THE SPATIAL DISTRIBUTION OF HOST-SEEKING MAMMALOPHILIC BLACK FLIES (DIPTERA: SIMULIIDAE) IN RELATION TO TERRESTRIAL HABITATS ON THE AVALON PENINSULA, NEWFOUNDLAND

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BY

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ABSTRACT

Female host-seeking black flies were collected using dry ice baited sticky traps, unbaited sticky traps and a sweep net to assess abundance in six habitats. Females of the *Simulium venustum/verecundum* complex were most abundant in peatlands and regrowth, whereas *P. mixtum* and *St. mutata* females were most abundant in balsam fir and black spruce forest, followed by regrowth and peatlands. Few black flies were collected on pastureland. Spatial distributions described were observed throughout the sampling day, and between sampling days and sampling years. The distribution of *S. venustum/verecundum* complex among the six habitats was similar in June and August, but in July there was a relative increase in the abundance of females in the forest. The paucity of females in the pasture was associated with relatively high wind speeds while the relatively small catches of *S. venustum/verecundum* complex in the forest in most months may be related to the low light levels in that habitat. Generally, the meteorological conditions 1 m above ground level were not good indicators of black fly spatial distribution. The relationships between black fly distribution and certain topographical factors, resting sites and nectar sources were discussed.

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INTRODUCTION

The adult females of certain black fly species (Diptera: Simuliidae) blood-feed and are vectors of parasites (Craig and Pledger, 1979; Fallis, 1964; Garms *et al.*, 1979; Moore and Noblet, 1974). The harassment, blood loss and disease resulting from transmitted parasites make black flies an important medical, veterinary and economic problem (Laird, 1981; NRCC, 1982). Black flies are a major human health problem in West Africa, and to a lesser extent elsewhere in Africa and South and Central America because they vector the causal agent of river blindness (onchocerciasis) (Laird, 1981). Black flies do not vector parasites of humans in North America, although they are an irritant and are responsible for large economic losses in industry, particularly forestry and agriculture (Cupp and Gordon, 1983; NRCC, 1982). In western Canada, massive attacks of *Simulium arcticum* Malloch on cattle resulted in temporary sterilization in bulls, interfered with breeding, induced weight loss and decreased milk production (Khan and Kozub, 1985; Rempel and Arnason, 1947; Ryan and Hilchie, 1982). During particularly severe attacks, blood-feeding resulted in the death of livestock (cattle, pigs, sheep and horses) due to severe blood loss or anaphylactic shock induced by the injection of anticoagulating enzymes (Fredeen, 1977a, 1977b; Ryan and Hilchie, 1982). In Newfoundland the major pests of humans and domestic mammals are the *S. venustum/verecundum* complex followed by *Prosimulium mixtum* Syme and Davies, *Stegopterna mutata* (Malloch), *Simulium vittatum* Zetterstedt and *Simulium decorum* Walker (Lewis and Bennett, 1973; McCreadie, 1983). Because black flies have a negative impact on a large number of animal species (Fredeen, 1977a, 1977b; Moore and Noblet, 1974; NRCC, 1982; Thing and Thing, 1983), they have received much research attention.

Black fly larvae and pupae are restricted to running water, whereas the adults are restricted to terrestrial environments. Newly emerged adults go through a species-specific sequence of postemergence behaviours that may include mating, nectar-feeding and dispersal from the emergence site (Wenk, 1981). Most pestiferous species require a blood-meal to complete the first ovarian cycle (Anderson and Shemanchuk, 1987; Wenk, 1981) but some, including *P. mixtum*, *St. mutata*, *S. vittatum* and *S. decorum* in Newfoundland, do not (Lewis and Bennett, 1973). Females in the various stages of the reproductive cycle (host-seeking, ovipositing, postovipositing and resting) orient to different environmental cues, therefore the biology of each group may not be directly comparable. The biology of the adults has been reviewed by D.M. Davies (1978) and Wenk (1981). There is a paucity of information on nectar-feeding, resting and mating behaviour of most species because these activities are seen infrequently in the field and under laboratory conditions the adults may be either inactive or difficult to maintain. Recently, some progress has been made in the laboratory rearing of certain species (Bernardo *et al.*, 1986; Edman and Simmons, 1985). Research on the adults has focused on the behaviour of host-seeking females, viz., mechanisms of host location (Sutcliffe, 1986) and diel activity (El Bashir *et al.*, 1976; Hocking and Pickering, 1954; Hunter and Moorehouse, 1976), particularly as it is influenced by meteorological conditions (Alverson and Noblet, 1976; Williams, 1962). In Newfoundland black fly distribution (Colbo, 1979; Lewis and Bennett, 1973; Pickavance *et al.*, 1970) and seasonal succession (Colbo and O'Brien, 1984; McCreadie, 1983) were studied in addition to the factors influencing host orientation (Bradbury and Bennett, 1974a, 1974b) and the influence of weather conditions on host-seeking and blood-feeding activity (McCreadie *et al.*, 1986). There is a limited amount of information on black fly host preferences (Pickavance *et al.*, 1970).

Movement of host-seeking females from the emergence site is an important event in the acquisition of a blood meal because it brings females into habitats where suitable hosts are likely to occur (Sutcliffe, 1986). Movement may be achieved through 1) long-range dispersal, which is mainly a wind-borne event and/or 2) short-range dispersal (spatial distribution), which is largely a result of the insects flight capabilities (modified from Wenk, 1981). Only recently black fly movement has been recognized to have important implications to pest management. Because black flies are capable of long-range dispersal (Cooter, 1982, 1983; Johnson *et al.*, 1982), necessary treatment areas may be too large to treat economically or existing control programmes may be seriously jeopardized (Garms *et al.*, 1979; Ryan and Hilchie, 1982). The latter problem has arisen in West Africa where there have been difficulties maintaining low numbers of the *S. damnosum* complex inside the treatment area due to the influx of adults from a source approximately 300 km away (Garms *et al.*, 1979). Females of this complex are capable of moving over long distances (56-79 km) in relatively short periods (10-34 hours) through repeated bouts of wind-borne dispersal interspersed with nectar-feeding, blood-feeding and ovipositing (Cooter, 1983; Thompson, 1976a).

North American black flies are also capable of dispersing over long distances. In western Canada *S. arcticum* attacked and, in some instances, killed cattle that were gazing 95-160 km from black fly emergence sites (Fredeen, 1977a; Rempel and Arnason, 1947; Ryan and Hilchie, 1982). Even after pest management practices were implemented in Athabasca County, Alberta, considerable economic losses incurred as a result of migrating *S. arcticum* (Ryan and Hilchie, 1982). In southern Ontario Baldwin *et al.* (1975) trapped radioactively tagged adults, mainly the mammalophilic *S. venustum/verecundum* complex, up to 35 km from the tagging site, although most were trapped within 16 km of the emergence site. *Simulium jenningsi* Malloch, a major pest of humans in West Virginia, were collected as far as 25 km from their emergence site in New River (Amrine, 1982). In northern Ontario the ornithophilic species *S. rugglesi* Nicholson and Mickel and *Eusimulium euryadminiculum* Davies were trapped 3-8 km from the tagging site (Bennett, 1963; Bennett and Fallis, 1971) and in South Carolina female *S. slossonae* Dyar and Shannon, a vector of turkey leucocytozoa, were collected up to 13 km from the tagging site (Moore and Noblet, 1974).

Certain long-range dispersal studies indicated that the spatial distribution of immigrant black flies was non-random and dependent upon habitat (Baldwin et al., 1975; Garms et al., 1979). Garms et al. (1979) and Thompson (1976a) noted that females of the savanna sibling species of the *S. damnosum* complex were more abundant near their breeding sites than in nearby forest, whereas, the converse was true for the forest sibling species. Hunter and Moorhouse (1976) observed differences in the spatial distributions of two Australian mammalophilic species, *Austrosimulium pestilens* Mackerras and Mackerras and *A. bancrofti* (Taylor). *Austrosimulium pestilens* females were abundant close to the breeding sites, but were rare in woodland a short distance away. However, the opposite trend was observed for *A. bancrofti*. The distribution of both species varied with differences in microhabitat. Female *A. pestilens* were less abundant in very short grass and burnt or bare areas compared to long grass and female *A. bancrofti* were rare under *Eucalyptus* trees where the ground was covered with bark compared to under trees where the ground was covered with grass.

The most comprehensive studies of black fly spatial distribution in North America involved ornithophilic species. Bennett and Fallis (1971) and D.M. Davies and Peterson (1957) collected more female *Eusimulium euryadminiculum* at or near the shoreline of lakes compared to the middle of lakes or inland. A study designed to capture blood-fed black flies from sentinel birds indicated that ornithophilic species were vertically stratified within habitats; certain species were most abundant in the forest at ground level while others were most abundant in the forest canopy (Anderson and DeFoliart, 1961).

The spatial distributions of many North American mammalophilic species have not been quantified, but casual observations suggest that species-specific differences in distribution exist (Amrine, 1982; Anderson and DeFoliart, 1961; Fredeen 1977a). Lacey and Mulla (1977) noted that the spatial distribution of *S. vittatum* changed seasonally. Females were found exclusively near the emergence sites in the Colorado River Basin in the spring and early summer but moved up to 1 km inland in late summer. The vertical distributions of certain black flies within habitats has been studied, although little information is available. Fallis et *al.* (1967) collected more females of the *S. venustum/verecundum* complex on traps close to ground level than on traps at set distances above ground level.

While the influence of habitat on black fly distribution has been recognized by a few authors (D.M. Davies, 1978; Fredeen, 1961; Golini *et al.*, 1976; Service, 1981), it has been completely overlooked by others. A mark/recapture study conducted in southern Ontario by Baldwin *et al.* (1975) indicated that there was spatial heterogeneity in the distribution of mammalophilic black flies, but this was not discussed in the paper. Data collected by Craig and Pledger (1979) indicated that more *S. venustum/verecundum* complex were collected in the muskeg compared to the forest, but the authors did not comment on this finding.

The factors influencing spatial distribution of mammalophilic black flies are unknown. Certain meteorological factors influence general host-seeking activity (Williams, 1962) and may also influence black fly spatial distribution. Lacey and Mulla (1977) suggested that the vertical and lateral distributions of *S. vittatum* females were restricted to the emergence sites in the spring and early summer due to high air temperatures and low relative humidities. With the cooler air temperatures and higher relative humidities in the late summer this species tended to host-seek further inland. Another factor that may play an important role in spatial distribution is host distribution (D.M. Davies, 1978; Golini *et al.*, 1976). *Eusimulium euryadminiculum* females are generally most abundant in the areas of lakes where their host, the common loon (*Gavia immer* Brunnich), is likely to occur (Anderson and DeFoliart, 1961; Bennett and Fallis, 1971).

Beleaguered hosts may enter habitats where black fly activity is minimal to reduce black fly harassment (Fredeen, 1977a; Thing and Thing, 1983). Cattle will enter darkened shelters, rest on bare ground or stand in sloughs or bush to abate attack from *S. arcticum* (Fredeen, 1977a; Golini *et al.*, 1976). Caribou will rest in sandy patches (riverbanks, roadsides and sand pits) where black flies are not abundant (Helle and Aspi, 1984) and moose will lie under low shrubs for protection (Craig and Pledger, 1979). In Newfoundland, black fly activity appears to have a negative impact on cattle, moose and caribou (Colbo, pers. comm.). If the spatial distributions of the Newfoundland pest species were known then the impact of black flies on wild and domestic hosts may be more accurately assessed and possibly lessened by providing hosts with habitats not favourable to black fly activity.

This study was designed to assess the spatial distribution of host-seeking mammalophilic black flies among habitats in the boreal region, on the Avalon Peninsula, Newfoundland. The objectives of the study were fourfold, namely, (1) to establish, using a number of sampling methods, whether there are species-specific habitat differences in the distribution of mammalophilic black flies, (2) to determine whether the utilization of various habitats changes over the black fly season, (3) if differences in habitat utilization exist, to determine if certain environmental factors could be correlated with the observed distribution and (4) to assess whether the females are most abundant close to ground level.

MATERIALS AND METHODS

2.1. Study site

Sampling was conducted on the Harding dairy farm 16 km west of St. John's, Newfoundland, Canada (47°29'N, 52°51'W) from late May to late August in 1985 and 1986. This study site was chosen because it 1) had a diversity of vegetational types, including coniferous boreal forest, pasture, and extensive peatland, in close proximity to one another, 2) offered security from vandalism of sampling equipment, and 3) two studies of black flies had already been conducted in this area (Lewis, 1973; McCreadie, 1983).

2.2. Trapping sites

Six habitats, all within a distance of approximately 300 m (Fig. 2-1), were chosen for comparison of black fly abundance. The habitats were defined by the type of dominant vegetation cover and exposure to the wind. The peatlands were classified according to the scheme of Pollett and Wells (1980) and the vernacular plant names were taken from Peterson and McKenny (1968).

1. PASTURE - The pasture was a well drained fallow hayfield that contained a mixture of clover (*Trifolium* spp.), grass (*Phleum* spp.) and cow vetch (*Vicia cracca* L.) (Fig. 2-2). This 13 ha habitat was bordered by a mature balsam fir (*Abies balsamea* (L.) Mill) and black spruce (*Picea marina* (Mill.) BSP.) forest, but most areas in the rolling pasture received little shelter from the wind due to the relatively high altitude.

2. POORLY-DRAINED SLOPE BOG (PDSB) - Sphagnum moss (*Sphagnum* spp.) and small open pools of water were abundant in this habitat

Figure 2-1: Six habitats chosen for comparison of black fly abundance (PDSB = poorly-drained slope bog, WDSB = well-drained slope bog, (●) = sampling site).

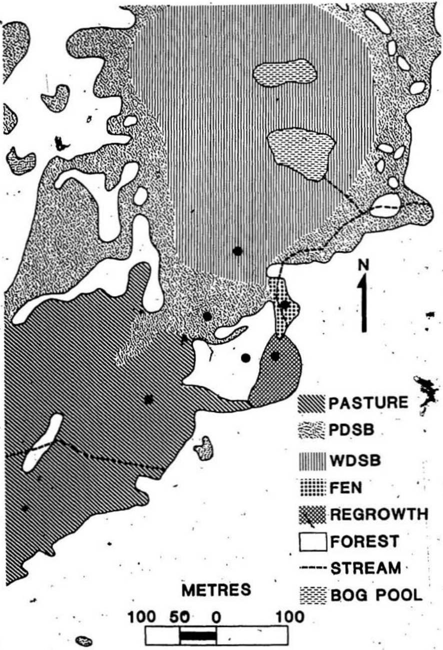
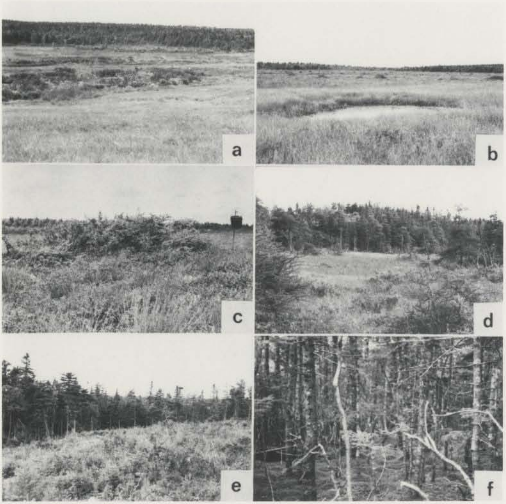

N
PASTURE
PDSB
WDSB
FEN
REGROWTH
FOREST
STREAM
BOG POOL
METRES
100 50 0 100

Figure 2-2: Six habitats in which black fly catch was assessed; (a) pasture (b) poorly-drained slope bog with the well-drained slope bog in the background (c) tuckamoor on the well-drained slope bog (d) slope fen (e) forest regrowth (f) mature forest.


a
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d
e
f

(Fig. 2-2). The PDSB was bordered on the east and west by mature balsam fir and black spruce forest, well-drained slope bog (WDSB) to the north, and pasture to the south. This relatively small habitat (ca. 1.5 ha) was exposed to the strong winds that swept across the WDSB.

3. WELL-DRAINED SLOPE BOG (WDSB) - This windswept bog was largely composed of caribou lichen (*Cladonia* spp.), followed by Labrador tea (*Ledum groenlandicum* Oeder), blueberry bushes (*Vaccinium angustifolium* Ait.) and tuckamoor. Tuckamoor are small thickets of procumbent coniferous shrubs (ca. 0.75 m high) consisting of larch (*Larix laricina* (Du Roi) K. Koch) and balsam fir or occasionally black spruce (Dodds, 1983) (Fig. 2-2). This 9 ha bog was surrounded by PDSB that was bordered by mature balsam fir and black spruce forest.

4. SHELTERED SLOPE FEN - The dominant vegetation in this habitat consisted of sphagnum moss, rushes (*Scirpus* spp.) and cotton grass (*Eriophorum* spp.) (Fig. 2-2). This poorly drained 0.2 ha habitat was sheltered from the wind by the mature balsam fir and black spruce forest that bordered it on all sides, except the northwest side where it drained into the slope bogs.

5. FOREST REGROWTH - This habitat was dominated by blueberry bushes, raspberry canes (*Rubus idaeus* L.) and regenerating larch and balsam fir (ca. 0.75 m high) (Fig. 2-2). The mature black spruce and balsam fir forest in this area was clear-cut approximately 10 years ago. This relatively small area (ca. 0.5 ha) was bordered on all sides by mature balsam fir and black spruce forest and had more protection from the wind than the four habitats described above.

6. MATURE FOREST - The mature forest was dominated by balsam fir and black spruce trees (Fig. 2-2). The forest floor, which was generally poorly drained, contained a few open pools of water (ca. 1 x 0.5 m) and was dominated by sphagnum moss. In areas of better drainage, corn-lilies (*Clintonia borealis* (Ait.) Raf.), bunchberries (*Cornus canadensis* L.) and twinflowers (*Linnaea borealis* L.) were present. The collector could move freely in the understory due

to the sparse vegetation and the spacing of the trees (ca. 1-2 m apart). Maximum tree height was only 5 m to 6 m which may reflect the poor drainage and low nutrient availability as a result of low soil pH and adverse climate in Newfoundland (Roberts, 1983). The trapping site inside the 1 ha forest was more sheltered from the wind compared to the trapping sites in the above habitats.

The streams running through the above habitats were permanent streams that were less than 1 m wide (Fig. 2-1). None of these streams had dense larval populations of black flies and, consequently, they were probably minor sources of adults (Colbo, pers. comm.).

2.3. Trap locations within habitats

Trapping was conducted in an area of the habitat where the vegetation cover and environmental factors typified conditions in that habitat. For each sampling method, collections were always taken at the same sites within habitats to decrease variability in black fly catch due to differences in the collection sites. In 1985 the pasture sampling site was less than 25 m from the forest edge. Compared to most areas of the pasture this site did not typify conditions in the pasture due to its relatively low altitude and shelter from the wind due to its close proximity to the forest. Therefore, in 1986 this site was moved closer to the center of the pasture to a location that was 69 m from the nearest forest edge. Trapping sites for the other habitats were located 24 m, 42 m, 12 m, and 15 m from the nearest forest edge in the PDSB, WDSB, fen, and regrowth, respectively. The trapping site in the forest was 19 m from the forest edge (Fig. 2-1).

2.4. Trap design

Assessment of black fly harassment, as indicated by abundance, may be biased by the sampling method used (Fredeen, 1961; Service, 1981; Shipp, 1985), therefore, three sampling methods were employed to assess black fly abundance and the results were compared. Dry ice baited sticky traps (DIB traps) were chosen because they attract and trap large numbers of black flies and operate over relatively long collection periods (Baldwin *et al.*, 1975; Shipp, 1985). The use of these traps in Newfoundland was experimental because they have been used in few studies in this region (Bradbury and Bennett, 1974a, 1974b), but the results from the 1985 sampling season indicated that the DIB traps were capable of collecting large numbers of black flies.

Because CO_2 is used in middle-range, as well as near-range orientation (Bradbury and Bennett, 1974b; Sutcliffe, 1986) a DIB trap may attract black flies from neighbouring habitats. However, a trap not baited with CO_2 will visually attract black flies over a relatively short distance (ca. 180 cm) through near-range orientation (Bradbury and Bennett, 1974b; Sutcliffe, 1986), although the number collected on the unbaited trap will be small compared to the DIB trap (Fallis *et al.*, 1967; Shipp, 1985). Based on the success of the DIB traps in 1985, it was expected that the unbaited traps could collect numbers of black flies large enough to include in an analysis. Thus, in 1986 visually attractive unbaited sticky traps were operated to assess black fly abundance within habitats.

The third trapping method, sweep netting, was employed because it is a proven method for collecting black flies (Wolfe and Peterson, 1960) and with it a large number of samples may be collected in a relatively short time, which allows for the detection of shifts in habitat utilization throughout the day. This method also had the advantage of involving a suitable mammalian host (human).

To make reliable within-month comparisons of the three sampling techniques, sampling was conducted on consecutive days, where possible, to decrease variability in catch as a result of black fly population fluxes (Wenk, 1981). Generally, DIB trapping and sweep netting were conducted on the same days and unbaited trapping was conducted on the days immediately following the completion of the former methods of sampling. The days on which samples were taken are recorded in Appendix A. Sampling was not conducted on days when activity was predicted to be marginal, that is, a day that had heavy rainfall, winds in excess of 8.0 km/hr or temperatures below 11°C (McCreadie *et al.*, 1986). Black flies were sampled on days when high activity was expected so that the numbers collected would be large enough to include in an analysis. There is no evidence to suggest that the spatial distribution changes with the activity level.

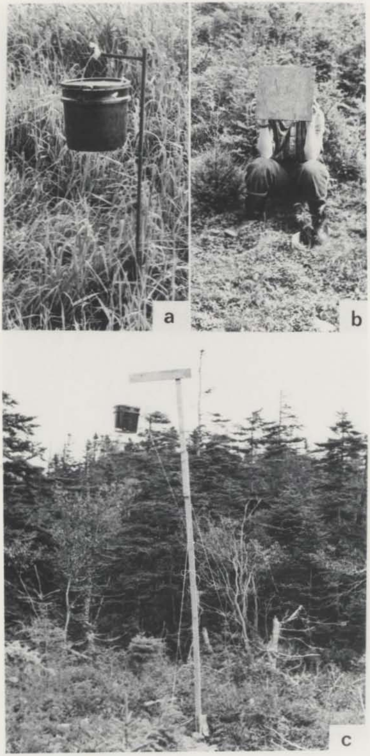
2.4.1. Dry ice baited and unbaited sticky traps

Plastic buckets (6 l capacity, 21 cm diameter, 19 cm high) and bucket lids were painted dark blue (Chevron Blue, Canadian Tire Corp., Toronto, Ont., Canada), a hue attractive to host-seeking black flies (Bradbury and Bennett, 1974a; D.M. Davies, 1972). Each bucket was suspended from a metal rod such that its top margin was 1 m above ground level. The handle and bottom of the bucket were fastened to the metal rod with string to prevent the bucket from moving in the wind (Fig. 2-3). Depending upon the sampling procedure, a bucket was either not baited or it was baited with a block of dry ice (ca. 250 g) wrapped in newspaper. Carbon dioxide vented through a set of five holes (9 mm diameter) drilled in the bottom of each bucket. No attempt was made to measure the rate of emission of CO_2. Black flies landing on the vertical sides of a bucket were trapped in a sticky substance (**Tanglefoot**, Tanglefoot Co., Grand Rapids, Mich., U.S.A.) that had been sprayed on an affixed sheet of plastic (Glad Cling Wrap, Union Carbide Canada Ltd., Toronto, Ont., Canada).

2.4.2. Sweep net

The sweep net had a total length of 1.04 m with a 34 cm (internal diameter) net opening. The collector held the sweep net with one hand near the butt of the handle and the other near the midpoint of the handle. The collector stood at the sampling site for a minimum of five minutes to attract black flies and then commenced sampling by moving the trap in a figure-of-eight motion from a maximum height of approximately 2 m above ground level to just above ground level. One sample consisted of the catch after 20 strokes were made. Black flies were transfered to a killing jar and later placed in labelled vials containing 70% ethanol.

Figure 2-3: Sticky traps employed in the collection of black flies; (a) dry ice baited or unbaited sticky trap elevated 1 m above ground level (b) human-baited sticky trap (c) sticky trap elevated 3 m above ground level.


a
b
c

2.5. Trapping schedule and procedure

2.5.1. Dry ice baited sticky trap

The purpose of this sampling was to compare black fly abundance in the six habitats described earlier over a relatively long collection period using traps baited with the middle-range and close-range attractive stimulus, CO_2 (Bradbury and Bennett, 1974b; Sutcliffe, 1986). In June 1985 the traps were baited at 0700 h (Newfoundland Standard Time) and operated until sunset (ca. 2030 h) when black fly activity ceased due to low temperatures and/or diminished illumination (El Bashir *et al.*, 1976; McCreadie *et al.*, 1986; Wolfe and Peterson, 1960). The dry ice bait dissipated prior to the end of this sampling day, therefore in the following months traps were baited with dry ice at 1430 h and operated until 2030 h to ensure dry ice remained in the traps throughout the sampling day. Three traps, each approximately 10 m from a neighbouring trap, were operated in each of the six habitats. Approximately 20 minutes were required to bait all of the traps with dry ice, affix the sheet of plastic, and spray with **Tanglefoot**. To correct for this time factor the first habitat in which traps were prepared for sampling was altered daily. Black flies were collected over three consecutive days, when possible, in June, July and August 1985 and 1986 (Appendix A).

2.5.2. Unbaited sticky trap

The purpose of this sampling was to assess black fly abundance within habitats using visually attractive traps. Five traps in each of the six habitats were operated from 0700 h until 2030 h over three consecutive days in June and July 1986 (Appendix A). This increased sampling effort was required due to the anticipated decrease in the number of black flies attracted to traps not baited with dry ice (Fallis *et al.*, 1967; Shipp, 1985). Collecting with unbaited traps was not carried out in August 1986 because of a sharp decline in the black fly population (0 black flies collected in the sweep net after three-days sampling and fewer than 20 black flies collected after two days using the DIB traps). Otherwise, the trapping schedule and procedure were the same as that described for the DIB traps.

2.5.3. Sweep net

The purpose of this sampling was to compare black fly spatial distribution among the six habitats throughout the day using a human host as an attractant. A set of three samples, taken as described above, were collected in each of the six habitats commencing at 1000 h, 1300 h and 1600 h. Samples were collected on three days in June 1985 and June, July and August 1986 (Appendix A). Approximately 45 minutes were required to collect three samples in each of the habitats, therefore the initial habitat sampled was altered daily to correct for the differences in the commencement time of sampling. Altering the sequence of sampling also reduced possible sampling bias resulting from black fly carry-over between habitats. All collections were made by the same collector to reduce variability in black fly catch due to differences in host attractiveness (Crosskey, 1955; Wolfe and Peterson, 1960). Sweep net sampling and DIB trapping were conducted concurrently, therefore the sweep net collector stayed a minimum of 10 m away from the DIB traps to minimize trap interaction.

2.6. Measurement of environmental factors

The meteorological factors recorded were relative humidity, ambient air temperature, wind speed or total wind passage and reflected light intensity. A set of wet/dry bulb thermometers was used to determine relative humidity, and ambient temperature (dry bulb). The thermometers were allowed to equilibrate for a minimum of five minutes before readings were taken. A totalizing cup anemometer (Qualmetrics, Inc., Sacramento, Ca., U.S.A.) was set up in the pasture and another in the regrowth to record total wind passage during the DIB trap collection periods in 1985. The anemometers were not operated in 1986 because they did not assess wind in all of the habitats. To assess wind speed in each habitat a hand-held floating ball wind meter (Dwyer Instruments, Inc. Michigan City, Ind., U.S.A.) was used. The floating ball wind meter was held facing into the wind and observed over a 30 second period before the median wind speed was recorded. A Luna 6 light meter (Lunasix, West Germany) was used to measure reflected light intensity 30 cm above a grey Kodak neutral test card (18% reflectance). Measurements from all instruments, except the light meter, were taken 1 m above ground level to follow the standard used by McCreadie *et al.* (1986). Measurements from all meteorological instruments, except the totalizing anemometers, were taken in each of the six habitats prior to each sweep net collection.

Prior to analysis of the data, relative humidity was converted to saturation deficit (SD) using the following formula:

$SD = (1 - RH)ES$, where

RH = relative humidity expressed as a proportion from 0 to 1

ES = saturation vapour pressure at temperature, T

Three topographical factors were measured and later examined for their relationship to black fly catch, viz., 1) distance from the sticky traps to the nearest forest edge, 2) distance from the sticky traps to the nearest stream edge, and 3) altitude, which was read from a 1:2500 topographical map (Newfoundland and Labrador Forest Resources and Lands Topographical Series 1N7-395).

2.7. Supplementary collections

2.7.1. Human-baited sticky trap

Preliminary results indicated there were differences in black fly abundance in the mature forest compared to the regrowth. To closely examine these differences in abundance, sampling was conducted in the regrowth 15 m from the forest edge, at the forest edge, and in the forest 19 m from the forest edge.

Sticky traps were deemed unsuitable due to the possibility of black flies following a chain of baits (Bennett and Fallis, 1971) and the sweep net was not used due to the possibility that the vegetation in the forest edge and forest may interfere with collecting. The trap used was a 30 cm^2 piece of plywood painted dark blue (Chevron Blue, Canadian Tire Corp., Toronto, Ont., Canada). **Tanglefoot** restrained black flies landing on the sheet of plastic that was affixed to the plywood's surface. While facing downwind and seated on the ground, the collector (human bait) held the trap at head level and parallel to the body (Fig. 2-3). Three samples were taken, each consisting of the catch collected over 10 minutes, in each of the three habitats. Samples were taken commencing at 1000 h, 1300 h, and 1600 h in May, June and July 1986 (Appendix A). Collections were taken over three consecutive days, excluding days when black fly activity was predicted to be marginal, and involved the same human bait for all sampling. The initial site sampled altered throughout the day to correct for sampling bias resulting from differences in the time sampling commenced and possible sampling bias that may arise from black fly carry-over between trapping sites.

2.7.2. Vertically stratified sampling

Casual observations indicated that black flies were most abundant close to ground level, therefore, trapping was conducted to assess the vertical distribution of females. DIB traps were prepared for sampling as described earlier and were suspended either 1 m above ground level from metal rods or were suspended 3 m above ground level from wooden supports (Fig. 2-3). Each trap was positioned a minimum of 10 m from a neighbouring trap to minimize trap interaction. A set of three traps was operated at 1 m above ground level and another set was operated at 3 m above ground level in both the forest and regrowth from 1400 h until 2030 h, June 25-27, 1986.

2.7.3. Tuckamoor collections

Sampling was conducted to assess black fly abundance near tuckamoor because preliminary investigations indicated that tuckamoor influenced black fly distribution on the WDSB. DIB traps were suspended from metal rods to a height of 1 m above ground level, as measured from the bucket's top margin, and were located as follows:

1. One metre upwind from a tuckamoor.
2. One metre downwind from a tuckamoor.
3. In the center of a tuckamoor with the bucket's bottom just above the surrounding vegetation.

Trapping positions 1 and 2 were determined on the basis of the forecasted prevailing wind direction. Only one trap was operated near each tuckamoor to prevent trap interaction. Three replicate samples were collected for each of the locations on July 17-19, 1986 using the trapping schedule and procedure described for the DIB trap collections.

2.8. Processing samples

The sheets of plastic collected from the sticky traps were placed on top of a sheet of plexiglass and examined under a dissecting microscope. A drop of mineral oil placed on a specimen facilitated its manipulation without damage. Specimens from the sweep net collections were examined in 70% ethanol under a dissecting microscope. Black flies were identified to species or species complex using the key provided by D.M. Davies *et al.* (1962), confirmed by M.H. Colbo, and the numbers of each recorded.

2.9. Analyses of data

Statistical procedures used included one way analysis of variance, Tukey's multiple range test, Kendall's coefficient of concordance, Pearson's product moment correlation, and the chi-square test for independent samples. The procedures were described by Elliott (1971), Siegel (1956) and Sokal and Rohlf (1981).

The data from the DIB trap, unbaited trap and the sweep net collections were analysed on a monthly basis due to the seasonality of black flies (McCreadie, 1983). Data were normalized by a logarithmic (base 10) transformation as follows:

$$\text{log black fly catch} = \text{log(black fly catch} + 1)$$

When fewer than five black flies were collected in at least four habitats on a minimum of two sampling days an analysis of the data was not conducted. Analysis of variance was used to test the hypothesis that there were no significant differences in mean black fly catch among the six habitats ($p<0.05$). When this hypothesis was false and significant differences were found, Tukey's multiple range test was used to indicate the habitats in which significantly different mean catches were collected ($p<0.05$). A similar procedure was used on the meteorological data to identify significant differences in conditions among the six habitats. Kendall's coefficient of concordance was used to assess change in habitat utilization over time and Pearson's correlation was used to compare the catches from the DIB traps, unbaited traps and sweep net, as well as to compare the catch from the DIB traps with environmental factors. The data for the supplementary collections were analysed using a chi-square test due to the small sample sizes involved. This analysis tested the hypothesis that there were no significant differences in the proportion of black flies collected among the habitats sampled.

RESULTS

3.1. Black flies present and relative abundance

Table 3-1 and 3-2 show the species and total numbers of black flies collected using the DIB trap, sweep net and unbaited trap. Males were infrequently collected and cursory examination of the females indicated that only non-gravid females were collected. All black flies trapped are mammalophilic species, except *Eusimulium* spp. and *Cnephia ornithophilia* which are ornithophilic species (Anderson and DeFoliart, 1961; Downe and Morrison, 1957; Golini *et al.*, 1976; Khan and Kozub, 1985; Schreck *et al.*, 1980). In 1985 and 1986 the *Simulium venustum/verecundum* complex were the most frequently encountered black fly taxon followed by *Prosimulium mixtum* and *Stegopterna mutata* (=*Cnephia mutata*) (Table 3-1 and 3-2).

3.2. Black fly spatial distribution

3.2.1. Dry ice baited sticky trap

Simulium venustum/verecundum complex females were most abundant in the WDSB and regrowth in June 1985, the fen in July 1985 and the PDSB in August 1985 (Fig. 3-1). These females were least abundant in the forest during those three months (Fig. 3-1). Analysis of variance indicated there were statistically significant differences in mean catches among the six habitats in June ($p<0.001$) and August ($p<0.001$), but not in July ($p>0.05$) (Appendix B). Tukey's multiple range test indicated that in June and August the mean catches in the forest were significantly lower than the mean catches from the five other habitats ($p<0.05$).

In June and July 1986 the greatest numbers of *S. venustum/verecundum*

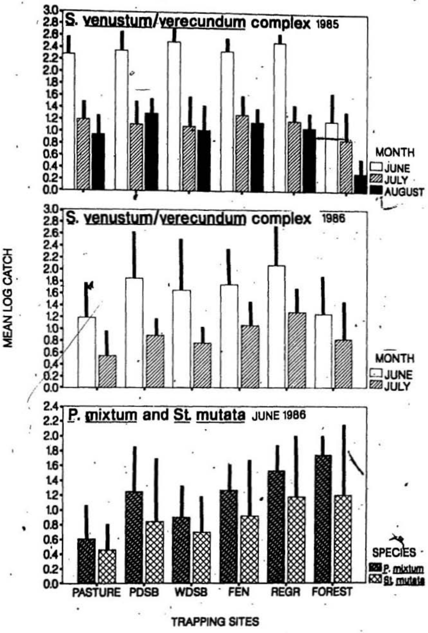
Table 3-1: Total number of female black flies collected in June, July and August in 1985 and 1986 using dry ice baited sticky traps and a sweep net.

Species	Sticky traps 1985 No.	Sticky traps 1986 No.	Sweep net 1985 No.	Sweep net 1986 No.	Total catch No.	Total catch %
Simulium venustum/ verecundum complex	15,217	11,835	1,234	3,877	32,163	85.5
Prosimulium mixtum Syme and Davies	127	2,178	48	970	3,323	8.8
Stegopterna mutata (Malloch)	19	1,769	1	112	1,901	5.1
Simulium vittatum Zetterstedt	1	61	1	53	116	<1.0
Eusimulium spp.	42	57	6	2	107	<1.0
Cnephia ornithophilia Davies, Peterson and Wood	0	4	0	7	11	<1.0
Simulium decorum Walker	0	2	0	7	9	<1.0
Totals	15,406	15,906	1,290	5,028	37,630	—

Table 3-2: Total number of female black flies collected in June and July 1986 using unbaited sticky traps.

Species	Collection date		Total catch	
	June	July	No.	%
Simulium venustum/ verecundum complex	1,228	100	1,328	98.6
Prosimulium mixtum Syme and Davies	1	0	1	<1.0
Stegopterna mutata (Malloch)	1	0	1	<1.0
Simulium vittatum Zetterstedt	1	2	3	<1.0
Eusimulium spp.	0	5	5	<1.0
Cnephia ornithophilia Davies, Peterson and Wood	1	0	1	<1.0
Simulium decorum Walker	8	0	8	<1.0
Totals	1,240	107	1,347	—

Figure 3-1: Mean log catch (+ one standard deviation) of black flies collected on three dry ice baited sticky traps operated in each of the habitats for three days per month (PDSB = poorly-drained slope bog, WDSB = well-drained slope bog, REGR = regrowth).


S. venustum/verecundum complex 1985
MONTH
JUNE
JULY
AUGUST
S. venustum/verecundum complex 1986
MONTH
JUNE
JULY
P. mixtum and St. mutata JUNE 1986
SPECIES
P. mixtum
St. mutata
MEAN LOG CATCH
PASTURE
PDSB
WDSB
FEN
REGR
FOREST
TRAPPING SITES

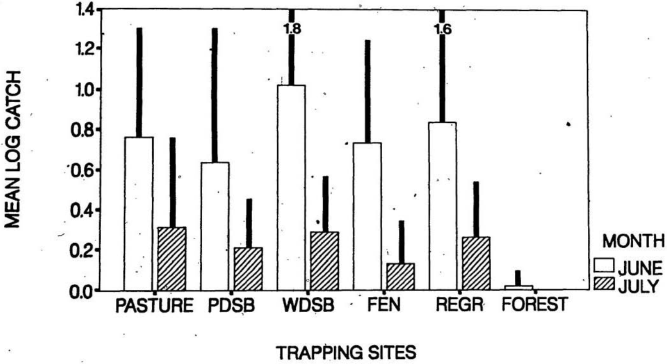
complex were observed in the regrowth and the smallest numbers were observed in the pasture (Fig. 3-1). There were no statistically significant differences in mean black fly catch among the six habitats in June ($p>0.05$), however, there were significant differences in mean catch in July ($p<0.05$) (Appendix B). Tukey's multiple range test indicated that the mean catch in the pasture was significantly smaller than the mean catch in the regrowth in July ($p<0.05$). The numbers of females collected in August 1986 were too small to be included in the analysis.

Prosimulium mixtum females were most abundant in the forest and least abundant in the pasture in June 1986 (Fig. 3-1). Analysis of variance indicated there were significant differences in mean catches among the six habitats ($p<0.05$) (Appendix B). Tukey's multiple range test indicated there were significantly larger catches in the fen, regrowth and forest compared to the other habitats and a significantly smaller catch in the WDSB compared to the forest ($p<0.05$). *Stegopterna mutata* females had a pattern of distribution similar to that of *P. mixtum* (Fig. 3-1), however, analysis of variance indicated that the differences in the mean catches among the six habitats in June 1986 were not significant ($p>0.05$) (Appendix B).

3.2.2. Unbaited sticky trap

In June and July 1986 fewer *S. venustum/verecundum* complex females were trapped in the forest compared to the other habitats (Fig. 3-2). The relative abundance of females in the pasture assessed by the unbaited traps (Fig. 3-2) was large compared to that assessed by the DIB traps (Fig. 3-1). Analysis of variance indicated there were significant differences in the mean catch of this complex among the six habitats in June ($p<0.001$) and July ($p<0.05$) (Appendix C). Tukey's multiple range test indicated that the mean catches of females in the pasture, WDSB, fen and regrowth were significantly greater than those in the PDSB and forest ($p<0.05$) in June. In July the mean catch in the forest was significantly smaller than that in the five other habitats ($p<0.05$).

Figure 3-2: Mean log catch (+ one standard deviation) of *S. venustum/verecundum* complex collected on five unbaited traps operated in each habitat for three days per month in 1986 (PDSB = poorly-drained slope bog, WDSB = well-drained slope bog, REGR = regrowth).


MEAN LOG CATCH
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.8
1.6
PASTURE
PDSB
WDSB
FEN
REGR
FOREST
TRAPPING SITES
MONTH
JUNE
JULY

3.2.3. Sweep net

Simulium venustum/verecundum complex females were most abundant in the peatlands and regrowth and were least abundant in the forest and pasture in June 1985 and June and July 1986. These trends in spatial distribution were observed in the morning, afternoon and evening collections (Fig. 3-3). Analysis of variance indicated that there were significant differences in the mean catches of black flies among the six habitats in all collections, except the evening June 1986 and the morning July 1986 collections (Appendix D). Where significant differences in mean catches existed, Tukey's multiple range test indicated that the mean catches of the females in the WDSB, fen and regrowth were frequently significantly larger than the mean catches in the pasture and forest ($p<0.05$) throughout the day and among the three sampling months (Appendix E).

Collections taken in June 1986 indicated that female *P. mixtum* were most abundant in the regrowth and were least abundant in the pasture in the morning and afternoon (Fig. 3-4). In the evening the largest catches were collected in the regrowth and forest and the smallest catch was collected in the pasture (Fig. 3-4). Analysis of variance indicated that there were significant differences in the mean catches of this species among the six habitats in the morning and afternoon ($p<0.05$ and $p<0.001$, respectively), but not in the evening ($p>0.05$) (Appendix D). In the morning significantly more females were collected in the regrowth compared to the pasture ($p<0.05$). In the afternoon significantly larger mean catches were collected in the WDSB, regrowth and forest compared to the pasture and the mean catch in the regrowth was significantly larger than the mean catches in the pasture, PDSB, WDSB and fen ($p<0.05$).

3.2.4. Comparison of sampling methods

The total daily log transformed catches of black flies from DIB traps, unbaited traps and the sweep net were compared using Pearson's correlation ($n=18$). The DIB trap and sweep net catches of *S. venustum/verecundum* complex were significantly positively correlated in June 1985 ($r=0.62$, $p<0.01$)

Figure 3-3: Mean log catch (+ one standard deviation) of *S. venustum/verecundum* complex from three sweep net collections taken in each of the habitats over three days per month (PDSB = poorly-drained slope bog, WDSB = well-drained slope bog, REGR = regrowth).

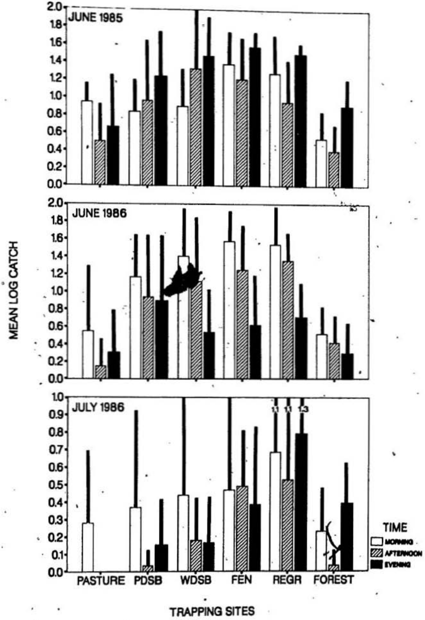
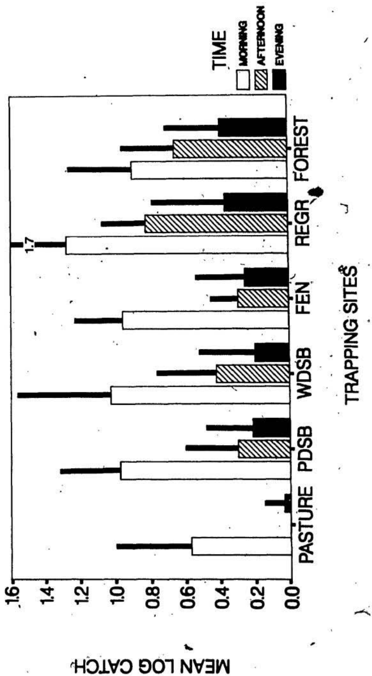

JUNE 1985
JUNE 1986
JULY 1986
MEAN LOG CATCH
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.9
0.7
0.5
0.3
0.1
1.1
1.1
1.3
PASTURE
PDSB
WDSB
FEN
REGR
FOREST
TRAPPING SITES
TIME
MORNING
AFTERNOON
EVENING

Figure 3-4: Mean log catch (+ one standard deviation) of *P. mixtum* from three sweep net collections taken in each of the habitats over three days in June 1986 (PDSB = poorly-drained slope bog, WDSB = well-drained slope bog, REGR = regrowth).


TIME
MORNING
AFTERNOON
EVENING
MEAN LOG CATCH
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.7
PASTURE
PDSB
WDSB
FEN
REGR
FOREST
TRAPPING SITES

and June 1986 ($r=0.83$, $p<0.001$), but not in July 1986 ($r=0.23$, $p>0.05$). The DIB trap catches and sweep net catches of *P. mixtum* were significantly positively correlated in June 1986 ($r=0.84$, $p<0.001$). The DIB trap and unbaited trap catches of *S. venustum/verecundum* complex were significantly negatively correlated in June 1986 ($r=-0.43$, $p<0.05$), but were significantly positively correlated in July 1986 ($r=0.43$, $p<0.05$). The sweep net catches and unbaited trap catches were not significantly correlated in June or July 1986 ($r=-0.13$, $p>0.05$; $r=0.097$, $p>0.05$, respectively).

3.2.5. Temporal changes in spatial distribution

Kendall's coefficient of concordance was used to indicate whether the pattern of black fly distribution among the six habitats changed within sampling days, and between sampling days and months. The significant coefficients of concordance from the analysis of the sweep net data indicated that the pattern of distribution for both *S. venustum/verecundum* complex and *P. mixtum* did not change within sampling days (Table 3-3).

Nonsignificant coefficients of concordance from the analysis of the catch of *S. venustum/verecundum* complex with DIB traps indicated that the pattern of distribution among the six habitats changed between sampling days in all sampling months, except August 1985 and June 1986 (Table 3-3). Generally, in June and August 1985 the forest had the lowest rank for catch of this complex and in June 1986 the pasture and forest generally had the lowest ranks for catch. The rank for the highest catch varied between the peatlands and regrowth in both sampling years (Appendix F). Thus, although the pattern of distribution as indicated by the coefficient of concordance appeared to change between sampling days for most months, the pattern of high catches in the peatlands and regrowth and low catches in the forest and pasture was consistent over the three sampling days in June and August 1985 and June 1986. Statistically significant ($p<0.05$) coefficients of concordance for *P. mixtum* and *St. mutata* catches indicated that their patterns of distribution did not change between sampling days in June 1986 (Table 3-3).

Table 3-3: Kendall's coefficients of concordance for black fly catch and habitat interactions within and between sampling days.

Date of collection	Coefficient of concordance, W within days sweep net	between days DIB trap[1]	between days sweep net
	S. venustum/verecundum complex		
June 1985	0.83*	0.64	0.75*
July 1985	—	0.39	—
August 1985	—	0.67*	—
June 1986	0.76*	0.86*	0.82*
July 1986	0.85*	0.58	—
	P. mixtum		
June 1986	0.92*	0.97*	0.78*
	St. mutata		
June 1986	—	0.87*	—

[1] DIB trap = dry ice baited sticky trap.

* Values significant at $W_{0.05}=0.65$, m=3, n=6.

There was a nonsignificant coefficient of concordance for the between days catch of *S. venustum/verecundum* complex collected on unbaited traps in June 1986 ($W=0.54$; $W_{0.05}=0.65$, $m=3$, $n=6$) indicating that the pattern of distribution changed between sampling days. However, the forest consistently had the lowest rank for catch, although none of the five other habitats consistently had the highest ranks for black fly catch (Appendix G). Black fly catch on the third day of sampling in July 1986 was extremely low (total daily catch = three black flies), therefore, the third sampling day was excluded from the analysis. As a result, a coefficient of concordance for the two remaining days could not be calculated.

In both sampling years the coefficients of concordance for between month comparisons of distribution of *S. venustum/verecundum* complex were not statistically significant (1985, $W=0.58$; 1986, $W=0.49$; $W_{0.05}=0.65$, $m=3$, $n=6$) indicating that the pattern of distribution, assessed using the DIB traps, changed between months. Similar to the above analyses, there was a pattern of high catches in the peatlands and regrowth and low catches in the forest and pasture for most sampling months in 1985 and 1986 (Appendix H). However, the distribution of *S. venustum/verecundum* complex in July 1985 and 1986 was different from that in June and August in both years. In July 1985 10.6% of all *S. venustum/verecundum* complex collected on DIB traps were trapped in the forest compared to 1.63% in June 1985 and 4.69% in August 1985. Similarly, a large relative abundance of females in the forest was observed in the July 1986 DIB trap collections (June, 4.69%; July, 24.33%; August, 1.50%) and in the July sweep net collections (June 1985, 3.92%; June 1986, 2.05%; July 1986, 5.09%).

The distribution of *S. venustum/verecundum* complex among the habitats was similar in the two sampling years, although the relative abundance of this complex in the pasture in 1985 was greater than that in 1986. This change in relative abundance was most likely due to the change in the trapping location within this habitat.

3.2.6. Comparison of black fly catch to environmental factors

Pearson's correlation was used to compare log black fly catch, assessed using DIB traps, with the environmental factors. The mean monthly meteorological data are recorded in Appendix I.

There were significant negative correlations between black fly catch and temperature in a few sampling months (Table 3-4). However, analysis of variance indicated there were nonsignificant variations in the mean temperature among the six habitats for most sampling months ($p>0.05$) (Appendix J).

Saturation deficit was negatively correlated with the catch of *S. venustum/verecundum* complex in most sampling months, however, most correlations were nonsignificant ($p>0.05$). The catches of *P. mixtum* and *St. mutata* were significantly negatively correlated with saturation deficit (Table 3-4). In all months the saturation deficit did not vary significantly among the six habitats ($p<0.05$) (Appendix J).

The catch of *S. venustum/verecundum* complex was nonsignificantly negatively correlated with wind speed in most months, although wind speed was significantly negatively correlated with *P. mixtum* and *St. mutata* catch (Table 3-4). Wind speeds recorded in the pasture, PDSB and WDSB in June 1985 and July 1986 were significantly greater than those recorded in the regrowth and forest ($p<0.05$) (Appendices J, K).

Reflected light intensity was significantly negatively correlated with the abundance of *P. mixtum*, only (Table 3-4). The reflected light intensity was comparable in all habitats (lux ca. 11,000), except the forest where significantly lower reflected light intensities were recorded (lux ca. 700, $p<0.05$) (Appendices J, K).

Black fly catch was more highly correlated with the distance of the DIB trap to the nearest forest edge compared to the other topographical factors

Table 3-4: Pearson's coefficients for log black fly catch, assessed using dry ice baited sticky traps, correlated with meteorological factors (n=54, except for reflected light in July 1986 where n=36).

Date of collection	Temp. °C	SD[1] mm Hg	Wind[2] km/h	Reflected light, lux
		S. venustum/verecundum complex		
June 1985	0.23	0.071	0.64***	—
July 1985	-0.17	-0.47***	0.75***	—
Aug. 1985	-0.072	-0.16	-0.21	—
June 1986	-0.60***	-0.56***	-0.12	0.22
July 1986	-0.46***	-0.20	-0.065	-0.026
		P. mixtum		
June 1986	-0.65***	-0.66***	-0.52***	-0.34***
		St. mutata		
June 1986	-0.67***	-0.70***	-0.35**	-0.17

[1]SD = saturation deficit.

[2] Total wind passage (km) in July and August 1985, only.

* Values significant at $p<0.05$.

** Values significant at $p<0.01$.

*** Values significant at $p<0.001$.

(Table 3-5). There were significant positive correlations between the catch of *S. venustum/verecundum* complex and the distance of the DIB traps to the nearest forest edge in June and August 1985. The significant correlation was negative in July 1986 (Table 3-5). The catches of *P. mixtum* and *St. mutata* were significantly negatively correlated with the distance of the DIB trap to the nearest forest edge (Table 3-5).

There were significant negative correlations between black fly catch and the distance of the DIB trap from the nearest stream edge in a few sampling months (Table 3-5). However, there was a significant intercorrelation between the distance of the trap from the nearest forest edge and stream edge (1985, $r=0.47$, $p<0.001$; 1986, $r=0.77$, $p<0.001$). The distance of the trap from the forest edge was more highly correlated with black fly catch, therefore it was deemed the more important topographical parameter.

Altitude was negatively correlated with black fly catch, although most relationships were nonsignificant ($p>0.05$) (Table 3-5). A positive, yet nonsignificant ($p>0.05$), relationship between altitude and wind speed was believed to account, in part, for the negative relationship between altitude and black fly catch.

3.3. Supplementary collections

3.3.1. Human-baited sticky trap collections

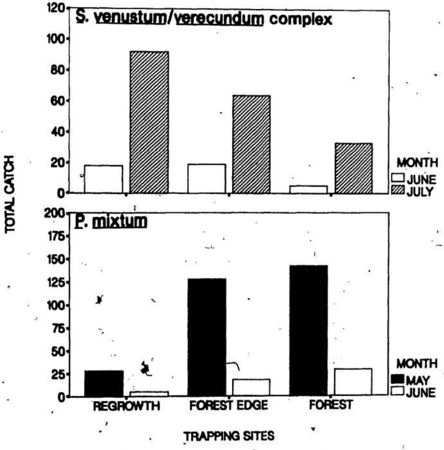
The morning, afternoon and evening black fly catches from each sampling day were combined to increase sample sizes. This was justified as the analysis of the sweep net data indicated that the pattern of distribution does not change significantly throughout the day (Table 3-3). *Simulium venustum/verecundum* complex and *P. mixtum* were collected in numbers large enough to be included in the analysis in June and July 1986, and May and June 1986, respectively. Chi-square analysis of the *Simulium venustum/verecundum* complex catch indicated there were statistically significant differences in the proportion of host-seeking

Table 3-5: Pearson's coefficients for log black fly catch, assessed using dry ice baited sticky traps, correlated with topographical factors (n=54).

Date of collection	Distance to forest	Distance to stream	Altitude
	S. venustum/verecundum complex		
June 1985	0.52***	0.014	-0.10
July 1985	0.11	-0.032	-0.016
August 1985	0.38**	0.053	-0.31*
June 1986	-0.10	-0.24*	-0.18
July 1986	-0.32**	-0.44***	-0.10
	P. mixtum		
June 1986	-0.64***	-0.47***	-0.13
	St. mutata		
June 1986	-0.33**	-0.041	-0.28*

* Values significant at $p<0.05$.
** Values significant at $p<0.01$.
*** Values significant at $p<0.001$.

Figure 3-5: Total daily catch of black flies collected using a 30 cm^2 sticky trap that was operated in the regrowth, forest edge and forest for nine, ten minute periods on one day per month in 1986.


S. venustum/verecundum complex
120
100
80
60
40
20
0
MONTH
JUNE
JULY
TOTAL CATCH
200
P. mixtum
175
150
125
100
75
50
25
0
MONTH
MAY
JUNE
REGROWTH
FOREST EDGE
FOREST
TRAPPING SITES

females collected in the regrowth, forest edge and forest (June, χ^2=8.71, df=2, p<0.05; July, χ^2=25.52, df=2, p<0.001). Females were most abundant in the regrowth and forest edge in June and most abundant in the regrowth in July. In both months females were least abundant in the forest (Fig. 3-5). Similarly, there were significant differences in the proportion of *P. mixtum* collected in the regrowth, forest edge and forest (May, χ^2=77.83, df=2, p<0.001; June, χ^2=16.65, df=2, p<0.001). In both months female *P. mixtum* were most abundant in the forest and least abundant in the regrowth (Fig. 3-5).

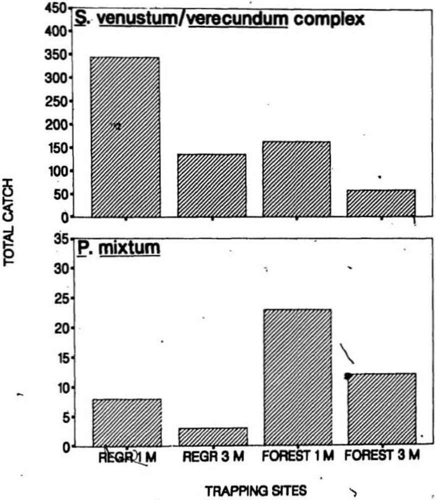
3.3.2. Vertically stratified sampling

A chi-square test was used to determine if there were significant differences in the proportion of host-seeking black flies collected at different elevations above ground level within two habitats. There were statistically significant differences in the proportion of *S. venustum/verecundum* complex collected at 1 m and 3 m above ground level in the regrowth (χ^2=90.13, df=1, p<0.001) and the forest (χ^2=49.89, df=1, p<0.001) (Fig. 3-6). Unlike *S.venustum/verecundum* complex, there were no statistically significant differences in the proportion of *P. mixtum* collected at 1 m and 3 m above ground level in the regrowth (χ^2=2.27, df=1, p>0.05) or the forest (χ^2=3.46, df=1, p>0.05) (Fig. 3-6).

3.3.3. Tuckamoor collection

The position of the DIB traps near tuckamoor significantly influenced the numbers of *S. venustum/verecundum* complex collected (χ^2=6.28, df=2, p<0.05). The largest catches of females were collected on traps 1 m downwind from tuckamoor (total catch = 200 black flies), followed by the traps placed 1 m upwind (total catch = 141 black flies) and traps placed in the center of the tuckamoor (total catch = 81 black flies).

Figure 3-6: Total catches of black flies from dry ice baited sticky traps (one metre and three metres above ground level) operated in the regrowth and forest for three days in June, 1986 (REGR = regrowth).


S. venustum/verecundum complex
P. mixtum
TOTAL CATCH
0
50
100
150
200
250
300
350
400
450
0
5
10
15
20
25
30
35
REGR 1 M
REGR 3 M
FOREST 1 M
FOREST 3 M
TRAPPING SITES

DISCUSSION

4.1. Black flies present and relative abundance

Mammalophilic black flies comprised greater than 99% of the total black fly catch, as only *Eusimulium* spp. and *Cnephia ornithophilia* are ornithophilic (Anderson and DeFoliart, 1961; Cupp and Gordon, 1983) (Table 3-1, 3-2). The mammalophilic black flies encountered, viz. *S. venustum/verecundum* complex, *P. mixtum*, *St. mutata*, *S. vittatum* and *S. decorum*, constitute taxa frequently encountered in this region (Lewis and Bennett, 1973; McCreadie *et al.*, 1985; Pickavance *et al.*, 1970). All females collected were non-gravid and many females attempted to blood-feed on the human bait, indicating that the majority of the females sampled were host-seeking. The small number of males collected probably oriented to the sticky traps as a visual marker as mating occurs in a swarm that forms around distinct visual markers, which can be the blood host (Wenk, 1981). On one occasion two black flies, probably *S. venustum/verecundum* complex, were observed copulating on the lid of a sticky trap, suggesting these traps could be used as visual markers by the males.

Simulium venustum/verecundum complex consists of at least 10 sibling species of *S. venustum* Say and 2 sibling species of *S. verecundum* Stone and Jamnback, which are distinguished in the larval stages on the basis of chromosome morphology (Rothfels *et al.*, 1978; Rothfels, 1981). Due to the difficulty in separating the adult siblings on a morphological basis, the two complexes have been grouped. In Newfoundland, the complex is multivoltine, anautogenous (Lewis and Bennett, 1973) and consists of five sibling species (Rothfels *et al.*, 1978). Females of the *S. venustum/verecundum* complex are the most abundant black flies in northeastern North America and are major pests of a large number of mammals, including humans (Abdelnur, 1968; Cupp and Gordon, 1983; Lewis and Bennett, 1973, 1974, 1979; NRCC, 1982). Greater than 85% of the black flies collected belong to this complex (Table 3-1, 3-2), which is greater than 73% reported by Lewis and Bennett (1979) and 63.7% reported by McCreadie *et al.* (1984). Such discrepancies in relative abundance of black flies may be attributed to annual fluctuations in black fly populations (Colbo, 1985), differences in trapping sites (this study; Service, 1981), and host attractiveness (Crosskey, 1955; Hughes and Daly, 1951; Wolfe and Peterson, 1960). In Newfoundland females of this complex reach peak abundance in mid-July (McCreadie *et al.*, 1985).

Prosimulium mixtum is included with *P. fontanum* Syme and Davies, *P. mysticum* Peterson and *P. fuscum* Syme and Davies in a complex of closely related species formerly known as the *P. hirtipes* complex (D.M. Davies and Syme, 1958; Peterson, 1970; Rothfels, 1956; Syme and D.M. Davies, 1958). Cytological examination of larval forms indicate that only *P. mixtum* are on the island of Newfoundland (Colbo, 1979). These females are univoltine and autogenous for the first ovarian cycle (Cupp and Gordon, 1983; L. Davies, 1961; Lewis and Bennett, 1973). Female *P. mixtum* are important pests of many mammals, including humans, but they are secondary in importance to *S. venustum/verecundum* complex (Cupp and Gordon, 1983; NRCC, 1982). The relative abundance of 8.8% reported for *P. mixtum* (Table 3-1) in this study was low compared to 31.6% reported by McCreadie *et al.* (1984). However, *P. mixtum* females were the second most abundant black flies in both studies. In Newfoundland *P. mixtum* females reach peak abundance in June (McCreadie *et al.*, 1985). Relatively few females were collected in 1985 because (Table 3-1) sampling commenced following a decline in the host-seeking population. Cursory sampling indicated that females of this species had been present earlier in the season.

Stegopterna mutata females are parthenogenetic, univoltine and autogenous in the first ovarian cycle (Back and Harper, 1979; Colbo, pres. comm.; Cupp and

Gordon, 1983; Lewis and Bennett, 1973). While blood-fed females have been collected from a large number of mammals (Abdelnur, 1968; Anderson and DeFoliart, 1961; Downe and Morrison, 1957; Fallis, 1964), they are a minor nuisance on the Avalon Peninsula due to their relatively low abundance (McCreadie *et al.*, 1984). *Stegopterna mutata* was the third most frequently encountered black fly species, accounting for 5.1% of the total collection (Table 3-1). A relative abundance of 2.0% was reported by McCreadie *et al.* (1984) who attributed this low value to the attraction of this species to a trap situated in a pasture: speculation that was supported by this study. In Newfoundland *St. mutata* females are most abundant in June (McCreadie *et al.*, 1985). Females were not frequently collected in 1985 (Table 3-1), although they were abundant earlier in June when cursory sampling was conducted.

Simulium vittatum females are multivoltine and autogenous for the first ovarian cycle (Cupp and Gordon, 1983; Lewis and Bennett, 1973). This species blood-feeds on several species of large mammals, but rarely on humans (Abdelnur, 1968; Anderson and DeFoliart, 1961; Cupp and Gordon, 1983; Lacey and Mulla, 1977; Peterson, 1956). Low relative abundances for this species were reported in this study (<1%, Table 3-1) and the studies conducted by McCreadie *et al.* (1984) (2.2%) and Ezenwa (1974). The small number of this species collected may reflect the distribution of the larval population which is restricted to lake outlets (Colbo, 1979).

Simulium decorum females are univoltine and autogenous for the first ovarian cycle (Cupp and Gordon, 1983; Lewis and Bennett, 1973). While this species will blood-feed on a variety of mammals (Abdelnur, 1968; Anderson and DeFoliart, 1961; Cupp and Gordon, 1983), it is not a major pest in Newfoundland due to its relatively low abundance (Lewis and Bennett, 1973; McCreadie, 1983). This species constituted less than 1% of the total black fly catch in this study (Table 3-1) and in the study conducted by McCreadie *et al.* (1984). Like *S. vittatum*, the larvae of *S. decorum* are restricted to lake outlets (Cupp and Gordon, 1983) and, as a result, this species may be abundant in localized areas, only.

4.2. Black fly spatial distribution

Only a limited number of comparisons between the findings of this study and other studies may be made due to the dearth of information on the spatial distribution of North American mammalophilic black flies. The DIB trap and sweep net collections will be discussed together as both collections were significantly correlated. Generally, fewer *S. venustum/verecundum* complex females were collected in the forest compared to the peatlands and regrowth, a trend also reported by Craig and Pledger (1979). *Prosimulium mixtum* females, which were most abundant in the forest, have been described by Lewis and Bennett (1979) as pests in forested areas, but unfortunately the authors did not elaborate on this observation. Indirectly certain authors may have indicated a recognition of the spatial distribution of these black flies because studies of *S. venustum/verecundum* complex have been conducted in clearings in a forested area (D.M. Davies, 1952; L. Davies, 1963; Fallis *et al.*, 1967), whereas studies of *P. mixtum* have been conducted in mature forest (L. Davies, 1961). In Quebec, Wolfe and Peterson (1960) collected more black flies (95% S. *venustum/verecundum* complex; <1% *P. mixtum*) in the mature forest compared to the regrowth. However, their sampling was conducted in early July so reliable comparisons of the relative abundance of *S. venustum/verecundum* complex and *P. mixtum* could not be made because the adult population of *P. mixtum* sharply declines in this region prior to the first of July (D.M. Davies, 1952; Wolfe and Peterson, 1959). A second consideration is that the large number of *S. venustum/verecundum* complex in the Quebec forests in early July may correspond to the large numbers observed in the Newfoundland forests in late July, with the delay resulting from the differences in the time of emergence of adults in the two regions (Colbo, 1979; Lewis and Bennett, 1974).

The relative abundance of *P. mixtum* in the forest when assessed using the sweep net was low compared to the relative abundance assessed using DIB traps (Figs. 3-1, 3-4). Possibly, the size of the area sampled in the forest was smaller than that in the other habitats due to the physical restriction of using a sweep net in the forest.

Stegopterna mutata females were most abundant in the forest, but unfortunately no reference to the spatial distribution of the adults was found in the literature. However, Colbo (1979) collected few *St. mutata* larvae in outflows on the barrens and speculated that it could be related to adult biology if open expanses were unfavourable to the adults. The low numbers of this species taken in the pasture, peatlands and regrowth and the high numbers collected in the forest support this speculation.

Simulium vittatum and *S. decorum* were collected in such low numbers that a reliable pattern of distribution was not discernible. Craig and Pledger's (1979) study indicates that these species are marginally more abundant in the muskeg [peatland] compared to the forest.

The distribution of the females among the six habitats was non-uniform and could not be accounted for simply by the dispersal of females by the prevailing west southwest wind. The spatial distributions described indicate that *S. venustum/verecundum* complex mainly occupy open areas, whereas *P. mixtum* and *St. mutata* are primarily forest dwellers.

4.2.1. Temporal changes in spatial distribution

Changes in the pattern of spatial distribution within and between sampling days were not observed for *S. venustum/verecundum* complex, *P. mixtum* or *St. mutata*. Similarly, in studies conducted in Africa, Australia, Colombia and North America changes in distribution within and between sampling days were not observed (Craig and Pledger, 1979; Garms and Vajime, 1975; Guttman, 1972; Hunter and Moorehouse, 1976). However, changes in distribution between months, like the one observed in July for *S. venustum/verecundum* complex, have been reported. A change in distribution may be a result of at least three factors.

Temporal changes in spatial distribution have been reported for *P. mixtum*, *P. fuscum* and *S. damnosum* complex and were related to age-dependent behaviour differences (L. Davies, 1961; Duke, 1975). The nulliparous females generally dispersed away from the emergence sites, but the parous females tended to remain near the streams in which they recently oviposited. To determine if the change in *S. venustum/verecundum* complex spatial distribution is associated with a change in the parous rates, females taken from different habitats should be examined for changes in parity throughout the black fly season. It was not possible to examine the females taken for this study for parity due to the difficulty of determining parity with preserved specimens (Colbo, pers. comm.).

Changes in the spatial distribution of *S. venustum/verecundum* complex throughout the sampling season may be related to changes in the predominant sibling species. Studies conducted in Africa indicate that the various sibling species of the *S. damnosum* complex have distinct spatial distributions; certain siblings are restricted to the savanna while others are restricted to the forest (Duke, 1975; Meredith *et al.*, 1983). The seasonal succession of *S. venustum/verecundum* complex in Newfoundland is not well understood, although preliminary investigations indicate there is a shift in the predominant sibling species in July from that in June or August (McCreadie, pers. comm.). Possibly, the predominant July siblings are more inclined to host-seek in the forest than the June or August siblings. Elucidation of the relationship between changes in spatial distribution of the complex and the succession of siblings is dependent upon the development of methods to identify the adult members of the *S. venustum/verecundum* complex.

Thirdly, the July increase in relative abundance of *S. venustum/verecundum* complex in the forest may be related to a change in biting habits. This has been observed by El Bashir *et al.* (1976) who reported that *S. griseicolle* Becker, generally ornithophilic, was collected from mammals, including humans, towards the end of the day. Temporal changes in biting habits have also been reported for the ornithophilic species *S. meridionale* Riley by DeFoliart and Rao (1965) who attributed this phenomenon to blood-hungry females becoming non-selective in order to obtain a blood-meal. Females of the *S.*

venustum/verecundum complex have been collected from birds indicating that they may have catholic tastes, at least under certain circumstances (Pickavance *et al.*, 1970). If the less attractive hosts occupy habitats different from those of the preferred host, certain females may host-seek in habitats different from those in which the preferred hosts most frequently occur.

The spatial distribution of *S. venustum/verecundum* complex in 1985 was similar to that in 1986. The distributions were similar even though the two summers were different meteorologically (Appendix L). Similarity in spatial distribution between sampling years was reported by Guttman (1972) and Rivosecchi (1972).

4.2.2. Unbaited sticky traps

The negative correlation of the unbaited trap catch with the catches from the DIB traps and the sweep net in June 1986 could not be explained. However, the results from all three trapping methods indicated that *S. venustum/verecundum* complex were generally most abundant in the peatlands and regrowth. Since unbaited traps may attract females from within habitats only, the similarity in the pattern of distribution assessed by the three trapping methods may indicate that the DIB trap and sweep net collections are good indicators of within habitat black fly abundance. That is, few adults in one habitat may have been attracted to the DIB traps or the sweep net collector in a neighbouring habitat.

4.2.3. Influence of environmental factors on distribution

4.2.3.1. Air temperature

The catches of *S. venustum/verecundum* complex and *P. mixtum* were significantly negatively correlated with air temperature in a few months (Table 3-4). While Alverson and Noblet (1976) believed black fly activity was temperature independent within the critical range, D.M. Davies (1952) and Hunter and Moorehouse (1976) observed increasing flight activity with increasing temperature up the the critical high temperature limit. McCreadie *et al.* (1986) reported significant negative correlations between *S. venustum/verecundum* complex and *P. mixtum* catch and air temperature when the temperature was 16-25 °C and 14-29 °C, respectively. The mean monthly temperature range in most months was 16.1-24.7 °C (Appendix I), which falls into the lower end of the range reported by McCreadie *et al.* (1986). The negative correlations observed in the present study indicate that activity was being suppressed by high air temperatures. The nonsignificant difference in mean temperatures among the six habitats in most months provides no evidence to suggest that black fly habitat selection is based upon air temperatures 1 m above ground level (Appendix J).

4.2.3.2. Saturation deficit

Saturation deficits were significantly negatively correlated with black fly catch in a few months (Table 3-4). Although McCreadie *et al.* (1986) reported nonsignificant correlations between black fly catch and saturation deficits, all relationships were negative. Certain authors reported significant relationships between black fly catch and saturation deficit (D.M. Davies, 1952; Lacey and Mulla, 1977), whereas others believed it accounted for a minor part of the variation in black fly catch (Alverson and Noblet, 1976; El Bashir *et al.*, 1976; Ogata, 1954). Low saturation deficits are important to adult survival as laboratory studies indicate that female *S. verecundum* have a survival time of only a few days when incubated at a saturation deficit as small as 6 mm Hg (Martin, unpublished data). The nonsignificant differences in saturation deficit among the six habitats suggests that saturation deficits 1 m above ground level are not good indicators of black fly spatial distribution.

4.2.3.3. Wind speed

Wind speed or total wind passage was negatively correlated with black fly catch in most sampling months and was significantly positively correlated in a few (Table 3-4). Bennett and Coombs (1975) and McCreadie *et al.* (1986) considered wind to be one of the most important meteorological factors limiting black fly activity in Newfoundland. Anderson and DeFoliart (1961), El Bashir *et* *al.* (1976), Guttman (1972), Lacey and Mulla (1977) and Ogata (1954) considered moderate to light wind speeds to be a major factor limiting black fly activity, particularly when the prevailing wind was steady rather than gusty. Brown and Bennett (1980) and Hunter and Moorehouse (1976) observed lower numbers of black flies in exposed sites compared to sheltered ones. The relatively high wind speeds in the pasture (Appendix K) may contribute to the relatively low numbers of black flies collected there and the relatively low wind speeds in the fen and regrowth may have contributed to relatively large catches in these habitats. Although lower wind speeds were recorded in the forest (Appendix K), the collections of *S. venustum/verecundum* complex in this habitat were relatively small. Thus, some other critical factor(s) apparently influenced their distribution.

4.2.3.4. Light intensity

Reflected light intensity was negatively correlated, although generally not significantly correlated (Table 3-4), with black fly catch in most sampling months. El Bashir *et al.* (1976) and Lacey and Mulla (1977) reported that high light intensities suppressed black fly activity. Many studies indicate that light intensity has a major influence on black fly activity, particularly during sunrise and sunset, providing that other meteorological factors are favourable for activity (Anderson and DeFoliart, 1961; El Bashir *et al.*, 1976; Lacey and Mulla, 1977; McCreadie *et al.*, 1986). Ogata (1954) reported that the optimum light intensity for *S. venustum* was 3,000-14,000 lux. The daily mean light intensity in the forest was approximately 700 lux compared to approximately 11,000 lux in the other habitats. Thus, the light intensity in the forest was lower than the reported optimum and may account for the relatively low number of *S. venustum/verecundum* complex in this habitat. Females of the *Simulium venustum/verecundum* complex will not enter barns to blood-feed on cattle, whereas *P. mixtum* females will, indicating that the former may not enter areas of low light intensity (Anderson and DeFoliart, 1961; Fredeen, 1977a). Thompson (1976b) found that the savanna sibling species of the *S. damnosum* complex mainly relied on visual stimuli, whereas the forest siblings mainly relied on olfactory stimuli. Perhaps, *P. mixtum* has a greater reliance on olfactory stimuli compared to *S. venustum/verecundum* complex which may enable *P. mixtum* to host-seek in the forest where light levels are low.

4.2.3.5. Proximity to the forest

Given that the *S. venustum/verecundum* complex primarly occurs in open areas, the negative relationship between catch and distance to the forest in 1986 (Table 3-5) indicates that this complex may have received shelted from the wind by the forest and, as a result, were most abundant in the habitats where the sampling sites were nearest the forest. The positive correlations between wind speed and distance to the forest (June 1986, $r=0.67$, $p<0.001$; July 1986, $r=0.85$, $p<0.001$) supports this hypothesis. The positive correlation between *S. venustum/verecundum* complex catch and the distance of the sticky traps from the forest in 1985 were unexpected and no explanation for such relationships can be made. The difference in the direction of the correlation between proximity to the forest and black fly catch observed in 1985 and 1986 indicate that other factors may be influencing distribution; other factors whose influences are not well understood.

Based on the findings from the DIB trapping and sweep netting, the significant negative correlations between *P. mixtum* and *St. mutata* catch and the distance to the forest (Table 3-5) supports the hypothesis that these species are primarily forest dwellers, which will leave the forest to host-seek in nearby habitats.

4.2.3.6. Proximity to streams

Most of the correlations between black fly catch and distance to the nearest stream were negative indicating that the females may have been residing near streams (Table 3-5). This is an unexpected result as the streams in the study site were not major breeding areas for black flies. The negative relationships between catch and distance to the streams may reflect the significant positive correlation between the distances to the streams and distances to the forest.

4.2.3.7. Altitude

Although most of the correlations between black fly catch and altitude were nonsignificant, all relationships were negative (Table 3-5). This negative relationship is associated with a positive correlation between altitude and wind speed. As discussed in a previous section, moderate to strong winds suppress black fly activity. Thus, the pasture, which had the highest altitude and the strongest winds, also had the lowest black fly catches.

4.2.4. Other factors influencing spatial distribution

4.2.4.1. Resting sites

While there were significant relationships between meteorological factors and black fly catch, the differences in meteorological conditions among the six habitats rarely corresponded to black fly spatial distribution. Possibly, black fly distribution is more influenced by changes in meteorological conditions in black fly resting sites rather than the conditions 1 m above ground level; a conclusion also made by Alverson and Noblet (1976). D.M. Davies (1952) noticed that when the subsoil temperatures were below 26 °C half as many black flies, mainly *S. venustum/verecundum* complex, were collected compared to times when subsoil temperatures were above 26 °C. Suitable resting sites are critical to adult survival because exposure to conditions outside of the resting sites can be lethal over short exposures (Hunter and Moorehouse, 1976; Lacey and Mulla, 1977). Possibly, the relatively small catches in the pasture result from a paucity of suitable resting sites due to the low plant diversity and the thin humus layer. The meteorological conditions in the resting sites most likely strongly influences the spatial distribution of the adults, although elucidation of a relationship between these two factors awaits identification of black fly resting sites in Newfoundland.

4.2.4.2. Food sources

Black flies feed on the nectar of flowers to provide energy for metabolic processes, as well as for flight involved in long-range and short-range dispersal (Cooter, 1982, 1983; Peterson and Wolfe, 1958). Because of the importance of sugar-feeding and blood-feeding, the most suitable habitats for black flies should have access to both food sources. Stone and Snoddy (1969) frequently collected *S. vittatum* from flowers near the habitat in which the females blood-feed. Wenk (1965) (cited in Sutcliffe, 1986) suggested that the flowers used as nectar sources may double as resting sites, which emphasizes the importance of nectar sources. *Simulium venustum* sugar-feeds on *Ledum groenlandicum* Oeder, *Rubus acaulis* Michx., and *Vaccinium angustifolium* Ait. flowers (Hocking and Pickering, 1954; Wolfe and Peterson, 1959). At least one of these plant species or a member of the genera was present in all of the habitats, except the pasture. The scarcity of suitable sugar sources in the pasture may have contributed to the low numbers of black flies collected in this habitat. The relatively large number of black flies collected in the regrowth may have been influenced by edge effects, which is the tendency for increased variety and density of species in an ecotone compared to the climax communities that flank it (Odum, 1971). Thus, the relatively large numbers of *S. venustum/verecundum* complex, *P. mixtum* and *St. mutata* collected in the regrowth may reflect the diverse flora and mammalian fauna in this habitat.

4.3. Supplementary collections

4.3.1. Human-baited trap collection

The differences in the numbers of *S. venustum/verecundum* complex and *P. mixtum* females attracted to a human host in nearby habitats suggests that black flies may severly harass a host in one habitat, but not in a neighbouring habitat, particularly if the two areas differ greatly in dominant vegetation cover. These results support the hypothesis that there may be little movement of black flies between habitats. The results of the human-baited trap collections coupled with the results from the DIB trapping indicate that the relatively low number of *P. mixtum* collected in the forest with the sweep net was an anomaly.

4.3.2. Vertical stratification of black flies

Significantly more *S. venustum/verecundum* complex were collected 1 m above ground level compared to 3 m above ground level. Similarly, Fallis *et al.* (1967) collected the most *S. venustum/verecundum* complex closest to ground level and Adler *et al.* (1983) collected *S. vittatum* 0.3 m above the surface of streams. Choe *et al.* (1984) purposed that black flies generally fly [short-range dispersal] within the boundary layer where they are able to control their flight (Taylor, 1974). Since *S. venustum/verecundum* complex females mainly occupy open areas that are exposed to the wind, the boundary layer in these habitats may be within 1 m of ground level, explaining the small number of this complex collected 3 m above ground level.

The vertical distribution of *P. mixtum* was unexpected in light of this species preference for large mammals (Anderson and DeFoliart, 1961; Cupp and Gordon, 1983) and the absence of the less attractive arboreal mammals on the Avalon Peninsula (Dodds, 1983). However, *P. mixtum* females occupy a habitat that is sheltered from the wind and, as a result, this habitat may have a boundary layer greater than 3 m above ground level enabling females to be more vertically distributed.

4.3.3. Tuckamoor collections

The small number of *S. venustum/verecundum* complex collected on traps placed in the center of tuckamoor compared to traps placed upwind or downwind of tuckamoor may be a result of at least two factors. One, based on the findings from the vertically stratified sampling and the studies conducted by Fallis *et al.* (1967), females appear to fly near ground level and, therefore, may fly around the tuckamoor rather than over it, resulting in few females coming into visual contact with the traps placed in the center of the tuckamoor. Two, Bradbury and Bennett (1974a) speculated that objects whose colour strongly contrast with the environment may be better visual targets than objects that blend in with the colours in the background vegetation. If the contrast between the colour of a sticky trap and caribou lichen was greater than the contrast between a sticky trap and tuckamoor, then a sticky trap placed 1 m away from the tuckamoor may be better visual target and, as a result, attract more females than a trap in the center of the tuckamoor.

SUMMARY

1. A total of 38,977 female black flies were collected using dry ice baited traps, unbaited traps and a sweep net at the study site 16 km west of St. John's, Newfoundland, from 28 June to 21 August 1985, and 30 May to 7 August 1986. Greater than 99% of the females collected were mammalophilic, of which approximately 85% were *S. venustum/verecundum* complex, 8% *P. mixtum* and 5% *St. mutata*.

2. Females of the *S. venustum/verecundum* complex were most abundant in the peatlands and regrowth, whereas *P. mixtum* and *St. mutata* females were most abundant in the forest. Few black flies were collected in the pasture.

3. The spatial distribution of black flies was similar within sampling days, between sampling days and sampling years. However, in July the relative abundance of *S. venustum/verecundum* complex females in the forest was greater than that in June or August. The reasons for this change in distribution were not evident, although age-dependent behaviour differences, changes in the predominant sibling species and changes in biting habits were thought to play an important role.

4. The high wind speeds in the pasture may have contributed to the low number of black flies collected in this habitat while the low light levels in the forest may have contributed to the low numbers of *S. venustum/verecundum* complex generally taken in this habitat.

5. Many of the environmental factors measured did not correspond to the spatial distribution of the adults. Intercorrelations between environmental factors

and the poorly understood influences of other factors makes elucidation of the relationship between a single environmental factor and black fly catch difficult.

6. Although no evidence was presented, changes in the meteorological conditions in the resting sites were suspected to have a greater influence on black fly spatial distribution than the meteorological conditions 1 m above ground level.

7. There may be little movement of adults to a host in a neighbouring habitat, particularly if the habitats differ greatly in dominant vegetation cover.

8. More *S. venustum/verecundum* complex females were collected close to ground level than above ground level, whereas *P. mixtum* females have a greater vertical distribution.

9. Given the occurrence of *Simulium venustum/verecundum* complex in open areas, this complex may become a greater problem to mammals if clearing of forested land is encouraged. Based on the spatial distribution and seasonal succession of the major pest species in Newfoundland, providing mammals with open windy areas in June and forested or dimly light shelters in July and August may reduce black fly harassment.

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APPENDIX A

Dates of black fly sampling during the summers of 1985 and 1986.

Sampling method	Date of collection
Dry ice baited sticky trap	June 28, 29 and July 5, 1985
	July 22-24, 1985
	August 19-21, 1985
	June 7, 8, 13, 1986
	July 10, 11, 14, 1986
	August 5-7, 1986
Unbaited sticky trap	June 16, 18, 19, 1986
	July 22-24, 1986
Sweep net	June 28, 29 and July 5, 1985
	June 7, 8, 13, 1986
	July 10, 11, 14, 1986
	August 5-7, 1986
Human-baited sticky trap	May 30, 1986
	June 20, 1986
	July 1, 1986
Vertically stratified sampling	June 25-27, 1986
Tuckamoor collections	July 17-19, 1986

APPENDIX B

Source tables for analysis of variance of the log transformed black fly catches from dry ice baited sticky traps (DF=degrees of freedom; SS=sum of squares; MSS=mean sum of squares).

S. venustum/verecundum complex

June 1985

Source	DF	SS	MSS	F ratio	p
Between	5	11.42	2.28	22.83	0.000
Within	48	4.80	0.10		
Total	53	16.22			

July 1985

Source	DF	SS	MSS	F ratio	p
Between	5	0.92	0.18	1.01	0.42
Within	48	8.73	0.18		
Total	53	9.65			

August 1985

Source	DF	SS	MSS	F ratio	p
Between	5	5.38	1.08	11.31	0.000
Within	48	4.57	0.095		
Total	53	9.95			

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	5.40	1.08	2.09	0.082
Within	48	24.76	0.52		
Total	53	30.16			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	2.90	0.58	2.94	0.021
Within	48	9.45	0.20		
Total	53	12.35			

P. mixtum

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	7.61	1.52	7.09	0.000
Within	48	10.31	0.21		
Total	53	17.92			

St. mutata

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	3.61	0.72	1.26	0.30
Within	48	27.49	0.57		
Total	53	31.10			

APPENDIX C

Source tables for analysis of variance of the log transformed black fly catches from unbaited sticky traps. (DF=degrees of freedom; SS=sum of squares; MSS=mean sum of squares).

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	8.38	1.68	4.69	0.000
Within	83	29.67	0.36		
Total	88	38.05			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	1.03	0.21	2.72	0.025
Within	84	6.38	0.076		
Total	89	7.41			

APPENDIX D

Source tables for analysis of variance of the log transformed *S. venustum/verecundum* complex and *P. mixtum* sweep net catches (DF=degrees of freedom; SS=sum of squares; MSS=mean sum of squares).

S. venustum/verecundum complex

June 1985, morning

Source	DF	SS	MSS	F ratio	p
Between	5	4.28	0.86	5.96	0.000
Within	48	6.90	0.14		
Total	53	11.18			

June 1985, afternoon

Source	DF	SS	MSS	F ratio	p
Between	5	6.29	1.26	4.59	0.002
Within	48	13.16	0.27		
Total	53	19.45			

June 1985, evening

Source	DF	SS	MSS	F ratio	p
Between	5	6.12	1.22	6.78	0.0001
Within	48	8.67	0.18		
Total	53	14.79			

June 1986, morning

Source	DF	SS	MSS	F ratio	p
Between	5	10.43	2.09	8.02	0.000
Within	48	12.49	0.26		
Total	53	22.92			

June 1986, afternoon

Source	DF	SS	MSS	F ratio	p
Between	5	10.53	2.11	7.83	0.000
Within	48	12.91	0.27		
Total	53	23.44			

June 1986, evening

Source	DF	SS	MSS	F ratio	p
Between	5	2.48	0.50	1.68	0.16
Within	48	14.15	0.29		
Total	53	16.63			

July 1986, morning

Source	DF	SS	MSS	F ratio	p
Between	5	1.78	0.24	0.99	0.43
Within	48	11.42	0.24		
Total	53	12.60			

July 1986, afternoon

Source	DF	SS	MSS	F ratio	p
Between	5	2.58	0.52	5.76	0.000
Within	48	4.29	0.089		
Total	53	6.87			

July 1986, evening

Source	DF	SS	MSS	F ratio	p
Between	5	3.49	0.70	6.65	0.0001
Within	48	5.04	0.11		
Total	53	8.53			

P. mixtum

June 1986, morning

Source	DF	SS	MSS	F ratio	p
Between	5	2.32	0.46	2.74	0.030
Within	48	8.14	0.17		
Total	53	10.46			

June 1986, afternoon

Source	DF	SS	MSS	F ratio	p
Between	5	3,84	0.77	10.63	0.000
Within	48	3.47	0.072		
Total	53	7.31			

June 1986, evening

Source	DF	SS	MSS	F ratio	p
Between	5	0.75	0.15	1.58	0.18
Within	48	4.54	0.095		
Total	53	5.29			

APPENDIX E

The results of Tukey's multiple range test identifying the habitats that have significant differences in *S. venustum/verecundum* complex sweep net catch in 1985 and 1986 (* denotes pairs of habitats significantly different at $p<0.05$; Past=pasture; PDSB=poorly-drained bog; WDSB=well-drained bog; Regr=regrowth; For=forest).

June 1985, morning

	For	PDSB	WDSB	Past	Regr	Fen
For						
PDSB						
WDSB						
Past						
Regr	*					
Fen	*	*				

June 1985, afternoon

	For	Past	Regr	PDSB	Fen	WDSB
For						
Past						
Regr						
PDSB						
Fen	*					
WDSB	*	*				

June 1985, evening

	Past	For	PDSB	WDSB	Regr	Fen
Past						
For						
PDSB						
WDSB	*					
Regr	*					
Fen	*	*				

June 1986, morning

	For	Past	PDSB	WDSB	Regr	Fen
For						
Past						
PDSB						
WDSB	*	*				
Regr	*	*				
Fen	*	*				

June 1986, afternoon

	Past	For	PDSB	WDSB	Fen	Regr
Past						
For						
PDSB	*					
WDSB	*					
Fen	*	*				
Regr	*	*				

July 1986, afternoon

	Past	PDSB	For	WDSB	Fen	Regr
Past						
PDSB						
For						
WDSB						
Fen	*	*	*			
Regr	*	*	*			

July 1986, evening

	Past	PDSB	WDSB	Fen	For	Regr
Past						
PDSB						
WDSB						
Fen						
For						
Regr	*	*	*			

APPENDIX F

The rankings of abundance for *Simulium venustum/verecundum* complex collected on dry ice baited sticky traps in 1985 and 1986. These ranks were used in the calculation of Kendall's coefficient of concordance for between days comparison of distribution (Past=pasture; PDSB=poorly-drained slope bog; WDSB=well-drained slope bog; Regr=regrowth; For=forest; habitats were ranked from minimum abundance (1) to maximum abundance (6)).

Sampling day	Past	PDSB	WDSB	Fen	Regr	For
			June 1985			
1	2	4	6	3	5	1
2	5	3	4	2	6	1
3	3	4	2	5	6	1
			July 1985			
1	3.5	3.5	6	5	1	2
2	5	3	2	6	4	1
3	4	2	1	5	6	3
			August 1985			
1	2	5	3	4	6	1
2	2	6	5	4	3	1
3	5	6	2	3.5	3.5	1
			June 1986			
1	2	5	3	4	6	1
2	1	4	2	5	6	3
3	1	5	4	3	6	2
			July 1986			
1	2.5	4	2.5	5	6	1
2	1	2	3	4	5	6
3	1	4	2	3	6	5

APPENDIX G

The rankings of abundance for *Simulium venustum/verecundum* complex collected on unbaited sticky traps in 1986. These ranks were used in the calculation of Kendall's coefficeint of concordance for between months comparison of distribution (Past=pasture; PDSB=poorly-drained slope bog; WDSB=well-drained slope bog; Regr=regrowth; For=forest; habitats were ranked from minimum abundance (1) to maximum abundance (6)).

Sampling day	Past	PDSB	WDSB	Fen	Regr	For
			June			
1	5	2	4	6	3	1
2	4	5	6	2	3	1
3	3	2	5	4	6	1
			July			
1	6	3.5	2	3.5	5	1
2	6	4	5	2	3	1

APPENDIX H

The rankings of abundance for *Simulium venustum/verecundum* complex collected on dry ice baited sticky traps in 1985 and 1986. These ranks were used in the calculation of Kendall's coefficient of concordance for between months comparison of distribution (Past=pasture; PDSB=poorly-drained slope bog; WDSB=well-drained slope bog; Regr=regrowth For=forest; habitats were ranked from minimum abundance (1) to maximum abundance (6)).

Sampling month	Past	PDSB	WDSB	Fen	Regr	For
			1985			
June	3	4	6	2	5	1
July	4	3	5	6	2	1
Aug.	2	6	4	5	3	1
			1986			
June	1	5	4	3	6	2
July	1	3	2	4	6	5
Aug.	2	5	6	4	3	1

APPENDIX I

Monthly meteorological data recorded at one metre above ground level (Past=pasture; PDSB=poorly-drained slope bog; WDSB=well-drained slope bog; Regr=regrowth; For=forest; Temp=temperature (°C); SD=saturation deficit (mm Hg); Wind=wind speed (km\hr); TP=total wind passage (km)).

Month		Past	PDSB	WDSB	Fen	Regr	For
June	Temp	21.9	23.1	23.1	23.1	24.7	22.4
1985	SD	7.3	8.7	9.2	9.5	12.0	7.3
	Wind	6.0	6.3	5.5	3.0	4.0	0.0
July	Temp	20.9	19.8	19.8	19.5	19.0	18.4
1985	SD	7.4	5.9	5.3	7.4	6.5	5.2
	TP	74.1	—	—	—	55.5	—
Aug.	Temp	18.2	17.5	17.2	17.7	17.3	17.2
1985	SD	10.6	4.3	4.4	4.6	3.4	4.6
	TP	52.1	—	—	—	53.2	—
June	Temp	17.2	16.7	17.7	17.7	17.3	16.1
1986	SD	9.8	9.1	8.8	9.6	11.1	7.4
	Wind	6.1	4.1	4.1	0.7	1.4	0.0
July	Temp	18.9	18.7	19.3	19.2	20.2	18.3
1986	SD	3.7	5.9	7.2	7.1	9.1	5.7
	Wind	10.2	6.6	8.0	4.3	3.0	0.0

APPENDIX J

Source tables for analysis of variance of the meteorological factors. (DF=degrees of freedom; SS=sum of squares; MSS=mean sum of squares).

Temperature

June 1985

Source	DF	SS	MSS	F ratio	p
Between	5	12.94	2.59	1.19	0.37
Within	12	26.00	2.17		
Total	17	38.94			

July 1985

Source	DF	SS	MSS	F ratio	p
Between	5	10.28	2.06	3.36	0.039
Within	12	7.33	0.61		
Total	17	17.61			

August 1985

Source	DF	SS	MSS	F ratio	p
Between	5	7.11	1.42	0.091	0.99
Within	12	186.67	15.56		
Total	17	193.78			

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	5.50	1.10	0.58	0.71
Within	12	22.56	1.88		
Total	17	28.06			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	7.11	1.42	0.26	0.92
Within	12	64.67	5.39		
Total	17	77.78			

Saturation deficit

June 1985

Source	DF	SS	MSS	F ratio	p
Between	5	46.16	9.23	0.38	0.85
Within	12	292.68	24.39		
Total	17	338.84			

July 1985

Source	DF	SS	MSS	F ratio	p
Between	5	13.25	2.65	0.21	0.95
Within	12	148.59	12.38		
Total	17	161.84			

August 1985

Source	DF	SS	MSS	F ratio	p
Between	5	5.48	1.10	0.68	0.65
Within	12	19.42	1.62		
Total	17	24.90			

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	17.22	3.44	0.55	0.74
Within	12	75.52	6.29		
Total	17	92.74			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	22.74	4.55	1.98	0.15
Within	12	27.57	2.30		
Total	17	50.31			

Wind speed

June 1985

Source	DF	SS	MSS	F ratio	p
Between	5	84.48	16.89	4.97	0.011
Within	12	40.76	3.40		
Total	17	125.24			

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	82.67	16.53	2.50	0.090
Within	12	79.33	6.61		
Total	17	162.00			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	209.11	41.82	6.49	0.000
Within	12	77.33	6.44		
Total	17	286.44			

Reflected light intensity

June 1986

Source	DF	SS	MSS	F ratio	p
Between	5	29.40	5.88	70.08	0.000
Within	12	1.01	0.084		
Total	17	91.21			

July 1986

Source	DF	SS	MSS	F ratio	p
Between	5	20.70	4.14	21.60	0.000
Within	6	1.15	0.19		
Total	11	21.85			

APPENDIX K

The results of Tukey's multiple range test identifying the habitats that have significant differences in environmental conditions in 1985 and 1986 (* denotes pairs of habitats significantly different at $p<0.05$; Past=pasture; PDSB=poorly-drained bog; WDSB=well-drained slope bog; Regr=regrowth; For=forest).

Air temperature

July 1985

	For	Regr	Fen	WDSB	PDSB	Past
For						
Regr						
Fen						
WDSB						
PDSB						
Past	*					

Wind speed

June 1985

	For	Fen	Regr	WDSB	Past	PDSB
For						
Fen						
Regr						
WDSB	*					
Past	*					
PDSB	*					

July 1986

	For	Regr	Fen	PDSB	WDSB	Past
For						
Regr						
Fen						
PDSB	*					
WDSB	*					
Past	*	*				

Reflected light

June 1986

	For	Regr	WDSB	Fen	PDSB	Past
For						
Regr	*					
WDSB	*					
Fen	*					
PDSB	*					
Past	*					

July 1986

	For	Regr	PDSB	Fen	WDSB	Past
For						
Regr	*					
PDSB	*					
Fen	*					
WDSB	*					
Past	*					

APPENDIX L

Comparison of meteorological conditions during the summers of 1985 and 1986 recorded at Environment Canada's weather station on Brookfield Road, St. John's, Newfoundland.

Month	Total precipitation (mm)		Mean wind passage (km)		Total sunshine (h)		Mean air temperature (°C)	
	1985	1986	1985	1986	1985	1986	1985	1986
June	101.3	104.8	281	200	186.2	202.5	10.7	12.1
July	98.6	114.4	210	214	243.5	193.5	17.8	13.6
Aug.	113.1	69.5	141	—	161.8	186.1	14.4	15.5