MONTANA STATE UNIVERSITY

The biology of Tephromyiella Atlanis (Ald.), a parasite of nymphal and adult grasshoppers
by Angus J Howitt

A THESIS Submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University
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Abstract:
There are many references in the literature concerning the control of locust and grasshopper outbreaks by parasites. Investigations are being conducted in Canada to obtain information on the parasite complex and evaluate its worth as a natural control factor. The biology of Tephromyiella atlanis. a late season parasite occurring generally throughout Canada, is discussed. Behavior of the adult including feeding, mating, larviposition, fecundity, hosts and activity in relation to meterological conditions, are discussed. Dissection records of grasshoppers collected in the Prairie Provinces during 1939-1945 show the incidence of parasitism by T. atlanis. The possible value of this parasite for use in the biological control of grasshoppers is discussed.

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Submitted to the Graduate Faculty

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Approved:

Head, Major Department

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ABSTRACT

There are many references in the literature concerning the control of locust and grasshopper outbreaks by parasites. Investigations are being conducted in Canada to obtain information on the parasite complex and evaluate its worth as a natural control factor. The biology of Tephromyiella atlanis, a late season parasite occurring generally throughout Canada, is discussed. Behavior of the adult including feeding, mating, larviposition, fecundity, hosts and activity in relation to meterological conditions, are discussed. Dissection records of grasshoppers collected in the Prairie Provinces during 1939-1945 show the incidence of parasitism by T. atlanis. The possible value of this parasite for use in the biological control of grasshoppers is discussed.

THE BIOLOGY OF TEPHROMYIELLA ATLANIS (ALD.), A PARASITE OF NYMPHAL AND ADULT GRASSHOPPERS

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INTRODUCTION

There are numerous references in the literature concerning outbreaks of locusts and grasshoppers that have been controlled or materially reduced by parasite attacks. Uvarov (1928) stated that the percentage of infestation by parasites is often very high and that records of 100 per cent infestation of swarms of locusts are not rare. Calvert (1882) reported Sarcophaga lineata Fall. as being destructive to locusts in the Dardanelles. Coquillet (1892) reported sarcophagids materially reducing the locust invasion of California in 1891. Kelly (1914) reported outbreaks of Melanoplus differentialis and Melanoplus bivittatus occurring near Wellington, Kansas, and at Wellston, Oklahoma, in 1913 being controlled by parasites. More recently Rehn and Rehn (1938) reported parasites causing a high mortality of Dendrotettix quercus, Packard, the post-oak locust, in the outbreak occurring at Mount Misery, New Jersey, in 1936. Approximately 25 per cent of the adult D. quercus were parasitized by a sarcophagid identified by Hallock (1940) as Sarcophaga atlanis Aldrich = (Tephromyiella atlanis (Aldrich)).

Attacks by parasitic flies cause varying effects upon grasshoppers.

"It is probable", stated Uvarov (1928), "that various species of flies have different feeding habits, and that, at least in some of them, must occur what Pantel (1912) found in a tachinid Thirixion halidayanam,

Rond., parasitizing stick insects of the genus Leptynia in Spain; here the fly larva does not feed even on the fat-body, but merely on the blood of its host without causing any direct injury to the latter." It is important then to differentiate between beneficial species and those which are considered to be of no practical value in the control of grasshoppers.

Investigations concerning parasites of pest species of grasshoppers in Canada are now being conducted cooperatively by the Unit of Biological Control and the Unit of Field Crop Investigations of the Division of Entomology, Dominion Department of Agriculture. The purpose of this study is to obtain information on the parasite complex in an effort to evaluate its worth as a natural control factor and to appraise the potential value of each parasite species for biological control purposes. Investigations to date have been confined largely to the Prairie Provinces. Particular attention has been given to parasites of the three pest species: Camnula pellucida (Scudd.), Melanoplus bivittatus (Say), and Melanoplus mexicanus mexicanus (Sauss.), although more than 20 different species of grasshoppers have been examined for parasites. Southern Manitoba, especially the Red River Valley and the southwestern area near the Canadian - U.S. border, has been surveyed most extensively. Saskatchewan material has been collected at widely separated points, and Alberta collections have been made near Carmangay and Drumheller. In British Columbia more limited collections have been obtained from the Nicola and Lac du Bois ranges near Kamloops. In Ontario the seasonal occurrence of parasites has been closely watched and recorded at Chatterton. A small number of collections have also been taken from points in Quebec, Prince Edward Island, New Bruns-

wick, and Ontario.

Smith (1944) and Smith and Finlayson (1950) have reported a total of 27 species of parasites that have been reared or dissected from nymphal and adult grasshoppers in Canada. Twenty-five of these are primary parasites, and two are secondary parasites.

Primary Parasites:

Diptera
- Sarcophagidae
  - Sarcophaga sinuta Meig.
  - Sarcophaga reversa Ald.
  - Sarcophaga "H"
  - Sarcophaga "C"
  - Sarcophaga "D"
  - Sarcophaga "E"
  - Acridiophaga aculeata (Ald.)
  - Blaesoxiphotheca coloradensis (Ald.)
  - Blaesoxiphotheca "A"
  - Blaesoxiphotheca "B"
  - Blaesoxiphotheca "C"
  - Blaesoxiphotheca caudata Tns.
  - Tephromyiella "A"
  - Tephromyiella atlanis (Ald.)
  - Opsophyto opifera (Coq.)
  - Protodexia hunteri (Hough)
  - Kellymyia kellyi (Ald.)
- Tachinidae
  - Hemithrixion oestriforme B.B.
  - Euacemyia tibialis (Coq.)
  - Paradionaea atra (Tns.)
  - Ceracia dentata (Coq.)
- Nemestrinidae
  - Parasymmictus clausus O.S.
  - Neorhynchocephalus sackenii (Will.)
- Anthomyiidae
  - Acridomyia canadensis Snyder

Nematoda
- Mermithidae
  - Agamermis decaudata Cobb, Steiner, Christie

Secondary Parasites:

Hymenoptera
Perilampidae
Perilampus hyalinus Say

Chalcididae
Brachymeria coloradensis Cress.

In addition to the above list, three South American species of Sarcophagidae have been released at the following points although as yet no recoveries have been made in dissection or rearing of grasshopper collections.

Acridiophaga caridei (Brethes) has been released in small numbers at Chatterton and Brighton, Ontario.

Tephromyiella neuquenensis B.I. has been released at Chatterton, Ontario, and Carmangay, Alberta.

Protodexia australis B.L. has been released at Chatterton, Ontario, Carmangay, Alberta, and in the Lac du Bois ranges of British Columbia.

To date, there has been little work published on the biology of grasshopper parasites. The purpose of this paper then will be to discuss, in some detail, the biology of one of the more important parasites of adult grasshoppers, *Tephromyiella atlanis*. Marlatt (1889) mentioned this species as *Sarcophaga* sp., and stated that about 5 per cent of the grasshoppers in the outbreak at Franklin, New Hampshire, contained dipterous larvae. In field studies made in western Canada during the summer of 1950 *T. atlanis* was found to be very abundant and the dominant species present at all collecting points visited during the mid July - September period. Dissection and rearing records of parasites compiled from grasshopper collections made

throughout Canada substantiate its predominance among late season parasites.

The synonomy of Tephromyiella atlanis is as follows:

Sarcophaga atlanis Aldrich, 1916, Sarcophaga and Allies, p. 100, pl. 4, fig. 40. Hallock, 1940, J. New York Ent. Soc., Vol. 48, p. 225, pl. 3, fig. 47, 48, 49, pl. 10, fig. 134, 135, 136.

Tephromyiella frankliniana Townsend, 1918, Ins. Ins. Mens., Vol. 5, p. 164.

Tephromyiella atlanis (Aldrich) Townsend, 1938, M. Myiology, Vol. 6, p. 94.

Smith and Finlayson, 1950, Can. J. Research, D, Vol. 28, p. 95, fig. 13, 19, 45.

The adult was first described as Sarcophaga atlanis by Aldrich in 1916. Aldrich used as the holotype a male specimen (No. 20506, U.S.N.M.) and for the allotype, female (No. 20506, U.S.N.M.). Both specimens were reared from Caloptenus atlanis Riley (= Melanoplus mexicanus (Saus.)), collected in Franklin, New Hampshire.

In 1918 Townsend established the new genus Tephromyiella with Tephromyiella frankliniana as the genotype. For the holotype of the new species Tephromyiella frankliniana, and therefore the type of this new genus, he selected the allotype of Sarcophaga atlanis Aldrich, which was assigned No. 21586, U.S.N.M. Townsend stated that this could not be the female of S. atlanis and was doubtful that frankliniana was congeneric with atlanis.

In 1938, however, Townsend transferred the species Sarcophaga atlanis Aldrich to the genus Tephromyiella, apparently assured that this species was congeneric with Tephromyiella frankliniana but incorrectly placed in the

genus Sarcophaga. The currently accepted name for this species seems to be Tephromyiella atlanis (Aldrich).

ACKNOWLEDGEMENTS

Grateful acknowledgement is due R. W. Smith of the Dominion Parasite Laboratory, Belleville, Ontario, for his proposal of the problem and his continued interest and aid in attacking the problems embodied in this paper. Special credit is due to the late H. W. Moore for his personal effort and interest in supervising the collecting and sorting of the western grasshopper material.

The writer wishes also to acknowledge his indebtedness to Dr. J. H. Pepper, Dr. J. A. Callenbach, and Dr. D. C. Quimby for their helpful suggestions and aid in preparing this paper.

LIFE HISTORY

Description of Stages

Adult

Tephromyiella atlanis (Fig. 1A) closely resembles Protodexia hunteri, but the yellow palpi and striking tuft of long hair on the anal forceps of hunteri distinguish the two species. The adult is fully described by Aldrich (1916) as follows:

> "Male. Front rather narrow, .144 of head (average of three - .133, .143, .155); frontal stripe at least twice as wide as one side; frontal bristles more numerous than usual, 11 to 13 in number; strongly divergent below, reaching below the middle of the second antennal joint. Parafrontals and parafacials shining gray pollinose, the latter with a row of coarse hairs or bristles. Antennae black; third joint slender, twice as long as second, reaching four-fifths of the way to the vibrissae; arista plumose as usual; vibrissae at oral margin, a few hairs above them on facial ridge. Palpi and proboscis black, ordinary. Bucca one-third of eyeheight. Back of head with three rows of black hairs behind the eye and abundant but not very long, whitish beard. Outer vertical bristles absent.
>
> "Thorax gray pollinose when viewed from behind with 3-5 black stripes; 3 posterior dorsocentrals and 2 pairs large anterior acrostichals; 1 large prescutellar; 3 stenopleurals; on scutellum there are two marginals, one preapical and one apical.
>
> "Abdomen gray pollinose with three stripes, the median one being quite constant, the lateral ones changeable; first segment with only lateral bristles; the second with a small pair of median marginal bristles; the third segment with a large pair of median marginal bristles and five laterals; the fourth segment with a row of about 16.
>
> "Hypopygium: first segment rather small, brown pollinose, with a row of six or eight small bristles near the apex; second segment small, reddish brown, subshining, with conspicuous hairs or bristles. Forceps slender, yellow, not divergent, strongly hooked forward and blackened at apex. Accessory plate short but with an acute tip. Posterior clasper slender, strongly hooked. Anterior clasper much stouter and shorter, broad at apex; penis with rather long basal, the distal one shining black, bent forward at an angle; its flat posterior part expanded apically into two lateral lobes, the median part black, compressed; fifth sternite with V-shaped opening bearing a few hairs and a delicate pubescence.

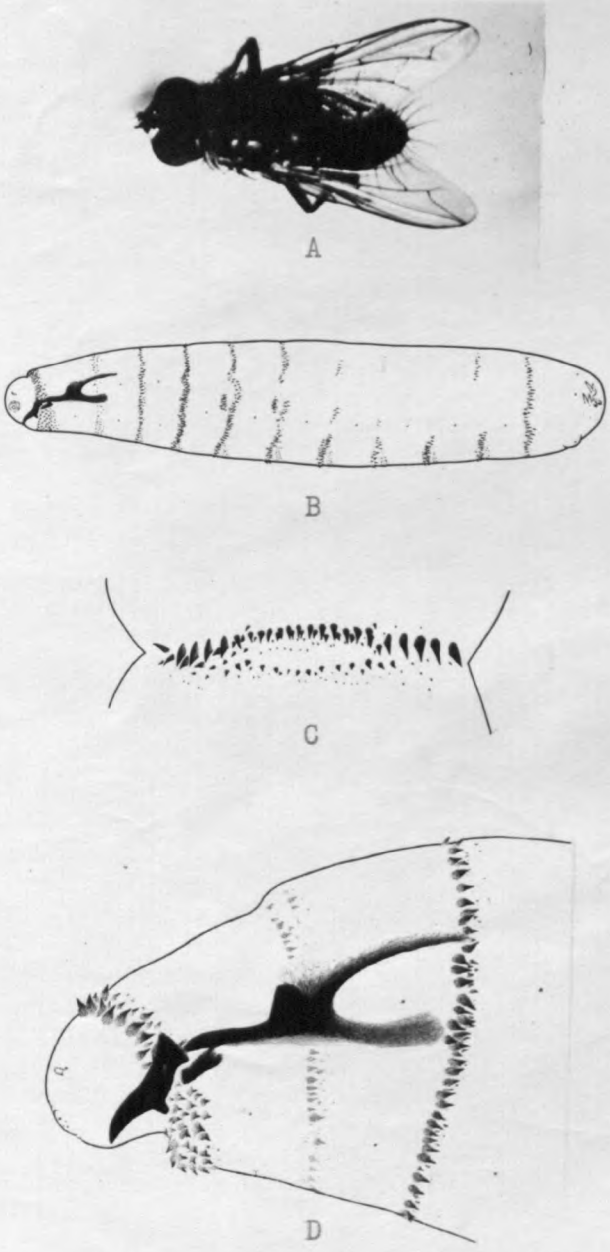


Fig. 1. Adult and First-Stage Larva of Tephromyiella atlanis
A - Adult
B - First-Stage Larva
C - Fusiform Area on Venter
D - Buccopharyngeal Armature and Anterior Segments

"Legs black; middle femur with short, well developed comb on hind side below; middle tibia with two bristles on outer front side; hind tibia without villosity.

"Wing subhyaline; no costal spine; third costal segment shorter than fifth; first vein hairy half way to crossvein.

"Female. Front .274 of head. The usual two orbital bristles; third antennal joint less slender than in the males. General color more grayish. Outer vertical bristles present. No apical bristles on scutellum. Second abdominal segment without median marginal bristles. Abdomen distinctly reddish; genital segment dull red opaque, enclosing a well developed, short larvipositor like that of Protodexia hunteri. Middle femur without comb. Length, $5\frac{1}{2}$ - 8 mm."

First-instar Larva

Smith and Finlayson (1950) have described the first stage larva as follows:

"First-stage larva (Fig. 1B) translucent white in color, cylindrical, tapering toward anterior end, more rounded on posterior end; approximately 1.2 mm. in length and 0.25 mm. in diameter. Segments 1 to 7 each almost completely encircled on anterior margin with backwardly directed spines. Segments 9 and 10 encircled with anteriorly directed spines on their posterior margins. The bands of spines on Segments 5 to 7 interrupted in pleural regions, and with a patch of spines between dorsal and ventral bands. Segments 8 and 9 without band of spines but occasionally with a few isolated spines on anterdorsal margins. Spines on first segment prickle-like with broad bases, band five rows wide ventrally, reduced to two dorsally. Spines on anterior margin of Segment 2 also somewhat prickle-like but smaller. Spines on Segments 3 and 4 stout, well pigmented, closely placed, cone-like in shape, and in bands one to two rows wide with a few smaller spines behind. Segments 6 to 10 with a single row of anteriorly directed spines on posteroventral margin. Fusiform band of spines on venter of each of Segments 5 to 10, five to six rows wide with largest spines in anterior row, spines short and cone-like, those in center of each area well spaced and discrete (Fig. 1C). Spines on anteroventral margin of Segment 11 similar to those on Segment 10 but without fusiform area.

"Buccopharyngeal armature (Fig. 1D) 0.22 mm. in length with oral hooks tapering toward tip. Ventral profile of hook relatively straight but depressed slightly on apical third; basal area of mandibular sclerite rectangular in outline and about twice as long as wide. Infrahypostomal bridge not fused but articulated with hypostomal scler-

ite; mandibular sclerite in length about three-quarters of the distance from tip of hypostomal sclerite to nearest point of sinus.

"Posterior cavity with a pair of two-lobed, sharp-tipped spiracles and a pair of claw-like processes with apical spines; spines not apparent on floor of cavity. A few spines present in region of anal opening.

"The antenno-maxillary complex present on the pseudocephalon and the usual papillae present on the thoracic and abdominal segments; the three bristled sensuria not apparent on the thoracic segments."

Second and Third-instar Larvae

No diagnostic characters were found on the second and third-instar larvae. Since identification of sarcophagid larvae is based on characteristics of the first-instar larvae, a description of the second and third instar larvae has not been included.

Puparium

The puparium (Figs. 2A, 2B) is described by Green (1921) as follows:

"small sized, dull, yellowish red. Posterior cavity quite small, shallow, located on the horizontal axis; no tubercules around the edge of the cavity; last two segments of puparium rather distinct. Each spiracular plate (Fig. 2C) is sub-shining, red with three yellow slits; the middle slits parallel, spiracular plates separated by a space about three-fourths the width of one plate; on the inside, near the lower edge of each spiracular plate is a small, wrinkled area. Anal opening small, inconspicuous, dark; on each side of the opening is a small, rounded depression; no anal tubercules. Anterior spiracles small, located close to the apex of the puparium; each spiracle has seven yellow lobes; spiracle dull, dark red at base."

This description agrees with the writer's observations except that each anterior spiracle (Fig. 2D) consists of ten yellow lobes. The lobes are sometimes grouped into two clumps, each clump consisting of six and four lobes respectively.

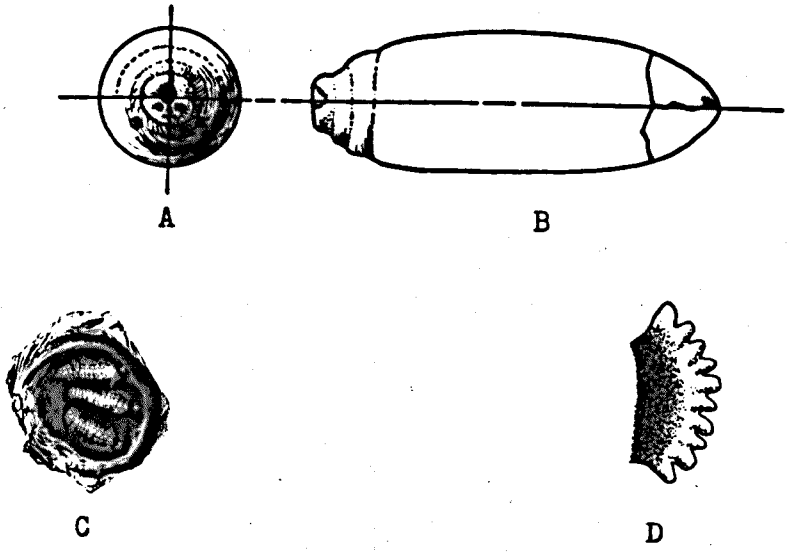


Fig. 2. Puparium of Tephromyiella atlanis
A - Puparium, Posterior View
B - Puparium, Lateral View
C - Spiracular Plate
D - Anterior Spiracle

Seasonal History

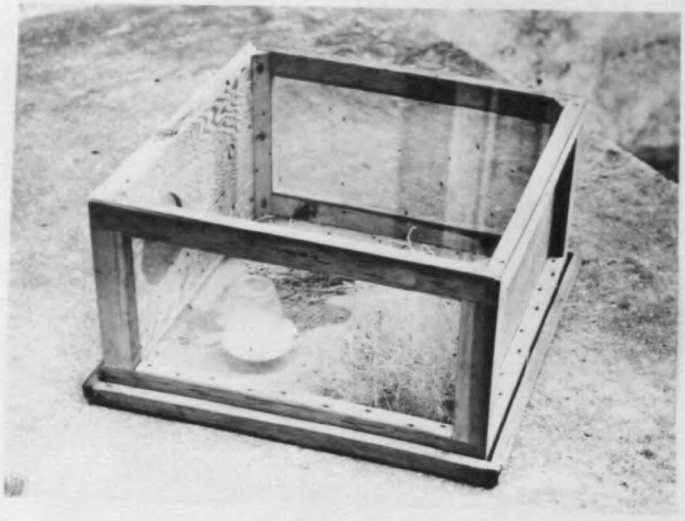
Dissection records and field observations made in Saskatchewan during the summers of 1949 and 1950 indicate that there is one generation a year. Tephromyiella atlanis passes the winter in the soil as a mature larva or pupa. Adults are present in the field from mid-July until late fall, although occasionally they may appear as early as late June. Gravid females are present from mid-July until the latter part of September. T. atlanis is a late season parasite that ordinarily attacks adults only, although occasionally grasshoppers in the fifth instar are parasitized.

BIOLOGY

Methods and Materials

In order to obtain details on the life history and morphology of Tephromyiella atlanis, it was necessary to rear it under cage conditions. Only fifth instar and adult grasshoppers (Fig. 3A) were used as host material. When field collected grasshoppers were used for hosts, it was necessary to hold them at 75° F. for at least two weeks to eliminate parasitized individuals.

Parasite stock was obtained from gravid females collected in the field, and from mated females reared from larvae that emerged from field collected grasshoppers. The following method was devised for facilitating propagation of T. atlanis and to give more definite information on its development. To secure the larvae it was necessary to kill the parasite so that it was important that only gravid females be selected for use. Since non-gravid females showed little interest in grasshoppers, the con-



A



B

Fig. 3. Grasshopper Cages
A - Cage Used for Rearing Host Grasshoppers
B - Cages Used for Handling of Parasitized Grasshoppers

dition of the flies could usually be determined by noting the interest they took in hosts presented to them. As a further check, the flies were examined for the presence of larvae under a dissecting binocular. This was done by etherizing the fly and gently compressing the abdomen with curved-tipped needles. If present, active larvae could be seen through the membraneous areas.

To obtain larvae from a gravid female, the abdomen was severed from the etherized fly and the uterus, containing the larvae, was removed. The mass of larvae was then placed on a black metal plate where they could be more easily seen and kept moistened with fresh water to keep them active and alive until placed on hosts.

To parasitize a host, its leg was snipped off at the tip of the femur with a pair of dissecting scissors, and the larvae were allowed to enter the severed tip. This was done by picking up one or two larvae on the moistened tip of a camel's hair brush and transferring them to the freshly-cut end of the femur, which was held in view under a dissecting binocular. With practice, this procedure could be carried out deftly and the larvae positioned to enter the leg quickly. The parasitized host was then placed in a cage and fed until the mature larvae emerged.

A convenient cage for the handling of parasitized grasshoppers consisted of a wire screen cylinder, 12 mesh per inch, six inches in diameter and ten inches in height, with a bottom of 12 mesh wire screen and a cap-like top of metal (Fig. 3B). Food was added through a hole in the lid of the cage. These cages were set in six-inch metal funnels so that emerging larvae escaped through the bottom of the cage and fell through the funnel

to a container below. The funnels were held upright in holes bored in a strip of wood (Fig. 3B).

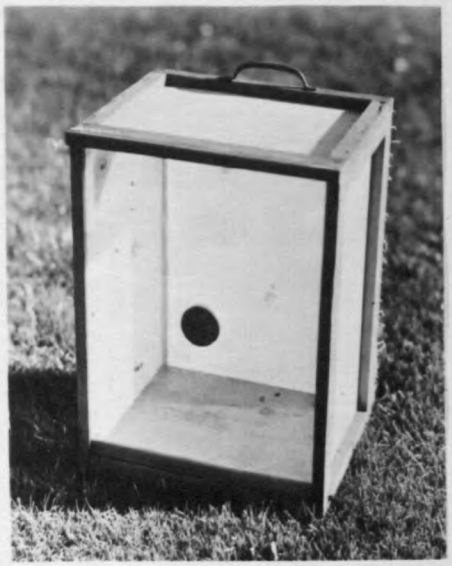
Emerged larvae were transferred to flower-pot saucer containers or to 15 x 55 mm. glass vials (Fig. 4C) with wire gauze stoppers for pupation and emergence of adults. The saucer containers consisted of two $4\frac{1}{2}$ inch flower-pot saucers with smooth ground edges, inverted one on the other. A small moistened pad of cheesecloth provided contact moisture for the larvae.

Adults were placed in cheesecloth covered cages 12" x 12" x 15" (Fig. 4A) for mating and holding during the prelarviposition period. Food was supplied in the form of sugar cubes and split raisins. Water was supplied by sprinkling the cages twice daily with water from an atomizer or wash bottle.

Duration of Stages

The life cycle of Tephromyiella atlanis was worked out under laboratory conditions with an average room temperature of 75° to 76° F., and a relative humidity of 50 to 60%. These conditions proved quite satisfactory. The mature larvae did not enter prolonged diapause as frequently as did many other parasitic sarcophagid larvae so that T. atlanis proved to be a very suitable grasshopper parasite to use for biological studies.

The larva develops through three stages, from first to third instar, within the host. The mature third-instar larva emerges from the host to pupate and transform to an adult. To determine the length of time spent in each stage within the host, dissection of parasitized host material was employed. Grasshoppers were parasitized in the manner previously described,



A



B



C

Fig. 4.
A - Cage Used for Mating and Holding Adults During the Prelarviposition Period
B - Mating Cage
C - Vials Used for Pupation and Emergence of Adults

dissected at specific intervals, and the stage of development of the parasite recorded. Frequently, when two first-instar larvae from the same female were placed on a single host at the same time, the larvae emerged from the host on different days. The difference in rate of development, however, was not extreme as indicated by the fact that never more than one instar separated the developing larvae within the host.

To determine whether there was a difference in rate of development or mortality of Tephromyiella atlanis in hosts containing one larva, as compared with hosts containing two larvae, the following procedure was carried out. A single larva was placed in hosts of one lot, while two larvae were placed in each host in a second lot of grasshoppers. The larvae used were taken from a single gravid female. The hosts consisted of adult Camnula pellucida and Melanoplus mexicanus mexicanus. Larvae deposited singly on hosts showed no significant difference in rate of development or mortality than larvae deposited in pairs on hosts.

There appears to be considerable variation in the length of time required to complete development within the host. Of a total of 167 emerged larvae, 153 or 91.6 per cent spent from 6 to 8 days in the host. Of the 91.6 per cent or 153 larvae, 62 or 37.1 per cent required 7 days, 49 or 29 per cent required 8 days, and 42 or 25.1 per cent required 6 days within the host before emerging as mature larvae (see Table I).

Table I. Number of Days Spent by Tephromyiella atlanis Larvae in Melanoplus mexicanus mexicanus and Camnula pellucida Adults

No. of larvae	No. of days spent in host
3	5
42	6
62	7
49	8
8	9
3	10

On emerging, 85 out of 101 larvae or 84.1 per cent of the total pupated on the second day after leaving the host (see Table II). Ninety-five of a total of 100 pupae spent from 9 to 11 days in the pupal stage. Of the 95 pupae, 15 pupated for 9 days, 58 pupated for 10 days, and 22 spent 11 days in the pupal stage (see Table III).

Table II. The Number of Days Tephromyiella atlanis Spent as Mature Larvae After Emerging From the Host Before Pupation

No. of larvae	No. of days spent as mature larvae
2	1
85	2
13	3
2	4
1	5

Table III. Number of Days Spent in the Pupal Stage by Tephromyiella atlanis

No. of pupae	No. of days spent in pupal stage
1	8
15	9
58	10
22	11
3	12
1	14

The sex ratio of adults emerging from the 100 pupae was evenly distributed, there being 50 females, 49 males and one pupa from which there was no emergence.

Habits of the Adult

Feeding

Tephromyiella atlanis has been observed feeding on the flowers of Symphoricarpos sp. and Helianthus annuus L. While nectar is frequently taken, adults have been occasionally noted feeding on honeydew. On July 25, 1950, at Dollard, Saskatchewan, they were observed feeding on honeydew secretions from aphids infesting Artemisia cana Pursh. They have been taken in sweeps and have been frequently observed resting on Agropyron smithii Rydb., although no records of feeding on this plant have been made. In confinement adults feed freely on sugar, diluted honey and split

raisins.

Mating

Copulation has never been observed in the field, but in the laboratory mating occurs quite readily in cages made of cheesecloth and wood (see Fig. 4B). Females are ready to mate almost immediately after emergence. Males usually do not mate until they are a few days old. In mating the male mounts the female from behind, resting its prothoracic legs on the head or the notal portion of the prothoracic region, with the tarsal claws of the mesothoracic legs firmly hooked to the anterior margins of the wings of the female near the wing bases. The metathoracic legs rest on the floor of the cage. At the beginning of copulation there are momentary adjustments in position before the mating pairs settle down. The flies remain together for varying lengths of time. Some have been observed to separate after 10 to 15 minutes whereas others have remained together for a period exceeding 6 hours. Ordinarily mating flies remain united for about 3 hours.

Larviposition

Field observations on the manner of parasite attack have not been made. Kelly (1914) reported that in no instance could a sarcophagid be observed depositing eggs or larvae on grasshoppers not in motion. He observed that in most cases the grasshoppers were struck while in flight, on the underside of the unfolded wing by sarcophagids, causing the grasshopper to drop to the ground.

Hunter (1899) thought that species of sarcophagids deposited their

eggs and larvae on the soft body of the grasshopper immediately after moulting had occurred. He observed that for some time after moulting the grasshopper was soft and inactive and crawled upon some vegetation where it hardened. Hunter noted that female sarcophagids flew among the vegetation where the grasshoppers were resting until their exoskeleton hardened, crawled upon them, and stuck living larvae beneath the posterior end of the pronotum.

Smith (1944) reported unidentified sarcophagids in the field attacking grasshoppers in flight. Smith and Finlayson (1950) reported that viviparous sarcophagids may deposit larvae on various parts of the body of hosts at rest or in the air.

Tephromyiella atlanis is viviparous, the female depositing well developed, naked larvae on the host. Under cage conditions it has been observed to deposit larvae on hosts at rest and in the air. It is probable that T. atlanis, in common with other sarcophagids that deposit larvae, parasitizes hosts in the field in the same manner.

To determine the prelarviposition period, newly emerged virgin females were placed in individual cages with males that were at least 2 days old. At intervals the females were dissected and the uterus examined for the presence of larvae. At 76° F. it was found that the prelarviposition period varied from 7 to 8 days.

Fecundity

The female produces from 20 to 80 larvae with 50 larvae per female being the average number produced. Insectory reared females produced

approximately the same number of larvae as did females captured in the field.

Activity in Relation to Meterological Conditions

During the summer of 1950 adults were collected at frequent intervals, and under varied weather conditions over widely scattered parts of Saskatchewan. The males prefer exposed places and are usually observed resting in open places on rock piles, roads, fence posts, and the exposed parts of vegetation. In dry weather the male behavior is characterized by quick, short, nervous flights after which it usually returns to the same resting place. Few females were observed in dry weather even though the males were present in large numbers (see Table IV). Sweeps made through the vegetation in making grasshopper collections contained no females. However, when the weather was damp, numerous females were observed resting on the drier, more open parts of the vegetation. On one occasion shortly after a rain, when the vegetation was beginning to dry, numerous females were taken in sweeps made through Agropyron smithii, although no females could be seen resting in the open. The females in this case were resting under cover in the uppermost, drier parts of the vegetation. When the weather was damp both males and females were in evidence but inactive. The females were observed resting on the exposed parts of the vegetation while the males were found on fence posts, rock piles and other exposed locations.

Habits of the Larva

First-Stage Larva

Under cage conditions Tephromyiella atlanis deposits larvae on hosts

Table IV. Distribution of Sexes in Saskatchewan During the Summer of 1950 Showing the Location and Time of Collection, Weather Conditions at the Time of Collection, and a Description of the Habitat from Which Tephromyiella atlanis Was Taken

Date and time of collection	Location	Where collected	♂	♀	Weather conditions at the time of collection
June 28, 1950 11:00 a.m. - 12:30 p.m.*	Herschel	At rest on road	7	0	Rel. humidity 68%, skies clear, temp. in shade 68° F., wind 0-3 MPH, conditions dry
July 24, 1950 1:00 p.m. - 4:00 p.m.	Herschel	Resting and feeding on Symphoricarpos foliage and blossoms	numerous**	1	Skies clear, temp. in shade 85° F., wind 0-3 MPH, conditions dry
July 25, 1950 12:00 noon - 2:30 p.m.	Dollard	Feeding on honeydew secretions from aphids infesting A. cana	5	0	Temp. 95° F. in shade, skies clear, wind 0, conditions dry
July 27, 1950 12:00 noon - 3:00 p.m.	Gravelbourg	Resting on fence posts	numerous	0	Temp. 89° F. in shade, skies clear, wind 0, conditions dry
Aug. 8, 1950 12:00 noon - 3:00 p.m.	Gravelbourg	Resting on fence posts	numerous	0	Rel. humidity 46%, temp. in shade 73° F., skies clear, wind 10-15 MPH, conditions dry
Aug. 8, 1950 5:00 p.m. - 7:00 p.m.	Coppen	Resting on car and on the road	numerous	0	Rel. humidity 42%, temp. in shade 74° F., skies clear, wind 5 MPH, conditions dry

Table IV. (Continued)

Date and time of collection	Location	Where collected	♂	♀	Weather conditions at the time of collection
Aug. 9, 1950 5:30 p.m. - 7:00 p.m.	Esme	Feeding and resting on blossoms and stems of wild sunflower	num-erous	0	Rel. humidity 42%, temp. in shade 71° F., skies overcast, wind 5 MPH, conditions dry
Aug. 25, 1950 12:00 noon - 1:30 p.m.	Dollard	At rest on *Symphoricarpos* vegetation	3	0	Skies partly cloudy, temp. 68° F. in shade, wind 5 MPH, conditions dry
Aug. 26, 1950 3:00 p.m. - 4:00 p.m.	Coppen	At rest on *Agropyron smithii*	num-erous	0	Temp. in shade 77° F., skies clear, wind 5 MPH, conditions dry
Aug. 26, 1950 5:40 p.m. - 6:30 p.m.	Hodgeville	At rest on stone pile	1	0	Temp. in shade 77° F., skies clear, wind 5 MPH, conditions dry
Aug. 27, 1950 1:00 p.m. - 2:00 p.m.	Gravelbourg	At rest on fence posts	num-erous	0	Temp. in shade 81° F., skies clear, wind 5 MPH, conditions dry
Sept. 12, 1950 12:00 noon - 2:30 p.m.	Herschel	At rest on road and on car	10	0	Air temp. 51° F., skies overcast, wind 0-2 MPH, conditions dry
Sept. 13, 1950 12:00 noon - 2:30 p.m.	Dollard	At rest on fence posts	7	0	Air temp. 54° F., skies overcast, wind 0-3 MPH, conditions dry

Table IV. (Continued)

Date and time of collection	Location	Where collected	♂	♀	Weather conditions at the time of collection
Sept. 13, 1950 5:00 p.m. - 7:00 p.m.	Glenbain	At rest on fence posts	8	0	Air temp. 54° F., skies overcast, wind 5 MPH, conditions dry
Sept. 14, 1950 12:00 noon - 2:00 p.m.	Gravel-bourg	At rest on fence posts	2	2	Air temp. 53° F., skies overcast with a light drizzle, conditions wet
Sept. 15, 1950 3:30 p.m. - 4:30 p.m.	Coppen	At rest on car	3	0	Air temp. 50° F., skies overcast with a light rain falling, conditions wet
Sept. 16, 1950 1:30 p.m. - 4:00 p.m.	Esme	♂'s on road and car; ♀'s from sweeps made through *A. smithii*	num-erous	num-erous	Air temp. 58° F., skies cloudy, wind 0-3 MPH, conditions wet
Sept. 16, 1950 5:00 p.m. - 7:00 p.m.	Hodge-ville	♂'s from road, car and rock pile; ♀'s from rock pile	6	2	Air temp. 59° F., skies cloudy, wind 0-3 MPH, conditions dry

* All times are M.S.T.
** In listing the numbers of *Tephromyiella atlanis* captured, the term "numerous" is used to indicate any number over 10.

at rest and in the air. These make their way to the more lightly sclerotized parts of the integument, such as those around the bases of the legs and wings, or in the region of the occiput. The larva gains entry to the body cavity by means of its well developed mouth hooks and rings of bristles which serve as a support when it burrows. Some larvae penetrate the integument quickly while others fail completely in the attempt. Larvae may be found anywhere within the body of the host, including the head. First-stage larvae are frequently found among the muscle bands. There was no evidence of attachment of larvae to the tracheae or air sacs of hosts.

Second-Stage Larva

The second-stage larva spends its entire life within the host. The newly moulted second-instar larva is more robust than the first and loses the dark-colored bristles becoming a creamy white color.

Third-Stage Larva

The third-stage larva retains the creamy white color of the second-stage until emergence from the host. The larva escapes from the host through the same passages that were used in gaining entry to the grasshopper, that is, through the more lightly sclerotized parts of the integument. In this stage the larva is a more opaque color appearing to contain a large amount of fat. The emerged larva does not feed. Under laboratory conditions, Tephromyiella atlanis larvae usually pupated the second day after emerging from the host (see Table II). In the field the larvae crawl from the body of the grasshopper and enter the soil to a depth of 2" to 6" to pupate.

Relation of the Activity of the Parasite within the Host

The problem of determining the manner in which grasshopper parasites feed within the host is a difficult one, and as yet there has been little work published on this subject. In reporting on this problem, Uvarov (1928) stated that "the very important problem of how the larva feeds inside its host is not yet quite clear". It is usually assumed that the larva feeds mainly on the fat-body, and devours more vital organs only toward the end of development. "It is probable", stated Uvarov (1928), "that various species of flies have different feeding habits, and that, at least in some of them, must occur what Pantel (1912) found in a tachinid Thirixion halidayanam, Rond., parasitizing stick insects of the genus Leptynia in Spain; here the fly larva does not feed even on the fat-body, but merely on the blood of its host without causing any direct injury to the latter."

Aldrich (1916), citing Pantel, stated, "that the larvae of Sarcophaga which are parasitic in Orthoptera, do not show any specialization for this mode of life, and simply lie among the tissues of the host, doing little damage until nearly full grown, and obtaining oxygen from the body fluid of the host."

To determine the effect on the behavior of Camnula pellucida and Melanoplus mexicanus mexicanus adults when parasitized, larvae were deposited on different parts of their bodies with a camel's hair brush. Other C. pellucida and M. mexicanus mexicanus adults were parasitized by presenting them to gravid females that deposited larvae on their bodies. Under cage conditions the host grasshopper displayed no marked irritation when larvae

were deposited on its body, crawled over its surface, or even when they penetrated the integument. The host showed no abnormal symptoms until some time after the parasite had gained entry to its body. When the larva began to increase in size, the host became sluggish and usually died shortly after the parasite had emerged. Some hosts survived for a time after the larvae had left their bodies, although dissection of such hosts showed some of their organs to be partially destroyed.

In some grasshoppers from which the parasites had emerged, the internal organs were completely destroyed and only the exoskeleton of the grasshopper remained. In other parasitized grasshoppers which were dissected at intervals of 3, 4 and 5 days, those containing first and second-stage larvae showed little evidence of feeding. In those containing third-instar larvae there appeared to be considerable variation in the amount of feeding. In some hosts there was little evidence of feeding, while in others internal organs showed evidence of considerable damage. It appeared probable that most of the destruction of tissue was done by third-instar larvae in the later stages of development just prior to emergence from the host.

Hosts

Uvarov (1928) stated that grasshopper parasites were able to develop throughout the season on various hosts and that this was an obvious advantage to them. Kelly (1914) reported that sarcophagids are often unable to distinguish grasshoppers from other insects. They were observed to strike and deposit larvae on moths and butterflies. However, attempts to rear the flies from moths and butterflies so attacked were unsuccessful. Further

illustrating the indiscriminate deposition by flies, Kelly crumpled a piece of tissue paper and threw it into the wind among them, when no less than half a dozen flies struck it. When the paper was examined tiny maggots were found clinging to it.

The writer believes that some grasshopper parasites are fairly specific in their host requirements, and that in many cases the parasite is restricted to a single genus, or a limited number of species within the genus. The present studies being conducted on grasshopper parasites in Canada indicate that species of grasshoppers within the same genus show great variation in their ability to resist parasite attacks. Thus a parasite attacking different species within a genus may survive on only a few of them. It follows then that a high percentage of parasites are lost through indiscriminate parasitism, not only on other insects, but on a great many species of grasshoppers in which the parasite cannot successfully complete its development.

The present study provides a good example of the specificity of some grasshopper parasites in host requirements. Tephromyiella atlanis will attack a number of grasshopper species in the field although it will not survive in many of these insects. T. atlanis has been recorded from the following grasshopper species:

Cyrtacanthacrinae

Melanoplus mexicanus mexicanus (Saus.)
Melanoplus packardii Scud.*
Melanoplus bivittatus (Say)*
Melanoplus dawsoni (Scud.)
Melanoplus foedus foedus Scud.
Melanoplus femur-rubrum femur-rubrum (deG.)
Phoetaliotes nebrascensis (Thom.)*

Acridinae

Ageneotettix deorum (Scud.)*
Chorthippus longicornis (Latreille)

Oedipodinae

Camnula pellucida (Scud.)
Spharagemon collare (Scud.)*

*Probably do not survive in host.

In dissecting preserved grasshoppers, the presence of Tephromyiella atlanis larvae is not a good criterion of parasite survival in these hosts. Many of the larvae showed signs of melanism (see Tables V and VI). Melanic larvae in preserved specimens indicated that the parasite had died some time before the death of the host. All larvae found in Spharagemon collare and Ageneotettix deorum and the majority of larvae found in Melanoplus bivittatus and Melanoplus packardii showed signs of melanism (see Tables V and VI). In many cases the parasite did not survive beyond the first or second instar. M. bivittatus showed considerable resistance to all sarcophagids, particularly to Sarcophaga reversa Ald. and Tephromyiella atlanis (see Tables V and VI). In attempted rearings under laboratory conditions, T. atlanis larvae did not develop beyond the first instar in M. bivittatus and beyond the second instar in M. packardii. The larvae showed a high rate of survival in M. mexicanus mexicanus and Camnula pellucida. Both of these hosts are readily attacked and appear to be the principal hosts of T. atlanis throughout most of its range (see Tables V, VI, VII, and VIII).

Table V. Dissection Record of Grasshoppers Collected in Alberta During 1943-44-45-46, Showing the Number and Species of Grasshoppers Collected, the Per Cent of Grasshoppers Parasitized by Tephromyiella atlanis, and the Per Cent of Tephromyiella atlanis Larvae Found Melanized

Period of collection	Melanoplus mexicanus	Melanoplus bivittatus	Camnula pellucida	Melanoplus packardii	Other species
		Number of grasshoppers examined (1943-46):			
July 1-15	117	42			151
July 16-30		17			103
Aug. 1-15	420	232	70	21	859
Aug. 16-31	316	64		85	97
Sept. 1-15	263	63	58	101	54
		Per cent parasitized with Tephromyiella atlanis:			
July 1-15	0.85	11.9			1.3
July 16-30		11.7			0.97
Aug. 1-15	3.33	6.8	1.4	4.7	2.09
Aug. 16-31	2.2	10.9		2.3	5.15
Sept. 1-15	10.2	6.3	1.7	4.9	1.85
		Per cent of Tephromyiella atlanis larvae found melanized:			
July 1-15		100			50
July 16-30		50			
Aug. 1-15		43.7	100		56.3
Aug. 16-31		42.8			
Sept. 1-15		25	100	20	

Table VI. Dissection Record of Grasshoppers Collected in Manitoba During 1941 and 1942 Showing the Number and Species of Grasshoppers Examined, the Per Cent Parasitism by Tephromyiella atlanis in Each Species, and the Per Cent of Melanized Tephromyiella atlanis Larvae

Period of Collection	Melanoplus mexicanus	Melanoplus bivittatus	Melanoplus femur-rubrum	Camnula pellucida	Melanoplus dawsoni	Chortithippus longicornis	Ageneotettix deorum	Melanoplus foedus	Melanoplus packardii
	Number of grasshoppers examined:								
June 16-30	92	399	0	683	19	0	0	31	0
July 1-15	352	369	57	525	159	96	37	19	44
July 16-31	498	770	84	437	27	0	12	21	31
Aug. 1-15	1957	664	599	1509	222	58	119	82	159
Aug. 16-31	1265	458	88	576	231	0	238	146	36
Sept. 1-15	268	129	199	171	19	11	0	0	14
	Per cent parasitism by Tephromyiella atlanis:								
June 16-30	0	0	0	0	0	0	0	0	0
July 1-15	0.59	0.54	0	0.19	0	1.04	0	0	2.27
July 16-31	1.4	4.15	0	1.83	0	0	0	4.76	16.3
Aug. 1-15	3.75	6.77	0.83	1.85	0	0	0.84	15.8	5.03
Aug. 16-31	3.55	7.20	0	3.12	1.29	0	3.36	6.85	11.1
Sept. 1-15	1.86	8.52	6.03	2.77	5.26	9.09	0	0	7.14
	Per cent of Tephromyiella atlanis found melanized:								
June 16-30	0	0	0	0	0	0	0	0	0
July 1-15	0	50.0	0	0	0	0	0	0	100
July 16-31	0	65.6	0	25.0	0	0	0	0	20.0
Aug. 1-15	1.4	44.4	0	17.8	0	0	100	7.7	12.5
Aug. 16-31	2.2	75.7	0	33.3	0	0	100	30.0	25.0
Sept. 1-15	20.0	81.8	0	20.0	0	0	0	0	0

Table VII. Dissection Record of Grasshoppers Collected in Manitoba during 1940-41-42-43-44-45, Showing the Number and Species of Grasshoppers Collected and Per Cent Parasitism by Tephromyiella atlanis

Period of collection	Melanoplus mexicanus	Melanoplus bivittatus	Melanoplus femur-rubrum	Camnula pellucida
Total number of grasshoppers examined (1940-45):				
June 1-15	1053	2472	145	2229
June 16-30	2005	4730	300	2624
July 1-15	2810	3802	652	1596
July 16-31	2451	2099	582	878
Aug. 1-15	2989	1695	1395	1832
Aug. 16-31	1246	571	306	741
Sept. 1-15	322	192	247	334
Per cent parasitized by Tephromyiella atlanis:				
June 1-15	0	0	0	0
June 16-30	0	0	0	0
July 1-15	0.035	0.026	0	0
July 16-31	0.204	0.52	0	0.58
Aug. 1-15	1.2	1.53	0.358	0.33
Aug. 16-31	1.92	1.57	0	1.08
Sept. 1-15	1.55	1.04	3.6	1.19

Table VIII. Dissection Record of Grasshoppers Collected in Manitoba During 1939-40-41, Showing Total Number of Grasshoppers Examined, the Total Percentage Parasitism by All Parasites, and the Percentage Parasitism by Tephromyiella atlanis

Period of collection	Total no. of grasshoppers examined		Total % parasitism by all parasites		% parasitism by T. atlanis	
	M. mex.	C. pell.	M. mex.	C. pell.	M. mex.	C. pell.
July 1-15	124	44	12.09	2.5	1.61	2.5
July 16-31	194	420	16.49	4.28	3.09	1.66
Aug. 1-15	605	413	14.48	2.66	7.27	1.69
Aug. 16-31	472	236	12.92	6.35	4.02	5.93

Secondary Parasites

It is conceivable that secondary parasites may place a serious limitation on the use of grasshopper parasites and make the difference between success and failure in the work of parasite introduction. The most important of these pests, affecting both tachinid and sarcophagid parasites of grasshoppers including Tephromyiella atlanis, is the chalcid, Perilampus hyalinus Say. Numerous sarcophagid and Perilampus adults were observed at Gravelbourg, Saskatchewan, on July 27, 1950. On a later trip at Esme, Saskatchewan, on August 9, 1950, numerous sarcophagids and Perilampus were observed feeding and resting on the blossoms of the common sunflower, Helianthus annuus. In dissecting grasshoppers it was found that a large percentage of them, as high as 60 per cent in some collections, contained the planidia of Perilampus hyalinus. Planidia were found to be present irrespective of whether or not the grasshoppers were infested by primary parasites. Examination of several thousand grasshoppers showed that the planidium could be found in almost any part of the body, although generally found in the body cavity.

Distribution

Tephromyiella atlanis has been taken in collections from British Columbia to Prince Edward Island and no doubt is generally distributed throughout Canada (Fig. 5). D. G. Hall and C. W. Sabrosky, United States Department of Agriculture (private correspondence), reported T. atlanis to be generally distributed throughout the United States.

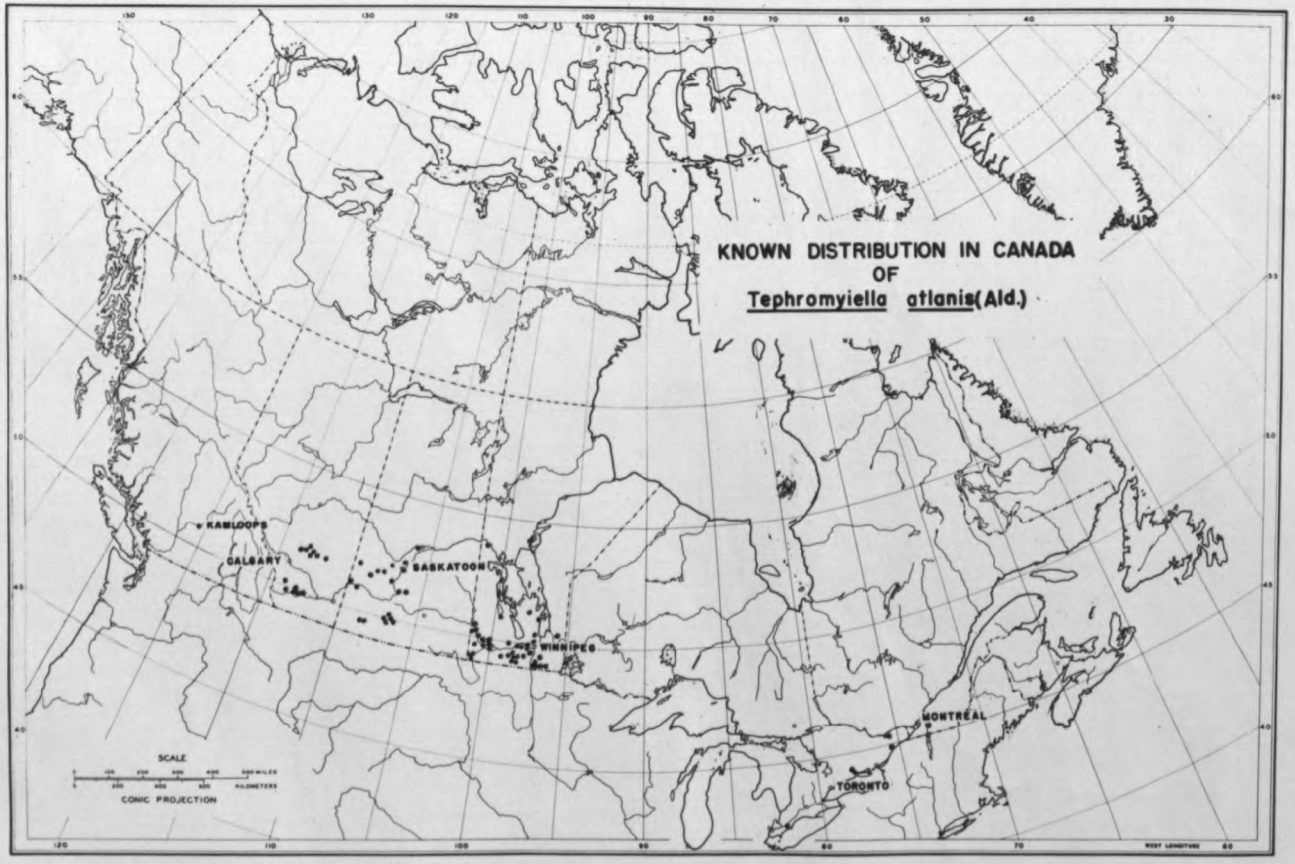


Fig. 5. The Known Distribution in Canada of Tephromyiella atlanis

POSSIBLE ECONOMIC IMPORTANCE OF PARASITES IN BIOLOGICAL CONTROL

The question of the practical importance of parasitic flies for the biological control of grasshoppers is not easy to answer. There is obviously a marked difference in the effect on the host by the activities of different species of flies. In order to make a study of the grasshopper problem and obtain information on the parasite complex in western Canada, Units of Biological Control, and of Field Crop Investigations, working cooperatively, established Permanent Survey Blocks in western Canada. In this way, it was possible to continue periodic collections and observations in areas where grasshoppers were known to be a recurrent problem.

In Manitoba, the Red River Valley Permanent Survey Blocks and the Southwestern Permanent Blocks have served this purpose very well in that population surveys have been continued between outbreaks, development of the population has been followed, and parasite records have been maintained.

In Alberta, the program was set up more on the study center idea than on the Permanent Survey Blocks and collecting point idea. Collecting points within the Permanent Survey Blocks in Alberta were not set up as replicates of species habitats within "climatic soil zones" as they were in the Manitoba Permanent Survey Blocks but were set up to represent variations of habitat within climatic zones.

In Saskatchewan, collections were made, not in blocks, but in representative locations within large climatic soil zones, or in relation to special studies. In Saskatchewan the "collecting point" program was not connected with Permanent Survey Blocks but with general grasshopper areas.

The main purpose of Permanent Survey Blocks was such that surveys and observations could be continued between outbreaks. Collecting points within the Permanent Survey Blocks were established to make possible periodic visits to specific areas between general survey periods, and to permit the continuation of special studies. Collecting points supplied information on nymphal development, embryological development and parasites. They were replicates of economic species habitats within the blocks; for example, two Melanoplus bivittatus habitats, two Camnula pellucida habitats and one combined habitat, all in the heavy soils areas of the Red River Valley near the Canadian - U. S. border. The collecting points were selected as close as possible to the same point each year. They were not moved unless the habitat was destroyed or changed so that the species could no longer be found there. If the collecting point was moved, it was moved to a similar habitat within the same area and as close to the former point as possible. It was not moved merely to select an easier collecting point with a higher grasshopper population. Six collections a year were made on each collecting point. These collections were made at bi-monthly intervals beginning about June 7 and continuing until September 21. Each collection, preferably containing about 300 specimens, was placed in 70 per cent methyl alcohol. The collecting time did not exceed one hour, and collecting was terminated at the end of one-half hour if 20 specimens were not taken in that time.

Samples were sorted to species and instar at Saskatoon, both for information on development, and in preparation for examining for parasites. Details of the contents of the samples were determined and recorded on collection record cards. Sarcophagid and tachinid adults present in the collec-

tions were retained and forwarded to the Parasite Laboratory at Belleville, Ontario, with the collections. These served as a check on the identification of the immature parasites and contributed useful biological information on seasonal occurrence and distribution. The sorted samples were examined at Belleville by dissection and the parasite content determined and recorded. Initial examination was done with an X18 to 20 magnification and parasite identification verified at X40 to X400 magnification when necessary. Records of dissection were completed for each host species examined. They included a record of the number and stage of grasshopper examined, and the number, species and stage of parasite present in each affected host. The record also indicated whether the parasite was dead or alive at the time the host was collected in the field. A dissection record card with a complete and detailed record of parasitism was prepared for each host species in a collection. Parasite records were summarized for each collection point for the year and the aggregate seasonal parasitism calculated for each parasite species on each host, for the parasite complex on each host and for each parasite and the parasite complex on the host complex.

Collections of living material were made at selected points in Saskatchewan, Alberta, and British Columbia, shipped to Belleville and reared for emergence of parasites. The adult parasites obtained served as a check on the identification of species encountered in their immature stages. They also provided stock for laboratory rearing in connection with biological studies. Collections were made at monthly intervals at the points selected and consisted of approximately 300 specimens. These were placed in stout paper bags with a small amount of food and forwarded to Belleville in car-

tons. On arrival at Belleville, each lot of material was placed in a separate cage, provided with fresh food and held two weeks or more for emergence of parasites. The drop of larvae and emergence of adults was recorded and the adults used for laboratory studies.

Collections of living grasshoppers were obtained from selected points in eastern Canada for information on the distribution and host associations of parasites, and on the parasite fauna with particular interest on the possible occurrence of species not present in other parts of Canada.

While there is considerable evidence to show that parasites have materially reduced outbreaks in the past, their utilization in the biological control of grasshoppers is still unknown. Uvarov (1928) noted the great difference in the effect on hosts between different species of parasites varying from no effect to fatal effects. In view of this, Uvarov (1928) stated that generalizations on the effects of parasites on locusts and grasshoppers are dangerous and that the inter-relations of each species of these flies with its host must be studied separately. This suggestion has been followed in carrying out investigations on the biological control of grasshoppers in Canada. Parasite records have been kept on the aggregate seasonal parasitism for each parasite on each host, for the parasite complex on each host, and for each parasite and the parasite complex on the host complex.

Data on species and stage of host attacked, and on seasonal and annual parasitism and its relation to host abundance, have been obtained mainly from dissection of grasshopper collections. This method has obvious disadvantages. In the first place, dissection is slow and tedious. Each specimen

requires a thorough and careful search for parasites. Determinations can be made only on the first larval stage, so that if the larva is in a later stage of development, the first larval cast with its buccopharyngeal armature must be found in order to make the identification. While the first stage larval cast is always present, it may require an hour or more to find it.

Because of the great amount of time required in dissecting collections, it is difficult to keep dissection records up to date and as a result the dissection records on grasshopper collections at Belleville are five and six years behind the actual collecting dates. Furthermore, dissections do not give a true picture of the effects of parasitism. For example, the dissection records of M. bivittatus show a relatively high percentage of parasitism (see Tables V, VI, VII and VIII). Yet experimental evidence, as previously pointed out, has shown that Melanoplus bivittatus possess a high resistance to most parasites, and in particular to Tephromyiella atlanis (see Tables V, VI). Under laboratory conditions M. bivittatus parasitized by T. atlanis appeared quite normal, ate as usual, mated and deposited eggs. In no case did T. atlanis larvae survive in the host beyond the first instar. Similarly, Melanoplus packardii showed no abnormal behavior, under cage conditions, when parasitized with T. atlanis, and the parasite larvae did not develop beyond the second instar.

As previously pointed out, dissections will indicate whether the parasite was dead or alive at the time the host was collected in the field. Larvae that were dead at the time of collection will show up as melanized larvae in contrast to the normal, white colored larvae that were alive when the

host was placed in preservative. However, this is not a true indication of parasite survival, since a parasite, although it will not mature in a host, will survive for a short time and these parasites will show up as normal larvae on hosts that were placed in preservative shortly after being parasitized.

In assessing the value of parasites in reducing grasshopper abundance, the effect of the total aggregate seasonal parasitism must be taken into consideration. For example, the total parasitism, in per cent, of Melanoplus mexicanus mexicanus in Manitoba during the years 1939-1941 inclusive for the periods July 1-15, July 16-31, August 1-15, and August 16-31 was 12.09, 16.49, 14.48 and 12.90, respectively (see Table VIII). For the sake of simplicity fractional parts may be omitted. Collections were made for the most part on the 7th and 21st of each month and as the parasites ordinarily leave the hosts within eight days (see Table I), any overlapping of parasitism would be negligible. Starting out with a hypothetical population of 100 grasshoppers and considering this a stable population then the 12 per cent parasitism during the July 1-15 period will reduce this population to 88 grasshoppers. The 16 per cent parasitism incurred during the July 16-31 period will act on the surviving 88 members and reduce the number to 74 grasshoppers. Similarly, the 14 per cent parasitism in the August 1-15 period will reduce the remaining population from 74 to 64 individuals. Finally, the 15 per cent parasitism incurred during the August 16-31 period will act on the remaining 64 grasshoppers and further reduce this number so that 54 grasshoppers remain out of the original population of 100. Thus the original population has been reduced 46 per cent by para-

sites acting over the whole season.

In assessing the importance of Tephromyiella atlanis, we must first consider the potential value of parasites for biological control purposes and then evaluate the importance of T. atlanis as part of this parasite complex. As previously shown, the grasshopper population is subjected to parasite attacks over the whole season. These attacks are made by different species of parasites acting at different times in the season. Some are early season parasites and confine their attacks for the most part to the nymphal grasshoppers, others are active over the whole season and attack both nymphal and adult grasshoppers, while still others are late season parasites and attack only adult grasshoppers. For example, the dissection records of Melanoplus mexicanus mexicanus for all parasite species in Manitoba for 1942 indicate parasitism from early June until late in September with a peak parasitism occurring early in the season and another peak occurring later in the season. The first peak was produced by Blaesoxiphotheca sp. "B" to which M. mexicanus seems particularly susceptible. The late season peak was due to an accumulation of several parasites, particularly Tephromyiella atlanis and tachinid species. Similarly the dissection records for Melanoplus bivittatus for the same period in Manitoba showed parasitism from early June until late September with a single peak parasitism occurring in mid season. This peak was caused by an early season parasite Sarcophaga reversa Ald. and to a lesser extent by the late season parasite T. atlanis. The overlapping of parasitism of the two species in mid season accounted for the peak.

Investigations on the control of grasshoppers by biological methods

are still in progress so that as yet no final conclusions can be given on the potential value of parasites. However, the results of the study carried on in western Canada to date indicate that, although parasites will help to reduce the intensity of grasshopper infestations, they are not the controlling factor influencing grasshopper abundance.

One of the major problems encountered in introducing grasshopper parasites has been the difficulty in rearing parasites in quantity for release in the field. Up to the present time all grasshopper parasites have to be propagated by the method described previously, that is by rearing them in living grasshoppers. This method of having to rear and maintain a host grasshopper for every parasite is too slow and costly for mass propagation of parasites. Investigations into the possibility of rearing grasshopper parasites in an artificial media are being carried out and if successful will greatly increase the chances of success in the control of grasshoppers by biological methods.

SUMMARY

Tephromyiella atlanis, which appears to be one of the most widely distributed of the late season grasshopper parasites, was selected for study. A review of synonomy and a description of diagnostic stages were completed. The life history was studied under cage conditions. Techniques for infesting hosts are described and development recorded. Most larvae spent from 6-8 days in the host and usually pupated on the second day after emergence. From 9-11 days were spent in the pupal stage.

Adults were observed feeding on the flowers of Symphoricarpos sp.,

Helianthus annuus, and occasionally on honeydew. Under cage conditions larviposition occurred at rest and in flight. It is probable that Tephromyiella atlanis parasitizes grasshoppers in the field in the same manner. The female produced from 20 to 80 larvae with 50 larvae per female being the average number produced. Adults in the field produced the same number of larvae as did those reared under cage conditions. Few females were observed in dry weather even though the males were present in large numbers. In damp weather both males and females were observed.

Tephromyiella atlanis was recorded from 11 species of grasshoppers. Melanoplus mexicanus mexicanus and Camnula pellucida appear to be the principal hosts. Some hosts, particularly Melanoplus bivittatus and Melanoplus packardii showed considerable resistance to the parasite. In dissecting grasshoppers it was found that as high as 60 per cent in some cases contained a hyperparasite.

Data on species and stage of host attacked, and on seasonal and annual parasitism were obtained mainly from dissection of grasshopper collections. One of the chief disadvantages in this method was that dissections did not give a true picture of the effects of parasitism.

Data indicates that Tephromyiella atlanis has a wide distribution throughout North America. Records show incidence of parasitism in susceptible hosts such as Melanoplus mexicanus mexicanus varying from 0 to 10 per cent. These figures are maximums since they do not take into account the effects of the secondary parasite, Perilampus hyalinus. Melanoplus bivittatus, a resistant species, showed a higher incidence of parasitism, but since the parasite did not survive or cause the grasshopper any appar-

ent harm, the effects of these insects must be considered as negligible. It is probable that the effectiveness of the parasite would be greatly increased in a dominant population of susceptible species such as Melanoplus mexicanus and Camnula pellucida. In a mixed population containing susceptible and resistant grasshopper species, it is likely that the effectiveness of the parasite must bear some relationship to the proportion of susceptible to resistant species, since the fly parasitizes grasshoppers indiscriminately.

From the study Tephromyiella atlanis, it is apparent that it is impossible to generalize on the possible control of grasshoppers by biological methods until each parasite is studied separately. In order to do this further studies will have to be made on the aggregate seasonal parasitism for each parasite on its host.

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