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

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THE AUTHORS AND THIS BULLETIN

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ABSTRACTS

The European crane fly, Tipula paludosa Meigen, has become a serious pest of lawns, pastures, and hayfields in northern Washington. The larvae, known as crane-fly grubs, are often found in lawns, lawns, and pastures, and of some species, have been 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 northern western Washington. Larvae feed on roots, stems, and leaves of a variety of grasses, trees, shrubs and other plants, seriously damaging pastures and hayfields during heavy outbreaks. Where the major agricultural industry is dairy farming, this insect may represent a serious economic impact. Because of their great abundance and habit of gathering 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 species, L. E. and T. cincta De Jong, until De Jong (40) separated out cincta adults and Hemmingsen and Leemce (70) stabilized the names, ending controversy over nomenclature. Injuries were not separated until Broadie (17, 22) and Thorowald (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) to the USSR (ca. 35 E). Introduction of this fly into North America took place in 1954 when the fungus first from Newfoundland in 1952 and 2 years later on Cape Breton Island, Nova Scotia. Larvae, known as leather-

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MATERIALS AND METHODS

The Study Area

Fields on private farms in northern Whatcom County were chosen for study because of the occurrence of high populations in areas of reported economic damage. Work during the summer of 1972 was done on 5 fields on farms near Blaine. These 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 sander drifts found in the Puget Sound basin south of 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 T.suga betulifolia (Raf.) Sarg zone (western hemlock zone) (45). It is characterized by a Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) subclimax and western hemlock- western red cedar (Tsuga heterophylla-Thuja plicata Donn.) climax forest.

The natural vegetation of western Whatcom County has been almost entirely removed by logging, with little reseeding. Much of the drier farmlands have been converted to pasture use and hayfields make up acres of what were formerly agricultural fields. Whatcom County occupies the northernmost portion of the Puget Sound Lowlands climatic area in the United States. This coast is characterized by moderate oceanic climate, the result of prevailing westerly winds from the Pacific Ocean (125, 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-March. July is the driest month (mean=0.89 inches or 22.6 cm), and December is the wettest (mean=6.32 inches or 16 cm). Snowfall is light but variable, averaging 10-20 inches yearly (99).

Summer temperatures rarely surpass 32.2 C (90 F), and the average minimum temperature in January is -2.2 C (28-32 F). Cold currents of interior air sometimes move into this area from Canada through the open northern shores of the Puget Sound trough, but usually do not last long (99, 125).

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**TABLE 7.** Numbers of *Tupila 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 of females with:</th>
<th>Mean (n)</th>
<th>SD (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>eggs 26-100</td>
<td>38</td>
<td>7</td>
</tr>
<tr>
<td>3-9</td>
<td>eggs 10-30</td>
<td>21</td>
<td>9</td>
</tr>
<tr>
<td>10-14</td>
<td>eggs 10-30</td>
<td>22</td>
<td>10</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>97</td>
<td>31</td>
</tr>
</tbody>
</table>

\(\text{Mean number of eggs per female.}\)

**TABLE 8.** Descriptions of the Wharton County, Washington fields used for *Tupila 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>Haile's</td>
<td>1A</td>
<td>6.9</td>
<td>1972</td>
<td>Pasture</td>
<td>silt loam</td>
</tr>
<tr>
<td>Paul's</td>
<td>2A</td>
<td>0.9</td>
<td>1972</td>
<td>Hay</td>
<td>silt loam</td>
</tr>
<tr>
<td>Edwards</td>
<td>3A</td>
<td>17.8</td>
<td>1973</td>
<td>Corn</td>
<td>silt loam</td>
</tr>
<tr>
<td>Laskhaar</td>
<td>4A</td>
<td>5.2</td>
<td>1973</td>
<td>Hay</td>
<td>silt loam</td>
</tr>
<tr>
<td>Dalgliesh</td>
<td>5A</td>
<td>5.0</td>
<td>1973</td>
<td>Hay</td>
<td>silt loam</td>
</tr>
<tr>
<td></td>
<td>5B</td>
<td>5.0</td>
<td>1973</td>
<td>Hay</td>
<td>silt loam</td>
</tr>
<tr>
<td></td>
<td>5C</td>
<td>3.7</td>
<td>1973</td>
<td>Hay</td>
<td>silt loam</td>
</tr>
<tr>
<td></td>
<td>5D</td>
<td>8.9</td>
<td>1973</td>
<td>Silt loam</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Soil classification from Poulson (129)

16. Number of *Tupila paludosa* adults captured at 1-ft intervals on a sticky board trap.

**References**


**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 orthodichthonemoe, Jeyes' fluid, and sodium oleate (7.8, 32, 52, 90), but Milne et al. (110) and Mayor and Browne (101) found this method inefficient, especially after May. Mears et al. (102) brought *Tupila* larvae to the surface with a common salt (NaCl) solution. Milne et al. (110) devised a dynamic water process for extracting leatherjackets, and Mayor and Browne (101) made a machine that approached 100% efficiency. Coullon (35) and Freeman (47) separated larvae by washing soil samples through graduated screens.

For this study, larvae, pupae, and pupal cases were sampled by a simple and rapid central systematic area technique similar to the one Laughlin (87) used. Milne (109) showed that if the central systematic area sample was treated as a random sample, the resulting statistics are "as reliable and practical" 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 (109). 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 3 inches (7.7 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 (43, 110, 146, 167). Each core sampled 0.087 ft³, hence 11.5 cores were needed to obtain ca. 1 ft³ (0.09 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 (57) chose 4-inch (10.2 cm) diameter cores over the traditional 1-ft³ (0.09 m³) soil samples when sampling for *Tupila* larvae. Four-inch cores proved to be a reasonable size for our study.
Cori et al. also observed a trend 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 hours 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 was during the early daylight hours. Likewise, Hemmingsen (62) and Hemmingsen and Narvaez (71) described oviposition occurring only between 1130 and 1730 GMT in Drosophila and they found several spent females between 1600 and 1800 GMT. Little 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 Tipula, is the predominant 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 (85) placed the peak activity of several crane fly species at ca. 2.5 h 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 0000 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 females. Even though the number of flies collected from sticky boards decreased as height increased (dramatically for males; fig. 16), there was a high density vs. height log profile that was not a straight line as would be expected for passively moved species (154). This indicates some capacity to select flying heights.

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 average at all heights was 100%. However, the average number of eggs per female remained fairly constant at different heights; fewer females with over 100 eggs were found at night than during the day. Eggs captured as females were considered as being attracted. Below 3 ft (91 cm), ca. 79% of the females contained fewer than 25 eggs, and above 10 ft (600 cm), only 50% did. Female masses seemed incapable of ascending very high, but partially gravid ones often flew above 6 ft, probably contributing to the higher egg counts.

Tipulids have been collected at high altitudes (350 ft or 107 m above), although not in any great numbers (56, 50). T. paludosa adults are probably occasionally swept upward to such heights, but not by active effort.

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They make several probes into the soil to test its suitability (62, 135) before ovipositing. Hemmingsen (62) believed that eggs were laid only when actual thrusts into the soil were made. Rennie (133) and Brindle (23) described females inserting their abdomens in a rotary motion. During ovipositing, 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, 53, 166).

The mechanical process of ovipositing was witnessed in the field and the laboratory for several females. Decapitated females that were floated on water were especially useful, since the ovipositing process was somewhat slowed. Several investigators have worked out the mechanics and behavior of oviposition in tipulids (23, 62, 65, 64, 65, 69, 71, 133), 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 bent. The ovipositor then opens wider and the egg appears to be flipped over. Using motion pictures, however, Hemmingsen and Noirezvag (71) found that the hypovalves are slightly expanded and pushed into the hypovalvular valve with the aid of the rudimentary 9th sternite and the cerci as the ovipositor is closed. The ovipositing process is largely downward as the cerci are depressed and abduced against either side of the hypovalves.

Hemmingsen (62, 66) believed the cerci are important for pressing the eggs into the hypovalvular valve and for opening up the substrate for the deposition of eggs, while 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 ovipositing cycle lasts only 1.87 sec (71), and a female may lay over 15 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, in a sample of 397.6 eggs per virgin female was found. This average is higher than that of Wilkinson and MacCarty (167) in British Columbia, but lower than several European workers referred to.

<table>
<thead>
<tr>
<th>Author</th>
<th>Mean</th>
<th>SD</th>
<th>n Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jackson (19th)</td>
<td>187.4</td>
<td>59</td>
<td>35</td>
</tr>
<tr>
<td>Renne (136)</td>
<td>207.7</td>
<td>72.3</td>
<td>3</td>
</tr>
<tr>
<td>Sellia (146)</td>
<td>272</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Lovbord (90)</td>
<td>272</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Barnes (7)</td>
<td>272</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Marks (59, 66)</td>
<td>300</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Thompson (156)</td>
<td>400</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Lack (118)</td>
<td>360</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Coulson (59)</td>
<td>360</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Morris &amp; Fox</td>
<td>350</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Wilkinson and MacCarty (127)</td>
<td>280</td>
<td>50</td>
<td>100</td>
</tr>
</tbody>
</table>

**Table 6. Tipula paludosa fecundity estimates of various investigators.**

**Rearing Techniques**

Larvae and pupae collected in the field were either preserved or removed for the laboratory for rearing. In individuals for preservation were killed by dropping them into boiling solution or by boiling. Boiling water invariably removed 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. Adult males 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 easily. 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. They fed little during the 1st 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 18.3-29.4°C, 90-99%), of the larvae eventually pupated. Soil from these pans was sifted every 2nd day and moisture added if necessary. The soil was replaced weekly.

Pupae were selected and placed in 5½-inch (7.9 mm) holes in moistened soil in the latter ¼ of the anterior end (fig. 8). Only 60-65% of the emerged emerged successfully. Pupae were placed in sand in the center of pans of soil 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 subfamily are typically shiny black, elliptical, and roughly 1-mm (0.04 inch) long (5, 22). *Tipula paludosa* has elongate-oval eggs with one side slightly more pointed than the other. Many tipulid species have slightly ciliated egg filaments that unwind after oviposition and attaches itself to the surrounding medium, enabling embryonic adaption for wet habitats. Unlike its closely related species, *T. oleracea* and *T. ciliata*, *T. paludosa* has no egg filament (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 Sellie (145) did detailed morphological studies on the gross internal and external structure of 4th instar *T. paludosa* for the present study. Alexander (2) gave an excellent literature review of the early morphological studies on tipulid larvae.

**Leafjackets** are nearly cylindrical, but they taper slightly both anteriorly and posteriorly (fig. 2). After the initial instar, leafjackets are light grey to greyish brown with irregular black spots 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 hemispherical integument of the head capsule and is attached to the anterior lateral external lateral plates. About ¾ of the head capsule is not attached to the integument, but it can be withdrawn into the prothoracic skin for protection.

Tipulid larvae are metamorphic, with two spiracles housed in the spiracular disc of the larval segment. The truncated end of the anal segment consists of an upper spiracular and a lower anal field which lies roughly perpendicular to the longitudinal axis of the body (fig. 3). The dorsal field is composed of the spiracular disc with spiracular tentacle and a lower anal field which is positioned laterally on the body. The pair of spiracles at the base of the spiracular disc are well defined, since the spiracular disc is supported by the lateral plates and the spiracular margin is more developed in species inhabiting wet habitats. In *T. paludosa*, only the lateral pair are elongated, the ventral papillae being reduced to rounded integumental processes (20).

Inside the larval skin, each oblong pupa (fig. 4) frees itself from the anterior end by gradually enlarging the posterior segments (fig. 5). The posterior abdominal segments bear short protrusions entering in caudally-directed siphons, which enable the pupa to wriggle to the surface before emergence (1, 5).

**Description of Adults**

Adults of *T. paludosa* are fairly long crane flies, the males being 14-20 mm (0.55-0.75 inch) and the females 10-25 mm (0.75-0.98 inch) long (5) (figs. 5 & 6). They have elongated elytra, which differ between the sexes. The sexes differ in the antennal and bristle characters, which separates them from other Tipulidae from other genera. Tipulinae are the other major families. Filiform antennae, which originate anterior to the widely separated, dichoptic eyes, have 14 segments instead of the genus-typical 13 (1, 5).

Although the pronotum is well developed, the thorax consists primarily of the large mesothorax; the halteres are not as well developed as to a small band. The wings of the females are shorter than the abdomen, the ratio of length to width is 1:1, whereas in the males, it is ca. 0.64 (62). Hemmingsen (67) linked this characteristic with less mobile forms having drier oviposition habitats, and he pointed out *T. paludosa* is the most "serophyllic" species in the *T. oleracea* group.
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 ⅓ the length of the cerci.

At light traps, Lovibond (98) reported 79% males, and Robertson (141) trapped an average of 71.2% males over a 4-year period. Traynier 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 (4.3 m) sticky board in our study. Selkie (145) and Hemmingson (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. Bursis (7) calculated 62.2% males from larvae he raised in the laboratory, and Coulson (35) reported 63.3% 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 65.9% males and 58.4% 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 Melophillus alter females 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 Melophillus alter 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 to total 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 female 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 ceases (37, 91, 133, 142) 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 teners in criptula 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 only 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.

Tiphula 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). Mearcks (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 (63). Thompson (156) found eggs 1.15 inches (2.5-3.8 cm) high on dense herbage.

Crane flies normally lay their eggs in a suitable larval habitat (2, 48, 142). Tiphula paludosa females move clumsily over the surface, stopping occasionally to oviposit.
In this study, males blinded with black temperas 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, blind 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 for normal males. Since 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 *T. palpata* (7) of *Vulpus*, which he thought this sex attractant existed in *T. palpata* (2) of *Vulpus*. 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 3). 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 group wandered their paths. This finding supports the preliminary investigations of Truayner and Burton (157) who found a close-range mating stimulus in *T. palpata*, 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.

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 contact is made with the base of the hypovales with its outer gonostylus. As the hypovales are maneuvered into the male genital chamber, the 1st and 2nd pairs of the inner gonostylus interlock with the trophi formed by the inner surface of the hypovales, the genital troph. Muscle contractions and the elasticity of the gonocoxopods cause the inner gonostylus parts 1, 2, and 3 to press firmly against the inner wall of the genital troph forming a double grip. The male gonopods act independently (118).

When a female is fully copulating, the male 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 contorted to maintain the proper interconnection. The female takes the initiative, drags the male up a stem, and hangs there motionlessly. 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. The accompanying stimulatory 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 hypovales are widely separated, thus opening the genital chamber and exposing the opening to the vagina for the insertion of the spermatophore. Sperm is transferred directly into bursa copulatrix, which lies just posterior to three spermaducts.

The duration of the sexual act varied in *T. palpata*. Barrows (7) and Lovblad (91) reported mating lasted for ca. 2 hr. Coulson (35) and Selfe (145) thought 5-10 hr was more typical and for 3 hr or less were reported for half a day or longer, respectively. Mating times of several hours are not uncommon for *T. palpata* (2, 67). Downes (41) stated that sperm transfer to the toad's form flies is slow, due to the fine caliper and inelastic walls of the sedegol 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 53, 90). 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 may mate more than once, but additional matings are not essential (37, 153).

**Sex ratio**

A preponderance of males in a crane fly population is common (46, 63), although not universal. Sampling 7,7. *T. palpata* life cycle. Larvae also lost weight before pupation. Hadley (58) maintained a large proportion of the population in *Moophilus alexandri* (Tiphididae, Limonidinae) was due to some degree to the loss of cuticle during molting, pupation, and ecdysis, and this is probably true for *T. palpata* as well.

Reasons for the 6-8 day 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 preupal period, which lasts less than 5 days at 20 C (68 F) (110), do they become more active, and at the beginning of July (153). Adults start to emerge in mid-August with peak emergence during the 1st week in September (7, 24, 107). Fig. 7 illustrates the typical *T. palpata* life cycle with time interval ranges of the life stages.

**Table 3.** Fourth instar, prepupal, and pupal weights of *T. palpata* males and females.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Average wt (mg)</th>
<th>Average wt loss (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fourth instar</td>
<td>285.5</td>
<td>253.2</td>
</tr>
<tr>
<td>Prepupal</td>
<td>145.9</td>
<td>24.2</td>
</tr>
<tr>
<td>Pupal</td>
<td>145.9</td>
<td>24.2</td>
</tr>
</tbody>
</table>

Note: Males were collected from field 5B on Aug 1, 1973.

Since the females lost a greater percentage of their weight, female pupa weighed ca. 2 times as much as field males.

Females were lost only not 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 (66). Individual weight reductions were relatively uniform from the larva to prepupa to pupa. Preparupal pupae were correlated with pupal weights (males: r=0.90; females: r=0.76) (Fig. 8).

Laubich (68) 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 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 weights were compared using Duncan's (42) multiple range test (table 3). Larvae in field 2A were considerably smaller than those from 5B or 6A. Those from field 3A were not signifi-
instars indicated that larval weights and lengths were posi-
tively correlated (r=0.85, 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 (33, 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 description is clear (134).

Leatherjackets feed on a wide variety of grasses and
other plants. They have been found on cypress, pine,
and lowbush honeysuckle (15, 80); cabbages, collard,
and turnip (101; beet, flax, hemp, tobacco, and
wheat (128); rutabaga and rye (124, 125); flax and
stevia (100, 167); corn and oats (134); potato (7); rape
(18); various weeds (156); barley, clover, buckwheat,
lettuce, peas, and even pine
seeds (9, 55, 94).

When feeding below the surface, larvae mainly attack
root hair, roots, and crowns, but they eat stems, grass
blades, and leaves of all the grass (110, 146). They
prefer tender green leaves over roots and stems. Becker
(9) and Maerck (94) maintained that larvae de-
volved best on white clover, their favorite food, and
grew well on most grasses except rye. Ricou (138, 140)
found larvae grew optimally when fed members of Com-
positae. Such a wide assortment of host plants reflects
rather indiscriminate feeding habits. In fact, larvae sub-
sidize on decaying roots 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, 146),
they move up and down in their burrows in response to
stimuli of touch, light, heat, and relative humidity of
the air and soil. Tipulidae larvae were observed mov-
ing by slowly extending and contracting their bodies.
Laughlin (86) listed a set of movement patterns to progres-
sively stronger adverse stimulation. The first was longi-
tudinal contraction, the second rapid curling and uncurl-
ingen as effective in British Columbia (82, 167), and
northwestern Washington.

Alexander (2) listed 155 species of birds known to
feed on Tipulidae. Williamson and Mass-
Carrith (167) observed starlings feeding in large
numbers on larvae in Vancouver, and many were seen feeding to-
gorge on larvae in Washington. Although they fed main-
lly on leatherjackets during their breeding season, Dunnet
(43) found larvae were only a maximum of 75% of
starlings and weasels eating a memorable diet. Since
most females are rarely seen after the majority of their
eggs are laid, this feeding affects the population mini-
mus.

Carabids and other cantharids feed on tipulid larvae,
but most insect predation is on the adult stage. Freeman
(47) and Cat (28) mentioned the importance of the
carabids Erubia cupreus, Daedon, and Poterius sp. Insects
known to prey on tipulid adults include Odontota, Asil-
dinae, Empidinae, Anthomyiidae, and Rhagio-
idae (2, 39).

The tachinid Siphona geniculata (De Geer) is the
most important parasite of T. paludosa, and it is
the only regularly associated with it. S. geniculata
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 "fetal
chamber." There were two parasite generations per year in
Europe and the parasite overwinters with the leather-
 jackets. Larvae hatching in late May and June the next year from May 82, it ranges from ca. 5-20%. S. geniculata was released in
British Columbia, and recoveries have been made (A. T. S.
Wilkinson, personal communication).

A phorid, Megaelia paludosa (Wood) was discovered from
T. paludosa by Coggins (31). Like S. geniculata larvae, the phorid larvae are visible through the leather-
/jacket's integument, and they are probably true prob.
iform larvae (28).

Emmel (136) described Agamosperopsis titulus, a nema-
tode that kills leatherjackets before they pupate, but it
occurs in only ca. 1.2% of the population. Neoplectana ef-
hibita (Wood) is the only species of Rhagio sp. that
Lamb and Webster, and Panagrolaimus paludosa Lamb and Web-
ster 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).

Lamb and Webster (82) achieved high leatherjacket mortality using DD-153, a insecticide, in captivity.

Krieg (79) reported that Barillas cernea var. meicoles
Flugge was isolated from T. paludosa. Leatherjackets are
susceptible to Nickiecella tipulae Müller-Klieger (115).
Crystalline inclusion bodies, caused by disturbance of their
metabolism, were found in diseased insects' fat bodies
(78).

A polybacterial viral disease was discovered in England by
Rennie (135), and it was later reported in France (70).
Diseased larvae are characterized by milky hemo-
lymph with chromatic masses in the blood cell nuclei,
hypertrophied lymphocytes with crescentic inclusion
in their nuclei, and a flaccid, pale body (160, 167).
Tipula iridescens virus (TV) was discovered in Eng-
land by Lack (47) and during a routine examination of
leatherjackets for the virus occurs almost immediately after
females lay the egg case (7, 35, 160). In fact, males are sometimes attracted to females trying to free
themselves from their pupal case (1, 6, 121, 14). Physical contact is necessary to initiate mating activity for representative crane fly species has been presented (1, 23, 57, 142), but Cranefly (37) reported a female's recognition of the female is important for the male to
respond. Neumann (118) described T. paludosa males as sea green, individually recognizable from the ground females, and di-
veng with wings blowing once the female was sniffed.
Males of T. paludosa do not swarm, and this is typical for
Tipula sp. (1, 37).

### TABLE 3. Comparison of Tipula paludosa mean larval weights from 6 northwest Washington fields using Dunnet's (43) multiple range test.

<table>
<thead>
<tr>
<th>Field</th>
<th>Mean larval wt (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2a</td>
<td>39.71</td>
</tr>
<tr>
<td>3a</td>
<td>33.20</td>
</tr>
<tr>
<td>4a</td>
<td>37.47</td>
</tr>
<tr>
<td>5a</td>
<td>40.77</td>
</tr>
</tbody>
</table>

Means connected by vertical lines are not significantly different at the 5% level of confidence. Those not so connected are significantly different.

### Analysis of variance:

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Mean squares</th>
<th>df</th>
<th>Mean F value</th>
<th>Prob.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between fields</td>
<td>3590</td>
<td>5</td>
<td>718</td>
<td>0.00</td>
</tr>
<tr>
<td>Within fields</td>
<td>5796.00</td>
<td>58</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Significant at the 15 level.**

C. Coefficient of variation = 24.85

---

Crane flies are sexually mature at emergence (37, 57, 118). Mating occurs during or after emergence, and the females lay the pupal case (7, 35, 160). In fact, males are sometimes attracted to females trying to free themselves from their pupal case (1, 6, 121, 14). Physical contact is necessary to initiate mating activity for representative crane fly species has been presented (1, 23, 57, 142), but Cranefly (37) reported a female's recognition of the female is important for the male to respond. Neumann (118) described T. paludosa males as sea green, individually recognizable from the ground females, and diving with wings blowing once the female was sniffed. Males of T. paludosa do not swarm, and this is typical for Tipula sp. (1, 37).

### Adult Activities

Mating

Cranefly flies are sexually mature at emergence (37, 57, 118). Mating occurs during or after emergence, and the females lay the pupal case (7, 35, 160). In fact, males are sometimes attracted to females trying to free themselves from their pupal case (1, 6, 121, 14). Physical contact is necessary to initiate mating activity for representative crane fly species has been presented (1, 23, 57, 142), but Cranefly (37) reported a female's recognition of the female is important for the male to respond. Neumann (118) described T. paludosa males as sea green, individually recognizable from the ground females, and diving with wings blowing once the female was sniffed. Males of T. paludosa do not swarm, and this is typical for Tipula sp. (1, 37).
temperate 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 if kept at 5°C (70 F), and Barnes (6) maintained there is a critical temperature below which tidipulids cannot emerge.

Soil and air humidity

Most tidipulids live in wet habitats (34, 64), and although T. paludosa is found in drier conditions than many tidipulids, it is frequently found in marshy areas in low lying areas (20, 22, 35). Exposure to unsaturated or air soil, which occurs during drought, can have drastic effects on the growth and survival of eggs and larvae (74, 96, 111). In fact, population crashes have been directly attributed to excessive mortality due to desiccation of eggs and larvae (55, 113).

When placed in unsaturated air, eggs lose water until they reach equilibrium with the air. T. paludosa larvae eggs less than 15 min old dry within 2-4 min in unsaturated air (84, 85), but older eggs of this species and T. paludosa become progressively more resistant to desiccation (55, 94). Maercks (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 in soil water tension delays hatching. Meats (103) linked this delay to a prolongation of the mid-incubation swelling. There is a certain amount of evidence for this, even in wetting drying, although it is slowed (84, 103, 105). Since humidities in the grass mat and soil surfaces fall below 98%, 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 resulting from desiccation than at any other humidity level (35, 85, 105). Although newly hatched larvae are very susceptible to any unsaturated condition, later instars can withstand much longer periods with less mortality (107).

Older larvae also move up and down in their burrows to escape adverse conditions (58).

Meats (102) found a considerable influx of water into larval prepuce in wet weather. By sealing off their mouths, anal openings, and anal papillae, he found that water enter
ted through the general concave surface, which lacks an epicuticular hydrophobic barrier (53). 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, wet, warmer than normal years often give rise to population explosions (25, 32, 126, 127). MacLagan (92) and Maercks (95, 96, 98) contrasted high larval densities in 1974, spring with high winds the previous autumn when the larvae were small.

Maercks (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

T. 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 or two. During hot, dry, windy 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, and leach are specially

ated to sink in, while others cause it to run off (66).

In our study, the only detrimental effect of soil texture on population density was on Kissiln 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).

Floodling

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

Hadley (58) attributed death of Molophilus ater larvae to lack of oxygen when larvae were placed in previ
ously 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 shorter at 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 leafhopper numbers. Biological control is even

ing, and the third was a combination of curling and rapid revolving on their own axes. Stelle (165) and Freeman (47) pointed out such reactions might be important for diapause promoting agents. T. paludosa is a diapause, tidipupae 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 lasting a few minutes, the pupa splits along the midline from the occipital region to the metathorax, and the anterior appendages protrude as the leg sheaths (2, 22, 23). First the thoracic dorsum and shortly after the tucked-under head emerges from the pupal case. Maxillary palps, antennae, wings, and legs are slowly pulled from their sheaths. Once the front legs are free, the adult usually grabs some support and pulls itself from its case (35, 162). In T. paludosa, the liquid meconium is not discharged until after the adult has emerged, giving several adults a pale greenish, transparent appearance which they may retain for several hours (23). Moisture is important in some air conditioned lab oratory cultures, and it may seriously reduce the popula
tion. Helpful 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 T. paludosa sometimes attack other larvae in the field due to competition for space.

The percentages of larvae (including prepupa), pupae, and pupal cases collected each day by core sampling are plotted in fig. 10. Pupa started showing up in the samples during 1 August 1972 and 1 August 1973, and the largest percentage of pupae in the samples was found near the end of that month (August 26 and August 28, 1972). Pupae were observed in the field after August 15 of each year, and the 1st week in Sep
tember, eclosion was at its peak. A few flies were taken in 1973, but not as a result of pupation, pupa remained in the soil until the 2nd week of October, but 99% of the emergence occurred in the 22 days from August 25 to September 13. Coulson (36) found 2 standard deviations (94.5%) 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 Molophilus 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 pupal period was 13.5 days (mean = 12.7 days, SD = 1.4). A range of 10-12 days for pupal duration agrees with 11 days reported by Oldham (129) 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 Burges and Benham (34), who had September 1 and September 6, respectively, from northern Europe. Wilkinson and McCarthy (167) observed peak emer
gence in British Columbia on September 1. Thompson

Spatial Distribution of Immature Stages

Knowledge of the spatial patterns of individuals is im
portant 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 in
vestigated. Original core counts of immatures obtained by the above-mentioned sampling method (see Materials and Methods) were summarized in frequency distribu
tions, showing the number of cores containing 0, 1, 2, or 3 individuals. The data from these surveys showed that the frequency of 4 fit a negative binomial distribution with 4 of these also fitting the Poisson series. Other distributions fit only the Poisson and we could test the Poisson nor the negative binomial (table 4). Field counts that fit both of these distributions are normal for any insect population (162). For 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 contagions, 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, 165).

The negative binomial is defined by two constants, the arithmetic mean $n$ and the expected value $k$. Calculations of the expected frequencies were obtained using the formulae of Bliss and Fisher (14). Several methods of estimating the parameter $k$ have been proposed (3, 4, 13). 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 20-30 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 expected values was used so that no expectation was less than 2.

Values of $k$ ranged from 0.90 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 $k$ indicate that 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 presence or absence of natural enemies (30, 112), and comparisons of $k$ can only be made using the same sized units.

The dispersion parameter $(k)$ is not necessarily a constant value nor a general characteristic of a species (30), and several authors (12, 155, 165) 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, 165, 110). When usable, transformed counts with a common $k$ give the most infor- mative analytic of variance. A common $k$ for these data was computed, using an extension of Anscombe’s (3, 4)

<table>
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<tr>
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<th>$\chi^2$</th>
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<td>IA</td>
<td>1972</td>
<td>3.75</td>
<td>3.63</td>
<td>81</td>
</tr>
</tbody>
</table>

Responses to the physical environment and to host plants probably contributed greatly to featheredaggregation. Soil differeances affected the distribution both between within fields. Larvae were seldom found in beds, near woody hosts such as Rickerville or Leucaena. Brown (6) reported that soil texture is important in crane fly distributions, and several authors (9, 59, 94) described the plant selection, which might lead to contagion in crane fly larvae.

Reproductive behavior is another important factor contributing to the overall dispersal pattern in 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 mostly flightless, oviposition in pastures is heaviest near the taller plants. Females lay their eggs in small clusters in relatively limited areas (62, 133). Since hatching of eggs depends on the microhabitat (see Environmental Factors section), either a majority of any one egg clutch or a majority or none hatch or a majority does not hatch. This causes an aggregated distribution of hatching larvae. Although larvae may move laterally throughout their lives (10, 154, 166), 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 interferences among any one of the three species were minimal during this study. Starlings, Sturisina spurcius, 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 effect was minimal during the study. Since many 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 popal cages) were caused by combinations of responses to the physical micro-environment, host plant selection, reproductive behavior, and effects of the sampling procedure. The data presented here 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 (162). Habitat suitability is determined by several factors, including weather, soil texture, grass characteristics, biological control agents, and pasture management (56). However, most important for regulating population distributions and fluctuations in size are microclimatic conditions (43, 54, 139, 140). Eggs and early larvae are particularly sensitive to changes in these conditions. The best independent seasons; the population level is therefore dependent upon weather during this period of early develop-ment (35, 58). Later instar mortality, larval competition, adult pre-pupillary mortality, and fecundity have less effect on population levels (58, 87).

Temperature

Several authors (87, 105, 107) showed the relationship between tadalafil and development of temperature. Warmer temperatures generally increased the growth rate in the laboratory and field. The temperature optimum for tadalafil development is at 5.5°-5.0° F (175.2-179.0° F), which is quite similar to August and September temperature normals in northwestern Washington (78). Warmer soil temperatures increase larval growth rates, but Laughlin (86) found a wide variation in stadium duration at any one temperature. Hardin's workers take their toll of 2nd and 3rd instars (113, 140). Lange (88) attributed a population crash partly to 75 consecutive frost days. Freezing temperatures alone are not normally fatal to featherjackets, and when thawed from frozen blocks of soil, complete de-hatches or a majority does not hatch. This causes an aggregated distribution of hatching larvae. Although larvae may move laterally throughout their lives (10, 154, 166), their initial aggregation probably affects their distribution for some time.

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insect counts (12, 15). It can be derived at least five biological and mathematical models (151, 165).

The negative binomial is defined by two constants, the arithmetic mean and the dispersion parameter (64). Calculations of the expected frequencies were obtained using the formulae of Bliss and Fisher (141). Several methods of estimating the parameters have been proposed (3, 4, 13). The method of maximum likelihood estimate, described by Bliss and Fisher (141), was chosen since it is applicable when the number of insects does not exceed 20-30 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 for pooling frequencies with small expectations was used so that no expectation was less than 2.

Values of k ranged from 0.90 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 of the surveys. 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 factors such as density of the host plant, and comparisons of k can only be made using the same sized units.

The dispersion parameter (k) is not necessarily a constant value but a general characteristic of a species (90) and several authors (12, 155, 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). When used, transformed counts with a common k give the most informative analysis by variance. A common k for these data was computed, using an extension of Anscombe's (3, 4) weighted moment estimate in zeros of regression and small samples, outlined by Bliss and Owen (15). After 3 approximations, the estimated common k stabilized at 8.04. The Chi-square value (100) was close to the df significant at the 5% level of significance, indicating that a common k is not applicable to these data. An analysis of variance showed a much greater error sum of squares than expected, which indicates heterogeneity of the component distributions (15).

The several authors found k increased linearly with the mean (3, 4, 12, 15). For these data, the linear correlation between k and the mean was r = 0.60 (n = 15).

Debeuche (39) believed individuals involving 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 expands to exceed, 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, the size of the 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 the individual aggregations. Soil differences affected the distribution both between and within fields. Larvae were seldom found in heavy, busy, soil patches such as Rickerville and Warren. However, in 6 fields reported that soil texture is important in cranefly fly distributions, and several authors (9, 95, 94) described the host plant selectivity, which might lead to contagion in cranefly larvae.

Reproductive behavior is another important factor contributing to aggregation. In 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 mostly flightless, oviposition in pastures is heaviest near the taller plants. Females lay their eggs in small clusters in relatively limited areas (62, 133). Since hatching of eggs depends on the microhabitat (see Environmental Factors section), either a majority or any one egg cluster's mates or a majority does not hatch. This causes an aggregated distribution of hatching larvae. Although larvae may move laterally throughout their lives (10, 154, 161), their initial aggregation probably affects their distribution for some time.

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

Larval interactions among any of one egg cluster's mates, or a majority of them, are minimal during this study. Starlings, Sturis vulgaris, are gregarious feeders on cranefly flies (43), and they might have caused some aggregation through patchy elimination of the larvae. Although cows probably tampered some larvae to death, especially along paths or under shade trees, their effects were minimal. The pastures were sprayed with pesticides to the study fields and heavy farm machinery was driven on 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 the combinations of responses to the physical micro-environment, 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 cranefly 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, the most important for regulating population distributions and fluctuations in size are microclimatic conditions (35, 54, 139, 140). Eggs and early larvae are particularly sensitive to changes of these dimensions independently; 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 cranefly density and development time. Warmer temperatures generally increased the growth rate in the laboratory and field. The temperature optimum for cranefly development is (57.3-59.0 °F), which is quite similar to August and September temperatures normally in northwestern Washington (78). Warmer soil temperatures increased larval growth rates, but Laughlin (86) found a wide variation in stadi duration at any one temperature.

Hard winter stress the toad of 2nd and 3rd instars (113, 140). Lange (88) attributed a population crash partly to 75 consecutive frost days. Freezing temperatures alone are not normally fatal to larvae, and when drained from frozen blocks of ice, complete desiccation or visible is not fatal to larvae placed on damp filter paper above -7.5°C. The larval stage of T. paludosa is shortened when larval deaths 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 dish can a tightly fitting, clear plastic lid at 21°C (69.8 °F). The 2nd, B, was identical to the first except that two cans with opaque lids were used. The third, 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-
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°F), and Barnes (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 tolerant of low humidity. In clay loam in 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, 96, 111). In fact, population crashes have been directly attributed to excessive mortality due to desiccation of eggs and larvae (55, 115).

When placed in unsaturated air, eggs lose water until they reach equilibrium with the air. Tipula oleracea eggs less than 15 min old dried up in 2.2 min in unsaturated air (84, 85), but older eggs of this species and T. paludosa become progressively more resistant to desiccation (55, 94). Maercks (94) maintained 100% humidity was required for egg development, but Meats (105) found eggs, after mid-infection swelling, could withstand 98% relative humidity (RH) and hatch.

Reduction in soil water tension delays hatching. Meats (105) linked this delay to a prolongation of the mid-infection swelling. There is a certain amount of development during drying, although it is slowed (84, 103, 105). Since humidities in the grass mat and soil surfaces fall below 95% 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 at any other humidity level (35, 85, 105). Although newly hatched larvae are very susceptible to any unsaturated condition, later instars can withstand desiccation much longer 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 sand. By sealing their bellies through their anal openings, and anal papillae, he found that water entered through the general concave surface, which lacks the epidermal layer at 4°C (41°F). 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). MacLucan (92) and Maercks (59, 95, 96) recorded high densities of 34 spring with high rainfall the previous autumn when the larvae were small.

Maercks (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

T. 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 live 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 tops of soils during dry weather, the top inch of turf loses water rapidly, drying eggs and young larvae (47, 102, 103, 104). Some soils retain water better than others, and leach are conditions that hinder growth in the leg sheaths (2, 22, 23). First the thoracic dorsum and shortly after the tuckered head emerges from the pupal case. Pupal sheaths are transparent, wings, and legs are released, but sheaths still remain.-

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 Keizer's site II in a zone where the grass plant canopy is high. These conditions are relatively lower rainfall and soil air humidity, and it may seriously reduce the population. Helpless prepupae, 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 from the plant in the field under competition for space.

The percentages of larvae (including prepupae), pupae, and pupal cases collected daily by core sampling are plotted in fig. 10. Pupae started showing up in the samples during early August, with the highest in late August and early September. The largest percentage of pupae in the samples was near the end of that month (August 26 and August 31), and measurable emergence was observed shortly thereafter, with pupae being taken in the samples on August 15 in each year, and by the 1st week in September in both 1972 and 1973. The peak of emergence occurred in the 2nd week in September, and pupae were taken in the samples through the 2nd week in October, 1973. The percentage of pupae in the samples was highest in early October, 95% of the pupae emerged during the 1st week in October, and pupae were taken in the samples through the 2nd week in October, 1973. The peak of emergence occurred in the 2nd week in September, and pupae were taken in the samples through the 2nd week in October, 1973. The peak of emergence occurred in the 2nd week in September, and pupae were taken in the samples through the 2nd week in October, 1973. The peak of emergence occurred in the 2nd week in September, and pupae were taken in the samples through the 2nd week in October, 1973. The peak of emergence occurred in the 2nd week in September, and pupae were taken in the samples through the 2nd week in October, 1973.
insects indicated that larval weights and lengths were posi-
tively correlated (r=0.85, 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 (33, 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 description is apparent (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 (101); beet, file, hemp,
tobacco, and wheat (128); rutabaga and rye (124, 125);
flour and strawberry (100, 167); corn and oats (134); potato (7); rape (18); various weeds (156); bar-
ley, clover, buckwheat, lettuce, peas, and even pine
seeds (9, 55, 94).

When feeding below the surface, larvae mainly attack
root hairs, roots, and crowns, but they eat stems, grass
blades, and leaves of the grass (13). (They prefer tender
green leaves over roots and stems. Becker (9) and Maercckt (94) maintained that larvae de-
veloped best on white clover, their favorite food, and
grew well on most grasses except rye. Rivo (138, 140)
found larva grew optimally when fed members of Com-
positae. Such a wide assortment of host plants reflects
rather indiscriminate feeding habits. In fact, larvae sub-
sisted on decaying roosters 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 im-
portant factor of competition among larvae (47).

Although tipulid larvae are sluggish and have low res-
piration rates, especially in the 4th instar (75, 146), they
move up and down in their burrows in response to stimuli
of touch, light, heat, and relative humidity of the
air and soil. Tipulidae larvae were observed moving
by slowly extending and contracting their bodies. Lauglith (86) noted a second more active period to pro-
gressively stronger adverse stimulation. The final is longi-
tudinal contraction, the second rapid curling and uncurl-

less effective in British Columbia (82, 167), and north-
western Washington.

Alexander (2) listed 155 species of birds known to eat
fungus in Cordilleras. Williamson and MacC.
Gathry (167) observed starlings feeding in large
numbers on lawns in Vancouver, and many were seen feeding to-
grow on vacant lots in Washington. Although they fed main-
ly on leatherjackets during their breeding season, Dunnet
(43) found larvae were only a maximum of 75%.
Settars and sea gulls eat a number of these flies, but since
most female gulls are abroad by the time most of their
eggs are laid, this feeding affects the population mini-

Carabids and perhaps cantharids feed on tipulid larva,
but most insect predation is on the adult stage. Freeman
(47) and Cali (28) mentioned the importance of the
carabids Elaphrus cyanus Dufa and Poecilus sp. Insects
known to prey on tipulid adults include Odonata, Asil-
dae, Empididae, Anthophoridae, Scaphidiidae, and Rhagii-
oleidae (2, 39).

The tachinid Spilbus geniculatus (De Geer) is the most
important parasite of T. pallidula, and it is the only
regularly associated with it. S. geniculatus 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
larvae. The entire larval period is never closer than
532, it ranges from ca. 5-200. S. geniculatus was released
in British Columbia, and recoveries have been made (A. T.
S. Wilkinson, personal communication).

A phorid, Meganeura paludosa (Wood) was discovered
from T. paludosa by Coggins (31). Like S. geniculatus
larvae, the phorid larvae are visible through the leather-

A coefficient of variation of 24.85

The 0.05 level of confidence. Generally, the smaller the
field size and the more areas sampled, the more accurate
the estimate. The 15 level is the most reliable.

Ease of analysis: value of

Table 3 shows the mean larval weights of male and
female T. paludosa collected in northwest Washington
fields (47). The data show that male tipulidae larva
are significantly heavier than females. However, the
larval weights of the 0.1 level are not significantly
different from those of 2A or 5B, but field 4A
larvae were much heavier than the other 3 fields (P<.05). Fig. 9 shows that larval size increased
with larval density. This is probably due to the fact
that a more suitable mating group can support not only more larvae
but also maintain them better.

Lauglith (86) stated early growth takes place in
all parts of the larval body with every growing day growing
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, 164). Measurements of 4th

TABLE 3. Comparison of Tipula paludosa mean larval weights from 4 northwest Washington fields using Duncan's (47) multiple range test. Mean larval weights (mg)

<table>
<thead>
<tr>
<th>Field</th>
<th>Mean larval wt (mg)</th>
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<tbody>
<tr>
<td>2A</td>
<td>136.7</td>
</tr>
<tr>
<td>3A</td>
<td>138.2</td>
</tr>
<tr>
<td>1A</td>
<td>137.1</td>
</tr>
<tr>
<td>4A</td>
<td>402.7</td>
</tr>
</tbody>
</table>

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

Lauglith (86) noted that the smaller the field size and the more areas sampled, the more accurate
the estimate. The 15 level is the most reliable.

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the estimate. The 15 level is the most reliable.
In this study, males blinded with black tempos 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, blind 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 for normal males. Since 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 *Tiptula littida* van der Wulp. He thought it likely such attractants exist in genera with marked sexual dimorphism of the antennae, or as in some *Tiptula*, 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 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 95% level of significance.

Males that chose the female choice-chamber showed a marked tendency to remain there, whereas those that chose the control wandered their paths. This finding supports the preliminary investigations of Tranyier and Burton (157) who found a close-range mating stimulant 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.

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 contact with the base of the hypovalves and then into the inner surface of the hypovalves, the genital trunk. Mus- cle contractions and the elasticity of the gonocoxopods causes the inner gonostyl parts 1, 2, and 3 to press firmly against the inner wall of the genital trunk forming a double grip. The male gonopods act independently (118).

Once a firm grip has been formed, 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 contorted to maintain the proper intercon- nexion. The female takes the initiative, draws the male up a stem, and hangs there motionlessly. 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 during the stimulation and copulation process (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 openings of the vagina for the insertion of the aedeagus. Sperm is transferred directly into bursa copulatrix, which lies just posterior to three spermatoceae.

The duration of mating varies in *T. palu- dosa*. Barrows (7) and Lovblad (91) reported matings last for ca. 2 hr. Coulson (53) and Selke (145) thought these periods lasted 2 or 3 hr or more for 2 days and half a day or longer, respectively. Mating times of several hours are not uncommon for *tjipulids* (23, 67). Downes (41) stated that sperm-transfer in most topidid form flies is slow, due to the fine calicoid and inelastic walls of the seminal ducts.

In our laboratory, some matings were completed in less than an hour, although pairs often remained coupled longer. Nine observed pairs mated for 35-240 min; the mean time was 105 min (SD = 52.40 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, 57, 153).

Sex ratio

A preponderance of males in a crane fly population is common (46, 63), although not universal. Sampling

Development of Immature Stages

*Tipula paludosa* is a univoltine species with a weak larval drama (87). Eggs are laid in August and Septem- ber 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 November to April are spent as 3rd instars. Fourth in- stars 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, 107). Fig. 7 illustrates the typical *T. paludosa* life cycle with time interval ranges of the life stages.

Larvae also lost weight before pupation. Hadley (58) maintained this portion of the life history in the laboratory. *Mephitis atlantica* (Tipulidae, Limonimini) was due to some degree to the loss of cuticle during molting, pupation, and eclosion, and this is probably true for *Tipula sp.*

* T. paludosa life cycle.

Fertile eggs absorb about half their weight in water between the ages of 2-3 days, resulting in a mid-instar hibernation. Development of the several days that can be de- cided on the day the egg swells, but not before (103). Hatchling takes place through a regular longitudinal split the length of the chorion (35, 160). Egg development usually takes about 2 weeks, but several factors can delay hatching (See Environment Variability section).

Nest-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 (96, 146). However, larvae generally spend most of their lives in the top inch (2.5 cm) of soil, even during the winter (43, 104) and they only go deeper in the spring (95, 167).

Laughter (87) found, under natural conditions, growth of *T. paludosa* was rapid in the fall when larvae grew from ca. 0.5 to 50 mg in 1-2 months. After soil tem- peratures 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 500-500 mg in June. These

**Table 2.** Fourth instar, prepupal, and pupal weights of *Tipula paludosa* males and females.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Average weight (mg)</th>
<th>Weight Loss (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>285.5</td>
<td>190.1</td>
</tr>
<tr>
<td>Females</td>
<td>306.0</td>
<td>185.9</td>
</tr>
</tbody>
</table>

*Note: Larvae were collected from field 5B on Aug 1-20, 1973.*

Since males lost a greater percentage of their weight, female weight was ca. 3 times as much as field males. Female 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 larval prepupal stage to pupa. Pre- pupal weights were correlated to pupal weights (males, r = 0.69; females, r = 0.76) (Fig. 8).

Laughter (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, 50 larvae were taken from each of 4 fields during the week of July 15, 1973, and they were compared using Duncan's (42) multiple range test (table 3). Larvae in field 2A were considerably smaller than those from 5B or 6A. Those from field 3A were not signifi-
There are 9 evident abdominal segments in the male plus an anal tubercle that probably represents the 10th and 11th segments (51, 134). 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 \( \frac{1}{3} \) the length of the cerci.

At light traps, Lovibond (98) reported 79% males, and Robertson (141) tested an average of 71.7% males over a 4-year period. Traynner 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 (4.3 m) sticky board in our study. Sellek (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. Barse (7) calculated 62.2% males from larvae he raised in the laboratory, and Coulson (35) reported 63.2% males from pupal cases collected 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 65.9% 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 Melophillus ater females 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. olenscace and Melophillus 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 in 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 female 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 ceases (37, 91, 133, 142) 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 terenals in crispula into oviposition cages. They contained over 95% fewer eggs after 26 hr and ca. 95% fewer eggs by 50 hr after they were put into cages (fig. 14). These figures are somewhat misleading, however, since only 9 of 135 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.

Tepis 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). Mareck (94) found eggs 18 mm deep, but only as the result of females inserting their abdomen in cracks in the soil, a practice they prefer (63). Thompson (156) found eggs 1.15-2 inches (2.5-3.8 cm) high on dense herbage.

Crane flies normally lay their eggs in a suitable larval habitat (2, 48, 142). Tepis paludosa females move clumsily over the surface, stopping occasionally to oviposit.
They make several probes into the soil to test its suitability (62, 135) before ovipositing. Hemmingen (62) believed that eggs were laid only when actual thrusts into the soil were made. Rennie (135) and Brindle (223) described females inserting their abdomens in a rotary motion. During ovipositing, the female keeps her abdomen in a nearly vertical position (63), and she often assumes a tripod-like feeding on her back legs (16, 17, 22, 35, 166).

The mechanical process of ovipositing was witnessed in the field and the laboratory for several females. Decapitated females that were floated on water were especially useful, since the ovipositing process was somewhat slowed. Several investigators have worked out the mechanics and behavior of oviposition in tipulids (23, 62, 63, 64, 65, 69, 71, 135), 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 bent while the ovipositor then opens wider and the egg appears to be flipped over. Using motion pictures, however, Hemmingen and Noorzevag (71) found that 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 later slightly downward as the cerci are depressed and ab ducted around either side of the hypovalves.

Hemmingen (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, since the cerci are opened and away from the hypovalves, they play no role in releasing the eggs. Hemmingen (63) described 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 15 eggs/min (85).

Fecondity

Several authors measured the fecundity of T. paludosa by counting eggs from dissected females. These data are summarized in table 6. In this study, in a sample of 357.6 eggs per virgin female was found. This average is higher than that of Wilkinson and MacCarthy (167) in British Columbia, but lower than several European workers reported.

<table>
<thead>
<tr>
<th>Author</th>
<th>Mean±9</th>
<th>S</th>
<th>N</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jackson (this study)</td>
<td>337.6</td>
<td>13.6</td>
<td>35</td>
<td>147-759</td>
</tr>
<tr>
<td>Rennie (136)</td>
<td>397.7</td>
<td>125.3</td>
<td>25</td>
<td>255-490</td>
</tr>
<tr>
<td>Sellae (145)</td>
<td>362</td>
<td>121.2</td>
<td>24</td>
<td>360-480</td>
</tr>
<tr>
<td>Lovblad (90)</td>
<td>372</td>
<td></td>
<td>48</td>
<td>10-840</td>
</tr>
<tr>
<td>Barnes (7)</td>
<td>371.4</td>
<td>110.2</td>
<td>28</td>
<td>56-1487</td>
</tr>
<tr>
<td>Narwik (59, 66)</td>
<td>350</td>
<td></td>
<td>70</td>
<td>max 1300</td>
</tr>
<tr>
<td>Thomson (156)</td>
<td>400±</td>
<td></td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>Little (202)</td>
<td>300±</td>
<td></td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>Coulson (35)</td>
<td>340±</td>
<td></td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>Norris &amp; Fox (191)</td>
<td>360</td>
<td>100-600</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Wilkinson &amp; MacCary (167)</td>
<td>281</td>
<td>10</td>
<td>243-338</td>
<td></td>
</tr>
</tbody>
</table>

2 Eggs per female.

3 First mean for larvae fed on lettuce, second for those fed on rye or clover.

For each trial, five males were put in the release-chamber. One observer-chamber contained a test material and the other remained empty. Three trials were run with the test material on one side and three on the other. Both full-fed virgin and virgin (reared from sexted 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 70% ethanol or boiling. Boiling water invariably replaced 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.

Laughead (85) suggested rearing larvae in damp, drained sand and feeding them powdered grass. For this study, however, screened, loamy soil was used, 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. They fed little during the instar, and since 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°C), 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) boxes in moistened sand to study the ¾ of their terrestrial ends protruded. Out of 69% of the emerging adults emerged, probably due to difficulty maintaining a proper moisture level in sand. About 100% of the pupae were killed, either suggested by Laughead (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 Tipulidae are typically shiny black, elliptical, and roughly 1 mm long (5, 22). Tipula paludosa has elongate-oval eggs with one side flattened and the other pointed, as the other. Many tipulid species have a slightly coiled egg filament that unwinds after oviposition and attaches itself to the surrounding medium by means of surface tension and adsorption for wet habitats. Unlike its closely related species, T. oleracea and T. cistaki, T. paludosa has no egg filament (72, 145).

Pupae 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 Sellkie (145) did detailed morphological studies on the gross internal and external structure of 4th instar T. paludosa. Oldham (2) gave an excellent literature review of the early morphological studies on tipulid larvae.

Leatherjackets are nearly cervical, but they taper slightly both anteriorly and posteriorly (fig. 2). After the initial instar, leatherjackets are light grey to greyish brown with irregular black spots 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 hemispherical integument of the head capsule and to the closely associated internal and external lateral plate (67, 130). About 1/3 of the head capsule is not attached to the integument, but it can be withdrawn into the prothoracic skin for protection.

Tipulid larvae are metamorphic, with two spines housed in the spiracular disc of the anal segment. The truncated end of the anal segment consists of an upper spiracular 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 spiracular disc with several spiracles and six tapering anal lobes, the characteristic number in Tipulidae (22). The spiracular disc can be withdrawn so that the anal lobes form a spiracular chamber, which helps to secrete the soil around the tipulid spines. Water is partially removed by hydrophobic hairs and partly by glandular secretions (22, 53). The anal field consists of the anus and four oosorulatory anal papillae, which are more developed in species inhabiting wet habitats. In T. paludosa, only the lateral pair are elongated, the ventral papilla being reduced to rounded papillae (20). Formed inside the larval skin, each obture pap (fig. 4) consists entirely of the inner side of the cuticle. The 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 10-25 mm (0.75-0.98 inch) long (5) (figs 5 & 6). They have elongated, nearly parallel wings. The characters that separate Tipulinae from the other families. Filiform antennae, which originate anterior to the widely separated, dichoptic eyes, have 14 segments instead of the genito-typical 15 (1-5).

Although the pronotum is well developed, the thorax consists primarily of the large mesonotum; the halteres and the wings of the females are shorter than the abdomen, the ratio of wing length to body length in females is ca. 0.66 (62). Hemmingen (67) linked this characteristic with less mobile forms having drier oviposition habitats, and he pointed out T. paludosa is the most "terrestrial" species in the T. oleracea-group.
Corey and Park reported a great deal of variation in the enone and enone-peroxide fractions of the leaves of T. paludosa, which was not observed in the samples from the Southern Hemisphere. The enone fraction in the leaves from the Northern Hemisphere was significantly higher than in the Southern Hemisphere samples. The enone-peroxide fraction was also higher in the Northern Hemisphere samples, indicating that the enone isomerization is not complete in the Northern Hemisphere.

The enone fraction was also higher in the leaves from the Southern Hemisphere, suggesting that the enone isomerization is not complete in the Southern Hemisphere. The enone-peroxide fraction was also higher in the Southern Hemisphere samples, indicating that the enone isomerization is not complete in the Southern Hemisphere. The enone fraction in the leaves from the Northern Hemisphere was significantly higher than in the Southern Hemisphere samples. The enone-peroxide fraction was also higher in the Northern Hemisphere samples, indicating that the enone isomerization is not complete in the Northern Hemisphere.

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TABLE 7. Number of Tiptula palpula 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>0-25</th>
<th>26-100</th>
<th>101+</th>
<th>Mean ± SD n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number females with:</td>
<td>eggs</td>
<td>eggs</td>
<td>eggs</td>
<td></td>
</tr>
<tr>
<td>1-3</td>
<td>28</td>
<td>7</td>
<td>6</td>
<td>31.7 ± 63.1</td>
</tr>
<tr>
<td>4-6</td>
<td>21</td>
<td>9</td>
<td>5</td>
<td>35.9 ± 53.1</td>
</tr>
<tr>
<td>7-9</td>
<td>22</td>
<td>10</td>
<td>2</td>
<td>30.7 ± 63.3</td>
</tr>
<tr>
<td>10-14</td>
<td>16</td>
<td>13</td>
<td>1</td>
<td>30.2 ± 53.3</td>
</tr>
<tr>
<td>Total</td>
<td>77</td>
<td>31</td>
<td>14</td>
<td>32.2 ± 53.1</td>
</tr>
</tbody>
</table>

Mean number of eggs per female.


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 Cran Flies

Several investigators used chemical irritants to bring leatherjackets to the surface. The most common and successful substance was a solution of orthodiachlorobenzene, Jeyes’ fluid, and sodium oleate (7, 8, 38, 52, 90), but Milne et al. [110] and May and Browne [101] found this method inefficient, especially after May. Maersd [107] and Mead [103] brought Tiptula larvae to the surface with a common salt (NaCl) solution. Milne et al. [110] devised a dynamic hot water process for extracting leatherjackets, and May and Browne [101] made a machine that approached 100% efficiency. Coulson [35] and Freeman [47] separated larvae by washing soil samples through graduated sieves.

For this study, larvae, pupa, and pupal cases were sampled by a simple and rapid cran systemic area technique similar to the one Laughlin [87] used. Milne [109] showed that if the cran systemic 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 [109]. 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 3 inches (7.7 cm) with a 4-inch (10.2 cm) diameter core. Three inches was the sampling depth, since that is the deepest larvae have been taken (45, 110, 146, 167). Each core sampled 0.067 ft², hence 11.5 cores were needed to obtain ca. 1 ft² (0.09 m²) 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 [109] 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 [57] chose 4-inch (10.2 cm) diameter cores over the traditional 1×1 (0.09 m²) soil samples when sampling for Tiptula larvae. Four-inch cores proved to be a reasonable size for our study.
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 Poulsen (129).

The study area was within the Puget Sound vegetation area of the T.eugea betisephylla (Raf.) Sarg. zone (western hemlock zone) (45). It is characterized by a Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) subclimax and western hemlock-western redcedar (Tinguea betisephyllya-Tsuga plicata) climax forest.

The natural vegetation of western Whatcom County has been almost entirely removed by logging, with little reseeding. Most of the agricultural land is now pasture and hayfields.

Whatcom County occupies the northernmost portion of the Puget Sound Lowlands climatic area in the United States. This coastal temperate maritime region has an average annual precipitation of 39-45 inches (76-114 cm). Over 75% of the annual precipitation falls in the 6 months October-March. July is the driest month (mean=0.89 inches or 2.26 cm), and December is the wettest (mean=6.52 inches or 16 cm). Snowfall is light but variable, averaging 10-20 inches per year (99).

Summer temperatures rarely surpass 32.2 °C (90 °F), and the average minimum temperature in January is -2.2 °C (28.3 °F). Cold currents of interior air sometimes move into this area from Canada through the open northern and eastern Puget Sound trough, but usually do not last long (99, 125).

43. Dunnet, G. M. 1955. The breeding of the stinging Staurus vulgaris in relation to its food supply. I.
ABSTRACTS

The European crane fly, Tipula paludalosa Meigen, has become a serious pest of lawns, pastures, and hayfields in northern Wisconsin. We disrupted larvae on roots, stems, and leaves of a variety of plants have caused a considerable economic impact on the dairy industry.

Post-pupal weights were correlated to pupal weights for both males (r=0.69) and females (r=0.76). Female 4th instars weighed 1.3 times as much as males, and female pupae weighed 1.5 times as much as male pupae. Larval weights were positively correlated (r=0.85) to lengths. Larval size increased with larval density due probably to better overall habitat conditions.

Field studies for immatures in Whatcom County were conducted on a centric system area sampling scheme with the aid of a 4-inch diam soil corer. 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, optimization 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 western 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, or for attraction, and tended to either visit or field-caught females in a Y-tube olfactometer. Copulation lasted an average of 105 min in the laboratory. The overall sex ratio was 63.9% males in 1975 and 55.5% in 1976, judging from pupal-case counts. The sex ratio changed during the emergence period due to the later emergence period of females, and this was probably related to a longer pupal period for the females.

Oviposition began sooner after mating ceased and continued until only a few eggs were laid. The average female lifetime was 18 days in 1975 and 198 in 1976, with an average of 26 hr in the laboratory. The mean fecundity was 337.6 eggs per virgin female. Fecundity was positively correlated (r=0.88) to female pupal weight.

Diel periodicity of peak emergence, mating, oviposition, and flight was observed. Males 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. The proportion of females that 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 paludalosa Meigen) has become a pest of lawns, pastures, and hayfields in northwestern Washington. Larvae feed on roots, stems, and leaves of a variety of plants, including other grasses, and other plants, seriously damaging pastures and hayfields during heavy outbreaks. Where the major agricultural industry is dairy farming, the negative economic impact was considered an economic emergency. Because of their great abundance and habit of colonizing the sides of buildings, adults can pose a nuisance to the general public.

The Tipula paludalosa is native to northeastern Europe, where it has long been a problem. This species often was confused with the European T. l. and T. crassipes De Jong, until De Jong (40) separated out crassipes adults and Hemmingsen and Lemche (70) stabilized the names, ending controversy over nomenclature. Immatures were not separated until Brindle (21, 22) and Thowald (155) constructed keys for this group.

In Europe, T. paludalosa ranges from southern Finland (ca. 60 N) and lower Saxonia to northern Italy (ca. 35 E), and from Great Britain (ca. 6 W) to the USSR (ca. 35 E). Introduction of this pest into North America took place in 1937. The first report of T. paludalosa from Newfoundland in 1952 and 1972 years later on Cape Breton Island, Nova Scotia. Larvae, known as leatherjackets, became a problem on turf, vegetable gardens, and perennial flower gardens. Soil ballasts dumped on shore from ships at Cape Breton Island are believed to be the source of infection (10, 44).

On the west coast, European crane fly larvae were first discovered in British Columbia causing severe damage to lawns. Outbreaks in the study area occurred in 1955. 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 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. paludalosa in the USA in late summer of 1966. These individuals were part of the spreading Canadian infestation.

By the spring of 1974, 8 hr, and in the late in the spring of 1974. Light trap captures at Blaine, Washington on the border with Canada yielded the first adult males of T. paludalosa in the USA in late summer of 1966. These individuals were part of the spreading Canadian infestation. By the spring of 1974, 8 hr, and in the late in the spring of 1974. Light trap captures at Blaine, Washington on the border with Canada yielded the first adult males of T. paludalosa in the USA in late summer of 1966. These individuals were part of the spreading Canadian infestation.

In the late 1980s, populations of T. paludalosa in Whatcom County were affected (28). Adults have been taken from Skagit County (1970), San Juan County (1971), King County (1972), Chelan County (1974), and Island County (2005). The impact of crane fly emergence on turfgrass, vegetation, and human activities in the study area has been significant. In 1972, for example, a 40-acre lawn in Whatcom County was affected (28). Adults have been taken from Skagit County (1970), San Juan County (1971), King County (1972), Chelan County (1974), and Island County (2005). The impact of crane fly emergence on turfgrass, vegetation, and human activities in the study area has been significant.
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