Biting flies attacking man and livestock in Canada

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INTRODUCTION

Canada has been afflicted with more than its fair share of bloodsucking flies. The number of species may not seem large compared to the faunas of tropical countries, but some of the pest species can be astonishingly numerous at certain times and places. Canada is so large that no one species is found in all parts of the country—problem species differ from region to region, from spring to fall, and even from one year to the next. Over much of the nation, poor drainage, resulting from bedrock or permafrost just below the surface, combined with ample rainfall and snowfall contribute immeasurably to their abundance. In some instances, by impeding or altering drainage patterns, man unwittingly creates conditions that augment their numbers.

The success of any counterattack on a pest species by man has usually been directly proportional to the extent of his knowledge of the life cycle, especially of the habitat of the larvae, for most bloodsucking flies are in the larval phase most of the year. Also, larvae of most species are aquatic or semiaquatic, and thus are usually concentrated in relatively small areas. An experienced observer can sometimes predict fairly accurately what species may occur in a given habitat, suggesting that the female fly is consistent in selecting a certain type of habitat for her offspring; however, the exact parameters are known only to the insects themselves. For example, female mosquitoes are also sensitive to odors left behind by larvae and pupae of the previous generation and consequently lay their eggs in that same habitat: nothing succeeds like success!

Bloodsucking species of flies (members of the order Diptera) attacking man or livestock in Canada belong to one of the following seven families: mosquitoes, black flies, biting midges (also called no-see-ums, punkies, or sand flies), horse flies and deer flies (collectively called tabanids), snipe flies, horn flies and stable flies, and sheep keds, or sheep ticks. Each family is treated in detail under the section on Families of biting flies. Horn flies and sheep keds do not bite man but are restricted to cattle and sheep, respectively. Insects other than Diptera that suck blood, such as fleas, lice, or bed bugs, and non-insects such as ticks and chiggers (Acarina) are not discussed here, nor are those bloodsucking Diptera (a few rare species in each of the families Corethrellidae, Psychodidae, and Ceratopogonidae) that bite only reptiles or amphibians.

MECHANISM OF BLOOD FEEDING

The females of many different kinds of flies depend on blood as a source of protein for their developing eggs. Insect blood was probably an important source, perhaps the major source, of food for the earliest ancestors of flies, and many species still catch their insect prey on the wing and feed only on its blood. The arrival of large terrestrial vertebrates, however, providing an almost inexhaustible supply of blood, must have presented a tempting alternative to insects, for whole families of extant flies now feed almost exclusively on vertebrate blood. One can only imagine the hordes of biting flies that the dinosaurs might have had to contend with!

Among mosquitoes, black flies, biting midges, tabanids, and snipe flies, it is only the female which sucks blood. The males are, without exception, innocuous, and subsist only on sugars such as nectar or honeydew secreted by aphids. In contrast, both sexes of horn flies, stable flies, and sheep keds suck blood. Furthermore, the mouthparts of the last named group are constructed on an entirely different plan, suggesting that the bloodsucking habit of this group was reacquired independently in the course of evolution after it had been lost.

The shift from preying on other insects to bloodsucking on vertebrates may have been a relatively easy step once the fly developed the ability to home in on carbon dioxide. All biting flies are extremely sensitive to this compound and can detect and follow an ''odor plume'' containing it, for great distances. Other odors from a potential host may also play a role in long-distance detection. The fly is also sensitive to heat and moisture as it approaches its host, and when quite close, perhaps only a few metres away, vision apparently comes into play. These responses are best known for mosquitoes, but observations on all biting flies suggest that they, too, are responding to the same cues.

The females of mosquitoes, black flies, biting midges, tabanids, and snipe flies (as well as those of the insect biters alluded to previously) all have the same set of mouthparts (labrum, mandibles, maxillae, and labium) that are common to other insects and all are similarly modified. The modifications to each of these appendages, however, are considerable. Both the mandibles and maxillae are blade- or sword-like, with serrated edges, and their musculature has been radically altered to allow them to be jabbed into skin. This commonality of structure has led investigators to conclude that the common ancestor of all these flies had similar mouthparts and was also a blood feeder.

When preparing to feed, the fly thrusts its maxillary blades, which have recurved teeth along their margins, into the skin as anchors, then snips the skin with its mandibles, which act like a pair of scissors, until blood begins to flow. As blood wells up in the wound, the fly pumps salivary fluid into it to prevent coagulation. This saliva, which contains protein, is allergenic, and causes the swelling and itching that make their attentions so unpleasant. The fly then draws blood up through a channel along the underside of the labrum. No solid tissue is taken, and the belief that black flies and tabanids take chunks of skin has no basis in fact. Of the flies mentioned here, only mosquitoes have evolved a more sophisticated form of feeding. Instead of snipping the skin, the long sword-like mandibles are jabbed deeply into the skin until a capillary is encountered. The mandibles then enter the capillary, and blood is pumped up via the channel along the labrum.

Unlike nectar or other sugar solutions which are stored in the crop, blood passes directly to the stomach, or midgut. The abdominal walls of a biting fly are exceptionally distensible—a mosquito may commonly double its own weight with a single blood meal, and may occasionally triple its own weight. With a full meal of blood, the insect can scarcely fly, and promptly seeks a resting place for several days while the blood is being digested. A week or so later, depending on the temperature, the eggs develop, and the female then seeks a suitable place to deposit them. After deposition, she is ready to search for another blood meal to repeat the process.

The blood meal is such an integral part of the physiology of female biting flies, that most of them cannot mature their eggs without one. Such species thus dependent are said to be anautogenous. In every family of biting flies, however, there are species that have escaped the need for a blood meal and have developed the ability to mature their eggs without one; these species are said to be autogenous. If they develop all their eggs without blood, and do not take blood, they may be called obligatorily autogenous. However, if a few eggs develop without blood, but many more can be matured with a blood meal, these species are said to be facultatively autogenous. In some species, the first cycle of the season is autogenous, whereas blood is required for subsequent cycles.

LIFE CYCLE

All biting flies pass through four major phases during their life cycle: egg, larva, pupa, and adult (Figs. 1, 2, 4, 6). The time of occurrence of each phase is essentially the same from year to year for any given species. Different species, however, usually differ from one another, often substantially, in the timing of each phase.

Most species complete only one cycle, or generation, annually, and are said to be univoltine. Others, which can complete more than one cycle per year, are multivoltine. Univoltine species, upon reaching a certain point in their life cycle, must enter a resting stage, or diapause, in which to pass the winter, the summer, or both. When the weather is favorable for development, multivoltine species can skip the diapause; for these species diapause becomes facultative, not rigidly programmed into the life cycle. Environmental signals such as shorter days or cooler conditions induce diapause, and development is then temporarily suspended either for a predetermined number of weeks or months or until some other environmental cues signal that the time has come when development can safely be resumed. A thorough knowledge of the timing of the life cycle of every pest species is a prerequisite to successful abatement.

Diapause may occur during any of the four phases, depending on the species. For example, most species of mosquitoes belonging to the genera *Anopheles* and *Culiseta* overwinter as adults. However, *Culiseta melanura* overwinters as a larva, whereas *Anopheles walkeri* and *Culiseta morsitans* overwinter as eggs. Most species of *Aedes* mosquitoes overwinter as eggs, which pass the summer, autumn, and winter in diapause, then hatch in the spring after the snow has begun to melt. Most species of black flies also overwinter in the egg stage, but a few species hatch in the fall and the larvae develop slowly all winter under the ice. These species appear as adults in early spring, and spend the summer as diapausing eggs. All tabanids overwinter as larvae, but they are inactive and are probably in diapause. A few tabanid species need more than one year to reach maturity. Horn flies and stable flies pass the winter as pupae. Sheep keds, because they are in a perpetually warm environment, have no diapause.

Egg. Eggs must be deposited in or above a suitable environment for larval development, because newly hatched larvae have severely limited powers of dispersal. The larval habitat is thus determined by the female. As some species oviposit (for instance, many mosquito and black fly species that develop in temporary pools or streams) after the water has dried up for the summer, she must rely on other cues. Some female mosquitoes have been shown to respond to odors left behind by developing larvae and pupae—if such odors could be generated in places unsuitable for larval development, or in combination with insecticides, females might be duped into depositing their eggs in unsuitable places.

Larva. All growth is done by the larva. An insect larva must shed its outer skin, or cuticle, periodically during growth, for the cuticle's ability to distend is limited. After shedding, or molting, its cuticle, the larva immediately swallows air or water to enlarge itself while the new cuticle stretches to its new capacity. Each period of growth is a stage; the larva itself during a given stage is said to be in a particular instar, first instar, second instar, third instar, and so forth. The number of instars larvae of biting flies have varies from three to seven, depending on the family. Mosquitoes, biting midges, and tabanids have four instars, black flies have up to seven, and horn flies, stable flies, and sheep keds have only three. Each successive instar is larger than the previous one, and is usually different not only in size but in structure as well. The first instar is usually markedly different from later instars. Identification aids are usually based on the final instar, and because of lack of knowledge, it is usually difficult to identify to species the other instars of most biting flies unless comparison to final instars is possible.

Larvae of almost all biting flies are aquatic or semiaquatic. Mosquito larvae are confined to standing (non-moving) water, whereas black fly larvae are found only in flowing water (preferences for rate of flow differ among species—for some the flow must be rapid, for others it may be scarcely detectable). Larvae of biting midges, tabanids, and snipe flies usually live in moist soil or moss, whereas those of horn flies can develop only in fresh cow dung. Stable fly larvae are able to develop in any decaying vegetation, including cow dung. All larval instars of the sheep ked are spent within the abdomen of the female, in an elaborate uterus adapted for nourishing developing larvae one at a time.

Pupa. The transition from larva to adult is accomplished in the pupa. Although the pupa develops within the skin of the last instar, it resembles an adult rather than a larva, for the outlines of eyes, legs, and wings can be readily seen on its surface. Normally the pupa sheds the cuticle of the last larval instar; some biting midge pupae remain partly enclosed by their larval cuticle. Pupae of horn flies, stable flies, and sheep keds remain completely enclosed by this cuticle, which becomes a tough barrel-shaped protective container (puparium) for the pupa. With the exception of overwintering horn flies and stable flies, the pupal phase lasts only a week or two. Pupae of mosquitoes can escape predators by swimming to the bottom of the pond. Black fly pupae remain under water, partially enclosed in a silken cocoon which offers little protection from predators. Pupae of biting midges and tabanids are helpless and vulnerable to predators; the most they are capable of is wriggling to the surface of the moss or soil so the adult can escape easily. Adults of horn flies and stable flies must force their way out of the puparium and surrounding soil by means of a distensible sac, called the ptilinum, on the front of the head, which exerts pressure on an obstacle, and in some flies is covered with teeth for rasping the soil ahead of it.

Adult. Emergence (i.e., escape from the pupa) usually occurs in the early morning, perhaps to avoid the many predators which become active later in the day. Freshly emerged adults are usually rather soft, and require a day or so for their cuticle to harden sufficiently. Black flies, however, must emerge under flowing water, for the pupa cannot leave its cocoon; their wings expand as they emerge. Although they are able to take flight as soon as they reach the surface, black fly adults still require several hours to become fully hardened.

A prerequisite of any activity for both sexes is a sugar meal—either in the form of nectar from flowers, as sap from tree wounds in spring, or as honeydew, a sugary solution produced by aphids and scale insects that is usually readily available on the leaves of many different kinds of plants. Water is also a regular requirement: sugar and water are presumably taken at least once every day of a fly's life.

Mating is presumed to be the next order of priority. Males of nearly all species of mosquitoes, black flies, biting midges, tabanids, and snipe flies assemble at particular sites within a few days of emergence, and they presumably spend their entire lives, when not resting or active at that site, commuting between such places and sources of sugar and water. A wide variety of male flies, as well as the males of many other insects, congregate at certain sites, and a particular species may be found there year after year. Females are believed to come to the site only briefly, presumably soon after their emergence. Because mating has been observed almost exclusively at such sites, it is now widely assumed that they are meeting places where the individuals of both sexes can find one another. Hilltops, valley floors, forest clearings, edges of water bodies, prominent trees or boulders, and many other irregularities in the environment have been identified as assembly sites for different species of flies. Male mosquitoes, black flies, and biting midges tend to assemble in the evening, often in swarms. They usually remain hovering or flying back and forth over or beside some prominent object, the "swarm marker." When the swarm is large, the noise of the wing beats may be audible for some distance. Females do not take part in the swarm, but on approaching or entering it they are instantly pursued by one, or more, males. The coupled pair immediately leaves the swarm, and mating is completed nearby in the vegetation. Males presumably reenter the swarm after mating; females may not need to mate again and hence may not return to the swarm, although this aspect of their behavior is not well known. On a warm spring or summer morning on an exposed hilltop, male tabanids, often of several species, may be seen hovering or resting, periodically chasing every passing insect, presumably in hopes of encountering a female. Males may be found there day after day, and experiments are under way to determine whether a particular individual spends all his time at one site or whether he visits other sites. Females are seldom seen, and then only briefly, usually departing with a male in tow. After females of mosquitoes, black flies, biting midges, tabanids, and snipe flies have mated, they are ready to seek a blood meal.

Unlike the aforementioned families, whose males cannot take blood, both sexes of horn flies, stable flies, and sheep keds suck blood. Sheep keds spend their entire lives in the wool of sheep and cannot survive elsewhere. Horn flies spend almost all their adult lives on the backs of cattle, leaving only for a few minutes at a time to lay their eggs on fresh dung. Stable flies are less strongly associated with livestock, and will attack man along beaches, often in remote areas, far from barnyards.

DISEASE TRANSMISSION

In contrast to most tropical and subtropical countries, Canada has relatively few diseases transmitted by biting flies that affect man and livestock. Insects that transmit disease are known as vectors; the disease organisms themselves are pathogens, whereas the victims are the hosts. To succeed, an epidemic (or epizootic in the case of animals) of an insect-borne disease requires suitably high populations, in close proximity, of the host or alternate host, the vector or vectors, and the pathogen.

Transmission of a pathogen may be of two types, mechanical (when the insect is merely a passive carrier, carrying pathogens on its body or mouthparts from a previous visit to an infected host), and biological (when the insect itself plays an essential role in the life cycle of the pathogen). Mechanical transmission is much less important in Canada than is biological transmission. Deer flies, horse flies, and stable flies, which tend to feed on small amounts of blood from several animals in succession, are believed to transmit the bacteria that cause tularaemia and anthrax by carrying these bacteria on their mouthparts from an infected host to an uninfected one. The flies themselves are not necessary steps in the life cycle of the bacteria.

The most important pathogens transmitted by the biting fly in Canada are the arboviruses (*arbo* from *ar*thropod *bo*rne). Canadian arboviruses are primarily pathogens of wild mammals and birds and their occurrence in man and livestock is sporadic, that is to say, only when populations of the vector mosquito rise to abnormally high levels. Four of these arboviruses, transmitted biologically by mosquitoes, cause encephalitis in man. Western equine encephalitis (WEE) and eastern equine encephalitis (EEE) affect horses as well as man, whereas St. Louis encephalitis (SLE) and the snowshoe hare (SSH) strain of the California group of viruses affect man but not livestock. Another strain of the California group, Powassen virus, is transmitted by ticks. Most persons contracting any of these viral infections will not suffer any serious effects, and may not be aware that they have the infection (blood tests taken after epidemics have shown that hundreds of people had the disease but did not report it, for every person who was hospitalized).

The cycles of WEE and SSH probably occur many times every summer, in many parts of Canada, but go undetected because they involve only wild animals. The viruses of SLE and EEE may not be present every year in Canada, although they are undoubtedly present in the USA, and have advanced northward on several occasions. Whether these viruses increase or decrease as summer progresses probably depends more on populations of the vector mosquitoes than on any other factor—in a wet summer these vectors can become enormously abundant, and the chances for an outbreak of the disease among humans and livestock become much greater. In a dry summer, the vectors, and subsequently the disease, become scarce.

WEE is predominantly a disease of the Prairie Provinces and is transmitted most commonly and effectively by a prairie mosquito, *Culex tarsalis*, although other mosquitoes such as *Culiseta inornata* also transmit it. These mosquitoes are partial to feeding on birds but will attack livestock and man when birds are not available. Horses seem particularly susceptible to WEE, and deaths among these animals are usually a prelude to a potential epidemic in the human population. The progress of WEE is monitored every summer at various points across the prairies by frequent testing of chickens maintained for the purpose (called sentinel flocks). Numbers of *tarsalis* are also monitored by means of special traps. When these chickens become infected, and when *tarsalis* reaches a critical level, a decision to spray for *tarsalis* must be made to prevent a potential epidemic of WEE.

SLE is a common disease in the eastern USA. It, too, is a disease of wild birds, and like WEE, infects man and livestock tangentially to the natural cycle. The most common vector, the northern house mosquito, *Culex pipiens*, is present everywhere in southern Ontario and southern Quebec, breeding in ditches and puddles as well as in man-made containers. Chickens and house sparrows may readily become infected, bringing the disease into an urban situation. Although it much prefers to bite birds, *pipiens* will also bite man, bringing SLE into the human population. SLE was unknown in Canada until the epidemic of summer 1975 in southern Ontario. The virus apparently spread north from the USA during a warm wet season in which *pipiens* became exceptionally abundant. There were 66 verified clinical cases, with five fatalities. Subsequent blood tests on a random basis have shown that hundreds more had the disease but did not have symptoms severe enough to be hospitalized. The infection rate dropped precipitously the following summer, and by 1977, the virus had apparently disappeared from Ontario and has not returned.

Although EEE virus has been responsible for deaths of horses in Quebec, no human cases in Canada have been documented. Its vector in the USA, *Culiseta melanura*, also a bird biter, is rare in Canada, and unless other species of mosquitoes can serve effectively as vectors, EEE is unlikely to become a problem.

SSH is apparently widely distributed across the north, where it is passed among small mammals, especially snowshoe hares, by a forest mosquito, *Aedes communis*. Both the wild hosts and the vectors are common and widely distributed, and *communis* readily attacks man, yet recorded cases of SSH in humans are rare. The apparent rarity may, however, be only a reflection of the paucity of medical services in the north, where most victims would recover from the disease before being able to seek treatment.

The only other arbovirus in Canada affecting livestock is bluetongue, a disease of deer, cattle, and sheep transmitted biologically by biting midges, especially *Culicoides occidentalis*. In Canada, the disease has been a threat only in central British Columbia.

Two other arboviruses, causing yellow fever and dengue, are exotic to Canada, occurring only in individuals that have recently returned from the tropics. Yellow fever used to occur in late summer along the eastern seaboard, when boats carrying populations of the mosquito vector, *Aedes aegypti*, and presumably also infected seamen, sailed north from southern harbors. The vector can breed in any water-filled container, and does particularly well in bilge water in wooden ships. The advent of modern steel vessels, along with efficient mosquito control, eliminated this hazard from North America. The lack of suitable vector mosquitoes in Canada precludes an epidemic of either of these diseases that might otherwise result from a returning infected tourist.

Malaria is a disease caused by a protozoan. Unlike viral infections, protozoa seem more resistant to the body's defense mechanisms, and once malaria is contracted, symptoms may occur again and again if not treated. Although various animals, including birds, lizards, and monkeys, may contract various kinds of malaria, human malarial organisms have no host other than man and therefore the disease cannot be contracted away from human habitation. Over 100 years ago human malaria flourished in Eastern Canada but has now been eradicated from Canada and the USA. It is transmitted biologically only by species of the mosquito genus *Anopheles*. At least five of the six species of *Anopheles* found in Canada have transmitted malaria experimentally. Transmissions of malaria occurred recently among campers in California, because one of them had the disease. However, this is an unlikely event in Canada, and it could only happen if someone, returning from the tropics with an active case of the disease, were to be bitten by an *Anopheles*.

ALLERGIC REACTIONS AND IMMUNITY

Every time a biting fly (or other biting insect or related arthropod) takes a blood meal it injects a small amount of salivary fluid to help prevent coagulation within and around its mouthparts. This fluid contains proteins which act as allergens, resulting in swollen, itchy welts. A more generalized anaphylactic reaction, though fortunately rare, can occur in a few individuals who are hypersensitive.

Some species of biting flies seem to have more allergenic saliva than others. Black flies may be worse than others in this regard, and one species of black fly, *Simulium arcticum*, has caused many deaths from anaphylactic shock among cattle in certain areas near the North Saskatchewan and Athabaska rivers.

As everyone who has been bitten frequently by mosquitoes knows, the site of the bite becomes itchy almost before the mosquito has finished feeding.

The itch continues for half an hour, or more (the initial reaction), before subsiding, only to return even more forcibly the following day (the delayed reaction). It has been suggested that initial and delayed reactions are responses to different substances. Experiments with rabbits have shown that an animal with no prior exposure will not react, but after only a few bites it will have a delayed reaction. After still more bites, an initial reaction occurs, followed by the delayed reaction as before. Many hundreds more bites are required to create immunity from the delayed reaction, but once this immunity is acquired it seems to last a lifetime. The severity of the initial reaction may also ameliorate after many bites have been received, but the reverse, hypersensitivity or a more intense reaction, may also occur.

The pattern described here, of sensitivity followed by gradually acquired immunity, applies to rabbits bitten by mosquitoes, but other evidence and experience seem to indicate that the same sequence of events occurs in humans, and also in response to bites from other biting flies. However, one may have to acquire an immunity to each group of biting fly separately, for immunity to mosquito bites seems to offer no protection from those of black flies or biting midges. Furthermore, immunity to the bites of one group of mosquitoes may not render the victim immune to those of others. The writer has developed immunity to bites of *Aedes* but not to *Anopheles, Culex,* or *Culiseta.* For black flies, immunity to bites of *Prosimulium* seems not to effect immunity to those of *Simulium.* A vaccine, prepared from the salivary glands, though theoretically possible, presumably would have to be prepared for each group of biting flies, and it would undoubtedly be less expensive to acquire one's immunity through exposure.

PERSONAL PROTECTION

Abatement, aimed at reducing the number of larvae, is a community undertaking, rarely feasible for an individual, even one owning hundreds of hectares; adult mosquitoes, black flies, and tabanids travel far from their breeding places and are likely to infest one's property from breeding places kilometres away. Fogging one's premises with insecticides, to reduce the adults that happen to be lurking in the vicinity, at best effective for only a few hours, is too expensive and time-consuming for most people. Because of the danger involved, and because legislation differs from one year to the next, and from one part of Canada to another, professional assistance should be sought before fogging equipment is rented or purchased. For hikers, campers, and other visitors to sparsely inhabited areas, and even for urban dwellers at times, repellents offer the only practical means of protection from biting flies.

The most effective repellent for mosquitoes is still diethyl toluamide, or deet, as it is usually called. It is a colorless liquid, and is marketed either in nearly pure form or diluted with alcohol. Because only deet is effective in repelling flies (the alcohol evaporates quickly and has no known repellent activity), the brand which provides the highest concentration of deet for the lowest price should be the most economical.

Despite its effectiveness against mosquitoes, deet is less effective against other biting flies and also has other disadvantages. Intended for use either on skin or on clothing, it may irritate some people's skin, and may damage some synthetic fabrics. It also dissolves some plastics, among them spectacle frames, watch crystals or straps, combs, and handles of pocket knives. Acrylic plastics and polyethylene seem unaffected, but vinyl is quickly softened. On exposed skin, deet must be reapplied every hour, or less, especially under windy conditions.

To overcome some of these deficiencies, a recently developed parka-like jacket, made of open-weave cotton and nylon impregnated before use with deet, provides much longer-lasting protection, up to a day or more. The mesh is coarse enough to admit black flies and mosquitoes, but the impregnated repellent discourages them from entering. The hood of the jacket is usually sufficient to keep black flies and tabanids from crawling into one's hair or under clothing. The open weave permits heat dissipation.

Unfortunately, neither direct application of deet nor use of deet-impregnated clothing kills the attacking insects, which continue to swarm around the head of the person even though they do not bite. Research is under way to test the efficacy of volatile insecticidal compounds such as synthetic pyrethroids, which might reduce their numbers without harming the user.

Electrocutors, which use an ultraviolet light source surrounded by a charged grid that electrocutes any insect approaching the light, remain popular items, especially in rural areas, despite several studies that have shown that such devices do not significantly reduce the numbers of attacking mosquitoes, although they kill many other insects. Apparently female mosquitoes, when searching for blood, are more attracted to people than to the light. Effectiveness in reducing biting midges, the only other biting flies active at night, has apparently not been tested.

Sonic devices emitting a high-pitched noise that supposedly repels blood-seeking mosquitoes have also been tested but found ineffective in protecting the user from attacking mosquitoes. Female mosquitoes are apparently deaf—only the males, which are not interested in blood, respond to sounds.

ABATEMENT STRATEGIES

Reduction in the numbers of biting flies, significant enough to bring relief from local attack for a short period of time, is the best one can hope for at present. Until some breakthrough can be made in genetic engineering, environmental manipulation, or biocontrol, using parasites or diseases of biting flies, most of Canada will continue to be infested annually with biting flies.

Responsibility for abatement legislation rests with the provincial and territorial governments, with the result that 12 different sets of legislation exist in Canada with regard to abatement procedures and licensing of exterminators. An up-to-date list of addresses of provincial officers responsible for administering this legislation may be obtained from the Canada Biting Fly Centre, Department of Entomology, University of Manitoba, Winnipeg, Man. The provincial governments may further delegate responsibility to municipalities, which may superimpose additional legislation of their own. The

Ottawa–Hull region, for example, is regulated by the federal government and two provincial, two regional, and several municipal governments, with the result that biting fly abatement on a community-wide scale has become impracticable.

At present, Alberta, Manitoba, and Yukon have the most ambitious mosquito abatement programs. The cities of Edmonton and Winnipeg each maintain a full-time trained staff to deal with their mosquito problems. The Yukon Territorial Government annually appoints an entomologist to undertake mosquito abatement in those municipalities desiring it. Many other municipalities have mounted sporadic abatement programs, either under threat of an encephalitis outbreak or when pest species reach intolerable levels. Any individual or municipality intending to initiate an abatement program should consult the appropriate provincial or territorial authorities.

Biological control (or biocontrol). Mosquito-fish may be the first organisms that were used specifically to combat biting flies: in 1925, some of these fish were introduced into the warm sulfur pools at Banff, Alta., to reduce the mosquito larvae developing there. The fish have reproduced themselves in these pools ever since, and have effectively eliminated the mosquito problem. In the southern USA, these fish have been introduced into canals, mangrove swamps, and other water bodies, but they are not hardy in Canada in normal waters. Research is currently testing hardier species, for example sticklebacks.

Birds, bats, and dragonflies are widely believed to be effective destroyers of mosquitoes. Undoubtedly these predators will eat mosquitoes when they can, but they cannot be expected to make a significant reduction to mosquito populations, for at least three reasons. Mosquitoes are not readily accessible to them but tend to remain in shaded places, in the shelter of vegetation, where birds and dragonflies cannot readily find them, and they tend to fly close to the ground where bats do not normally hunt. Mosquitoes are active at a time when there are far greater numbers of other, larger insects, such as mayflies, caddisflies, and nonbiting midges available for food. Predators can only eat so much at one time, and as they need a constant supply of food during their lifetime, their populations cannot increase indefinitely. Mosquitoes appear suddenly in large numbers, more than enough to feed all the predators combined, but then disappear for long periods, leaving predators to search for other food. The belief that dragonflies have been raised and released for mosquito abatement is without foundation. The larvae of dragonflies are also predators, and require a year, or more, to develop. A mass-rearing technique for dragonflies, which has not been developed, would likely be very expensive, and there is no assurance that the adults could make a significant contribution to biting fly abatement.

Parasites and pathogens. The most promising research today in biting fly abatement concerns the development and use of parasites and pathogens of the flies themselves. These organisms have the great advantage over predators in that they attack the biting flies specifically, not other organisms, and they do not require other food when the biting flies are not available, because their life cycles are geared to those of the flies. The bacterium, *Bacillus thuringiensis* var. *israelensis*, and the mermithid nematode worm, *Romanomermis culicivorax,* are now mass-produced and commercially available for abatement of mosquito larvae. These and related species are being tested against black fly larvae. Various species of fungal pathogens have also been discovered that afflict mosquito, black fly, and tabanid larvae, and their culture and exploitation for abatement are still in the experimental stage.

Environmental manipulation. Every species of animal and plant requires a particular habitat. Some are more tolerant than others of changes in their habitat, but for others, quite small changes may be sufficient to enhance or eliminate that species or to replace it with another. Man has often done this unwittingly by changing patterns of drainage, changing water levels or rates of flow, or changing the vegetation cover. The critical parameters for each biting fly species are imperfectly understood, but some generalizations about past manipulations are possible, and may provide suggestions for future alterations of habitat.

Mosquito larvae, which only inhabit standing water, are sensitive to changes in water level. Quite different species inhabit temporary ponds, semipermanent waters, or permanent waters. Problem species have often been permanently eliminated by draining and filling in the ponds in which they were breeding.

FAMILIES OF BITING FLIES

Mosquitoes (Culicidae)

Mosquitoes are found in every part of Canada except on a few of the small Arctic Islands. Other biting flies may be severe pests in certain areas, but mosquitoes are ubiquitous, and may be encountered both day and night, and from early spring until late summer, giving no respite even in autumn in some years. As if these obnoxious habits were not enough, mosquitoes are the only biting flies in Canada that transmit disease organisms to man (see section on Disease transmission).

At present, 74 species have been recorded in Canada. Their presence throughout the spring and summer is a result of a succession of different species, each appearing at different times, as well as a succession of generations of a few species during the summer and fall, provided rainfall is sufficient. Some of the larger species are long-lived, persisting from late May until August or even early September. Most species, however, do not live more than a month as adults. The first ones to appear in spring, sometimes before

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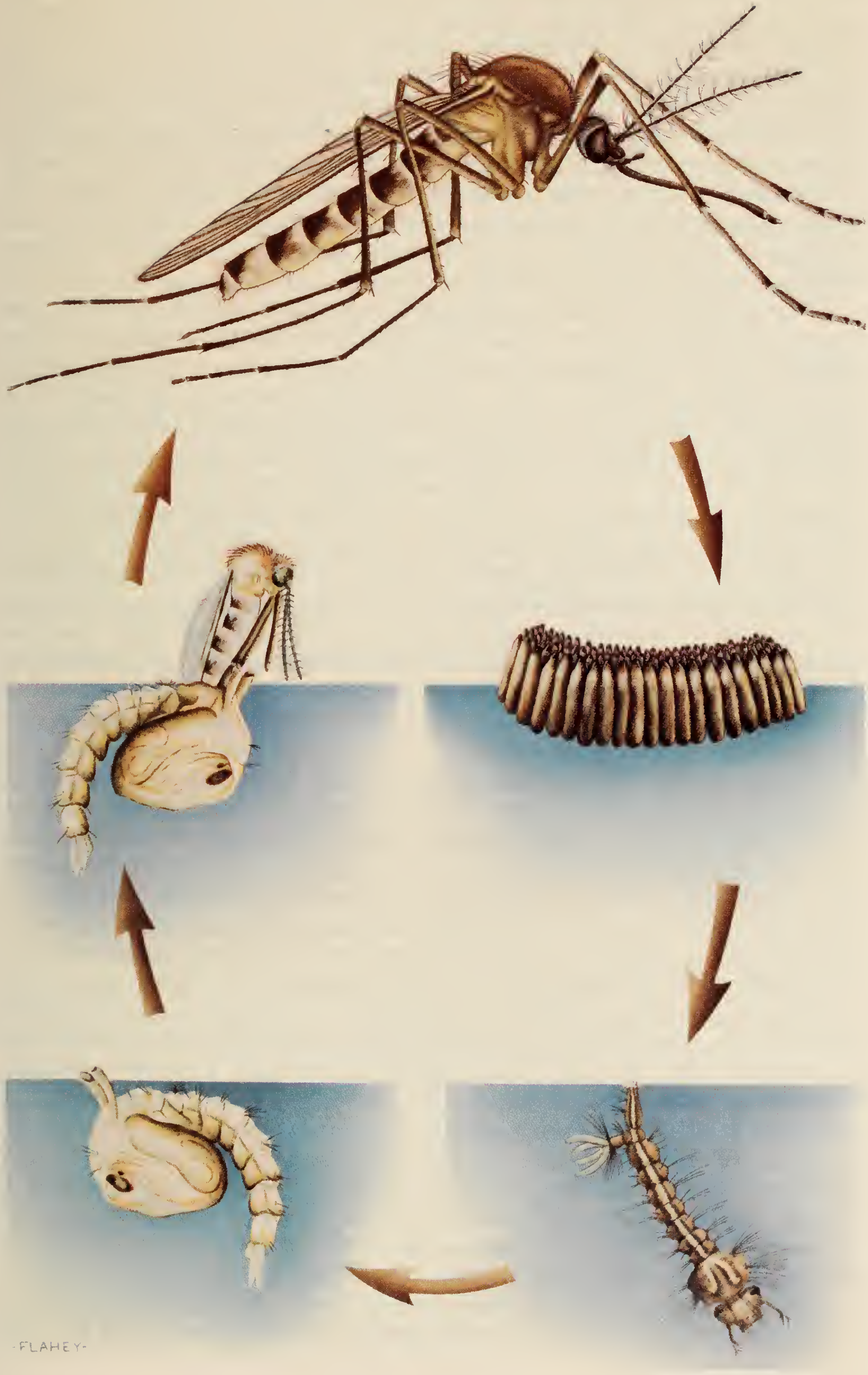
Fig. 1. Life cycle of the mosquito, *Culex pipiens.* Clockwise from top: adult female; eggs cemented together to form a "raft," floating on water surface; larva, suspended from surface film by apex of siphon, through which it breathes air; pupa also suspended at water surface by its two respiratory trumpets; adult emerging into air from floating pupal skin.



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all the snow has melted, are females of *Anopheles* and *Culiseta* that have just come out of hibernation. The majority of species (mostly belonging to the genus *Aedes*) hatch in early spring from overwintering eggs, and develop as larvae in pools of meltwater. These early species account for the great surge in numbers of mosquitoes as soon as the leaves appear on the trees. A few species (especially *Aedes vexans*, Canada's worst pest mosquito) that are capable of repeated rapid generations during hot weather may become unbelievably abundant during summers with heavy rainfall, resulting in a severe reduction in livestock gains and milk production. The prairies are acutely affected when such a wet summer occurs, but any part of southern Canada can experience outbreaks of *vexans*.

The presence of adults among grass or shrubs distant from water has led to the assumption that mosquitoes breed in long grass. However, this belief is without foundation. Larvae of all known species require standing water in which to develop. This water may be as little as a spoonful in a tree hole or leaf base, or as much as a marsh many hectares in extent. Virtually every type of standing water, except lake surfaces exposed to wave action, may support larvae of one or more species. Some species, for example *Aedes excrucians*, are tolerant of a variety of situations, breeding across Canada from the treeline south, but most have their preferred habitat. A few may be found only in large permanent marshes. Temporary snowmelt pools support the greatest number of species, mostly species of *Aedes*, and perhaps also the greatest number of individuals. The drying up of these pools in summer is of no consequence once adults have emerged from them, because their eggs survive desiccation, sometimes for many years. Even specialized habitats, such as the water in tree holes or pitcher-plant leaves, contain species of mosquitoes found nowhere else.

Temporary pools form ideal breeding places for species that can develop fast. Predators, which cannot develop appreciably more rapidly than the mosquitoes, face a glut of food for a few days which they cannot consume fast enough, followed by an abrupt disappearance of this food. Although many kinds of predators have evolved to exploit this abundant food source, few are effective enough at significantly reducing the numbers of larvae to be exploitable as biocontrol agents. Parasites and disease organisms also have their difficulties adapting to such a rapid change from feast to famine.

Mosquito larvae, also called wrigglers, are surprisingly complex animals anatomically. They have no legs but can swim rapidly by lashing their body from side to side. Although minute larvae may breathe through their skin, older larvae breath air at the water surface through a pair of small openings, or spiracles, at their posterior end. In most species, the spiracles are elevated on the end of a conical siphon, which gives the larvae a characteristic appearance. Larvae are often seen suspended from the surface film, each by the apex of its siphon, sustained by surface tension. One of the oldest methods of control is to disrupt the surface tension of the water with an oily substance, thus cutting off the air supply to the larvae beneath.

Except for a couple of rare species whose larvae are predaceous on aquatic organisms, especially other mosquito larvae, all mosquito larvae feed on plant material, either living (as algae or floating pollen) or dead. *Anopheles* larvae are specialized for feeding on material floating on the surface; the rest feed mostly at the bottom. Food particles are gathered with a pair of brushes, the labral brushes, on either side of the mouth. Each brush consists of tightly packed rows of hundreds of long hairs—the hairs may be extended simultaneously by internal blood pressure, or collapsed, row by row, by the pull of a complex set of muscles. Extension and collapse are rapidly repeated, several times per second, entrapping nearby particles as well as generating a current in the water which brings more particles into range. Entrapped food is then combed out and directed into the mouth by the remaining mouthparts (mandibles, maxillae, and so forth) which are among the most complex found in any animal. This type of feeding, called filter-feeding, is also practiced by larvae of black flies and by those of several other nonbloodsucking families of flies. Mosquito larvae of the genus *Aedes* are not dependent on particles already in suspension but can create them by rasping dead leaves and other submerged organic material with the comb-tipped hairs of their labral brushes. The sharp-tipped mandibles can also break up larger particles into ones small enough to be eaten.

The pupae, shaped like tiny tadpoles with the tail tucked underneath, normally rest motionless at the water surface, breathing through a pair of funnel-shaped structures, called trumpets, located just behind the head. When disturbed, they can swim rapidly to the bottom and hide among the debris there, an ability almost unique among insect pupae.

Adults emerge from their pupal skins at the water surface. When free of its pupal case, an adult can stand on the surface until its wings harden. Some species then undergo dispersal flights, which may take them kilometres from their emergence site. Males then assemble in certain areas appropriate to the species, usually clearings in the forest, where they take flight and form swarms at daybreak and again at dusk, in hopes of intercepting a female. Unmated females are also attracted to these clearings, and the hum of their approaching wing beats is detected by the long whorls of erect hairs on the antennal segments of the males. An approaching female, once detected, is immediately intercepted by one or more males; the successful suitor captures her in midair, and they mate in flight, completing the process either in the air or as they drift downward to land in the vegetation below. After mating, the male presumably returns to the swarm, whereas the female leaves the area to begin her quest for a suitable host and a meal of blood.

Pest species. Although more than 60 of the 74 recorded species in Canada take blood, only a few are so abundant that they may be considered serious pests. Perhaps the worst pest is *Aedes vexans*, discussed previously. On the prairies, *Aedes spencerii* and *A. dorsalis* are also regularly occurring nuisance species. Near salt marshes in the Maritime Provinces, *Aedes cantator* and *A. sollicitans* are pests throughout the summer. Near large permanent marshes in southern Ontario and southern Quebec, *Mansonia perturbans* is an abundant pest at dusk during summer. *Aedes sticticus* eggs may remain alive for many years along bottomlands of large rivers across southern

Canada, hatching en masse when inundated by flood waters in late spring or summer. *Aedes stimulans* and *A. excrucians* and their relatives are large aggressive reddish brown species with white-banded legs. They persist throughout the summer in wooded areas of southern Ontario and southern Quebec. Farther north, *A. punctor* and *A. communis* are the dominant species throughout the boreal forest. *Aedes punctor* prefers acidic muskeg, whereas *communis* develops in association with alluvial clay along stream valleys. The subarctic, in the vicinity of treeline, owes its formidable reputation as the worst place in the world for mosquitoes largely to *Aedes hexodontus.* Breeding in enormous numbers, estimated at 12.5 million to the hectare at Churchill, Man., *hexodontus* attacks day and night, under conditions of wind and cold that would subdue most other species. On the tundra, *Aedes nigripes* and *A. impiger* extend all the way to the northern tip of Ellesmere Island, but nowhere do they approach the ferocity of *hexodontus* near the treeline.

Black flies (Simuliidae)

No other biting flies inspire such apprehension, particularly among visitors to Canada, as do black flies. In the forested parts of the Canadian Shield in June and July this fear may be justified, for members of the *Simulium venustum* species complex can be so numerous and can attack so persistently that outdoor activity during the day without some protection becomes almost impossible. Black flies often land and take off repeatedly without biting. Their numbers, and their tendency to bite, increase as sunset approaches. Even when they are not biting, however, their buzzing presence and constant crawling is as irritating as the bloodsucking itself. Mercifully, relief comes after dark, for unlike mosquitoes and biting midges, black flies do not attack at night. Also unlike mosquitoes, black flies seldom attack indoors or even in a vehicle; once they sense being trapped their attention seems permanently diverted to escape and they spend the rest of their lives crawling up the screen or window pane.

Although they cannot bite through clothing, black flies have a predilection for crawling into hair or under clothing, biting in inaccessible places, such as the ankles and belt line. Tucking trouser cuffs into socks will normally prevent them from getting at the ankles, and the deet-impregnated jacket (see section on Personal protection) will discourage most of them from crawling under one's shirt or into one's hair. Black flies are strongly influenced by color—they find dark hues more attractive than pale ones, and blue, purple, brown, and black more attractive than white or yellow. A light-colored shirt, therefore, is a much better choice of clothing than a dark blue one. It is a moot point, however, whether blue jeans might not be better than

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Fig. 2. Life cycle of a black fly. Clockwise from top: adult female; eggs laid on emergent vegetation at surface of flowing water; larvae attached to stream bottom, with labral brushes, usually called labral fans in this family, extended in feeding position; pupae, each enclosed in its cocoon, attached to submerged vegetation; adult, enclosed in air bubble, escaping to surface of water from submerged pupal skin.

pale trousers: if they are carefully tucked in at the ankles and are without holes, jeans may help to attract the flies away from the head region.

In southern Canada, black flies are on the wing from early May (coincident with the bursting of buds of forest trees, especially sugar maple, before mosquitoes appear in numbers) until mid-June. Farther north, in the boreal forest, they may be present throughout June and July, whereas in the Yukon and mainland Northwest Territories, where rivers are usually ice cold until midsummer, black flies do not appear until late July or early August, after mosquitoes have nearly disappeared.

There are more species of black flies than of mosquitoes in Canada; over 100 have already been recorded, and there are more that have not even been named. Black flies are more selective in their choice of host than are mosquitoes, and comparatively few species take human blood. Most species seem to feed only on the blood of birds and a substantial percentage apparently do not take blood at all, because their mouthparts have degenerated and appear useless for bloodsucking. Bird biters may, however, be attracted to man, probably by the carbon dioxide he breathes out, and when numerous can be annoying, even though they do not bite.

Black fly larvae of various species may be found in every type of flowing water, from minute seepages in which the flow is scarcely detectable, to the largest rivers and waterfalls. Each species seems to have its preferences for streams of a certain width, velocity, and character; springs and seepages have their own particular black fly species, whereas large rivers and waterfalls support a different fauna. Most species seem rare; in contrast, some are so abundant that their larvae carpet thousands of square metres of river bottom. Each larva normally remains fixed in one place, clinging by means of a ring of numerous minute hooklets at its posterior end to a small pad of "silk," a salivary secretion that the larva attaches to an object in the current. Using the same structures as the mosquito larva (labral brushes, mandibles, maxillae, and so forth), though modified extensively for coping with moving water, the black fly larva filter feeds by straining small particles, in the form of algae and detritus, from the water that flows past. Larvae cannot easily discriminate between different types of particles and swallow everything within a certain size range that gets caught by their mouthparts, including the fecal pellets of larvae upstream. In this respect they are important recyclers of nutrient material. Their inability to discriminate between particles also renders them vulnerable to being fed insecticides in the form of tiny pellets.

Although black fly larvae can remain for long periods in one place, anchored to their small pad of silk, they are capable of changing positions. After attaching a new pad of silk, the larva grasps it with the hooklets at the end of its anterior proleg (a finger-like projection just behind and below the head), releases its posterior hold and brings the posterior hooklets forward to grasp the new pad. A larva can thus progress, albeit slowly, in a looper-like fashion. If irritated, however, the larva instantly attaches some silk to the substrate, then lets go completely, drifting downstream at the end of a dragline of silk like a spider, except that the silk is produced from its tongue rather than from spinnerets as in a spider. It can then either work its way back up the dragline or drift downstream indefinitely until a suitable situation is encountered again. This drifting habit explains why some species that are normally inhabitants of small streams are occasionally collected in large rivers.

When a larva is fully grown, it searches out a suitable place to spin its cocoon, in which it pupates. The cocoon, a sac-like or slipper-shaped structure, is made of the same salivary secretion with which the larva uses to anchor itself. The cocoon is always firmly attached to some underwater object, or even partially buried in the bottom silt, with the anterior end of the pupa protruding from the opening. All black fly pupae have a pair of filamentous gill-like organs, arising behind the head, for gas exchange; the number and shape of these organs is of diagnostic value in identifying the species. After a week, or more, just before the adult is ready to emerge, the pupa fills with gas. The adult emerges, expanding its wings as it does so, and, leaving the pupal skin behind in the cocoon, bobs to the surface completely surrounded by this protective film of gas. Like a mosquito, it too can stand on the water surface, and may ride downstream a short distance before taking flight.

Almost all species of black flies in Canada have a single annual generation (univoltine). Some of these, for example, several species of *Prosimulium*, spend the winter in the larval stage, often under the ice, where they slowly mature. They are thus ready to pupate as soon as breakup comes, and they are the first to appear as adults. With a single exception (*Simulium vittatum*, discussed next) these species are univoltine and pass the summer and autumn in the egg stage. Eggs hatch in October, or earlier in northern Canada. Of the remaining species, most are univoltine and pass the summer, fall, and winter in the egg stage. Larval development is usually rapid; most of these species occur in small, often rather warm streams and seepages. A few species are multivoltine, that is, they pass through more than one generation during the summer. *Simulium vittatum* is the multivoltine species that also overwinters as a larva.

Pest species. Only a small fraction of the species now recorded in Canada are pest species. In Eastern Canada, only two species complexes are severe pests. The first of these to appear (with the bursting of the buds of forest trees) is the *Prosimulium fuscum-mixtum* species complex. Adults are pale to dark brown and have uniformly brown legs, without white bands. The species of *Prosimulium* last only 1–2 weeks before being largely supplanted by the *Simulium venustum-verecundum* species complex, a group of blacker species with black and white banded legs. The peak of abundance of the *venustum* species complex is in June or early July, depending on latitude. Thereafter, the problem usually subsides, although a few species continue to create local problems. *Simulium decorum*, a multivoltine species, may become noticeable in autumn (though present all summer, this species either does not attack man or is so outnumbered by the *venustum* complex that it escapes detection). Near large rivers, the species *S. jenningsi*, also multivoltine, may be locally common; fortunately it does not seem to be the serious pest in Canada that it is farther south in the eastern USA. In New Brunswick, *S. parnassum* is a rather late species, common in midsummer. In Newfoundland, an early spring species, *Prosimulium pleurale*, is locally abundant.

In Western Canada, *S. arcticum* and *S. luggeri* are serious pest of livestock on the prairies. Before the advent of the Gardiner dam on the North Saskatchewan River, *arcticum* used to appear in such large numbers among herds of cattle that many were killed by anaphalactic shock (see section on Allergic reactions and immunity). Although *arcticum* is still a serious pest in the region of the Athabasca River, the Gardiner dam changed the rate of flow of the North Saskatchewan River and eliminated the rapids where *arcticum* used to breed; this species ceased to be a pest and *luggeri* took over the slower, weed-choked river. Although *luggeri* apparently does not kill cattle, it is multivoltine and therefore present all summer long, hardly a better substitute for the univoltine *arcticum*.

Biting midges (Ceratopogonidae)

Biting midges, also called sand flies, no-see-ums, and punkies, are the smallest of the biting flies. The victim is seldom aware of the fly's presence until it has already started to feed. The burning sensation this fly produces has earned it the name ''brulot'' in French Canada.

The family Ceratopogonidae is by far the largest, and least known, of the families of flies with bloodsucking members. With the exception of a few species of *Leptoconops*, however, those species of biting midges attacking man and livestock in Canada all belong to the genus *Culicoides*. More than 50 species of this genus occur in Canada, most feeding either on mammals or on birds, although a few attack only reptiles or amphibians. The remaining members of the genus have atrophied mouthparts and probably do not feed on blood. Aside from *Culicoides*, there are many other genera of Ceratopogonidae in Canada, encompassing hundreds of species, perhaps the majority not yet even named. They occur everywhere, even on the Arctic Islands. Some members of the genus *Forcipomyia* suck blood, almost like ectoparasites, from larger insects, either directly from the living insect or from carcasses trapped in spider webs (somehow avoiding capture themselves). A few species of *Atrichopogon* suck the contents from pollen grains. Most remaining female ceratopogonids are predaceous and even cannibalistic, capturing their prey on the wing and even consuming their mates during the mating process. As is the case with mosquitoes and black flies, only the females seek blood as well as nectar or other sugar sources; males feed only on sugars.

Ceratopogonid larvae are minute and not easily found or studied, although they occur in a wide variety of moist habitats, usually among decaying vegetation. Larvae either feed on plant material such as algae, fungi, or fungal spores or are carnivorous. The carnivorous larvae have bullet-shaped heads, and burrow, headfirst, into larger insect larvae. The plant

Fig. 3. Adult female of a biting midge belonging to the genus *Culicoides*.

feeders are usually terrestrial, in moist situations such as under the bark of dead trees. Carnivores are either aquatic or soil dwellers. *Leptoconops* larvae, whose feeding habits are unknown, have been found several centimetres below the surface of sand beaches.

Ceratopogonid larvae make no cocoons nor spin silk, but pupate in or near the larval habitat. Pupae of the aquatic species may float to the surface but cannot swim; those formed under bark are often partially enclosed within the last larval skin.

Pest species. Despite the large number of species found in Canada, relatively few are pest species. In the boreal forest, especially in eastern Quebec and the Atlantic Provinces, *Culicoides sanguisuga* and other species can make camping in forested areas intolerable in late June and July. In the Maritimes, adjacent to coastal salt marshes, *C. furens* can be abundant, although not the problem it is farther south in the USA. *Culicoides occidentalis* is believed to be the principal vector of the virus that causes bluetongue in livestock in central British Columbia.

Horse flies and deer flies (Tabanidae)

Tabanids, as these flies are usually collectively called, occur throughout Canada south of the treeline. In general, they are the most numerous in the boreal forest where vast boggy areas provide unlimited breeding grounds and where caribou and moose unwittingly provide blood for the females. Active only during the day, when the weather is warm, most species are prevalent only during summer, from June to August. Most of the species are thus present simultaneously.

There are about 135 species of tabanids in Canada. Most of these (75) are horse flies, belonging to the genera *Hybomitra* and *Tabanus*; 42 are deer flies, belonging to the genus *Chrysops*, whereas the remaining 18, most of which do not bite, belong to various other genera. Deer flies are smaller, and usually have boldly patterned wings; the wings of horse flies are usually transparent.

All tabanids overwinter in the soil as larvae. Most favor wet mud, near or under ponds, marshes or streams, or in sphagnum moss in bogs, although a small number of species live in drier habitats. A few rare species occur as larvae only in gravel under swiftly flowing water. Some species, especially in the last two categories, are choosy as to their habitat, but the larvae of perhaps the majority of species have been collected in a variety of wet muddy habitats near various water bodies. With present knowledge it is not as easy to predict what species might occur in a given habitat as it would be for mosquito or black fly larvae. Tabanid larvae are also fairly mobile, and as they live for many months, they may crawl considerable distances through the moss or mud.

Horse fly larvae are fierce predators, capturing their prey, usually the larvae of other insects, with their sharp sickle-shaped mandibles and paralyzing them with an injection of venom like a rattlesnake. A particularly large species in the southern USA can capture newly hatched toads and drag them under the mud. Each mandible is hollow, traversed lengthwise by a poison duct which opens near its tip; the poison gland is located farther back inside the body. An injection of the venom immobilizes the prey almost instantly and probably also aids in liquefying its tissues which are then sucked out leaving an empty skin. Horse fly larvae are capable of inflicting a painful bite if handled. Deer fly larvae are equipped with a similar set of mandibles with venom glands but no one is sure what their food consists of or how their mandibles are used. They are not cannabalistic, as are horse fly larvae, and often occur together, especially at pupation time. Pupae of all tabanids are formed in soil just below the surface, where they can wriggle out in time for adult emergence.

Fig. 4. Life cycle of a horse fly. Clockwise from top: adult female; egg mass deposited in cattail leaf above stagnant water; two larvae; two pupae, each containing a fully developed adult ready to emerge, protruding from the mud.

Adult males, especially of some of the larger species of *Hybomitra*, are spectacular fliers, hovering in one place for minutes at a time, then dashing off at top speed in pursuit of another insect, which presumably they hope is a potential female, only to return to the same spot and continue hovering. Such males must require relatively enormous amounts of nectar to provide the energy to remain airborne for such long periods. Hovering behavior is confined to "aggregation sites," usually hilltops, sunlit clearings, or forest paths, where a given species occurs regularly every year. Other tabanids do not hover, but nevertheless congregate at the same types of aggregation sites, waiting on foliage, then suddenly disappearing in pursuit of passing insects. More detailed knowledge of such sites, and of other aspects of male behavior, might lead to a method of abatement of males which could result in fewer tabanids the following year.

Adult females are serious pests of livestock. Cattle on pasture spend so much of their time fending off the flies that meat and milk production are curtailed. One cow can lose about one-quarter of a litre of blood per day under heavy attack, with more blood lost from the bite wounds. The flies are wary, and are easily interrupted while feeding, resulting in numerous bites in an effort to obtain a single blood meal. They move freely from one animal to another, and under experimental conditions have been shown capable of mechanical transmission of disease organisms, such as anthrax and tularemia, on their mouthparts. Both these diseases are essentially afflictions of animals, but they can occur in man when in contact with infected animals. Fortunately, disease transmission by tabanids to man does not seem to have occurred in Canada, although the potential danger should not be ignored.

Tabanids lay their eggs in a peculiar manner, usually in a dark-colored oval mass consisting of overlapping layers, on stems or leaves usually overhanging water that will, in a week or so, become the larval habitat. Eggs so laid on leaves or grass blades may escape many of the predators that would eat them if laid directly on land or into the water, but they do not always escape egg parasites.

Snipe flies (*Symphoromya* spp.—Rhagionidae)

Snipe flies resemble small, nondescript slender horse flies, and are pests in the mountains of British Columbia, Alberta, and southern Yukon. The eastern species are uncommon and rarely bite. In comparison to tabanids, snipe flies are unwary and easily swatted, but they may be abundant enough that swatting can become a full-time occupation. Some species spend all their time crawling on the skin but seem unwilling to take a blood meal; a few species apparently do not suck blood, and these may be autogenous.

There are at least 10 species of snipe flies in Canada, but they are not well studied, and more species remain to be described. Different species appear at different times throughout the summer. Snipe flies are most abundant in the wet coastal region of British Columbia, ranging from sea level to the alpine zone. Larvae of only a few species have been found in tundra meadows on south-facing slopes, among stands of cow parsnip and hellebore. Mouthparts of the larvae resemble those of larvae of tabanids, suggesting that they might be predaceous, but no one has observed their feeding habits. All the species appear to have only one generation per year. Male aggregation sites have been found along paths on hills in Alberta, in sunlit clearings beside rivers in British Columbia, and on hilltops in the East.

Horn flies and stable flies (*Haematobia irritans* and *Stomoxys calcitrans*—Muscidae)

Horn flies and stable flies were introduced from Europe, presumably along with cattle at the time of early settlement. Horn flies do not bite man but are almost exclusively associated with cattle and sometimes with horses. They spend almost their entire adult lives on and among the hair of their hosts, females leaving for only a few minutes to oviposit. They can feed whenever they wish, which they do often to the distress of cattle. Stable flies, also called biting house flies, are much less tied to livestock and will bite man readily. They remain on their hosts only while trying to feed, and travel widely in search of hosts or breeding sites.

In contrast to the preceding families, the mouthparts of both males and females of members of this family are essentially identical, and both sexes bite. Also, their mouthparts are constructed on an entirely different principle, indicating that blood feeding in these flies is an independent evolutionary event from the other biting flies. They have neither mandibles nor maxillae, and instead of snipping or slicing the skin, as do members of the preceding families, the entire proboscis, which is slender and pointed, is forced into the skin like a hypodermic needle, with a resulting painful effect on the victim. Small recurved spines at the tip of the proboscis dig into the skin and then are moved sideways away from each other to rasp a hole and pull the proboscis deeper and deeper.

Horn fly larvae develop only in fresh cow dung. In hot weather horn flies develop rapidly, completing a generation every 3 weeks or so at 30°C, or monthly at 25°C. The young larvae, which cannot survive desiccation, live at the moist surface of the dung; older larvae live within tunnels made in the drier dung by beetle larvae. Pupation takes place in the soil under the dung or nearby. In areas where dung beetles carry off and bury cow dung soon after it falls, horn flies are scarce, presumably because the larvae cannot find enough to eat.

Larvae of the stable fly also develop in cow dung, but they can develop in any decaying vegetation, such as lawn clippings, refuse from packing plants, or waterweed cast up on the shores of the Great Lakes. Stable flies also develop rapidly and can complete several generations each summer. Unlike members of the preceding families, horn flies and stable flies overwinter in the pupal stage. The pupa is enclosed within the last larval skin, which has become hardened and darkened, and is called a puparium. This puparium must offer some protection to the pupa from bacteria and fungi

Fig. 5. Adult female snipe fly.

but not from predators, such as mice or shrews, nor from parasitic wasps which drill a hole in it to insert their eggs.

A smaller relative of the horn fly, the moose fly, *Haematobosca alcis*, is the only blood-feeding member of the Muscidae native to North America. As its name implies, it is associated with moose, and has not been observed biting man or livestock.

Stable flies are suspected of being capable of mechanically transmitting bacteria on their mouthparts, such as those that cause tularaemia and anthrax. Like tabanids, they are wary feeders, and may bite several animals many times before feeding to completion. Evidence is lacking, however, as to whether such transmission has occurred in Canada.

Sheep keds, or sheep ticks (*Melophagus ovinus*—Hippoboscidae)

Sheep keds, which superficially resemble ticks rather than flies, are wingless, brown, stout-bodied insects that pass their entire life cycle in the wool of their only host, sheep. Adults creep about in the wool, feeding whenever hungry. Their mouthparts are constructed like those of horn flies and stable flies—the entire proboscis is forced into the skin by means of sets of recurved teeth at the tip which work away from each other to pull the proboscis into the skin.

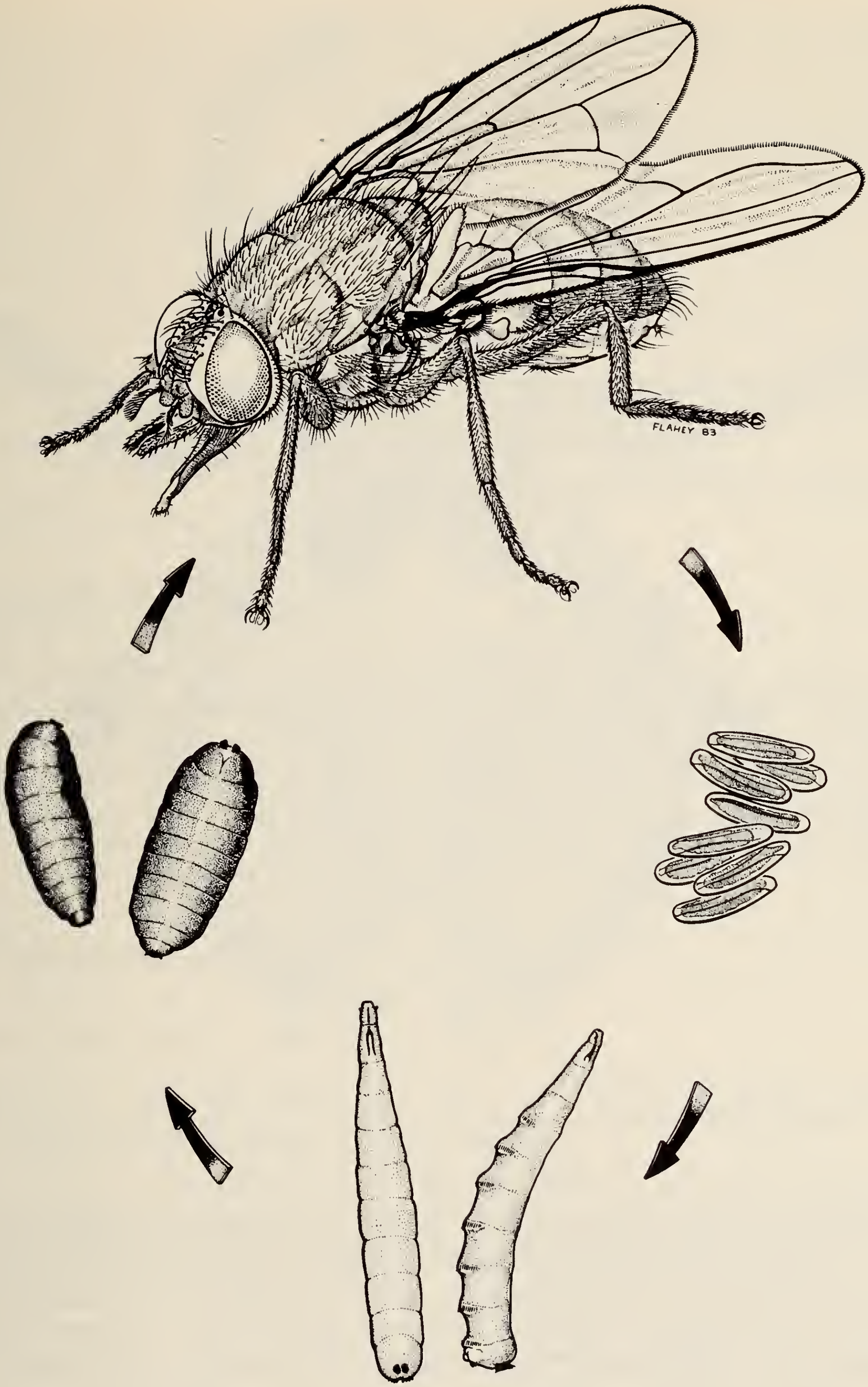

Fig. 6. Life cycle of the horn fly, *Haematobia irritans.* Clockwise from top: adult female; eggs; larvae; puparia (the hardest skin of the mature larva), each containing a pupa.

Fig. 7. Adult female sheep ked.

Sheep keds are members of a small family of flies that are all ectoparasites, mostly of birds. Usually called louse flies, they are strongly flattened from top to bottom, presumably the easier to creep about through fur or feathers. Most species of Hippoboscidae are winged, and thus are more readily recognizable as flies. None attacks domestic fowl, although wild game birds are sometimes afflicted. One species of hippoboscid, *Lipoptena cervi*, found on deer in British Columbia, starts its adult life with a useable pair of wings, then sheds them as soon as it has found a host, possibly because the wings interfere with movement through the hair. However, wings seem to be of no impediment to those species that live on birds, for most of these species are winged and keep their wings throughout life.

All louse flies, including sheep keds, share with the tsetse flies (Glossinidae) of Africa and the bat flies (Nycteribiidae and Streblidae), the remarkable ability to retain their larvae in utero. One larva develops at a time, from egg to maturity, in a special enlargement of the oviduct, where it is nourished entirely with secretions of specialized accessory glands, called "milk glands." When mature, the larva is ejected by the female, and it promptly darkens and hardens to form a puparium, inside which the pupa forms a few days later. Female sheep keds deposit their mature larvae in the wool of the host; other hippoboscids leave the host temporarily to deposit their larvae in suitable places on the ground. A female can presumably nourish several larvae in succession during the course of her lifetime.

The sheep ked, living in a perpetually heated environment, has no need for an overwintering phase. Other louse flies overwinter as puparia presumably on or under the surface of the soil.

The "dip" with which sheep are annually treated is usually sufficient to control the sheep ked population.

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Further information may be obtained from the Canada Biting Fly Centre, Department of Entomology, University of Manitoba, Winnipeg, Manitoba.