Biology of the European Crane Fly, *Tipula paludosa* Meigen, in Western Washington (Tipulidae; Diptera)

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THE AUTHORS AND THIS BULLETIN

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David M. Jackson
ABSTRACTS

The European crane fly, Tipula paludosa Meigen, has become a serious pest of lawns, pastures, and hayfields in northwestern Washington. Larvae feeding on roots, stems, and leaves of a variety of plants have caused a considerable economic impact on the dairy industry.

Tipula paludosa is a univoltine species whose eggs hatch in September. Larvae feed voraciously and complete their first 2 instars in less than 2 months. They usually spend the winter as 3rd instars. Third and 4th instars feed rapidly in the spring, but remain relatively inactive during the summer until pupation. Pupae were first found during early August. The duration of the pupal stage was 10.5-11.5 days. Peak emergences were on September 1, 1972, and September 6, 1973, and 95% of the adults were taken from August 25 to September 13.

Prepupal weights were correlated to pupal weights for both males (r=0.69) and females (r=0.76). Female 4th instars weighed 1.5 times as much as males, and female pupae weighed 1.5 times as much as male pupae. Larval weights were positively correlated (r=0.83) to lengths. Larval size increased with larval density due probably to better overall habitat conditions.

Field surveys for immatures in Whatcom County were conducted on a centric systematic area sampling scheme with the aid of a 4-inch diam soil core. Most larval core frequencies fit the negative binomial distribution, which implies a contagious distribution of crane fly immatures. This overdispersion is probably attributable to responses to the physical microenvironment, host plant selection, ovipository preferences, and effects of the sampling procedure.

Immatures are susceptible to drought, especially as 1st and 2nd instars. Cold temperatures, flooding, and poor soil conditions also may be detrimental to growth and development. Little evidence of natural biological control was found in northwestern Washington.

Adults are sexually mature at eclosion; and mating, which often involves tenereal females, occurs immediately. Experiments showed males do not rely on vision for finding females, and males were not attracted to either virgin or field-caught females in a Y-tube olfactometer. Population level averages an average of 105 min in the laboratory. The overall sex ratio was 63.9% males in 1972 and 55.1% in 1973, judging from pupal-case counts. The sex ratio changed during the emergence period due to the later recruitment of females into the population, and this was probably related to a longer pupal period for the females.

Oviposition began shortly after mating ceased and continued until nearly all eggs were laid. The average female laid 50% of her eggs within 8 hr, and 99% within 26 hr in the laboratory. The mean fecundity was 337.6 eggs per virgin female. Fecundity was positively correlated (r=0.08) to female pupal weight.

Diet periodicity of peak emergence, mating, oviposition, and flight was observed. Adults typically emerged shortly after sunset and finished mating by midnight. Oviposition was mostly completed by dawn, but some females retained part of their egg complement into the next day. A large proportion of these females were captured flying above 6 ft from the ground on a sticky board trap. These daytime-flying individuals probably contribute to the species' dispersal.

INTRODUCTION

The European crane fly (Tipula paludosa Meigen) has become a pest of lawns, pastures, and hayfields in northwestern Washington. Larvae feed on roots, stems, and leaves of a wide variety of grasses, legumes, and other plants, seriously damaging pastures and hayfields during heavy outbreaks. Where the major agricultural industry is dairy farming, these depredations have been of considerable economic importance. Because of their great abundance and habit of collecting upon the sides of buildings, adults can be a nuisance to the general public.

Tipula paludosa is native to northwestern Europe, where it has long been a problem. This species was often confused with two European ones, T. oleracea L. and T. ciceki De Jong, until De Jong (40) separated out ciceki adults and Henningsson and Lemche (70) stabilized the names, ending controversy over nomenclatorial priority. Immatures were not separated until Brindle (21, 22) and Theewald (155) constructed keys for this group.

In Europe, T. paludosa ranges from southern Finland (ca. 60 N) and lower Scandinavia to northern Italy (ca. 35 E), and from Great Britain (ca. 6 W) into the USSR (ca. 35 E). Introduction of this pest into North America took place in eastern Canada. The fly was reported first from Newfoundland in 1952 and 2 years later on Cape Breton Island, Nova Scotia. Larvae, known as leatherjackets, soon became a problem on turf, vegetable gardens, and perennial flower gardens. Soil ballsants dumped on shore from ships at Cape Breton Island are believed to be the source of infestation (10, 44).

On the west coast, European crane fly larvae were first discovered in British Columbia causing severe damage to lawns on the outskirts of Vancouver in 1965. The source of this introduction is not known. By 1966, they were firmly established and were the focus of much concern (167). Leatherjackets had spread over the entire lower Fraser River farming district by the spring of 1974.

Light trap captures at Blaine, Washington on the border with Canada yielded the first adult males of T. paludosa in the USA in late summer of 1966. These individuals were part of the spreading Canadian infestation. By the spring of 1974 over 50,000 acres of Whatcom County were affected (26). Adults have been taken from Skagit County (1970), San Juan County (1971), King County (1972), Clallam County (1974), and Island Coun-
ty (1 male taken by D. M. Jackson on July 12, 1973 at Oak Harbor; determined by W. J. Turner). The infestation has been spreading slowly but steadily southward (fig 1).

1. Distribution of Tipula paludes in SW British Columbia and NW Washington.

It is hard to assess the full social and economic impact this pest has made upon the farming regions of southwestern British Columbia and northwestern Washington. This is in part due to the fact that despite the efforts of several investigators, no consistent relationship between leatherjacket numbers and crop damage exists (52). Differences in the growing seasons, diversity of host species, and fluctuations in dairy farm economics are possible causes of these inconsistencies. It is also difficult to place monetary values on the nuisance factor or damage to lawns, golf greens, and gardens.

Leatherjacket damage can be a major economic factor for individual dairy farmers. Control programs have taken a high priority in Europe during years of high population levels (85), and chemical controls have been used in western Whatcom County for the past 3 years.

In 1970, the Plant Protection Division of the USDA Agricultural Research Service issued an emergency plant pest regulation for Whatcom County covering interstate commerce (158). A similar regulation was made by the state of Washington for intransit movements of potentially infected materials. These regulations remained in effect until early in 1973. Then they were removed because they were deemed ineffective in stopping the movement of the crane fly infestation southward. The prevailing attitude is that advance warning of high larval levels and sound control advice are practical methods for dealing with the leatherjacket problem.

MATERIALS AND METHODS

The Study Area

Fields on private farms in northern Whatcom County were chosen for study because of their moderate to high populations in areas of reported economic damage. Work during the summer of 1972 was done in 3 fields on 2 farms near Blaine. These same fields could not be used in 1973 since they suffered dramatic population declines during the fall of 1972. Therefore it was necessary to find new fields near Lynden and Sumas for the 1973 work. A total of 10 fields on 5 farms were included in this study. Tabulated descriptions of these sites are in table 1, where each farm and field is identified with a number and letter.

The Puget Sound area of Whatcom County, where this study was conducted, consists of extensive alluvial flats, low glacial and postglacial fluvial or marine terraces, and low rolling glacial ground-moraine plains. Whatcom County soils are far more diverse than the more sandy drifts found in the Puget Sound Basin south of the Cascade Mountain spur at Bellingham. Generally, these soils are friable, and tend to form granules that are hard and durable in water. Although they are somewhat leached, these soils have a high inherent mineral fertility and respond favorably to fertilizers and good farming. Drainage ranges from well-drained and gravelly sections to poorly-drained, iron-laden soils. Details of these soils were presented by Poulson (129).

The study area was within the Puget Sound vegetation area of the Tsuga heterophylla (Raf.) Sarg. zone (western hemlock zone) (45). It is characterized by a Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) subclimax and western hemlock-western redcedar (Tsuga heterophylla-Triodia plicata Donn) climax forest.

The natural vegetation of western Whatcom County has been almost entirely removed by logging, with little reseeding. Much of this area is now in agriculture, but there are some small second-growth woodlots. Since dairying is the major agricultural industry of the county, pastures and hayfields make up much of the farm acreage.

Whatcom County occupies the northernmost portion of the Puget Sound Lowlands climatic area in the United States. This county has a mild, somewhat modified oceanic climate, the result of prevailing westerly winds from over the Pacific Ocean (123, 129). Average annual precipitation for this area ranges from 30-45 inches (76-114 cm). Over 75% of the annual precipitation falls in the 6 months October 1-March 31. July is the driest month (mean: .080 inches or 2.26 cm), and December is the wettest (mean: .632 inches or 16 cm). Snowfall is light but variable, averaging 10-20 inches year (99).

Summer temperatures rarely surpas 32.2° C (90° F), and the average minimum temperature in January is -.2° to 0° C (28-32° F). Cold currents of interior air sometimes move into this area from Canada through the open northern end of the Puget Sound trough, but usually do not last long (99, 132).
TABLE 1. Descriptions of the Whatcom County, Washington fields used for *Tipula paludosa* field studies:

<table>
<thead>
<tr>
<th>Farm</th>
<th>Field</th>
<th>Acres</th>
<th>Year</th>
<th>Farmer’s use</th>
<th>Soil type a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heins’, 2 miles ESE of Blaine on Swede Rd, 122°31’W, 49°56’N.</td>
<td>IA</td>
<td>6.9</td>
<td>1972</td>
<td>Pasture and hay</td>
<td>Hemen silt loam</td>
</tr>
<tr>
<td>Paul’s, 5 miles ESE of Blaine on Delta Line &amp; Highway No. 122°37’N; 49°53’N.</td>
<td>2A</td>
<td>0.9</td>
<td>1972</td>
<td>Hay</td>
<td>Tranp silt loam</td>
</tr>
<tr>
<td>2B</td>
<td>4.5</td>
<td>1972</td>
<td>Pasture</td>
<td>Tranp silt loam</td>
<td></td>
</tr>
<tr>
<td>Edwards’, 1 mile east of Sumas on Jones Rd, 122°15’W, 49°N.</td>
<td>3A</td>
<td>17.8</td>
<td>1973</td>
<td>Corn</td>
<td>Nooksack silt loam</td>
</tr>
<tr>
<td>3B</td>
<td>7.4</td>
<td>1973</td>
<td>Hay</td>
<td>Nooksack silt loam</td>
<td></td>
</tr>
<tr>
<td>Lankmead’s, 1 Mile NNE of Lynden on Double Ditch Rd. 122°28’W, 49°57’N.</td>
<td>4A</td>
<td>5.2</td>
<td>1973</td>
<td>Hay</td>
<td>Woodly silt loam</td>
</tr>
<tr>
<td>Dahlgren’s, 4 miles N of Lynden on C. Boundary Rd. 122°28’W, 49°N.</td>
<td>5A1</td>
<td>5.0</td>
<td>1973</td>
<td>Hay and pasture</td>
<td>Kickerville silt loam</td>
</tr>
<tr>
<td>5A2</td>
<td>5.0</td>
<td>1973</td>
<td>Hay and pasture</td>
<td>Riffe peat</td>
<td></td>
</tr>
<tr>
<td>5B</td>
<td>4.1</td>
<td>1973</td>
<td>Peat</td>
<td>Riffe peat</td>
<td></td>
</tr>
<tr>
<td>5C</td>
<td>3.7</td>
<td>1973</td>
<td>Corn</td>
<td>Riffe peat</td>
<td></td>
</tr>
<tr>
<td>5D</td>
<td>8.9</td>
<td>1973</td>
<td>Pasture</td>
<td>Kickerville silt loam</td>
<td></td>
</tr>
</tbody>
</table>

a Soil classification from Poulison (129).

Temperatures for the Puget Sound were generally cooler than normal during the 1971-73 period. Precipitation was heavier than normal during 1971 and the first 9 months of 1972. A dry spell followed and lasted until the fall of 1973, at which time normal precipitation began.

**Sampling for Immature Crane Flies**

Several investigators used chemical irritants to bring leatherjackets to the surface. The most common and successful substance was a solution of orthodichlorobenzene, Jeyes’ fluid, and sodium oleate (7, 8, 52, 58, 52, 90), but Milne et al. (110) and Mayor and Brownie (101) found this method inefficient, especially after May. Marseck (97) and Meats (102) brought *Tipula* larvae to the surface with a common salt (NaCl) solution. Milne et al. (110) devised a dynamic hot water process for extracting leatherjackets, and Mayor and Brownie (101) made a machine that approached 100% efficiency. Coulson (59) and Freeman (47) separated larvae by washing soil samples through graduated sieves.

For this study, larvae, pupae, and pupal cases were sampled by a simple and rapid centric systematic area technique similar to the one Laughlin (87) used. Milne (100) showed that if the centric systematic area sample was treated as a random sample, the resulting statistics are “as reliable and precise” as those obtained from ordinary random sampling. We used stratified random sampling to check the efficiency of the systematic method, since the former gives more consistent statistics than unrestricted random sampling (169). In no case was there any significant difference between the results obtained by these two methods. All soil samples were therefore treated as if they had been obtained randomly.

Each field was subdivided into 50 x 50-ft or 100 x 100-ft (15.2 or 30.5 m square) sections, and a soil core was taken from the center of each section. Dimensions of the subdivisions were determined on the basis of the size of the field and the thoroughness of sampling desired. A grid system was devised, giving each sample a designated position.

Cores were taken to a depth of 5 inches (12.7 cm) with a 4-inch (10.2 cm) diam. soil corer. Three inches was the sampling depth, since that is the deepest larvae have been taken (45, 110, 146, 167). Each core sampled 0.087 ft³, hence 11.5 cores were needed to obtain ca. 1 ft³ (0.03 m³) of soil. Rocks were seldom encountered, but when they were a problem, a new sample was taken as close to the original attempt as possible.

Several investigators showed the size of the sampling unit greatly affects the estimated parameters of the population distribution. Yates and Finney (169) found 4-inch (10.2 cm) diameter cores preferable to either 2- or 6-inch (5.1 or 15.2 cm) ones. The 4-inch cores provided a reasonable balance between labor and precision when sampling wireworm populations. Likewise, George (52) chose 4-inch (10.2 cm) diameter cores over the traditional 14x1 (0.04 m²) soil samples when sampling for *Tipula* larvae. Four-inch cores proved to be a reasonable size for our study.
Cores were taken apart over a series of graduated screens in the field. This method approached 100% efficiency, since 4th instars could not pass through the smallest mesh.

Examination of fields 2B and 5B led to the estimation that 9% of each pasture was covered by dung piles by the end of August. Waterhouse (190) found the average bovine drop ca. 12-inch (30.5 cm) of diameter. Thirty cows, each pastured 50 hr/wk for 150 days (mid-April to mid-August) on field 2B would cover 0.2 acres (0.8 ha) or 4.9% of the field; 9% is a reasonable estimate. Soil beneath dung piles contained few larvae, and pupal cases were seldom found protruding through fresh manure. It was not determined whether the larvae were killed or migrated from under dung piles, but helpless pupae and immobile pupae were probably killed.

Individual larvae severed by the edge of the corer were counted only if the head end remained with the sample. This is the standard procedure in quantitative sampling (119), but led to some problems in scoring pupae since genital sheaths are used for that purpose.

Sampling for Adults Crane Flies

Adults were sampled in several ways. The simplest method, the use of a standard light-weight sweep net, worked well in short or tall grass and weeds. Short sessions of uniform sweeping were done over selected areas, regardless of the type or condition of the herbage. The net was emptied often into screened cages or adults were examined directly from the net. Sweeping was convenient and it gave valuable information about the population composition, but it was limited to dry conditions. Also, high-flying adults, noticed during the late mornings and afternoons, could not be reached with the net. By the time they had landed several yards away they were indistinguishable from other individuals.

Emergence cages were used in one effort to get quantitative data on adult emergence. These enclosures consisted of wooden frames with inside dimensions of 12 x 12 x 12 inches (30.5 x 30.5 x 30.5 cm). This framework was covered with saran screening except for the bottom, which was left open, and half of one side containing a door. A 2-inch (5.1 cm) galvanized metal strip was nailed around the bottom of the frame so that 1½ inches (3.8 cm) extended below. This flange was pushed into the soil until the wooden frame rested on the ground to prevent adults and most larvae from escaping. Each cage covered exactly 1 ft² of turf, and the screened volume slightly exceeded 1 ft³ (0.03 m³).

Immediately after each cage was in place, the surrounding larval density was determined by taking 8 core samples within 2 ft (61.0 cm) of the cage. Grass within each cage was clipped quite short so that adults could be found. This might have contributed to the high mortality observed, since protection from the sun was decreased. These cages were examined every other day during 1972 and adults collected. When these cages were removed, the sum of the pupal cases and pupae was found to be 92.1% of the original larval density, but the cumulative number of adults totalled only 73.1% of the original larval density; 26% of the population was still in the pupal stage at that time. Additional cores taken near the removed cages contained pupae and pupal cases totaling 93.2% of the original larval density, and 5.9% of the sample were pupae. Pupal case counts gave as good an estimate of emerging adults as did emergence cages; therefore, the cages were not used in 1973.

Pupal cases were easily found since they protruded 1/3 to 2/3 of their length out of the soil, with some hung up in the grass or enwined in heavy trash. Samples were taken by marking off 1-ft² (0.9 m²) areas and collecting the pupal cases within, or by using the soil corer. Pupal cases were used on the basis of their various genital sheaths.

During the 1972 flight period, a 6 x 2-ft (182.9 x 61.0 cm) yellow plywood board covered with Tanglefoot, a sticky resin, was erected on field 1A. Many crane flies were trapped, but several were observed escaping by the board by vibrating their wings vigorously and pulling their legs free. Only flies that had their wings or body stuck were held permanently. For the 1973 flight period, a larger board was constructed in order to sample high-flying adults. This 14 x 2-ft (426.7 x 61.0 cm) board was marked off in foot-high (30.5 cm) sections and fastened to an existing telephone pole in field 5B. A polystyrene compound, Tack Trap, which proved to be more viscos than the former substance, allowed fewer flies to escape. Adults were removed from it and transferred to pieces of paper. Information concerning location on the board, sex, and time of capture for each adult was recorded directly on these papers, and they were frozen for later examination. Females were removed from the papers with ethyl acetate and dissected under a mixture of ethyl alcohol and paint thinner to obtain egg counts.

Over 200 hours were spent in the laboratory studying the behavior of confined adults, including observations of males blinded with black tempera paint. Over 500 hours were spent doing field-related work during this study.

Y-Tube Experiment

Existence of a chemical sex attractant in the adult female was tested, using a Y-tube olfactometer similar to the one used by Heuzel et al. (75). This apparatus was made of 2-inch (5.1 cm) i.d. clear glass tubing and consisted of a 12-inch (30.5 cm) stem and two 12-inch (30.5 cm) arms separated by a 60° angle. The extremity of each arm was fitted with a 4-inch (10.2 cm) cubic choice-chamber of translucent plastic, and the stem ended in 4 x 6 x 4-inch (10.2 x 15.2 x 10.2 cm) release-chamber of the same material. These compartments had air-tight snap-on lids, and their attachment points with the glass tubing were sealed with a silicone sealer. A small suction fan fastened to the lid of the release-chamber pulled a steady flow of air through the tube from the choice-chambers. An identical number of 1/8-inch (0.35 cm) holes, drilled in the backs of the choice-chambers, were covered with tape to regulate the air flow. Enough air was drawn through the tubes to be noticeable, but not enough to impair the male's travel through the tubes.
For each trial, five males were put in the release-chamber. One choice-chamber contained a test material and the other remained empty. Three trials were run with the test material on one side and three with it on the other. Both field-captured and virgin (reared from seeded pupae) males were tested against 5 virgin females (expt 1) and 5 field-females (expt 2). The Y-tube and chambers were washed between trials.

Rearing Techniques

Larvae and pupae collected in the field were either preserved or removed to the laboratory for rearing. Individuals for preservation were killed by dropping them into water near boiling. Boiling water invariably ruptured pupae. After 5 min, specimens were transferred to 10% formaldehyde and left for several weeks. Then they were placed in 70% ethanol for permanent storage. Adults were killed in cyanide vials and dry mounted or put directly in 70% ethanol. Pupal cases were also kept in alcohol.

Laughlin (85) suggested rearing larvae in damp, drained sand and feeding them powdered grass. For this study, however, screened, loamy field soil was better, since the moisture content could be regulated more evenly. One hundred fifty 4th instars were placed in 12 x 18-inch (30.5 x 45.7 cm) pans containing 4 or more inches (10 cm) of soil. Because they feed little during the final instar and because the larvae were not crowded, cannibalism was minimal. Powdered alfalfa pellets were spread over the soil, but little feeding was observed.

When held at room temperature (65-85 F or 18.3-29.4C), 90-99% of the larvae eventually pupated. Soil from these pans was sifted every 2nd day and pupae were removed; the soil was replaced weekly.

Pupae were sexed and placed in 5/16-inch (7.9 mm) holes in moistened sand so that about ⅓ of their anterior ends protruded. Only 60-65% of the pupae emerged, probably due to difficulty maintaining a proper moisture level in sand. The use of holes in plaster of paris, as suggested by Laughlin (85), or in paraffin proved even less successful. Adults emerging into screened cages were removed daily. Males and females, held separately in screened cages at opposite ends of the laboratory, were provided with water but no food.

RESULTS AND DISCUSSION

Description of Immature Stages

Eggs of the subspecies Tipulinae are typically shiny black, elliptical, and roughly 1-mm (0.04 inch) long (5, 22). *Tipula paludosa* has elongate-oval eggs with one side flattened and one end more pointed than the other. Many tipulid species have a tightly-coiled egg filament that unwinds after oviposition and attaches itself to the surrounding substrate, thus providing an anchoring adaptation for wet habitats. Unlike its closely related species, *T. olacea* and *T. czekie*, *T. paludosa* has no egg filaments (72, 145).

Tipulids have 4 instars; the last 3 are quite similar in appearance, and most morphological works have been concerned with the final instar. Oldham (120) and Sellike (145) did detailed morphological studies on the gross internal and external structures of 4th instar *T. paludosa*. Alexander (2) gave an excellent literature review of the early morphological studies on tipulid larvae.

Leatherjackets are nearly cylindrical, but they taper slightly both anteriorly and posteriorly (fig. 2). After the initial instar, leatherjackets are light grey to greyish brown with irregular black specks of various sizes. Their cuticle is somewhat translucent and it reveals the two longitudinal tracheal trunks and alimentary canal.

The thoracic integument is attached to the hemichephalous head capsule over a section of the closely associated internal and external lateral plates (67, 130). About ⅓ of the head capsule is not attached to the integument, but it can be withdrawn inside the prothoracic skin for protection.

Tipulid larvae are metamorphic, with two stigmata housed in the spicular disc of the anal segment. The truncated end of the anal segment consists of an upper spicular and a lower anal field which lie roughly perpendicular to the longitudinal axis of the body (fig. 3). The dorsal field is composed of the spicular disc with rounded stigmata and six tapering anal lobes, the characteristic number in Tipulinae (22). The spicular disc can be withdrawn so that the anal lobes form a spicular chamber, which helps keep soil particles out of the stigmata. Water is partially retracted by hydrophobic hairs and partly by glandular secretions (22, 53). The anal field consists of the anus and four osmoregulatory anal papillae, which are more developed in species inhabiting wet habitats. In *T. paludosa*, only the lateral pair are elongated, the ventral papillae being reduced to rounded protuberances (20).

Formed inside the larval skin, each obrect pupa (fig. 4) frees itself through the anterior end of the old cuticle by spasmodic movements (142, 145). The five posterior abdominal segments bear short protuberances ending in caudally-directed spines, which enable the pupa to wriggle to the surface before emergence (1, 5).

Description of Adults

Adults of *T. paludosa* are fairly large crane flies, the males being 14-19 mm (0.55-0.75 inch) and the females 19-25 mm (0.75-0.98 inch) long (5) (figs. 5 & 6). They have elongate maxillary palpi, a character that separates Tipulinae from other subfamilies. Filiiform antennae, which originate anterior to the widely separated, dichoptic eyes, have 14 segments instead of the genus-typical 15 (1, 5).

Although the pronotum is well developed, the thorax consists primarily of the large mesothorax; the halteres-bearing metathorax is reduced to a small bulb. The wings of the females are shorter than the abdomen, the ratio of wing length divided by total body length being ca. 0.64 (62). Hemingssen (67) linked this characteristic with less mobile forms having drier ovipository habitats, and he pointed out *T. paludosa* is the most "xeroephilic" species in the *T. olacea* group.
There are 9 evident abdominal segments in the male plus an anal tubercle that probably represents the 10th and 11th segments (51, 151). The 9th segment, which bears a pair of gonopods, is often referred to as the hypopygium.

The female abdomen consists of 10 clearly defined segments, the 8th through 10th being modified into a functional "ovipositor." It is formed by the cerci, which are continuous with the 10th tergum, and a pair of blade-like hypovalves (8th sternum) that extend only \( \text{\frac{3}{4}} \) the length of the cerci.

2. Ventral view of a 6th instar *Tipula paludosa*.

3. Caudal view of a 6th instar *Tipula paludosa*.

4. Side view of female and male *Tipula paludosa* pupae.

5. Adult female *Tipula paludosa*.

6. Adult male *Tipula paludosa*.
Development of Immature Stages

*Tipula paludosa* is a univoltine species with a weak larval diapause (87). Eggs are laid in August and September and hatch in 11-15 days in the field (7, 134). Larvae feed ravenously and usually complete the first 2 instars in less than 2 months (7, 94). Typically, the winter months of November to April are spent as 3rd instars. Fourth instars feed briefly and then remain inactive until pupation, which begins as early as the middle of July (35). Adults start to emerge in mid-August with peak emergence during the 1st week in September (7, 24, 167). Fig. 7 illustrates the typical *T. paludosa* life cycle with time interval ranges of the life stages.

![Diagram of T. paludosa life cycle]

Fertile eggs absorb about half their weight in water between the ages of 2-3 days, resulting in a mid-incubation swelling. Development of the second cuticle can be detected on the day the egg swells, but not before (105). Hatching takes place through a regular longitudinal split the length of the chiton (55, 106). Egg development usually takes about 2 weeks, but several factors can delay hatching (See Environment Factors section).

Newly-hatched larvae live just below the surface of the soil, but many are found 3-6 cm (1.2-2.4 inches) deep within a month (94, 146). However, larvae generally spend most of their lives in the top inch (2.5 cm) of soil, even during the winter (45, 104) and they only go deeper in the spring (93, 167).

Laughlin (87) found, under natural conditions, growth of *T. paludosa* was rapid in the fall when larvae grew from ca. 0.3 to 50 mg in 1-2 months. After soil temperatures dropped, growth was much slower, and the larvae only doubled their weight during the winter. Spring feeding and development was again rapid until the 4th instars reached a peak of 300-500 mg in June. These larvae also lost weight before pupation. Hadley (58) maintained part of the loss of biomass in *Molopbus ater* (*Tipulidae, Limoninae*) was due to some degree to the loss of cuticle during molting, pupation, and eclosion, and this is probably true for *Tipula* sp.

Reasons for the 6-8 week delay from the end of feeding until pupation remain unknown. The larvae are relatively inactive at this time, but they do respond to normal external stimuli. Only during the prepupal period, which lasts less than 5 days at 20 C (68 F) (110), do they descend in the soil, contract, and remain quiescent (2, 142). The prepupa cannot move for several days before pupation since many of their muscles are detached (110).

Fourth instars were collected from the field, weighed on a Mettler balance, and placed individually into 6 oz (177 ml) paper cups containing field soil. Every 2nd or 3rd day, the larvae and new pupae were weighed and returned to their cups. A record of initial field weight, prepupal weight, and pupal weight was obtained for each individual (table 2).

<table>
<thead>
<tr>
<th>4th Instar wt (mg)</th>
<th>Prepupal wt (mg)</th>
<th>Pupal wt (mg)</th>
<th>Avg % wt loss from prepupa to pupa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>288.5</td>
<td>253.2</td>
<td>145.9</td>
</tr>
<tr>
<td>30</td>
<td>75.1</td>
<td>52.4</td>
<td>30.6</td>
</tr>
<tr>
<td>n</td>
<td>34</td>
<td>34</td>
<td>34</td>
</tr>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>383.1</td>
<td>363.8</td>
<td>216.2</td>
</tr>
<tr>
<td>50</td>
<td>106.0</td>
<td>106.0</td>
<td>56.4</td>
</tr>
<tr>
<td>n</td>
<td>29</td>
<td>29</td>
<td>29</td>
</tr>
</tbody>
</table>

**NOTE:** Larvae were collected from field SB on Aug. 1-20, 1973.

Since males lost a greater percentage of their weight, female pupae weighed ca. 1.5 times as much as the males; male larvae from the field weighed ca. 1.3 times as much as field males. Females were not only larger than males, but they also lost a smaller weight percentage during pupation. Some of the larval weight losses were due to defecation, shedding of the larval skin, cuticular water loss, and expenditure of reserves during pupal formation (86). Individual weight reductions were relatively uniform from the larva to prepupa and from prepupa to pupa. Prepupal weights were correlated to pupal weights (males: r=0.69; females: r=0.70) (fig. 8).

Laughlin (88) found a significant heterogeneity in larval weights collected from areas greater than 5 yd apart. He also (87) reported a greater variation between peak larval weights from year to year than from place to place during the same year. For our study, 30 larvae were taken from each of 4 fields during the week of July 15, 1973, and their mean larval weights were compared using Duncan’s (42) new multiple range test (table 3). Larvae in field 2A were considerably smaller than those from 3B or 4A. Those from field 3A were not signifi-
instars indicated that larval weights and lengths were positively correlated \((r = 0.83, n = 60)\).

Leatherjackets make burrows through the root systems of plants up to the surface. During the day they usually feed just below the ground (53, 156), but they often surface to feed on warm nights (110, 146) and on damp, cloudy days when the humidity is high or there is a dew (121). Larvae sometimes wander or migrate over the surface in search of food, although no relation between this and larval density has been established (10, 86, 154).

Leatherjackets feed on a wide variety of grasses and other plants. They have been found on city lawns, golf and bowling greens (38); meadows and pastures (25, 80); cabbage, cauliflower, and turnip (70); beet, flax, hemp, tobacco, and wheat (128); rutabaga and rye (124, 125); flowers and strawberry (100, 167); corn and oats (134); potato (7); rape (18); various weeds (156); barley, clover, buckwheat, lettuce, peas, and even vine seedlings (9, 93, 94).

When feeding below the surface, larvae mainly attack root hairs, roots, and crowns, but they eat stems, grass blades, and leaves when above the ground (118, 167). They prefer tender green leaves over roots and stems. Becker (9) and Marckks (94) maintained that larvae developed best on white clover, their favorite food, and grew well on most grasses except oats. Ricou (138, 140) found larvae grew optimally when fed members of Compositae. Such a wide assortment of host plants reflects rather indiscriminate feeding habits. In fact, larvae subsisted on decaying rootlets and vegetative matter in soil that was completely devoid of living material (134). Food supply is rarely scarce, and it is unlikely to be an important factor of competition among larvae (47).

Although tipulid larvae are sluggish and have low respiration rates, especially in the 4th instar (75, 145), they move up and down in their burrows in response to stimuli of touch, light, heat, and relative humidity of the air and soil. *Tipula paludosa* larvae were observed moving by slowly extending and contracting their bodies. Laughlin (86) listed a series of three responses to progressively stronger adverse stimulation. The first was longitudinal contraction, the second rapid curling and uncurling differently from those of 2A or 3B, but field 4A larvae were significantly larger than those from the other 3 fields \((P = 0.05)\). Fig. 9 shows that larval size increased with larval density. This is probably due to the fact that a more suitable habitat can support not only more larvae but also maintain them better.

Laughlin (86) stated early growth takes place in all parts of the larval body with every organ growing day by day and the cuticle at the molts. By the last instar the larva has grown to almost its full length, but it is thin. Additional feeding causes development of the fat bodies and an increase in girth (86, 154). Measurements of 4th

---

**Table 3.** Comparison of *Tipula paludosa* mean larval weights from 4 northwest Washington fields using Duncan's (42) new multiple range test.

<table>
<thead>
<tr>
<th>Field</th>
<th>Mean larval wt (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2B</td>
<td>296.7</td>
</tr>
<tr>
<td>2A</td>
<td>338.0</td>
</tr>
<tr>
<td>3A</td>
<td>324.7</td>
</tr>
<tr>
<td>5B</td>
<td>420.7</td>
</tr>
</tbody>
</table>

Means connected by vertical lines are not significantly different from each other at the 0.05 level of confidence. Those not so connected are significantly different.

**B. Analysis of variance:**

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Mean squares</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Across fields</td>
<td>3</td>
<td>83,450.0</td>
<td>16.6*</td>
</tr>
<tr>
<td>Within fields</td>
<td>118</td>
<td>7,480.0</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>119</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Significant at the 0.05 level.

**C. Coefficient of variation = 24.05**
ing, and the third was a combination of cutting and rapid revolving on their own axes. Sellek (143) and Freeman (47) pointed out such reactions might be important for dislodging predators.

Like most nematomorphs, tipulid pupae can move up and down in their burrows in response to various stimuli (142). This movement is enhanced by the curved spines on the abdomen. After moving to the surface and resting a few minutes, the pupa splits along the mid-line from the occipital region to the metathorax, and between the antennal sheaths and pronotum as far down as the leg sheaths (2, 22, 23). First the thoracic dorsum and shortly after the tucked-under head emerges from the pupal case. Maxillary palpi, antennae, wings, and legs are slowly pulled from their sheaths. Once the front legs are free, the adult usually grasps some support and pulls itself from its case (33, 142). In Tipulinae, the liquid mesonotum is not discharged until after the adult has emerged, giving teneral adults a pale greenish, transparent appearance which they may retain for several hours (23).

Cannibalism is common in crowded or confined laboratory cultures, and it may seriously reduce the population. Helpless prepupa, pupae, and larvae in poor physical condition are particularly liable to be eaten by healthy larvae (7, 85, 87). Freeman (47) found circumstantial evidence that *Tipula* larvae sometimes attack other larvae in the field due to competition for space.

The percentages of larvae (including prepupae), pupae, and pupal cases collected each day by core sampling are plotted in fig. 10. Pupae started showing up in the samples during the 1st week of August of both 1972 and 1973, and the largest percentage of pupae in the samples was found near the end of that month (August 26 and August 31). Measurable emergence was observed shortly after August 15 of each year, and by the 1st week in September, eclosion was at its peak. A few flies were taken in early July (earliest on July 9), and some remained into October, but 99% of the emergence occurred in the 22 days from August 23 to September 13. Coulson (34) found 2 standard deviations (94.9%) from the peak emergence date was 23 days.

Hadley (58) used the difference between the dates on which 75% of the adults emerged as the duration of the pupal stage of *Melophillus ater* Meigen. Measured this way, the length of *T. paludosa*'s pupal stage was 11.5 days in 1972 and 10.5 days in 1973. The method gives no measure of pupal stage duration variability, however. Eighteen larvae were reared to adults in the laboratory; the average pupal duration at ca. 18.5 °C was 11.5 days (range=8-14, SD=4-6). A range of 10-12 days for pupal duration agrees with 11 days reported by Oldham (120) and 10 days by Ricou (140). Other workers (7, 87, 156) reported the pupal period was about 14 days.

Peak emergences were September 1 and September 6 for the 2 years. These figures are remarkably similar to Barnes' (7) and Cameron's (24), who had September 1 and September 6, respectively, from northern Europe. Wilkinson and MacCarthry (167) observed peak emergence in British Columbia on September 1. Thompson


Spatial Distribution of Immature Stages

Knowing the spatial pattern of individuals is important because of the biological and ecological inferences that can be drawn, although one must use caution in doing so. The distributions of European crane fly immatures for 16 separate surveys from 10 fields were investigated. Original core counts of immatures obtained by the above-mentioned sampling method (see Materials and Methods) were summarized in frequency distributions, showing the number of cores containing x=0, 1, 2, ... n individuals. The data from these surveys showed that the frequency of 14 fit a negative binomial distribution with 4 of these also fitting the Poisson series. One distribution fit only the Poisson and one fit neither the Poisson nor the negative binomial (table 4). Field counts that fit both of these distributions are normal for any insect population (162).

Several models describing the aggregative tendencies of individuals have been devised for use in basic ecological research. The negative binomial was the most applicable of these contagious, or overdispersed distributions for many pasture species (139) and for *T. paludosa* in this study. The negative binomial is the most versatile and generally used contagious distribution for the analysis of
insect counts (12, 15). It can be derived by at least five biological and mathematical models (151, 163).

The negative binomial is defined by two constants, the arithmetic mean ($\mu$) and a positive exponent ($k$). Calculations of the expected frequencies were obtained using the formula of Bliss and Fisher (14). Several methods of estimating the exponent $k$ have been proposed (3, 4, 15). The method of maximum likelihood estimate, described by Bliss and Fisher (14), was chosen since it is applicable when the number of insects does not exceed 20-20 per unit.

Goodness-of-fit tests for the Poisson and negative binomial were by a Chi-square of the observed and expected values at the 5% level of significance. Paul's (122) procedure of pooling frequencies with small expectations was used so that no expectation was less than 2.

Values of $k$ ranged from 0.0 to infinity. This exponent was computed for all the surveys since its validity as a measure of aggregation is not impaired by the Poisson (162). $k$ values in excess of 8 indicate the distribution is approaching randomness (151), a situation existing in only 3 surveys of this study. $k$ expresses the expansion potential of the population, but only in the prevailing conditions of the habitat at the time of sampling. $k$ values are influenced by the sampling unit size (60, 112), and comparisons of $k$ can only be made using the same sized unit.

The dispersion parameter ($k$) is not necessarily a constant value nor a general characteristic of a species (39), and several authors (12, 153, 163) had trouble fitting a common $k$ value to samples from different localities. A common $k$ is essential, however, for the underlying model of sequential sampling plans for populations fitting the negative binomial (112, 119, 161). When usable, transformed counts with a common $k$ give the most informative analysis of variance. A common $k$ for these data was computed, using an extension of Aronson's (3, 4)

**TABLE 4. Statistical data from 16 surveys for T. pulmonis larva in NW Washington.**

<table>
<thead>
<tr>
<th>Survey</th>
<th>Field</th>
<th>Year</th>
<th>$\mu$</th>
<th>Variance</th>
<th>$n$ (cores taken)</th>
<th>$k$</th>
<th>Poisson $\chi^2$</th>
<th>Negative Binomial $\chi^2$</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1A</td>
<td>1972</td>
<td>2.59</td>
<td>3.40</td>
<td>312</td>
<td>7.47</td>
<td>13.41**</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>1A</td>
<td>1972</td>
<td>2.91</td>
<td>3.43</td>
<td>183</td>
<td>12.84</td>
<td>6.58</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>2A</td>
<td>1972</td>
<td>2.75</td>
<td>3.39</td>
<td>83</td>
<td>3.27</td>
<td>0.85</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>2A</td>
<td>1972</td>
<td>0.46</td>
<td>0.62</td>
<td>122</td>
<td>1.16</td>
<td>0.08</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>2A</td>
<td>1972</td>
<td>2.08</td>
<td>2.15</td>
<td>143</td>
<td>1.36</td>
<td>4.65</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>6</td>
<td>3A</td>
<td>1972</td>
<td>0.39</td>
<td>0.41</td>
<td>72</td>
<td>6.35</td>
<td>2.47</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>7</td>
<td>3A</td>
<td>1972</td>
<td>0.72</td>
<td>1.08</td>
<td>55</td>
<td>1.31</td>
<td>0.19</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>4A</td>
<td>1972</td>
<td>2.88</td>
<td>3.53</td>
<td>183</td>
<td>13.45</td>
<td>2.68</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>9</td>
<td>5A</td>
<td>1972</td>
<td>0.24</td>
<td>0.40</td>
<td>72</td>
<td>0.39</td>
<td>0.01</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>5A</td>
<td>1972</td>
<td>0.67</td>
<td>2.31</td>
<td>46</td>
<td>0.30</td>
<td>13.68**</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>11</td>
<td>5B</td>
<td>1972</td>
<td>0.41</td>
<td>2.53</td>
<td>97</td>
<td>1.35</td>
<td>13.52</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>12</td>
<td>5B</td>
<td>1972</td>
<td>1.40</td>
<td>2.19</td>
<td>218</td>
<td>2.46</td>
<td>1.74</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>13</td>
<td>5B</td>
<td>1972</td>
<td>2.78</td>
<td>4.31</td>
<td>170</td>
<td>2.74</td>
<td>6.02</td>
<td></td>
<td>7</td>
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<tr>
<td>14</td>
<td>5B</td>
<td>1972</td>
<td>3.08</td>
<td>6.13</td>
<td>76</td>
<td>3.37</td>
<td>7.08</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>15</td>
<td>5C</td>
<td>1972</td>
<td>0.16</td>
<td>0.16</td>
<td>88</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>16</td>
<td>5C</td>
<td>1972</td>
<td>1.16</td>
<td>2.51</td>
<td>44</td>
<td>0.89</td>
<td>0.84</td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>

*Significant at 5% level.
**Significant at 1% level.
*Mean number of larvae per core.

weighted moment estimate in terms of regression and small series, outlined by Bliss and Owen (15). After 3 approximations, the estimated common $k$ stabilized at 5.04. The Chi-square value (109.0 with 12 df) was significant at the 1% level of significance, indicating that a common $k$ is not applicable to these data. An analysis of variance showed a much larger error sum of squares than expected, which indicates heterogeneity of the component distributions (15).

Several authors found $k$ increased linearly with the mean (3, 4, 12, 163). For these data, the linear correlation between $k$ and the mean was $r=0.0$ ($n=15$).

Debaise (35) believed individuals invading an area of low population density appear to arrange themselves randomly (i.e., Poisson Distribution) if there is a large number of suitable habitats. A population rarely remains in a random distribution once it begins to expand, however, since changes in insect population densities lead to changes in their distributions. In addition, a good fit to the Poisson might be obtained when the population is not random, if the population density is too small in comparison to the size of the sampling unit. When a population is sparse in respect to the sampling unit size, the chances of individuals occurring in any one unit is so small that the distribution is effectively random (151).

Waters (162) listed five behavioral responses of individuals of a species that might lead to contagion:
1. responses to the physical environment
2. responses to host plants
3. reproductive behavior
4. mutual attraction of individuals
5. interactions with other organisms.

These biological bases are continuously interacting, so any statistical measure of aggregation applies only to a defined set of biological conditions.
Responses to the physical environment and to host plants probably contributed greatly to leatherjacket aggregation. Soil differences affected the distribution both between and within fields. Larvae were seldom found in hard, stony soils such as Kickerville silt loam. Barnes (5) reported that soil texture is important in crane fly distribution, and several authors (9, 93, 94) described host plant selectivity, which might lead to contagion in crane fly larvae.

Reproductive behavior is another important factor contributing to overdispersion. As much as the female typically pulls the male up a stem during copulation, many mating pairs collect on the few patches of tall herbage in pastures. Hay fields have a more uniform stand and mating pairs are less aggregated. Since gravid females are nearly flightless, oviposition in pastures is heaviest near the taller plants. Females lay their eggs in small clusters in relatively limited areas (62, 131). Since hatching of eggs depends on the microhabitat (see Environmental Factors section), either a majority of any egg cluster hatches or a majority does not hatch. This causes an aggregated distribution of hatching larvae. Although larvae may move laterally throughout their lives (10, 134, 146), their initial aggregation probably affects their distribution for some time.

Mutual attractions of larvae are minimal, as far as could be ascertained. Competition for space and resultant cannibalism are common, but these are dispersive forces.

Larval interactions with other organisms were minimal during this study. Starlings, Sturnus vulgaris, are gregarious feeders on crane flies (43), and they might have caused some aggregation through patchy elimination of the larvae. Although cows probably trampled some larvae to death, especially along paths or under shade trees, their effects were minimal over most of the pasture. Since no pesticides were applied to the study fields and heavy farm machinery was driven across them only occasionally, these human-related activities were disregarded.

It seems, therefore, that the observed aggregations of larvae (and subsequently pupae and pupal cases) were caused by combinations of responses to the physical microenvironment, host plant selection, reproductive behavior, and effects of the sampling procedure. The data presented here are by no means conclusive, and further investigation of this interesting ecological situation is needed.

Environmental Factors

The presence of an adequate larval habitat determines whether a crane fly species can maintain itself in a given area (142). Habitat suitability is determined by several factors, including weather, soil texture, grass characteristics, biological control agents, and pasture management (50). However, most important for regulating population distributions and fluctuations in size are microclimatic conditions (35, 54, 139, 160). Eggs and early larvae are particularly susceptible to extremes of these density-independent factors; the population level is therefore dependent upon weather during this period of early development (35, 58). Later instar mortality, larval competition, adult pre-oviposition mortality, and fecundity have less effect on population levels (58, 87).

Temperature

Several authors (87, 105, 107) showed the relationship between tipulid egg development and temperature. Warmer temperatures generally increased the growth rate in the laboratory and field. The temperature optimum for egg development is 14-15°C (57.2-59.0°F), which is quite similar to August and September temperature normals in northwestern Washington (78). Warmer soil temperatures also increased larval growth rates, but Laughlin (86) found a wide variation in stadium duration at any one temperature.

Harsh winters take their toll of 2nd and 3rd instars (113, 160). Lange (83) attributed a population crash partly to 75 consecutive frost days. Freezing temperatures alone are not normally fatal to leatherjackets, and when thawed from frozen blocks of ice they may complete development (25, 83). Freeman (47) observed little mortality of larvae placed on damp paper in the field, but 7.5°C. The larval stage of T. paludosa is shortened when larvae are raised in the laboratory at a constant temperature (A. T. S. Wilkinson, personal comm.).

An experiment to determine the effects of cold and darkness on the initiation of pupation was run. Sixty 4th instars from field 4A were placed in soil in 1 of 3 situations. The 1st, A, was a 6-inch diam. can with a tightly fitting, clear plastic lid at 21°C (69.8°F). The second, B, was identical to the first except that two cans with opaque lids were used. The third group, C, consisted of 2 cans with opaque lids held at 5°C (41.0°F). The cans were cleaned weekly and the pupae removed.

Results of this experiment are in Fig. 11. Clearly, tem-

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perature limited the initiation of pupation more than darkness.

Duration of the pupal stage is also dependent upon the temperature (22, 75). Laughlin (85) showed emergence could be delayed by keeping pupae at 5 C (41.0 F), and Barns (6) maintained there is a critical temperature below which tipulids cannot emerge.

Soil and air humidity

Most tipulids live in wet habitats (34, 64), and although T. paludosa is found in drier conditions than many tipulids, it is quite susceptible to drought in its early instars (20, 22, 35, 47). Exposure to unsaturated air or soil, which occurs during drought, can have drastic effects on the growth and survival of eggs and larvae (74, 94, 95, 111). In fact, population crashes have been directly attributed to excessive mortality due to desiccation of eggs and larvae (35, 111).

When placed in unsaturated air, eggs lose water until they reach equilibrium with the air. Tipula oleracea eggs less than 15 min old dip into 2-4 min in unsaturated air (84, 85), but older eggs of this species and T. paludosa become progressively more resistant to desiccation (35, 94). Marecks (94) maintained 100% humidity was required for egg development, but Meats (105) found eggs, after mid-incubation swelling, could withstand 98% relative humidity (RH) and hatch.

Reduction of the soil water tension delays hatching. Meats (105) linked this delay to a prolongation of the mid-incubation swelling. There is a certain amount of development even during drying, although it is slowed (84, 103, 105). Since humidities in the grass mat and soil surfaces fall below 59% RH only during a short period of the afternoon (123), eggs run little risk of heavy mortality due to drying, except when newly laid (35, 74, 84).

First instars are as much as 40 times more vulnerable to death from desiccation than eggs at any one humidity level (35, 85, 105). Although newly hatched larvae are very susceptible to any unsaturated condition, later instars can withstand severe conditions much longer and with less mortality (104). Older larvae also move up and down in their burrows to escape adverse conditions (58).

Meats (102) found a considerable influx of water into larvae placed in wet tubes. By sealing off their mouths, anal openings, and anal papillae, he found that water entered through the general cuticular surface, which lacks an epicuticular layer (55). The 1972 population crashes on fields 1A, 2A, and 2B might be related to dry fall conditions.

Just as dry seasons may cause population crashes, wetter than normal years often give rise to population explosions (25, 32, 126, 127). Mclaren (92) and Marecks (95, 96, 98) correlated high larval densities in the spring with high rainfall the previous autumn when the larvae were small.

Marecks (95) found cool summers, mild winters, and rainfall in excess of 24 inches (61 cm) per year provide ideal conditions for the European crane fly. The maritime climate of the coastal areas of British Columbia, Washington, Oregon, and northern California appears to be suitable for this pest.

Soil conditions

Tipula paludosa larvae have been found in all types of soils including marl, peat, sand, clay, mineral soils, alluvial soils, and marshy soils (20, 21, 22, 34). Since eggs, larvae, and pupae lie near the soil surface, the moisture and temperature of both the soil and the air affect them. Soil water tension and soil air humidity vary considerably in the top inch of pasture soil. During hot, dry weather, the top inch of turf loses water rapidly, drying eggs and young larvae (47, 102, 103, 104, 105). Some soils retain water better than others; some allow precipitation to sink in, while others cause it to run off (63). Coulson (35) found mineral soils are best for crane fly development, since they have a greater capacity to raise water from the water table during drought.

In our study, the only detrimental effect of soil texture on population density was on Kickerville silt loam. This is a rapidly draining soil with high gravel content and shallow root penetration. Because of cementation of the loose, coarse subsoil it contained few larvae, even adjacent to areas of high larval densities. The undulating to rolling surface added to the rapidity of the drainage (129). See table 1 for the locations of this soil type. Hemmi silt loam, Temp silt loam, Woodlyn silt loam, Noonack silt loam, and Rifle peat are all imperfectly drained, so more water was available. The silt loams were formed from silty, clayey alluvium that retains water quite well. Rifle peat is found in ancient marshy areas where water availability is still high (129).

Floodling

Low-lying pastures and hayfields are subject to occasional flooding and prolonged periods of wet conditions. Ricou (140) reported that flooding kills all immature stages. Rogers (143) attributed a decrease in tipulid populations to flooding, which killed many 4th instars and pupae.

Hadley (58) attributed death of Molophilus ater larvae to lack of oxygen when they were placed in previously boiled water. Meats (106, 107), however, showed that eggs and larvae died in flooded soil before the water was completely deoxygenated because it became putrid and toxic to the larvae. Survival times were longer with lower temperatures, implying that winter flooding is less hazardous than summer flooding.

Meats (105, 107) found delayed hatching caused by dry soil, cold, or soil flooding is of survival value to this species since young larvae are more susceptible under these circumstances than eggs. Conditions that kill young larvae often do not prevail long enough to harm eggs.

Biological control agents

Although several predators, parasites, and microbial agents are associated with T. paludosa in Europe, none of these natural biological control elements effectively reduces leathertip numbers. Biological control is even
less effective in British Columbia (82, 167), and northwestern Washington.

Alexander (2) listed 155 species of birds known to feed on immature and adult tipulids. Wilkinson and MacCarthy (167) observed starlings feeding in large numbers on lawns in Vancouver, and many were seen feeding together on pastures in Washingom. Although they fed mainly on leatherjackets during their breeding season, Douglas (45) found larvae were only reduced a maximum of 75%. Starlings and sea gulls eat a number of adult flies, but since most females are on the wing after the majority of their eggs are laid, this feeding affects the population minimally.

Carabids and perhaps cantharids feed on tipulid larvae, but most insect predation is on the adult stage. Freeman (47) and Carl (28) mentioned the importance of the carabid Elaphrus capitis Dufault and Pocillus sp. Insects known to prey on tipulid adults include Odonata, Assilidae, Embiididae, Anthomyiidae, Scaphidiidae, and Rhagidiidae (2, 56).

The tachinid Sphincticus goniculata (De Geer) is the most important parasite of T. paludosa larvae, and it is the only one regularly associated with it. S. goniculata larvae enter their host, become attached to the tracheal trunks by means of a chitinous sheath-like structure, and establish a common respiratory system called the "felt chamber." There are two parasite generations per year in Europe and the parasite overwinters with the leatherjacket (132, 137). The level of parasitism is never high, it ranges from ca. 5-20%. S. goniculata was released in British Columbia, and recoveries have been made (A. T. S. Wilkinson, personal comm.).

A phorid, Megaselia paludosa (Wood) was discovered from T. paludosa by Coggins (31). Like S. goniculata larvae, the phorid larvae are visible through the leatherjacket's integument, and they are probably true parasites of T. paludosa (28).

Rennie (136) described Aganomorpha tipuloides, a nematode that kills leatherjackets before they pupate, but occurs in only ca. 1.2% of the population. Neop teroctaena affinis Bovine, N. bhiinos Bovine, Rhabditis tipuliformis Lam and Webster, and Panagrolaimus tipuliformis Lam and Webster were found capable of entering larvae per os, but they were unable to penetrate the gut wall into the hemocoel. They feed on and multiply in the insect only after it is dead or dying (19, 81).

Lam and Webster (82) achieved high leatherjacket mortality using DD-166, a nematicide of Neop teroctaena affinis Weiser with its associated bacterium Achrobacter nematophilus Poinar and Thomas, but only at high doses. They also discovered that preparations of β-exotoxin of Bacillus thuringiensis var. thuringiensis caused leatherjackets mortality, but spores and crystals of the same bacterium did not. Larvae that survived the β-exotoxin treatment often produced morphologically abnormal pupae and adults.

Krieg (79) reported that Bacillus cereus var. mycoides Flügge was isolated from T. paludosa. Leatherjackets are susceptible to Ricetella tipuloides Müller-Krüger (115). Crystalline inclusion bodies, caused by disturbance of their metabolism, were found in diseased insects' fat bodies (76).

A polyhalad viral disease was discovered in England by Rennie (135), and it was later reported in France (108). Diseased larvae are characterized by milky hemo- lymph with chromatic masses in the blood cell nuclei, hypertrophied lymphocytes with crescent-shaped inclusions in their nuclei, and a flaccid, pale body (150, 165). Tipla iridescens virus (TIV) was discovered in England by Xeros (168) during a routine examination of leatherjackets for the polyhalad virus. Darkly staining, icoshedral bodies were described from the fat bodies. These give infected larvae their characteristic blue iridescence (131, 148). Both viral types are sometimes found in the same larva (149).

The most common and effective fungal infection is Entomophthora (Ennopa) aereonecta Giard. It is lethal but not very contagious (2, 114). Other reported fungi associated with T. paludosa are Cordyceps militaris Fr., Cylindrocladium sulphuratum Petch, Beauveria bassiana (Bals.), and Spicaria heliothidis Charles (116, 117, 152). Janisch (78) described an unknown black spot disease on T. paludosa, and Coolson (35) found an undescribed fungal infection on leatherjacket tracheae.

Several protozoan representatives have been found in T. paludosa, Vickerman (165) found Herpetomonas indi- sulgi (Kramer), a flagellate, and Carl (27) reported an undescribed Microsporidia. Representing other sporozoans were Haptodiscus tipulae Hugg (77), Adelina tipulac Leger (164), and Gregarina longa (Leger) (27, 28). Unidentified gregarines were discovered in British Columbia and Washington, but no connection with larval survival has been established (A. T. S. Wilkinson personal comm.).

Adult Activities

Mating

Crand flies are sexually mature at emergence (37, 57, 118), and mating occurs almost immediately after the females leave the pupal case (7, 35, 130, 166). In fact, males are sometimes attracted to females trying to free themselves from their pupal cases, and they may wait beside females until they are free or actually help dislodge them (1, 2, 57, 142, 157). Females invariably are attended before they lose their teneral appearance, and often several males can be found around one emerging female. Traynor and Burton (157) found males were attracted to females trying to emerge but not to intact pupae.

Males have been described as walking and flying awkwardly over plants and tree trunks while searching for females (6, 121, 142). Evidence that physical contact is necessary to initiate mating activity for representative crane fly species has been presented (1, 23, 57, 142), but Catherson (57) and Neumann (118) believed visible recognition of the female is important for the male to respond. Neumann (118) described T. paludosa males searching individually along the ground for females, and diving with wings buzzing once a female was sighted. Males of T. paludosa do not swarm, and this is typical for Tipla sp. (1, 37).
In this study, males blinded with black tempera paint were hyperactive for a short time after the paint was applied. During this period no mating attempts were made with either virgin or field-females, even when physical contact with them was made. Soon, however, blinded males settled down and most hung from the sides of the cages. Occasionally they moved in a normal fashion or tried to mate, but only when there was physical contact with the female. Although blinded males acted normally once they were in copula, the number of mating pairs was never as high as for normal males. Since most mating took place after dark in the field, the males could not rely on vision for finding females.

Freeman (48) reported the existence of a sex attractant in Tiphula lirvisda van der Wulp. He thought it likely such attractants exist in genera with marked sexual dimorphism of the antennae, or as in some Tiphula, including T. paludosa, in which the male antenna is larger than the female's.

Information gathered from a Y-tube olfactometer suggested that no long-range sexual attractant exists in T. paludosa. No differences were found between the average number of virgin and field-males attracted to either virgin or field-females. Also, no differences were found in the number of males attracted to the female-containing choice-chamber when it was reversed in position with the control. Therefore, these data were pooled, and a paired t-test was run on the average number of males attracted to the female-containing choice-chamber and the average number attracted to the control for each experiment (Table 5). In neither case was there any significant difference between the means at the 5% level of significance.

Males that chose the female choice-chamber showed a marked tendency to remain there, whereas those that chose the control often reversed their paths. This finding supports the preliminary investigations of Trendier and Burton (157) who found a close-range mating stimulus in T. paludosa, but were unable to isolate it. Since males were attracted to emerging females (35, 157), some sex attractant might exist in callow females; this has not been investigated.

TABLE 5. Paired t-test between the average number of Tiphula paludosa males attracted to female-containing choice-chambers and the controls of a Y-tube olfactometer.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Avg number per trial (J)</th>
<th>Number of trials (n)</th>
<th>SD</th>
<th>Paired-t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males in the control</td>
<td>2.08</td>
<td>12</td>
<td>0.90</td>
<td>1.40 with 22 df</td>
</tr>
<tr>
<td>Males attracted to virgin females</td>
<td>1.92</td>
<td>12</td>
<td>0.67</td>
<td></td>
</tr>
</tbody>
</table>

After a male locates a mate, he lands above the female and takes a firm hold on her with his long legs. He then bends his upturned genitalia under her abdomen and moves the hypopygium, with widely spread gonopods, around until he resets the base of the hypovalves with his outer gonostyl. As the hypovalves are massed into the male genital chamber, the 1st and 2nd parts of the inner gonostyli interlock with the trough formed by the inner surface of the hypovalves, the genital trough. Muscle contractions and the elasticity of the gonocoxopodites cause the inner gonostyli parts 1, 2, and 3 to press firmly against the inner wall of the genital trough forming a double grip. The male gonopods act independently (118).

Once a firm grip is formed between the genitalia, the male lets go with his legs and the pair assume a tail-to-tail mating position. The genitalia are arranged so the male dorsal surface is rotated 180° from that of the female. This temporary torsion (145) is achieved mainly through the twisting motion of the male abdomen, but the female may also be conorted to maintain the proper intercomexion. The female takes the initiative, drags the male up a stem, and hangs there motionless. The male is usually suspended head-downward for the duration of mating, but this varies. Pairs may even take to the air while still in copula.

Two pairs of hair tufts located on the male's 9th sternum move alternately along the base of the female's cerci, which occasionally brush along the sides of the male hypopygium. These stimulus activities diminish as copulation progresses (66, 118). Periodic quiverings of the antennae, wings, and halteres have been reported (37, 153).

During copulation, the cerci and hypovalves are widely separated, thus opening the genital chamber and exposing the opening into the vagina for the insertion of the semealag. Sperm is transferred directly into bursa copulatrix, which lies just posterior to three spermathecae.

The duration of mating is quite variable in T. paludosa. Barone (7) and Lovibond (91) reported matings lasted for ca. 2 hr. Coulson (35) and Sellke (145) thought pairs remained in copula for 3 hr or more and for half a day or longer, respectively. Mating times of several hours are not uncommon for riputilids (23, 67). Downes (41) stated that sperm-transfer in most riputilid forms is slow, due to the fine caliber and inelastic walls of the semealag ducts.

In our laboratory, some matings were completed in less than an hour, although pairs often remained coupled longer. Nine observed pairs mated in 35-240 min; the mean time was 105 min (SD=65 min). Mating in the field was often quicker, since pairs uncoupled when disturbed. It was not determined whether females that mated for only a short time contained enough sperm to fertilize their full complement of eggs. Both males and females can mate more than once, but additional matings are not essential (7, 37, 153).

Sex ratio

A preponderance of males in a crane fly population is common (46, 65), although not universal. Sampling
at light traps, Lovibond (90) reported 77% males, and Robertson (141) trapped an average of 71.2% males over a 4-year period. Traynor and Burton (157) collected over 80% male T. paludosa from sticky board traps in British Columbia, and 67.8% males were collected from a 14-ft (4.5 m) sticky board in our study. Selike (145) and Hemmingsen (62) also reported a high proportion of male T. paludosa. However, these studies probably gave a distorted sex ratio, since they did not allow for differential mortality, differences in emergence times of the sexes, and behavioral influences.

Attempts at getting an absolute sex ratio have also been made. Barnes (7) calculated 62.2% males from larvae he raised in the laboratory, and Coulson (35) reported 63.2% males from pupal cases counted over the whole emergence period. For our study, the total, overall sex ratio was determined from pupal case counts after emergence was completed. In 1972 there was 63.9% males and 55.1% in 1973 on the final day of counting.

There is evidence, however, that the sex ratios of many tipulids are not constant throughout the emergence period (46, 57, 62, 68, 93). Moreover, an increase in the proportion of female pupal cases was observed over the emergence period during this study (Fig. 12). Since pupal cases accumulated from preceding days, the increase in female pupal cases gave only a relative estimate of the increase in female emergence.

Authors working on several crane flies reported that males emerged before females (1, 37, 75). Hadley (57) attributed the changing sex ratio to the later recruitment of Moleophilus atrofemales into the population. Delay in female emergence is due either to her having a longer larval period or a longer pupal period than the male. Laughlin (86) and Hadley (59) ascribed the later recruitment of female T. oleracea and Moleophilus ater into the population to a difference in the length of the larval period between the sexes, not to any difference in pupal period length.

For our study, however, the percentage of total female pupae plus female pupal cases increased only slightly during the emergence period, indicating that females pupated at nearly the same time as males. A difference in pupal period length probably accounted for most of the later recruitment. Evidence for this is that the proportion of females pupae obtained in the sample increased faster than the increase of female pupal cases, since females remained as pupae longer than males (Fig. 13); i.e., the increase in the proportion of female pupae found was due to more males emerging before females, even though they pupated at nearly the same time.

Oviposition

Female tipulids usually begin egg laying shortly after mating (37, 91, 133, 162) and continue until nearly all their eggs are laid. In this study, females contained an average of over 50% fewer eggs than virgin females by the 8th hour after they had been placed as teneral in pupae into oviposition cages. They contained over 95% fewer eggs after 26 hr and ca. 97% fewer eggs by 50 hr after they were put into cages (Fig. 14). These figures are somewhat misleading, however, since only 9 of 133 females after 26 hr and 4 of 91 females after 50 hr contained over 50 eggs; most contained a residual of fewer than 10 eggs per female. Several females that were found dead contained over 200 eggs, indicating that females do not always successfully deposit their eggs in the field.

T. paludosa females typically insert only the last few abdominal segments just below the soil surface usually no more than 5 mm deep (35, 37, 62, 146). Mears (94) found eggs 18 mm deep, but only as the result of females inserting their abdomens in cracks in the soil, a practice they prefer (65). Thompson (156) found eggs 1½ inches (2.5-3.8 cm) high on dense herbage.

Crane flies normally lay their eggs in a suitable larval habitat (2, 48, 142). T. paludosa females move clumyly over the surface, stopping occasionally to oviposit.
They make several probes into the soil to test its suitability (62, 153) before ovipositing. Hemmingsen (62) believed that eggs were laid only when actual thrusts into the soil were made. Rennie (133) and Brindile (22) described females inserting their abdomen in a rotary motion. During oviposition, the female keeps her abdomen in nearly a vertical position (63), and she often assumes a tripod-like position on her back legs (16, 17, 22, 33, 165).

The mechanical process of oviposition was witnessed in the field and the laboratory for several females. Decapitated females that were floated on water were especially useful, since the ovipository process was somewhat slowed. Several investigators have worked out the mechanics and behavior of oviposition in Tipulidae (25, 62, 63, 64, 65, 69, 71, 153), so only a short synopsis of this process is needed.

Initially the ovipositor is closed tightly, but upon the release of an egg from the gonopore into the genital chamber, the cerci and hypovalves are slightly parted and downwardly directed. The ovipositor is then opened wider and the egg appears to be flipped over. Using motion pictures, however, Hemmingsen and Noerzvang (71) found the eggs are simply tipped up and pushed into the hypovalvular boat with the aid of the rudimentary 9th sternite and the cerci as the ovipositor is closed. The ovipositor is then tilted slightly downward as the cerci are depressed and abducted around either side of the hypovalves.

Hemmingsen (62, 66) believed the cerci are important for pressing the eggs into the hypovalvular boat and for opening up the substrate for the deposition of eggs, but since the cerci are opened and away from the hypovalves, they play no role in releasing the eggs. Hemmingsen (63) demonstrated that females released their eggs normally when their cerci were removed. Eggs are held tightly between the two hypovalves before they are ejected forcefully, accompanied by an upward movement of the cerci. The eggs are released with such force that they can fly up to 1 meter through the air (144). Each ovipository cycle lasts only 1.87 sec (71), and a female may lay over 25 eggs/min (85).

Fecundity

Several authors measured the fecundity of *T. paludosa* by counting eggs from dissected females. These data are summarized in Table 6. In this study, a mean of 337.6 eggs per virgin female was found. This average is higher than that of Wilkinson and McCarthy (167) in British Columbia, but lower than several European workers report.

<table>
<thead>
<tr>
<th>Author</th>
<th>Mean²</th>
<th>50</th>
<th>n</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jackson (this study)</td>
<td>337.6</td>
<td>136.6</td>
<td>35</td>
<td>147-759</td>
</tr>
<tr>
<td>Rennie (133)</td>
<td>397.7</td>
<td>123.5</td>
<td>3</td>
<td>255-490</td>
</tr>
<tr>
<td>Sellke (145)</td>
<td>36</td>
<td>500</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locjord (50)</td>
<td>272</td>
<td>44</td>
<td>28</td>
<td>48-429</td>
</tr>
<tr>
<td>Barnes (27)</td>
<td>273.4</td>
<td>110.2</td>
<td>28</td>
<td>48-487</td>
</tr>
<tr>
<td>MacCracken (19)</td>
<td>50</td>
<td>300</td>
<td></td>
<td>max 1300</td>
</tr>
<tr>
<td>Thompson (156)</td>
<td>400</td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laughlin (87)</td>
<td>400</td>
<td>400</td>
<td></td>
<td>931</td>
</tr>
<tr>
<td>Coulson (35)</td>
<td>360</td>
<td>24</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morris &amp; Fox (113)</td>
<td>350-600</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wilkinson and McCarthy (167)</td>
<td>281</td>
<td>10</td>
<td>243-330</td>
<td>281</td>
</tr>
</tbody>
</table>

² Eggs per female.
winds, which cause high evaporation rates (48, 49, 142), and they often avoid these conditions. Barnes (7) kept T. paludosa males alive for up to 14 days (mean 7) and females for up to 10 days (mean 6.5) by giving them only water. Morris and Fox (115) claimed females live 10-12 days in eastern Canadian fields. During our study, few adults lived more than 48 hr in the laboratory cages. Most were dead by the middle of the day following emergence. Adults were kept alive longer in glass jars with moistened cotton.

Adult mortality normally has little effect on population fluctuations, since most females have completed oviposition before they die.

Diel periodicity and flight

Diel periodicity of peak emergence, number of mating pairs, oviposition, and flight activity for T. paludosa were observed in this study and have been described by several investigators (35, 89, 167). Adult eclosion showed the greatest regularity. Coulson (35) and Wilkinson and MacCarthy (167) described a crepuscular emergence pattern, but Barnes (7) reported from England that emergence began in the morning and was completed by 1100 GMT. During our study, teneral females were found only shortly after or just before dark, but male teneral were occasionally found in the afternoon. In British Columbia (157) and England (35), mating begins immediately after emergence and peaks at 2300. In northwestern Washington, mating occurred at all times of the day, but the largest number of flies in copula were observed from just after dark (ca. 1900 PDT) on Sept. 1 until midnight. Oviposition started shortly after mating ceased and peaked in the early morning hours. Most females deposited a large proportion of their eggs by dawn (35, 87). During our study, over half the eggs were deposited within 8 hr after females were put into oviposition cages (see Oviposition and fig. 15).

Contrary to the crepuscular and nightly pattern described above, Barnes (7) believed the majority of mating went on in the early daytime hours. Likewise, Henningsten (62) and Henningsten and Norelvang (71) described oviposition occurring only between 1130 and 1730 GMT in Denmark, and they found several spent females between 1600 and 1800 GMT. Little afternoon or early evening oviposition was observed in northwestern Washington, however.

Lewis and Taylor (89) reported that crepuscular emergence pattern of short-lived species, such as tipulids, is the dominant factor in determining the diel periodicity of flight activity. Using suction traps in England, they obtained a maximum number of adults at ca. 2115 GMT. Service (147) placed the peak activity of several crane fly species at ca. 2.5 hr after sunset. The greatest mating activity and male movement of T. paludosa in northwestern Washington occurred between 1800 and 2300 PDT, but this included little flight. The majority of adults were captured above 3 ft on the sticky boards after 0900 PDT and throughout the afternoon. Lewis and Taylor (89) found the amount of flight activity is related to temperature, and below a minimum threshold, flight does not occur (35). In our study, no adults were collected above 3 ft on the sticky boards during cold night and morning hours.

Unlike small insects, which are often carried passively by the wind, larger ones, including Tipula, can select a particular altitude of flight. Their densities do not decrease continuously or regularly with an increase in height as occurs with passive, wind-borne arthropods (154). Although the number of flies collected from sticky boards decreased as height increased (dramatically for males; fig. 16), the log density vs. log height profile was not a straight line as would be expected for passively moved species (154). This indicates some capacity to select flying height.

In egg counts from females captured at various heights on the boards (table 7), a substantial proportion of females contained more than a residual number of eggs; the overall mean was 32.2 eggs per female. Even though the average number of eggs per female remained fairly constant at different heights, fewer females with over 100 eggs, but a greater proportion of females with 25-100 eggs were captured as height increased. Below 3 ft (91 cm), ca. 75% of the females contained fewer than 25 eggs, and above 10 ft (609 cm), only 50% did. Fully-laden females seemed incapable of ascending very high, but partially-gravid ones often flew above 6 ft, probably contributing to the species dispersion.

Tipulids have been collected at high altitudes (350 ft or 107 m and above), although not in any great numbers (56, 61). T. paludosa adults are probably occasionally swept upward to such heights, but not by active effort.
16. Number of *Tipula paludosa* adults captured at 1-ft intervals on a sticky board trap.

LITERATURE CITED


———. 1931. Number of *Tipula paludosa* females containing different numbers of eggs, and the average number of eggs per female collected at various heights on a sticky board trap.

<table>
<thead>
<tr>
<th>Height (ft)</th>
<th>Number females with:</th>
<th>Mean ± SD n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3</td>
<td>28</td>
<td>31.7 ± 6.1 53</td>
</tr>
<tr>
<td>4-6</td>
<td>21</td>
<td>35.9 ± 5.1 35</td>
</tr>
<tr>
<td>7-9</td>
<td>22</td>
<td>30.7 ± 6.7 34</td>
</tr>
<tr>
<td>10-14</td>
<td>16</td>
<td>30.2 ± 2.3 30</td>
</tr>
<tr>
<td>Total</td>
<td>97</td>
<td>32.2 ± 5.5 150</td>
</tr>
</tbody>
</table>

Mean number of eggs per female.


Un.) 5: 12-17.
92. Maseeks, H. 1939a. Die Wiesenschnecken und ihre
93. ———. 1959b. Untersuchungen zur Biologie und
94. ———. 1941. Das Schadmaß von Tipula
95. ———. 1943c. Über die Ursachen des Schad-
96. ———. 1943b. Versuche zur Bekämpfung
97. ———. 1953. Über den Massenwechsel von
Tipula paludosa Meig. in den Jahren 1917-1953 und
Deut. Pflanzenschutzdienst. (Braunschweig)
1: 177-181.
summary of the United States. Section 1—Western Washington.
99. Massie, A. M. 1940. Notes on some interesting
insects observed in 1930. Rev. Appl. Entomol. 29:
283. (Abstr.)
100. Mayor, J. G. and K. W. Browne. 1964. A ma-
chine for separating leafhoppers from turf sam-
101. Meets, A. 1967a. The relation between soil wa-
ter tension and growth rate of larvae of Tipula oleracea and T. paludosa (Diptera) in turf.
102. ———. 1967b. The relation between soil wa-
ter tension and rate of development of the eggs
of Tipula oleracea and T. paludosa (Diptera, Nema-
103. ———. 1967c. The relation between survival and water loss in larvae of Tipula oleracea and
Tipula paludosa (Diptera) on exposure to unsatu-
104. ———. 1968. The effect of exposure to un-
saturated air on the survival and development of
eggs of Tipula oleracea L. and T. paludosa Meigen.
105. ———. 1970. Susceptibility of the leathery-
jackets Tipula oleracea and T. paludosa to soil flood-
106. ———. 1972. The effect of soil flooding
on the survival and development of the eggs of
Tipula oleracea L. and T. paludosa Meigen (Dip-
Virose à corps d'inclusion chez Tipula paludosa
Agr. Fr. 45: 113-118.
108. Milne, A. 1959. The cinctid systematic area-sample
phased treated as a random sample. Biometrics
15: 270-297.
The determination of numbers of leatheryjackets in
The 1959 and 1960 population crashes in the leathery-
jacket, Tipula paludosa Meigen, in Northumberland.
111. Morris, R. F. 1954. A sequential sampling tech-
nique for spruce budworm egg surveys. Can. J.
Zool. 32: 302-313.
112. Morris, R. F. and C. S. Fox. 1963. Control of the
European spruce bark beetle in Newfoundland and
113. Müller-Kögler, E. 1957. Über eine Mykose der
Larven von Tipula paludosa Meig. durch Enopos sp.
Z. Pflanzenkr. Pflanzenpathol. Pflanzenschutz 64:
529-534.
114. ———. 1958. Eine Rickettsiose von Tipula
paludosa Meig. durch Ricketssia tipulae nov. spec.
Naturwissenschaften 45: 248.
115. ———. 1960. Descripción de souches de germes
entomopathogénés. Sûmme entomographique
Pflie im Institut für biologische Schädlingbekämpf-
ung der Biologischen Bundesanstalt für Land-und
116. ———. 1965. Cordyceps sp. (Fr.)
Link: Beobachtungen und Versuche anlässlich eines
Fundus auf Tipula paludosa Meig. (Dipt., Tipul.)
117. Neumann, H. 1958. Der Bau und die Funktion
der männlichen Genitalapparate von Tribocera an-
ulata Meig. und Tipula paludosa Meig. (Dipt.,
Nematocera). Deut. Entomol. Z. (N. S.) 5: 255-
298.
118. Oakland, G. B. 1930. An application of sequen-
tial analysis to whitefish sampling. Biometrics
119. Oldham, J. N. 1928. On the final larval instar of
Tipula paludosa, Meig. and Tipula lateralis, Meig.
121. Paul, P. J. 1969. On testing goodness-of-fit of the
negative binomial distribution when expectations are
Climatography U.S. No. 50-45.
123. Plantengymnogamie i Danmark 1928. 1930. Plant
diseases and pests in Denmark 1928. Rev. Appl.
Entomol. 18: 43. (Abstr.)
Zoolog. 18: 695. (Abstr.)
126. Plantseygdomme i Danmark 1930. 1932. Plant dis-
Zoolog. 20: 144 (Abstr.)
127. Plantseygdomme i Danmark 1936. 1937. Plant dis-
Zoolog. 27: 766 (Abstr.)
128. Plantseygdomme i Danmark 1944. 1946. Plant dis-
Zoolog. 34: 116 (Abstr.)
Ser. 1941 No. 7. 153 pp.
130. Pritchard, G. and H. A. Hall. 1971. An introduc-
tion to the biology of craneflies in a series of aban-
doned beaver ponds, with an account of the life cycle of *Tipula sacra* Alexander (Diptera; *Tipul-
131. Rees, B. E. and G. F. Perris. 1939. The mor-
phology of *Tipula reci* Alexander (Diptera: *Tipul-
dae*). Microm. Ultrastr. 4: 143-178.
132. Rennie, J. 1912. Note on a Tachinid parasite (*Bu-
ceites genuinata* de Geer) of *Tipula* sp. Proc. Roy.
133. ———. 1916. On the biology and economic signi-
134. ———. 1917. On the biology and economic signi-
116-137.
137. Rennie, J. and C. H. Sutherland. 1920. On the life history of *Bucectes* (Siphon) *genuinata* (Dip-
tera: Tachinidae), parasite of *Tipula paludosa* (Dip-
tera) and other species. Parasitology 12: 199-211.
138. Ricou, G. 1967a. L’alimentation des larves de *T
tipulidae* (T. *paludosa* Meig.). Ann. Naut. Ali-


