THE BIOLOGY OF SOME BLACK FLIES (DIPTERA : SIMULIIDAE) OF ALBERTA

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The biology of 15 simuliid species in northern Alberta was studied. Simulium vittatum *Zetterstedt and* Simulium venustum *Say were the most abundant;* Prosimulium travisi *Stone and* Prosimulium onychodactylum *Dyar and Shannon were rare. Characterictically, the univoltine species (except* Cnephia mutata *Malloch) were autogenous throughout the area.* C. mutata *was represented by both the triploid (parthenogenetic) and the rare diploid sexual forms. A key for the identification of the 31 species reported from Alberta is given. Regular sampling of simuliid larvae in the rivers and creeks shows that there are several peaks of abundance every year (1963-1965) due to the occurrence of the larvae of more than one species in the breeding localities, and that the dates, numbers, and composition of these differ slightly depending on the date of the ice break-up and the march of temperature during the season. The overwintered larvae of* S. vittatum *were present in the water and the ice. The susceptibility of the larvae to DDT was measured and their migration downstream was investigated by the use of plastic sampling cones. The infection rates of the adults and aquatic stages by nematodes and microsporidian protozoans and an evaluation of both predators and parasites as control agents are given.*

Fredeen (1958) and Fredeen and Shemanchuck (1960) investigated the simuliids of Alberta, Saskatchewan and Manitoba. Strickland (1938, 1946) recorded eight species of black flies in Alberta; the number is now 31.

In the United States additional regional lists of black flies have been published: Western U.S.A., Stains and Knowlton (1940); Minnesota, Nicholson and Mickel (1950); Alaska, Stone (1952) and Sommerman (1953); Utah, Peterson (1955, 1960); New York, Stone and Jamnback (1955).

Ecological and biological studies were included in most of the above papers. The control of black flies using chemicals was started in Canada by Prevost (1947). Hocking, Twinn and McDuffie (1949) investigated various insecticides. Further reports on this subject were published by Arnason et al. (1949), Brown (1952), Brown et al. (1951), Hocking (1950, 1953), Hocking and Richards (1952), Peterson and Wolfe (1958), Peterson and West (1960), and West, Brown and Peterson (1960).

Cytological studies on black flies commenced with the work of Rothfels and Dunbar in 1953. Additional studies were reported by Rothfels (1956), Dunbar (1958), Basrur and Rothfels (1959), Landau (1962) and Pasternak (1964). The following species have been studied cytologically in North America: *Simulium vittatum* Zetterstedt, *Simulium tuberosum* Lundstroem, *Simulium aureum* Fries, *Simulium latipes* Mg., *Cnephia mutata* Malloch, *Prosimulium fontanum* Syme and Davies, *Prosimulium hirtipes* Fries, *Prosimulium frohnei* Sommerman, *Prosimulium fulvum* Coquillett, *Prosimulium travisi* Stone, *Prosimulium formosum* Shewell, *Prosimulium fuscum* Syme and Davies, *Prosimulium mixtum* Syme and Davies.

STUDY AREA

The Flatbush study area is about 100 miles north of Edmonton (54° 15'-50' N, 113° 30'-114° 15' W) and lies within the boreal forest region of central Alberta. The field station was seven miles west of Flatbush village (54° 40' N, 114° 10' W). Smith is 50 miles north of Flatbush, Athabasca town is 40 miles east, and Hinton 200 miles west. All these localities were used as centres during the survey.

The aspen and spruce forest is intact in long stretches and the cultivated land (farms and pastures) is located away from the rivers. There are no large urban centres (Happold 1965a & b).

Hinton (elevation 3265 feet) is about 177 miles west of Edmonton. It lies on the bank of the Athabasca River which has many riffles in which S. *arcticum* and S. *tuberosum* breed.

Muskuta Creek and three other creeks flowing into the Athabasca River above Hinton were surveyed for black fly species present. S. *vittatum*, S. *venustum* and S. *arcticum* were collected. Adults of *Prosimulium travisi* and *P. onychodactylum* were captured in netsweeps.

Athabasca town is 40 miles east of Flatbush, situated on the Athabasca River. In one locality downstream from the town, and many localities above the town, *S. arcticum* was collected but in small numbers. Muskeg Creek and three other creeks yielded large samples of black fly larvae, *S. venustum* being the dominant species.

Climate

The long cold winter, characteristic of the continental climate, commences in November and ends in March. The snow melts in April and the ice breaks in the rivers and creeks in April and May. During April the temperature rises to 40 F by day and drops to 20 F by night. In May the temperature reaches 80 F and drops to 35 F at night. The average maximum and minimum temperatures in June are 78 F and 42 F. July and August are warm and the temperature stays above 40 F. In September low temperatures are recorded.

The relative humidity records indicate an overall average of 61% (40-92%) during the May to September period. The diurnal records show fluctuations of relative humidity especially before sunset and for a short period after sunrise. There seems to be a peak in the morning followed by a drop at noon and a rise in the afternoon which continues well into the night. Temperature (air), relative humidity and rainfall records are given in table 1. The average date of ice break-up in the Pembina River over 10 years was April 17.

Vegetation

The forest plants include besides aspen and spruce, many shrubs such as rose, cranberry, raspberry, and other berries; horsetails, and grasses (Happold 1965a).

The plants come into leaf in May and by the end of September the herbaceous plant life has ended and the leaves have fallen. The insect population of this area is closely associated with the flora. All the species of black flies were collected feeding or resting on plants.

TABLE 1. Temperature, relative humidity and rainfall records in the field station at Flatbush : 1961-1965.

	May		June	
	Temp. F.	R.H. %	Temp. F.	R.H. %
1961				
Average	58.9	63.5	63.1	68.3
Mean max.	66.1	87.4	75.0	89.2
Mean min.	41.7	39.7	51.3	47.5
Rainfall total in.	0.30		4.49	
1962				
Average	50.3	68.2	58.1	67.5
Mean max.	61.8	94.8	69.7	93.5
Mean min.	38.8	41.7	46.5	43.5
Rainfall total in.	0.32		3.99	
1963				
Average	51.2	64.3	63.2	69.4
Mean max.	62.1	92.1	67.7	91.5
Mean min.	40.7	40.5	43.4	47.8
Rainfall total in.	1.37		2.97	
1964				
Average	50.2	65.5	64.2	70.2
Mean max.	62.1	90.0	68.3	93.4
Mean min.	41.2	41.7	44.6	42.8
Rainfall total in.	0.94		3.24	
1965				
Average	51.4	63.5	62.1	71.1
Mean max.	64.5	92.1	70.2	93.4
Mean min.	42.6	40.5	47.1	49.8
Rainfall total in.	1.41		4.89	

TABLE 1 (cont.).

	July		August		September	
	Temp. F.	R.H. %	Temp. F.	R.H. %	Temp. F.	R.H. %
1961						
Average	62.7	69.9	64.3	67.2	58.4	69.9
Mean max.	74.0	89.7	77.6	90.0	66.5	94.4
Mean min.	51.4	39.7	51.1	42.6	40.1	44.8
Rainfall total in.	4.38		0.88		2.15	
1962						
Average	60.0	72.0	60.3	72.7	57.6	74.3
Mean max.	71.0	94.7	71.4	94.8	67.4	97.8
Mean min.	49.0	49.3	49.2	50.9	38.6	57.7
Rainfall total in.	4.08		2.49		2.01	
1963						
Average	64.1	70.6	60.2	71.5	52.4	72.2
Mean max.	70.5	90.8	69.4	90.5	65.1	93.2
Mean min.	46.9	48.9	46.1	46.6	39.2	50.1
Rainfall total in.	3.12		0.94		1.65	
1964						
Average	65.7	71.5	62.2	71.3	59.3	74.1
Mean max.	71.2	91.2	70.4	94.4	69.1	94.8
Mean min.	46.9	46.9	45.5	48.8	39.7	53.3
Rainfall total in.	3.51		1.21		1.98	
1965						
Average	63.9	72.4	62.4	75.5	59.7	77.7
Mean max.	72.1	92.4	70.0	90.8	64.8	95.5
Mean min.	49.8	47.8	48.2	46.5	41.1	54.5
Rainfall total in.	4.74		1.21		2.11	

In the study area in running water very few aquatic plants were encountered. There were distinct differences in the composition and density of the vegetation in the various streams. The vegetation near the water is composed of horsetails, mosses, and algae. The banks of the rivers are steep and devoid of vegetation but further away from the rivers the valleys are forested. The creeks have low banks and the vegetation is dense and in shallow water extends into the creek bed.

The following aquatic plants were found in the simuliid breeding sites: Chlorophyceae: *Stigeodonium, Pediastrum* ; Fragilariaceae: *Asterionella* ; Fontinalaceae: *Fontinalis dalecarlica* Linn. ; Equisetaceae: *Equisetum* sp. ; Typhaceae: *Typha latifolia* Linn. ; Sparganiaceae: *Sparganium hyperboreum* Laestad, *S. multipedunculatum* Morang; Najadaceae: *Potamogeton americanus* C. and S., *P. richardsonii* (Benn.) Rybd. ; Alismaceae: *Sagittaria australis* J. G. Sm. ; Butomaceae: *Elodea canadensis* (Pursh), *Vallisneria spiralis* Linn. ; Pontederiaceae: *Pontederia* (*cordata* Linn. ?); Ceratophyllaceae: *Ceratophyllum* spp., (*C. demersum* Linn. ?); Cruciferae: *Radicula* sp. ; Haloragidaceae: *Myriophyllum spicatum* Linn.

Association with other Aquatic Organisms

Jamnback and Collins (1955) and Jamnback and Eabry (1962) used standard nets to measure quantitatively the stream organisms, in relation to blackfly control. Other workers had listed the groups of organisms encountered (Anderson and Dicke 1960, Hocking 1950 and Hocking et al. 1949).

In the present study a 20 mesh per inch screen (5 x 5 feet) was used to investigate the association of simuliid larvae and other stream organisms. The screen was fixed among the rocks in the breeding sites and supported by diagonal poles in the back. The collector worked downstream from a point about 100 yards up from the screen, disturbing the bottom substrata and turning stones and logs to dislocate the fauna which was trapped on the screen. The following organisms were collected:

Mollusca -	Gastropoda Pulmonata	
Annelida -	Hirudinea	*Helobdella stagnalis* Linn.
		Theromyzon occidentalis Verrill
		Moorebdella ferrida Verrill
Arthropoda -	Crustacea	*Daphnia* sp.
		Gammarus sp.
	Insecta	
	Ephemeroptera (nymphs)	*Heptagenia* sp.
		Ephemerida sp.
	Odonata (nymphs)	*Aeshna* sp.
		Agrion sp.
	Plecoptera (nymphs	*Nemoura* sp.
	Trichoptera	*Limnephilus canadensis* Banks
		Brachycentrus occidentalis Banks
		Helicopsyche borealis Hagen
		Hydropsyche recurvata Banks
		Hydropsyche sp.

	Trichoptera (cont.)	*Leptocella* sp.
		Athripsodes sp.
		Polycentropus sp.
		Mayatrichia sp.
	Diptera (Chironomidae)	
	Coleoptera (Hydrophilidae) (Dytiscidae)	
	Hemiptera (Corixidae)	
Chordata -	Pisces	*Esox lucius* Linn.
		Catostomus commersonii Lacepede
		Moxostoma sp.
		Pimephales promelas Rafinesque

No phoretic association was observed between the simuliid larvae and any other organism. At the start of the season and when the water levels were high the number of organisms was small but the populations built up following the rise in water temperature and decrease in flow which resulted in the formation of side pools in the rivers and areas of shallow flow in the creeks.

The crustaceans and snails were late-comers in each season while the other groups were usually present, in different numbers, in all stations all the season.

Rivers and Creeks

Some of this information was kindly provided by the District Engineer, Water Research Branch, Department of Mines and Technical Surveys (Calgary).

Athabasca River

The drainage area of this river is 29,600 sq. miles. It flows north from the Rocky Mountains and pours into Lake Athabasca. The mean discharge in April is 4,700 cubic feet per second, in May 21,200 ft^3/sec, in June 33,000 ft^3/sec, in July 32,000 ft^3/sec, in August 29,200 and in September 25,300 ft^3/sec. The mean velocity increases from 1.8 ft/sec in April to 2.8 ft/sec in June and is nearly uniform in the period June-September. The effects of the rains and melting ice in the mountains are seen in the study area.

The river bed is sandy with coarse gravel but a mud layer is slowly deposited at the end of the June floods. The main stream is devoid of vegetation except for some algal growth on rocks under the water, and a narrow zone of horsetails and reeds at the edge.

Due to the gentle slope of the land in the study area there are no rapids in the river but a few isolated riffles are present and *S. arcticum* Malloch and *S. tuberosum* were found breeding in these.

Pembina River

The drainage area of this river is 4,550 sq. miles. The Pembina flows north from the Rocky Mountains and conjoins the Athabasca River

10 miles north of Flatbush. From the low discharge of 320 ft^3/sec in April it reaches 2,230 ft^3/sec in May 1,320 ft^3/sec in June and July, 995 ft^3/sec in August and 2,000 ft^3/sec in September. The velocity of the current ranges from less than 1.5 ft/sec in April to more than 2.3 ft/sec in May.

The river banks are steep and the river valley is bare but a fringe of vegetation is present at the edge of the water consisting of horsetails and willows. The stream bed is a mixture of fine sand, clay and gravel. This condition resulted in a better crop of aquatic foliage than in the Athabasca River. The Pembina River has large stretches of riffles which extend at low water level. At low water also algae cover stones and rocks, and their filaments and the stones provide suitable substrates for attachment of black fly larvae. Seven species of simuliids, *S. arcticum* , *S. tuberosum* , *S. luggeri* Nicholson and Mickel, *S. venustum* Say, *S. vittatum* Zetterstedt, *S. decorum* Walker and *S. latipes* , were found breeding in the Pembina River.

Irish Creek

Irish Creek crosses Highway 44 65 miles north of Edmonton. It drains the marshes east of the highway and flows into the Pembina River. The creek is about 10 feet wide with steep banks. The water depth ranges from 1 to 3 feet. It flows in part in the shade of forest. The creek is rich in vegetation and although no overwintering larvae were found in it, the larvae of four species of black fly, *Prosimulium decemarticulatum* (Twinn), *Cnephia dacotensis* (Dyar and Shannon), *Cnephia mutata* (Malloch), and *C. emergens* Stone, were collected in May. *Simulium vittatum* Say, *Simulium vittatum* Zetterstedt, and *Simulium latipes* (Meigen) were the dominant species later in the season.

French Creek

This creek drains Cross Lake and flows west to the Pembina. The creek is up to 18 feet wide and the water is one to two feet deep. The current varies from one to two ft/sec near the junction of the creek and the Pembina River. The creek is rich in vegetation especially reeds. The effluence point and the numerous beaver dams provided suitable breeding sites for black flies. The larvae and eggs of six species of black flies were collected. The overwintering larvae of *S. vittatum* were present in water under the ice in 1963, 1964, 1965.

Cross Lake Creek

This creek flows into Cross Lake draining swamps and small lakes north of Cross Lake. The creek is eight to ten feet wide but the maximum water depth is one foot. It flows through dense growth of vegetation and is therefore shaded thus providing ideal breeding habitat for *S. decorum* .

Flatbush (Andy's) Creek

This creek flows into the Pembina at Flatbush draining the swamps east of the village. The creek channel is choked with vegetation in some places, dammed in two places, but receives many small rills. Some observations on repopulation of the creek by aquatic fauna especially

black flies were made, after it was dammed.

Chisholm Creek

This creek flows into the Athabasca River at Chisholm (25 miles north of Flatbush). It is dammed near the junction with the Athabasca to provide water for the lumber mills in the village. The creek channel is 15 feet wide and the water depth varies from nine inches to 1.5 feet. The overwintering larvae of *S. vittatum* were abundant and the highest rates of infestation by parasitic nematodes were recorded here in three consecutive years.

Water Analysis

The chemical and physical analyses of the water in the two rivers and in the creeks gave closely similar results. The two rivers were slightly cooler than the creeks; Irish and French creeks were cooler than the others. The pH readings ranged from 7.5 to 8.5. It has been reported in the literature that black fly breeding streams are slightly alkaline (Anderson and Dicke (1960), Fredeen and Shemanchuck (1960), Peterson and West (1958) and Sommerman et al. (1955). Albeit Peterson and Wolfe (1960) mentioned that black flies can breed in water with pH 5.8 to 8.5: Anderson and Dicke (1960) recorded pH values as high as 8.15 and 8.95 in Wisconsin. The dissolved oxygen concentration ranged from 8.1 ppm to 10.0 ppm and the calculated per cent of saturation showed fluctuations over 100%. Wu (1931), Petersen (1924) and Radzivilovskaya (1950) strongly upheld the theory that the function of the current is to maintain the oxygen saturation. Rubtzov (1939) and Zahar (1951) came to the conclusion that above a certain saturation there is no necessary current requirement.

TAXONOMIC PROCEDURE

The family is very poor in fossil records (Smart 1945, Stone 1964). Specimens recovered from Oligocene amber (English Purbeck) were described by Westwood (1854) and Handlirsch (1908). Two species belonging to two genera have been named: *Simulium priscum* Westwood 1854 orthotype of *Simulidium* Westwood 1854 and *Simulium humidum* Brodie 1906 orthotype of *Pseudosimulium* Handlirsch 1906.

Black flies are distinct and well separated from the other nematocerous families yet they share the biting habit with the Ceratopogonidae. There are no species in the simuliids with affinities to the latter, nor to the chironomids although Shewell (1958) and Davies, L. (1961) reported on the similarities between the primitive simuliids and chironomids, especially in the larval stages. Grenier and Rageau (1960) suggested that this highly evolved nematocerous family is a precursor of the Brachycera.

Seven subfamilies have been named by Enderlein (1937): Simuliinae, Prosimuliinae, Hellichiinae, Ectemniinae, Cnesiinae, Stegopterninae, and Nevermanniinae. Other authors have accepted 2 or 3:
Edwards (1939), Stone (1964), and Stone and Jamnback (1955); Simuliinae, and Prosimuliinae.

Smart (1945): Simuliinae and Parasimuliinae.
Dumbleton (1963), Grenier and Rageau (1960), and Shewell (1958): Simuliinae, Prosimuliinae and Parasimuliinae.
Rubtzov (1959): Simuliinae and Gymnopaidiinae.

There are 80 generic names and 1300 specific names in the literature. The genera and subgenera accepted in North America are:

Simulium
- *Simulium*
- *Eusimulium*
- *Byssodon*
- *Psilozia (Neosimulium)*
- *Hagenomyia*
- *Gnus*

Cnephia
- *Cnephia*
- *Stegopterna*
- *Ectemnia*

Prosimulium
- *Prosimulium*
- *Helodon*

Parasimulium
- *Parasimulium*

Twinnia

Gymnopais

The family is cosmopolitan; *Simulium* and *Cnephia* are the most widespread genera. There are species common to most of the adjacent zoogeographical regions.

Materials and Methods

Aquatic stages and adults were collected from the field and preserved in 95% ethyl alcohol; some of the adults were pinned or mounted by gluing them on paper points. Laboratory rearing was also used in the taxonomic study. The eggs of some species were collected easily but other species proved difficult as the eggs are scattered on the river bottom and no efficient method was found for their extraction. It was found that by combining the eggs, larvae, and pupal skins with the adult, identification is feasible. The pupae are more diagnostic than any other stage. Dissection of some stages was of value. The linear dimensions of eggs of the species studied have an overlapping range so that eggs of the different species proved difficult to identify positively.

On the other hand, the larval head capsule and its different structures were repeatedly employed in keying the species. The antenna has four articles and their colour and length are useful. The cephalic apotome (frontoclypeus) has head spots which occur where the muscles attach to the dorsal surface of the head capsule. These spots are constant in anterior and posterior median, and anterior and posterior lateral groups. The ventral side of the head capsule has a number of structures widely used in identification of the species. The shape and size of the postgenal cleft (throat, occipital, epicranial) vary from a slight groove extending to less than one-fifth the distance between the occipital pits and the base of the submental teeth, to a large bulbous opening with an apex almost touching the base of the hypostomial teeth. The submentum (hypostomium, mentum) has three sets of teeth: median tooth, lateral teeth (2 or 3) and a single corner tooth on each side of the laterals (fig. 1c, d. The cephalic fans (head fans or brushes) have short stalks (stems) and the number of rays in the mature larva is fairly constant (usually inc-

reases with each instar). Under each primary fan there is a secondary fan. The labrum, mandibles and maxillae are present. The hypopharynx is of no taxonomic value.

The larval proleg has a circlet of hooks at its apex used for locomotion. The lateral sclerite (plate) of the proleg is of subsidiary importance in identification of the species as it varies little from one species to another. The pupal respiratory organ histoblast is of considerable value.

The abdominal features utilized in the study are scales or setae, coloration, ventral papillae (anal tubercles), anal sclerite (anal crosspiece) and the posterior sucker (posterior circlet of hooks).

The pupa is usually surrounded by a cocoon, the shape of which is characteristic. The pupal respiratory organ consists of two to forty filaments arising from a different number of stalks (trunks, petioles). The filaments may be grouped or not. The hooks on the abdominal segments and the terminal spines are specific. The pupa proved to be a reliable tool of the utmost taxonomic value.

The adult black fly is very difficult to identify. The antennal flagellum has 7-9 articles. The maxillary palpus contains a sensory organ in its third segment. The comparative length of vein R (stem vein, the common base of R and Rs) and the distance to wing apex from the base of Rs are widely used. The basal cell may be present in some species (fig. 1e). The presence of setae or hairs on the ventral and dorsal sides of the veins is a good character for keying some species. The first tarsal article of the hind leg (the basitarsus) may be extended posteriorly in a flattened lobe (calcipala) and the second article may be notched dorsally (pedisulcus). The tarsal claws are simple or toothed (forked, bifid) (fig. 1 a, b).

The sexes are dimorphic and the males are holoptic; the upper facets of the eye in the males are larger than the lower ones. The male genitalia consist of dark pigmented sclerites that can be used to separate the species groups. On each side of the tip of the abdomen lies dorsally the basistyle (coxite, basimere) and attached to it is the clasper (dististyle, distimere) which has a single or many teeth on the inner side. Between the basistyle and clasper is found a ventral plate, a median sclerite and a paramere consisting of two arms and a fringe of hooks (phallosome and aedeagus pile respectively). The female genitalia consist of an ovipositor lobe attached to sternite eight, a genital fork under tergite nine, an anal lobe and a cercus.

Key to the Genera of North American Simuliidae

(Adapted in part from: Davies, Peterson, and Wood 1962, and Wood, Peterson, Davies, and Gyorkos 1963).

Adults

1. Costa with fine hairs only (microtrichia) no spiniform setae (macrotrichia); Rs forked apically (fig. 1); no calcipala or pedisulcus. .2
- Costa with macrotrichia intermixed with microtrichia; Rs not forked at apex; or with a small fork at the extreme portion; calcipala and pedisulcus present 5

2. A slight or well developed bulla behind the eye; antennal flagellum with 7-9 articles 3
- No bulla behind the eye; antennal flagellum with 9-11 articles . . . . . *Prosimulium* Roubaud
3. R joins the costa near the middle of wing; submedian fold apparently not branched; Rs fork distinctly ending before the termination of costa at apex of wing; flagellum with 9 articles. . . . . *Parasimulium* Malloch
- R joining costa well beyond middle of wing; submedian fold forked; Rs fork reaching to or beyond termination of costa 4
4. Scutum with stout, erect hairs but no fine recumbent hairs; flagellum with 7-9 articles . . . . . *Gymnopais* Stone
- Scutum with fine recumbent hairs only; 7-9 articles; male clasper with one apical spine; female ovipositor short, not reaching the anal lobes . . . . . *Twinnia* Stone
5. Basal cell usually present; pedisulcus very small; length of R more than one-third the distance from base of Rs to the wing apex, with hairs dorsally . . . . . *Cnephia* Enderlein
- Basal cell absent or very small and incomplete; pedisulcus well developed; R with or without hairs dorsally; its length less than one-third the distance from base of Rs to wing apex . . . . . *Simulium* Latreille

Pupae

The pupa of *Parasimulium* has not been described.

1. Cocoon irregular, shapeless and reduced; abdomen with a pair of large terminal spines 2
- Cocoon well developed with definite anterior opening; abdomen without terminal hooks 6
2. Almost no cocoon; dorsum without hooks; abdomen with ten hooks on sternites four to six in more than one transverse row; respiratory filaments four (subarctic genus) . . . . . *Gymnopais*
- Cocoon covering part of the body; dorsum with hooks on some of the tergites; if present, hooks on the sternites are in transverse rows 3
3. Tergites 6-8 with anterior row of hooklets 4
- Tergites 6-8 without row of hooklets: a) Pupa 4.0 mm long; respiratory organ with three stout trunks branching in 16 filaments. . . . . *Twinnia*
- b) Pupa 2.0-3.0 mm long; respiratory organ with two trunks branching in 15-23 (average 19) pale slender filaments . . . . . *Cnephia abdita* Peterson
4. Respiratory filaments arising from a rounded knob on a short petiole . . . . . *Cnephia*
- Respiratory filaments not arising from a rounded knob on a short petiole 5
5. Respiratory filaments 12 (rarely 14) or less arising from two trunks . . . . . *Cnephia*
- Respiratory filaments more than 12, if less than 12 not arising from two trunks . . . . . *Prosimulium*

6. Cocoon stalked and anterior margin not well developed . . *Cnephia*
- Cocoon not stalked and anterior margin well developed; lateral margin of terminal segments without short, curved hooks, although setae may be present . . . . . .*Simulium*

Larvae

1. Larva without cephalic fans; anal sclerite Y-shaped 2
- Larva with two cephalic fans; anal sclerite X-shaped or absent. .3
2. Labrum normal; antenna extending beyond the short cephalic apotome; mandible with no teeth on the subapical margin; submentum with distinct teeth . . . . . .*Twinnia*
- Labrum enlarged; antenna not extending beyond the narrow and elongated cephalic apotome; mandible with small teeth on outer subapical margin; submentum with no distinct teeth . . . . . .*Gymnopais*
3. Anal sclerite absent . . . . . *Cnephia* (in part)
- Anal sclerite present 4
4. Antenna with articles one and two pale, three and four darkly pigmented; secondary fan filaments form a straight line at their tips when extended; median tooth of submentum tridentate (fig. 1d) anal gills with three simple lobes . . . . . *Prosimulium*
- Antenna with articles one and two yellow to brown and three and four rarely dark brown; secondary fan filaments form an arc; median tooth of submentum not tridentate (fig. 1c);anal gill with three simple or compound lobes 5
5. Submentum with corner and median teeth large and subequal, lateral teeth three and subequal (fig. 1c) 6
- Submentum not as above; anal lobe with three simple lobes . . . . . *Cnephia* (in part)
6. Ventral papillae absent or small; postgenal cleft either pointed apically or suboesophageal ganglion and/or epidermis of postgenal cleft distinctly dark, or both; head spots light or dark; anal gill with three compound lobes (except *Psilozia*) . . . . . .*Simulium*
- Ventral papillae well developed; anal gill with three simple lobes (except *latipes*); postgenal cleft not pointed apically; suboesophageal ganglion and epidermis of postgenal cleft not black; head spots dark . . . . . (*Eusimulium*)

List of Species of Simuliidae Recorded from Alberta

(Publisher's or collector's name and date of publication or collection follow the colon.)

Simulium *(Simulium)*

decorum Walker 1848 : Strickland 1938.
hunteri Malloch 1914 : Strickland 1938.
tuberosum Lunstroem 1911 : Fredeen 1958.
luggeri Nicholson and Mickel 1950:Fredeen 1958.
venustum Say 1823 : Strickland 1938.
verecundum Stone and Jamnback 1955 : Abdelnur.
meridionale Riley 1886 : Fredeen 1958.
malyshevi Dorogostajakij, Rubtzov and

		Vlasov 1934 : Fredeen 1958
		piperi Dyar and Shannon 1927 : Fredeen 1958.
	(Byssodon)	*rugglesi* Nicholson and Mickel 1950 : Fredeen 1958.
		transiens Rubtzov 1949 : Fredeen 1958.
	(Gnus)	*arcticum* Malloch 1914 : Strickland 1938.
		corbis Twinn 1936 : Fredeen 1958.
	(Psilopelemia)	*griseum* Coquillett 1898 : Fredeen 1958.
		bivittatum Malloch 1914 : Fredeen 1958.
	(Psilozia)	*vittatum* Zetterstedt 1838: Strickland 1938.
	(Eusimulium)	*aureum* Fries 1824 : Fredeen 1958.
		latipes (Meigen) 1804 : Fredeen 1958.
		pugetense Dyar and Shannon 1927 : Fredeen 1958.
	(Hagenomyia)	*pictipes* Hagen 1880 : Strickland 1938.
Cnephia	*(Cnephia)*	*dacotensis* Dyar and Shannon 1927 : Abdelnur 1965.
		emergens Stone 1952 : Abdelnur 1965.
		saskatchewana Shewell and Fredeen 1958 : Shewell and Fredeen 1958.
	(Stegopterna)	*mutata* (Malloch) 1914 : Abdelnur 1965.
	(Cnetha)	*saileri* Stone 1952 : Fredeen 1958.
Prosimulium	*(Prosimulium)*	*fulvum* (Coquillett) 1902 : Strickland 1938.
		pleurale Malloch 1914 : Strickland 1938.
		travisi Stone 1952 : Abdelnur 1965.
		decemarticulatum (Twinn) 1936 : Abdelnur 1965.
		onychodactylum Dyar and Shannon 1927: Abdelnur 1965.
Twinnia biclavata	Stone and Jamnback 1955 : D. M. Wood 1964.	

Key to the Species Recorded from Alberta

(Adapted in part from Peterson (1960b), and Davies, Peterson and Wood (1962).

Prosimulium

Adult females

1. Antenna with 11 articles 2
- Antenna with 9 or 10 articles . . . . . *decemarticulatum*
2. Claw with a strong thumb-like basal projection 3
- Claw simple 4
3. Integument yellow or orange, frons narrow, nearly parallel sided. . . . . *onychodactylum*
- Integument black, frons normal . . . . . *pleurale*
4. Integument yellow to orange . . . . . *fulvum*
- Integument brown or black . . . . . *travisi*

Adult males

1. Antenna with 9 or 10 articles, clasper with one spine apically . ..

. . . . . *decemarticulatum*

- Antenna with 11 articles 2
2. Hind femora at least, yellow 3
- Hind femora brown or blackish, antenna black, ventral plate apically with sharp lateral prongs between which lies a two-tined fork . . . . . *pleurale*
3. Integument of thorax orange, clasper with a single apical spine . . . . . *fulvum*
- Integument of thorax dark or brown-black 4
4. Apex of clasper pointed with two terminal spines; ventral plate broad, shallow and V-shaped; basal articles of hind tarsus swollen and thus broader than other articles . . . . . *onychodactylum*
- Apex of clasper rounded, with two apical spines; ventral plate with a narrow and sharply pointed median recurved lip; tarsal articles not swollen . . . . . *travisi*

Pupae

1. Respiratory organ consisting of two stout divergent trunks on a short petiole, from the former arise 12-20 slender filaments . . . . . *onychodactylum*
- Respiratory organ not as above 2
2. Respiratory filaments 9, arranged in a whorl from a short base. . . . . *decemarticulatum*
- Respiratory filaments 16 or more 3
3. Respiratory filaments 21 or more . . . . . *pleurale*
- Respiratory filaments 14 or 16 4
4. Respiratory filaments closely clumped together; dorsum of head and thorax strongly rugose . . . . . *travisi*
- Respiratory filaments 16; not closely clumped together; dorsum of head and thorax not rugose; pupa orange . . . . . *fulvum*

Larvae

1. Submental median tooth distinctly shorter than corner tooth . . 2
- Submental median tooth distinctly longer than corner tooth . . . 3
2. Submental lateral teeth longer than other teeth; antenna longer than cephalic fan stalk, 45 rays in cephalic fan; nine filaments in respiratory histoblast; anal sclerite subrectangular, lateral plate of proleg very narrow . . . . . *decemarticulatum*
- Submental corner tooth longest; antenna longer than cephalic fan stalk, 54 rays in cephalic fan, 21 or more filaments in respiratory histoblast . . . . . *pleurale*
3. Postgenal cleft simple, antenna reaches tip of cephalic fan stalk. 4
- Postgenal cleft biarctate, antenna extending three-fourths length of cephalic fan stalk; respiratory histoblast with many filaments arising from two trunks . . . . . *onychodactylum*
4. Postgenal cleft slight, last lateral tooth on submentum as long as median tooth, head capsule pale, dorsal pattern absent, 17-19 rays in cephalic fan, 16 filaments in respiratory histoblast . . . *fulvum*
- Postgenal cleft pronounced, last lateral tooth on submentum shorter

than median tooth, head capsule pattern consisting of a median broken line and two lateral spots on each side of it with a broad dark area posteriorly . . . . . *travisi*

Cnephia

Adult females

1. Tarsal claws simple 2
- Tarsal claws each with a distinct basal tooth or a large projection. 3
2. Maxilla with retrorse teeth, mandible serrate, calcipala large, broad, rounded . . . . . *mutata*
- Maxilla without teeth, mandible not serrate, calcipala short, pointed . . . . . *emergens*
3. Tarsal claws with distinct teeth basally, calcipala small, pedisulcus indistinct or absent, scutum brownish with three narrow pale lines . . . . . *dacotensis*
- Tarsal claws with large basal projections 4
4. Scutum with three pale gray vittae, median narrow and straight, lateral broader and sinuous; scutellum with long, erect, white and few black hairs . . . . . *saskatchewana*
- Scutum gray, clothes with yellow recumbent hairs, scutellum reddish brown with long, erect pale hairs . . . . . *saileri*

Adult males

1. Clasper with one apical tooth 3
- Clasper with two teeth 2
2. Galea of maxilla reduced, shorter than labrum-epipharynx . . . . . *emergens*
- Galea of maxilla normal, as long as labrum-epipharynx . . . . . *mutata*
3. Upper facets not distinctly enlarged . . . . . *dacotensis*
- Upper facets distinctly enlarged 4
4. Clasper apical tooth very small, basistyle large irregular with an inner apodeme . . . . . *saskatchewana*
- Clasper apical tooth well developed, basistyle stout, subquadrate. . . . . *saileri*

Pupae

1. Respiratory filaments 12, arising from two main trunks (dorsal 7, ventral 5) . . . . . *mutata*
- Respiratory filaments 12 or more arising from more than two trunks 2
2. Respiratory filaments 12 arising from 3 main trunks; dorsal with 4, lateral with 3 and ventral with 5 filaments . . . . . *emergens*
- Respiratory filaments more than 12 3
3. Respiratory filaments 17-19 on very short trunks arising from a bulbous base . . . . . *saskatchewana*
- Respiratory filaments more than 30 4
4. Respiratory filaments 30-40 in 6 or 7 main groups arising from a

short bulbous base . . . . . *dacotensis*
- Respiratory filaments 35-45 arising near base, no trunks . . *saileri*

Larvae

1. Postgenal cleft reaching base of submentum 2
- Postgenal cleft not reaching base of submentum 3
2. Postgenal cleft reaches beyond base of submentum, 57 rays in fan, 35-45 filaments in respiratory histoblast, submentum teeth very small . . . . . *saileri*
- Postgenal cleft reaches only the base of the submentum, latter with 13 blunt teeth, 17-19 filaments in respiratory histoblast . . . . . *saskatchewana*
3. Antenna shorter than the cephalic fan stalk . . . . . *dacotensis*
- Antenna long extending well beyond cephalic fan stalk 4
4. Head capsule with distinct brown spots on cephalic apotome and posterior region of gena, entire margin of postgenal cleft narrowly pigmented, submentum teeth heavily sclerotized, distal two articles of antenna darker than basal articles, eye spots normal . . *mutata*
- Head capsule with indistinct spots, postgenal cleft with lateral margins heavily pigmented, submentum teeth weakly sclerotized, eye spots reduced . . . . . *emergens*

Simulium

Adult females

1. Vein R with hairs dorsally 2
- Vein R without hairs dorsally 4
2. Postnotum with a patch of yellow hairs (recumbent scales); scape and pedicel pale brown; legs bicolored; tarsal claws bifid . . . . *aureum*
- Postnotum bare; antenna dark; claws bifid 3
3. Legs brown with distal portion of each part dark; basitarsus of fore-leg long and slender; seven to eight times as long as wide; arms of genital fork diverging from stem at a point half way of total length of fork . . . . . *pugetense*
- Legs uniformly brown; basitarsus of fore-leg short and broad: five to six times as long as wide; arms of genital fork diverging from stem at a point two-thirds the total length of fork . . . *latipes*
4. Tarsal claw with a small subbasal tooth or a basal projection . . 5
- Tarsal claw simple 9
5. Claw with a strong basal projection 6
- Claw with a small subbasal tooth 7
6. Frons and terminal abdominal segments shining; fore coxa yellow . . . . . *rugglesi*
. . . . . *transiens*
- Frons and terminal abdominal segments pollinose; fore coxa dark . . . . . *meridionale*
7. Scutum without vittae; hair on stem vein pale . . . . . *arcticum*
. . . . . *corbis*
. . . . . *malyschevi*

- Scutum with distinct dark vittae 8
8. Pale species, fore coxa yellow, tibia with white pollinose, legs bicolor . . . . . *hunteri*
- Dark species, fore coxa dark, no white pollinose on tibia . . *piperi*
9. Abdomen with distinct black and light grey pattern; fore coxa dark; precoxal bridge absent; fore tibia with conspicuous broad white patch anteriorly, extending two-thirds the length of tibia; vittae on dorsum . . . . . *vittatum*
- Abdomen without pattern 10
10. Abdomen blackish or brown 12
- Abdomen greyish-yellow 11
11. Yellowish species; scutum with orange stripes (vittae) or mesonotum with seven stripes of contrasting colors; frons and abdominal segments pollinose . . . . . *bivittatum*
- Yellowish-grey species; no vittae or stripes; frons and terminal abdominal segments pollinose . . . . . *griseum*
12. Frons and terminal abdominal tergites distinctly pollinose; anal lobe large, subquadrate but narrow dorsally and broadening ventrally, anteroventral margin rounded with a short posteroventral projection under cercus 13
- Frons and terminal abdominal tergites shining black; anal lobe not as above 14
13. Fore tibia with a very distinct patch of white pollen . . . . *decorum*
- Fore tibia with no distinct patch of white pollen . . . . . *pictipes*
14. Fore tibia with a narrow greyish-white streak on anterior surface covering not more than one-third the width of tibia; small dark species . . . . . *tuberosum*
- Fore tibia with a bright yellowish-white patch on anterior surface covering more than one-half the width of tibia 15
15. Subcosta without a row of hairs on ventral surface . . . . *luggeri*
- Subcosta with a row of hairs ventrally 16
16. Inner margin of ovipositor lobe straight, anterior margin of lobe not more sclerotized than rest of lobe . . . . . *venustum*
- Inner margin of lobe concave (with an oval space between the two lobes); anterior margin of lobe distinctly more sclerotized than rest of lobe . . . . . *verecundum*

Adult males

1. Vein R with hairs dorsally 2
- Vein R without hairs dorsally 4
2. Postscutum with a patch of appressed yellow hair; legs bicolored; ventral plate with a laterally compressed median keel . . *aureum*
- Postscutum bare; legs uniformly brown; ventral plate with no median keel 3
3. Ventral plate broad with a medial V-shaped depression . . *pugetense*
- Ventral plate broad with no depression . . . . . *latipes*
4. Clasper with 3 or more apical spines . . . . . *vittatum*
- Clasper with 2, 1 or no apical spines 5
5. Clasper with a stout spine or tubercle at base internally 6
- Clasper without spine or tubercle at base 8

6. Base of clasper with a stout spine internally . . . . . *hunteri*
. . . . . *piperi*
- Base of clasper with a distinct rounded tubercle internally . . . 7
7. Basistyle with a number of short stout spines . . . . . *tuberosum*
- Basistyle with hairs only . . . . . *rugglesi*
. . . . . *transiens*
8. Ventral plate compressed, with denticles on margins 9
- Ventral plate broadly rounded, without denticles on margins . . .
. . . . . *meridionale*
. . . . . *pictipes*
9. Ventral plate narrow (compressed), an inverted Y, with a ventral process or keel 11
- Ventral plate broad, without a ventral process or keel 10
10. Toothed (serrated) margins of ventral plate pointing outwards, visible in profile . . . . . *venustum*
- Toothed margins folded inwards, not visible in profile or dorsally.
. . . . . *verecundum*
11. Ventral keel of ventral plate setose, forming an angle before apex of median portion of plate . . . . . *decorum*
- Ventral keel of ventral plate concave in profile, the angle it forms being at apex of plate 12
12. Clasper shorter than basistyle, former flat, quadrate 13
- Clasper longer than basistyle, cylindrical 14
13. Thorax grey with greenish tinge, median area of scutum not orange
. . . . . *griseum*
- Thorax dark brown to black, with two anterior pollinose spots . .
. . . . . *bivittatum*
14. Basal arms of ventral plate each with a prong but parameral hooks are small . . . . . *malyschevi*
. . . . . *luggeri*
- Basal arms of plate without prongs, some parameral hooks large.
. 15
15. Parameral hooks consist of distinct small hooks and much larger ones, intermingled. . . . . *arcticum*
- Parameral hooks gradually lengthening towards center . . *corbis*

Pupae

1. Respiratory filaments 4 2
- Respiratory filaments more than 4 4
2. Anterior margin of cocoon with a long median projection anteriorly
. . . . . *latipes*
- Anterior margin of cocoon without a projection 3
3. Dorsal respiratory filament strongly diverging from other three. .
. . . . . *aureum*
- Dorsal respiratory filament not divergent 4
a) Respiratory filaments paired, distinctly petiolated . . . *pugetense*
b) Petioles very short . . . . . *transiens*
4. Six respiratory filaments . . . . . *tuberosum*
. . . . . *verecundum*
. . . . . *venustum*

- Respiratory filaments more than 6 5
5. Respiratory filaments 8 6
- Respiratory filaments 9 or more 9
6. Cocoon loosely woven anteriorly; respiratory filaments in more than three groups 7
- Cocoon variably thickened anteriorly; respiratory filaments in three groups 8
7. Respiratory filaments thick, in three short-petiolate pairs, plus two singly . . . . . *decorum*
- Respiratory filaments thin, in 4 petiolate pairs . . . . . *rugglesi*
8. Respiratory filaments whitish, long and slender, the dorsal and medial groups on short petioles, the ventral group on a long petiole; anterior margin of cocoon with only slightly thickened, narrow rim . . . . . *griseum*
- Respiratory filaments shorter and thicker, branching fan-like near base of short petioles; anterior margin of cocoon broader and distinctly thickened . . . . . *bivittatum*
9. Respiratory filaments 9, diverging in a semicircle from center; cocoon boot-shaped . . . . . *pictipes*
- Respiratory filaments 10 or more 10
10. Respiratory filaments 10 11
- Respiratory filaments 12 or more 12
11. Cocoon boot-shaped . . . . . *corbis*
- Cocoon with an anterior projection . . . . . *piperi*
12. Respiratory filaments 12 13
- Respiratory filaments 14 or more 14
13. Cocoon with broad collar and many openings anteriorly . *arcticum*
- Cocoon with narrow collar and one large opening anteriorly . . . . . *luggeri*
14. Respiratory filaments 14 or 16; cocoon slipper-shaped . *vittatum*
- Respiratory filaments 16; cocoon boot-shaped . . . . *malyschevi*
- Respiratory filaments more than 16 15
15. Respiratory filaments 22-26 . . . . . *meridionale*
- Respiratory filaments 100 or more . . . . . *hunteri*

Larvae

1. Anal gill with three simple lobes 2
- Anal gill with three compound lobes 4
2. Ventral papillae conspicuous, conical; head spots dark; suboesophageal ganglion and epidermis in postgenal cleft pale; respiratory filaments in histoblast 4 3
- Ventral papillae small or absent; suboesophageal ganglion and/or epidermis in postgenal cleft usually black; respiratory filaments in histoblast variable 4
3. Antenna dark and conspicuous; submentum darker than adjacent area; lateral head spots double; anal gill lobes with secondary bumps . . . . . *pugetense*
- Antenna pale; posterior half of submentum concolorous with adjacent area; dorsal head pattern consisting of longitudinal patches . . . . . *aureum*

4. Submentum with median tooth as long as corner teeth; second antennal article with a single lobed ventral pale spot; anal gill with no accessory lobes; postgenal cleft slight and rounded apically . . . . . *vittatum*
- Submentum with median tooth longer than corner teeth; second antennal article with a bilobed ventral spot; anal gill with numerous accessory lobes; postgenal cleft extending to more than half the distance to the base of submentum . . . . . *pictipes*
5. Pigmented area anteroventral to eye conspicuous, suboesophageal ganglion and epidermis in postgenal cleft pale, second antennal article more than twice as long as third, respiratory histoblast with 4 filaments . . . . . *latipes*
- No pigmented area anteroventral to eye 6
6. Suboesophageal ganglion and epidermis in postgenal cleft pale . . . . . *piperi*
- Suboesophageal ganglion and/or epidermis in postgenal cleft dark 7
7. Spots on cephalic apotome (head spots) dark; antenna shorter than cephalic fan stalk; abdomen pale yellowish-brown; respiratory histoblast with 12 filaments; postgenal cleft bulbous extending one half the distance to base of submentum . . . . . *luggeri*
- Head spots pale 8
8. Antennae longer than the cephalic fan stalk; the entire two distal articles extending beyond apex of stalk of cephalic fan 9
- Antennae shorter than cephalic fan stalk 12
9. Respiratory histoblast with 6 or 10 filaments 10
- Respiratory histoblast with 12 or 16 filaments 11
10. Respiratory histoblast with 6 filaments; postgenal cleft uniformly tapering; 43 rays in cephalic fan . . . . . *tuberosum*
- Respiratory histoblast with 10 filaments; dorsal head pattern lacking isolated spots; postgenal cleft extending to just below the base of submentum, approximately 50 rays in cephalic fan . . . . *corbis*
11. Respiratory histoblast with 12 filaments; submentum teeth equal in length, 50 rays in cephalic fan . . . . . *arcticum*
- Respiratory histoblast with 16 filaments, postgenal cleft extends to base of submentum; the submentum with long, distinct median tooth; 49 rays in cephalic fan . . . . . *malyschevi*
12. Ventral papillae conspicuous . . . . . *rugglesi*
. . . . . *transiens*
- Ventral papillae absent 13
13. Postgenal cleft extending to less than half the distance to base of submentum . . . . . *hunteri*
- Postgenal cleft extending to more than two-thirds the distance to base of submentum 14
14. Infuscation around head spots wide and extending beyond outer edge of anterolateral spots; arms of anal sclerite broadly fused medially 15
- Infuscation around head spots narrow, not extending beyond inner edge of anterolateral spots; arms of genital sclerite narrowly fused medially; respiratory histoblast with 8 filaments . . . . *decorum*

. . . . . *griseum*
. . . . . *bivittatum*

15. Lateral plates of proleg lightly sclerotized; cephalic fan with about 52 rays; anal hooks in 66 rows; postgenal cleft not bordered by a fulvous area . . . . . *verecundum*
Lateral plates of proleg heavily sclerotized; cephalic fan with less than 42 rays; anal hooks in about 70 rows; postgenal cleft bordered by a narrow fulvous band . . . . . *venustum*

HABITATS, BEHAVIOR AND LIFE HISTORIES

Alberta Simuliids in General

Eggs

Simuliid females lay eggs in running water. There is no record of oviposition in stagnant water. Cameron (1922), Edwards (1920), and O'Kane (1926) suggested that the eggs of some species of black flies (*S. arcticum* , *S. latipes* and *P. hirtipes* respectively) withstand desiccation. They may be subjected to this through water receding or the drying up of intermittent streams. Jobbins-Pomeroy (1916), Smart (1944), and Wu (1931) concluded from field observation and experimental evidence that the eggs are not resistant to desiccation. Fredeen (1959b) devised a method for the extraction, sterilization and low temperature storage of black fly eggs collected from the field. He found that the eggs of arctic and temperate species overwinter and remain viable for longer periods in storage than the eggs of those species which pass the winter as larvae.

I tested batches of eggs of *Simulium venustum* , *S. vittatum* , and *S. decorum* for desiccation resistance as follows: egg batches were obtained from the breeding places and divided into three groups. The first group was used as a control and was firmly anchored or clearly marked in the breeding site. The second group was left on filter paper in the laboratory during the test periods (48, 144, and 264 hr) and then returned to water. The third group of eggs was used as a laboratory control, covered by water in clean, open museum jars. The results are shown in table 2.

The recorded (room) relative humidity was 67-74% and the temperature was 56-69 F. The eggs of these species need water for hatching and show no resistance to desiccation.

Table 3 shows the average number of eggs laid by the females of ten species. The eggs of a batch mature at the same time but there are differences in the numbers of eggs laid within and between species. This was also recorded by Davies and Peterson (1956) for many species, in most genera. In a few species there is usually a decrease in the number of eggs in the second gonotrophic cycle. This results from degeneration of some ovarioles in which the eggs from the previous ovarian cycle were retained.

The simuliid egg is conical in ventral view and sub-triangular in lateral view. There is a bulge on one side of the egg and the side opposite that is the longest in profile.

Linear measurements were taken from the lateral view. The length

was taken as the maximum measurement along the egg axis parallel to the longest side and the width dorsoventrally and perpendicular to this (table 4). Davies (1950) and Davies and Peterson (1956) compared the dimensions of eggs of various species belonging to all the North American simuliid genera. The eggs of *Gymnopais* and *Prosimulium* were found to be larger than these of *Cnephia* and *Simulium* except for *S. pictipes*, also the eggs of *Prosimulium* and *Cnephia* are narrow and eggs of other genera are subtriangular in profile.

The angles, table 5, were measured with an eyepiece goniometer.

TABLE 2. The progress of hatching of the eggs of three simuliid species in relation to drying.

Species	Field control	Lab. control	In air at 67-74% relative humidity
S. vittatum			
48 hr	10% hatch	13% hatch	no hatch
144 hr	96% hatch	80% hatch	no hatch
264 hr	infected	infected	no hatch
S. venustum			
48 hr	48% hatch	35% hatch	no hatch
144 hr	87% hatch	88% hatch	no hatch
264 hr	100% hatch	94% hatch	no hatch
S. decorum			
48 hr	38% hatch	47% hatch	no hatch
144 hr	35% hatch	96% hatch	no hatch
264 hr	infected	infected	no hatch

Larvae

Breeding sites - The simuliid larvae were found only in rivers and creeks. The young larvae of some species aggregate at the exits of creeks from lakes and bogs. The older larvae are more evenly distributed downstream and the mature ones are in the pupation sites which are in slow water and usually near the bank.

The head waters of the Pembina and the Athabasca rivers are at an altitude of about 3800 feet and the altitude is 2000 feet at Flatbush and 1690 feet at Athabasca town.

For about 4 to 7 miles downstream from big villages and towns there was a decreased population of simuliids. I attribute this to the influence of domestic and industrial waste disposal in the rivers. The creeks may be dammed for agricultural or industrial purposes for short or long periods during the season. Although they may be dry for some time, when there is a leak or overflow they get repopulated in the same season. Beaver dams are common in the area, usually giving rise to favorable breeding sites.

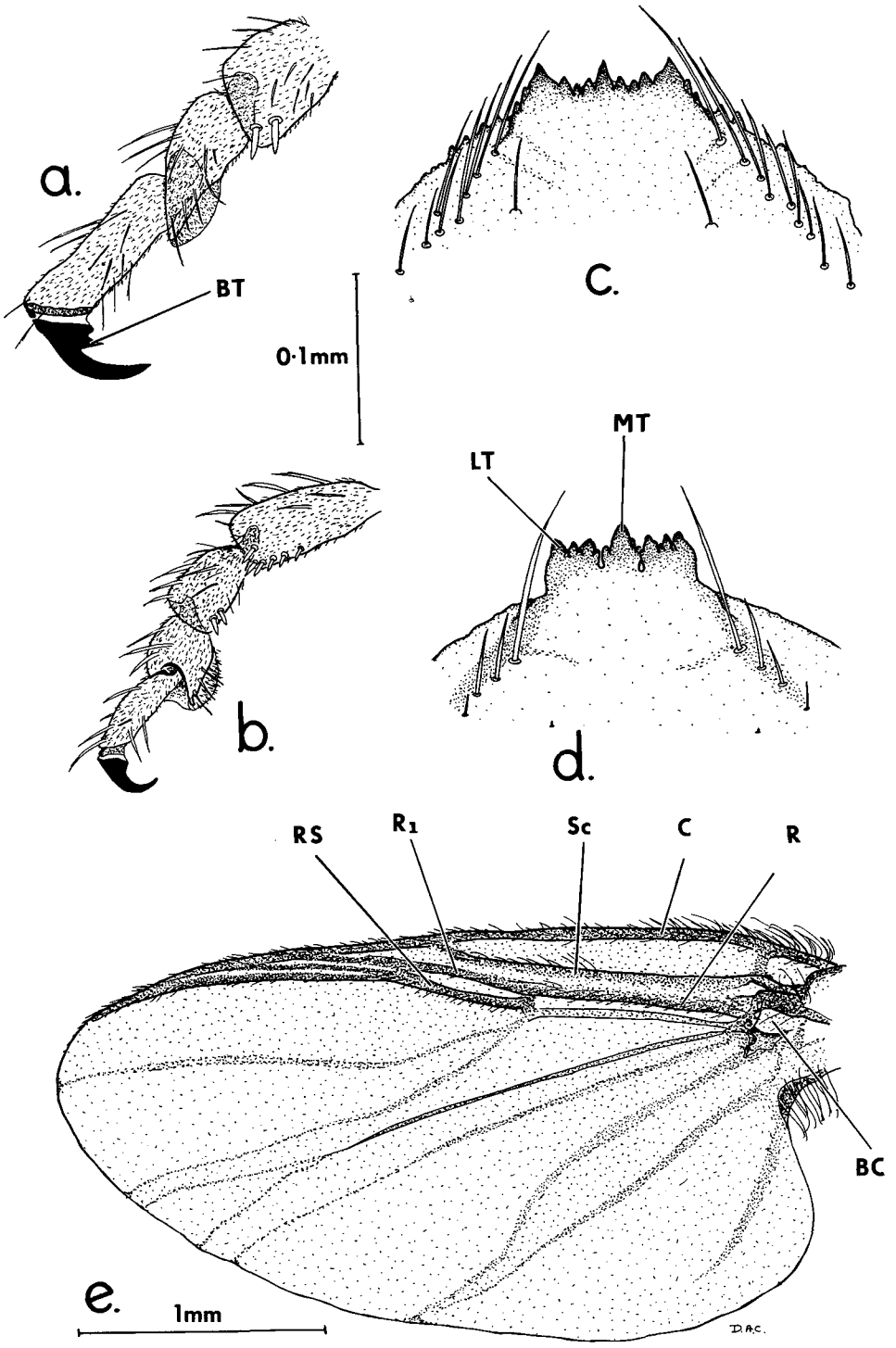

Fig. 1. a. Bifid claw of *Cnephia* sp., BT = basal tooth; b. Simple claw of *Simulium* sp.; c. Submentum of *Simulium* sp.; d. Submentum of *Prosimulium* sp., MT C median tooth, LT = lateral and corner teeth. e. Wing of *Prosimulium* sp. female, BC = basal cell.

TABLE 3. Number of eggs per gonotrophic cycle in some Simuliids, counts and published records, means ± standard deviations, number of counts in brackets, range.

Species	No. of eggs per female				Authority
	Mean	S.D.	No. of counts	Range	
S. arcticum	135	-	-	162-	Peterson 1959a
nulliparous	165	± 27.8	(22)	204-123	Count
parous	139	± 24.0	(20)	177-116	Count
S. aureum	750	-	-	823-	Davies & Peterson 1956
	745	± 13.4	(21)	810-686	Count
S. decorum	475	-	-	580-	Davies & Peterson 1956
nulliparous	550	± 51.0	(18)	594-479	Count
parous	436	± 20.7	(15)	467-411	Count
S. latipes	275	± 26.7	(16)	312-222	Count
S. luggeri	154	± 14.0	(12)	174-135	Count
S. tuberosum	202	-	-	264-	Davies & Peterson 1956
	225	-	-	--	Peterson 1959 a
nulliparous	227	± 7.4	(16)	218-234	Count
parous	196	± 17.0	(14)	212-145	Count
S. venustum	455	-	-	553-	Davies & Peterson 1956
	594	-	-	--	Hocking & Pickering 1954
nulliparous	513	± 28.7	(16)	572-465	Count
parous	481	± 24.8	(15)	511-441	Count
S. vittatum	312	-	-	395-	Davies & Peterson 1956
nulliparous	380	± 12.2	(17)	398-363	Count
parous	285	± 17.2	(16)	311-254	Count
C. dacotensis	287	-	-	348-	Davies & Peterson 1956
	281	± 17.2	(16)	288-276	Count
C. emergens	174	-	-	--	Davies & Peterson
	163	± 7.4	(20)	211-125	Count

TABLE 4. The length and width of mature eggs of some simuliid species.

Species	Length		Width		
	Mean ± S.D.	Range	Mean ± S.D.	Range	No.
S. arcticum	0.38 ± 0.033	0.32-0.44	0.25 ± 0.044	0.23-0.27	16
S. aureum	0.19 ± 0.049	0.16-0.22	0.14 ± 0.048	0.11-0.16	17
S. decorum	0.27 ± 0.052	0.23-0.29	0.16 ± 0.039	0.14-0.17	12
S. latipes	0.22 ± 0.035	0.20-0.24	0.14 ± 0.035	0.12-0.16	8
S. luggeri	0.34 ± 0.059	0.31-0.37	0.23 ± 0.035	0.21-0.255	10
S. tuberosum	0.21 ± 0.040	0.19-0.23	0.12 ± 0.036	0.10-0.14	12
S. venustum	0.25 ± 0.037	0.23-0.27	0.18 ± 0.037	0.14-0.19	19
S. vittatum	0.26 ± 0.040	0.25-0.29	0.16 ± 0.00	0.00-0.00	9
C. dacotensis	0.27 ± 0.0245	0.26-0.29	0.14 ± 0.39	0.12-0.16	15
C. emergens	0.29 ± 0.0	0.00-0.00	0.13 ± 0.0245	0.11-0.14	7

TABLE 5. Egg angles of three simuliid species measured in lateral view using eyepiece goniometer.

	Angles (degrees)					
	Head		Bulge		Third (tail)	
	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.
S. venustum	35-55	45.5 ± 5.9 (18)*	89-101	95.6 ± 4.4 (18)	41-55	49.0 ± 5.6 (18)
S. vittatum	35-58	45.3 ± 4.6 (9)	91-116	104.3 ± 9.9 (9)	42-61	51.2 ± 7.9 (9)
S. decorum	34-56	45.2 ± 8.3 (11)	88-102	95.7 ± 5.8 (11)	41-57	49.5 ± 6.8 (11)

* Number of readings, range.

The larvae of *S. arcticum* were limited in their distribution to the two rivers in the study area, albeit they have been collected from streams elsewhere (Fredeen (1958), Fredeen and Shemanchuk (1960) in southern Alberta, Peterson (1956) in Utah, and Sommerman et al. (1955) in Alaska). The current velocity was 1.5 to 5 ft/sec throughout the breeding sites except that mature larvae pupated in slower water near the banks of the rivers. The water was about three feet deep over the young larvae but only 8 to 14 inches above the pupae. Frequently pupae were exposed when the water receded; *Equisetum* stems are preferred pupation sites as the plant grows near the water edge and in the water. The water temperature ranged from 32 to 61 F during occupation by the species collectively.

Closely associated with *S. arcticum* in the Pembina River was *S. luggeri*. The latter was sparsely distributed on the same substrata although stones and rocks were utilized especially for pupation. It was collected also from the lower reaches of French Creek in similar positions.

S. tuberosum larvae aggregated on stones and vegetation exposed to the sun; the preferred current velocity was 0.6 to 3.5 ft/sec and the water depth was 3 to 18 inches. This species bred in the rivers and creeks.

S. verecundum, *S. venustum* and *S. vittatum* bred more in the creeks than in the rivers; the Pembina River usually had a bigger population of aquatic stages per square foot than the Athabasca (fig. 4). The current speed ranged from a trickle in one inch of water to about 5 ft/sec in more than three feet of water. The first two species appear when the temperature rises to 40 F.

S. decorum larvae were found to concentrate on shaded substrata in 3 to 12 inches of water and 0.5 to 1 ft/sec current. During the occupation of this species the temperature was 51 to 72 F.

The larvae of *S. aureum* were encountered only at above 50 F on trailing vegetation in streams with patchy growth in the water. The preferred current velocity was 0.5 to 2 ft/sec in 5 to 12 inches of water. The maximum temperature was 71 F.

The distribution of the larvae of *S. latipes* indicated a discontinuity in the rivers and abundance in the creeks. The larvae were attached to the vegetation, sticks and pebbles in the *S. aureum* breeding sites except that the temperature requirements were more eurythermic (starting from 40 F).

The larvae of *C. dacotensis* and *C. emergens* were collected from vegetation, logs, and bottom stones in 1.5 to 2.5 ft/sec current speed in one to three feet of water. The temperature was 38 to 51 F. The overwintered larvae of *C. mutata* were attached to the bottom pebbles and sticks in the same conditions.

Prosimulium decemarticulatum was well distributed in Irish and Flatbush Creeks. The larval attachment substrata were dead or trailing vegetation, sticks, stones, and logs under 4 to 13 inches of water and 0.5 to 2 ft/sec of current. The water temperature reached 36 F before the larvae appeared.

Population density assessment - Two methods were employed in determining population densities. The first method was the direct counting of the numbers of larvae in a square foot of the river bottom. Two weekly col-

lecting stations were selected in the Pembina River, one in the Athabasca River and one in each creek. Each station was about three miles long. A wooden frame was applied to a selected area (with suitable attachment substrata) delimiting one square foot of the bottom and the substrata were investigated (average 8 ft^2 counts). Bottom pebbles, debris, vegetation, sticks, stones, rocks and logs constituted the substrata (the last two usually encompassing more than one square foot). This method has been used in ecological studies and control assessments. Arnason et al. (1949), Anderson and Dicke (1960), Fredeen et al. (1953), Jamnback and Eabry (1962), Metcalf (1932) and Sommerman et al. (1955), and Wolfe and Peterson (1959) used a five minute stone count in selected areas.

The second method was based on artificial attachment sites. These consisted of hollow, white matt surfaced polystyrene-butadiene rubber ("high impact polystyrene") cones, 0.01 inch final thickness, 20 cm long, with a 10 cm base diameter and 30° apex, vacuum formed from 0.03" sheet by Spencer-Lemaire Plastics of Edmonton. One set of these was freely suspended by wire through the apices to wooden spikes fixed in the collection stations. Depth adjustment was attained by using cork or lead weights. Another set was fixed with the apices pointing upstream by fixing them to pegs through holes in the spikes. A similar method was employed by Peterson and Wolfe (1958), Phelps and DeFoliart (1964) and West et al. (1960).

In every collecting station there were control cones which were not changed during the season; but the other were checked and the larvae removed for counting every week.

Although the projected area of the cone is only approximately 1/9th of a square foot, the number of larvae on a trailing cone was subequal to the number of larvae in a square foot of bottom. This may be due to attraction of simuliid larvae to bright objects or perhaps to the nature or shape or movement of the surfaces. This is supported by the finding that cones painted yellow, brown, red, green or blue yielded less larvae than the white cones (table 6). The relative brightness of the cones to insects was estimated for me by Mr. Peter Kevan who photographed them by diffuse daylight through a quartz lens. Except for yellow, a fairly good direct relationship between brightness and numbers of larvae attaching is seen. Most measurements of spectral sensitivity in insects indicated low sensitivity in the yellow (Dethier 1963). Similar trends were observed by Wolfe and Peterson (1959) using painted parts of a spruce log.

The fixed cones gave very low numbers at all depths, the freely suspended cones had an optimum depth between 2 and 11 inches with a roughly inverse relationship between turbidity and optimum depth.

Peterson and Wolfe (1960) interpreted the population graph obtained in their study as representing three generations of all the species encountered in the period June to July with a small peak in May which resulted from the overwintered larvae and egg hatch (of all species) in spring. In my study area there was overlapping of the generations of one and all species whenever they were associated. This resulted in peaks in the population graphs (figs. 2-7) corresponding to the life histories of more

than one species in any station. For ease of comparison data have been adjusted in such a way as to synchronise the date of ice break-up.

TABLE 6. Numbers of simuliid larvae on plastic cones of different colors at different depths in the Pembina River, weekly collections, July and August 1965.

Depth in inches:-			2	4	6	8	10	12	14	16
	Relative brightness		Average number of larvae per cone/week (5 counts)							
Color	Visual	Visual + UV								
white	50	10	147	181	386	634	943	858	900	154
yellow	30	7	8	14	11	8	-	-	-	-
green	10	5	17	57	48	31	31	60	94	46
brown	9	1	7	11	13	7	-	-	-	-
red	8	3	11	33	21	9	-	-	-	-
blue	7	2	13	34	59	43	76	87	88	97

TABLE 7. Average numbers of simuliid larvae picked up per cone in six hour period (in the Pembina River, July and August 1965).

		Time				Moon			Sun	
Date	Means	6 to 12	12 to 18	18 to 24	00 to 6	rise	set	phase	rise	set
July 22	383	31	17	101	234	23:31	13:39	last $\frac{1}{4}$	4:00	20:23
July 25	371	31	17	99	224	0:20	17:52	last $\frac{1}{4}$	4:00	20:23
July 27	340	21	14	84	221	2:02	20:04	none	4:08	20:04
Aug. 2	280	18	13	77	172	10:48	22.17	1st $\frac{1}{4}$	4:16	19:55
Aug. 5	219	13	10	76	120	14:45	23:07	1st $\frac{1}{4}$	4:16	19:55

The spring peak depends on the abundance of the overwintered larvae and eggs and the effect of winter on both stages. The high water of spring flood is of great advantage to the larvae as more substrata and organic drift are provided by the invasion of new areas (Anderson and Dicke (1960), Carlsson (1962 & 1966), Fredeen and Shemanchuk (1960), Peterson and Wolfe (1960), and Phillipson (1956 & 1957). There are adverse

effects of the high water as some of the larvae may be washed away and perish and there may be depositions of silt over the substrata.

The summer peak (or peaks) may result from the combined presence of the first generation larvae of those simuliid species with high temperature requirements, successive ovipositions of some species in the first generation and influx of larvae of the second generation. This may be prolonged until August and overlap the small fall generation.

Anderson and Dicke (1960) recorded 2000 to 4000 larvae/ft^2 (300 to 800 larvae on grass blade 0.5" wide and 6" long). Metcalf (1932) recorded 2880 and 1500 larvae on two rocks and 300 larvae/ft^2. Peterson and Wolfe (1960) reported 2400 larvae/cone.

According to Hocking and Pickering (1954) the current gradient is important in the positioning of larvae on the substrata after the larvae attach. The fact that the cones suited the requirements of larvae is illustrated by the high catch recorded.

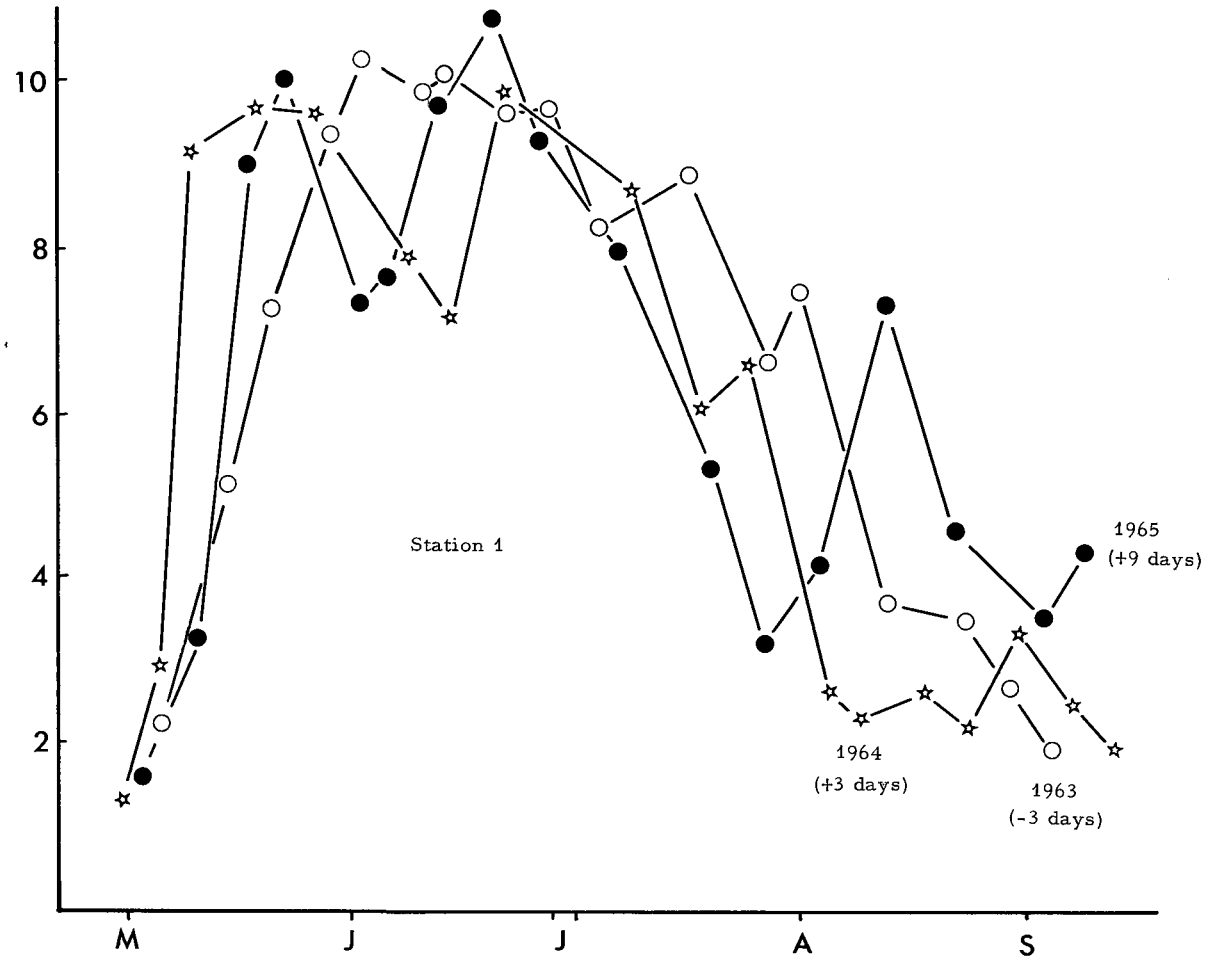

Fig. 2. Total population densities of simuliid larvae in the Pembina River : May to September 1963-1965 (adjusted for dates of ice break-up).

Larval migration - The adult females fly upstream and oviposit, their eggs hatch and the larvae accumulate in these oviposition sites for short periods. They are passively carried downstream by the current. These young larvae were reported by Peterson and Wolfe (1960) to secrete silk threads to suspend themselves in the current. The larvae populate all the favorable breeding sites in the streams and the mature larvae migrate to slower water to pupate.

Rubtzov (1939) concluded from his studies on the migration of simuliid larvae that they migrate downstream continuously during the night and settle on different substrata in the day. He attributed the migration to the decrease in current velocity in one site inducing the larvae to seek higher velocity levels. Radzivilovskaya (1950) reported the larvae migrating during the day and settling during the night and attributed this to lowered oxygen content at the attachment site. Peterson and Wolfe (1960) reported the larvae migrating during the night and settling during the day. Yakuba (1959) suggested that migration may be stimulated by the rapid rise in water level.

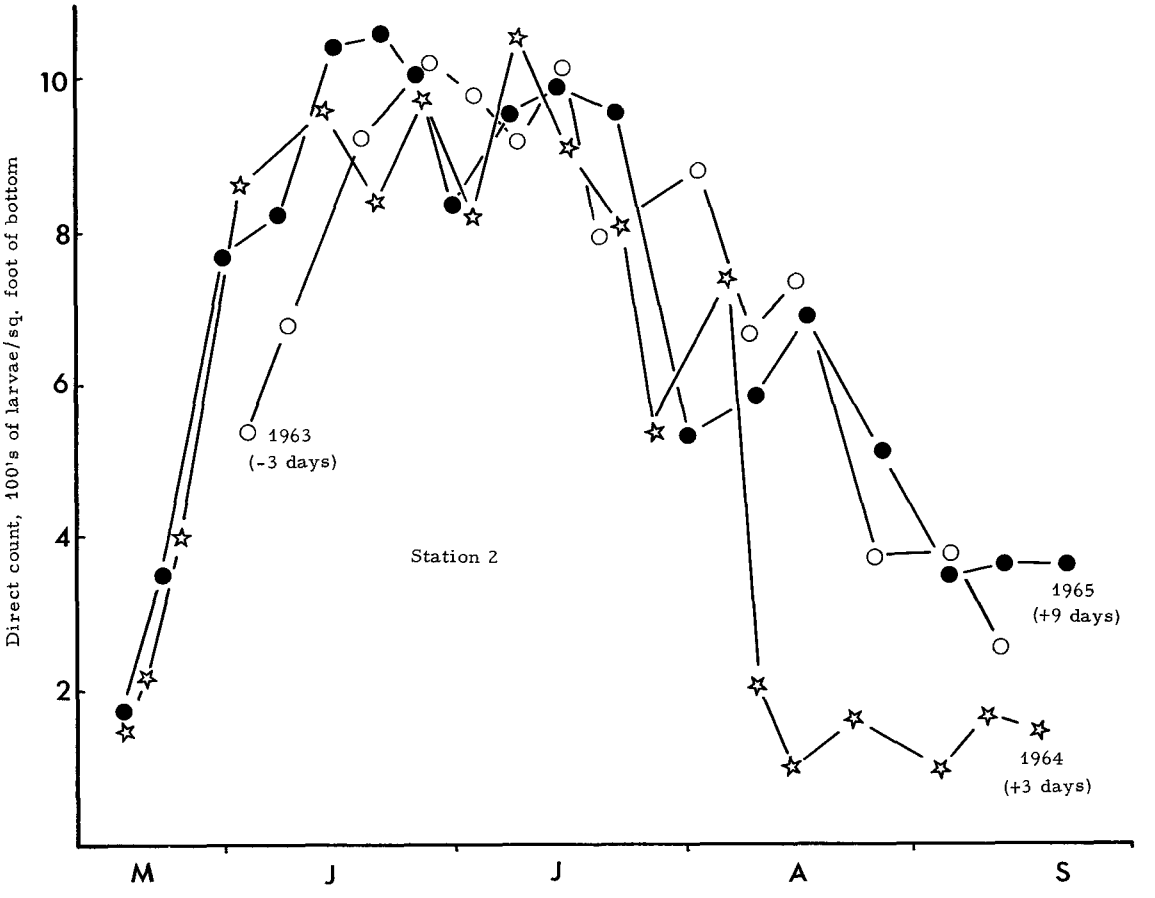

Fig. 3. Total population densities of simuliid larvae in the Pembina River : May to September 1963-1965 (adjusted for dates of ice break-up).

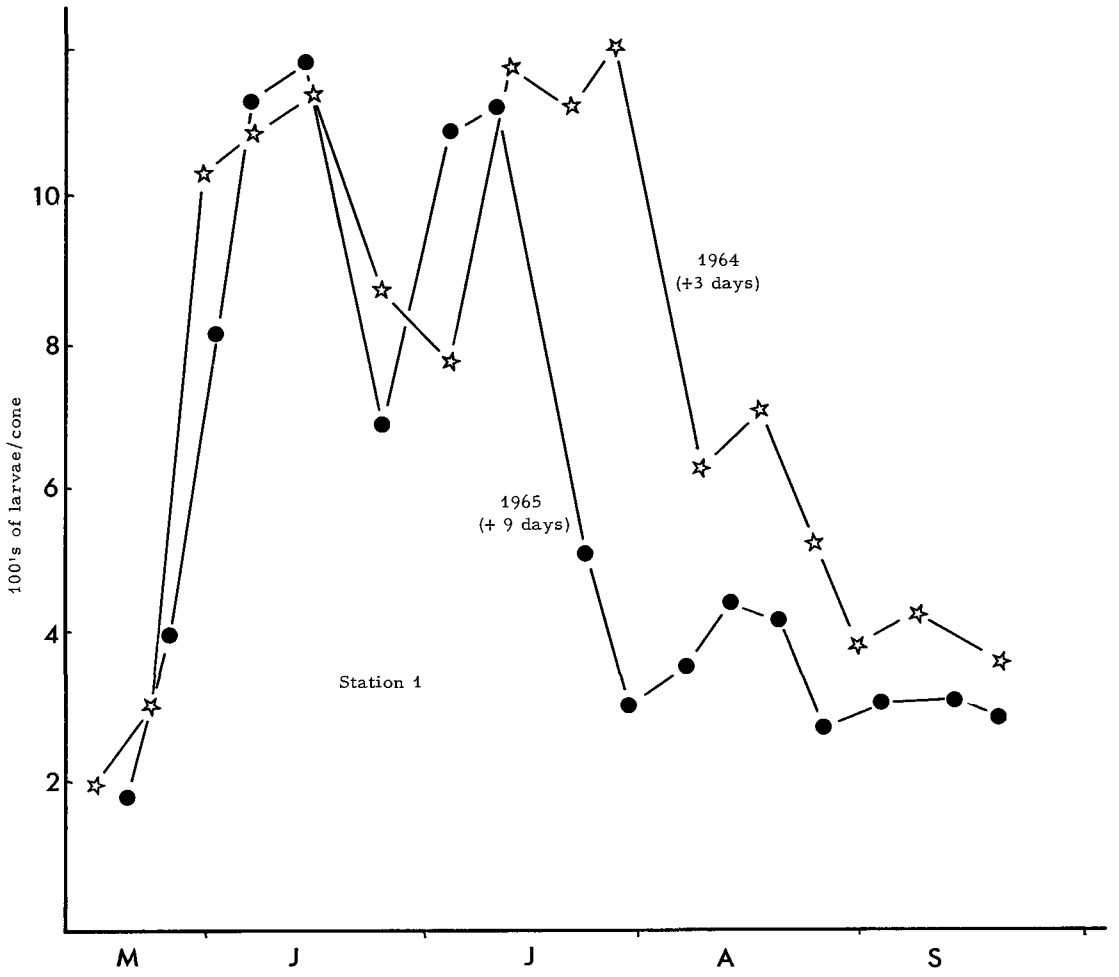

Fig. 4. Total population densities of simuliid larvae in the Pembina River : May to September 1964-1965 (adjusted for dates of ice break-up).

The total numbers attaching decreased with the advancing season in a comparable manner to the total larval density (fig. 2). Attachment, and hence probably numbers migrating downstream seems to be greatest when light intensity is increasing, and to be restricted by the very low light intensity when there is neither moon nor sun. Perhaps decreasing light intensity invokes release, and increasing light, attachment. They may be dislodged by other larvae, drifting objects or as a result of the movement of the attachment object.

Flatbush Creek was dammed in July 1963 and the bottom of the stream below the dam was dry. No eggs were found in June 1964, but the water overflowed the dam in July and continued to flow up to the end of the season. The stream was repopulated by simuliids in July and this was mainly done by females ovipositing below the dam and by larvae migrating from above the dam. In 1965 the simuliid populations in this creek were as high as in other creeks and the species of simuliids were: *C. mutata* , *P. decemarticulatum* , *S. venustum* , *S. vittatum* , *S. latipes* , and *S. aureum* .

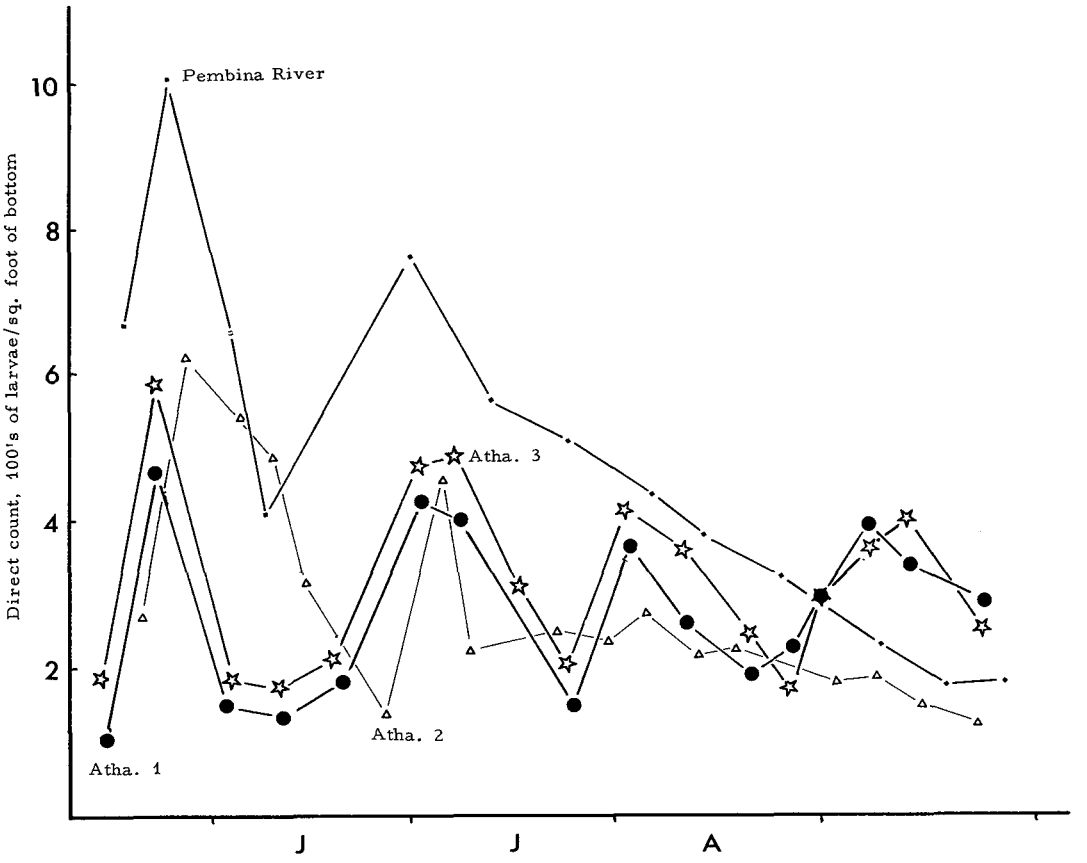

Fig. 5. Total population densities of *S. arcticum* larvae in the Athabasca (3 sites) and Pembina Rivers, 1965.

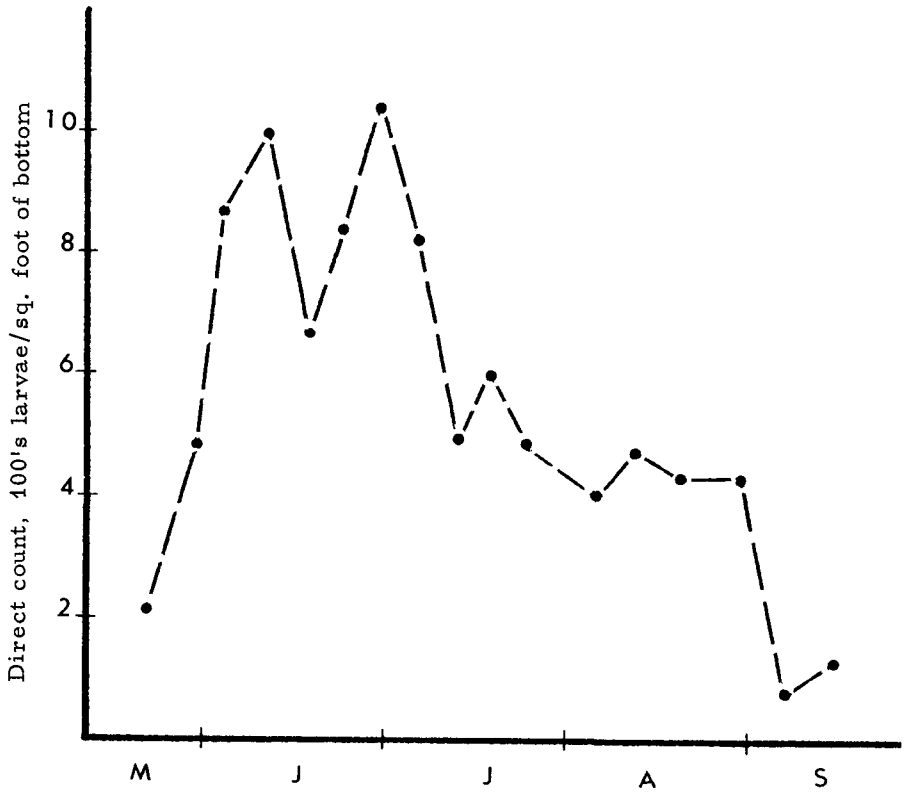

Fig. 6. Total population densities of simuliid larvae in French Creek, 1964.

Laboratory Rearing

Laboratory rearing of simuliid larvae was attempted by Fredeen (1959a), Hocking and Pickering (1954), Mackerras and Mackerras (1948), Puri (1925), Smart (1934), Dalmat (1955), Wood and Davies (1965) and Wu (1931). Only *Boophthora erythrocephala* de Geer has been reared from the pupa through two generations (Wenk 1963).

The methods employed were compressed air to circulate the water in breeding jars, using stone or fritted glass air breakers, and the movement of water: by the shaking or rotation of a platform carrying the breeding jars, by flow through tanks and troughs or by propulsion with propellers. The water used was chlorinated tap water, from aquarium tanks rich in algae or stream water. Rubtzov (1956a) suggested that the maintenance of larvae in the laboratory may be facilitated by rearing them in water rich in micro-organisms. This was attempted by some workers; by supplying bakers' yeast, powdered skim milk and bacteria. At optimum temperature, oxygen saturation and current velocity, food was not an important problem in the laboratory rearing of simuliids.

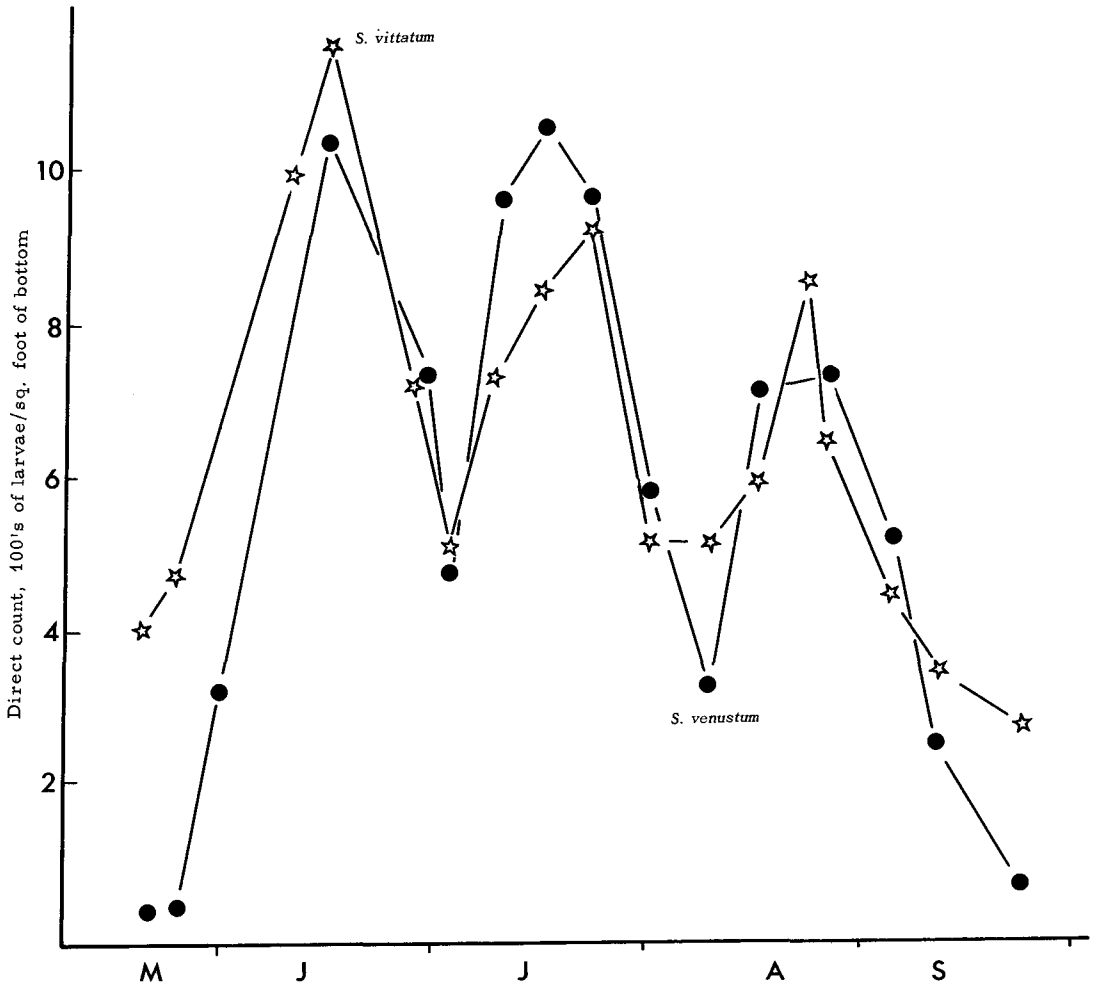

Fig. 7. Total population densities of *S. vittatum* and *S. venustum* larvae in Chisholm Creek, 1964.

In the present study two methods were successfully utilized in the study of life histories and other investigations. Compressed air was bubbled into breeding bowls and museum jars. This method was found satisfactory in raising early stages of *S. venustum*, *S. vittatum*, and *S. decorum* and for insecticide susceptibility tests. Larvae were induced to attach on glass plates facilitating the change of water. As Hocking and Pickering (1954) suggested, autointoxication may be responsible for the mortality observed in jars after four to six days when the water was not changed. 15% to 30% mortality was recorded in 500 cc jars with less than 75 larvae; 40 to 80% in jars with more than 75 larvae. The average used was 250 larvae per 1500 cc bowl with the mortality increasing with increase in the number of larvae.

Two acrylic plastic troughs (described under DDT susceptibility tests) were used in rearing efforts. These simulated breeding conditions in streams and the young larvae from the jars were transferred to the troughs and easily reared to pupae. Water was collected from breeding sites and bakers' yeast was the only food added. The larvae of *S. venustum* were observed to scrape the aggregated yeast cells off the walls of the containers. Algal growth and other microorganisms in the water were not removed.

Field investigations of nutrition were conducted by Anderson and Dicke (1960), Davies and Syme (1958), Hocking and Pickering (1954), Fredeen (1958 and 1964b) and Peterson (1956). The larval gut contents yielded soil particles (sometimes 100%), organic debris : diatoms, algal filaments, spores, pollen grains, pieces of green and decayed vegetation and chitinous pieces of invertebrate body.

In the laboratory the larvae filled their guts with yeast cells, phytoplankton and other inorganic particulate matter. Starved mature larvae emptied their guts in 9 to 17 days; 67% pupated and 12% survived for 21 days without filling their guts again. Larvae of *S. vittatum* without distinct visible histoblasts took 4 to 7 days to empty their guts and survived for 11 to 18 days.

The feeding process was as described by Hocking and Pickering (1954), Peterson (1956) and Osborn (1896). Internal fluid pressure and the current may be responsible for extending the fans. The fans were closed (drawn towards the mouth) two to 23 times in a minute. The secondary fan filaments may be employed to decrease the area between the filaments of the primary fan, thus enabling the larva to strain out smaller particles, e.g., yeast cells.

Puri (1925), Peterson (1956), and Wu (1931) described cocoon spinning. The observed procedure agrees with previous descriptions except that the larvae of *S. venustum*, *S. vittatum*, and *S. decorum* took more than 60 minutes to finish the cocoon in the laboratory.

Pupae

Pupae of *P. decemarticulatum* were recovered mainly from the bottom sand of Irish Creek and in the laboratory the mature larvae pupated in the bottom of the rearing bowls where they spun loose cocoons. Pupal aggregates were encountered in vegetation, rocks, and other substrata located in slow and shallow water. Peterson (1959b) suggested that there

may be a positive thigmotropic response facilitating the pupal development. Stranded pupae of *S. arcticum* , *S. decorum* , *S. venustum* , and *S. vittatum* were observed exposed as a result of a drop in water level. The pupal mass was kept moist by the fine spray from the water splash but when dried the pupae perished.

Carlsson (1966) indicated that each species has a certain pupal optimum temperature but the range between the maximum and minimum developmental temperatures is broad. In the laboratory I noticed that the duration of the pupal stage of *S. vittatum* , *S. venustum* , *S. decorum* , and *S. arcticum* (obtained from the same batch of mature larvae of each species) took from three to eleven days, and that the position of the pupa in the mass did not influence its duration; but as in the field the emerging adult may be trapped under the pupal mass and perish. Organic and inorganic drift sediment piling above the pupal mass may interfere with the emergence of the adult.

Rubtzov (1956b) indicated that there is a correlation between the number of pupal respiratory filaments and the character of the stream in relation to oxygen supply, i. e., pupae in swift water have less filaments than those in slow current. I found that *S. latipes* with four filaments breeds in the same stream as *C. dacotensis* which has numerous filaments, *S. vittatum* with 16 filaments and *S. venustum* with 6 filaments. Pupae kept in vials with moist cotton pads matured in less time than others of the same group left in the breeding troughs.

The adult emerged through a longitudinal split on the dorsal surface of the pupal skin pushing its thorax out first followed by the head and swiftly rising in a bubble of gas to the surface where it took off or was carried by the current to a near support.

Adults

Various methods have been used in studying populations of adult simuliids. Davies (1950), Davies and Syme (1958), Hocking and Richards (1952) and Ide (1940) used emergence traps. Light traps were employed by Davies (1955), Davies and Williams (1962), Fredeen (1961) and Williams (1948). The baited trap was preferred by Anderson and DeFoliart (1961), Bennett (1960) and Fallis (1964). Fredeen (1961) utilized "silhouette traps" which consisted of wooden frames in shape of animals (cow, sheep and horse) and covered by cloth of appropriate color to match the animal it represented. Hocking and Richards (1952) and Davies (1961, 1963) applied sweep-netting and fly-boy-hour counts. The latter method was recommended by the World Health Organization in relation to control.

I used a light trap (ultraviolet) in the period July to September 1963 and June to August 1964, at the field station (4 miles from the river); the total catch was: 91 female *S. venustum* , 49 female *S. decorum* , 36 female and 24 male *S. arcticum* and 18 female *S. latipes*. This represents a low yield compared to some records by the above workers.

Nylon gauze and paper coated with castor oil and sticky traps (tanglefoot and fly paper) were hung near bird nests and on vegetation near the breeding sites. The adults caught were utilized in the life histories studies. Quantitative study of the abundance of adult simuliids was attempted by sweep netting of flying, feeding, and resting flies; the average

number of flies in ten sweeps is plotted in figure 8.

The diurnal activity pattern consisted of a peak of activity two hours after sunrise and a peak starting from two hours before sunset and continuing until after dark. The latter peak was more conspicuous as it consisted of many species and more individuals than the former.

The emergence pattern of the adults was investigated in the laboratory and the field using emergence cages (20 mesh per inch nylon screens). The investigation was on *S. vittatum* in July 1965; approximately 100 pupae were selected from the breeding site for each period (two hour observation); to obtain pupae of similar age dark colored individuals were used. In general agreement with the published data, the observed adult emergence in the field was between 5:30 AM and 1:30 PM. In the laboratory it commenced two hours before sunrise and reached a climax at 9:00 AM but continued throughout the rest of the day in a random pattern (fig. 8).

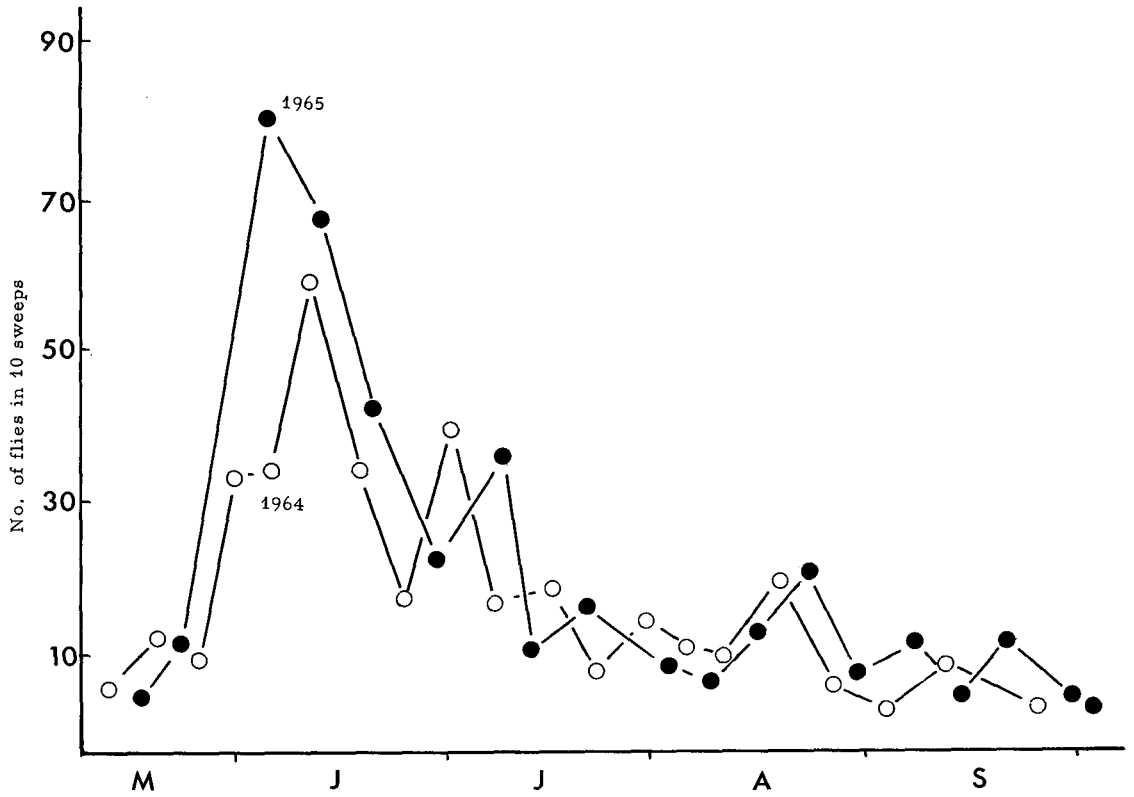

Fig. 8. Populations of adult simuliids, all species (sweep-netting) Flatbush, 1964 and 1965.

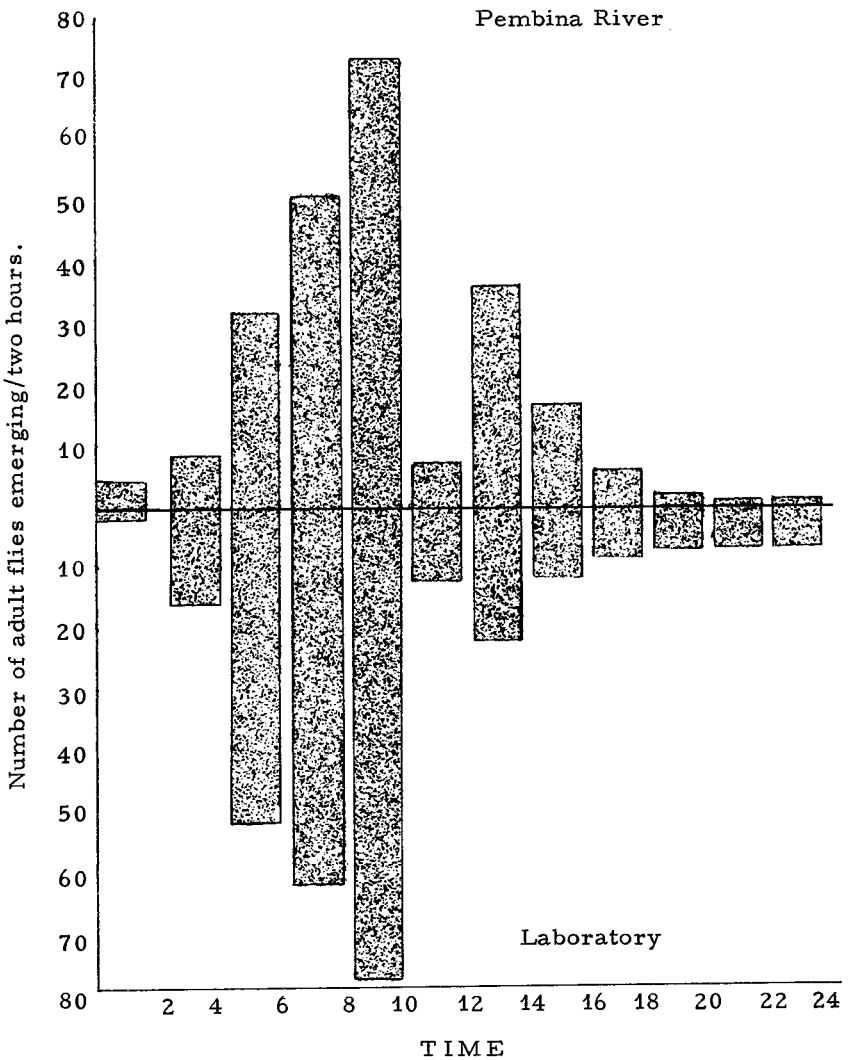

Fig. 9. Adult *S. vittatum* emergence pattern, July 1965.

Species and their Life Histories

Prosimulium (P.) decemarticulatum

This ornithophilic species was collected in 1965 from Irish and Flatbush creeks. The larvae were abundant in May but not before that, indicating that the species passes the winter as eggs. Mature larvae and pupae were taken on June 17. The first adult (a male) emerged in the laboratory on June 24, the females emerged on June 26. In the field a net collection on June 27 yielded only males, later collection yielded both sexes. The females showed no maturation, but were fertilized and most of them had fed on blood. These blood fed females matured their eggs in six days in the laboratory. A few parous females were also collected indicating that the females completed more than one gonotrophic cycle. After July 20 the aquatic stages were encountered singly or in a very random pattern. Similar data were reported by Anderson and Dicke (1960) from Wisconsin. Davies (1950) and Davies et al. (1962) from Ontario, and Sommerman et al. (1955) from Alaska.

Although females did not feed on sparrows in captivity most of the trap collections were from near nests of birds. Females were aspirated from young sparrow chicks in the nests. This is in accordance with the reported host preference for the species (Bennett 1960, Davies and Peterson 1956, and Davies et al. 1962).

Prosimulium (P.) onychodactylum

Three larvae and two pupae of this species were collected in July 1965 and four females and one male were collected on October 2-4, 1964. Except for *P. travisi* this was the rarest species in the study area. Aquatic stages were collected only from the Athabasca River in the Hinton area, above 3000 ft. Both sexes were attracted to the collector but neither landed nor fed on him. Two dissected females contained well-developed ovaries, i.e. the eggs more than half mature.

Sommerman et al. (1955) reported this species to overwinter in the eggs in Alaska and to have one generation annually extending from April to September. Peterson (1959b) collected only larvae in Utah and suggested that the species has one generation a year there.

Prosimulium (P.) travisi

On October 4 in the Hinton area a single male of *P. travisi* was collected in a net sweep from the vegetation on the bank of the Athabasca River, together with six females of *S. arcticum*. Neither aquatic stages nor females of this species were encountered.

Sommerman et al. (1955) collected *P. travisi* from July to September. It was suggested that it has one generation a year with the eggs hatching in June.

Cnephia (S.) mutata

Basrur and Rothfels (1959) discovered that the populations of *C. mutata* in southern Ontario contain bisexual diploid forms and parthenogenetic triploid forms (females only). Davies (1950), Davies and Peterson (1956),

and Davies et al. (1962) found that 90-100% of the individuals collected in Ontario were triploid females.

Basrur and Rothfels (1959) reported the species as univoltine in Peel County; the eggs of the diploid form hatch in January to February and the triploid form then dominates from mid-April to May.

Anderson and Dicke (1960) found that this species passes the winter as eggs in southern Wisconsin and as larvae in the north.

Davies (1950) collected males and females of the diploid form of the species emerging in mid-May and the peak of emergence of the triploid was in late May extending into June (with an odd female collected in August). This attenuated emergence led Basrur and Rothfels to suggest two generations for this species in southern Ontario.

In the study area larvae of *C. mutata* were collected after the ice break-up. They commenced to pupate on May 14 (1965). The females emerged ten to fifteen days later with their ovaries well-developed, containing between 190-250 eggs three-fourths mature. These eggs took five to seven days to mature in the laboratory, without fertilization, the females being fed on water and sugar crystals. In the field unfertilized females were collected feeding on horses and to a lesser extent on cows. These females were examined by me and showed indications of a previous ovarian cycle. There were mature eggs in one or both ovaries intermixed with very immature eggs and plenty of follicular relics.

Fallis (1964) quoted various authors reporting *C. mutata* feeding on deer, hare, cow, and man (ear).

On one occasion an ovipositing female was observed flying low over the surface of water against the current and tapping the water with the tip of its abdomen, it finally fell into the water.

There were no collections of adults or aquatic stages after June.

Cnephia (C.) dacotensis

C. dacotensis is univoltine and fully autogenuous species. It breeds in Irish Creek and was not collected from any other locality. The eggs hatched after the ice break-up and the larvae appeared in May and commenced to pupate in May 17-20. The first male was collected on May 20 and the females two days later. In the laboratory the females raised from pupae showed the eggs almost three-quarters mature. The females fed on water and sugar, matured their eggs in four to six days. In the field females netted from the vegetation on May 24 were all fertilized, their eggs three-fourths mature and the abdomens distended with liquid in the stomach, diverticula and oesophagus. Mating took place on rocks and stones near the water edge occupying from less than a minute to three minutes. No fertilization plugs or spermatophores were detected.

The females oviposited while flying low over the water. The total number of eggs in their ovaries was 276 to 288. Gravid females netted from the vegetation showed indications of partial oviposition, i.e. 20 to 30 ovarioles extended although the eggs were in the same degree of maturation.

The mouthparts of the female were reported as weak, reduced and incapable of feeding (Krafchick 1943, Peterson and Wolfe 1960. Nicholson 1945 and Stone 1964). Twinn (1936), Davies (1950) and Davies and Pet-

erson (1956) compared the size of the male eye with other species and concluded that the eyes are reduced and there is a lack of phototaxis rendering this species incapable of forming a mating swarm. In the present study no feeding or blood engorged females were encountered.

The last date on which the aquatic stages were seen was June 29; although Fredeen (1961 in Davies et al. 1962) reported some eggs hatching in autumn.

My findings are in accordance with the reports of Anderson and Dicke (1960), Davies (1950), Davies and Peterson (1956), Davies et al. (1962) and Nicholson and Mickel (1950), Sommerman et al. (1955), Stone (1964) and Stone and Jamnback (1955).

Cnephia (C.) emergens

C. emergens was taken as larvae and pupae on May 27 and June 10 respectively from Irish and Flatbush creeks. As no overwintered larvae were detected it is considered to pass the winter in the egg. No females were taken in the field but laboratory raised females contained half mature eggs. The eggs ranged from 125 to 211 per female. The females fed on water and sugar crystals but not on a sparrow, a cat or my arm. In describing the species Stone (1952) pointed out the reduction in armament of the mandibles and maxillae which indicated inability to feed on blood. The same condition was reported by Davies and Peterson (1956) and Peterson and Wolfe (1958). Davies et al. (1962) and Sommerman et al. (1955) found a single generation annually, which I confirm.

Simulium (G.) arcticum

This species is the cattle pest of western Canada. Serious outbreaks have been reported since 1912 in Saskatchewan (Arnason et al. 1949, Cameron 1918 and 1922, Curtis 1954, Fredeen 1958 and 1960, Fredeen et al. 1951 and 1953, Hearle 1932 and Rempel and Arnason 1947). The life history and control measures were studied in detail by these authors.

On no occasion were the eggs of this species collected from the breeding sites although presumed ovipositing females were captured in several instances from the Athabasca and less frequently the Pembina rivers. Ovipositing females were seen flying over the breeding sites which were mainly rapids and ripples in the rivers. They lay the eggs singly and they do not dive under water to lay (Cameron 1922 and Fredeen 1958 and 1960). The eggs are scattered in the bottom of the river but my efforts to recover them by brine flotation were not successful. Females captured while ovipositing were kept alive in vials in the laboratory for four days; they did not oviposit and the dissected eggs did not hatch.

Larvae were collected on May 10 1964 and May 11 1965. They accumulate in favorable sites within the breeding localities. They attach to pebbles, stones, rocks and vegetation, although the first three are more abundant in these breeding stations than vegetation it was noticed that there was an aggregation of larvae in the different instars on particular substrates, i.e. up to the third instar larvae are found on smaller pebbles and stones, later instars on stones and rocks, and mature larvae and pupae on rocks and vegetation in slower flowing water. This

indicates a definite migration pattern. Larvae and pupae were collected from the two rivers only although in the southern parts of the province they have been collected from the tributaries of the South Saskatchewan River and from irrigation canals (Fredeen 1958 and 1960).

The data indicate that there are four generations per year with an obvious overlapping of successive generations (as indicated by larval density assessment, fig. 5). The species overwinters in the egg stage as no larvae were collected from under the ice and because the larvae appear after the ice break-up in April. These newly hatched larvae reach maturity at different times in the period from April 20 to May 19 (1964-1965). Pupation of these larvae commences on May 28 and the adult emerges in six to ten days. In the field males were collected two days before the first females were encountered. The overall ratio of females to males was 1 : 4 near the breeding sites and 16 : 1 near grazing cattle and horses; random samples of pupae in the laboratory yielded a 1 : 1 ratio. Average date of pupation for the first complete summer generation is July 1, second generation August 2, the last seasonal generation September 1.

Females emerging from the overwintering eggs have their ovaries well-developed indicating an autogenous condition: thus this species fits into Rubtzov's (1955, 1956a, and 1958) category of "facultative blood suckers" which includes all the species of blood sucking groups that utilize the larval food reserves for the development of the first batch of eggs. Fredeen (1963) and Fredeen et al. (1951) observed this fact and were able to determine the number of previous ovarian cycles using the criterion of the follicular relics. Females that seek a blood meal have mated, oviposited, and usually have fluid in their crops sweet to taste and giving a positive reaction with Benedict solution. In the present study females feeding on cattle and horses were dissected and the ovaries were noticed to be empty except for a few (1-3) mature eggs and in an expanded condition.

Simulium (S.) aureum

Dunbar (1958, 1959) reported seven cytological forms of this species from larvae collected within its range. The two forms studied were:

Form A: Southern and central Ontario (the only form in Algonquin Park, Davies et al. 1962), with two generations extending from May-October (Davies and Peterson 1956) and females feeding on birds on trees about 20 feet above the ground (Davies et al. 1962, Bennett 1960). Form B: southern Ontario; two or more generations a year.

Jobbins-Pomeroy (1916) reported that *S. aureum* has five or six generations annually in southern California; two generations were reported from Illinois (Forbes 1912), Britain (Edwards 1920), France (Pacaud 1942), Ontario (Davies 1950), Davies and Peterson 1956), New York (Stone and Jamnback 1955) and Ontario (Davies et al. 1962). Stone (1964) reported two or more generations annually from Connecticut; Peterson (1956) reported three or four generations a year in Utah and Sommerman et al. (1955) reported one or two generations per annum in Alaska.

This species passes the winter in the egg stage throughout its range. In the study area eggs hatch in late May or early June but adults were

first collected in the period June 17-19 (1963-1965). The second generation pupated from July 11 to 17 and the third pupated from August 9 to 15. Adult collections indicated three peaks corresponding to the observed increases in the aquatic stages.

Females emerged with their ovaries very small and the eggs not developed (stage 1: Christophers' classification 1960). No mating swarms were seen although females collected feeding on cattle and on sticky traps were fertilized. These showed no follicular relics. It may be concluded that *S. aureum* requires a blood meal for each gonotrophic cycle. They were not attracted to humans or to other moving objects.

Ovipositing females were observed and sampled from Irish and Flatbush creeks only, which may explain the deficiency in larval contribution to adult nutrients and the slow maturation of the larvae as these are clear streams with only patchy vegetation.

Simulium (S.) decorum

The species is abundant in the area. The overwintering eggs hatch in May and mature larvae and pupae were encountered in 1964-65 between May 30-June 7. These aquatic stages are found as aggregates on undersurfaces of stones, culvert walls, embankments, beaver dams and vegetation leaves. Three more generations were recorded: the pupation commenced in June 16-20, third July 22-25, and fourth August 11-19 (1963-65). Apparent overlapping is observed between the first and second generations early in the season and third and fourth generations later in the season. Previous records show the species with two or more generations from Alaska southwards (Davies 1950, Sommerman et al. 1955, Stone and Jamnback 1955, Peterson and Wolfe 1960, Anderson and Dicke 1960, and Davies et al. 1962).

Ovipositing females were observed on beaver dams, sticks, stones, logs, cement embankments and vegetation, dipping their abdomens in the water and laying the eggs in mats; up to seven females used the same spots (cumulative ovipositing), 1500 eggs were counted; often dead females were found stuck to these mats.

No mating swarms were encountered but all the females collected were fertilized. Females of the first generation emerged with their ovaries well-developed (eggs in third stage) and the eggs in the laboratory reached maturity without the females mating or feeding; in the later generations there was a decrease in the ovarian development and females failed to develop their eggs without feeding. Fertilized females were collected from feeding swarms of *S. venustum*; attracted to the collector, females started biting on the neck and arm. Females were observed feeding on horses (June 14-17 1964, July 18-21 1965). Up to 70 flies were counted on a single horse at one time.

Simulium (E.) latipes

This is a holarctic species complex. In the palearctic it was reported that the overwintered larvae gave rise to a single generation a year and adults feed on cattle and humans (Davies et al. 1962, Edwards 1920, Smart 1944, and Steward 1931).

In North America the species passes the winter in the egg stage, has

one to three generations a year, feeds on birds, chickens, and man (Anderson 1956, Anderson and DeFoliart 1961, Bennett 1960, Davies 1950, Davies et al. 1962, Davies and Peterson 1956, Fallis 1964, Fallis and Bennett 1958, Hearle 1932, Hocking and Richards 1952, Peterson 1958, Shewell 1958, Sommerman et al. 1955, Stone and Jamnback 1955, and Stone 1964).

In the study area *S. latipes* has two generations per annum. The overwintered eggs hatch in May and mature larvae and pupae appear between June 17 and 20 (1963-65). Commencing on August 17, pupae and mature larvae of the second generation were encountered in increasing numbers.

Females of this species emerged with no ovarian development (eggs in stage II - Christophers' classification 1960). Females induced to feed on chickens and young sparrows failed to develop their eggs beyond stage III and died four days after a blood meal. Fertilized females netted in the field took blood meals from a chicken, a sparrow and the collector's arm, developed their eggs to maturity in 11 days but all died before laying. Davies and Peterson (1956) stated that *S. latipes* developed its eggs in captivity in 5 days at room temperature. Parous females took less than 11 days to develop their eggs in the second ovarian cycle, i.e. it takes less time for each successive cycle due to the fact that the first blood meal is utilized in overall development of the gonads and the eggs. Other likely factors may be the decrease in the number of functional ovarioles and higher temperatures.

Simulium (S.) luggeri

S. luggeri is not a common species in the area. It breeds in the rapids and riffles of the Pembina River. The dates of pupation of the three annual generations are June 13-20, July 21-28 and August 20-26. Nicholson and Mickel (1950) described the species as having three generations in Minnesota, Fredeen collected pupae from mid-June to early July (the first generation) on the Canadian prairies; Hocking and Pickering (1954) collected pupae in northern Manitoba in August; Anderson and Dicke (1960) recorded two generations per annum in Wisconsin; Twinn (1936) as *S. nigroparvum*) described three generations of the species in eastern Canada (Mostly from the Ottawa River, Ontario). *S. luggeri* passes the winter in the egg stage. Adults mated in small swarms near the breeding sites; fertilized females developed their first batch of eggs without blood meals but fed on horses and cattle before the second gonotrophic cycle. After that no females were encountered. Oviposition was not observed and no egg aggregations were detected, it is assumed that, since the known breeding sites yielded no eggs, the females scatter the eggs in the river.

Simulium (S.) tuberosum

Cytologically this Holarctic species was reported by Landau (1962) to consist of "four well-defined breeding units and a likely fifth, all sympatric" in Ontario and with no evidence of hybridization. Davies et al. (1962) suggested the presence in Ontario of two or more undescribed forms of the species which are different from the Palearctic form of *S. tuberosum* .

Previous records revealed two to four generations a year (Smart 1944, Davies 1950, Sommerman et al. 1955, Stone and Jamnback 1955, Anderson and Dicke 1960, Davies et al. 1962). In the study area as elsewhere *S. tuberosum* overwinters as eggs. It has three generations per annum: maturing larvae and pupae were collected on June 14-17, July 19-24 and August 20-24.

Larvae were seen to occur in dense mats on submerged surfaces or rocks and stones exposed to the sun in the Pembina and Athabasca rivers; they were usually well inside the stream and away from the banks.

Females required a blood meal for the first gonotrophic cycle and after mating they attacked cattle and were attracted to the collector in large numbers but only a few fed on my arms and legs and rarely on the neck or face.

Oviposition probably was on the surface of the water when the females were observed to descend from the air and settle on the water; eggs scattered in the water.

Larvae of *S. tuberosum* were closely associated with those of *S. venustum*. At low water larvae of the latter shared most of the substrates previously occupied by *S. arcticum* and *S. tuberosum*.

The last (third generation was more abundant in the southern part of the study area than in the north.

Simulium (S.) verecundum

Separated from *S. venustum* in 1955 (Stone and Jamnback), this species proved difficult to study separately. Stone and Jamnback (1955) suggested two or three generations a year; Davies et al. (1962) found the same in Ontario. In the study area the collection of aquatic stages from the Pembina River revealed a prolonged duration of larvae and pupae from May to August. This suggests three generations per annum. Adults were not attracted to the collector but were captured feeding on cattle.

Simulium (S.) venustum

This Holarctic species was second only to *S. vittatum* in abundance; aquatic stages were discovered in every breeding site and adults were regularly captured in the period May-September.

Stone and Jamnback (1955) questioned the value of the previous biological record of the species as a complex containing *S. verecundum*. They suggested that *S. venustum* has one generation annually (obligatory diapause). The *S. venustum* - *S. verecundum* complex was shown to have more than one generation resulting in a build-up of an almost continuous population of adults in each season (Smart 1944, Davies 1950, Hocking and Richards 1952, Sommerman et al. 1955, Fredeen 1958 and 1960, Anderson and Dicke 1960 and Davies et al. 1962).

In this study three definite peaks were detected in the larval and pupal densities suggesting a three generation pattern for the species: The generation derived from the overwintered eggs is extremely large and reached a peak on June 10-17. The other two generations are smaller but they overlap to cover the rest of the season. Eggs are abundant as they are laid by females in mats sometimes twenty eggs deep and containing more than 1000 eggs. Females dive under water, settle on water,

vegetation, rocks, stones or logs and usually share an oviposition site together. Eggs were recovered easily up to Setpember 20. July 10-15 and August 14-17 were the dates of pupation of the second and third generations respectively.

Females require a blood meal for the first gonotrophic cycle. Mating swarms were encountered and sometimes induced by the presence of the collector or the white top of a car. Females showed a definite preference for humans over cows and for cows over horses. After they land on a cow, a calf or a horse they are difficult to attract, but before landing they were observed to assemble towards a human host in the presence of other hosts. Females were collected feeding on a dog, on young sparrows and on pigs inside a barn.

Simulium (S.) vittatum

S. vittatum was the most abundant species in the study areas. Its aquatic stages were encountered in all the breeding sites examined. In the Athabasca River there was a noticeable decrease in the density of aquatic stages in the Hinton area but a gradual increase downstream (northwards).

Overwintered larvae were detected under the ice in the Pembina River, French, Chisholm and Blackmud (12 miles south of Edmonton) creeks. After the ice break-up the larvae of this species are predominant; they mature and pupate by May 11 to 13. Another peak of mature larvae and pupae was observed on May 28 to 30; this may be an emergence from overwintered eggs. *S. vittatum* was reported to pass the winter in the larval and egg stages in Alaska (Sommerman et al. 1955), British Columbia (Hearle 1932, Saskatchewan (Cameron 1922, 1918), Ontario (Davies 1950), Connecticut (Stone 1964) and Wisconsin (Anderson and Dicke 1960).

Pupation of the second generation commences on June 25 to 28, of the third generation on July 27 to 30 and the last generation on August 24 to 29. Overwintering larvae were common in September. Anderson and Dicke (1960) reported the species to have four to five generations a year in Wisconsin; Davies (1950) reported two generations in Ontario; Davies et al. (1962) recorded *S. vittatum* as multivoltine in Ontario; DeFoliart (1951) assigned three or four generations to *S. vittatum* in the Adirondack Mountains (New York State); Fredeen and Shemanchuck (1960) found the species to pass through four generations in a season; Sommerman et al. (1955) recorded two and three generations of *S. vittatum* depending on the habitat; Stone and Jamnback (1955) reported three to four generations in New York; Stone (1964) reported one to five generations in Connecticut; Twinn (1936) described two to three generations in eastern Canada.

Females developing from overwintered larvae had well-developed ovaries with the eggs almost mature on emergence. Mating swarms were observed from 1800-1900 hours; fertilized females from these were gravid five days later in the laboratory as also were females reared from pupae and not mated. Ovipositing females settled on different substrates mainly well to the middle of the creeks and started depositing eggs in strings. The communal oviposition method was observed with

four to seven females laying on the trailing leaves of vegetation. Females were collected later in the season, including those from overwintered larvae which had oviposited, feeding on horses and cows (mainly on the ear of the latter).

The females of this species were attracted to the collector in large numbers; they crawled inside the front of the shirt thus gaining access to the body. They started biting on the chest and the belly. Those outside the clothing started biting on the back of the neck and the arms. Females still feeding on cattle were carried inside the barns. They accumulated on windows where they were collected dead. Ants and spiders shared the daily crop of flies. Engorged females were seen flying under the barn lights at night. The preferred regions of feeding on cattle seem to be the ears and to a lesser extent the underside of the belly and the inside of the thighs. Only ear-feeding resulted in severe wounds. The swarming females are common; cattle and horses in the pastures are annoyed by these which are attracted to both moving and stationary objects. Females striking against the collector's face are inhaled and taken in the mouth.

Anderson and DeFoliart (1961) in Wisconsin and Wu (1931) in Michigan found the females to feed on cattle and horses but not to bite man although they are attracted to him. Zoophilic and anthropophilic tendencies were reported by Cameron (1922), Davies (1950), Davies et al. (1962), Hearle (1932), Hocking (1953), Jobbins-Pomeroy (1916), Jones (1961), Knowlton (1935), Knowlton and Maddock (1944), Malloch (1914), Sailer (1953), and Stone and Jamnback (1955).

CONTROL

Susceptibility of Larvae to DDT

Fairchild and Barreda (1945) investigated DDT as a larvicide against simuliid larvae in Guatemala and reported the effectiveness of the method. This led to further investigations and resulted in widespread black fly control for medical veterinary and agricultural purposes (Africa: Barnley (1958), Brown (1960 and 1962), Garnham and McMahon (1947), Hitchen and Goiny (1966), McMahon (1957 and et al. 1958), Wanson et al. (1949 and 1950). North America: Arnason et al. (1949), Gjullin et al. (1949 and 1950), Goulding and Deonier (1950), Hocking (1950, 1953), Hocking and Richards (1952), Hocking et al. (1949), Jamnback and Collins (1955), Jamnback and Eabry (1962), Kindler and Regan (1949), Peterson and Wolfe (1960), Peterson and West (1958), Twinn (1950), Travis et al. (1951) and West et al. (1960), and Prevost (1947). Central America: Lea and Dalmat (1954), Vargas (1945). Europe: Petrishcheva and Saf'yanova (1956) and Rubtzov and Vlasov (1934)). Various insecticides and formulations were investigated for the control of both aquatic stages and adults. Albeit eradication was not feasible, spectacular results were obtained.

Laboratory studies were started by Lea and Dalmat in 1954 using screened tubes for containers and circulating river water through them. One and ten parts per million of toxicant in water were used. This method was adopted by the W. H. O. (W. H. O. tech. Rep. ser. 87, 1954, pp. 21-

24). 820 chemicals were investigated in the period Jan. 1952 to Jan. 1953.

Jar tests

Muirhead-Thomson (1957) reported on the reaction of the larvae in the laboratory to DDT and Dieldrin using compressed air to circulate water in test jars.

Jamnback (1962) suggests two methods. The first method involves the use of a pump to circulate water in a reservoir pan to induce the larvae to detach from field substrata, insecticide exposure bags and then employing compressed air to circulate the water in the observation jars. The second method (W. H. O., 1964) employs wooden troughs, the water circulated by a pump from a reservoir tank. This method was modified by Travis and Wilton (1965). They used V-shaped metal troughs for the tests and nylon bags to return the larvae to the stream for the observation period.

I used 500 cc museum jars fitted with glass plates (3.25" x 4"), compressed air, and stream water. The larvae were introduced into the jars and left overnight to attach to the glass plates. After the larvae were selected and the jars were cleaned of excess larvae and substrata, the insecticide was introduced (solutions of DDT in ethanol added to the water to give the required concentration). The exposure time was one hour and after rinsing the jars to remove the insecticide, 500 cc of river water were added to commence the 24 hour observation period. The tests were carried out at room temperature (63 to 67 F); the insecticide was supplied by the W. H. O. in their mosquito larvae test kit (pp' isomer in ethanol). The species composition of the larvae tested was *S. vittatum* 40%, *S. venustum* 30%, *S. tuberosum* 10%, *S. decorum* 10%, and *S. arcticum* 10%. Results are given in table 8.

Trough tests

Two plastic (acrylic) troughs approximately 6 ft long, 7.5 inches wide and 2 inches deep (corrugated transversely; the ridges one inch apart and 3/8 inch deep), were used as simulated breeding sites. The water circulated from a "baby" bathing tub (22 liters capacity) using a 3-gallons per minute discharge pump. One trough and one tub (reservoir) were used in the tests with insecticides, the other was used for the control. It was found necessary to allow more time for attachment of larvae than the overnight period for the jars. It is easier to use the troughs as there is no handling of the larvae (usually a calculated risk). The disadvantage is the amount of water needed to conduct the tests and the large number of troughs required for a set of tests for various concentrations.

Results

Results are given in table 8.

Biotic Control

Predation on adults was not studied. The larvae associated with other stream organisms were accessible for study. In the study it was observed that predators play a minor part in regulating the numbers of

larvae present at any one point. The larvae of Trichoptera, nymphs of Plecoptera, Ephemeroptera, and Odonata were limited in their distribution within a single breeding site and therefore they had access to

TABLE 8. Results of tests of susceptibility of black fly larvae to DDT, Flatbush 1964 and 1965.

Test no.		Concentration of DDT (ppm) 0.002	0.004	0.005	0.010	0.020	control (0)
Jar method							
1)	8.11.1964						
	No. of larvae	50	50	50	60	70	70
	% mortality	40	80	80	100	100	0
2)	8.23.1964						
	No. of larvae	70	80	75	70	65	75
	% mortality	50	100	100	100	100	0
3)	7.18.1965						
	No. of larvae	65	65	65	60	60	65
	% mortality	47	80	100	100	100	0
4)	7.23.1965						
	No. of larvae	55	50	50	50	55	65
	% mortality	40	74	100	100	100	0
5)	8.7.1965						
	No. of larvae	50	55	55	50	60	65
	% mortality	46	71	100	100	100	0
Trough method							
6)	8.8.1965						
	No. of larvae	216	-	-	-	-	207
	% mortality	47	-	-	-	-	0
7)	8.10.1965						
	No. of larvae	-	194	-	-	-	203
	% mortality	-	83.3	-	-	-	0
8)	8.13.1965						
	No. of larvae	-	-	211	-	-	253
	% mortality	-	-	100	-	-	4.4

Percentage mortalities corrected by Abbott's formula

limited populations of simuliid larvae. The above groups were positively recorded as larval predators when their guts on dissection yielded whole larvae or remains of larvae. Other important groups consisted of leeches, birds, and fish. The leeches increased in the creeks, especially late in the season, and the fish and birds were uniformly scarce throughout the season. The two protozoan genera *Thelohania* and *Caudospora* (Protozoa: Microsporidia) are the most common of the simuliid parasites. Davies (1957) recorded *T. bracteata* Strickland and *T. fibrata* Strickland from *Simulium* spp. and *Caudospora* sp. from *Prosimulium*. The infection rates were 4 to 36%. In the present study the infection rate with microsporidians was estimated as 27 to 33% in the creeks and 0 to 45% in the Pembina and Athabasca rivers. It was observed that the infection with these parasites increased in the second generations but decreased rapidly in the middle of August and did not recover again until the end of the season. Adult infection was highest in May-June (2 to 8%).

Nematodes - Mermithid nematodes are parasites of invertebrates and Welch (1963) collected 153 world records of simuliids parasitized by species belonging to the five aquatic genera: *Isomermis* , *Limnomermis* , *Gastromermis* , *Mesomermis* and *Tetradonema* . Rubtzov (1964) reported simuliid parasitism by sphaerularids (Nematoda: Sphaerularidae) in Russia. The overwintered larvae of *S. vittatum* had infection rates of 7 - 47%, mean 26.1% (22 samples from seven localities in 1963 - 1965 seasons). The only species of mermithid parasitizing these larvae was *Gastromermis viridis* Welch. A single record of 79% infection was obtained in a sparse population in Chisholm Creek, in July 22 1964. Other species breeding in the same locality were not infected. *S. venustum* was infected by *Mesomermis flumenalis* Welch. The infection rates were 35 to 64%, mean 45.1% (approximately 89 samples from 7 to 13 sites per season: 1963 to 1965). Sparse and isolated populations of this species, especially in the creeks and the Pembina River reached 94% infection rates. *S. arcticum* , *S. aureum* and *S. tuberosum* were infected at very low rates. Their parasites were *Limnomermis* sp. Pupal and adult infections were estimated as 14 to 23% and 7 to 9% respectively (calculated on the basis of total collections: 1963 - 1965). In the laboratory seven females and four males of *S. vittatum* (raised from infected larvae) emerged in July 1964 with nematode infections. The above data indicate that the parasites are specific, infected larvae were retarded (metathetely), most of them died and pupal and adult infection contributed to the infestation of the upper reaches of the streams. Dr. H.E. Welch kindly helped with the identification of the mermithid nematodes.

DISCUSSION AND CONCLUSIONS

The 15 simuliid species recorded in this study represented the common species in central and central western Alberta. The study area extended from the southern limit of the boreal forest and the northern boundary of the Parkland to the eastern edge of the boreal cordilleran vegetation region (Moss 1955).

The seasonal differences in the dates of ice break-up, river discharge and weather conditions were slight in 1963 and 1964 but 1965 river discharge was higher than the average. This seemed to be without effect on the populations of the aquatic stages.

The systematics of the family are not clear; *Cnephia* overlaps *Prosimulium* and *Eusimulium* (subgenus of *Simulium*); the two new genera, *Paracnephia* Rubtzov and *Crozetia* Davies were erected to accommodate species included in *Cnephia* (in the Ethiopian region). The same problem of *Cnephia* species exists here. The lack of distinctive morphological characteristics at the species level has resulted in the species complexes encountered in the simuliid fauna here. Cytological investigations have revealed distinct forms within the species of many genera in the Arctic simuliids.

S. vittatum underwent no diapause, while the univoltine species *C. dacotensis*, *C. emergens*, *C. mutata*, and *Prosimulium decemarticulatum*, and probably *P. onychodactylum* and *P. travisi* underwent obligatory diapause. The other species were facultative with the eggs only overwintering but there was no indication of summer aestivation.

Mating swarms were not commonly observed but the females attracted to the collector, to other animals, moving objects, and in birds' nests were fertilized. It is suggested that mating precedes blood feeding; this may be the reason why many species failed to feed in the laboratory as they did not mate in captivity. It follows that parthenogenetic species should be easily induced to feed and oviposit. Two species (*Boophthora erythrocephala* DeGeer and *Wilhelmia salopiensis* Edwards) are now known to mate, feed, and oviposit in the laboratory (Wenk 1963, 1965). The oviposition of females in captivity has rarely been reported. *C. mutata* was the only parthenogenetic species in the area. cytological investigations (Basrur and Rothfels 1959) revealed the presence of both the triploid (parthenogenetic) and the diploid bisexual forms in Ontario. Only females were captured in the 1965 season in the study area but a few males were bred out of pupae collected in 1963 and 1964.

Autogeny was exhibited by univoltine species with weak mouthparts which are incapable of piercing the vertebrate skin, e. g., *C. dacotensis* and *C. emergens*; females of the former had their eggs almost mature on emergence, the females of the latter species had much stored nutrients and eggs were only half developed. Other species (*S. arcticum*, *S. vittatum*, and *S. decorum*) were autogenous in the first gonotrophic cycle in the first generation, taking a blood meal for the second ovarian cycle in the first generation and for the first cycle in the subsequent generations. Fredeen (1963) observed that *S. arcticum* females accumulate after oviposition in the first generation and attack in swarms under favorable weather conditions, to obtain a meal for the second gonotrophic cycle.

The third group of females were anautogenous. These were characterized by the large number of eggs in each ovarian cycle, usually laid in masses. These build up large populations of larvae in the breeding sites (*S. venustum*, *S. aureum*, *S. latipes* and *P. decemarticulatum*). This crowding led to competition among the larvae for food and substrata, and might have contributed to the lack of stored nutrients carried over to the adult stage. Lack of stored nutrients could be also inferred from

the quality and quantity of food available to the larvae, the morphology of the cephalic fan (spacing of the filaments) being an important factor. The adult feeding habits of these females indicated no preference. Mammalophilic *S. venustum* fed on 5 different hosts, including a sparrow; the other 3 species fed on different bird hosts. They were at an advantage as they were not exposed to the risks of long flights. Securing a blood meal with such ease contributed to the longevity of the females and ensured repeated ovarian cycles.

The larval development commenced before the growth of vegetation but the species differed in their developmental thresholds of temperature. These differences occurred in all generations of all species in each year. The overwintered larvae have low, and the overwintered egg (embryo) have high temperature requirements.

The seasonal prevalence of the different species indicated by the total population densities of the larvae in the rivers and creeks did not show much fluctuation in the last three years. In June 1965 there was an apparent reduction in the total larval population which could have been due to the effect of adverse weather conditions on the adult population of *S. arcticum* , and other riverine factors.

Larval migration downstream from upstream oviposition sites as well as the influx of migrant females accounted for the repopulation of streams. Predators and parasites would migrate or drift downstream also. There is a possibility that the eggs of those species that lay them singly drift or are washed downstream by the current. It has been reported that inseciticides in the stream induce the larvae to release their grip and be carried downstream where they perish. In the present study, laboratory tests of susceptibility of the larvae to DDT indicated the extreme toxicity of the insecticide to the larvae; calculated LC_{50} was 0.00213 ppm DDT for 1 hour (pp' isomer in ethanol). Similarly, high mortalities resulting from field applications and laboratory tests with low doses of insecticides have been reported.

Laboratory rearing of simuliids ended with the emergence of the adults from the pupae. As Wenk (1965) reported, the problems involved were mating, feeding, and oviposition in the laboratory and these difficulties were overcome with the discovery of two laboratory mating species in Europe. All other species fed on blood developed sterile eggs and oviposited without mating. Eggs dissected out of wild gravid mated females did not hatch. The latter phenomenon suggests that eggs are fertilized in the common oviduct prior to oviposition.

Emergence of aquatic as of many other species follows a diel periodicity, c.f. chironomid pupae (Palmén 1958), gall midges (Barnes 1930) and *Drosophila* (Brett 1955). Davies (1950) studied the factors that affect the emergence of adult simuliids. There was general agreement that light intensity was the main stimulus and that emergence was temperature independent, although the temperature exerted some control on the hourly emergence. I observed that in the laboratory there existed an attenuated emergence between 10 PM and 3 AM (two hours after sunset to about an hour before dawn). In the field the adult yield in the emergence traps dropped considerably after sunset and did not recover except at dawn. The variations in these emergence patterns are likely due

to temperature fluctuating less indoors than in the stream, or to lights being on at night. Temperature may be responsible for initiation of emergence.

Adult activity observations revealed a diurnal periodicity. There were two peaks of flight activity; the first commenced about two hours after dawn, continued for three hours after sunrise and the second occurred irregularly two to three hours before sunset and for sometime in the night. The same pattern of activity was described by Davies (1957) for *S. ornatum* Mg. Davies (1963) and Wolfe and Peterson (1960) reported on studies on the nulliparous and parous females concluding that parous females tended to fly in the late afternoon. Lewis (1958, 1960) observed *S. damnosum* to fly at noon. My studies were on *S. venustum*, *S. vittatum*, *S. arcticum* (mammalophilic species), and *S. latipes* and *S. aureum* (ornithophilic species). Sweep-netting near the breeding sites yielded a large number of nulliparous and a few gravid females and males. The composition of the population of females on the wing was varied. The emergence of the adults of a species of any of the above groups changed the age composition of the flying simuliids. Nulliparous females were dominant at the beginning of the season (late May and early June). The number of flies eventually decreased, and the parous females outnumbered the nulliparous. This pattern continued throughout the season.

Diurnal activity was influenced by the daily weather and meteorological conditions as reported by Dalmat (1954, 1955), Davies (1952), Davies (1957), Wolfe and Peterson (1959, 1960), Wenk (1963, 1965), and Zahar (1951), which indicated a similarity in different regions. In the present study no species exhibited any preference for any set of conditions but there was a uniformity in abundance in both periods of activity with a slight increase in numbers in the afternoon-evening peak. The low light intensity, moderate wind and high relative humidity were the main factors concerned and these were fulfilled in the above periods.

Biotic control agents of simuliids included mermithid nematodes, microsporidians, and predators. The value of Gregarinida (Protozoa: Sporozoa) was not investigated as these parasites were not very common. Microsporidian infections were fatal to the larvae and adults but their importance as biotic control agents of simuliids was not definite. The low incidence of infection with this parasite suggested a secondary value. On the contrary, the mermithid nematodes were efficient parasites reaching 94% in some larval populations (although it may be said here that infected larvae were slow to migrate and to pupate and this led to isolations of these populations which contributed to the high rate of infection observed). Host specificity of the nematodes was significant and was considered a disadvantage from the control viewpoint. The value of the predators (on the aquatic stages) might not exceed that of the microsporidian infection.

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