examined changed in favour of females from close to 1:1 during the first week of excavation to 3:2 after 10 days and 2:1 after 13 days. Also, a sample of beetles which had emerged from a log attacked 10 to 14 days previously contained mostly males, all of which were flight positive. It seems that, unlike the females, some males are capable of flight throughout the first three weeks of gallery construction and that if all the males originally involved in the galleries examined had been present in the samples taken, the positive response of males would have been more common. The lack of positive response by either sex after 25 days may indicate that any beetles which leave their galleries following the first four weeks are unable to fly.

THE EFFECT OF INCREASED STIMULATION ON THE FLIGHT RESPONSE

A sample of 100 young adult beetles was taken from the May emergence and stored overnight in petri dishes of moist paper. The following day at 73° F. each beetle was tossed ten times and the response resulting from each toss was recorded. The results of this test, presented in Table VI show that the number of beetles which responded positively increased with stimulation up to and including the sixth toss.

TABLE VI

Results of increased flight stimulation on 100 Douglas-fir beetles

Toss	Response		No. changed to a positive response
	Negative	Positive	
1	39	61	
2	22	78	17
3	16	84	6
4	12	88	4
5	11	89	1
6	10	90	1
7	10	90	*

* No additional changes up to and including the tenth toss

C. DISCUSSION

Most of the nematodes occurring internally were Aphelenchulus spp., Aphelenchoides sp., and Sphaerularia spp., which are believed to be true parasites (Van Zwaluwenberg, 1928; Massey, 1956). The most commonly occurring nematodes under the elytra were Rhabditoids and Diplogaster stercorarius Bovien, believed to be commensals or mechanical associates (Van Zwaluwenberg, 1928) and Aphelenchoides sp. The Aphelenchoides found externally were invariably in the larval stage and may have been mechanical associates. Fuchs (1930) stated that larval Diplogaster spp., and Rhabditoids carried under the elytra of bark boring beetles were in a resting stage and thus named them "Dauerlarven".

The mites which occurred externally were mostly nymphs of the genera Digamasellus or Dendrolaelaps and adults Vidia sp., and Dropoda sp. found under the elytra, where there is evidence that they feed on the nematodes

occurring in that region. The internal mites identified were all hypopi of Vidia sp.

The genus Digamasellus is usually found associated with bark beetles and may be predaceous or mycetophagous. Vidia are usually found associated with wasps although they comprise a group about which very little is known. Uropoda are of no economic or medical importance but frequently attach themselves to insects for dissemination and probably do not harm their hosts (Morgan in corres.).

On the basis of the identification and biology of the associates, one would expect the internal species to represent the most serious drain on the beetles' reserves and have the greatest effect on their behaviour. Since these studies have shown that the nematodes did not affect the flight response, it might be reasoned that the beetles are agents of nematode dissemination and are thus unaffected by their presence at this stage, although Massey (1956) and Reid (1958) suggest that they affect the beetles during other activities.

The effect of temperature on flight response might be an important factor during the spring flight period owing to the lower temperatures which occur at that time of year. If the air temperature was below 68° F., as it often is during May in the interior of British Columbia, the beetles would require some additional flight stimulus. This would have to be in the form of sunlight since the chances of large numbers of beetles being stimulated by loss of tarsal contact are small. If the cool conditions were accompanied by cloudy weather, the periods suitable for the initiation of flight would be limited. During such years the population might be forced to limit its activity to the immediate vicinity of the previous infestation, whereas in a year with a warm and/or clear spring the population might disseminate more widely and start new centres

of infestation.

The tests on the effect of relative humidity on the flight response indicated that the moisture content of the air acted by changing the body temperature of the beetles. At 68° F., which is sub-optimal for spontaneous flight, a few flights occurred when the air was almost saturated. This may be important in the spring when temperatures from 68° to 70° F., are often accompanied by high air moisture. The humidity had little effect at 75° F., which is very suitable for flight in this species. On the other hand, at higher temperatures, lower humidity is more beneficial.

The studies involving light intensity indicate that the Douglas-fir beetle does not fly during the night, but is capable of taking flight under almost all daytime intensities. However, since the speed of response increases with the light intensity, light may be an important factor during overcast weather when low light intensities in the forest might be inter-related with other factors falling near the threshold for flight. The Douglas-fir beetle will fly in complete darkness when supported, but is incapable of free flight under such conditions.

The observations on flight response during gallery construction indicate that some rapid internal changes affected the flight response of females within one day of the initiation of their galleries. Since this coincided with the beginning of oviposition it may, at first, have been due to the maturation of the ovaries and their intrusion into the pterothorax. The fact that some females reacted positively to flight stimulation from 15 to 25 days after attack is of interest, since it coincided with the time that most of the second attacks occurred in cage studies. Examination of the indirect flight muscles made in preliminary studies on their degeneration (Atkins and Farris, 1958) showed that changes occurred in the flight muscles of females soon after the galleries were

initiated and that there was no sign of regeneration even after 50 days, as was found in the mountain pine beetle, Dendroctonus monticolae Hopk., (Reid, 1958). Nevertheless, there were always a few females taken at each gallery age which did not show flight muscle degeneration. These apparently normal females would appear to be the only ones capable of a second flight 2 to 3 weeks after the first attack. Furthermore, since the muscles of these females do not change, it is possible that they are predestined to make a second attack. Some would be prevented from showing a positive flight response during the first two weeks of gallery extension by the production and deposition of eggs. Those which could fly during this period probably left their galleries and thus were not included in the samples taken.

McMullen and Atkins (unpublished data) have shown that after 30 days the percentage of parents which abandoned their galleries increased with attack density and that fewer eggs were laid per inch of gallery at higher attack densities. It seems either that the greater number of females which left their galleries at higher densities may be related to the deposition of fewer eggs, or that some of the females that left were not capable of flight and were lost.

FLIGHT ATTITUDE

Many insects have a definite flight attitude or posture (see Atkins, 1958). Since it is difficult to observe the details of the flight attitude in small or fast flying insects, the Douglas-fir beetle was observed on fixed mounts. The most successful type of mount consisted of a small balance made from a piece of glass capillary tubing bridged across the edges of two razor blades. This balance permitted the beetle to acquire its own angle of flight and thus gave a more natural picture of the flight attitude.

In most cases the body took on a horizontal position with the head directed slightly downward, the thorax humped and the abdomen arched downward. The antennae and forelegs were directed forward and slightly away from the body with the foretarsi held upward. The femoral and tibial portions of the mesothoracic legs were held upward and at right angles to the body while the tarsi were held still higher and directed towards the body. The metathoracic legs were sloped backwards and spread slightly away from the body with the tarsi held almost vertically. It was noted that the tarsal segments often changed their position during slight movements of the insect's body, possibly functioning as organs of finite balance. The flight posture on the up and down stroke is shown in Figs. 7 and 8.

THE FLIGHT MOVEMENTS

A. INTRODUCTION

The study of flight movements is important since it is these actions that propel the insect through the air and control the direction and magnitude of dissemination. A beetle may take flight when the basic requirements for flight are sub- or supra-optimal due to stimulation by a secondary factor, but it is important to know whether or not and how successfully flight can continue under various conditions. If, for example, an insect is stimulated by exposure to sunlight to fly on a cool day would flight continue once the insect entered a shaded area in the forest? Questions such as this are particularly applicable to spring flying insects like the Douglas-fir beetle, because of the frequency with which the basic conditions of flight are outside the limits of the activity. Adaptation to various conditions prior to activity may also be significant (Gunn & Hopf, 1942), but it will not be considered here. The experiments devolved concern only the flight movements themselves and how they are

affected by changes in the beetles' environment. Aerodynamics is not within the scope of this paper since it is a study apart from behaviour and since the forces produced can be expected to change in relation to changes in the flight movements.

The main movements to be considered in this section are the wing beat frequency, amplitude of the wing beat and elytra, and the deflection of the wings.

B. METHODS AND RESULTS

THE NORMAL WING-BEAT AMPLITUDE AND DEFLECTION

The wing-beat amplitude and wing deflection were studied with the aid of photography and the stroboscope, while the beetles flew on either a fixed mount or a balance.

Observed from a point at right angles to the stroke plane, the amplitude of wing-beat of various insects varies from 70° in Aeshna (Odonata) to 160° and 180° in Lucanus cervus and Priacma serrata (Coleoptera) respectively (Magnan, 1934 and Atkins, 1958), while Pringle (1957) noted the possibility of it being greater than 180° in some beetles. In the Douglas-fir beetle the wing-tips initially describe arcs of 187 degrees, while the broader anal portions travel farther due to wing deflection. At the top of the stroke the wings come together for their full length, although the broader portions touch only slightly after the tips, as the wings undergo a pronation twist. At the bottom of the stroke the wings stop at the vertical, with the exception of the broader portions, which touch as the wings rotate on their long axis. The tip of each elytron describes an arc of 40° to 45° upwards from the horizontal movement considerably more than is reported for beetles by Pringle (1950, 1957) (Figs. 7 and 8). The amplitudes pictured in Fig. 9 are considered normal for D. pseudotsugae although variations do occur.

Figure 7. The flight posture of the Douglas-fir beetle
showing wings and elytra elevated.

Figure 8. The flight posture of the Douglas-fir beetle
showing wings and elytra depressed.

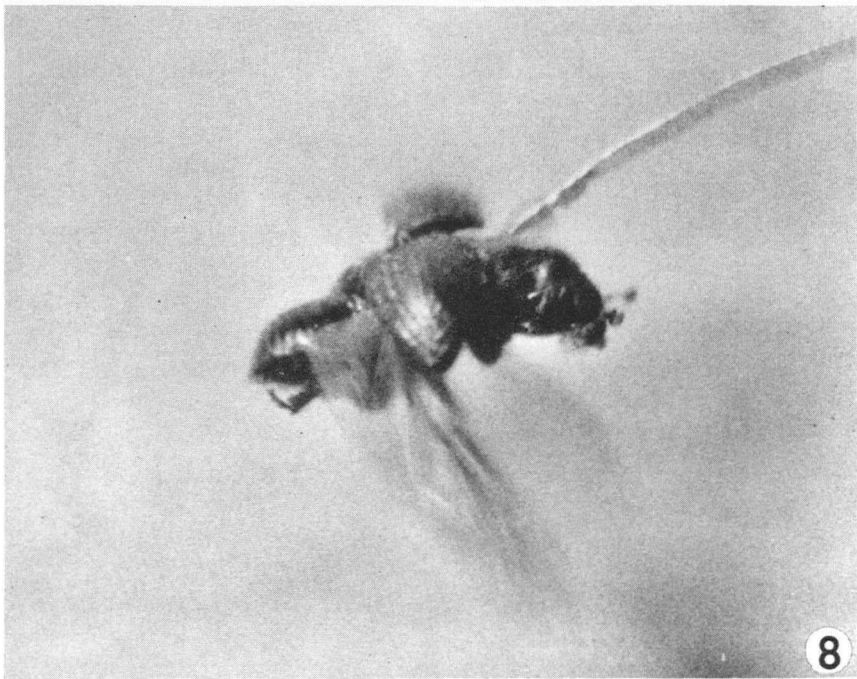
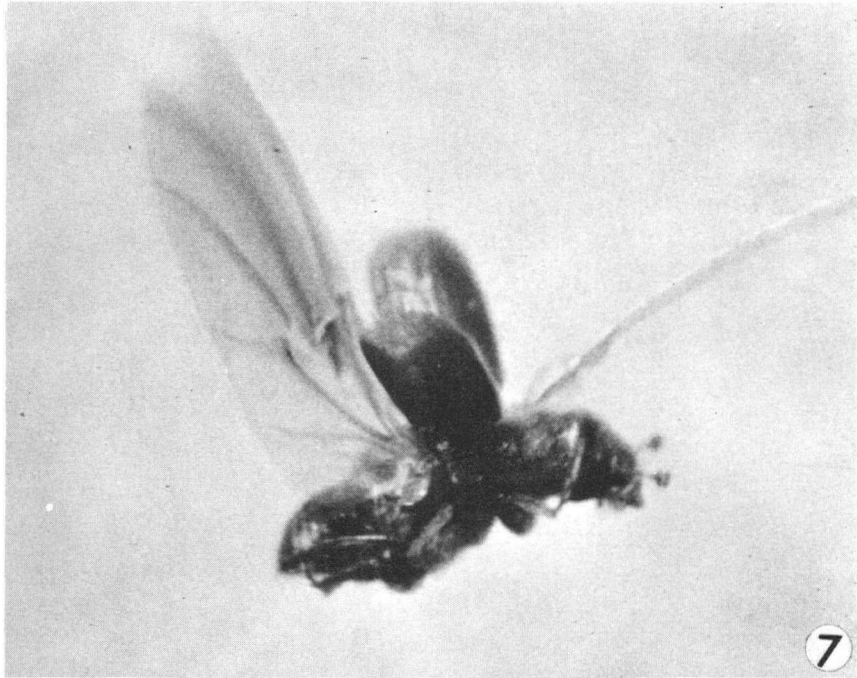


Figure 9. The wing-beat amplitude of the Douglas-fir beetle
(black indicates amplitude of the elytra).

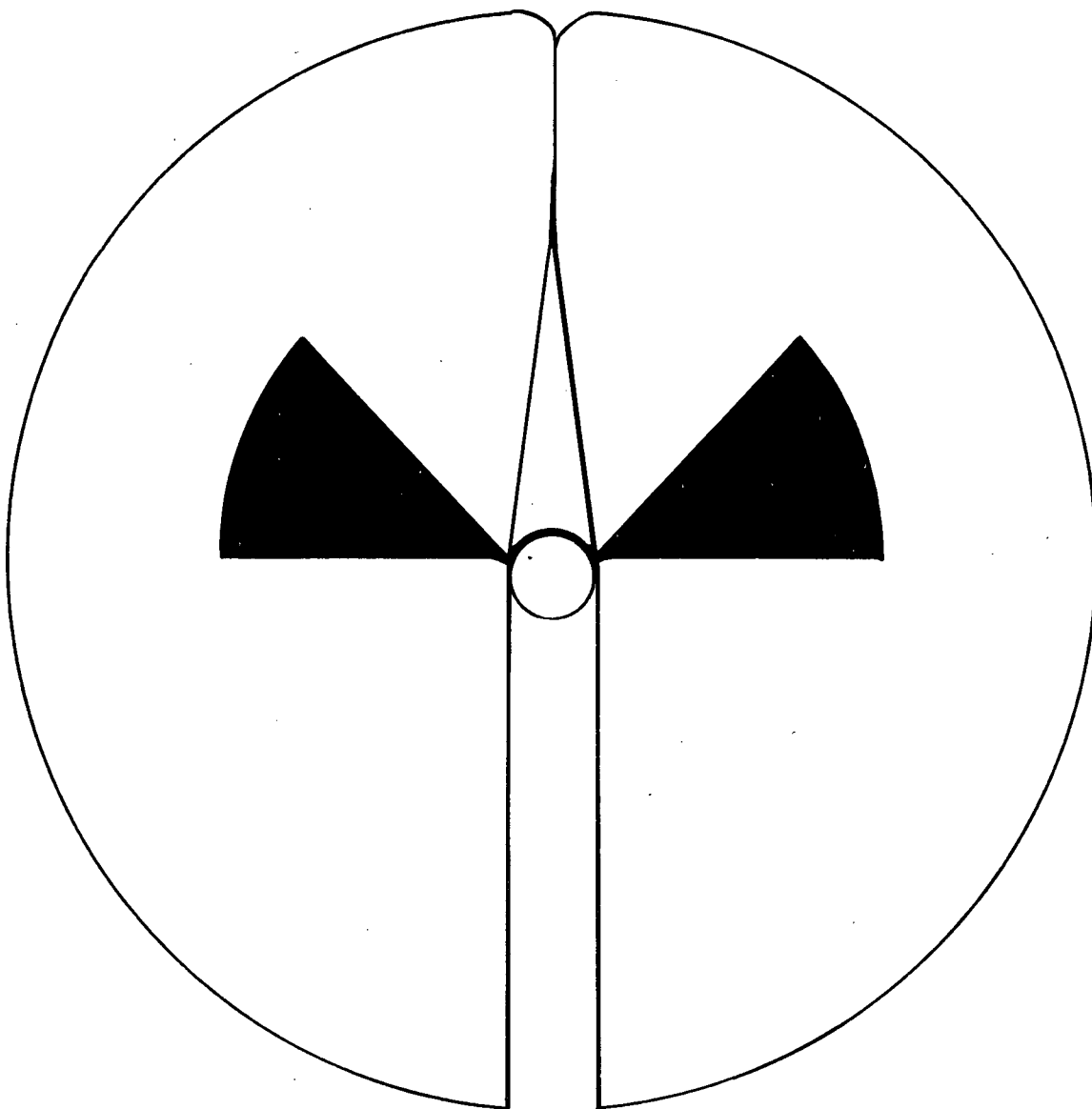


FIGURE 9

By adjusting the stroboscope so that the flashing tube was one or two cycles out of phase with the wing-beat, the secondary wing movements could easily be observed. On a fixed mount with a gentle flow of air directed from in front of the beetle, the wing tip curve was similar to that reported for many other insects, moving forward and downward with a positive angle of attack and returning backward and upward.

THE EFFECT OF ASSOCIATES ON THE WING-BEAT FREQUENCY AND AMPLITUDE

Young adult beetles which emerged from their brood logs at various times of the year were collected and subjected to flight stimulation by tossing. Those showing a strong positive response were used in the following tests. Four samples of 100 spring-emerged beetles, two from each of two years, and one sample of 100 summer-emerged beetles were used.

Each beetle was mounted on an aluminum foil point fastened to the prothorax by wax. The stroboscope method of determining the wing-beat frequency (Chadwick, 1939) was used. The calibration of the stroboscope used for the two initial samples was checked by an oscilloscope screen against an Audio Generator, which was checked at the 60 cycle point with line frequency. The overall accuracy was estimated at ± 5 per cent. All later tests were made with a Nicols Probostrobe with an accuracy of ± 1 per cent.

In all experiments involving the wing-beat frequency the readings were not taken until the insect had been flying for some seconds, because during the first few seconds the rate of beat reaches a value above the steady level later adopted. However, these changes occurred too rapidly for quantitative observation.

Following the wing-beat frequency readings for each individual, the beetles were dissected, sexed and examined for the presence or absence of nemic and mite associates. Only the adult nematodes were counted. Relative expressions were used to describe the number of larval forms due

to their occurrence in large numbers.

The temperature throughout these tests ranged between 72.6 and 75.0° F., and was disregarded since Rudinsky and Vité (1956) found that the wing-beat frequency of the Douglas-fir beetle changed only slightly between these levels.

The first two samples of spring emerged beetles had ranges of wing-beat frequency of 78 to 100 and 76 to 105 cycles per second, with means of 90.2 and 89.4 cycles per second respectively. The sample of summer emerged beetles had a range of 78 to 105 cycles per second with a mean of 89.9 cycles per second. The remaining two samples of spring emerged beetles had ranges of 60 to 97 and 73 to 97 cycles per second, with means of 87.4 and 88.0 cycles per second respectively.

Student's "t" test was used to analyse the data. No significant difference was found between uninfested males and females in any of the samples, so the total number of uninfested beetles in each sample was used as a basis for comparison with the infested groups of the corresponding sample. Preliminary analysis showed that mites had no effect on the wing-beat frequency, except in a special case described later, so they were eliminated from the final analysis. In each sample the uninfested beetles were compared with those infested with internal nematodes, external nematodes, and both internal and external nematodes. The means, degrees of freedom, and "t" values are presented in Table VII.

In the first sample, the significant difference between the uninfested beetles and those infested by internal nematodes alone is not considered solely due to the nematodes. If these had an effect by themselves they also should have shown an effect in the group infested by both internal and external nematodes.

TABLE VII

Analysis of the wing-beat frequency of 5 samples of 100 Douglas-fir beetles with various degrees of nematode infestation

Sample	Comparison	Mean frequency in cycles/sec.	d.f.	"t"
1	Uninfested	88.9		
	Infested			
	(A) External nematodes only	90.4	70	1.1737
	(B) Internal nematodes only	93.7	45	3.3426**
	(C) Internal & external nematodes	90.7	51	.9419
2	Uninfested	89.2		
	Infested			
	(A) External nematodes only	88.5	72	.4711
	(B) Internal nematodes only	91.8	45	1.614
	(C) Internal & external nematodes	89.8	43	.3768
3	Uninfested	90.6		
	Infested			
	(A) External nematodes only	91.1	71	.1509
	(B) Internal nematodes only	91.0	40	.1227
	(C) Internal & external nematodes	89.9	49	.2113
4	Uninfested	87.4		
	Infested			
	(A) External nematodes only	87.2	67	.1512
	(B) Internal nematodes only	87.8	47	.2841
	(C) Internal & external nematodes	88.5	54	.3928
5	Uninfested	88.4		
	Infested			
	(A) External nematodes only	87.9	81	.3049
	(B) Internal nematodes only	87.2	24	.4954
	(C) Internal & external nematodes	86.8	31	.3871

** Significantly different at the 1 per cent level.

A histogram of frequency distribution of the wing-beat frequencies of 500 Douglas-fir beetles taken between 72.6° and 75.0° F., and 45 per cent relative humidity is shown in Fig. 10.

The exceptional case in which mites affected the wing-beat frequency occurred when they formed a cluster on the tips of the elytra. The mean wing-beat frequency of 11 beetles infested with mites in this manner was 84 cycles per second compared with a mean of 89.3 cycles per second for the remaining 489 beetles. The mites probably acted as a loading mechanism reducing the wing-beat frequency through their weight on the elytra.

Throughout the last two samples of beetles, observations were made on the wing-beat amplitude to determine whether or not the associates caused any reduction which might result in changes in the wing-beat frequency. The amplitude described earlier was considered normal and reductions were estimated in degrees at both the top and bottom of the stroke. However, there was no correlation between reduced amplitude and differences in wing-beat frequency. The mean frequency for 37 beetles with reduced amplitude was 86.2 cycles per second compared with 86.3 cycles per second for the remaining 163 with normal amplitude. Furthermore, there was no definite correlation between nematode infested beetles and reduced amplitude, although the incidence of amplitude reduction was higher in the group of beetles infested by internal nematodes.

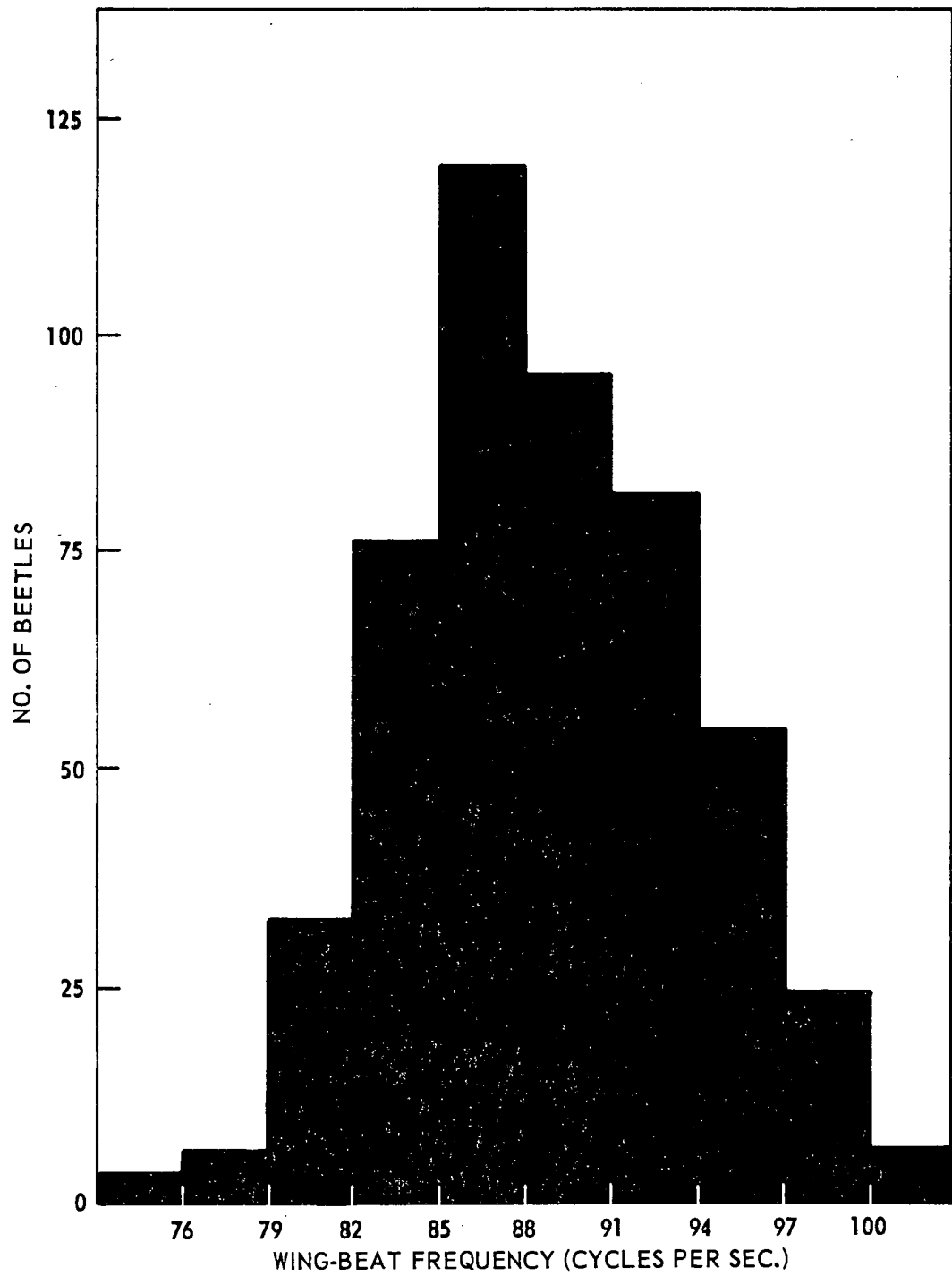


Figure 10. Frequency distribution of wing-beat frequencies of 500 Douglas-Fir Beetles

THE EFFECT OF TEMPERATURE ON WING-BEAT FREQUENCY AND AMPLITUDE

Initially, 5 samples of 50 flight positive spring-emerged beetles were tested. Each individual was mounted on an aluminum foil point and stimulated to fly near the flashing tube of the "Nichols" probostrobe in order to observe the wing-beat frequency and amplitude at the prevailing temperature. This procedure was followed with one of the samples at one of the following temperatures: 70°, 76°, 80°, 84° and 90° F. The resulting ranges and means are presented in Table VIII. Although the means showed a definite increase with temperature, the extremes did not, due to natural variation between the samples.

TABLE VIII

Results of wing-beat frequency readings for five samples of Douglas-fir beetles at different temperatures

Sample	Temperature (°F.)	Mean	Extremes
1	70	92.8	82 - 105
2	76	94.0	87 - 102.5
3	80	94.9	81 - 102
4	84	95.8	86 - 103
5	90	96.6	88 - 102

In order to control the variation between the samples, six groups of 20 beetles were taken from the same source as those in the preceding experiment and each group was studied throughout a temperature range. Following the wing-beat frequency and amplitude observations at one temperature, the beetles were put to rest until the temperature changed a few degrees, at which time another set of observations was made. This was

repeated until each sample had been observed at four different temperatures. Three of the samples were studied with increasing and three with decreasing temperature. With this method, both the extremes and means increased with temperature. The results are presented in Table IX. Additional observations indicated that at temperatures above 100° F., the wing-beat frequency of the beetles dropped as the thermal death point (118° to 120° F.) was approached and heat prostration occurred. The results of these studies are shown in Fig. 11.

Temperature did not affect the wing-beat amplitude. In cases where the amplitude changed there was no relation to temperature but rather to the duration of flight activity. This was evident mostly in the last observations. These changes were probably due to fatigue (see p. 38).

THE EFFECT OF RELATIVE HUMIDITY ON WING-BEAT FREQUENCY AND AMPLITUDE

The wing-beat frequencies and amplitudes of a number of beetles mounted on aluminum foil points were observed with the aid of the "Nichols" stroboscope. The observations were made at various relative humidities ranging from 25 to 98 per cent at 67° F., 18 to 96 per cent at 75° F., and 25 to 96 per cent at 85° F. At least 20 beetles were used at each temperature and humidity. The resulting mean of each sample was used in the graphical presentation in Fig. 12.

The wing-beat frequency increased as the RH increased through its lower range, the degree of increase varying inversely with the temperature. At higher RH the wing-beat frequency decreased quite sharply. No changes in amplitude were noted.

TABLE IX

Results of wing-beat frequency readings for six samples
of Douglas-fir beetles with varying temperatures

Sample	Temperature (°F.)	Mean frequency in cycles/sec.	Frequency extremes in cycles/sec.
1 *	64	79.7	72 - 87
	72	88.9	78 - 97
	75	89.1	80 - 98
	79	91.4	80 - 102
2	68	92.1	88 - 97
	75	94.9	88 - 100
	78	96.2	87 - 102
	88	96.6	88 - 103
3	65	86.7	79 - 93
	76	95.7	89 - 103
	80	96.9	92 - 103
	90	97.1	92 - 105
4 *	72	95.5	88 - 103
	76	97.3	90 - 104
	80	97.9	90 - 105
	86	98.1	91 - 105
5	76	94.8	87 - 100
	80	95.8	87 - 102
	85	96.2	88 - 100
	90	96.4	88 - 100
6 *	64	86.8	83 - 95
	76	92.8	87 - 100
	80	94.5	87 - 102
	86	94.9	88 - 102

* Sample studied under decreasing temperature.

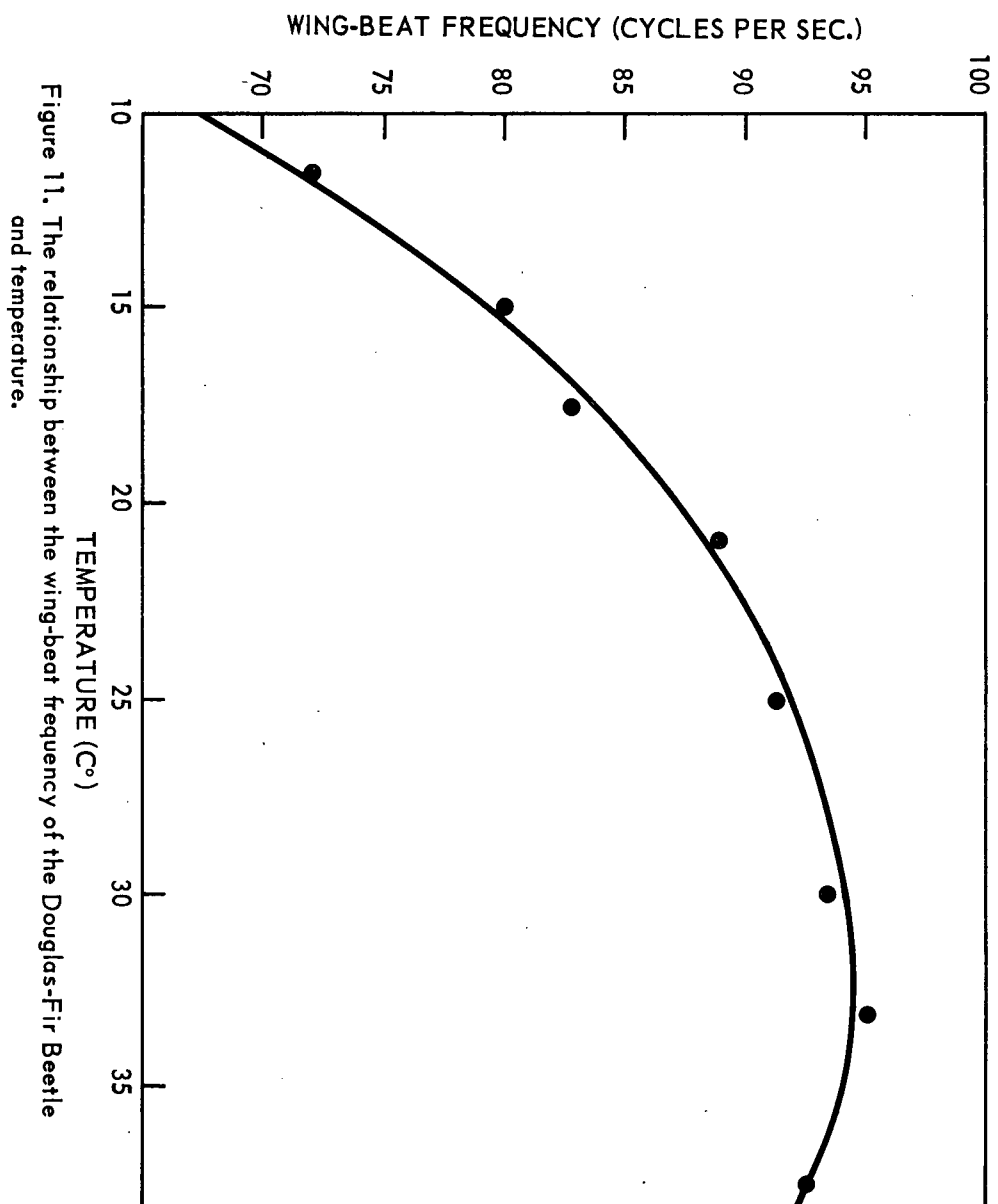


Figure 11. The relationship between the wing-beat frequency of the Douglas-Fir Beetle and temperature.

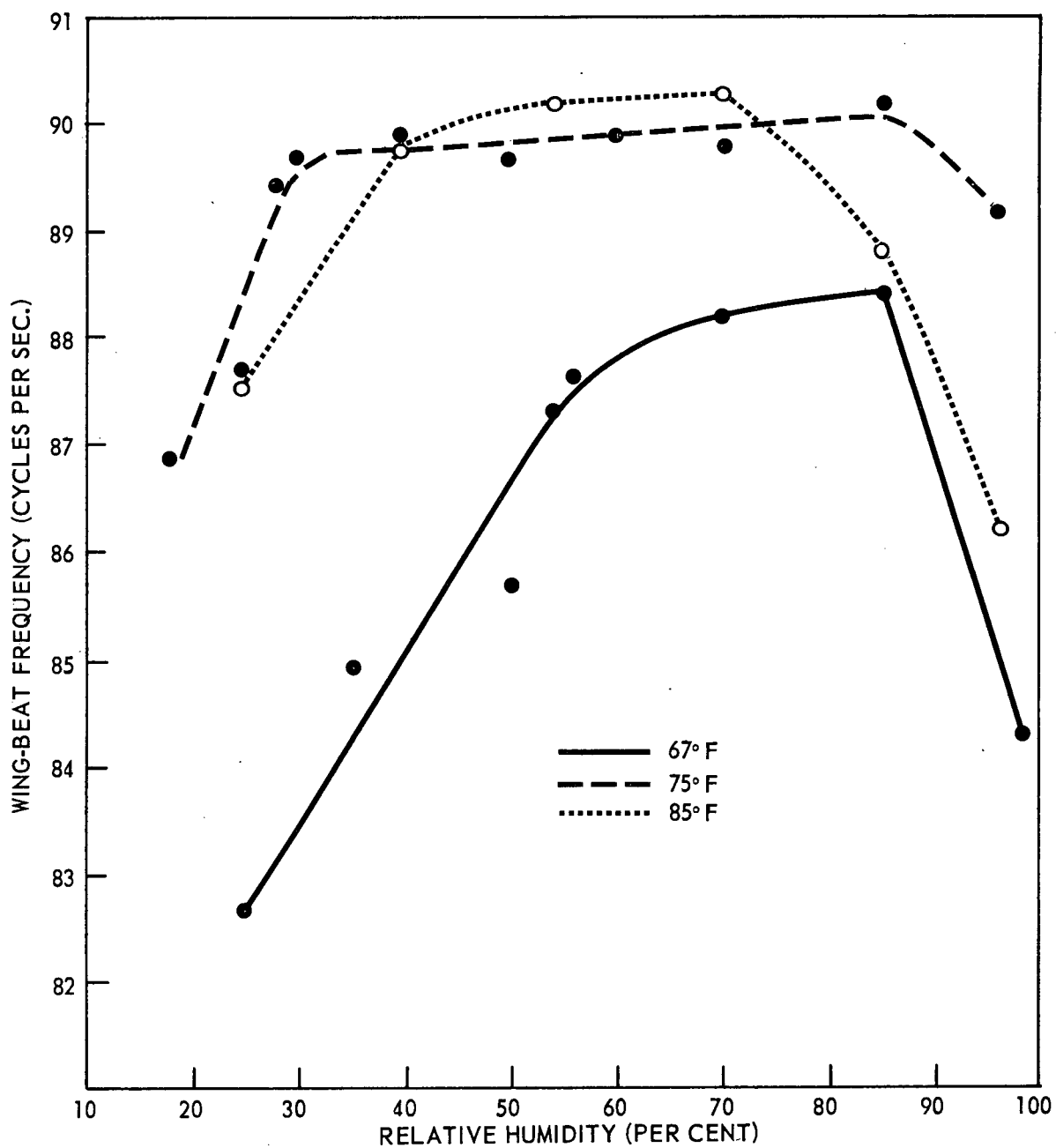


Figure 12. The relationship between the wing-beat frequency of the Douglas-Fir Beetle and relative humidity

THE EFFECT OF LIGHT INTENSITY ON WING-BEAT FREQUENCY AND AMPLITUDE

Young adults which emerged during the winter from spring-attacked logs brought into the laboratory were used. Six samples of 10 beetles that showed a strong flight inclination were tested at each of the following light intensities: 15, 60, 100 and 300 foot candles (72° F., 50 per cent RH). Three samples were observed with increasing, and three with decreasing light intensity, thus reducing any error due to fatigue. The beetles were allowed 10 minutes for adaptation at each light intensity prior to the wing-beat frequency readings, since the rate of activity under one light intensity may continue during the early stages of subjection to another intensity (Digby, 1957). The light intensity was controlled with incandescent lamps separated from the experimental area by a water bath to prevent large changes in temperature. The lowest light intensity used was considerably higher than that at which flight will occur (see p. 12). However, this intensity constituted the light produced by the flashing tube of the stroboscope. The results are presented graphically in Fig. 13. The value shown for 10 foot candles was estimated from indications obtained by filtering down the intensity of the strobe-light, although the frequency reading was not satisfactory. The wing-beat frequency increase with increase in light intensity, the greatest increase occurring between 60 and 100 foot candles.

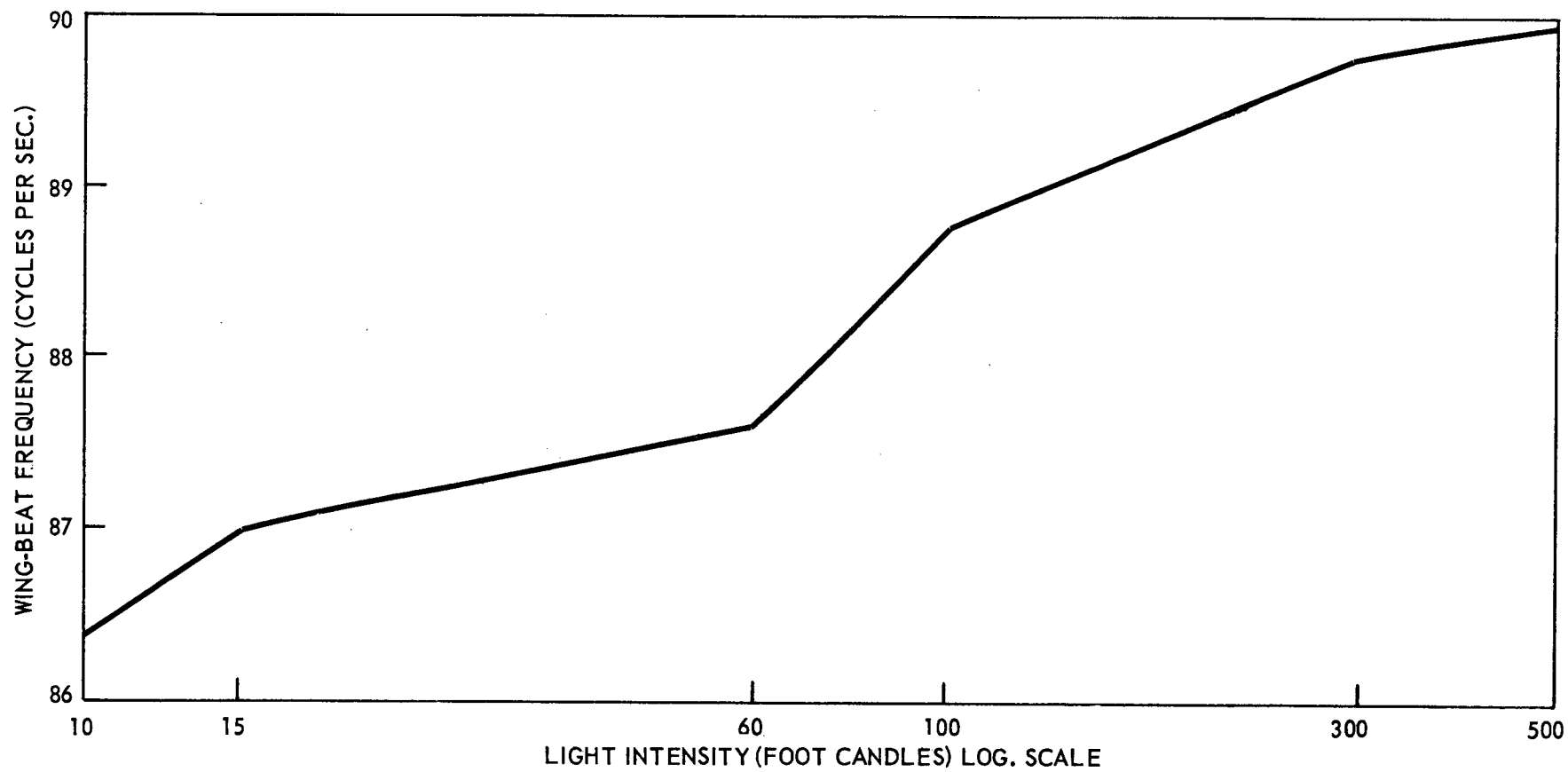


Figure 13. The relationship between the wing-beat frequency of the Douglas-Fir Beetle and light intensity

THE EFFECT OF REDUCED ATMOSPHERIC PRESSURE, WING-CLIPPING AND WING-LOADING ON WING-BEAT FREQUENCY AND AMPLITUDE

The effects of reduced atmospheric pressure and wing mutilation on the wing-beat frequency and amplitude of the Douglas-fir beetle, suggested by the work of Chadwick (1939), were investigated briefly. As in Drosophila (Chadwick and Williams, 1949) and many other insects (Sotavalta, 1952), a reduction of the atmospheric pressure increased the wing-beat frequency of the Douglas-fir beetle. Several beetles mounted on aluminum foil points were held by pins in a cork used to seal an inverted vacuum-flask. The wing-beat frequencies were taken at 1010 millibars and 10, 15, 20 and 25 pounds vacuum. The wing-beat frequencies showed a mean increase of 1.6 cycles per second for each 5 pounds increase in vacuum.

The clipping of either or both wings by approximately one-third was found to increase the beat frequency from one to six cycles per second, while small quantities of melted wax placed on the wing-tips decreased the beat frequency.

The wing-beat amplitude was unchanged, except in the case of wing loading, when the amplitude was reduced by varying degrees that depended upon the amount of loading.

THE EFFECT OF FATIGUE ON WING-BEAT FREQUENCY AND AMPLITUDE

Twenty beetles were mounted on aluminum foil points and stimulated to fly. The light intensity was 30 foot candles, the temperature 73° F., and the relative humidity 45 per cent throughout the tests. The wing-beat frequency was measured and the amplitude observed every 6 minutes for four hours with the Nichols Probastrobe. Some representative changes

in the wing-beat frequency are shown in Fig. 14. The average reduction in wing beat frequency for the 20 beetles tested after four hours flight was 17.95 per cent; this reduction being due almost certainly to fatigue. In Drosophila repleta, Chadwick (1939) found that the frequency after complete fatigue was 50 to 60 per cent of the starting rate, while Magnan (1934) noted a reduction of one-third during experiments with a sphingid, Macroglossa stellatarum.

The wing-beat amplitude was reduced in some individuals but not in others. Those changes which did occur failed to follow a definite pattern; in some cases recovery from previous reduction occurred. It was noted that changes in amplitude occurred at both top and bottom of the stroke, which is contrary to that found in some Diptera (Hollick, 1940), but in agreement with observations made on another beetle (Atkins, 1958).

It was noted in a few cases that, after flying on a mill for several hours, the beetle diminished or suspended the action of the outer wing, maintaining flight at a greatly reduced velocity. Hocking (1953) reported that Simulium and Apis mellifera also reduced the outer wing amplitude on flight mills. He suggested that this was an attempt by the insect to steer out of the circular path enforced by the mill.

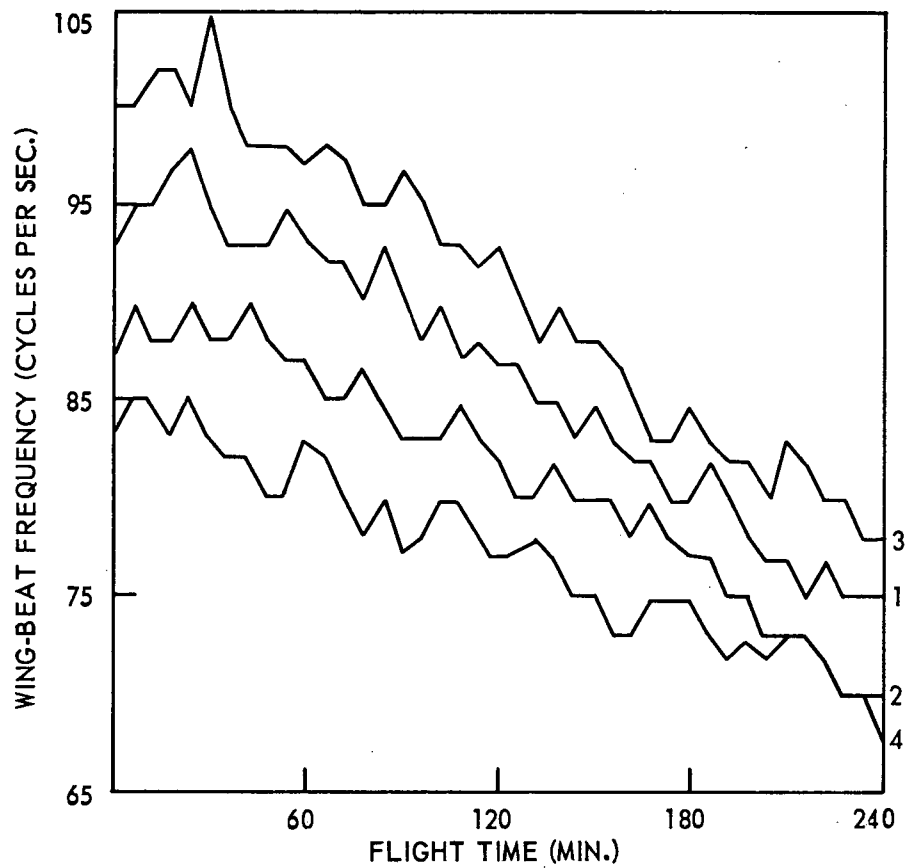


Figure 14. The variation in the wing-beat frequency and the effect of fatigue on the Douglas-Fir Beetle for four representative individuals

C. DISCUSSION

It is interesting that the internal nematodes appeared to have no effect on the beetles' flight movements even though some of the species that were present, Aphelenchulus spp., Aphelenchoides sp., and Sphaerularia spp., are known to be true parasites (Van Zwaluwenberg, 1928; Massey, 1956). If the significant difference noted in the first sample was actually due to the nematodes and not to sampling as suspected, it is interesting to note that the work of Fuchs (1920) and Reid (1955) shows that the wing-beat frequency was increased rather than decreased. Weis-Fogh (1956) noted that mermithids reduced or impeded the flight of locusts, while Moeller (1956) noted that bees were stimulated to fly by the presence of nosema parasites. It is possible that some internal nematodes would increase the wing-beat frequency by excitation, but difficulties in nematode identification prevent analysis of the data by nemic species.

It seems noteworthy that the wing-beat frequency increased rapidly with temperature to 68° to 72° F., the point at which spontaneous flight occurs. Once the optimal temperature for flight was reached the wing-beat frequency increased by only a few cycles per second with an additional rise of 18° F. in temperature.

The increase in wing-beat frequency resulting from an increase in relative humidity was probably due to changes in the insects' ability to cool themselves by evaporation of body water, since the temperature of insects indoors does not generally differ greatly from that of the environment, although it is definitely lower in dry air and higher in moist air (Krogh and Zeuthen, 1940). The decrease in wing-beat frequency evident at higher relative humidity was probably due to heat prostration resulting

from the inability to cool. This is further exemplified by the fact that the wing-beat frequency decreased at a lower relative humidity when the air temperature was highest.

At temperatures below the optimum for flight the relative humidity appeared to be quite significant in increasing the wing-beat frequency and may be important during the spring flight period when temperatures are generally lower and humidities higher. At 75° F., which is very suitable for Douglas-fir beetle flight, there is little change in the wing-beat frequency over the more common range of relative humidity.

The relative humidity did not generally affect the wing-beat amplitude, although a number of beetles observed at 96 and 98 per cent showed a slight reduction in amplitude at the top of the beat. This may have been due to the increased density of the air.

The changes in wing-beat frequency that occurred with changes in light intensity were of low magnitude compared with those resulting from changes in temperature and humidity. They are probably due to differences in the intensity of the stimulus entering the insects' eyes. Such stimulation has been demonstrated in eye-patching experiments where light entering only one eye stimulates the muscles on the opposite side of the body to greater activity, producing a turn towards the light (Chen & Young, 1943; Popam, 1952).

The increase in wing-beat frequency resulting from an increase in vacuum can be most easily explained by the reduced resistance offered to the wings. The fact that clipping either or both wings had the same effect on the beat frequency is contrary to the findings of Roch (1922) and Chadwick and Williams (1949), but in agreement with Sotavalta (1947, 1952). Sotavalta (1952) presents four theories to explain the increase

in frequency resulting from wing clipping. (1) The frequency increases as a compensation for the reduced wing area within the requirements of a constant aerodynamic force to be produced. (2) The frequency increases because the air resistance offered the wings is less. (3) The frequency increases because the inertia of the oscillating system is reduced. (4) The frequency is altered due to a disturbance of the sensory balance. Sotavalta feels that the changes are due to reduction of the inertia. His findings may be supported by the fact that small quantities of melted wax placed on the wing-tips of the Douglas-fir beetle, which would tend to increase the inertia without altering the area, decreased the wing-beat frequency.

The relationship between the wing-beat frequency, wing-stroke amplitude and the flight velocity is not fully understood, due to widespread variation between individuals, but it seems likely that they are all closely integrated and that the influence of the above-mentioned factors on wing-beat frequency and amplitude would be passed on to the flight velocity. In this case, the speed with which the beetles could reach new areas for infestation and the distance they might spread in a unit of time would vary widely from season to season.

The reduction in the wing-beat frequency that could be attributed to fatigue was considerably lower than that reported by other workers. However, the reduction shown here might be somewhat larger if the readings were carried on to the point of complete exhaustion as they were with D. repleta. This point, however, would follow more than eight hours of flight in the Douglas-fir beetle.

THE FLIGHT CAPACITY

A. INTRODUCTION

The flight capacity (duration and velocity) is an important phase of the behaviour of economically significant insects such as the Douglas-fir beetle, because it governs the feasibility of any control or preventive measures which may be developed. An understanding of the flight capacity and how it varies in relation to various factors is necessary to evaluate the beetles' power of dispersal under various seasonal conditions. This would be an aid in the detection of new areas of infestation by, in part, directing the search. It would help in evaluating the hazard at hand in terms of the surrounding timber. It would be an aid in determining the size of areas of sanitation or sanitation salvage required as a safety zone around a comparatively beetle-free stand.

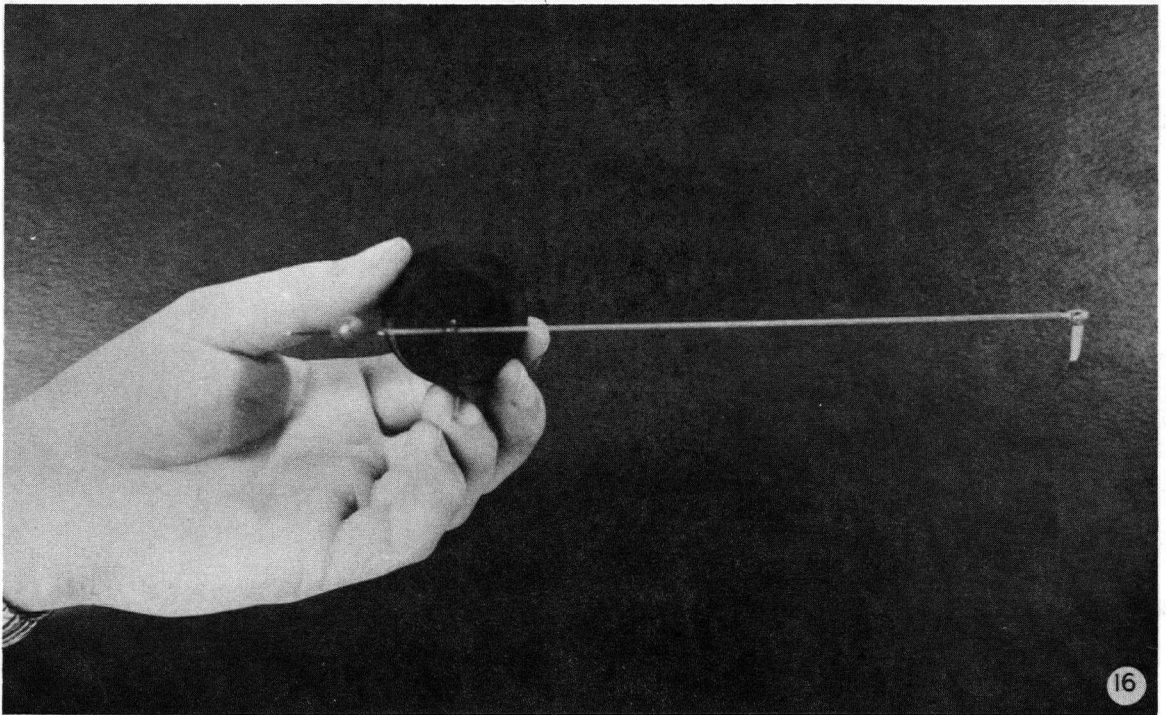
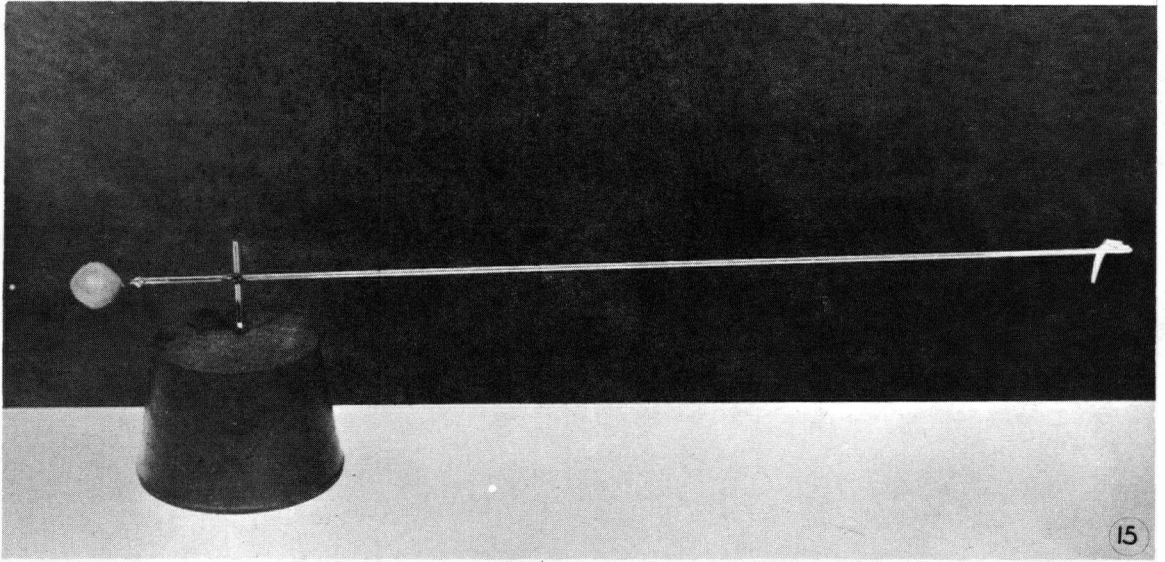
B. METHODS AND RESULTS

THE EFFECT OF ASSOCIATES ON FLIGHT DURATION

A number of spring emerged beetles were subjected to flight stimulation by tossing. Thirty of those which showed a "good" response were used in the initial trial. The beetles were flown for four hours on balsa-arm flight mills similar to those described by Chapman (1954). Another sample of 60 young beetles and a sample of 15 young beetles were flown for four and eight hours respectively on similar flight mills made from capillary tubing and having a small sliding ball of modelling clay which facilitated balancing of the mill once the beetles were attached (Fig. 15 and 16). A sample of 30 beetles which emerged from their egg galleries in July, presumably to make a second attack, also were tested for a four hour period.

Figure 15. Glass-arm flight mill in normal operating position.

Figure 16. Glass-arm flight mill turned on side to show balance obtained by sliding counter-weight at the left.



The starting and stopping times were recorded for each beetle to obtain the total flying time, the duration of the initial flight and the number of stops. At the conclusion of each test the beetles were dissected to determine the sex and degree of infestation by associates.

Students' "t" test was used to compare the mean flying times, mean duration of initial flight and the mean number of stops of various groups of beetles within each sample. In every case there was no significant difference between the mean flying times of males and females, so the mean of all uninfested beetles from each sample was used as a standard with which to compare other groups from the same sample. Each sample was broken down into groups on the basis of the presence of associates, viz: internal nematodes only, external nematodes only, mites only, and internal nematodes regardless of the presence of other associates. However, not all of the categories occurred in every sample. The means, degrees of freedom and values of "t" obtained from the four hour tests are presented in Tables X to XII.

The results obtained from the beetles flown for eight hours presented in Table XIII show great variation in the flight duration and the initial flight between beetles with similar infestation. Only 13 of the 15 beetles used are represented in Table XIII as two were eliminated on account of damaged wings.

TABLE X

Analysis of the flight during a four hour period of 30 Douglas-fir
beetles with various degrees of infestation

Comparison and infestation	df	Mean flying time (min.)	"t"	Mean initial flight (min.)	"t"	Mean no. of stops	"t"
Uninfested		152		109.0		5.8	
Infested							
1. External nematodes only	17	152	.000	87.9	.540	6.8	.126
2. Internal nematodes only	13	148	.091	35.8	2.245*	9.2	1.021
3. Internal and external nematodes	12	181	.950	47.8	2.054 ^{2/}	3.6	.708
4. Internal nematodes ^{1/}	28	163	.457	41.3	2.391*	6.6	.278

^{1/} Include all beetles infested by internal nematodes regardless of the presence of other associates.

^{2/} "t" value for significance at the 5 per cent level = 2.179.

* Significant at the 5 per cent level.

TABLE XI

Analysis of the flight during a four hour period of 60 Douglas-fir
beetles with various degrees of infestation

Comparison and infestation	df	Mean flying time (min.)	"t"	Mean initial flight (min.)	"t"	Mean no. of stops	"t"
Uninfested		170.9		130.3		4.86	
Infested							
1. Mites only	17	204.6	1.066	170.8	.781	6.06	.197
Uninfested ^{1/}		179.8		151.5		5.32	
Infested							
1. External nematodes only	44	159.5	.899	108.4	1.792	4.00	.557
2. Internal nematodes only	24	160.6	.563	65.0	2.320*	7.90	.955
3. Internal and external nematodes	24	198.3	.879	72.6	2.313*	2.71	1.261
4. Internal nematodes ^{2/}	31	179.4	.016	68.8	3.057**	5.29	.013

^{1/} Includes beetles with mites only.

^{2/} Includes all beetles infested by internal nematodes regardless of the presence of other associates.

* Significant at the 5 per cent level.

** Significant at the 1 per cent level.

TABLE XII

Analysis of the flight during a four hour period of 30 re-emerged Douglas-fir
beetles some of which were infested by internal nematodes

Comparison and infestation	df	Mean flying time (min.)	"t"	Mean initial flight (min.)	"t"	Mean no. of stops	"t"
Uninfested vs.		229.2		169.3		1.52	
Internal nematodes only ^{1/}	28	219.9	.978	94.3	2.063*	2.10	.533

^{1/} Only associates present in this sample.

* Significant at the 5 per cent level.

TABLE XIII

The flight pattern and dissection results of 13

Douglas-fir beetles flown for 8 hours

No.	Initial flight (min.)	Total flight (min.)	Internal nematodes	External nematodes	Mites
1	104	252		X	
2	480	480		X	X
3	*	*		X	X
4	8	49	X	X	
5	*	*		X	
6	33	429			X
7	16	88	X	X	X
8	23	241			
9	85	198			
10	388	475			
11	1	340		X	X
12	480	480		X	
13	365	398			X

* No single flights over one minute.

X Associate present.

THE EFFECT OF TEMPERATURE ON FLIGHT DURATION

Four samples of 20 spring emerged adults that showed a strong inclination to fly were flown on the glass-arm flight mills for four hours. Each sample was studied under one of four temperatures at 60 per cent relative humidity, viz: 62°, 72°, 80° and 90° F. The starting and stopping times of each beetle were recorded as before to obtain a complete picture of the flight pattern.

Temperature, over the range used, seemed to have little effect on the total time the beetles would fly during a four hour period, the means for the above temperature being 186.3, 172.8, 177.9 and 174.7 minutes respectively. However, there was a more pronounced effect on the duration of the initial flight. The mean initial flights for the same four temperatures were 46.5, 89.5, 90.5 and 99.5 minutes. The mean number of stops made by the beetles in four hours were 3.4 at 62° F., 2.6 at 72° F., 2.5 at 80° F., and 2.0 at 90° F. Several representative flight patterns which occurred under the above temperature conditions are presented pictorially in Fig. 17.

THE EFFECT OF RELATIVE HUMIDITY ON FLIGHT DURATION

Five samples of 20 spring emerged beetles with a strong flight response were flown for four hours on glass-arm flight mills. Each sample was studied under one of five relative humidities at 72° F., viz: 25, 45, 60, 75 and 95 per cent. A complete picture of the flight pattern during the four hour test period was recorded as before.

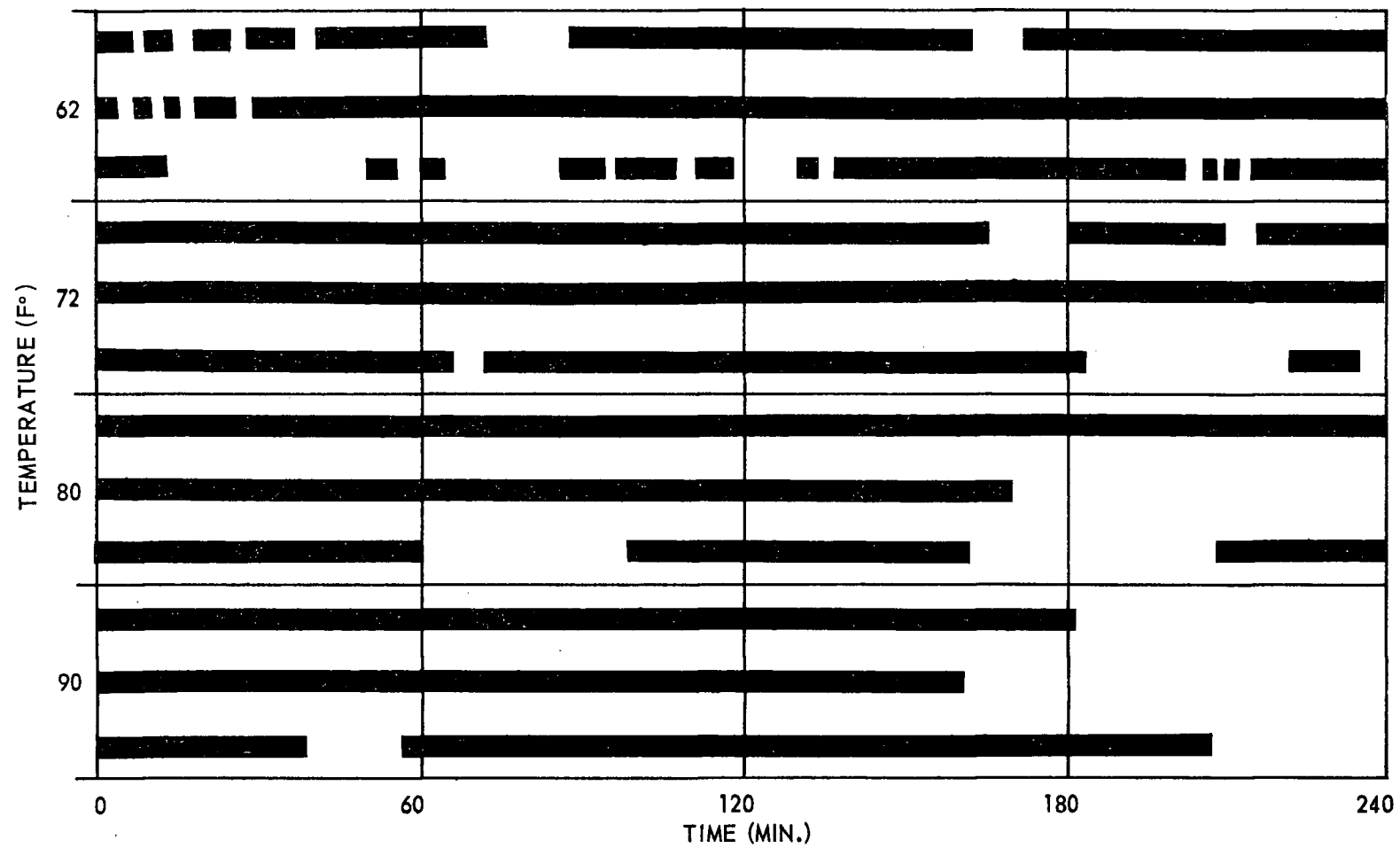


Figure 17. Representative flight patterns of Douglas-Fir Beetles flown for four hours at different temperatures with constant relative humidity (60 per cent). Black indicates flight.

As with temperature, the relative humidity had little effect on the total flying time, the means for the above humidities being 180.8, 181.5, 172.75, 183.45 and 185.25 minutes respectively. Again the major effect was on the duration of the initial flight, the corresponding means being 56.7, 80.9, 89.45, 85.75 and 95.25 minutes. The mean number of stops for the five humidities were 3.75, 2.3, 2.65, 2.6 and 2.15 respectively. Representative flight patterns that occurred with various degrees of air moistures are presented pictorially in Fig. 18.

THE EFFECT OF GALLERY CONSTRUCTION ON FLIGHT DURATION

Since parent beetles removed from their galleries at all but a few times throughout the season are flight refractory, the 30 beetles used in this study were collected as they emerged from their tunnels after approximately two weeks of gallery construction. The sample was flown for a four hour period on the glass-arm mills and the stops and starts were recorded as before. The results obtained were compared with those from a sample of 30 spring emerged beetles flown on the same mills. Student's "t" test was used for the comparison. The resulting means, degrees of freedom and values for "t" are shown in Table XIV.

TABLE XIV

Comparison of the flight over a four-hour period of 30
spring-emerged and 30 re-emerged Douglas-fir beetles

Treatment	d.f.	Total flying time (min.)	"t"	Initial flight (min.)	"t"
Spring-emergence	58	188.9	3.297**	134.5	.272
Re-emergence		225.0		141.8	

** Significant at the 1 per cent level.

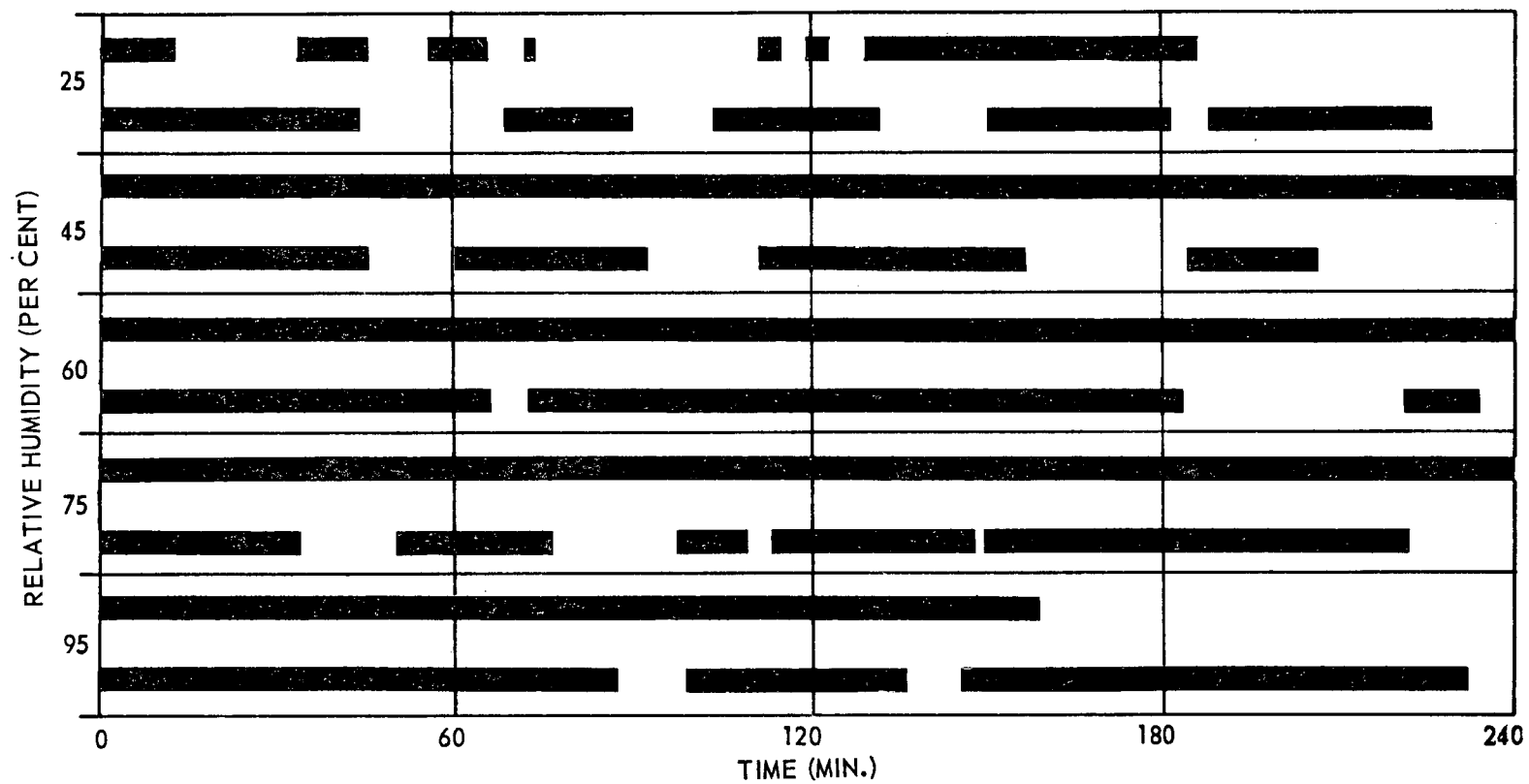


Figure 18. Representative flight patterns of Douglas-Fir Beetles flown for four hours at different relative humidities at constant temperature (72° F.). Black indicates flight.

THE FLIGHT VELOCITY ON FLIGHT MILLS

The beetles were fastened on glass-arm flight mills which described a one-metre circle. The number of evolutions per minute (counted against a stop watch) gave the flight velocity in metres per minute. Fifty beetles were observed between 72° and 77° C. Since the flight velocity of the Douglas-fir beetle varies according to the angle of the body as it does in the fly Muscina stabulans (Hollick, 1940), the beetles were placed in the near horizontal position assumed in natural flight. The flight velocity ranged from 48 to 88 metres per minute. The most common velocities (46 per cent) were between 65 and 74 metres per minute, which is approximately double that found by Rudinsky and Vité (1956) and is probably due to the construction of the flight mills.

THE FREE FLIGHT VELOCITY

The free flight velocity was obtained by releasing the beetles in a wind-free room and timing their flight over a measured course to a window. To prevent the initial velocity, which is slower due to the inclination of the insect's body, from reducing the level flight velocity, the beetles were not timed until they had flown several feet. The velocity varied considerably according to the manner of flight, that is, whether it was level, inclined, or zig-zagged. In a sample of 60 beetles tested, the velocity ranged from 50 to 150 metres per minute. The straight level fliers had velocities which usually fell between 90 and 115 metres per minute (3.3 to 4.2 miles per hour), comparable to the findings of Rudinsky and Vité.

THE EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON FLIGHT-MILL VELOCITY

The flight velocities of the beetles used in the tests on flight duration and temperature and humidity were recorded at the initiation of flight. The mean velocities of the samples show a similar relationship to temperature and air moisture as does the wing-beat frequency; they change rapidly at sub-optimal temperatures and low humidity, but change only slightly once conditions were suitable for the beetle to start flying. The average velocity when the relative humidity was 60 per cent was: at 62° F., 56.2 m/min. (metres per minute); at 72° F., 66 m/min.; at 80° F., 66.7 m/min.; and at 90° F., 67 m/min. When the temperature was 72° F. the average velocity was 60 m/min. at 25 per cent, 64.3 m/min. at 45 per cent, 66 m/min. at 60 per cent, 66.4 m/min. at 75 per cent, and 65.6 m/min. at 95 per cent.

THE EFFECT OF FLIGHT DURATION ON THE FLIGHT VELOCITY

Three samples of 10 beetles each were flown on glass-arm mills for a period of four hours. The flight velocity was recorded for each beetle as soon as it started to fly and each hour thereafter for four hours. The means for the 30 beetles showed very little reduction in flight speed with increased flying time. The means starting with the initial velocity were 66.8, 64.7, 62.6, 61.7 and 59.5 metres per minute.

C. DISCUSSION

It seems strange that the internal nematodes, whether alone or present with other associates, affected the duration of the initial flight but neither the total flight duration nor the number of stops. Because a number of internal nematodes from the Douglas-fir beetle are known to be true parasites one would expect any effect on the beetles' vigor to show as fatigue over a long period rather than in the early

stages of flight. It may be that during the first rest period there is some internal adjustment which compensates for or nullifies the effect of the worms. The nature of such a phenomenon is not here apparent. The fact that the initial flight period is reduced by 40 to 50 per cent may be significant in the dispersion of a population and the concentration of its nematode associates. It is evident that more work is needed on factors causing the wide range of nemic incidence one encounters when working with bark beetles.

The lack of effect of temperature and humidity on the total flying time seems reasonable within the range of conditions used, since once the beetles started to fly they could maintain their flight at sub-optimal temperatures due to increased body temperature arising from muscle activity. The same would be true of low humidities at the threshold temperature causing cooling which could be overcome by physiological warmth. At temperatures below those used in these tests, 11.5° to 12.5° C., Rudinsky & Vité found the flight ability decreased markedly. These temperatures were probably too low to permit sufficient heating through activity.

At high temperatures and humidity the flight was terminated sooner (at 90° and 72° F., and 60 and 95 per cent humidity respectively, only one of 40 beetles flew for the whole four-hour period) but was broken by fewer stops and thus the total flight averaged close to that under the other conditions. The earlier termination of flight at higher temperatures, whether direct or brought about by high humidity, is probably due to fatigue occurring more rapidly than under the more favourable conditions. However, the effect of temperature and humidity on the rate of fatigue will not be considered here. The greater number of stops which occurred at sub-optimal temperatures and low relative humidity were due to the

start-stop behaviour, possibly internal conditioning, which preceded the longer flights (Figs. 15 and 16).

Although fewer beetles completed the four-hour period flying at 72° and 90° F., at 95 and 60 per cent humidity respectively, they seemed to be the most suitable conditions for long unbroken flights. Further work is needed on the relation of internal temperature and environmental conditions.

Significantly greater total flight duration of beetles recently involved in gallery construction over that of newly emerged young adults, is difficult to reconcile with the similarity of the initial flights. One might expect it to be lower as a result of energy expended in excavation and the deposition of eggs. It seems unlikely that this could be a mechanism for creating heterogeneous groups through greater dispersion of one facet of the population.

The effect of temperature and humidity on the flight velocity follows a similar pattern to the effect on wing-beat frequency. It would appear that the flight velocity is controlled largely by the wing-beat frequency, but an attempt to relate the two along with wing-beat amplitude and beetle size failed to yield a positive relationship. Nevertheless, when the wing-beat frequency of an individual changed the velocity changed similarly.

The observations on the flight velocity over a long period of flight indicated that fatigue does take place after an hour or less but even after four hours the changes were only slight. The rate of fatigue would appear to depend primarily on the temperature and humidity.

CONCLUSIONS

Considering the flight activity of the Douglas-fir beetle as a whole, the flight performance is strong and relatively uniform despite the complexity of the factors affecting the different components of the activity. Although the environmental factors, with the exception of associates, have a marked effect on the flight response, the threshold condition leading to a flight attempt was invariably higher than that necessary for continuation of the activity. This means that once in flight the Douglas-fir beetle can pass through areas where the conditions fall below the threshold for spontaneous flight. In addition, rapid changes in the flight components due to the influence of changing environmental factors tend to lessen in the vicinity of the threshold of the particular factor.

Relative humidity influences the various phases of flight activity possibly through its effect on the body temperature.

The ability to initiate flight could vary widely from season to season depending on the weather. During a cool cloudy spring, the conditions suitable for spontaneous flight would be confined to short periods of sunshine which may tend to dilute the attacking population. On the other hand, several weeks of conditions suitable for emergence but not suitable for flight initiation, followed by several days of optimal flight conditions could cause an increased impact on the forest through concentration of the attacking population. The more suitable the conditions following emergence, the faster the beetles would fly, find new host material and make their attack. This would reduce the length of time they would be exposed to predacious animals wandering over the logs.

The Douglas-fir beetle is capable of flight under almost all day-time light intensities even in the most shaded forest, but is not capable

of free flight in darkness. Since beetles will fly in darkness on a mount, it would seem that vision plays an important role in free flight.

Of the flight movements, the wing-beat frequency is most affected by environmental factors. These effects are passed on to the flight velocity, although the relationship does not follow a definite pattern. Temperature probably has a combined effect; direct action on the biochemistry of the flight muscles and indirect action through sensory mechanisms. The reduction in wing-beat frequency demonstrated at high relative humidities is probably due to the onset of thermal paralysis, which may be supported by the earlier occurrence of rate reduction in the test conducted at 85° F.

The effect of light is probably due to sensory stimulation rather than an action on the physiology of the flight muscles. The effect of light intensity may be reduced following adaptation and sensory equalization as it is during the turning reaction.

Fatigue has a direct effect on the flight mechanism and would probably have a more pronounced effect than shown in this paper if the observations were carried out to a point of complete flight cessation.

With regard to the flight capacity, it appears that the initial flight rather than the total flight duration is the most important. While the total flight capacity remains relatively unchanged throughout the range of conditions used, the initial flight and flight velocity increased with the temperature and humidity, to an optimum under the conditions usually encountered during fair weather. Computations based on the experiments indicate that the Douglas-fir beetle is capable of flights up to 7 miles immediately following take-off. This is a most conservative estimate when one considers the fact that a number of individuals had their initial flight arbitrarily terminated after four hours, whereas

they may have flown considerably longer. Some may have flown for more than 8 hours. In addition some of the values for initial flight were taken from tests under sub-optimal conditions. From the evidence it seems a fair assumption that the Douglas-fir beetle is capable of an average initial flight, in still air, in excess of 10 miles and is capable of travelling 15 to 20 miles a day for several days. If one considers the enormous possibilities of dissemination by air currents the potential dispersal becomes astounding. We cannot overlook the fact that the beetles' flight is primarily one in search of suitable new host material. It appears as though it would be virtually impossible to isolate a population through silvicultural practice. It is necessary for a high concentration of beetles to make a successful attack before they are able to kill a tree, and this may be prevented by long distance flights diluting the population.

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