SEX ATTRACTION AND REPRODUCTIVE BIOLOGY OF *Lambdina fiscellaria lugubrosa* (LEPIDOPTERA: GEOMETRIDAE)

by

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ABSTRACT

The western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst.) was in the second year of epidemic conditions at Coquitlam Lake, B.C. in 1971 when attraction tests were run. More males were attracted to traps containing virgin females than to empty control traps, but only during the first half of the moth flight. Most moths were trapped in sample plots close to the lakeshore. Board and yellow carton "sticky" traps were superior to 3M-type and white carton traps. Behavioral observations suggest that a sex attractant may serve as an excitant as well as/or instead of an attractant, stimulating the male to searching activity.

Active release of sex attractant or "calling" occurred when terminal abdominal segments 8-10 were protracted, exposing an enlarged region in the intersegmental membrane between segments 8 and 9. Calling commenced 15 hours after the onset of the light period; copulation commenced 0.5 to 1.5 hours later and moths remained *in copulo* an average of 3.45 hours.

The highest degree of mating success occurred between 2-4 day-old males and females up to 4 days old. Peak oviposition occurred on the day after mating. Egg maturation was stimulated by mating. Mean longevity of mated and unmated females in the laboratory was 18.1 and 20.8 days respectively. Mating success was greatest at a 6:1, male to female sex ratio, and progressively less at a 1:1 and 1:6 sex ratio. Males mated only once within a 24-hr. period but were capable of multiple mating. Females would accept up to 3 spermatophores.

The internal reproductive system is typical of ditrysian type Lepidoptera. Mating resulted in the transfer of a single, plum-shaped spermatophore with a long collum. The spermatophore was placed in the

bursa copulatrix such that spermatozoa could exit through the aperture into the ductus seminalis.

A structure resembling known sex pheromone glands was elucidated by histological studies. The gland differs from that in other Lepidoptera, particularly in its paired structure and ventrolateral position.

ACKNOWLEDGEMENTS

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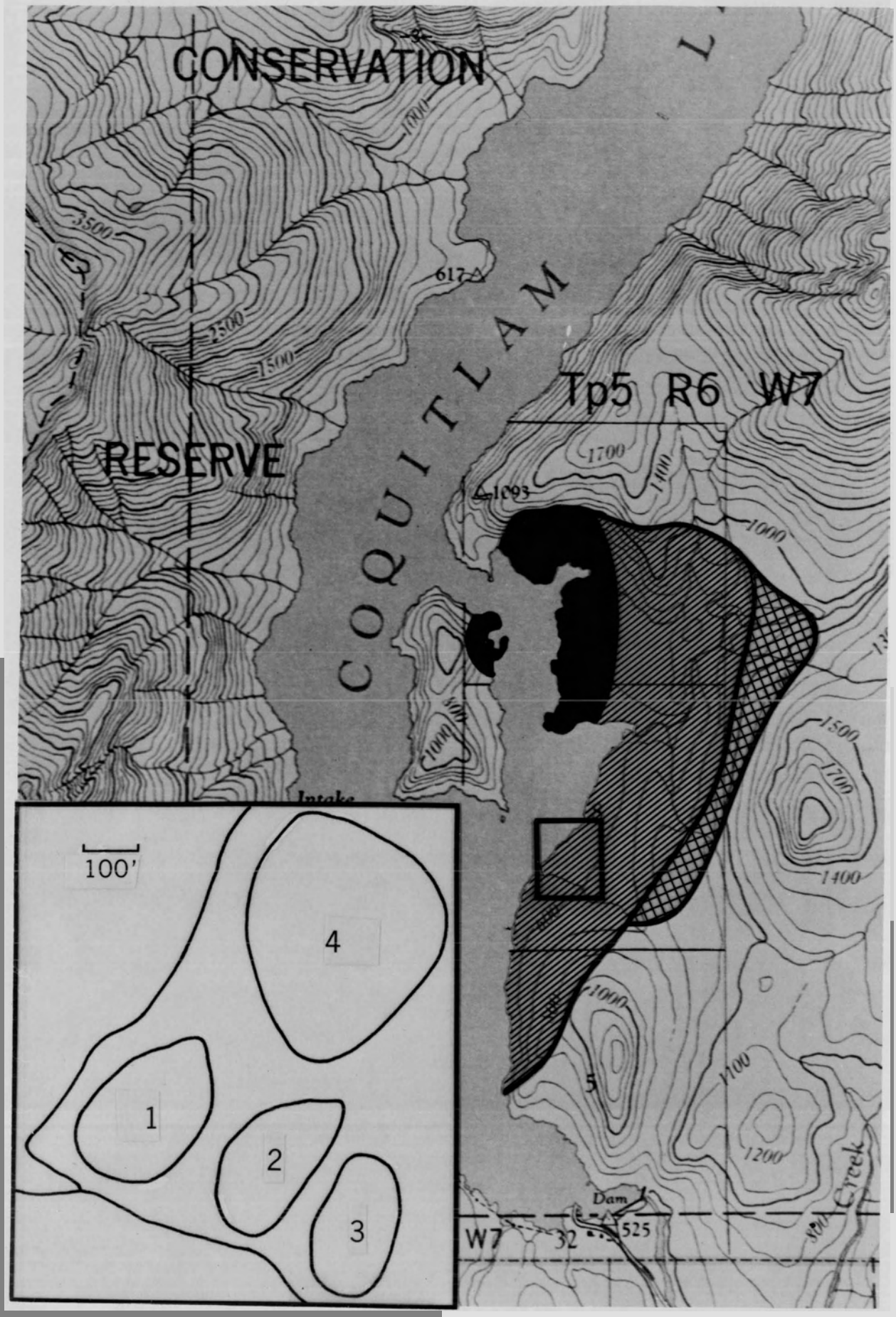
INTRODUCTION

The western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst.) and the eastern hemlock looper (*L.fiscellaria fiscellaria* Guenee) are serious defoliators of western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and balsam fir [*Abies balsamea* (L.) Mill.], respectively. In southwestern British Columbia, there have been 3 major outbreaks of *L.f. lugubrosa* on the mainland, which resulted in extensive tree mortality: 1911-13, in Stanley Park, Vancouver; 1928-30, from west of Howe Sound to Harrison Lake; and 1945-47, from Salmon Inlet to Stave Lake (Cottrell and Monts 1970). In 1970, moderate to severe defoliation occurred in 200 acres of western hemlock and amabilis fir [*Abies amabilis* (Dougl.) Forbes] on the east side of Coquitlam Lake (Allen and Koot 1971). Increased populations, severe defoliation, and some tree mortality occurred in the same area in 1971 (Fiddick 1971) with an extension of the defoliated area to 625 acres (Anonymous 1971) (Fig. 1).

The life history of the hemlock looper has been investigated by Hopping (1934) and Jardine (1969). It is univoltine. Eggs are laid from mid-September to mid-October, deposited singly onto lichen and moss on limbs and tree trunks. The larvae hatch in May to early June and feed first on the new needles. There are 5 larval instars, the fifth being the most damaging to foliage. Needles are often chewed off at the base. In severe infestations all the trees and much of the understory may be defoliated. Pupation occurs in mid to late August in bark crevices, under limbs, in crotches of limbs, and under extreme conditions of crowding, in the soil and in old decaying logs littering the forest floor. Adults emerge from early to late September.

Fig. 1. Western hemlock looper infestation levels in the Coquitlam Lake watershed in 1971 showing location of study area and plots. Light, medium and heavy infestation levels are indicated by cross-hatched, diagonal-lined and darkened areas, respectively.


CONSERVATION
RESERVE
COQUITLAM
Tp5 R6 W7
100'
4
1
2
3
Intake
Dam
W7
32
525
Creek

Sex pheromones may be useful in devising alternative strategies to insecticidal control of pest species. They have been demonstrated in the following forest Lepidoptera: *Choristoneura fumiferana* (Clemens) (Findlay and MacDonald 1966), *Dioryctria abietella* (Denis and Schiffermuller) (Fatzinger and Asher 1971), *Erannis aurantiaria* Hübner and *E.defoliaria* Clemens (Tvermyr 1969), *Estigmene acrea* (Drury)(MacFarlane and Earle 1970), *L.fiscellaria fiscellaria* (Otvos 1972), *Malacosoma disstria* Hübner (Strubble 1970), *Orgyia leucostigma* J.E. Smith (Percy, Gardiner and Weatherston 1971), *Porthetria dispar* (L.) (Collins and Potts 1932), *Rhyacionia buoliana* (Schiffermuller)(Pointing 1961), and *R.frustrana* (Comstock)(Berisford and Brady 1972; Wray and Farrier 1963). The pheromone compounds of some species are known, e.g. *C. fumiferana* (Weatherston, Roelofs, Comeau and Sanders 1971), and *P.dispar* (Bierl, Beroza and Collier 1972).

Sex pheromones can be used as trapping agents to manipulate populations in either of two ways (Shorey, Gaston and Jefferson 1968): 1) as direct trapping agents to survey insect populations (Daterman and McComb 1970; Dean and Roelofs 1970; Madsen and Davis 1971; Maksimovic 1964), or to mass-trap large numbers of individuals (Guerra, Garcia and Leal 1969; Roelofs *et al.* 1970); or 2) to disrupt orientation between sexes (Gaston, Shorey and Saario 1967; Sanders and Lucuik 1972; Shorey *et al.* 1972).

An understanding of reproductive biology and behavior of the insect species is essential before sex pheromones can be utilized in pest management. This information is available for only a limited number of forest Lepidoptera such as: *C.fumiferana* (Outram 1971a,b; Sanders 1971), *P.dispar* (Doane 1968), and *R.buoliana* (Pointing 1961).

Sex pheromone glands of several lepidopteran species have been described, yielding data on the source and production of the pheromone. The glands are characteristically associated with the intersegmental membrane between the eighth and ninth abdominal segments (Götz 1951). The gland is either a dorsal eversible sac (Jefferson, Shorey and Gaston 1966; Jefferson, Shorey and Rubin 1968), or a ventral eversible sac (Jefferson and Rubin 1970), but on occasion, may be a modified intersegmental membrane (MacFarlane and Earle 1970; Percy and Weatherston 1971; Percy *et al.* 1971). In the Geometridae, no sex pheromone glands have been located.

Published information on other Lepidoptera, particularly *L.f. fiscellaria* (Otvos 1972), suggested that females of *L.f.lugubrosa* could also attract males by secreting a sex pheromone. My objectives were to examine this hypothesis by investigating whether or not virgin female *L.f. lugubrosa* would attract males to traps, by observing mating behavior of both sexes before, during and after copulation, and by histologically examining females for the presence of a pheromone gland. Other objectives were: to determine the effect of age and varying sex ratio on mating ability and frequency; to determine the reproductive potential of females; and to elucidate the morphology of the female reproductive system.

FIELD TRAPPING WITH VIRGIN FEMALES

Materials and Methods

The study was conducted in an area of medium defoliation in a forest of old growth western hemlock and western red cedar (*Thuja plicata* Donn.) at the southeast end of Coquitlam Lake (49° 24' N latitude - 122° 47' W longitude)(Fig. 1). There was a dense understory comprising *Oplopanax horridum* (Sm.) Miq., *Rubus parviflorus* Nutt., *R.spectabilis* Pursh, and *Vaccinium parvifolium* Smith.

Four types of traps baited with virgin females were used. All were designed to catch moths on surfaces coated with Stickem Special[1]. Each had a 12-dram plastic snap cap vial suspended in the middle of the trap (Figs. 2-4). The vial, which served as a chamber for virgin females, allowed free air circulation through approximately 75, 1/16" diameter holes in the bottom and a cheesecloth-covered window in the cap. Each chamber was supplied with a glass tube containing a wick soaked in a 10% sucrose solution as food for the caged females.

The first type of trap consisted of 1/2 gallon, white, cylindrical cardboard food cartons, 19 x 13.5 cm (Fig. 2). Half of the lid and bottom of the cardboard carton was removed. The stickem-coated inner surface area of the trap was 650 sq. cm. The second type of trap was similar to the first type except that the outer surface was painted with yellow enamel (Humbrol 8). Yellow coloured traps have been reported to increase the number of trapped individuals of the apple maggot (Kring 1970) and black and western cherry fruit flies (Banham, unpubl.[2]). The third type of trap consisted

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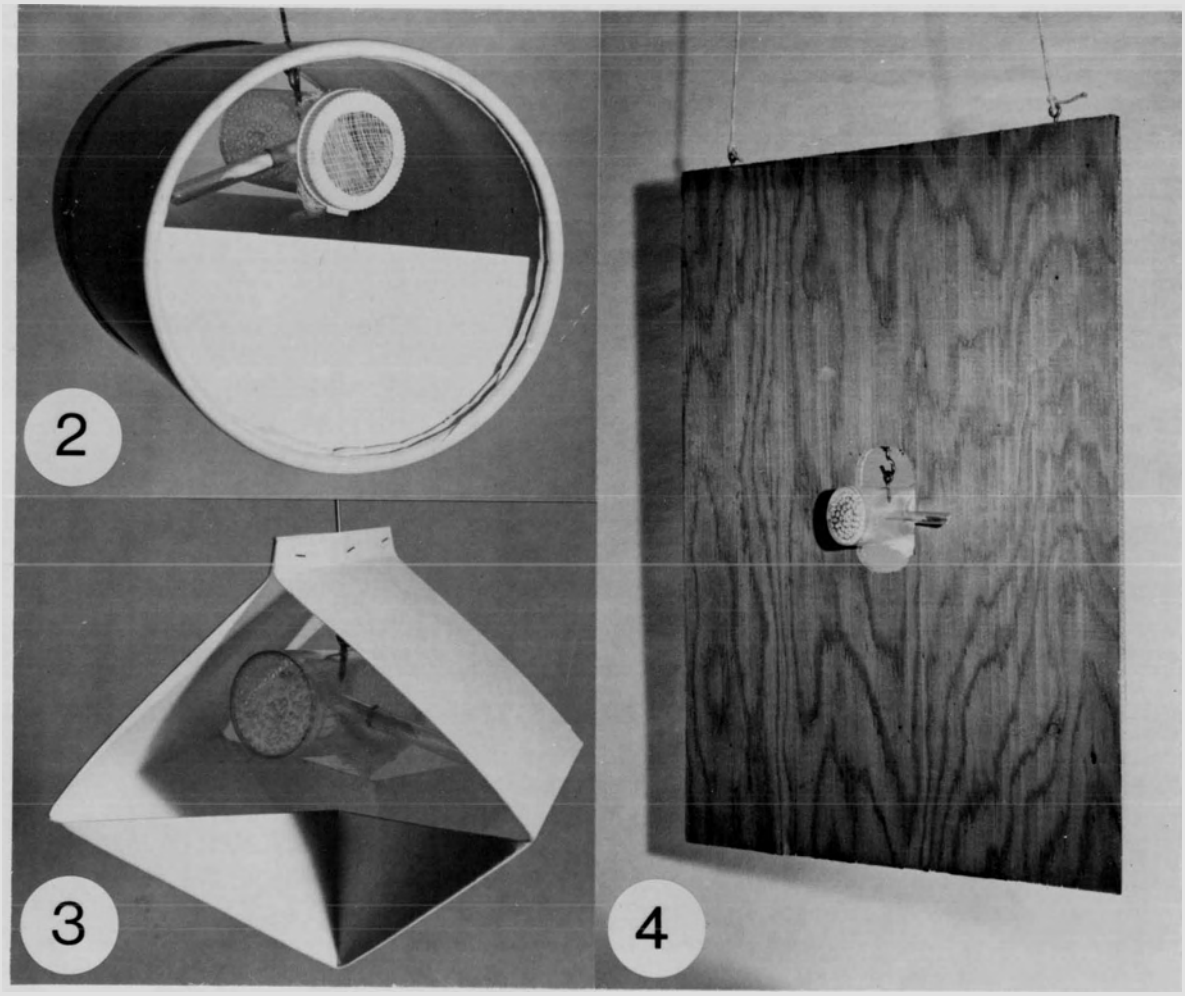
[1]Michel and Pelton Co., Manufacturing Chemists, Emeryville, California.

[2]F.L. Banham, report to Pool of Information on Fruit Pests. 1971 Research Summaries, Canada Department of Agriculture Research Station, Summerland, B.C.

Figs. 2-4. Sticky traps used for field trapping *L.f.lugubrosa*: 2, half gallon food carton; 3, modified 3M type trap; 4, board. Chamber used to confine virgin female hemlock loopers is suspended in each trap.


2
3
4

of an enlarged replica of the commercially produced 3M sectar trap[3] (Fig. 3). The inner, sticky surface area was slightly less than that of the cylindrical cardboard food carton. The fourth set of traps consisted of 3/8" plywood boards 30 x 43 cm with a 7.5 x 4 cm window in the centre in which the source chamber was suspended (Fig. 4). Both surfaces of the board were coated with Stickem Special.

The chamber in each experimental trap was baited with 3 female pupae obtained from fourth and fifth instar larvae reared on hemlock foliage under laboratory conditions. Traps were baited only once. Throughout the trapping season, each trap contained up to 3 virgin females. There was also a variable number of traps containing "calling" female moths during the collection periods. Chambers were not placed in the control traps.

The study area was divided into four roughly elliptical plots, 3 of which were approximately one acre in size and one plot approximately 3 acres in size (Fig. 1, insert). Elliptical plots eliminated possible bias from traps placed at the end of a linear sequence. Each plot contained 16 traps, 3 baited and one unbaited control of each type. Traps were suspended 1.5-2 m above ground on overhanging limbs and spaced approximately 25 m apart in the following sequence: Board, Yellow Carton, White Carton, White Carton Control, 3M, Board, Yellow Carton, Yellow Carton Control, White Carton, 3M, Board, Board Control, Yellow Carton, White Carton, 3M, 3M Control.

Traps were set in early September at the commencement of moth flight. The number of male moths caught was recorded every two days until the middle of October, the termination of moth flight.

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[3] 3M Co., St. Paul, Minnesota.

Additional trapping studies and behavioral observations of field populations were made during a single 24-hr. period on 7 September, 1972 at Mica Creek, British columbia.

Results and Discussion

Males were attracted in significant numbers by virgin females (Tables I-III), indicating that female *L.f.lugubrosa* may produce a sex pheromone.

All catches were recorded as number of individuals per 100 cm^2 of sticky surface because of the differences in sticky surface area between trap types. In all trap types there was a significant difference between catches in baited traps and control traps (Table I). The large board traps, when baited, caught the greatest number of moths. When adjusted for surface area, they were more effective than the 3M type or white carton traps, but were no more efficient than yellow carton traps (Table I). The open trap type may allow more effective dispersion of pheromone molecules, possibly attracting males from a greater distance. The exposed sticky surface of the board traps may be more effective than inside surfaces; since in some cases, males were observed to land on the outer surface of the closed traps before entering, and leave without entering. The yellow carton traps, which were more efficient than the white carton type traps (Table I), may have attracted male moths because of a response to the yellow color. The plain white carton recorded the lowest catches of the four trap types in both baited and control traps. There was no significant difference between catches when 1, 2, or 3 virgin females were in the chambers.

Traps in Plot 3 which was located approximately 170 m from the lakeshore caught the lowest number of moths (Table II). There were no significant differences between the remaining areas. These data indicate that most flight activity probably occurred near the lakeshore.

A highly significant difference between catches in baited traps

Table I. The effect of trap type on the mean catch of male *L.f.lugubrosa* in baited and unbaited traps in all sample plots at Coquitlam Lake, 1971.

Trap Type	Catch/trap/day/100 cm^2 sticky surface Baited[x]	Control[x]	Probability Level[x] Baited vs. Control
Board	.61 a	.28 a	***
Yellow Carton	.41 ab	.12 ab	***
3M	.38 bc	.19 a	*
White Carton	.28 c	.07 b	***
Mean for all traps	.43	.16	***

[x] All statistics, Mann-Whitney U Test modified for large sample sizes (Siegel 1956). Means followed by same letter not significantly different, $P<.05$. Probability levels: $P<.001$, ***; $P<.05$, *.

Table II. The effect of sample plot position on mean catches of male *L.f. lugubrosa* for all trap types at Coquitlam Lake, 1971.

Plot	Catch/trap/day/100 cm^2 sticky surface Baited[x]	Control[x]	Probability Level[x] Baited vs. Control
4	.56 a	.21 a	***
1	.49 a	.20 a	***
2	.40 ab	.11 a	***
3	.29 b	.14 a	**
Mean for all Plots	.43	.16	***

[x] All statistics, Mann-Whitney U Test modified for large sample sizes (Siegel 1956). Means followed by same letter not significantly different, $P<.05$. Probability levels: $P<.001$, ***; $P<.01$, **.

and control traps was recorded for the first 8 out of the 15 moth counts (14 September - 28 September) after which no significant difference occurred except for one collection (collection 14, on 10 October)(Table III). Early in the trapping season, virgin females in baited traps were apparently able to compete with field-emerged females. As the number of calling females in the field increased the virgin females in the traps possibly could not compete or ceased to release significant amounts of pheromone, as occurs in the gypsy moth (Richerson, pers. comm.[4]). Collections of adult moths in a sweep net during the time period of the first 8 counts revealed a decreasing male to female sex ratio (i.e. 25:0, 30:0, 20:1, 18:1, 10:1, 9:1, 6:1, and 3:1). The fourteenth collection (10 October) resulted in a significant difference in catches between baited and control traps (Table III). At this time, the field population of females was decreasing. Moreover, the females probably were releasing less pheromone if they had mated and were engaged in oviposition. Thus, virgin females in the traps could apparently again successfully compete for male moths.

Trapping of male moths with virgin females during one night, 7 September, at Mica Creek, B.C., resulted in no significant difference between catches in baited and unbaited traps. A possible explanation follows from the data in Table III. Moths were reported to have been flying for 2 weeks prior to 7 September and the field population of females was high. Thus, caged virgin females may not have been able to compete with females in the field. Males were active on tree trunks from ground level to 3 m, with

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[4] J.V. Richerson, Department of Entomology, Pennsylvania State University, University Park, Pennsylvania 16802.

Table III. Collection sequence of the mean catch of male *L.f.lugubrosa* in all trap types and sample plots combined at Coquitlam Lake, 1971.

Collection[+]	Catch/trap/day/100 cm^2 sticky surface Baited	Control	Probability Level[x] Baited vs. Control
1	.09	0	
2	.27	0	
3	.12	.02	***
4	.37	.03	***
5	.06	.03	***
6	.33	.10	*
7	.91	.13	***
8	.20	.06	*
9	.38	.18	
10	.80	.39	
11	.48	.37	
12	.30	.21	
13	.42	.45	
14	.67	.28	*
15	.06	.16	
Mean	.43	.16	***

[x] Mann-Whitney U Test modified for large sample sizes when $n_2 > 20$ (for collections 6-15)(Siegel 1956). Probability levels: $P < .001$, ***; $P < .05$, *.

[+] All collections at 2-day intervals from 14 September to 14 October except for collection 15 which occurred 4 days after collection 14.

the greatest activity concentrated at a level of up to 1 m. Female moths were observed calling from tree trunks. They are heavy-bodied and not easily disturbed and probably did not move far from their pupation sites. However, if disturbed they dropped to the ground rather than fly away as did males. Searching males walked rapidly up and down the tree trunks. The sex pheromone may serve as an excitant as well as or instead of an attractant, stimulating the male to search actively. Such a searching response, particularly when populations of females in the field were high, could explain the high catches in the unbaited control traps (Tables I-III) and in *L.f.fiscellaria* (Otvos 1972). Excited, searching males would blunder more frequently onto any sticky surface during their search as compared to non-stimulated males. Catches of *L.f.lugubrosa* in baited traps were lower than for such forest Lepidoptera as *Acleris variana* Fern. (R.F. Shepherd, pers. comm.[5]), *C.fumiferana* (Sanders 1971), *C.pinus pinus* Freeman (Sanders 1971), and *M.disstria* (Strubble 1970). This lower catch level may indicate a weaker pheromone than in other Lepidoptera or may support the hypothesis of a stronger excitatory than attraction function.

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[5]Pacific Forest Research Centre, Canadian Forestry Service, Department of the Environment, Victoria, B.C.

REPRODUCTIVE BIOLOGY OF *L.f.lugubrosa*

Materials and Methods

Experimental adult insects were obtained by two rearing methods. Larvae emerging from eggs, held at 0°C for 17 weeks to break diapause, were reared on an artificial diet (McMorran 1965) at 22°C and 80% relative humidity for the first two instars. Third instar larvae were transferred to hemlock foliage and reared to adulthood at 22°C and 80% R.H. Alternatively, third and fourth instar larvae were field collected and reared in the laboratory on hemlock foliage. Sexes were identified and separated at the pupal stage.

Six cages, each 24 x 16 x 4 cm were used for observation of mating behavior, i.e. pre-copulatory and copulatory movements, female "calling" position and diel periodicity. Cylinders of dental cotton wicks soaked with a 10% sucrose solution were supplied as food sources for the emergent adult moths. The front of the cage was made of plexiglass and the back of the cage was covered with a double layer of cheesecloth to provide oviposition sites for females. A red light behind the cages allowed observation of nocturnal behavior.

The cages were held in a growth chamber at 20°C, 60% R.H., and a diel light cycle of 14L:10D for the life span of the moths. One pupa of each sex was placed in each cage and, following emergence, adult behavior was observed for 10 days. Periods of observation commenced 2 hours prior to the onset of darkness and continued until 2 hours after the onset of light. Courtship and copulatory positions were recorded photographically[6].

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[6] 35 mm Kodak Panatomic X Film, Asahi Pentax Spotmatic camera with 50 mm/F4 Takumar Lens.

Mating and spermatophore transfer were investigated with moths held in 50 cages made from 1/2 gallon Sealrite food cartons[7], with both ends replaced with cheesecloth. Each cage was stocked with a pair of 1-4 day old moths. The cages were held at 20°C, 50% R.H. and a diel cycle of 12L:12D. Cages were checked every 15 minutes during the dark period and the initiation and duration of mating recorded. Upon termination of mating, a female was removed and its abdomen was excised and placed in a vial containing Benz's (1969) Preservative. The number and size of spermatophores were determined by dissection of the bursa copulatrix.

The effect of age on mating success was investigated by pairing all combinations of the following age classes: < 0.5, 1, 2, 4, and 8-day old males and females. Each combination had 20 replicates of one pair per cage. The cheesecloth cage-end served as an oviposition site. Each pair was confined overnight (18 hours) at 20°C and 50% R.H. Males were then removed and females left to oviposit. Eggs laid were counted daily, and new cheesecloth was supplied. Upon death of the female, the bursa copulatrix was dissected to determine spermatophore transfer.

The effect of sex ratio on mating frequency, was determined by combining 6 males and 6 females, 6 males and one female, and one male and 6 females in 26 x 42 x 26 cm cages on the day of emergence. There were 60 cages, 4 groups of 5 each per combination. Females from the first group of 5 cages for each combination were removed after 10 hours and their abdomens excised and preserved in Benz's (1969) Preservative. The females were

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[7]Crown Zellerbach Co., New Westminister, B.C.

removed from the remaining cages after 2, 4, and 6 days. The number of times a female had mated was determined by dissecting the bursa copulatrix and counting the spermatophores. Dissections of 1-2 day-old females were made to determine the internal reproductive anatomy, spermatophore position, and the potential egg complement.

Results and Discussion

Mating Behavior

Active release of sex attractant or "calling" (Doane 1968; Fatzinger and Asher 1971; Strubble 1970) is a necessary preliminary to the copulatory behavior of adult moths. Females characteristically emerged from the pupal stage shortly after the onset of darkness and were capable of assuming the calling position that same night. In preparation for calling, female *L.f.lugubrosa* clung to either the sides or top of the cage. Wings were held vertically over the body. Terminal abdominal segments 8-10, which are normally retracted within the seventh segment, began to protract (Fig. 7). Upon full extrusion (Fig. 8), the female began a slight rhythmical protraction and retraction of the terminal segments. There appeared to be a pumping action into the protracted segments causing a swelling in the intersegmental membrane (Fig. 8). Only females with the terminal abdominal segments fully protracted were considered to be calling. Some females retracted the last segments briefly, often on readjustment of calling position, change of area, or when disturbed by the activity of the male. Other females ceased calling and relaxed into a resting position but some started calling again before the lights switched on. The majority of the females maintained the calling position without interruption, some until the end of the dark period. The calling position of *L.f.lugubrosa* differed from that described for other Lepidoptera (Doane 1968; Leppla 1972; Percy *et al.* 1971; Sanders 1969; Strubble 1970).

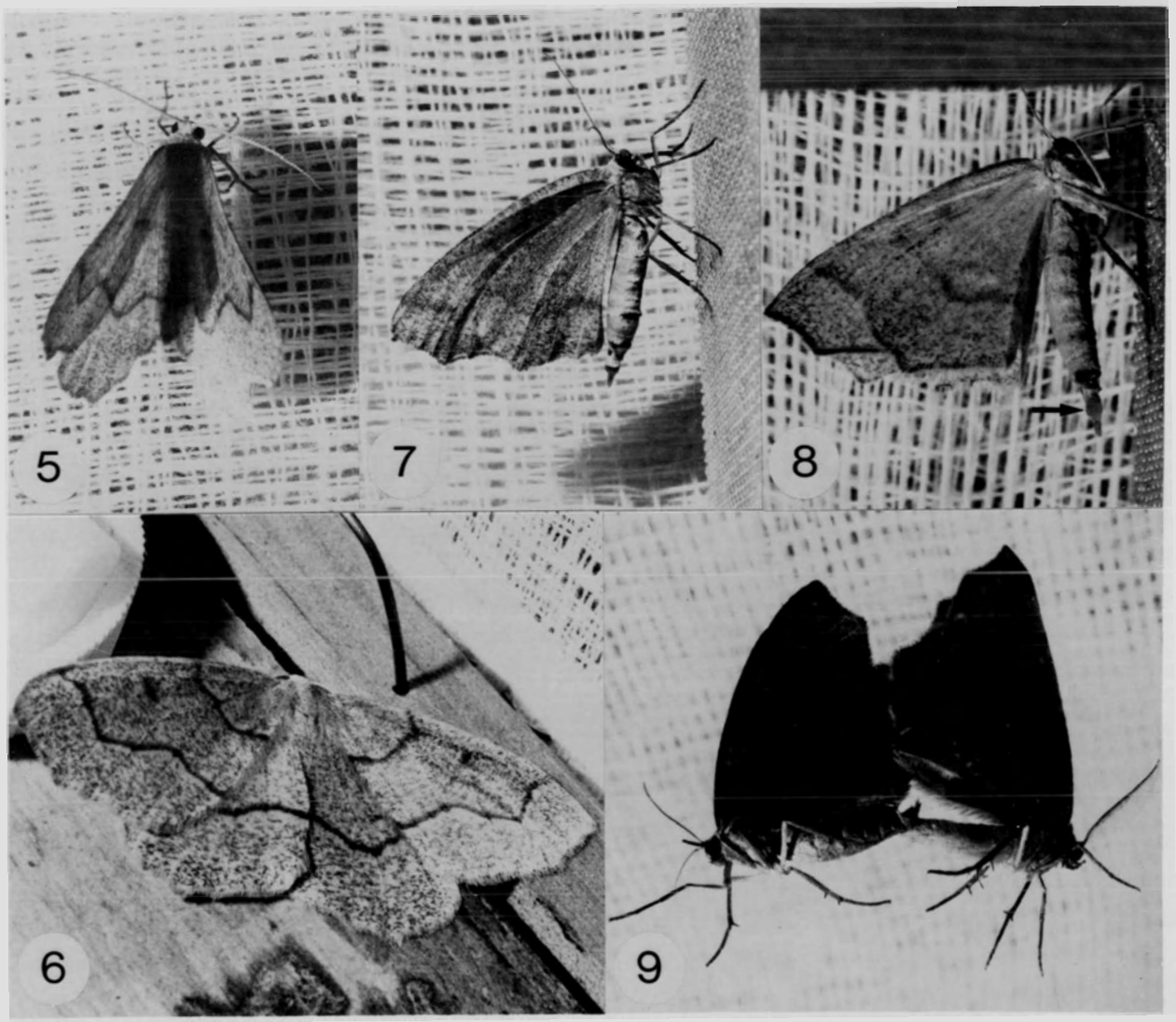
At night, except for brief periods of activity, males usually remained in a resting position (Fig. 5) with the wings held in a V at an approximate angle of 60^{o} above the horizontal and the antennae directed

Figs. 5,6. Resting positions of male *L.f.lugubrosa*: 5, in the dark; 6, in the light.

Fig. 7. Female *L.f.lugubrosa* immediately prior to assuming calling position. Note last few segments slightly protracted.

Fig. 8. Calling female *L.f.lugubrosa* with terminal abdominal segments fully protracted. Arrow indicates suggested location of the sex pheromone gland.

Fig. 9. *L.f.lugubrosa in copulo*. Male on the right, female on left.


5
7
8
6
9

posteriorly 45° from the body midline. This position differs from the one assumed by both sexes during daylight hours (Fig. 6) when the wings are held horizontally on the substrate with the linear pattern of the mesothoracic wings meeting that of the metathoracic wings and the antennae directed posteriorly beneath the wings. When the male perceived the calling female the following sequence of activity occurred in rapid succession in less than 2 minutes: 1) the antennae were brought forward and vibrated alternately with increasing rapidity, "fanning" the air, (2) the wings were vibrated from a 90° to 45° plane with increasing frequency, (3) the male started walking in a highly agitated manner. When the male came within 1-2 cm of a receptive female, the 2 insects faced each other and engaged in slight antennal "fencing". The male circled the female and tapped her abdominal segments alternately with one antenna and then the other. The male, with abdomen arched downwards and claspers visible, proceeded forward to a position alongside the female, curved his abdomen toward the abdominal tip of the female and quickly seized her with the exposed claspers. The pair, *in copulo* moved directly into a position with heads facing in opposite directions and the wings held vertically over the body (Fig. 9). The pair remained motionless for the duration of copulation. Immediately prior to separation, the female began walking, dragging the male behind her until the male released her. The male remained motionless for approximately 5 minutes following separation, with the copulatory apparatus still visible. The female moved about and, in some instances, began to oviposit almost immediately.

Antennal contact with the terminal segments of the calling female

did not always precede copulation. Shorey (1964) suggests that such contact may serve to perceive high concentrations of a pheromone stimulus until the effective level of excitation necessary to release the copulatory act had been reached.

Under laboratory diel light cycles of 14L:10D, where the dark period occurred at 2130 hours, female *L.f.lugubrosa* demonstrated a distinct periodicity of calling (Fig. 10). The calling commenced at 2145 hours, peaked 4 hours later and by 0445 hours all calling had ceased. A 24-hr. observation of moths in the field at Mica Creek in early September 1972, disclosed similar activity cycles. Caged virgin females began calling at 2200 hours with a peak activity 3 1/2 hours later and ceased calling by 0500 hours. Photoperiod under these conditions was 12L:12D (sunrise at 0700 hours and sunset at 1900 hours).

Sanders and Lucuik (1972) showed that onset of the previous light period acts as a cue for the start of calling in *C.fumiferana*. This stimulus may also be used by the hemlock looper. Under laboratory conditions (14L: 10D), calling commenced at 2145 hours while under field conditions (12L:12D, with sunrise at 0700 hours) calling commenced at 2200 hours. In both cases calling commenced approximately 15 hours after the onset of the light period.

Copulation commenced 0.5 to 1.5 hours after the onset of calling, with peak mating occurring between 1.5 and 2 hours after the peak calling period (Figs. 10,11). Fifty mating pairs were *in copulo* an average time of 3.45 $\pm$1.32[8] hours (range, 0.5 to 7 hours)(Fig. 12).

Effect of Age on Mating Ability

Table IV indicates the mating success of *L.f.lugubrosa* at different

[8]All means reported in text followed by $\pm$ one standard deviation.

Fig. 10. Time of initiation of calling behavior by female *L.f.lugubrosa* after lights-off at 2100 hours, measured for 6 females at 15 minute intervals throughout the dark period, for 10 days. Total of 38 incidences of calling initiation. Diel light cycle, 14L: 10D.

Fig. 11. Time of initiation of copulation of 50 *L.f.lugubrosa* pairs after lights-off at 1930 hours, examined at 15 minute intervals during the dark period of a 12L:12D diel light cycle.

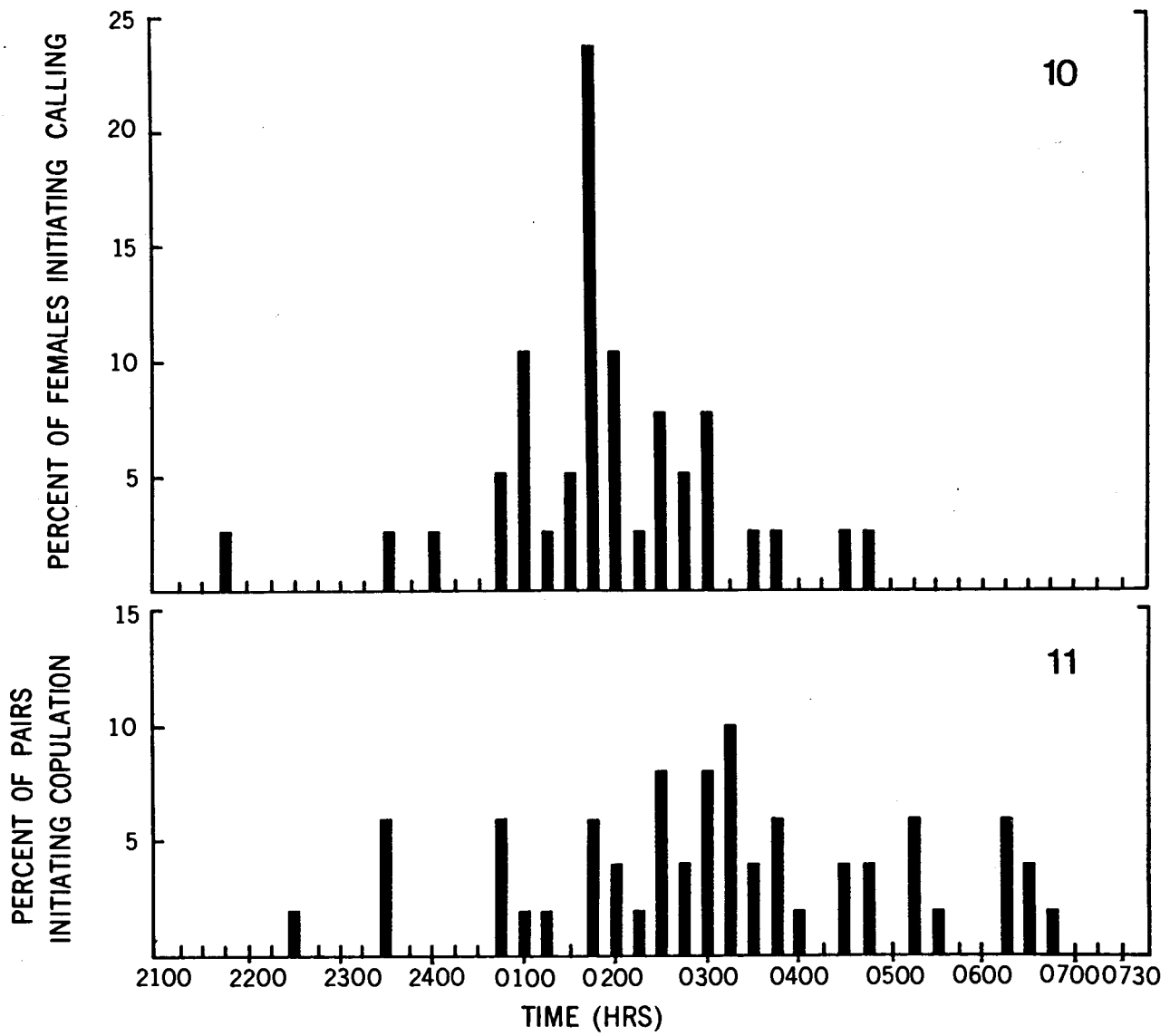

PERCENT OF FEMALES INITIATING CALLING
25
20
15
10
5
10
PERCENT OF PAIRS INITIATING COPULATION
15
10
5
11
2100
2200
2300
2400
0100
0200
0300
0400
0500
0600
0700
0730
TIME (HRS)

Fig. 12. Percentage of 50 *L.f.lugubrosa* pairs remaining *in copulo* for time periods measured at 15 minute intervals during the dark period of a 12L:12D diel light cycle.

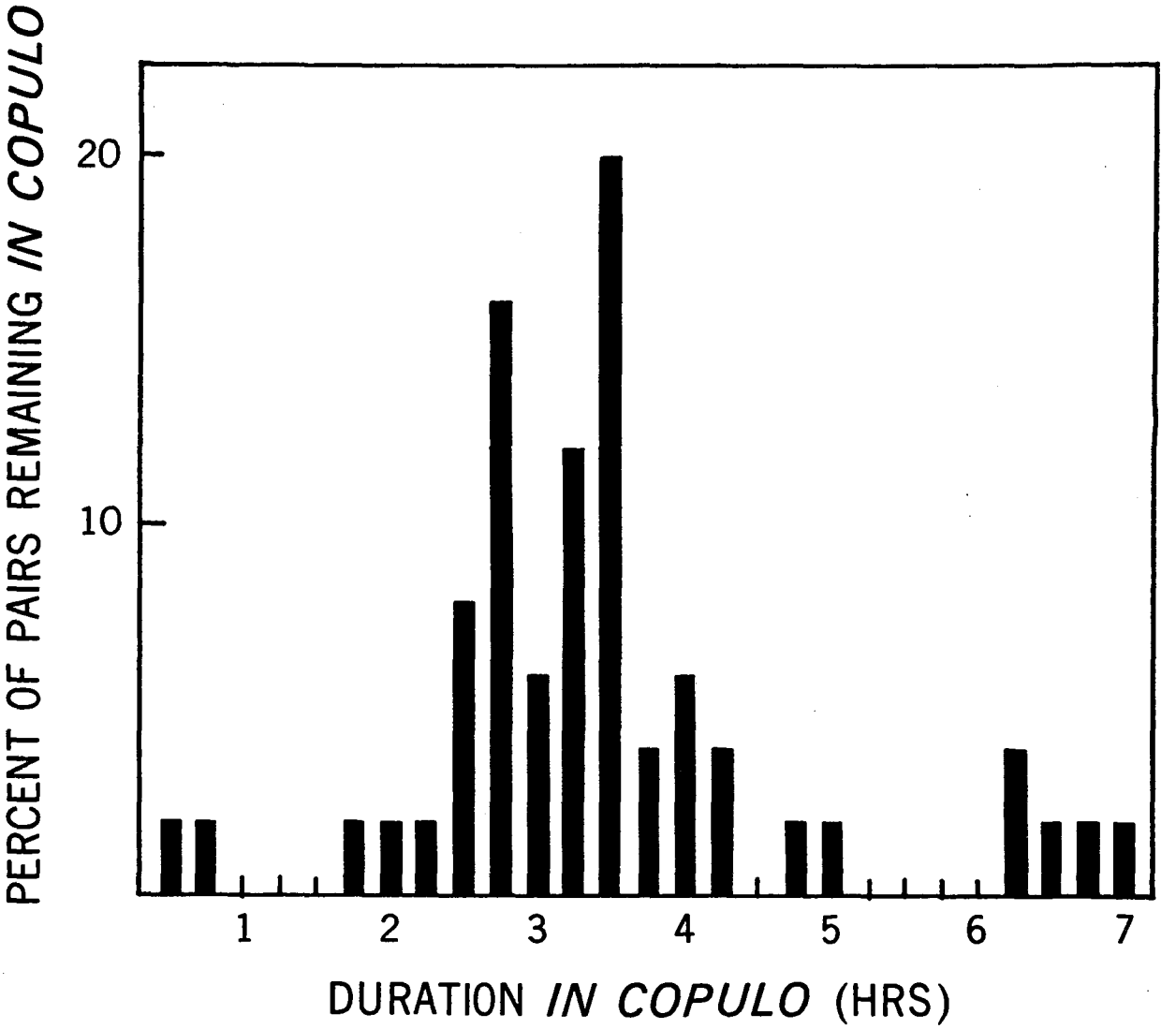

PERCENT OF PAIRS REMAINING *IN COPULO*
20
10
1
2
3
4
5
6
7
DURATION *IN COPULO* (HRS)

Table IV. Mating success of *L.f.lugubrosa* at different male and female age combinations as expressed by the number of females inseminated out of 20 replicates. Diel light cycles 12L:12D.

Male Age (Days)	Female Age (Days)					Total
	0.5	1	2	4	8	
0.5	3	0	0	3	0	6
1	12	12	13	9	2	48
2	18	16	10	13	6	63
4	15	16	16	14	6	66
8	6	8	14	13	-	41
Total	54	52	53	52	14	

age combinations. Females were able to mate immediately after emergence with a drop in frequency of mating at 8 days of age. Few males less than 0.5 days old mated. Mating increased sharply after one day and reached a peak in 2-4 day-old males. The highest degree of mating success occurred between 2-4 day-old males and females up to 4 days old.

Peak oviposition by fertilized females occurred on the day after mating (Fig. 13). Increased age of females before mating resulted in more eggs being laid immediately after mating. In all cases where females were mated, 90% of the eggs were deposited within 6 days after mating. Unmated females survived longer than mated females (Fig. 14), possibly because of the availability of metabolic reserves which would otherwise have been utilized in oogenesis and yolk production. The mean longevity of mated and unmated females respectively was 18.1 $\pm$3.8 and 20.8 $\pm$3.8 days (significant difference, t-test, $P<.005$). Unmated females, 1-2 days old, contained a primary stock of approximately 80 eggs. Unmated females oviposited a mean total of 74.5 $\pm$32.6 eggs. However, mated females of the same age oviposited significantly more eggs per female (Table V). As in *Zeiraphera diniana* (Guenee)(Benz 1969), mating stimulated oviposition and apparently indirectly stimulated egg maturation.

Effect of Sex Ratio on Mating Frequency

The low number of spermatophores transferred within the first 24 hours of emergence indicated the lack of successful matings during this period (Table VI). Mating activity increased on the second day after emergence and reached a maximum on the sixth day. The mean number of spermatophores transferred per male was greatest when there were 6 times as many females as males present (1:6 male to female sex ratio), indicating that males tended

Fig. 13. Number of eggs laid per day by female *L.f.lugubrosa*. Mated females were <0.5, 1, 2, 4, and 8 days old prior to being paired with a male for 24 hours. Diel light cycle, 12L:12D. All age groups combined for unfertilized females.

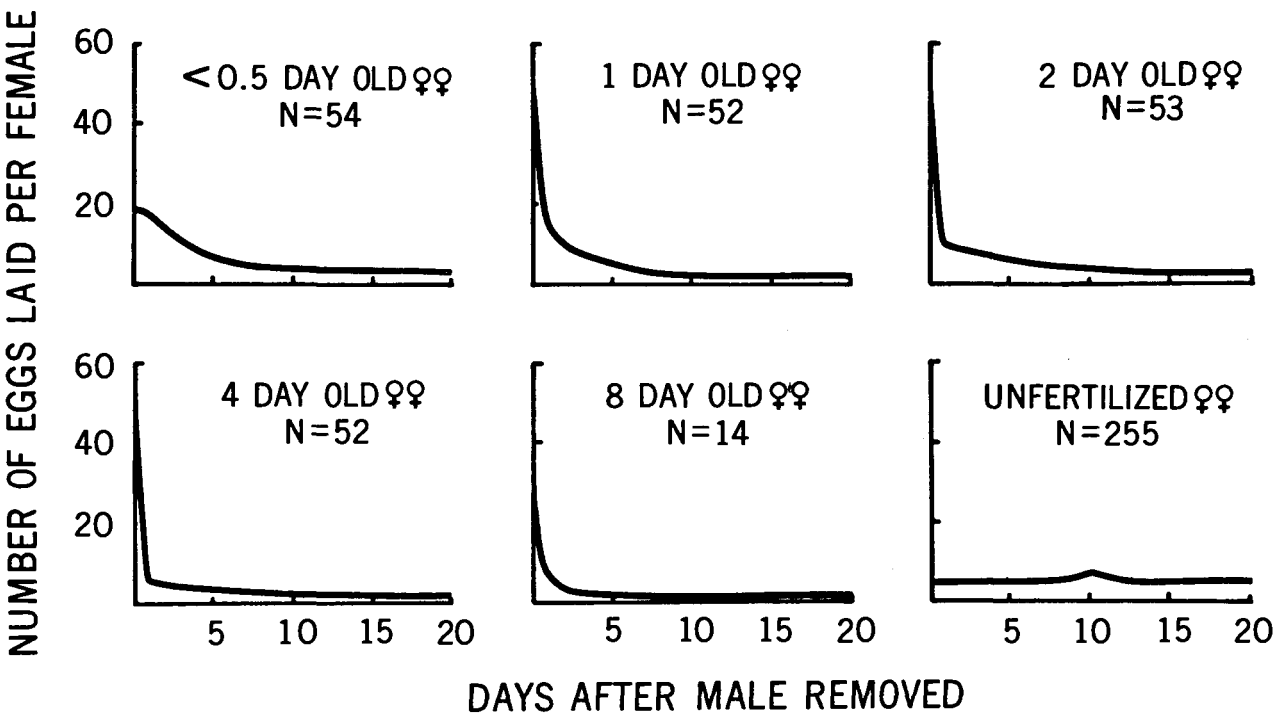

NUMBER OF EGGS LAID PER FEMALE
60
40
20
<0.5 DAY OLD ♀♀
N=54
1 DAY OLD ♀♀
N=52
2 DAY OLD ♀♀
N=53
4 DAY OLD ♀♀
N=52
8 DAY OLD ♀♀
N=14
UNFERTILIZED ♀♀
N=255
5
10
15
20
DAYS AFTER MALE REMOVED

Fig. 14. Survivorship of 225 mated and 255 unmated female *L.f.lugubrosa*. Diel light cycle, 12L:12D.

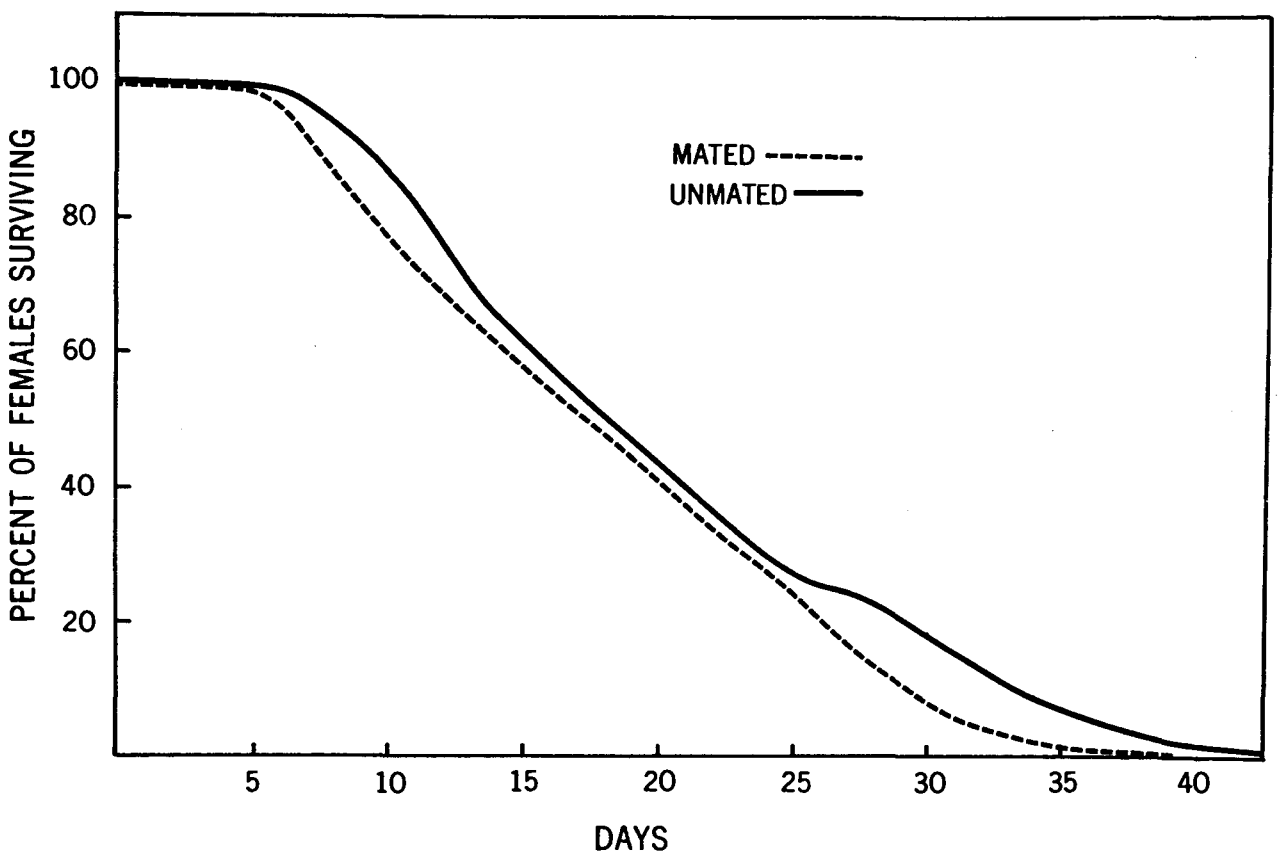

PERCENT OF FEMALES SURVIVING
100
80
60
40
20
MATED
UNMATED
5
10
15
20
25
30
35
40
DAYS

Table V. Number of eggs in mature females and total fecundity by mated and unmated *L.f.lugubrosa*. All females 2 days old or less at time of dissection or start of observation period.

No. of eggs per Female	Number of Females Occurring in Each Egg Class		
	Dissected	Ovipositing	
	N=70	Unmated N=141	Mated N=159
< 20	-	5	2
21-40	6	12	2
41-60	13	36	10
61-80	16	31	23
81-100	20	23	28
101-120	14	21	31
121-140	1	9	36
141-160	-	4	17
161-180	-	-	4
181-200	-	-	5
>200	-	-	1
Mean no. of eggs/Female	79.2 ±24.4	74.5 ±32.6	108.8[x] ±36.4

[x] Number of eggs laid by mated females significantly greater than those laid by unmated females, t-test, $P < .001$.

Table VI. Effect of different sex ratios on mating frequency of female *L.f.lugubrosa*, based on spermatophore counts. Five replicates for each sex ratio per day. Diel light cycles, 12L:12D.

Sex Ratio ♂ : ♀	Days after emergence	No. of Females with indicated no. of spermatophores				Percent of Females Mated
		0	1	2	3	
1:1 (6 ♂♂ : 6 ♀♀)	1	26	4	0	0	13.3
	2	15	15	0	0	50.0
	4	5	22	2	1	83.3
	6	1	17	10	2	96.7
	Total	47	58	12	3	
6:1	1	4	1	0	0	20.0
	2	0	4	1	0	100.0
	4	0	4	1	0	100.0
	6	0	5	0	0	100.0
	Total	4	14	2	0	
1:6	1	30	0	0	0	0
	2	27	3	0	0	10.0
	4	21	9	0	0	30.0
	6	17	12	1	0	43.3
	Total	95	24	1	0	

to mate more frequently when unmated females were present (Table VII). Similar results were obtained in other Lepidoptera (Dustan 1964; Gehring and Madsen 1963; Outram 1971b). Some mated females remained receptive to males and contained 2 or 3 spermatophores in the bursa copulatrix (Table VI). This observation corroborates data from field collections at Mica Creek, B.C., on 7 September 1972, in which some females contained up to 3 spermatophores. Percent of successfully mated females was greatest at a 6:1 and least at a 1:6 male to female sex ratio (Table VI). As the duration of copulation averaged 3.45 hours, a recovery period similar to that in *C.fumiferana* (Outram 1971b) was probably necessary for the secretion of new spermatophore material. It is probable that males of *L.f.lugubrosa* did not mate more than once per 24-hr. period. In cases where more than one spermatophore was transferred by a single male (i.e. in a 1:6 male to female sex ratio), the average spermatophore dimensions were: corpus length, 1.19 $\pm$.1 mm; corpus diameter, .87 $\pm$.2 mm; and collum length, 2.87 $\pm$.3 mm, significantly less in all dimensions (t-test, $P<.005$) than when only one spermatophore was transferred. Apparently, later spermatophores transferred are smaller than the first, as was found in *C.fumiferana* (Outram 1971b) and *Grapholitha molesta* (Busck)(George and Howard 1968).

Morphology of the Spermatophore and the Female Reproductive System

Each of the 50 mated females contained one well formed spermatophore in the bursa copulatrix (Fig. 15) except for 2 females which terminated copulation after 30 and 45 minutes respectively and contained no spermatophores. The spermatophore has a long collum fitting into a groove along the side of the plum-shaped corpus (Fig. 16). The average dimensions of 50 spermatophores measured were: corpus length, 1.42 $\pm$.2 mm; corpus width,

Table VII. Effect of different sex ratios on spermatophore transfer of male *L.f.lugubrosa*, based on spermatophore counts. Five replicates for each sex ratio per day. Diel light cycles, 12L:12D.

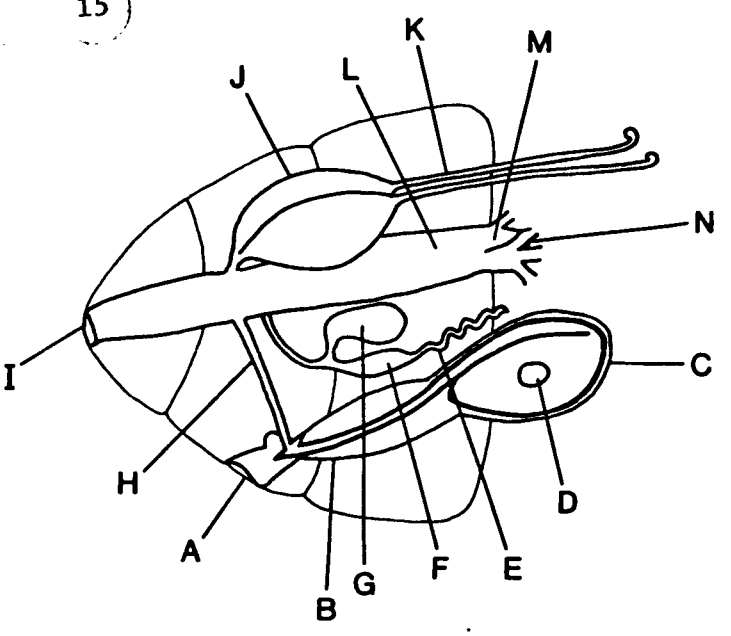
Sex Ratio ♂ : ♀	Days after emergence		Total spermatophores transferred	Mean spermatophore per male
1:1 (6♂♂:6♀♀)	1		4	.13
	2		15	.50
	4		29	.97
	6		43	1.43
		Total	91	
6:1	1		1	.03
	2		6	.20
	4		6	.20
	6		5	.17
		Total	18	
1:6	1		0	0
	2		3	.60
	4		9	1.80
	6		14	2.80
		Total	26	

Figs. 15,16. Lateral view of the posterior region of the reproductive system of female *L.f.lugubrosa* with spermatophore *in situ* (Fig. 15), and removed from the bursa copulatrix (Fig. 16). Structures are as follows:

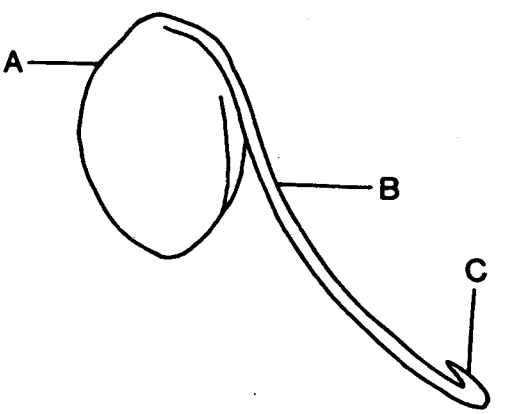
Fig. 15, A, ostium bursae; B, ductus bursae; C, bursa copulatrix; D, signum; E, spermathecal gland; F, utriculus of spermatheca; G, lagina of spermatheca; H, ductus seminalis; I, ostium oviductus; J, accessory gland reservoir; K, accessory gland; L, common oviduct; M, lateral oviduct; N, calyx.

Fig. 16, A, corpus of spermatophore; B, collum; C, aperture and frenulum of spermatophore.

15



16



1.05 ±.1 mm; and collum length, 3.25 ±.2 mm.

The terminology used in this description follows that of Callahan and Chapin (1960). The corpus lies within the bursa copulatrix with a small amount of white viscous material adhering to the lower portion of the corpus. According to Callahan and Chapin (1960) and Outram (1971a) this material is the residue of the spermatophore precursor which has been constricted off by the heavy muscular area of the cuticular simplex of the male. The collum extends the full length of the ductus bursae and is held by a frenulum such that the aperture, through which sperm escape, leads into the ductus seminalis. As in some other Lepidoptera (Callahan and Chapin 1960), the frenulum maintains the contiguity of the aperture and ductus seminalis, whereas in *C.fumiferana*, contiguity is maintained by a spring-like action of a loop in the collum (Outram 1971a).

The female has 2 external openings directly concerned with reproduction. As typical for ditrysian type Lepidoptera (Imms 1957), the ostium oviductus, occurring on sternite 9 just below the anus, serves as the opening for oviposition. The ostium bursae, on sternite 8, is the opening for the transfer of the spermatophores into the bursa copulatrix (Fig. 15). Spermatozoa probably migrate down the ductus seminalis to the ostium oviductus (Williams 1941) where the accessory gland and spermathecal gland also open (Fig. 15). Presumably spermatozoa can be utilized for immediate fertilization of ova or may migrate to the spermatheca and be stored for later fertilization.

A SEX PHEROMONE GLAND IN *L.f.lugubrosa*

Materials and Methods

Abdomen tips were forcibly extruded and excised from 1-2 day-old virgin females, fixed in alcoholic Bouin's solution and dehydrated in ethanol. The tissue was softened and cleared in methyl benzoate and 1% celloidan in methyl benzoate solution (Percy *et al.* 1971), infiltrated under vacuum with Tissuemat and embedded in Paraplast. Sections were made at 5 microns and stained with Mallory's triple stain (Humasson 1967). Photographs were taken with a Zeiss Ikon 35 mm camera mounted on a Carl Zeiss microscope.

Results and Discussion

Extrusion of the terminal abdominal segments by calling female *L.f.lugubrosa* (Figs. 7,8) suggested that an intersegmental membrane is exposed through which a sex pheromone may be secreted as was described by Percy *et al.* (1971) in other Lepidoptera. Paired glands and reservoirs were found situated ventrolaterally in the eighth segment and were presumed to be the pheromone glands. The gland itself (Figs. 17-19) consists of a single, uniform layer of goblet-shaped glandular cells (Figs. 19,20) resting on a basement membrane (Fig. 19), similar to those described by Percy *et al.* (1971). There is a large lumen between the glandular cells and the uniform, dark-staining cuticle of the eighth abdominal segment. Under microscopic examination of whole abdomens, the intersegmental membrane between segments 8 and 9 can be seen to extend anteriorally as ventral folds between the sclerites of the eighth abdominal segment posterior to the sternite of the ostium bursae. These ventral folds are also present in sectioned preparations

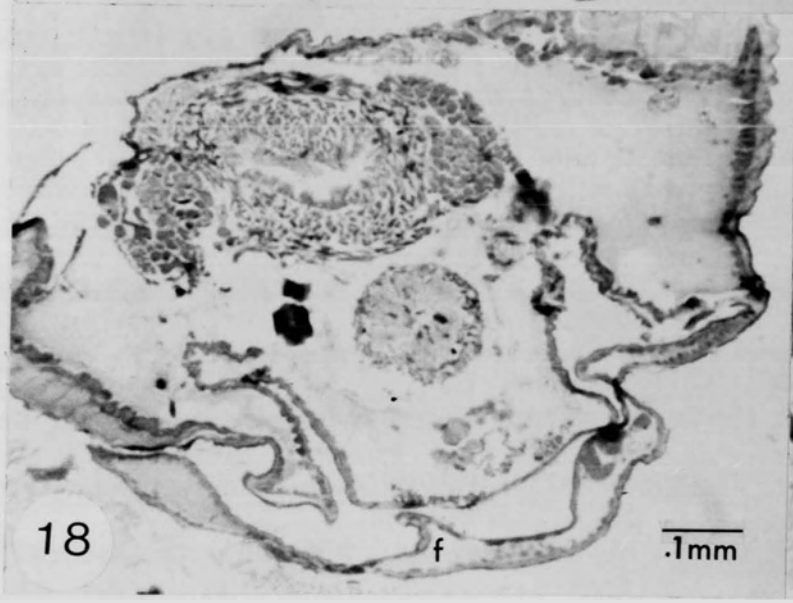
Figs. 17,18. Cross-sections of eighth abdominal segment of *L.f.lugubrosa* showing position of possible sex pheromone gland (g)(Fig. 17), and anterior ventral fold (f)(Fig. 18).

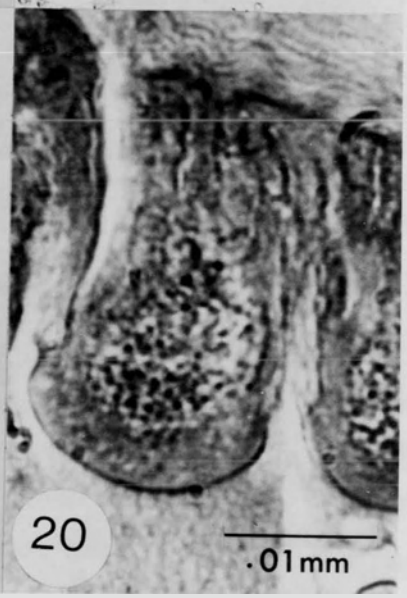
Fig. 19. Cross-section through one side of possible pheromone gland to show arrangement of the modified epidermal cells. c, cuticle of eighth abdominal segment; e, glandular epithelium; l, lumen.

Fig. 20. Goblet-shaped glandular cells.


g
g
17
.2 mm


c
l
e
19
.1mm


18
f
.1mm


20
.01mm

and extend ventrally from the glands and their reservoirs (Fig. 18).

The calling position of female *L.f.lugubrosa* exposes a swelling between segments 8 and 9, exterior to the paired glands (Fig. 17) and involving the ventral folds of the intersegmental membrane (Fig. 18). Therefore, I hypothesize that the glands identified in histological sections represent the pheromone glands of female *L.f.lugubrosa*.

According to Götz (1951), pheromone glands have originated from an intersegmental fold typically situated between abdominal segments 8 and 9, and occur in one of 5 types: displaceable scent field, protrusible scent ring, protrusible scent fold, protrusible scent sac, or paired glandular ducts penetrating deep into the eighth abdominal segment. The placement between the eighth and ninth abdominal segments is consistent with almost all Lepidoptera examined to date. Jefferson and Rubin (1970) described the pheromone gland of the noctuid *Prodenia litura* (F.) as a single eversible sac of glandular epithelium situated ventrally in the intersegmental membrane similar to that in *P.ornithogalli* Guenee. In *Autographa californica* (Speyer) and *Rachiplusia ou* (Guenee) the sex pheromone gland can occur as either an eversible sac or eversible fold situated dorsally in the intersegmental membrane (Jefferson *et al.* 1968). A similar eversible sac of glandular epithelium occurs in *Pseudoplusia includens* (Walker), *Spodoptera exigua* (Hübner) and *Feltia subterranea* (F.) (Jefferson *et al.* 1968), and *Trichoplusia ni* (Hübner)(Jefferson *et al.* 1966). In *Heliothis zea* (Boddie), *H.virescens* (F.), and *H.phloxiphaga* Grote and Robinson, the sex pheromone gland is a complete ring of glandular epithelium between the eighth and ninth abdominal segments (Jefferson *et al.* 1966). Percy and Weatherston (1970) described pheromone glands in 3 forest•

Lepidoptera: a modified intersegmental membrane appearing as a dorsal saddle in *C.fumiferana*, a similar gland with a different arrangement of dorsal folds in *C.pinus pinus*, and a large, smooth glandular dorsal saddle in *M.disstria*. In *O.leucostigma*, the pheromone gland is crescent-shaped and located dorsally in the intersegmental membrane (Percy, Gardiner and Weatherston 1971). The gland in *L.f.lugubrosa* is the first described in the family Geometridae, and differs from that in other Lepidoptera, particularly in its paired structure and ventrolateral position.

CONCLUDING DISCUSSION

This study has demonstrated sex attraction in *L.f.lugubrosa*, disclosed a structure characteristic of known lepidopteran pheromone glands, and elucidated the reproductive biology. These data may be useful in the development of a pest management system.

Females attract males in the field (Tables I-III) and begins mating soon after emergence (Table IV) but if not mated, will continue to attract males to traps (Table III). Calling behavior (Figs. 7,8) and what is hypothesized to be a pheromone gland (Figs. 17-20) are fairly typical of Lepidoptera. The periodicity of *L.f.lugubrosa* in the laboratory (Figs. 10, 11) and field observations indicate the periods of peak activity and the times at which behavioral manipulation could possibly be successful.

As practiced or proposed for other species, sex pheromones may play an important role in: monitoring population levels and the onset of flight activity (Madsen and Davis 1971), detecting populations at low density levels (Collins and Potts 1932; Daterman and McComb 1970; Dean and Roelofs 1970), mass trapping males (Guerra, Garcia and Leal 1969; Roelofs *et al.* 1970), or disrupting male response (Gaston *et al.* 1967; Sanders and Lucuik 1971; Shorey *et al.* 1967; Shorey *et al.* 1972). However, response of male *L.f.lugubrosa* (Tables I-III) was lower than in other Lepidoptera (Sanders 1971; Strubble 1970), possibly because of weak flight, or excitation of males rather than attraction. Alternatively, more than one female in a chamber may mutually inhibit pheromone production and/or release, or females may release large amounts of pheromone only in response to stimulation from responding males (Shorey 1964). In spite of low response levels, trapping records of males early in the flight season suggests that the

pheromone may be used effectively in survey and detection programs. Control by disruption or mass trapping may also be possible early in the flight period (Table III) or at low population levels particularly if a synthetic pheromone is available and it is released in optimal concentrations at appropriate times. If forest management changes to intensive use of high yield, accessible growing sites and if trees are grown in blocks or pure stands of one species as in orchard situations, the development of sex pheromones for survey, detection and direct control may prove feasible and economically sound. Refinements such as the Sectar-1, 3M trap, a daylight yellow trap which fluoresces under black light, and modified shape and dimensions of traps may prove valuable.

L.f.lugubrosa is ready to mate and oviposit within 24 hours after emergence (Tables IV,V), and at emergence carries approximately 75% of the mean total number of eggs to be laid (Table V). Although unmated females oviposit at a constant low rate, oviposition was markedly stimulated by mating (Fig. 13). There appears to be no hormonally regulated, prolonged maturation period necessary, as in some other insects (Barth 1965; Menon 1970). Therefore, *L.f.lugubrosa* adults are an unlikely target for hormonal control or behavioral disruption. However, experiments with *L.f.lugubrosa* and the juvenile hormone mimic ZR-0451 (512)(Zoecon Corporation, Palo Alto, California) indicate a promising possibility of using this hormone as a foliar, larvicidal spray (R.F. Shepherd and T. Sahota, pers. comm.[9]). The compound remains on the tree for a sufficient period to kill larvae, cause supernumerary molts, or extend pupation time. After a population knock-down with juvenile hormone or other insecticidal sprays, the emergent

[9] Pacific Forest Research Centre, Canadian Forestry Service, Victoria, B.C.

adult population could be reduced further in an integrated control program by using sex pheromone traps or male disruption techniques.

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