# ASPECTS OF THE BIOLOGY OF ADULT TABANIDAE (DIPTERA) OF SOUTHWESTERN QUEBEC

by

© Daniel J. Leprince

A thesis submitted to the Faculty
of Graduate Studies and Research in
partial fulfilment of the requirements
of Doctor of Philosophy (Ph.D.)

Department of Entomology
McGill University
Montreal, Quebec
Canada

February 1984

Short title:

# BIOLOGY OF ADULT TABANIDAE (DIPTERA)

Daniel J. Leprince

## ABSTRACT

Ph.D.
D.J. LEPRINCE
ENTOMOLOGY

# BIONOMICS OF THE TABANIDAE (DIPTERA) OF SOUTHWESTERN QUEBEC

An aggregation site of male tabanids was discovered on a mountain summit. Males were more abundant and usually had a longer seasonal distribution than females of the same species. Two main types of male behavior have been associated with mating: hovering and waiting. Prevalence of sugar feeding was 43% in waiting males and 84% in hovering males. The range of climatic factors during male activity, and the species of flowering plants visited are also presented.

Of 3418 female horse flies (9 *Hybomitra* species and 5 *Tabanus*) collected in 2 sampling years, 3187 were dissected. Among dissected specimens, 70% were nulliparous, 87% were sperm positive, 86% were sugar positive and 3.3% retained blood. Populations of *H. frontalis* were autogenous; anautogeny is reported in 7 other species. Relative abundance, seasonal distribution, the range of atmospheric conditions during female activity, the stage of development of ovarian follicle, attractiveness of carbon dioxide to females, wing length and number of ovarioles are also presented.

## RESUME

DOCTORAT
D.J. LEPRINCE
ENTOMOLOGIE

# BIONOMIE DES TABANIDAE (DIPTERA) DU SUD-OUEST DU QUEBEC

Un site d'aggrégation de tabanides mâles fut découvert au sommet d'un mont. Les mâles furent plus abondants et ont généralement eu une période de vol plus longue que les femelles de la même espèce. Chez les mâles deux types de comportements furent associés à l'accouplement: "hovering" et "waiting". L'incidence des repas de sucre fut de 43% chez les mâles en attente (waiting) et de 84% chez les mâles volants sur place (hovering). La variation des facteurs climatiques durant l'activité des mâles, et les espèces de fleurs visitées sont présentées.

Des 3418 femelles de taons à cheval (9 espèces d'*Hybomitra* et 5 de *Tabanus*) récoltés au cours de 2 saisons d'échantillonnage, 3187 furent disséquées. Parmi les spécimens disséqués, 70% étaient nullipares, 87% contenaient du sperme, 86% des sucres et 3.3% du sang. Les populations *H. frontalis* furent autogènes; l'anautogénie est rapportée chez 7 autres espèces. L'abondance relative, la distribution saisonnière, la variation des facteurs climatiques durant l'activité des femelles, le stade de développement des follicules ovariens, l'attraction du bioxyde de carbone sur les femelles, la longueur de l'aile et le nombre d'ovarioles sont aussi présentés.

Short title:

BIOLOGY OF ADULT TABANIDAE (DIPTERA)

Daniel J. Leprince

## CLAIM TO ORIGINALITY

The study of a male aggregation site provided original information on (1) 2 main types of male behavior associated with mating (hovering and waiting), (2) prevalence of sugar feeding by males, (3) male longevity, (4) the effect of climatic factors on male activity and (5) a list of flowers visited by males based on pollen identification.

The type of male behavior is not related to generic classification since both hovering and waiting behavior were found in different species of *Hybomitra*.

For the first time in Quebec, host-seeking tabanid females (*Hybomitra* and *Tabanus*) were dissected to determine (1) parity rates, (2) the incidence of anautogeny among tabanid species, (3) the oviposition period based on ovariole sheath dilatation, (4) the incidence of sugar and blood meals, (5) the range of atmospheric conditions during female activity.

Seasonal fluctuations of sperm presence in nullipars and pars of *Hybomitra* and *Tabanus* species are reported for the first time.

The attractiveness of carbon dioxide to parous tabanid females, the linear regression between wing length (as a body parameter) and the number of ovarioles (potential fecundity) of *Tabanus* species are original contributions.

## ACKNOWLEDGMENTS

This project was financially supported by Agriculture Canada through a research grant to Dr D.J. Lewis. Personal support was provided by the Faculty of Agriculture of McGill University (W.M. Stewart Scholarship), the Department of Entomology (McGill) and Service des prêts et bourses aux étudiants, Ministère de l'Education, Gouvernement du Québec. Dr D.M. Wood, (Biosystematics Research Institute, Ottawa) kindly loaned his tabanid material collected on Mount Rigaud from 1978 to 1980. Dr D.C. Dondale (BRI, Ottawa) identified the crab spider (Araneae: Thomisidae). Miss Johanne Parent, Université du Québec à Rimouski, performed the pollen identification. Miss Martha Farkas and Mr Pierre Langlois, respectively, provided assistance in the collection of tabanids and technical support. Dr D.J. Lewis gave me invaluable time and assistance throughout the course of this investigation. My wife, Jacqueline Garand, helped me with her love, courage and moral support.

TABLE OF CONTENT

ABSTRACT . . . . . ii
RESUME . . . . . ii
SHORT TITLE . . . . . iii
CLAIM TO ORIGINALITY . . . . . iv
ACKNOWLEDGMENTS . . . . . v
TABLE OF CONTENT . . . . . vi
LIST OF TABLES . . . . . viii
LIST OF FIGURES . . . . . ix

I INTRODUCTION . . . . . 1

II REVIEW OF LITERATURE . . . . . 2
1.0 Economic and medical importance . . 2
2.0 Quebec literature . . . . . 2
3.0 Male biology . . . . . 3
4.0 Female . . . . . 3
4.1 Reproductive system . . . . . 3
4.2 Follicle development . . . . . 3
4.3 Age grading . . . . . 3
4.4 Sperm presence . . . . . 4
4.5 Sugar and blood feeding . . . . . 4
4.6 Trapping . . . . . 4
4.7 Diurnal activity . . . . . 5
4.8 Parasitism . . . . . 5

III AGGREGATION OF TABANID MALES ON A MOUNTAIN SUMMIT IN SOUTHWESTERN QUEBEC . . . . . 7
1.0 Introduction . . . . . 7
2.0 Materials and methods . . . . . 7
2.1 Sampling site and collection of specimens . . . . . 7
2.2 Dissection . . . . . 7
2.3 Nectar detection and pollen analysis . . . . . 7
2.4 Longevity studies . . . . . 8
3.0 Results . . . . . 8
3.1 Seasonal distribution . . . . . 8
3.2 Male behavior . . . . . 8
3.3 Effect of climatic factors on male behavior . . . . . 9
3.4 Nectar feeding and longevity . . 9
3.5 Pollen spectrum on *H. sodalis*. 10
3.6 Interspecific mating . . . . . 10
3.7 Predation and parasitism . . . . 10
4.0 Discussion . . . . . 10

IV ASPECTS OF THE BIOLOGY OF FEMALE HORSE FLIES IN SOUTHWESTERN QUEBEC . . . . . 17
1.0 Introduction . . . . . 17
2.0 Materials and methods . . . . . 17
2.1 Sampling site and collection of specimens . . . . . 17
2.2 Dissection . . . . . 17
2.3 Incidence of nectar feeding and flowers visited . . . . . 17
2.4 Fecundity . . . . . 18
3.0 Results . . . . . 18
3.1 Seasonal distribution and relative abundance . . . . . 18
3.2 Parity rates . . . . . 19
3.3 Oviposition . . . . . 19
3.4 Egg retention . . . . . 20
3.5 Sperm presence . . . . . 20
3.6 Anthrone positivity and flowers visited . . . . . 21
3.7 Blood meal presence . . . . . 21
3.8 Effect of carbon dioxide . . . . 22
3.9 Atmospheric conditions during female activity . . . . . 22
3.10 Fecundity . . . . . 22

3.11 Endoparasites . . . . . 22
4.0 Discussion . . . . . 23
4.1 Seasonal distribution . . . . . 23
4.2 Parity rates and physiological age . . . . . 23
4.3 Oviposition. . . . . 24
4.4 Egg retention . . . . . 25
4.5 Sperm presence . . . . . 25
4.6 Sugar presence . . . . . 26
4.7 Blood presence . . . . . 27
4.8 Carbon dioxide . . . . . 28
4.9 Atmospheric conditions. . . . . 28
4.10 Fecundity . . . . . 29
4.11 Endoparasites . . . . . 29

V GENERAL DISCUSSION AND FUTURE AREAS OF RESEARCH . . . . . 58

VI LITERATURE CITED . . . . . 60

## LIST OF TABLES


Table 1. Incidence of nectar feeding, as detected by the cold anthrone test and abundance of fat body in male tabanids collected on Mount Rigaud, Quebec, 1981 . . . . . 14

Table 2. Prevailing atmospheric conditions during male tabanid activity on the summit of Mount Rigaud, Quebec, 1981 15

Table 3. Pollen spectrum for 22 *Hybomitra sodalis* males collected from 28 June to 30 July 1981 from Mount Rigaud, Quebec . . . . . 16

Table 4a. Summary of parity rates, sperm presence, and anthrone positivity of horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec in 1980–1981. . 39

Table 4b. Summary of parity rates, sperm presence, and anthrone positivity of horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec in 1980–1981. . 40

Table 5. Parity rates, sperm presence, and anthrone positivity of *Hybomitra affinis* and *Hybomitra illota* in southwestern Quebec in 1980 and 1981 41

Table 6. Parity rates, sperm presence, and anthrone positivity of *Hybomitra epistates* in southwestern Quebec in 1980 and 1981 . . . . . 42

Table 7. Parity rates, sperm presence, and anthrone positivity of *Hybomitra frontalis* in southwestern Quebec in 1980 and 1981 . . . . . 43

Table 8. Parity rates, sperm presence, and anthrone positivity of *Hybomitra lasiophthalma* in southwestern Quebec in 1980 and 1981. . . . . 44

Table 9. Parity rates, sperm presence, and anthrone positivity of *Hybomitra nuda* and *Hybomitra microcephala* in southwestern Quebec in 1980 and 1981 45

Table 10. Parity rates, sperm presence, and anthrone positivity of *Hybomitra pechumani* and *Hybomitra sodalis* in southwestern Quebec in 1980 and 1981 46

Table 11. Parity rates, sperm presence, and anthrone positivity of *Tabanus catenatus* and *Tabanus lineola* in southwestern Quebec in 1980 and 1981 47

Table 12. Parity rates, sperm presence, and anthrone positivity of *Tabanus quinquevittatus* in southwestern Quebec in 1980 and 1981. . . . . 48

Table 13. Parity rates, sperm presence, and anthrone positivity of *Tabanus similis* in southwestern Quebec in 1980 and 1981 . . . . . 49

Table 14. Percentage of parous females which retained eggs in 1980 and 1981 50

Table 15. Parity rates, anthrone positivity and attraction to carbon dioxide of unmated horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec in 1980–81 . . . . . 51

Table 16a. Attractiveness of carbon dioxide to nullipars and pars of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in southwestern Quebec in 1980–1981. . . . . 52

Table 16b. Attractiveness of carbon dioxide to nullipars and pars of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in southwestern Quebec in 1980–1981. . . . . 53

Table 17. Percentage of parous specimens collected in non-baited and carbon dioxide-baited Canopy traps in 1980 and 1981 . . . . . 54

Table 18. Variation of climatic factors during female tabanid activity in 1980–81 . . . . . 55

Table 19. Wing length and number of ovarioles of *Tabanus* females from southwestern Quebec 1980–81 . . . . . 56

Table 20. Comparison of wing length and potential fecundity of *Tabanus* females collected in 1980 and 1981 . . . . . 57

## LIST OF FIGURES

Figure 1. Seasonal succession of tabanids collected on the summit of Mount Rigaud, Quebec, 1978-81 . . . . . 12

Figure 2. Location of canopy traps near the entrance of the Morgan Arboretum (Sainte-Anne-de-Bellevue), Quebec, 1980-81 . . . . . 31

Figure 3. Seasonal succession of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in Sainte-Anne-de-Bellevue, Quebec, 1980-81 . . . . . 33

Figure 4. Potential fecundity of *Tabanus lineola* and *Tabanus similis* in southwestern Quebec. . . . . 35

Figure 5. Potential fecundity of *Tabanus quinquevittatus* in southwestern Quebec . . . . . 37

# I INTRODUCTION

The Tabanidae (Diptera) is a relatively large cosmopolitan group of flies commonly referred to as horse flies and deer flies. Adult females are strong fliers and have been notorious pests of livestock and other warm-blooded animals; males do not blood-feed. At their peak of abundance tabanids may seriously interfere with human outdoor activities, and as a result of their feeding behavior may cause significant losses in livestock productivity. Larvae are usually found in semi-aquatic habitats but some develop in semi-arable lands. Larval development may require several years.

There is little information available on the biology of male tabanids. Most trapping methods are designed to collect host-seeking females; therefore males are rarely collected. Diurnal patterns of male activity, male behavior, and mating sites are unknown for most tabanid species.

An aggregation site of male tabanids was discovered on a mountain summit in southwestern Quebec. Aspects of male biology and environmental conditions at the site were studied in order to provide information on tabanid mating systems. Seasonal and diurnal activity of males were recorded along with climatological factors; it was believed that males of different species would share the use of the site so as to avoid competition. Sugar feeding was studied to determine to what extent males rely on sugar for their energy requirements; results were correlated with behavior. Pollen analysis was performed on males of one species to identify the most important nectariferous flowers visited.

In southwestern Quebec, tabanid females are known to be pests of humans and livestock. Certain aspects of tabanid biology were investigated as these were felt to be relevant to the potential pest status of the insects. It is unknown whether tabanid females in this area rely on blood for their first gonotrophic (blood feeding-oviposition) cycle and how many cycles can be completed by a single female. As an alternative to laboratory rearing, ovarian dissection can be used to obtain information on autogeny and ovarian cycles. This approach, already proven for mosquitoes, was attempted for tabanids. The number of ovarioles was correlated with wing length for *Tabanus* spp. females and results compared between species. The number of ovarioles, found by dissection, was also used to estimate the potential number of eggs that could be laid per gonotrophic cycle.

Sperm presence in the three spermathecae was checked to determine if insemination occurs prior to host-seeking. Sugar presence was detected by the cold anthrone test to assess the extent to which tabanid females depend on carbohydrate sources to meet their energy requirements. Carbon dioxide was used in conjunction with Canopy traps to evaluate its efficiency as an attractant for nulliparous and parous tabanid females. An attempt was made to study the effect of climatic factors on female diurnal activity.

# II - REVIEW OF LITERATURE

## 1.0 ECONOMIC AND MEDICAL IMPORTANCE

Tabanids have an economic and medical impact on humans and livestock. In New York State as a whole tabanids ranked second only to mosquitoes as annoying pests of domestic and wild animals (Pechuman 1981). In Canada, the economic impact of biting flies of livestock, in terms of non-realized animal production, has been estimated to be $104 million per year (Laird *et al.* 1979). Females of many species are mammalian blood feeders. They usually feed on cattle (Shemanchuck 1978; Magnarelli and Anderson 1980a; Lewis and Leprince 1981; Lane and Anderson 1982), horses (Magnarelli and Pechuman 1975; Magnarelli and Anderson 1980a; Pechuman 1981) and other mammals (Smith *et al.* 1970; Magnarelli and Anderson 1980a; Lane and Anderson 1982). Most species prefer landing and feeding sites on cattle (Mullens and Gerhardt 1979; Magnarelli and Anderson 1980a).

Medically important animal disease agents (viruses, bacteria, protozoa and helminths) transmitted by horse flies and deer flies were reviewed by Krinsky (1976). In Wisconsin, DeFoliart *et al.* (1969) isolated Jamestone Canyon serotype (California group) from 1 pool of *Hybomitra lasiophthalma* (Macquart) and 1 pool of *Chrysops cincticornis* Walker. In west central Wisconsin, Wright *et al.* (1970) isolated LaCrosse virus (California group) from 3 pools of *H. lasiophthalma*. Recently Miller *et al.* (1983) found no replication of Jamestown Canyon and Keystone (California group) viruses after inoculation in 4 species of tabanids. They concluded that other members of the family should not be ruled out as reservoirs or vectors of California group viruses on the basis of their experiment. According to the small number of viral isolations from tabanids and their potential to mechanically transmit certain viruses for which other effective means of transmission are known, Krinsky (1976) suggested that tabanids play a minor role in the transmission of viruses but may increase the size of epizootics in localized situations in which large numbers of acutely infected animals are in proximity to suceptible hosts.

## 2.0 QUEBEC LITERATURE

There are approximately 132 species of tabanids known to occur in Canada (Teskey 1979). Before 1981, published information on the tabanids of Quebec consisted of lists of species (Winn and Beaulieu 1932; Freeman 1953; Philip 1962; Pechuman 1964; Thomas 1980), outdated systematic studies (Chagnon and Fournier 1943) and brief notes on the seasonal distribution of some species in the Laurentians (Robert 1958). In their study of latitudinal distribution of the Quebec tabanid fauna, Baribeau and Maire (1983a) critically reviewed the literature published on Quebec tabanids. They reported the presence of 82 species in six genera: *Chrysops* (31 species), *Hybomitra* (28 species), *Tabanus* (15 species), *Atylotus* (5 species), *Stonemyia* (2 species) and *Haematopota* (1 species).

Recently, there has been a renewed interest in this group of biting flies. Lewis and Leprince (1981) studied tabanids feeding on cattle in southwestern Quebec. Several studies considered the abundance and seasonal distribution of tabanids in temperate and subartic Quebec localities (Leprince and Lewis 1982; Baribeau and Maire 1983b, 1983c; Thibault and Harper 1983). Baribeau and Maire (1983b) also studied the spatial distribution and larval density of tabanids in two southern Quebec bogs and Thibault and Harper (1983) gave an account of the activity and habitat preferences of adult tabanids. Leprince and Lewis (1983) studied aspects of the biology of *Chrysops univittatus* Macquart including parity rates, sugar feeding, sperm presence and potential fecundity as determined by the number of ovarioles.

## 3.0 MALE BIOLOGY

There is little information available on the biology of male tabanids. Males are rarely collected because they do not feed on blood and most trapping methods are designed to collect host-seeking females. Males feed on nectar [65% of males collected in West Germany contained nectar sugars (Kniepert 1980)]. Two main types of male tabanid behavior have been associated with mating: hovering (Bailey 1948; Blickle 1959) and waiting (Catts and Olkowski 1972). In both types of behaviors males share common characteristics: they are motionless with respect to their environment (hovering males remain stationary in the air, waiting males on a substratum) and they are alert to movement near them and usually respond by active flight pursuit.

In North America, aggregation of 5 species of male tabanids on hilltops in Nevada has been recorded by Chapman (1954). Downes (1969) suggested that the silhouette of the hill served as an optical marker and that insects oriented to it and were finally led to the peak itself.

## 4.0 FEMALE

## 4.1 REPRODUCTIVE SYSTEM

The reproductive system of female tabanids consists of 2 ovaries, an oviduct, a vagina, 3 spermathecae and 2 accessory glands (Surcouf 1908). Spermathecae are long and bent in their middle, their apex is located near their base. Inside each ovary there is an internal oviduct into which ovarioles run radially. The number of ovarioles is not constant for one species (Leprince and Lewis 1983). Each ovariole consists of a growth zone or germarium, situated in its proximal portion; and in the case of gonoactive females there are usually 2 follicles. The follicle lying nearest to the oviduct will develop completely after a blood meal.

## 4.2 FOLLICLE DEVELOPMENT

A follicle contains an oocyte and 7 nurse cells which are of the polycentropic type. Each follicle is surrounded by a follicular epithelium, which is formed when the follicle comes away from the germarium. The developing follicle passes through a number of phases described by Christophers (1911) and Mer (1936). The stages are classified according to the following characteristics: (N)-a follicle consisting of 8 undifferentiated cells. The follicle is sperical and the follicular cells compose a regular cubical epithelium. (I)-1 oocyte, situated in the distal portion of the follicle, is clearly visible. Above the oocyte lie 7 nurse cells. The follicle either retains its spherical shape or becomes slightly oval. (I-II)-a crown of 1 or 2 rows of yolk granules appears around the nucleus in the oocyte protoplasm. The follicle takes on an oval shape. (II)-larger and more numerous yolk granules are seen in the protoplasm of the oocyte around the egg. The egg grows, becomes considerably larger than the nurse cells and takes up about half the follicle. (III)-the egg gradually increases its share of the follicle space from one half to three-quarters. Its nucleus is no longer visible through the mass of yolk. The follicle becomes somewhat elongated. (IV)-the follicle becomes longer and the nurse cells occupy only the uppermost part of it. The oogonium, full of yolk, is well developed and occupies more than nine-tenths of the follicle. (V)-the chorion covers the whole egg. The remains of the nurse cells are found at the proximal end of the follicle. The egg is now ready for laying.

## 4.3 AGE GRADING

Female tabanids that have not laid eggs (nulliparous flies or nullipars) may be distinguished from those that have oviposited (parous flies or pars) by having retained eggs in one or both ovaries, expended ovarioles containing follicular debris, or by the presence of dilatations in

contracted ovarioles. Polovodova's (1949 in: Detinova 1962) technique of counting the number of ovariole dilatations, each of which corresponds to a previous oviposition, is the best available for determining the number of ovarian cycles completed by flies.

Some tabanids produce their first batch of eggs and sometimes a second without a blood meal (Lane and Anderson 1983); others require a full blood meal prior to oviposition. Roubaud (1929) proposed the term "autogeny" to denote egg production by mosquitoes that had not fed upon blood, while "anautogeny" was applied to the more common obligate requirement of vertebrate hosts. Spielman (1971) proposed a broader definition to include other insects as nonhematophagous species; thus "anautogeny" denotes a situation wherein there is a specific food mediated arrest, and "autogeny" the absence of such a diapause.

## 4.4 SPERM PRESENCE

Lane and Anderson (1982) reported that mating preceded blood feeding in *Chrysops hirsuticallus* Philip based on sperm presence in 17 host-seeking nullipars. From the dissection of 293 specimens, Lutta (1970 in Chvala *et al.* 1972) observed that 99.9% of females contained sperm and concluded that females only seek blood after mating. Leprince and Lewis (1983) observed that 96% of the nullipars and pars of *C. univittatus* were mated. They suggested that mating generally occurs prior to host-seeking in nullipars and that enough sperm are contained in parous flies for a second gonbtrophic cycle.

## 4.5 SUGAR AND BLOOD FEEDING

Like the mosquito *Culiseta inornata* (Williston) (Friend 1978, 1981), female *Tabanus nigrovittatus* Macquart displays 3 modes of feeding in the laboratory: (1) a drinking mode where a small quantity of water goes to the midgut, (2) a nectar or sugar-feeding mode in which a large quantity of sugar solution is directed to the crop, and (3) a blood feeding mode where a large quantity of blood or diet containing an appropriate phagostimulant is sent to the midgut (Friend and Stoffolano 1984). A previous meal of sugar or blood does not prevent immediate feeding on the other substance (Stoffolano 1983).

In southwestern Quebec, the incidence of sugar positivity was 90% in blood-feeding tabanids (Lewis and Leprince 1981), and 75% in both nullipars and pars of *C. univittatus* (Leprince and Lewis 1983). In Connecticut, prevalence of sugar positivity was 71% in nullipars and 72% in parous tabanids (Magnarelli and Anderson 1981). In West-Germany, 53% of the females were sugar positive (Kniepert 1980).

Incidence of partial blood meals reported in tabanids from previous studies varied from 2 to 10 %: 5.9% by Bosler and Hansens (1974), 2% by Magnarelli (1976), 10% by Magnarelli and Anderson (1980a), 9% by Kniepert (1980), and 10% by Lane and Anderson (1982).

## 4.6 TRAPPING

Various trapping methods have been used to collect tabanids. Host-seeking female tabanids have been collected on live animals or in animal bait-traps (Tashiro and Schwardt 1949, 1953; Roberts 1965, 1969, 1972a; Thompson and Pechuman 1970; Smith *et al.* 1970; Lewis and Bennett 1977; Shemanchuk 1978; Mullens and Gerhardt 1979; Magnarelli and Anderson 1980a; Lewis and Leprince 1981). In human bait studies, the human bait uses an aerial sweep net to collect tabanids as they fly around the bait (Thompson 1967, 1969; Smith *et al.* 1970; Troubridge and Davies 1975; Lewis and Bennett 1977; Thibault and Harper 1983). Chrysopsinae are known to be more attracted to humans, Tabaninae generally prefer larger hosts (Thompson 1969; Smith *et al.* 1970). Aerial sweep net collections are made manually and are necessarily employed during shorter periods, nevertheless this method is efficient,

mobile and gives a good representation of the Chrysopsinae (Thompson 1969).

Malaise traps are often used to collect male and female tabanids. The Malaise trap operates on the assumption that flying insects blunder or wander into the structure, are stopped by the internal baffle, and work upward into the collection apparatus as they attempt to extricate themselves (Townes 1962). Roberts (1970) showed that the entrance of tabanids in different Malaise traps was not correlated with the size of the traps as a result of wandering but with the color and reflectance of the trap from the background. Roberts (1972b) compared the effectiveness of several types of Malaise traps for the collection of tabanids, he reported that the Stoneville Malaise trap with natural saran screen was the most effective; its efficiency was increased by 3-fold when a 23 cm-diameter plastic decoy painted with black acrylic paint was added to it. Tabanids, which are most active in bright sunlight, are attracted by the reflectance of a glossy black sphere; this sphere has become an integral part of many tabanid traps including the Manitoba trap (Thorsteinson *et al.* 1965). Roberts (1976) compared the efficiency of 6 traps types (Stoneville Malaise trap, Canopy trap, modified Canopy trap, California Malaise trap, Plexiglass trap and Manning trap) and reported carbon dioxide baited Canopy traps second after carbon dioxide Stoneville Malaise trap. Although highly efficient, Malaise traps are expensive, difficult to built, bulky and not easily transported. Canopy traps are inexpensive, easy to build, set up and transport by one person. Like Malaise traps, Canopy traps are continuously self operating during tabanid activity. According to Pechuman (1981), the Canopy trap is less effective in attracting Chrysopsinae than Tabaninae and rarely collects male specimens.

The release of 4.0 l/min of carbon dioxide was shown to increase the catch of tabanids by 13-fold in Malaise traps (Roberts 1975). The attraction of tabanids to carbon dioxide varied with the amount released per minute (Roberts 1975), trap type (Roberts 1976), trap location, species and date of collection (Roberts 1971). Roberts (1970) suggested that tabanid females use carbon dioxide in host location.

## 4.7 DIURNAL ACTIVITY

In New York State, Tashiro and Schwardt (1949) found little biting activity of tabanids below 22.2°C and above 32.2°C and Miller (1951) showed that among Canadian prairie species maximum activity occurred between 20°C and 22.8°C. In California, Anderson *et al.* (1975) observed that daily host-seeking activity was suppressed below 23.9°C and above 32.2°C; normal host-seeking times for most species were markedly altered on days with maximum temperatures above 32.2°C. In temperate regions of Quebec, the average maximum air temperature was above 20°C during tabanid activity (Baribeau and Maire 1983c); Thibault and Harper (1983) observed little activity when maximum daily temperatures failed to reach 21°C. In subartic Quebec, tabanids were collected when the daily maximum temperature was above 13°C (Baribeau and Maire 1983c).

Diurnal activity of female tabanids has been studied in relation to several meteorological factors (temperature, solar radiation, relative humidity, barometric pressure, wind velocity, cloud cover, etc.) by multivariate analysis in Alabama (Daie and Axtell 1975; Burnett and Hays 1974) and in South Carolina (Alverson and Noblet 1977). Factors of greatest influence varied between the 3 studies. Alverson and Noblet (1977) concluded that differences presented in the 3 models suggested that the effects may be dependant upon trap type, location or the species sampled.

## 4.8 PARASITISM

Several larval and pupal parasites have been recorded from Canadian tabanids; a tachinid [*Carinosillus tabanivorus* (Hall)] (Teskey 1969; James 1963), a bombyliid [*Villa lateralis* Say] (Teskey 1969), a

nematode [*Bathymermis* sp.] (James 1963) and 2 gregarious hymenopteran parasites: a pteromalid [*Diglochis occidentalis* (Ashmead)] and a diapriid [*Trichopria* spp.] (Cameron 1926; Miller 1951; James 1963; Teskey 1969). Parasitism of tabanid immatures has been estimated to be 2% by Teskey (1969) after rearing several hundred larvae to adults.

# III AGGREGATION OF TABANID MALES ON A MOUNTAIN SUMMIT IN SOUTHWESTERN QUEBEC

## 1.0 INTRODUCTION

An aggregation site of male tabanids was discovered on a mountain summit in southwestern Quebec. Studies were conducted to observe the behavior of male tabanids, to describe their seasonal distribution, to determine the effect of climatic factors on their activity, to estimate the rate of nectar feeding, and to identify the species of flowering plants visited.

## 2.0 MATERIALS AND METHODS

### 2.1 SAMPLING SITE AND COLLECTION OF SPECIMENS

Mount Rigaud (45°27'N, 74°18'W), located near the community of Rigaud in southwestern Quebec, is 220 m above sea level. Rigaud River, a suspected tabanid breeding site, is approximately 800 m from the mountain. The summit of the mountain consists mainly of exposed rocks interspersed with herbaceous and shrubby vegetation. The highest point is an oak tree (*Quercus rubra* L.) 3-4 m high. The area was visited at least 1 day each week from early June to late August 1981 between 0700 and 1400 h, and occasionally until 1700 h (eastern standard time). Every half hour tabanids were collected with an insect net in the vicinity of the oak tree and along a rocky path (100 m long) leading to the summit. Waiting males were swept from the foliage, and hovering males were caught by placing the net under them at a hovering station and moving it quickly upward. Occasionally females were collected as they landed on the investigator or in tandem with males.

Specimens were placed in vials and frozen on ice packs in the field; they were later stored at -20°C in the laboratory. Observations on behavior and the time of collection were recorded for each specimen. A sling psychrometer was used every hour to measure air temperature and relative humidity (RH); measurements were made 1 m above ground near the oak tree.

Specimens have been deposited in the Lyman Entomological Museum of McGill University.

### 2.2 DISSECTION

Male tabanids were dissected within 3 weeks of collection. The tip and the side of the tabanid abdomen were cut with fine scissors, and internal structures were pulled out with a pair of fine forceps and placed in a drop of saline solution on a microscopic slide for examination. Fat body was qualitatively assessed, and considered abundant when it was one of the most prominent internal structures. The presence of endoparasites was recorded.

### 2.3 NECTAR DETECTION AND POLLEN ANALYSIS

Fructose and sucrose were detected by an anthrone test, which was modified from that of Van Handel (1972). Diverticula were placed into wells on a ceramic spot plate, and 0.25-ml aliquot of cold anthrone reagent was added to each well. Results of reagent activity were recorded within 30 minutes.

Pollen analyses were performed on 22 *Hybomitra sodalis* males collected between 28 June and 30 August 1981. Due to the amount of work involved, only one species was selected for pollen analysis. Specimens retained for pollen analysis were first screened with a dissecting stereomicroscope at 70X for various pollen types to obtain a complete spectrum of the flowers visited. One cubic millimetre of cold glycerin-gelatin (1.5 ml of alcoholic solution of basic fushin 0.1% in 10 ml of glycerin-gelatin) was placed on the tip of a pin and pressed on the specimens to collect pollen. The cube was then melted on

a slide, covered with a cover slip, luted with paraffin, and sealed with synthetic resin. Up to 500 pollen grains were identified from each specimen by using a reference collection located in the Laboratoire de Paléobiogéographie et de Palinologie, Université de Montréal.

## 2.4 LONGEVITY STUDIES

Twenty males each of *Hybomitra affinis* and *H. sodalis* (collected during the 1st week of their flight period) were individually placed in 500-ml plastic containers with a mesh screen on top and maintained at 24°C, 70% RH, and 12 h of light per day in an incubator.

Specimens were divided equally between control and treatment containers. Each control container had 2 vials of distilled water, and each treatment container had a vial of distilled water and a vial of 10% sucrose solution. The time of death of each specimen was recorded.

# 3.0 RESULTS

## 3.1 SEASONAL DISTRIBUTION

Males of 17 species of *Chrysops*, *Hybomitra*, and *Tabanus* were collected on the summit of Mount Rigaud. The seasonal distribution of all adult tabanids collected on the summit from 1978 to 1981 is presented in Fig. 1. The seasonal distribution of females was also included to give an overall view of the species frequenting the summit; males of some species were not collected. Male flight activity extended from late May to late August, reaching its greatest diversity in mid-June. Males of *C. cincticornis*, *H. affinis*, *H. lasiophthalma*, *H. microcephala*, and *T. reinwardtii* were present, when conditions were suitable, for more than 40 days. Males were more abundant and usually had a longer seasonal distribution than females of the same species. Mated couples of *C. mitis*, *H. affinis*, *H. lasiophthalma*, *H. nuda*, *H. microcephala*, and *T. similis* were collected at the beginning of their seasonal flight activity. No males were collected on a nearby summit (2 km from the Rigaud River) on days when conditions were favorable for male activity.

## 3.2 MALE BEHAVIOR

Waiting species comprised all *Chrysops*, and *H. microcephala* males (Table 1), which spent a considerable proportion of time on vegetation. They were observed chasing other flies (the more individuals, the more time spent chasing). Most *C. mitis* and *C. cincticornis* males were collected on small shrubs (*Vaccinium* spp., *Amelanchier* sp., and *Rhus typhina*). The remaining specimens of *Chrysops* and half of the *H. microcephala* males were usually collected as they waited on foliage of the oak tree. The other half of the *H. microcephala* males were collected as they landed on the outstretched white net. These were collected only when the collector faced the sun and the oak tree and quickly moved the net back and forth at the level of the upper oak foliage. Usually when the net stopped, 1 *H. microcephala* male flew from the oak foliage to land on the net. *Hybomitra microcephala* males also were collected in the forest well below the summit, waiting on the ground in sunlit patches; these males did not morphologically differ from those collected on the summit of the mountain. *Tabanus catenatus* and *T. reinwardtii* males were collected while resting on rocky surfaces or tree bark exposed to sunlight at the summit. It was uncertain whether they were warming up or exhibiting waiting behavior. Lavigne *et al.* (1968) reported that male *T. reinwardtii* rested on a sunlit exposed drainage pipe and rocks to warm up before chasing each other in rapid flight.

Hovering species included all *Hybomitra* except *H. microcephala* (Table 1). Although clearly viewed while hovering, their pursuit flight speed was too great to be observed by the human eye. Hovering males were divided into 2 groups depending

on their hovering site; *H. lasiophthalma* hovered above the oak tree, while *H. affinis*, *H. lurida*, *H. nuda*, and *H. sodalis* hovered near the ground. Species hovering near the ground were found along the rocky path leading to the summit, or in depressions such as those between clumps of shrubs. No hovering markers were detected on the summit, even though different specimens and species were collected at specific hovering stations that share a "U" shape (0.5 to 3 m wide). The orientation of the flies was parallel to the path, facing the wind on windy days; or either downhill or uphill on calm days. Males hovered parallel to the ground along the path, moved back and forth 1 to 6 m depending on male density, and returned to their hovering stations. The hovering height was usually a few cm above the surrounding vegetation (0.5 m). After being missed by the net, disturbed males would disappear and then shortly return to the same hovering station.

As many as 5 males of *H. nuda* hovered along the same path coincidentally maintaining an interval of 1 m between each other. They moved as a group slowly back and forth depending on the wind. Whenever one began to chase another insect, others followed; they chased each other for a few seconds, then resumed their stationary hovering. Contact between flies was audible.

## 3.3 EFFECT OF CLIMATIC FACTORS ON MALE BEHAVIOR

A summary of male activity as related to air temperature, RH and hour of day is presented in Table 2. Flies were present during bright and sunny periods; none were seen during cloudy periods. Male flight activity ceased when clouds interfered with sunlight or was delayed on cloudy mornings until the sky cleared. On partly cloudy days, the hovering behavior of tabanid males was several times turned on and off by passing clouds. Except for *H. nuda*, which was still flying at 1700 h, most male flight activity terminated around 1400 h. On sunny mornings, most *Chrysops* and *Tabanus* males were collected before 1000 h. Flight activity did not appear to be influenced by RH, however, it was affected by wind. Waiting males preferred areas of tree foliage or other vegetation that were protected from the wind, while hovering males adjusted their flight height inversely to wind strength (10 to 15 cm above ground during strong winds versus 1.5 m during calm periods at the same hovering site).

No intraspecific competition was observed at a hovering station, but with an increasing density of males there was a decreasing area available to each male which restricted their horizontal movements. The potential for interspecific competition among males of *H. affinis*, *H. nuda* and *H. sodalis* could be expected since they share the same hovering station and peak temperature activity (Table 2). Because *H. nuda* is an early season tabanid, there is little competition with the other species, but males of *H. affinis* and *H. sodalis* have similar seasonal distributions (Fig. 2); males of the former species are larger than those of the latter, are active at lower temperatures (Table 2), and are not displaced by *H. sodalis* males.

## 3.4 NECTAR FEEDING AND LONGEVITY

The prevalence of anthrone positive tabanids was 73% (Table 1), with 84% in hovering flies and 43% in waiting flies. The percentage of specimens with abundant fat body was almost the same in hovering and waiting flies (Table 1), indicating that differences in anthrone positivity could be related to behavior.

Under laboratory conditions, *H. affinis* and *H. sodalis* males maintained on a 10% sucrose diet lived 12.1 $\pm$ 3.41 ($\bar{X} \pm$ SD) and 8.5 $\pm$ 4.3 days, respectively; those maintained on water only lived 1.5 $\pm$ 0.53 and 1.2 $\pm$ 0.42 days, respectively.

### 3.5 POLLEN SPECTRUM ON *H. sodalis*

The pollen spectrum on *H. sodalis* is presented in Table 3; some pollen could not be identified beyond family level. The most common and abundant pollen or pollinia present on these flies were *Asclepias syriaca, Chrysanthemum leucanthemum* type, *Cirsium* sp., Umbelliferae, *Rhus typhina, Rumex* type, *Spiraea latifolia* and *Tilia americana*. All these nectariferous plants have large inflorescences, which are probably used as landing platforms by male tabanids. Nearly 40% of all *H. sodalis* males caught had pollinia, specimens had from 1-12 pollinia, with a mean of 4 per fly. The pollen spectrum of *H. sodalis* males changed during the season according to the seasonal succession of flowers, and each fly had its own pollen spectrum.

### 3.6 INTERSPECIFIC MATING

A male of *C. niger* was captured in copula with a female of *C. mitis* in late June. They were placed in a vial where they remained in copula even after freezing. The female was nulliparous; sperm were found in her genital chamber.

### 3.7 PREDATION AND PARASITISM

A *Vespula maculata* (L.) (Hymenoptera: Vespidae) female captured a male of *C. callidus* resting on the top foliage of the oak tree at 0900 h in late June when the temperature was 15.6°C. Even though they were immediately collected, half of the deer fly's head had already been consumed. An *Asilus* (*Machimus*) sp. (Diptera: Asilidae) female was collected after it caught a *C. cincticornis* female in flight at 0930 h in late July when the temperature was 17.7°C. The prey was punctured in the thorax.

Encysted parasites thought to be hymenopteran were found in the abdomen of 5 males of *H. nuda*, 3 *H. lasiophthalma* and 1 *H. affinis*. The number of endoparasites varied from 1 to 6. They were usually coiled around 1 Malpighian tubule of their host, in which a variable degree of degeneration was observed. No apparent damage was done to the reproductive system. Since all endoparasites were keratinized and melanized, they were probably acquired before the adult stage.

## 4.0 DISCUSSION

The proximity of a breeding site might be an important factor in the determination of a hilltop male tabanid aggregation site since no males were collected on a nearby summit 2 km from the Rigaud River. In the search for an aggregation site, preference should be given to bare or exposed hilltops since sunlight is an important factor in tabanid activity.

According to Wellington (1974), overhead polarization is strongest near sunrise and sunset and weakest near noon; it may also be eliminated at any time by a patch of thick clouds drifting across the zenith. Blickle (1959) and Catts and Olkowski (1972) found no correlation between the start of male activity and light intensity and stated that temperature was the main factor influencing the beginning of male flight activity. Since there was no flight activity on top of Mount Rigaud on cloudy days and since such behavior was delayed on cloudy mornings or stopped momentarily by a passing cloud when temperature was suitable, polarized light may well influence male tabanid activity.

The rate of anthrone positivity (73%, Table 1) was similar to the figure (69%) reported by Kniepert (1980) in West Germany. The presence of fructose and sucrose in the diverticula of tabanids was first considered to be in relation with fat body depletion. The percentage of specimens with abundant fat body was almost the same in hovering (54%) and in waiting (58%) specimens (Table 1). The high incidence of anthrone positive flies in hovering specimens probably reflects a greater storage of fuel energy and perhaps

a greater incidence of carbohydrate meals in order to fulfill the energy requirements of this behavior. The high incidence of nectar feeding and the short life span of tabanid males without sugar suggests that floral nectars or other sources of carbohydrates are used for survival and flight activity. Magnarelli and Anderson (1981) also reported a relatively high incidence of sugar feeding by female tabanids and suggested that these carbohydrates are important dietary nutrients.

Most pollen identified are not carried by wind and can only be acquired by visits to the flowers. In their search for nectar, *H. sodalis* males are probably opportunistic in their visit to the flowers. Most abundant pollen or pollenia probably reflect that more time was spent by males *H. sodalis* on their respective flowers. It is unknown whether these flowers were more nectar rewarding or more abundant in the field. Further studies comparing the pollen found in diverticula (where the nectar meal is stored) with the pollen found on the fly would help to define the flowers visited versus the ones providing nectar.

In Delaware, Catts and Olkowski (1972) explained the interspecific mating between a male of *C. fuliginosus* and a female of *C. atlanticus* by a seasonal and microclimate overlap in the 2 populations, particularly a delayed male *C. fuliginosus* migration into the *C. atlanticus* mating area. Since *C. niger* apparently transferred sperm to *C. mitis*, it seems that specific sexual recognition failed between these individuals.

Hines (1906) reported that predation of *Vespula maculata* on both sexes of *T. sulcifrons* Macquart was common, and Blickle (1959) suggested that *Bembix belfragei* Cresson, a predatory wasp, may have contributed to the decrease of the male population of *T. bishoppi*. Based on hundreds of hours of observations, the low numbers of asilids and yellowjacket wasps on top of Mount Rigaud and their lack of host specificity, it is unlikely that these predators significantly reduce male tabanid populations at the aggregation site.

The presence of encysted endoparasites indicates that some tabanids can harbor a small number of them and survive.

Figure 1. Seasonal succession of tabanids collected on the summit of Mount Rigaud, Quebec, 1978-1981

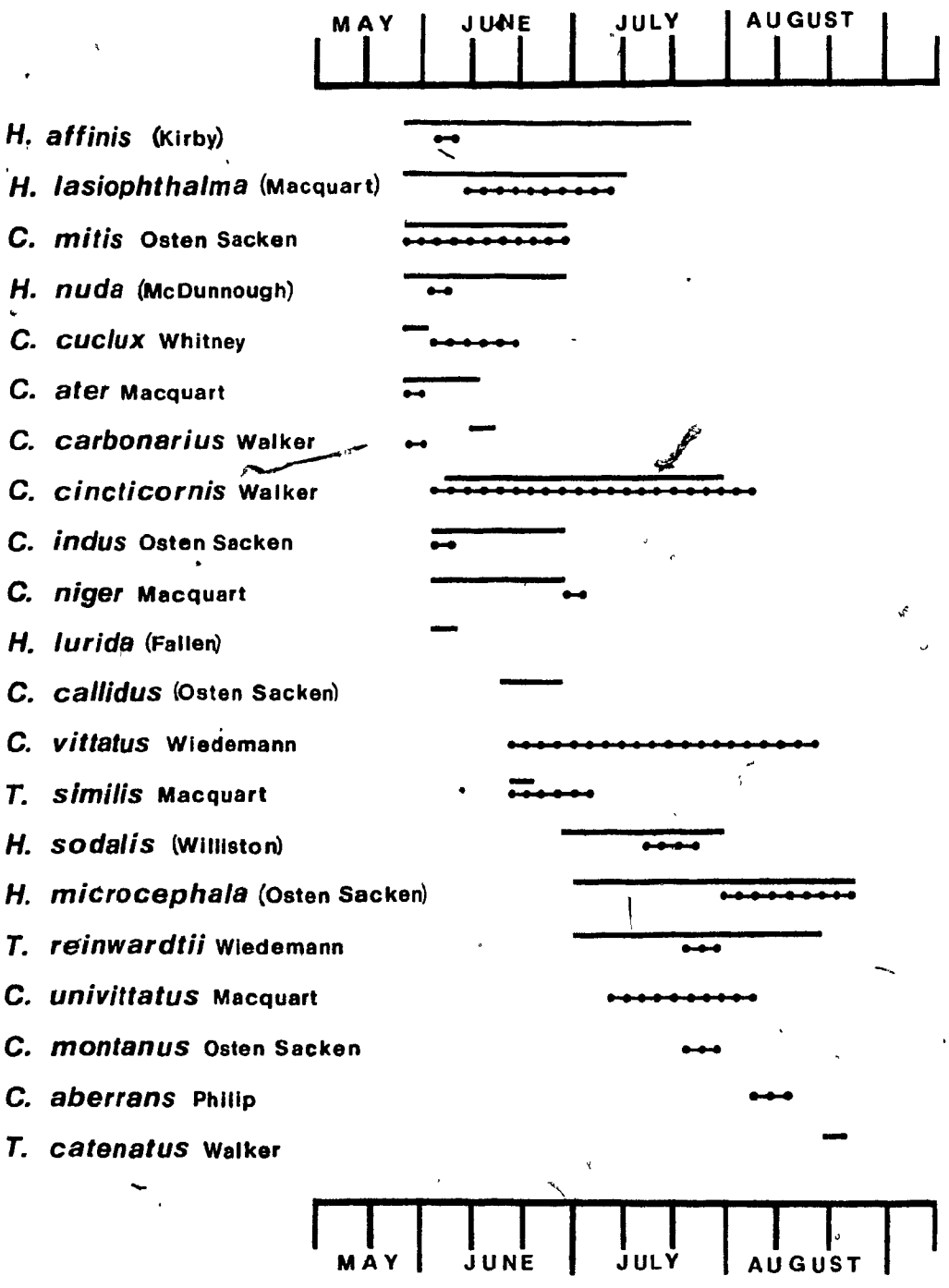
MAY
JUNE
JULY
AUGUST
H. affinis (Kirby)
H. lasiophthalma (Macquart)
C. mitis Osten Sacken
H. nuda (McDunnough)
C. cuclux Whitney
C. ater Macquart
C. carbonarius Walker
C. cincticornis Walker
C. indus Osten Sacken
C. niger Macquart
H. lurida (Fallen)
C. callidus (Osten Sacken)
C. vittatus Wiedemann
T. similis Macquart
H. sodalis (Williston)
H. microcephala (Osten Sacken)
T. reinwardtii Wiedemann
C. univittatus Macquart
C. montanus Osten Sacken
C. aberrans Philip
T. catenatus Walker
MAY
JUNE
JULY
AUGUST
MALES
FEMALES

Table 1. Incidence of nectar feeding, as detected by the cold anthrone test, and abundance of fat body in male tabanids collected on Mount Rigaud, Quebec, 1981

| Behavior | Species | # | At+ | Fb+ |
|---|---|---|---|---|
| Waiting | *C. callidus* | 6 | 33 | 50 |
| | *C. cincticornis* | 12 | 42 | 33 |
| | *C. indus* | 9 | 44 | 33 |
| | *C. mitis* | 6 | 17 | 33 |
| | *C. niger* | 10 | 80 | 0 |
| | *H. microcephala* | 64 | 38 | 80 |
| | *T. catenatus* | 1 | 100 | 100 |
| | *T. reinwardtii* | 5 | 80 | 40 |
| Subtotal | | 113 | 43 | 58 |
| Hovering | *H. affinis* | 35 | 91 | 51 |
| | *H. lasiophthalma* | 82 | 74 | 77 |
| | *H. lurida* | 2 | 100 | 100 |
| | *H. nuda* | 124 | 85 | 44 |
| | *H. sodalis* | 56 | 89 | 39 |
| Subtotal | | 299 | 84 | 54 |
| Total | | 412 | 73 | 55 |

\# Number of specimens analysed

At+ Percentage of anthrone positive specimens

Fb+ Percentage of specimens with abundant fat body.

Table 2. Prevailing atmospheric conditions during male tabanid activity on the summit of Mount Rigaud, Quebec, 1981

| Species | # | h | RH (%) | Temperature (°C) | |
|---|---|---|---|---|---|
| | | | | Range | Peak |
| *C. callidus* | 6 | 0700-0900 | 58-74 | 15.6-17.2 | |
| *C. cincticornis* | 12 | 0700-0830 | 46-74 | 13.9-19.4 | |
| *C. undus* | 6 | 0630-1100 | 35-60 | 15.6-16.7 | |
| *C. mitis* | 7 | 0700-0900 | 55-84 | 12.7-16.1 | |
| *C. niger* | 9 | 0630-1100 | 35-58 | 15.6-20.0 | |
| *H. affinis* | 54 | 0700-1430 | 37-91 | 13.9-29.4 | 23.9-28.9 |
| *H. lasiophthalma* | 82 | 0700-1130 | 35-74 | 13.9-21.7 | 15.0-20.0 |
| *H. lurida* | 2 | 1000-1030 | 48 | 21.1 | |
| *H. microcephala* | 64 | 0800-1300 | 31-74 | 16.1-25.0 | 18.3-23.3 |
| *H. nuda* | 123 | 0800-1600 | 33-57 | 16.7-28.3 | 23.9-28.3 |
| *H. sodalis* | 76 | 0700-1300 | 33-91 | 18.3-28.9 | 23.9-28.9 |
| *T. catenatus* | 1 | 0730-0800 | 63 | 15.0 | |
| *T. reinwardtii* | 5 | 0700-0930 | 46-80 | 15.0-19.4 | |

\# Number of specimens collected

h Eastern standard time

RH Relative humidity

Table 3. Pollen spectrum for 22 *Hybomitra sodalis* males collected from 28 June to 30 July 1981 from Mount Rigaud, Quebec

| | |
|---|---|
| Asclepiadaceae | *Asclepias syriaca** |
| Anacardiaceae | *Rhus typhina** |
| Butomaceae | *Butomus ombellatus* |
| Caryophyllacea | |
| Compositae | *Ambrosia* sp. |
| | *Artemisia* sp. |
| | *Cirsium* sp.* |
| | *Chrysanthemum leucanthemum* type* |
| | *Solidago* type |
| | *Taraxacum officinale* type |
| Corylacea | *Betula* sp. |
| | *Corylus cornuta* |
| Cruciferae | *Brassica kaber* |
| | others |
| Cyperaceae | |
| Graminaeae | |
| Guttiferae | *Hypericum perforatum* |
| Leguminosae | *Melilotus* sp. |
| | *Trifolium hybridum* |
| Labiatae | *Mentha* type |
| Umbelliferae* | |
| Pinaceae | *Picea mariana* |
| | *Pinus* sp. |
| | *Pinus divaricata* |
| | *Thuja occidentalis* |
| Plantaginaceae | *Plantago* sp. |
| Polygonaceae | *Fagopyrum saggittatum* |
| | *Rumex acetosella* |
| | *Rumex* type |
| Ranunculaceae | *Caltha palustris* type |
| | *Ranunculus acris* |
| | *Thalictrum* |
| Rosacea | *Potentilla* sp. |
| | *Spiraea latifolia** |
| | others |
| Salicaceae | *Salix* sp. |
| Tiliacea | *Tilia americana** |
| Typhaceae | *Typha* type |

* most common pollen or pollinia

# IV ASPECTS OF THE BIOLOGY OF FEMALE TABANIDS IN SOUTHWESTERN QUEBEC

## 1.0 INTRODUCTION

The purpose of this investigation was to determine the seasonal distribution and relative abundance of female horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec, the incidence of insemination, and sugar meals (as detected by the cold anthrone test), the influence of dry-ice baited and unbaited Canopy traps on parous females and the variation of climatic factors during female activity. Assessment of potential fecundity, as determined by the number of ovarioles, was performed on *Tabanus* females.

## 2.0 MATERIALS AND METHODS

### 2.1 SAMPLING SITE AND COLLECTION OF SPECIMENS

The study was conducted in the Morgan Arboretum, adjacent to the farm of the Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue (45°25'N, 73°56'W), Quebec, from early June to early September in 1980 and 1981. Most specimens were collected in unbaited and dry-ice baited canopy traps (Catts 1970); some were also collected with an insect net as they flew around the investigator. Six sampling stations were used in 1980 (Fig. 2). In 1981, only stations 1 to 4 were sampled; stations 5 and 6 were not used because of their low productivity in 1980. Half the stations were baited with 10 kg of dry-ice placed at the base of the trap; the release rate of carbon dioxide varied between 4.0-8.0 l/min. Carbon dioxide-baited stations were selected at random every week. In 1980, 23 heifers were kept in pastures around Stoneycroft Pond (Fig. 2), and 21 in 1981. Herbaceous areas were cut twice in 1980 but only once in 1981.

The area was sampled weekly on sunny days conducive to tabanid flight activity. Traps were set from 0700 to 2100 h (eastern standard time). Specimens were collected hourly, placed in a vial and frozen on ice-packs in the field. They were later stored at -20°C in the laboratory. A sling psychrometer was used every hour to measure air temperature and RH. Solar radiation measurements were obtained from the meteorological station Jean Brébeuf (Montréal) which is approximately 15 km from the research area. Specimens have been deposited in the Lyman Entomological Museum of McGill University.

### 2.2 DISSECTION

Dissections were performed within 3 to 30 months after capture and physiological age was determined by Polovodova's method (Detinova 1962) on the basis of the number of dilatations of ovarioles e.g. when one yellow body or one dilatation was present the fly was recorded as uniparous. The tip and the side of the abdomen were cut with fine scissors, internal structures were pulled out with a pair of fine forceps and placed in a drop of saline solution on a slide. The stage of follicular development in terminal follicles was recorded for each specimen using the classification established by Christopher (1911) and modified by Mer (1936). The diverticulum was retained for sugar analysis. The 3 spermathecae were cut and examined under a compound microscope (400X) for sperm. The presence of endoparasites was recorded.

### 2.3 INCIDENCE OF NECTAR FEEDING AND FLOWERS VISITED

Fructose and sucrose were detected by an anthrone test which was modified from that of Van Handel (1972). Diverticulae were placed into wells on a ceramic spot plate, and 0.25-ml aliquot of cold anthrone reagent was added to each well. Results of reagent activity were recorded within 30 minutes. On sampling days, flowers were

observed regularly to record those visited by tabanids.

## 2.4 FECUNDITY

Potential fecundity was determined by doubling the total number of ovarioles found in one ovary of randomly selected *Tabanus* females. Each ovary was placed in a 50% alcohol solution for a few seconds and then transferred to a saline solution where ovarioles were gently teased apart and counted. The number of ovarioles was correlated with insect body size (as measured by wing length) by a simple linear regression analysis. Wings were placed between 2 microscope slides and measured from the base of the costa to the tip of the wing.

# 3.0 RESULTS

## 3.1 SEASONAL DISTRIBUTION AND RELATIVE ABUNDANCE

Females of 14 species of horse flies (9 *Hybomitra* and 5 *Tabanus*) were collected in the Morgan Arboretum in Sainte-Anne-de-Bellevue, Quebec. Their seasonal distribution is presented in Fig. 3. and their seasonal abundance is presented in Tables 5 to 13. Male data have also been included. Horse fly activity extended from late May to early September, reaching its greatest diversity from mid-June to mid-July. In both years females of *H. epistates, H. frontalis, T. lineola* and *T. quinquevittatus* were in flight for more than 40 days; *H. lasiophthalma* and *T. similis* had similar flight periods in 1980 and 1981 respectively. According to the number of canopy traps used each year (6 in 1980, 4 in 1981), more females of *H. epistates* (Table 6), *H. microcephala* (Table 9) and *T. quinquevittatus* (Table 12) were collected in 1980 than 1981, but less females of *T. lineola* (Table 11) and *T. similis* (Table 13), and almost equal numbers of *H. frontalis* (Table 7) and *T. sodalis* (Table 10). Females of *H. lasiophthalma* and *H. nuda* might have been more abundant in 1981, but sampling started later in 1980 and a portion of the populations may not have been collected.

The relative abundance of horse flies is presented in Table 4a and 4b. More specimens belonged to *Hybomitra* (56%, n = 3418) than *Tabanus*. Three species accounted for more than 88% of the total catch: *T. quinquevittatus* (39.2%), *H. lasiophthalma* (38.6%) and *H. epistates* (10.5%). Although some species were abundant certain days, no horse flies attempted to bite humans. On rare occasions, *T. similis* and *T. quinquevittatus* landed on the collector.

Females of *H. epistates* were abundant from early June to late July (Table 6) and represented 18.7% (n = 1912, Table 4a) of the *Hybomitra* community. Females of *H. frontalis* were most abundant from mid-June to early July but were never collected in great numbers. Females of *H. lasiophthalma* were most abundant from early to late June and represented 69% (n = 1912, Table 4a) of the *Hybomitra* specimens. Females of *H. nuda*, one of the first species to appear with *H. lasiophthalma* (Fig. 3), were most abundant from late May to early June (Table 9). Females of *H. microcephala* were present from late July to late August (Table 9); they were one of the latest *Hybomitra* to fly. Females of *T. lineola* were present from mid-June to late August (Fig. 3) but were most abundant in mid-July (Table 11). Females of *T. quinquevittatus*, comprising 89% (n = 1506) of the *Tabanus* community, appeared in early July, reached maximum abundance from mid to late July, and gradually decreased in number during August and early September (Table 12). Females of *T. similis*, the second most abundant *Tabanus*, were present for a long period in both sampling years (Table 13), but very few specimens were collected on any given day. Females of *H. affinis* and *H. illota* were present in June (Fig. 3, Table 5). Females of *H. pechumani, H. sodalis, T. atratus* and *T. catenatus* were collected in July or August (Fig. 3, Tables 10 and 11).

Males were rarely collected. One anthrone negative male of *T. catenatus* was collected resting on a sandy path exposed to sunlight in a forest trail in mid-July (Station 1, Fig. 2) at 1000 h, when the temperature was 23.9 °C and RH 62%. A male of *T. atratus* was collected in late July while resting on vegetation. Eleven males of *H. lasiophthalma* were collected from early to late June. Among 9 specimens dissected, 8 were anthrone positive and all contained sperm. Most of them were collected in carbon dioxide baited canopy traps #1 and #2 (Fig. 2) between 1400-1900 h, when temperatures were 21.1-27.2 °C and RH 33-62%. Only 1 *H. lasiophthalma* was collected while hovering in a forest trail near station 1 (Fig. 2). Most males of *H. lasiophthalma* were collected in Canopy traps probably while pursuing females. Most males of *H. epistates* (n = 16) were collected approximatively 1 m from a forest margin near an open field in early July 1981; no specimens were collected in the field. Males were hovering a few cm over the surrounding vegetation (some were collected from 10 to 90 cm from the ground) 0600-0900 h when temperatures were 19.4-23.9 °C and RH 63-67%.

## 3.2 PARITY RATES

A summary of parity rates, sperm presence and anthrone positivity is presented in Table 4a and 4b. Specimens dissected represented 93% (n = 3418) of the collection. Almost 88% (n = 229) of the non-dissected females were *H. lasiophthalma* which were collected on June 13, 1981 during the peak of abundance. Almost 70% of the *Hybomitra* and *Tabanus* specimens collected were nulliparous. Generally nulliparous females appeared a week earlier than parous females of the same species. In both years, the peak of abundance of parous females of *H. epistates, H. lasiophthalma* and *T. quinquevittatus* occurred generally during the peak of nulliparous females (Tables 6, 8 and 12). Dissection revealed that only parous females were collected in the following species: *H. frontalis, H. pechumani, H. microcephala*, and *T. catenatus*. The percentage of parous females (1980,1981,1980-81) ranged between 0 to 50% and was quite variable from year to year: *H. epistates* (38,15,32), *H. illota* (0,50,43), *H. lasiophthalma* (37,20,24), *H. nuda* (40,12,15), *T. lineola* (39,44,42), *T. quinquevittatus* (31,35,32) and *T. similis* (45,17,27) (Tables 4-6, 8-13). Percentages of parity of *H. lasiophthalma* and *H. nuda* were probably overestimated in 1980 since sampling started later than 1981.

Follicle development was in stage I-II or II for most specimens dissected, it was sometimes in stage I in parous females with sac-stage ovarioles. Stage N was not seen in dissected specimens. Stage III or IV follicles were found in 6 nulliparous females with fresh or partially digested blood meals: 1 *H. epistates*, 3 *H. lasiophthalma* and 2 *T. quinquevittatus*. No more than one yellow body or one dilatation was found at the base of ovarioles of all parous females dissected. Yellow bodies were sometimes of an uneven shape but only one dilatation was observed. In these cases the fly was recorded as uniparous and registered as parous.

## 3.3 OVIPOSITION

The ovarioles of some parous females had a sac-like dilatation (those with distended follicular tubules), indicating recent oviposition. Apart from *H. epistates, T. catenatus* and *T. lineola* (Table 6 and 11), percentages of parous females with sac-stage ovarioles were well over 50% each year in the remaining species (Tables 5, 7-10 and 12-13). In both sampling years, oviposition usually occurred 1 or 2 weeks after the appearance of nulliparous females of *H. epistates, T. lineola* and *T. similis* (Tables 6, 11, 13), only in 1981 in *H. lasiophthalma* and *H. nuda* (Tables 8 and 9), and in 1980 in *T. quinquevittatus* (Table 12). Oviposition occurred from the end of June to early August in *H. epistates* but most egg laying activity was concentrated in early to mid-July in 1980 and in mid-June in 1981 (Table 6). Females

of *H. frontalis* had one of the longest oviposition periods in both sampling years; it started in the first half of June and ended in mid-August in 1980 and late July in 1981; a peak was observed between the end of June and early July (Table 7). Females of *H. illota* oviposited in mid-June and *H. nuda* laid eggs during early to late June (Tables 5 and 9). Oviposition extended from early June to mid-July in *H. lasiophthalma*, but was concentrated mainly in June (Table 8). Females of *H. microcephala* layed eggs in late July till mid-August in 1980 but only in late July in 1981 (Table 9). Oviposition of *H. pechumani* and *H. sodalis* occurred during mid to late July (Table 10). In 1981 *T. catenatus* oviposited in late July (Table 11); oviposition of *T. lineola* females lasted for 3 weeks each year, starting in mid-July in 1980 and in early July in 1981 (Table 11). Females of *T. quinquevittatus* laid eggs from mid-July to early September in 1980 and from early to late July in 1981; most egg laying activity occurred during mid-July to early August (Table 12). The oviposition period of *T. similis* extended from mid-July to late August in 1980 and from mid-June to mid-July in 1981 (Table 13).

## 3.4 EGG RETENTION

Among the parous females dissected 12% (n = 972) retained eggs; 14% (n = 487) were *Hybomitra* and 10% (n = 485) were *Tabanus* (Table 14). In 1980, 14% (n = 566) of parous females retained eggs versus 9% (n = 404) in 1981 (Table 14). Apart from *H. illota* and *H. nuda*, percentages of parous females with retained eggs were generally higher or equal in 1980 than 1981 (Table 14). Great variations were observed in 1980 (64%, n = 14) and 1981 (11%, n = 9) for *T. similis* (Table 14). Greater incidence of egg retention generally occurred after the peak of abundance of parous females. Few eggs were retained per parous females, 74% (n = 115) retained 2 eggs or less and 54% had only one.

Apart from two females of *T. quinquevittatus* (one female containing 198 eggs, the other with one ovary containing 105 eggs and the second ovary without eggs), the mean number of eggs retained per ovary (pooled data) was 0.50 ± 0.71 (n = 1 female, X ± SD) in *H. illota*, 1.38 ± 1.83 (n = 17) in *H. epistates*, 1.03 ± 1.06 (n = 16) in *H. frontalis*, 1.17 ± 1.63 (n = 26) in *H. lasiophthalma*, 0.50 ± 0.71 (n = 1) in *H. microcephala*, 2.38 ± 3.50 (n = 4) in *H. nuda*, 0.50 ± 0.71 (n = 1) in *H. sodalis*, 3.00 ± 0 (n = 1) in *T. catenatus*, 0.67 ± 0.82 (n = 3) in *T. lineola*, 2.28 ± 5.41 (n = 32) in *T. quinquevittatus* and 1.75 ± 2.40 (n = 10) in *T. similis*. The mean length of *T. quinquevittatus* eggs was 2.65 ± .08 mm (n = 23).

## 3.5 SPERM PRESENCE

Sperm were found in the spermathecae of 87% (n = 3187) of the females dissected, 94% (n = 972) in parous and 84% (n = 2215) in nulliparous females (Table 4b). Among the different species, variation in sperm presence ranged from 71 to 90% in nulliparous females (Table 4a-b; when more than 5 individuals were dissected) and from 90 to 100% in parous females. In both years, the percentage of sperm positive nulliparous females of *H. epistates*, *H. lasiophthalma* and *T. quinquevittatus* was lower but related to the percentage found in parous females (Tables 6, 8, 12). Lower percentages of sperm presence were found before the peak of seasonal abundance, and from this point percentages usually remained higher for most of the season (*H. epistates* in 1980, *H. lasiophthalma* in 1981 and *T. quinquevittatus* in 1980 and 1981) (Tables 6, 8 and 12). Some dramatic variations in the percentage of sperm positive nulliparous and parous females were noticed in both sampling years. In 1980, 83% (n = 159) of the nulliparous and 96% (n = 97) of the parous females of *H. epistates* contained sperm, versus 60% (n = 79) of the nulliparous and 64% (n = 14) of the parous females in 1981 (Table 6).

Although variable between sampling years and among species, percentages of unmated parous females were 6% (n = 972)

in 1980-81, 8% (n = 485) in *Hybomitra* and 3% (n = 485) in *Tabanus* (Table 4a-b).

Almost 85% (n = 421) of the parous and nulliparous sperm negative females were collected in carbon dioxide baited Canopy traps (Table 15). Carbon dioxide attracted a similar proportion of mated nulliparous and parous females (Table 16). Anthrone positivity was 73% (n = 368) in nulliparous and 85% (n = 53) in parous sperm negative females (Table 15). Percentages of anthrone positivity in sperm negative nullipars were generally lower (especially in the nulliparous *T. quinquevittatus* females, Table 15) than the ones found in sperm positive nulliparous females (Table 4a-b).

## 3.6 ANTHRONE POSITIVITY AND FLOWERS VISITED

Results of the anthrone test performed on the diverticula of horse flies are presented in Table 4a and 4b. Anthrone positive flies represented 86% (n = 3187) of the horse fly population, results being almost equal in the two genera (Table 4a,b). The incidence of anthrone positivity was higher in pars than nullipars of *T. quinquevittatus* in 1980 and 1981; similar rates were found between pars and nullipars of the other species (Tables 5-13). Apart from *H. sodalis* and *T. lineola*, percentages of anthrone positive nulliparous and parous flies were almost equal or greater in 1980 than 1981 (Tables 5-13); overall results being 89% (n = 1610) in 1980 and 83% (n = 1577) in 1981. Except for *T. catenatus*, anthrone positivity was well over 60% in parous and nulliparous flies.

On July 24, 1981, one female *T. quinquevittatus* was observed feeding for 5 minutes (1000 h, 26.1°C, 63% RH) on honeydew on an *Asclepias syriaca* leaf. The fly was later found covered with pollen, parous, sperm and anthrone positive. On July 11, 1981, one female of *T. quinquevittatus* was caught by a crab spider (*Misumena vatia* (Clerck), Thomisidae) at 1100 h, 28°C and RH 43% on an *Asclepias syriaca* inflorescence. The fly was visiting *Asclepias* flowers prior to capture. No other tabanids were found feeding on flowers although many were covered with pollen grains or pollinia. During July, *Asclepias syriaca* pollinia were found of 2 females *H. epistates*, 18 *T. quinquevittatus*, 2 *T. lineola* and 1 *T. similis*. All females were found to be anthrone positive, and 12 were parous. The number of pollinia ranged from 1 to 3 in *H. epistates*, from 1 to 2 in *T. quinquevittatus*, from 2 to 4 in *T. lineola* and 4 in *T. similis*. The mean number of pollinia per specimen was 1.52 ± 0.75 (X ± SD). Only 1 female of *T. quinquevittatus* had pollenia in 1980 (912 females collected), and 17 in 1981 (428 females collected).

## 3.7 BLOOD MEAL PRESENCE

Fresh, partially digested or old blood was found in 3.3% (n = 3187) of the horse flies dissected. Blood was found only in the midgut of the specimens dissected, not in the diverticula. Among the 106 specimens collected, 88% were in carbon dioxide-baited traps, 56% were parous, 96% were sperm positive and 78% were anthrone positive. In 1980 blood presence in the horse fly population was 4.4% (n = 1610); in 1981 it was 2.2% (n = 1577). Fresh blood was present in nulliparous (31%, n = 106) and parous (26%) females; old or partially digested blood was found in nulliparous (12%) and parous (30%) females. Fresh blood was found in 1 nulliparous female of *H. affinis*, 6 nulliparous and 2 parous females of *H. epistates*, 7 nulliparous and 11 parous females of *H. lasiophthalma*, 1 nulliparous female of *H. nuda*, 18 nulliparous and 14 parous females of *T. quinquevittatus* and 1 parous female of *T. similis*. Old or partially digested blood was present in 1 nulliparous and 3 parous females of *H. epistates*, 1 parous female of *H. frontalis*, 5 nulliparous and 11 parous females of *H. lasiophthalma*, 7 nulliparous and 17 parous females of *T. quinquevittatus*. Compared to the number of specimens dissected, more parous females had fresh blood in *H. lasiophthalma* (4.0%, n = 272 versus 0.8%,

n = 847 in nulliparous females) and in *T. quinquevittatus* (3.3%, n = 427 versus 2.0%, n = 906 in nulliparous females), than in *H. epistates* (1.8%, n = 111 versus 2.5%, n = 238 in nulliparous females).

## 3.8 EFFECT OF CARBON DIOXIDE

More than 85% (n = 3289) of the horse flies collected were trapped with the carbon dioxide baited Canopy traps (Table 16a-b); similar proportions were found in both genera. Except for *T. atratus*, more specimens were collected in carbon dioxide baited Canopy traps than unbaited ones.

Percentages of tabanids attracted to carbon dioxide baited Canopy traps were relatively constant from year to year and generally greater than 80% in the most abundant species: *H. epistates* (84,78,82) (1980,1981,1981-82; results derived from Table 17), *H. nuda* (80,82,82), *T. lineola* (92,97,95) and *T. quinquevittatus* (85,90,87) but more variable in *H. lasiophthalma* (79,88,86) and *T. similis* (59,81,73).

Each sampling year, a similar proportion of pars of *H. lasiophthalma* were collected in non-baited and carbon dioxide-baited Canopy traps, although more pars of *T. quinquevittatus* but less of *T. lineola* were collected in non-baited traps (Table 17). No definite trend can be given for *H. epistates*, *H. nuda* and *T. similis* because there was considerable variation in the proportion of pars from year to year in non-baited traps. From pooled data (1980-81), pars of *H. epistates* and *H. nuda* showed no preference between baited and unbaited-traps, whereas more pars of *T. similis* were present in non-baited traps (Table 17).

## 3.9 ATMOSPHERIC CONDITIONS DURING FEMALE ACTIVITY

The climatic factors observed during female horse fly activity are presented in Table 18. Horse fly females were active from 0600 to 1900 h, when solar radiation varied from 0.25 to 3.39 $MJ/m^2$, temperature ranged from 15.6 to 31.7°C and relative humidity was 33 to 91%. Few specimens were collected when temperatures were below 20°C; no activity was detected under 16°C (Table 18).

Early season species like *H. epistates*, *H. illota*, *H. lasiophthalma*, *H. nuda*, *T. similis* (Fig. 3) were generally active at lower temperatures than species which occurred later in the season.

## 3.10 FECUNDITY

Mean wing length and number of ovarioles found in *Tabanus* species are presented in Table 19. Wing length and number of ovarioles significantly differ at the .01 level between *T. lineola*, *T. quinquevittatus* and *T. similis*. Highly significant differences (.01 level) were detected in wing length and number of ovarioles of females of *T. lineola* collected in 1980 and 1981; no statistical differences (.05 level) were detected in *T. quinquevittatus* and *T. similis* (Table 20).

The correlation between the number of ovarioles and wing length as analysed by linear regression is presented in Fig. 4 for *T. lineola* and *T. similis*, and in Fig. 5 for *T. quinquevittatus*. Number of ovarioles was found to vary proportionately with the size of specimens.

## 3.11 ENDOPARASITES

Encysted endoparasites, probably *Diglochis occidentalis*, were found in the abdomen of 2 males and 4 females of *H. lasiophthalma*, and 1 female of *H. nuda*. They were generally coiled around Malpighian tubules of their host. The number of encysted endoparasites was 25 in each male, and varied from 2 to 11 in females. No apparent damage was done to the reproductive system. They were found from early to late June in both sampling years.

# 4.0 DISCUSSION

## 4.1 SEASONAL DISTRIBUTION

Seasonal flight periods were generally similar to those of comparable latitudes (Teskey 1960; Pechuman and Burton 1969, Smith *et al.* 1970, Matthysse *et al.* 1974, Magnarelli and Pechuman 1975; Magnarelli 1976, Golini and Wright 1978; Lewis and Leprince 1981; Leprince and Lewis 1982; Baribeau and Maire 1983b, 1983c, Thibault and Harper 1983). Variations could be attributed to species abundance, altitude and climatic factors of different years. Only one generation a year was detected among the various species. Species collected in the present study have been reported in the temperate region of Quebec (Baribeau and Maire 1983a).

## 4.2 PARITY AND PHYSIOLOGICAL AGE

Most females dissected had stage I-II or II terminal follicles characteristic of ovarian diapause and blood seeking behavior. This ovarian arrest is known to be food-mediated in anautogenous populations but also in autogenous populations after their first oviposition (Spielman 1971). One exception is known among autogenous tabanids, a pangoniine horse fly, *Apatolestes actites* Philip and Steffan, whose immatures inhabit coastal sandy beaches in California, was found to be bi-autogenous (Lane and Anderson 1983; Lane *et al.* 1983).

Conclusive proof of autogeny is obtained only when eggs develop completely without the female taking a blood meal. Autogeny may be inferred indirectly if there is an absence of nulliparous host seeking females in the field at the beginning of the flight season (Thomas 1972; Troubridge and Davies 1975). In southwestern Quebec, *H. frontalis* would be autogenous since no nullipars were collected in both sampling years. Species which showed nulliparous flies in ovarian diapause troughout most of their seasonal flight period were considered anautogenous. Anautogenous species in southwestern Quebec would include *H. epistates, H. lasiophthalma, H. nuda, H. sodalis, T. lineola, T. quinquevittatus* and *T. similis*. In most of these species, fresh blood was found in the midgut of nullipars supporting the evidence for anautogeny.

Anautogeny has been reported for *H. affinis, H. pechumani* (Thomas 1972, the latter as *H. typhus*, Thomas personal communication 1980), *H. epistates, H. illota, T. lineola, T. similis* (Troubridge and Davies 1975, Magnarelli 1976), *H. lasiophthalma, H. nuda* (Thomas 1972, Magnarelli 1976), *H. sodalis* (Magnarelli 1976), and *T. quinquevittatus* (Magnarelli and Pechuman 1975; Magnarelli 1976). Autogeny of *H. frontalis* was noted by Thomas (1972).

Based on the rapid rate of increase of the proportion of parous females which remained at high levels thereafter Troubridge and Davies (1975) suggested that *H. lasiophthalma* and *T. quinquevittatus* were capable of facultative autogeny (i.e., affecting only a part of the population) in southern Ontario. In southwestern Quebec, total percentages of parous females never exceeded 36% and the rate of increase of parous females during each season was much lower in both species and sampling years than the ones reported by Troubridge and Davies (1975). Facultative autogeny does not seem to occur in these species in the area studied.

Auroi (1982) stated that variations in the total number of captures were not taken into account in the criteria set by Troubridge and Davies (1975) for facultative autogeny. From Troubridge and Davies (1975) data, Auroi (1982) noted that the number of nulliparous females captured during 1 week was always greater than the number of unipars captured the next week (the only exception was in the first week) and concluded that *H. lasiophthalma* was anautogenous.

Several factors might influence the rate of increase and the proportion of

parous females in anautogenous populations' pattern of adult emergence, blood feeding success, species abundance, climatic conditions during female host-seeking activity, nectar or carbohydrate resources, sampling (effort, frequency and habitat), selectivity of trapping methods on species, parous and nulliparous females. Therefore, in absence of laboratory rearing, careful examination of the field data is mandatory before suggestion of facultative autogeny.

Flies were considered uniparous because only one dilatation of the wall of the ovariole was present in dissected parous females. No biparous flies were identified by ovarian dissection as in earlier studies (Thomas 1972, Troubridge and Davies 1975; Magnarelli and Pechuman 1975; Magnarelli 1976); it is perhaps related to the importance given to the number of dilatations of the wall of ovariole during dissection instead of the number of yellow bodies as in the studies mentioned above. Magnarelli and Stoffolano (1980) reported that only 1 follicular relic (= dilatation) per ovariole was found after 2 ovarian cycles in *Tabanus nigrovittatus* Macquart females. They hypothesized that dilatations do not form separately after each ovarian cycle but that contraction of tissues results in the creation of a single, largely expanded unit resulting in an inaccurate estimation of physiological age of the specimens. They also mentioned that similar problems in dilatation formation in known multiparous individuals were reported for *T. quinquevittatus* and *Chrysops atlanticus* Pechuman. Perhaps the species studied in southwestern Quebec do not develop more than one dilatation after 2 ovarian cycles, thus explaining the absence of biparous individuals among nearly a thousand parous females dissected in two sampling years. The presence of fresh blood in pars of *H. epistates, H. lasiophthalma, T. quinquevittatus* and *T. similis* is a further indication that females were trying to start a second gonotrophic cycle.

Lane and Anderson (1982) found 1 to 3 ovariole dilations in females of *Chrysops hirsuticallus* Philip during a two year study in California. They concluded that Polovodova's method of counting the number of ovariole dilatations (each of which corresponds to a previous oviposition) was reliable for this species to determine the number of ovarian cycles.

Although the number of heifers in the study area remained approximately the same during the two sampling years, the percentage of parous females in anautogenous species was variable from year to year. A comparison of parity rates of the most abundant species (year, total number of specimens collected, percentage of parous females, anthrone positivity of nulliparous females) is presented: *H. epistates* (1980,262,38,95), (1981,96,15,82), *H. lasiophthalma* (1980,317,37,83), (1981,622,31,82 comparison started June 13), *T. lineola* (1980,27,38,100), (1981,43,44,75), *T. quinquevittatus* (1980,912,31,87), (1981,428,35,85), *T. similis* (1980,34,45,76), (1981,55,17,60). Parity rates were more variable in species at low densities. High density and high or constant anthrone positivity rates (as in *H. epistates* in 1980, *H. lasiophthalma* and *T. quinquevittatus* in 1980 and 1981) were accompanied by high parity rates. Low density and anthrone positivity rates (as in *H. epistates* and *T. similis* in 1981 but not in *T. lineola* in 1981) were accompanied by lower parity rates. It is unknown to what extent lower parity rates were related to a lower incidence of a carbohydrate diet in nulliparous flies or more likely unfavorable climatic conditions which could both affect blood and nectar feeding activity.

## 4.3 OVIPOSITION

Immediately after oviposition, the posterior part of the follicular tube of a tabanid female is sac-like and about the size of a recently shed egg, it will contract further and debris inside will form a distinct "yellow body" in about 2 days (Thomas 1972). It then follows that

evaluation of egg laying period based on the presence of distended follicular tubes in tabanid females could be at the most 2 days earlier than recorded by dissection. Apart from *H. epistates*, *T. catenatus* and *T. lineola*, percentages of parous females with sac-stage ovarioles were well over 50% each year in remaining species which means that host-seeking behavior started less than 2 days after oviposition for most parous females in southwestern Quebec. A systematic record of pars with sac-like dilatations has only been mentioned by Magnarelli and Pechuman (1975) for *T. quinquevittatus* in New York State. They reported an incidence of 71% (n = 96) and 44% (n = 181) pars with sac-like dilatations for two different localities (a mean of 54%) and occurring from early July to early September with a peak in mid to late July. Similar occurrence and incidence (pooled data) were found in southwestern Quebec (Table 12) indicating that peak and period of oviposition were similar.

## 4.4 EGG RETENTION

Egg retention could not be used solely to determine parity in female horse flies since it only occurred in 12% (Table 14) of the parous females dissected and was quite variable among species and between sampling years. Morris and DeFoliart (1971) reported that 30% of parous females of *H. lasiophthalma* retained eggs. According to the present study, incidence of egg retention generally increased after the peak of parous females. Their results are perhaps overestimated because a greater proportion of specimens were dissected at the end of the flight period. Similar rates of egg retention were reported in Alberta by Thomas (1972) in *H. frontalis* (20%), *H. lasiophthalma* (10%), *H. nuda* (28%) and *H. pechumani* (6%, as *H. typhus*) and in New York State by Magnarelli and Pechuman (1976) for *T. quinquevittatus* (7.6%).

## 4.5 SPERM PRESENCE

Sperm were not present in the spermathecae of 16% of the nullipars and 6% of the pars dissected (Table 15). The higher proportion of sperm positive parous females as compared to nullipars is perhaps related to the older age of parous females and greater chances to be intercepted by a male. It is further substantiated by the high percentage of unmated nulliparous females at the beginning of the flight season which decreased thereafter.

Population peaks were related with peak of pars and high rates of sperm presence (*H. epistates* in 1980, *H. lasiophthalma* in 1981 and *T. quinquevittatus* in 1980 and 1981). Since males usually emerged 1 to 3 days before females, their peak of abundance would have coincided with female population peaks. The abundance of males would then benefit the unmated female population (blood-fed and non blood-fed nullipars and pars).

The proportion of sperm negative pars and nullipars attracted to carbon dioxide baited traps was similar to sperm positive females, and their stage of follicular development was I-II or II which means that these females were seeking a host without having mated. In southwestern Quebec, mating generally occurred prior to blood feeding but did not seem prerequisite to host-seeking behavior. Furthermore host-seeking behavior, intake of blood, sugar feeding, egg maturation and oviposition would normally occur in unmated females as confirmed by the presence of sperm negative pars.

Lane and Anderson (1982) reported that mating preceded blood feeding in *C. hirsuticallus* based on sperm presence in 17 host-seeking nullipars. From the dissection of 293 specimens, Lutta (1970 in Chvala *et al.* 1972) observed that 99.9% of females contained sperm and concluded that females only seek blood after mating. Leprince and Lewis (1983) observed that 96% of the pars and nullipars were mated and suggested that mating occurs prior to host-seeking in nulliparous females and that enough sperm is contained in parous females for a second gonotrophic cycle.

The presence of sperm negative pars could also be explained by sperm exhaustion during oviposition. Then mating would refresh or replenish the sperm reserve of parous females. It would also be highly detrimental to egg fertility and to subsequent ovarian cycles because mating would be required after every oviposition while male density is continuously decreasing. It would be of a definite advantage that the amount of sperm transferred to a female remain viable and last for several ovarian cycles.

The absence of sperm in parous females could be used as a relative estimate of the number of unfertilized egg masses laid by females under field conditions. Although variable between sampling years and species, percentages of unfertilized egg masses would have been 6% (n = 972) in horse flies in 1980-81, 8% (n = 485) in *Hybomitra* and 3% (n = 485) in *Tabanus* (Table 4a-b). A portion of the population of parous females might mate after oviposition, or exhaust their sperm reserve before completion of oviposition; both events might counterbalance each other.

Compared to 1980, the population of *H. epistates* in 1981 decreased by almost half (considering the trapping effort; Table 4a), the incidence of parous females decreased by more than half (38 to 15%; Table 6), and only 64% of the parous females were mated (93% in 1980; Table 6). A significant drop in the number of fertilized eggs occurred in 1981 as compared to 1980. Different productivity of fertile eggs between years might help to explain yearly fluctuations in population density in a given habitat. Population fluctuations could then perhaps be predicted from sperm presence, proportion of pars and population density.

## 4.6 SUGAR PRESENCE

The incidence of sugar feeding (as detected by the presence of fructose by anthrone test) was similar to the one reported by Lewis and Leprince (1981) in their study of tabanids feeding on cattle at the same locality. It is important to note that negative tests do not demonstrate that females have never sugar fed (Bidlingmayer and Hem 1973). Magnarelli and Anderson (1981) reported lower incidence of sugar feeding among tabanids collected in Connecticut by the anthrone test: *H. epistates* 81%, *H. lasiophthalma* 81%, *H. sodalis* 58% and *T. quinquevittatus* 71%. Discrepancies between the two studies might be related to a greater incidence and concentration of fructose in sugar sources (floral nectars, plant juices and honeydew) in southwestern Quebec or a greater incidence of glucose in sugar sources in Connecticut which might have been undetected by the anthrone test. But it could also be related to the methodology employed. Magnarelli and Anderson (1981) crushed the body parts of the specimens with a glass rod and recorded the results within 30 min of reagent activity. Specimens with a small amount of fructose might have been overlooked due to reaction of sulfuric acid with the crushed body parts of the insect. In the present study, only the diverticula were tested instead of the whole insect body. Lall (1969; 1970a) with *Chrysops vittatus* Wiedemann, and Stoffolano (1983) with *T. nigrovittatus* demonstrated that sugars were directed to the crop (diverticula) and blood to the midgut.

Glucose has been detected by thin-layer chromatography from the crushed bodies of tabanids (Magnarelli *et al.* 1979; Magnarelli and Anderson 1981) but its origin was questionable since glucose is a component of vertebrate blood and may also result from enzymatic hydrolysis of stored energy reserves (glycogen) carried over from immature stages (Magnarelli and Anderson 1981). Lall (1970b) demonstrated the presence of glucose and fructose by paper-partition chromatography of the crop fluid of *C. vittatus*. The anthrone test should be conducted on the diverticula of tabanids instead of the whole body to provide more accurate and comparative results and prevent contamination from crushed body of insects. It would then allow

the detection of glucose and other sugars from the carbohydrate meal by proper detection methodology.

Sugar meals appeared to be insufficient to promote ovarian development since host-seeking females had oocytes in stage I-II and II. Similar results were reported by Magnarelli and Anderson (1981).

Higher rates of sugar presence in both sampling years of pars of *T. quinquevittatus* might reflect a depletion of the fat body reserves after oviposition. Parous females of other species might have sugar requirements similar to nulliparous females.

Most sperm negative nullipars acquired a sugar meal before mating (Table 15). Magnarelli and Anderson (1979) reported that some females of *C. fuliginosus* acquired nectar sugars prior to mating and oviposition; and that they oviposited more readily if fed on 10% sucrose solution. Magnarelli and Stoffolano (1980) noted that vertebrate blood appeared insufficient to maintain all *T. nigrovittatus* through the minimum period required for oocyte maturation and oviposition without sucrose supplement. Hocking (1953) reported that survival and flight of blood seeking females were dependant upon carbohydrates and other nutrients in nectar. Stoffolano (1983) confirmed that a previous meal of sugar or blood did not preclude immediate feeding on the other sustance in *T. nigrovittatus*. In Germany, Kniepert (1980) mentioned that 53% of the females and 69% of the males were anthrone positive. Magnarelli and Anderson (1981) noted that the majority of females (nullipars and pars) contained nectar sugars, and suggested that carbohydrates were essential dietary nutrients. According to the high incidence of fructose in host-seeking tabanids in the present study and the preceding literature it is suggested that carbohydrates are essential dietary nutrients during the entire adult life of tabanids by providing the energy for basic metabolic activities.

Paired pollenia of *Asclepias syriaca* have already been reported on females of *T. atratus, T. quinquevittatus* and *T. similis* (Lewis and Leprince 1981) and males of *H. sodalis* (Leprince *et al.* 1983) in southwestern Quebec. Their presence on females of *H. epistates* and *T. similis* is reported herein for the first time in Quebec. Only 1 female of *T. quinquevittatus* had pollenia in 1980 (912 females collected) as compared to 17 in 1981 (428 females collected). The incidence of pollenia was not related to the density of the tabanid population but to the availability of flowers since in 1980 forest margins where most *A. syriaca* plants were growing was cut twice thus preventing flowering. Since incidence of anthrone positivity was approximately the same for *T. quinquevittatus* during the 2 sampling years, it is implicit that females were opportunistic and relied on other carbohydrate sources in 1980.

## 4.7 BLOOD PRESENCE

Blood meals were found in the midgut of 3% of the females horse flies collected in southwestern Quebec. The midgut has already been reported as the destination of blood meal in tabanids: Lall (1969), Bosler and Hansens (1974), Magnarelli (1976), Magnarelli and Anderson (1980a), Kniepert (1980), Friend and Stoffolano (1983, 1984), and Stoffolano (1983). Incidence of partial blood meals reported in tabanids from previous studies varied from 2 to 10 %: 5.9% by Bosler and Hansens (1974), 2% by Magnarelli (1976), 10% by Magnarelli and Anderson (1980a), 9% by Kniepert (1980), and 10% by Lane and Anderson (1982).

Anthrone positivity was 78% in specimens with blood in the midgut. Bosler and Hansens (1974) reported that the crop of 77% of the blooded females of *T. nigrovittatus* were distended; it is assumed that crop contained carbohydrate meal as shown in previous studies (see sugar feeding). From laboratory experiments, Stoffolano (1983) demonstrated that a previous meal of sugar

or blood does not preclude immediate feeding on the other substance.

Despite the presence of fresh blood in the midgut of host seeking pars and nullipars, females with a full blood meal were rarely collected. It seemed that unless a sufficient amount of blood is taken to allow the development of a maximum number of oocytes, the fly still remains in the host seeking behavior thus enhancing its vector potential. Fully blood fed females would exhibit a cessation of host seeking behavior and would not be collected by the Canopy trap designed to attract host seeking females. As the cessation of blood feeding behavior of *Rhodnius prolixus* Stal has been shown to be under the control of an abdominal stretch receptor (Maddrel 1963; Anwyl 1972), it is suggested that a similar mechanism exists in tabanid females.

The presence of fresh blood in host seeking pars and nullipars is interpreted as an indication of multiple feeding resulting from feeding interruption. Based on visual examination of tabanids on cattle, Magnarelli and Anderson (1980a) estimated the frequency of interrupted feeding of *H. epistates* to 54%, 32% in *H. lasiophthalma* and *H. sodalis*, 84% in *T. atratus*, 25% in *T. lineola* and 26% in *T. quinquevittatus*. They stated that the possibility of mechanical transmission of pathogens by tabanids increases with the frequency of interrupted feeding.

## 4.8 CARBON DIOXIDE

Carbon dioxide increased by almost 6-fold the number of horse flies collected in Canopy traps. It therefore represents an advantage in studies where large numbers of specimens are required for biological studies or pathogen screening. Roberts (1976) reported an increase in the tabanid catch from 2 to 4-fold in different Canopy traps when carbon dioxide was released at a rate of 100 ml/min. The release of 4.0 l/min of carbon dioxide was shown to increase the catch of tabanids by 13-fold in Malaise traps (Roberts 1975). Roberts (1972) estimated the release of carbon dioxide of lactating dairy cows to 3.5 l/min.

Parous flies of *T. quinquevittatus* but not of *T. lineola* were more abundant in non baited Canopy traps than baited traps but no preference was shown by pars of *H. lasiophthalma*. Trends observed in pars of the two dominant horse flies, *H. lasiophthalma* and *T. quinquevittatus*, were consistent each sampling year and are believed to be reliable. Mixed attraction to non baited traps occurred from year to year in pars of *H. epistates*, *H. nuda* and *T. similis*. Variability in the response of pars of these species is perhaps related to low population levels of pars in one of the sampling year. At low densities, the response of pars to carbon dioxide is more likely to be skewed from the general trend of high populations densities. The interpretation of the attractiveness of carbon dioxide to nullipars and pars of horse flies should be made with caution especially if it is based on a secondary species and one sampling season.

## 4.9 ATMOSPHERIC CONDITIONS

The lowest temperature threshold of host seeking activity for 10 of 13 tabanid species ranged from 15.6 to 22.2°C. Specimens collected between 15 to 20°C probably warmed up in sunlit exposed places before flight. This range is close to the one reported by Anderson *et al.* (1974), 20 to 21.7°C, in northern California. In New York State, Tashiro and Schwardt (1949) found little biting activity below 22.2°C. In Quebec, little flying activity was recorded in the temperate climatic zone when temperatures were below 21°C in the Laurentians (Thibault and Harper 1983), or below 20°C in the Trois-Rivières area (Baribeau and Maire 1983).

Climatic factors surveyed in the present study are more or less linked to each other. A multivariate analysis should be carried on the data before one can assess the relative importance of each factor on the host seeking activity of horse flies in southern Quebec.

## 4.10 FECUNDITY

The number of ovarioles of different *Tabanus* species collected in southwestern Quebec showed considerable variation (Table 19). Although conclusive proof could only be derived from a greater sample size, females of *T. lineola* were significantly larger and had greater number of ovarioles in 1980 than 1981. No differences were observed between the number of ovarioles of *T. quinquevittatus* and *T. similis* in both sampling years. Similar results were obtained in both sampling years for *Chrysops univittatus* Macquart (Leprince and Lewis 1983). In mosquitoes, Colless and Chellapah (1960) found that number of oocytes varied with body weight of *Aedes aegypti* (Linnaeus).

Ratio of wing length (mm) divided by mean number of ovarioles could be used to compare different species. A lower ratio was found in *T. atratus* (28.9), *T. catenatus* (32.3) and *T. quinquevittatus* (26.5), as compared to those found in *T. lineola* (49.5) and *T. similis* (53.6). The rate of increment varied differently between species of the same genus. The ratio of *C. univittatus* would be (50.9) from Leprince and Lewis (1983) data. I suggest that the ratio is species specific. Variations in the number of ovarioles of specimens belonging to the same or different geographical areas would vary along a species specific regression line. Leprince and Lewis (1983) suggested that the number of ovarioles in tabanids is probably related to the amount of stored nutrient carried over from the immature stage, its considerable variation may reflect a variety of larval habitats. They also suggested that the number of ovarioles could be used as an index of species condition and perhaps used to assess the quality of larval habitat of one species over its geographical range.

The number of ovarioles and the ratio could be used by taxonomists as a tool to explain taxonomic relations between species or group of species. It could also be used by ecologists to understand the dynamics and the reproductive strategy of populations of tabanids. Knowledge of the number of ovarioles of different species with the number of eggs after an anautogenous or autogenous oviposition would help to assess the validity of the evaluation of physiological age by Polovodova's method (e.g. if only half of the oocytes develop after a full blood meal and the remaining part after a second, this could lead to an underestimation of the number of ovarian cycles and vector potential of a biting fly).

Bi-autogeny implies that the fat body reserve exceeds the potential egg production of one ovarian cycle. Then, in the absence of ovarian diapause and egg retention, follicle development would occur without a blood meal in previously used ovarioles. Otherwise bi-autogeny could refer to 2 batches of eggs laid at different periods by the same female but by different set of ovarioles; bi-autogeny would then refer to asynchrony of follicle development.

Engelman (1970) stated that number of eggs possible per batch is determined by number of oocytes present in ovaries, suboptimal food quantity lower egg production by allowing maturation of only a fraction of the primary oocytes. The evaluation of the number of ovarioles could also help to determine the proportion of active ovarioles based on the number of eggs laid after each gonotrophic cycle.

## 4.11 ENDOPARASITES

Gregarious endoparasites of tabanid larvae and pupae are known from 2 families of Hymenoptera: Diapriidae (*Trichopria* spp.) and Pteromalidae (*Diglochis occidentalis* Ashmead) (James 1963; Teskey 1969; Magnarelli and Anderson 1980b). The number of encysted endoparasites varied from 2 to 25 in horse flies in southwestern Quebec; these parasites could belong to one or both of these hymenopteran parasitic groups. This suggests that immature tabanids can survive a parasitic infection and still become functional adults.

Figure 2. Location of Canopy traps near the entrance of the Morgan Arboretum (Sainte-Anne-de-Bellevue), Quebec, 1980-81

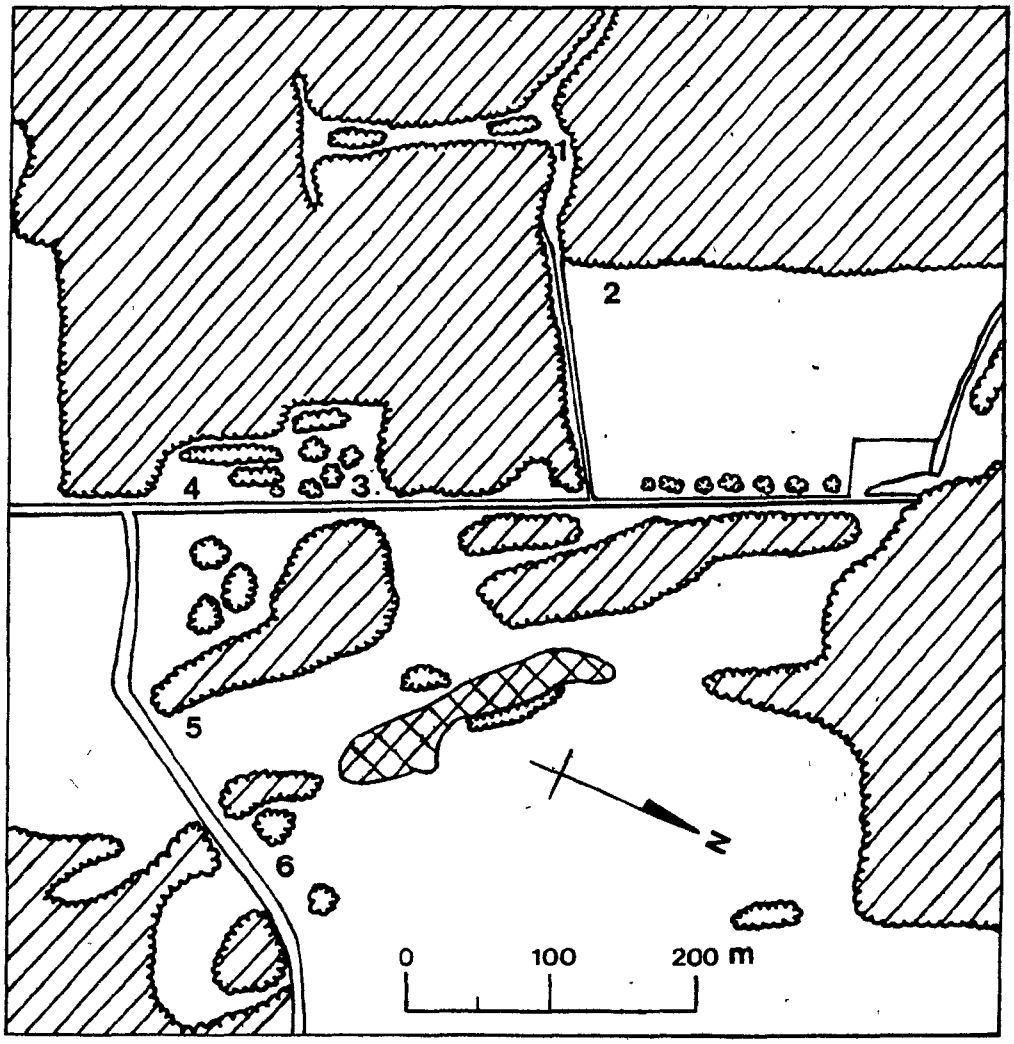
1
2
3
4
5
6
N
0
100
200 m
Forested area
Stoneycroft Pond
Herbaceous area

Figure 3. Seasonal succession of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in Sainte-Anne-de-Bellevue, Quebec, 1980-81

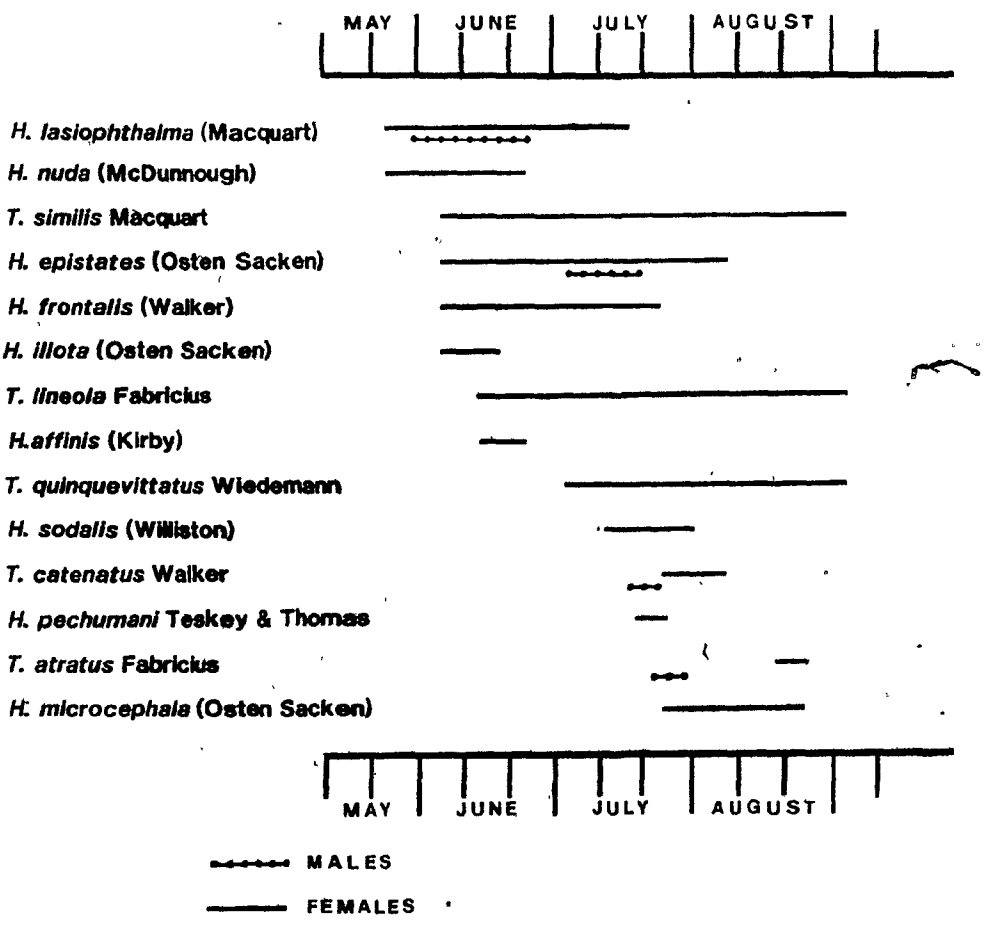
MAY
JUNE
JULY
AUGUST
H. lasiophthalma (Macquart)
H. nuda (McDunnough)
T. similis Macquart
H. epistates (Osten Sacken)
H. frontalis (Walker)
H. illota (Osten Sacken)
T. lineola Fabricius
H.affinis (Kirby)
T. quinquevittatus Wiedemann
H. sodalis (Williston)
T. catenatus Walker
H. pechumani Teskey & Thomas
T. atratus Fabricius
H. microcephala (Osten Sacken)
MAY
JUNE
JULY
AUGUST
MALES
FEMALES

Figure 4. Potential fecundity of *Tabanus lineola* and *Tabanus similis* in southwestern Quebec

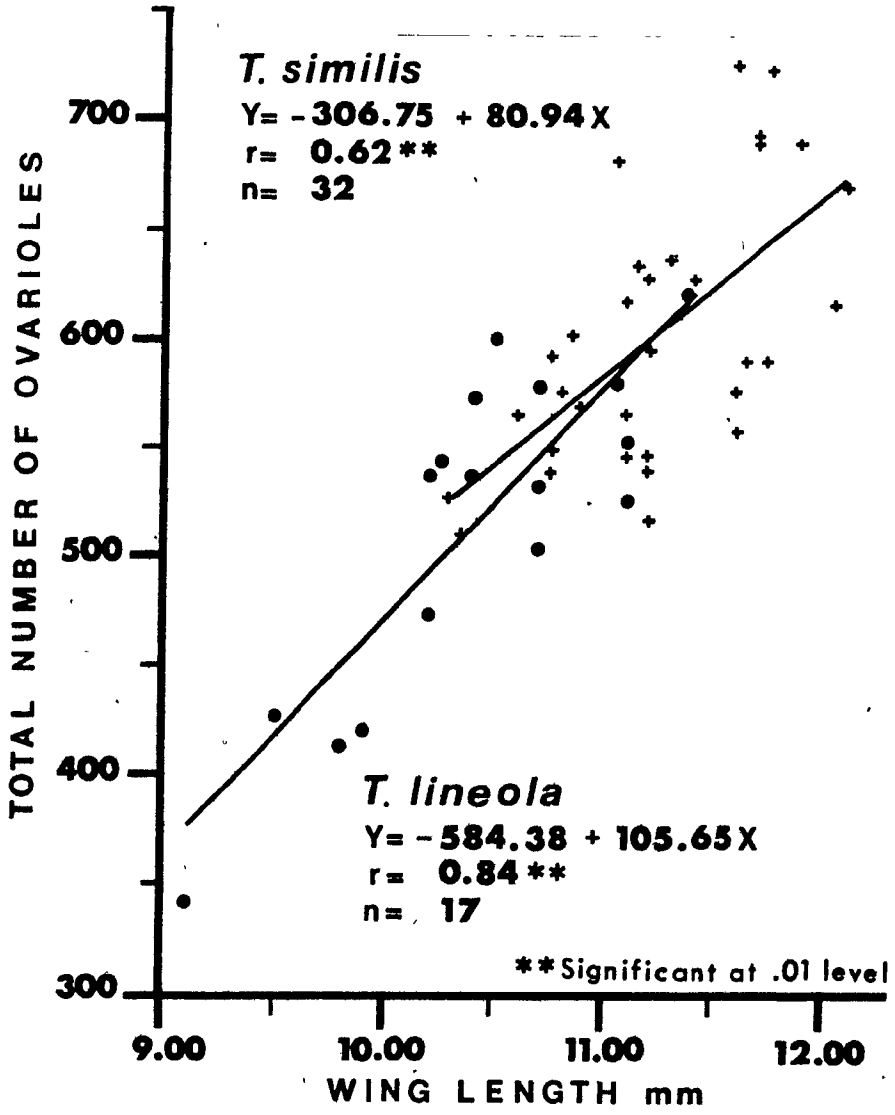
T. similis
Y= -306.75 + 80.94X
r= 0.62**
n= 32
T. lineola
Y= -584.38 + 105.65X
r= 0.84**
n= 17
**Significant at .01 level
TOTAL NUMBER OF OVARIOLES
700
600
500
400
300
9.00
10.00
11.00
12.00
WING LENGTH mm

Figure 5. Potential fecundity of *Tabanus quinquevittatus* in southwestern Quebec

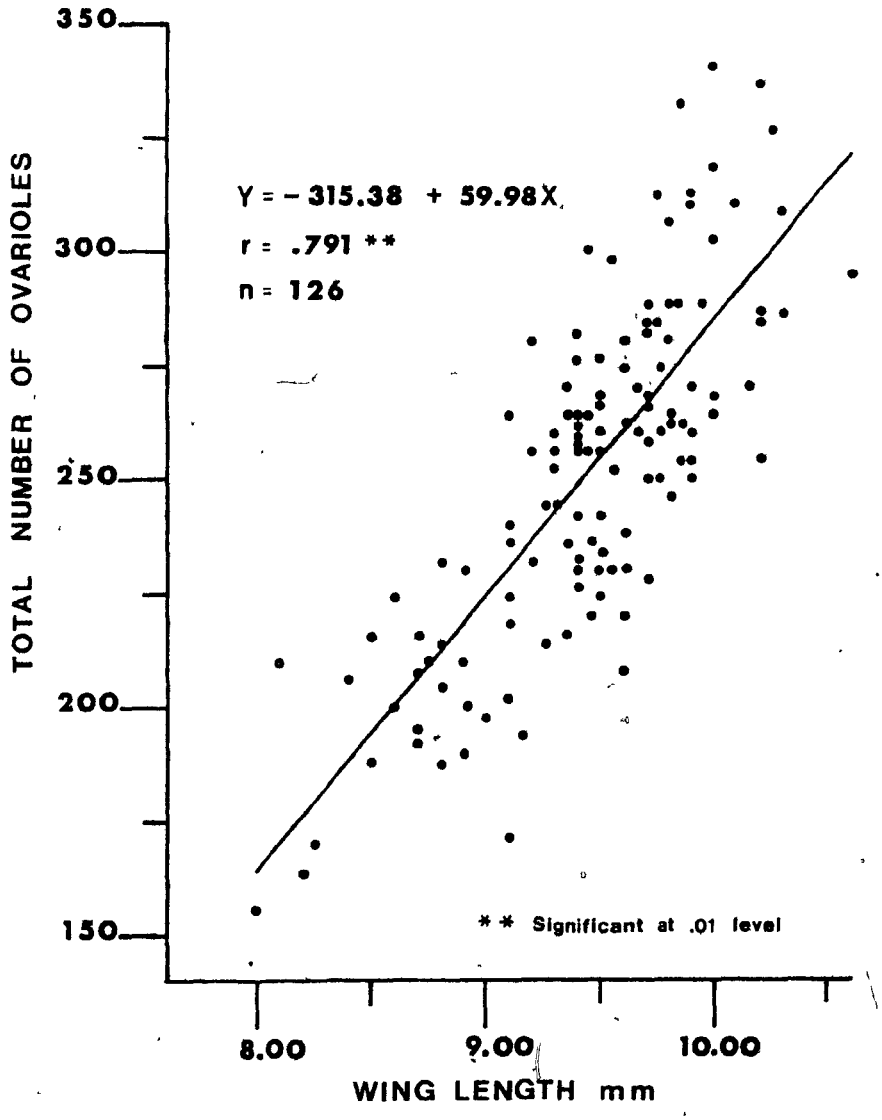
350
300
250
200
150
TOTAL NUMBER OF OVARIOLES
Y = - 315.38 + 59.98X
r = .791 **
n = 126
** Significant at .01 level
8.00
9.00
10.00
WING LENGTH mm

TABLE 4a. Summary of parity rates, sperm presence, and anthrone positivity of horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec 1980–1981

| | | Nulliparous | | | Parous | | |
|---|---|---|---|---|---|---|---|
| Species | # | An. | Sp+ | At+ | An. | Sp+ | At+ |
| *H. affinis* | 5 | 5 | 40 | 80 | 0 | - | - |
| *H. epistates* | 358 | 238 | 75 | 91 | 111 | 92 | 91 |
| *H. frontalis* | 63 | 0 | - | - | 61 | 93 | 74 |
| *H. illota* | 7 | 4 | 75 | 100 | 3 | 100 | 100 |
| *H. lasiophthalma* | 1320 | 847 | 82 | 85 | 272 | 90 | 83 |
| *H. nuda* | 106 | 85 | 87 | 85 | 15 | 100 | 87 |
| *H. microcephala* | 14 | 0 | - | - | 14 | 100 | 71 |
| *H. pechumani* | 2 | 0 | - | - | 2 | 100 | 100 |
| *H. sodalis* | 37 | 27 | 89 | 78 | 9 | 100 | 89 |
| Sub-total | 1912 | 1206 | 81 | 86 | 487 | 92 | 84 |

TABLE 4b. Summary of parity rates, sperm presence, and anthrone positivity of horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec 1980-1981 [continued]

| Species | # | Nulliparous An. | Nulliparous Sp+ | Nulliparous At+ | Parous An. | Parous Sp+ | Parous At+ |
|---|---|---|---|---|---|---|---|
| *T. atratus* | 1 | 1 | 100 | 100 | 0 | - | - |
| *T. catenatus* | 6 | 0 | - | - | 6 | 100 | 33 |
| *T. lineola* | 70 | 40 | 90 | 85 | 29 | 93 | 83 |
| *T. quinquevittatus* | 1340 | 906 | 89 | 85 | 427 | 98 | 95 |
| *T. similis* | 89 | 62 | 71 | 65 | 23 | 96 | 61 |
| Sub-total | 1506 | 1009 | 88 | 84 | 485 | 97 | 92 |
| TOTAL | 3418 | 2215 | 84 | 85 | 972 | 94 | 88 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

TABLE 5. Parity rates, sperm presence, and anthrone positivity of *Hybomitra affinis* and *Hybomitra illota* in southwestern Quebec in 1980 and 1981.

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| *Hybomitra affinis* | | | | | | | | |
| 800624 | 3 | 3 | 33 | 100 | 0 | - | - | - |
| 810613 | 1 | 1 | 100 | 0 | 0 | - | - | - |
| 810618 | 1 | 1 | 0 | 100 | 0 | - | - | - |
| TOTAL | 5 | 5 | 40 | 80 | 0 | - | - | - |
| *Hybomitra illota* | | | | | | | | |
| 800613 | 1 | 1 | 100 | 100 | 0 | - | - | - |
| 810605 | 5 | 3 | 67 | 100 | 2 | 100 | 100 | 50 |
| 810618 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| TOTAL | 7 | 4 | 75 | 100 | 3 | 100 | 100 | 67 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 6. Parity rates, sperm presence, and anthrone positivity of *Hybomitra epistates* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| 800613 | 4 | 4 | 75 | 50 | 0 | - | - | - |
| 800621 | 4 | 4 | 50 | 100 | 0 | - | - | - |
| 800624 | 52 | 40 | 73 | 95 | 11 | 100 | 91 | 18 |
| 800703 | 62 | 43 | 88 | 100 | 18 | 94 | 89 | 67 |
| 800711 | 29 | 15 | 93 | 93 | 12 | 100 | 100 | 50 |
| 800718 | 51 | 21 | 86 | 100 | 30 | 93 | 90 | 47 |
| 800725 | 43 | 23 | 87 | 91 | 18 | 94 | 100 | 33 |
| 800731 | 14 | 8 | 88 | 88 | 6 | 100 | 67 | 17 |
| 800807 | 3 | 1 | 100 | 100 | 2 | 100 | 100 | 100 |
| Subtotal | 262 | 159 | 83 | 95 | 97 | 96 | 92 | 44 |
| 810605 | 11 | 11 | 55 | 100 | 0 | - | - | - |
| 810613 | 30 | 19 | 63 | 79 | 8 | 63 | 88 | 13 |
| 810618 | 28 | 23 | 48 | 74 | 5 | 60 | 80 | 20 |
| 810624 | 3 | 3 | 100 | 100 | 0 | - | - | - |
| 810702 | 9 | 8 | 63 | 88 | 1 | 100 | 100 | 0 |
| 810711 | 4 | 4 | 75 | 75 | 0 | - | - | - |
| 810716 | 2 | 2 | 0 | 0 | 0 | - | - | - |
| 810724 | 9 | 9 | 78 | 100 | 0 | - | - | - |
| Subtotal | 96 | 79 | 59 | 82 | 14 | 64 | 86 | 14 |
| TOTAL | 358 | 238 | 75 | 91 | 111 | 92 | 91 | 41 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

Table 7. Parity rates, sperm presence, and anthrone positivity of *Hybomitra frontalis* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| 800613 | 2 | 0 | - | - | 2 | 100 | 100 | 50 |
| 800624 | 10 | 0 | - | - | 10 | 90 | 90 | 60 |
| 800703 | 15 | 0 | - | - | 13 | 100 | 69 | 54 |
| 800711 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| 800718 | 4 | 0 | - | - | 4 | 100 | 100 | 100 |
| 800807 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| 800818 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| Subtotal | 34 | 0 | - | - | 32 | 97 | 84 | 66 |
| 810605 | 1 | 0 | - | - | 1 | 0 | 100 | 100 |
| 810613 | 8 | 0 | - | - | 8 | 100 | 63 | 38 |
| 810618 | 6 | 0 | - | - | 6 | 83 | 67 | 83 |
| 810702 | 9 | 0 | - | - | 9 | 89 | 44 | 78 |
| 810711 | 2 | 0 | - | - | 2 | 100 | 50 | 50 |
| 810716 | 2 | 0 | - | - | 2 | 100 | 100 | 50 |
| 810724 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| Subtotal | 29 | 0 | - | - | 29 | 90 | 62 | 66 |
| TOTAL | 63 | 0 | - | - | 61 | 93 | 74 | 66 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 8. Parity rates, sperm presence, and anthrone positivity of *Hybomitra lasiophthalma* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| 800613 | 84 | 58 | 71 | 86 | 14 | 93 | 93 | 100 |
| 800621 | 47 | 30 | 87 | 83 | 17 | 88 | 94 | 71 |
| 800624 | 145 | 90 | 93 | 81 | 53 | 83 | 91 | 53 |
| 800703 | 33 | 12 | 67 | 75 | 21 | 90 | 95 | 67 |
| 800711 | 5 | 0 | – | – | 5 | 80 | 60 | 20 |
| 800718 | 3 | 2 | 50 | 100 | 1 | 0 | 100 | 100 |
| Subtotal | 317 | 192 | 89 | 83 | 111 | 86 | 91 | 63 |
| 810523 | 1 | 1 | 100 | 100 | 0 | – | – | – |
| 810531 | 47 | 39 | 88 | 97 | 0 | – | – | – |
| 810605 | 333 | 311 | 75 | 87 | 19 | 84 | 89 | 68 |
| 810613 | 472 | 220 | 91 | 84 | 82 | 96 | 83 | 60 |
| 810618 | 139 | 85 | 85 | 79 | 54 | 89 | 67 | 61 |
| 810624 | 9 | 4 | 100 | 75 | 5 | 100 | 80 | 80 |
| 810702 | 2 | 1 | 0 | 0 | 1 | 100 | 100 | 0 |
| Subtotal | 1003 | 655 | 82 | 85 | 161 | 93 | 78 | 61 |
| TOTAL | 1320 | 847 | 82 | 85 | 272 | 90 | 84 | 61 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 9. Parity rates, sperm presence, and anthrone positivity of *Hybomitra nuda* and *Hybomitra microcephala* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| *Hybomitra nuda* | | | | | | | | |
| 800613 | 7 | 5 | 100 | 100 | 2 | 100 | 100 | 100 |
| 800624 | 4 | 1 | 100 | 0 | 2 | 100 | 100 | 100 |
| 810523 | 2 | 2 | 100 | 100 | 0 | - | - | - |
| 810531 | 33 | 28 | 75 | 79 | 1 | 100 | 100 | 0 |
| 810605 | 49 | 45 | 91 | 87 | 4 | 100 | 75 | 75 |
| 810613 | 11 | 4 | 100 | 100 | 6 | 100 | 83 | 50 |
| TOTAL | 106 | 85 | 87 | 85 | 15 | 100 | 87 | 67 |
| *Hybomitra microcephala* | | | | | | | | |
| 800731 | 2 | 0 | - | - | 2 | 100 | 100 | 100 |
| 800807 | 8 | 0 | - | - | 8 | 100 | 63 | 88 |
| 800813 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| 800824 | 2 | 0 | - | - | 2 | 100 | 100 | 0 |
| 810724 | 1 | 0 | - | - | 1 | 100 | 0 | 100 |
| TOTAL | 14 | 0 | - | - | 14 | 100 | 71 | 79 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 10. Parity rates, sperm presence, and anthrone positivity of *Hybomitra pechumani* and *Hybomitra sodalis* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| *Hybomitra pechumani* | | | | | | | | |
| 800718 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| 800725 | 1 | 0 | - | - | 1 | 100 | 100 | 100 |
| TOTAL | 2 | 0 | - | - | 2 | 100 | 100 | 100 |
| *Hybomitra sodalis* | | | | | | | | |
| 800711 | 2 | 2 | 100 | 100 | 0 | - | - | - |
| 800718 | 15 | 12 | 92 | 83 | 2 | 100 | 50 | 100 |
| 800725 | 5 | 4 | 75 | 50 | 1 | 100 | 100 | 100 |
| 800731 | 3 | 1 | 100 | 100 | 2 | 100 | 100 | 50 |
| 810711 | 5 | 4 | 100 | 75 | 1 | 100 | 100 | 100 |
| 810716 | 5 | 3 | 100 | 100 | 2 | 100 | 100 | 100 |
| 810724 | 2 | 1 | 0 | 0 | 1 | 100 | 100 | 0 |
| TOTAL | 37 | 27 | 89 | 78 | 9 | 100 | 89 | 78 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 11. Parity rates, sperm presence, and anthrone positivity of *Tabanus catenatus* and *Tabanus lineola* in southwestern Quebec in 1980 and 1981.

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| *Tabanus catenatus* | | | | | | | | |
| 800807 | 1 | 0 | - | - | 1 | 100 | 100 | 0 |
| 810724 | 3 | 0 | - | - | 3 | 100 | 33 | 33 |
| 810731 | 1 | 0 | - | - | 1 | 100 | 0 | 100 |
| 810807 | 1 | 0 | - | - | 1 | 100 | 0 | 0 |
| TOTAL | 6 | 0 | - | - | 6 | 100 | 33 | 33 |
| *Tabanus lineola* | | | | | | | | |
| 800711 | 1 | 1 | 100 | 100 | 0 | - | - | - |
| 800718 | 11 | 8 | 100 | 100 | 3 | 100 | 67 | 33 |
| 800725 | 8 | 5 | 100 | 100 | 3 | 100 | 67 | 33 |
| 800731 | 4 | 1 | 100 | 100 | 2 | 100 | 100 | 0 |
| 800807 | 2 | 1 | 100 | 100 | 1 | 100 | 100 | 100 |
| 800821 | 1 | 0 | - | - | 1 | 100 | 100 | 0 |
| Subtotal | 27 | 16 | 100 | 100 | 10 | 100 | 80 | 30 |
| 810613 | 3 | 3 | 33 | 67 | 0 | - | - | - |
| 810681 | 3 | 2 | 50 | 100 | 1 | 100 | 100 | 0 |
| 810702 | 9 | 4 | 100 | 100 | 5 | 60 | 100 | 80 |
| 810711 | 7 | 5 | 80 | 60 | 2 | 100 | 100 | 50 |
| 810716 | 15 | 7 | 100 | 57 | 8 | 100 | 88 | 25 |
| 810724 | 5 | 3 | 100 | 100 | 2 | 100 | 100 | 50 |
| 810731 | 1 | 0 | - | - | 1 | 100 | 100 | 0 |
| Subtotal | 43 | 24 | 83 | 75 | 19 | 89 | 95 | 42 |
| TOTAL | 70 | 40 | 90 | 85 | 29 | 93 | 90 | 38 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 12. Parity rates, sperm presence, and anthrone positivity of *Tabanus quinquevittatus* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| 800703 | 21 | 20 | 60 | 70 | 0 | - | - | - |
| 800711 | 23 | 21 | 90 | 100 | 2 | 100 | 100 | 100 |
| 800718 | 230 | 189 | 84 | 87 | 41 | 100 | 100 | 68 |
| 800725 | 320 | 217 | 94 | 87 | 101 | 97 | 96 | 35 |
| 800731 | 167 | 100 | 98 | 89 | 66 | 100 | 92 | 62 |
| 800807 | 96 | 59 | 97 | 85 | 36 | 100 | 89 | 78 |
| 800814 | 22 | 8 | 100 | 100 | 14 | 100 | 100 | 57 |
| 800821 | 18 | 7 | 100 | 86 | 11 | 91 | 100 | 36 |
| 800903 | 15 | 7 | 71 | 57 | 8 | 100 | 100 | 13 |
| Subtotal | 912 | 628 | 90 | 87 | 279 | 99 | 95 | 53 |
| 810702 | 57 | 54 | 76 | 74 | 3 | 100 | 100 | 33 |
| 810711 | 78 | 59 | 73 | 68 | 18 | 94 | 100 | 67 |
| 810716 | 105 | 60 | 95 | 85 | 45 | 96 | 91 | 53 |
| 810724 | 118 | 77 | 91 | 94 | 41 | 98 | 95 | 34 |
| 810731 | 62 | 26 | 81 | 85 | 36 | 94 | 94 | 67 |
| 810814 | 4 | 2 | 100 | 100 | 2 | 100 | 100 | 0 |
| 810820 | 2 | 0 | - | - | 2 | 100 | 100 | 0 |
| 810826 | 2 | 0 | - | - | 1 | 100 | 100 | 0 |
| Subtotal | 428 | 278 | 84 | 82 | 148 | 96 | 95 | 51 |
| TOTAL | 1340 | 906 | 89 | 85 | 427 | 98 | 95 | 52 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

TABLE 13. Parity rates, sperm presence, and anthrone positivity of *Tabanus similis* in southwestern Quebec in 1980 and 1981

| | | Nulliparous | | | Parous | | | |
|---|---|---|---|---|---|---|---|---|
| DATE | # | An. | Sp+ | At+ | An. | Sp+ | At+ | SSO |
| 800613 | 2 | 2 | 100 | 100 | 0 | – | – | – |
| 800624 | 2 | 1 | 100 | 100 | 0 | – | – | – |
| 800703 | 4 | 1 | 0 | 0 | 2 | 50 | 0 | 0 |
| 800711 | 1 | 0 | – | – | 1 | 100 | 100 | 100 |
| 800718 | 8 | 5 | 80 | 60 | 2 | 100 | 0 | 50 |
| 800725 | 5 | 4 | 75 | 100 | 1 | 100 | 100 | 0 |
| 800731 | 7 | 1 | 100 | 100 | 6 | 100 | 83 | 83 |
| 800814 | 1 | 0 | – | – | 1 | 100 | 100 | 100 |
| 800821 | 3 | 2 | 100 | 50 | 1 | 100 | 100 | 100 |
| 800903 | 1 | 1 | 100 | 100 | 0 | – | – | – |
| Subtotal | 34 | 17 | 82 | 76 | 14 | 93 | 64 | 64 |
| 810605 | 1 | 1 | 100 | 100 | 0 | – | – | – |
| 810613 | 17 | 17 | 53 | 59 | 0 | – | – | – |
| 810618 | 15 | 10 | 90 | 60 | 4 | 100 | 25 | 75 |
| 810624 | 3 | 2 | 50 | 50 | 1 | 100 | 100 | 100 |
| 810702 | 13 | 11 | 55 | 55 | 2 | 100 | 50 | 100 |
| 810711 | 5 | 4 | 100 | 75 | 1 | 100 | 100 | 100 |
| 810716 | 1 | 0 | – | – | 1 | 100 | 100 | 0 |
| Subtotal | 55 | 45 | 67 | 60 | 9 | 100 | 56 | 78 |
| TOTAL | 89 | 62 | 71 | 65 | 23 | 96 | 61 | 70 |

\# Number of specimens collected

An. Number of specimens analysed

Sp+ Percentage of specimens containing sperm

At+ Percentage of anthrone positive specimens

SSO Percentage of specimens with sac-stage ovariole

Table 14. Percentage of parous females which retained eggs in 1980 and 1981

| Species | 1980 | 1981 | 1980-1981 |
|---|---|---|---|
| *H. epistates* | 16/97 = 16.5 | 1/14 = 7.1 | 17/111 = 15.3 |
| *H. frontalis* | 10/32 = 31.3 | 6/29 = 20.7 | 16/61 = 26.2 |
| *H. illota* | 0/0 = - | 1/3 = 33.3 | 1/3 = 33.3 |
| *H. lasiophthalma* | 13/111 = 11.7 | 13/161 = 8.1 | 26/272 = 9.6 |
| *H. microcephala* | 1/13 = 7.7 | 0/1 = 0 | 1/14 7.1 |
| *H. nuda* | 1/4 = 25.0 | 4/11 = 36.4 | 5/15 = 33.3 |
| *H. pechumani* | 0/2 = 0 | 0/0 = - | 0/2 = 0 |
| *H. sodalis* | 1/5 = 20.0 | 0/4 = 0 | 1/9 = 11.1 |
| Sub-total | 42/264 = 15.9 | 25/223 = 11.2 | 67/487 = 13.8 |
| *T. catenatus* | 1/1 = 100 | 0/5 = 0 | 1/6 = 16.7 |
| *T. lineola* | 1/10 = 10.0 | 2/19 = 10.5 | 3/29 = 10.3 |
| *T. quinquevittatus* | 25/279 = 9.0 | 9/148 = 6.1 | 34/427 = 8.0 |
| *T. similis* | 9/14 = 64.3 | 1/9 = 11.1 | 10/23 = 43.5 |
| Sub-total | 36/304 = 11.8 | 12/181 = 6.6 | 48/485 = 9.9 |
| TOTAL | 78/568 = 13.7 | 37/404 = 9.2 | 115/971 = 11.8 |

Table 15. Parity rates, anthrone positivity and attraction to carbon dioxide of unmated horse flies (*Hybomitra* and *Tabanus*) in southwestern Quebec in 1980-81

| | | Nulliparous | | | Parous | | |
|---|---|---|---|---|---|---|---|
| Species | # | Sp- | $CO_2$ | At+ | Sp- | $CO_2$ | At+ |
| *H. affinis* | 3 | 3 | 100 | 100 | 0 | - | - |
| *H. epistates* | 68 | 60 | 78 | 80 | 8 | 88 | 88 |
| *H. frontalis* | 4 | 0 | - | - | 4 | 100 | 75 |
| *H. illota* | 1 | 1 | 100 | 100 | 0 | - | - |
| *H. lasiophthalma* | 192 | 164 | 84 | 79 | 28 | 79 | 89 |
| *H. nuda* | 11 | 11 | 91 | 82 | 0 | - | - |
| *H. sodalis* | 3 | 3 | 100 | 33 | 0 | - | - |
| Sub-total | 282 | 242 | 83 | 79 | 40 | 83 | 88 |
| *T. lineola* | 7 | 5 | 100 | 80 | 2 | 100 | 100 |
| *T. quinquevittatus* | 115 | 105 | 89 | 62 | 10 | 80 | 80 |
| *T. similis* | 17 | 16 | 75 | 56 | 1 | 0 | 0 |
| Sub-total | 139 | 126 | 87 | 62 | 13 | 77 | 77 |
| TOTAL | 421 | 368 | 85 | 73 | 53 | 81 | 85 |

\# Total number of sperm negative females

Sp- Number of sperm negative females

$CO_2$ Percentage of specimens collected in carbon dioxide baited canopy traps

At+ Percentage of anthrone positive specimens

TABLE 16a. Attractiveness of carbon dioxide to nullipars and pars of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in southwestern Quebec in 1980-1981

| | Non $CO_2$ baited traps | | | | $CO_2$ baited traps | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | ND | Nu. | Pa. | Sto | ND | Nu. | Pa. | Sto | TOT |
| *H. affinis* | 0 | 20 | 0 | 20 | 0 | 80 | 0 | 80 | 5 |
| *H. epistates* | 0.6 | 11.3 | 6.2 | 18.1 | 0.8 | 56.8 | 24.3 | 81.9 | 354 |
| *H. frontalis* | 0 | 0 | 27.9 | 27.9 | 1.6 | 0 | 70.5 | 72.1 | 61 |
| *H. illota* | 0 | 0 | 0 | 0 | 0 | 57 | 43 | 100 | 7 |
| *H. lasiophthalma* | 2.0 | 8.7 | 3.0 | 13.7 | 12.8 | 55.5 | 18.0 | 86.3 | 1227 |
| *H. nuda* | 1.0 | 14.1 | 3.0 | 18.2 | 6.1 | 65.7 | 10.1 | 81.8 | 99 |
| *H. microcephala* | 0 | 0 | 21.4 | 21.4 | 0 | 0 | 78.6 | 78.6 | 14 |
| *H. pechumani* | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 100 | 2 |
| *H. sodalis* | 0 | 8.1 | 0 | 8.1 | 2.7 | 64.9 | 24.3 | 91.9 | 37 |
| Sub-total | 1.5 | 9.1 | 4.6 | 15.2 | 9.3 | 54.0 | 21.5 | 84.8 | 1806 |

ND Percentage of specimens not dissected

Nu. Percentage of nulliparous specimens

Pa. Percentage of parous specimens

Sto Sub-total percentage of one treatment

TOT Total number of specimens collected

TABLE 16b. Attractiveness of carbon dioxide to nullipars and pars of horse flies (*Hybomitra* and *Tabanus*) collected in Canopy traps in southwestern Quebec in 1980-1981 [continued]

| | Non $CO_2$ baited traps | | | | $CO_2$ baited traps | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | ND | Nu. | Pa. | Sto | ND | Nu. | Pa. | Sto | TOT |
| *T. atratus* | 0 | 100 | 0 | 100 | 0 | 0 | 0 | 0 | 1 |
| *T. catenatus* | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 100 | 5 |
| *T. lineola* | 0 | 4.3 | 0 | 4.3 | 1.4 | 52.9 | 41.4 | 95.7 | 70 |
| *T. quinquevittatus* | 0 | 7.8 | 5.4 | 13.2 | 0.1 | 60.4 | 26.3 | 86.8 | 1320 |
| *T. similis* | 3.5 | 14.9 | 10.4 | 28.7 | 2.3 | 44.8 | 24.1 | 71.3 | 87 |
| Sub-total | 0.2 | 8.1 | 5.4 | 13.7 | 0.3 | 58.9 | 27.1 | 86.3 | 1483 |
| TOTAL | 0.9 | 8.7 | 4.9 | 14.5 | 5.3 | 56.2 | 24.0 | 85.5 | 3289 |

ND Percentage of specimens not dissected

Nu. Percentage of nulliparous specimens

Pa. Percentage of parous specimens

Sto Sub-total percentage of one treatment

TOT Total number of specimens collected

Table 17. Percentage of parous specimens* collected in non-baited and carbon dioxide baited Canopy traps in 1980 and 1981

| Species | Year | Non $CO_2$ baited traps | $CO_2$ baited traps |
|---|---|---|---|
| *H. epistates* | 1980 | 20/42 = 47.6 | 75/215 = 34.9 |
| | 1981 | 2/20 = 10.0 | 11/72 = 15.3 |
| | 1980-81 | 22/62 = 35.5 | 86/287 = 30.0 |
| *H. lasiophthalma* | 1980 | 19/47 = 40.4 | 77/177 = 43.5 |
| | 1981 | 18/97 = 18.6 | 144/725 = 19.9 |
| | 1980-81 | 37/144 = 25.7 | 221/902 = 24.5 |
| *H. nuda* | 1980 | 0/1 = 0 | 3/4 = 75.0 |
| | 1981 | 3/16 = 18.8 | 7/71 = 9.9 |
| | 1980-81 | 3/17 = 17.6 | 10/75 = 13.3 |
| *T. lineola* | 1980 | 0/2 = 0 | 11/25 = 44.0 |
| | 1981 | 0/1 = 0 | 18/41 = 43.9 |
| | 1980-81 | 0/3 = 0 | 29/66 = 43.9 |
| *T. quinquevittatus* | 1980 | 50/130 = 38.5 | 221/763 = 29.0 |
| | 1981 | 21/44 = 47.7 | 126/381 = 33.1 |
| | 1980-81 | 71/174 = 40.8 | 347/1144 = 30.3 |
| *T. similis* | 1980 | 8/12 = 66.7 | 6/17 = 35.3 |
| | 1981 | 1/10 = 10.0 | 8/44 = 18.2 |
| | 1980-81 | 9/22 = 40.9 | 14/61 = 23.0 |

* Most abundant species

Table 18. Variation of climatic factors during female tabanid activity in 1980-81

| Species | h | * | °C | RH |
|---|---|---|---|---|
| *H. affinis* | 1100-1700 | 1.65-2.91 | 26.1-31.7 | 39-61 |
| *H. epistates* | 0800-1900 | 0.39-3.39 | 18.9-31.7 | 38-75 |
| *H. frontalis* | 0900-1800 | 1.00-3.39 | 20.6-31.7 | 34-72 |
| *H. illota* | 0900-1800 | 1.11-3.34 | 18.9-27.2 | 33-61 |
| *H. lasiophthalma* | 0700-1900 | 0.39-3.36 | 15.6-31.7 | 33-89 |
| *H. nuda* | 0900-1800 | 1.06-3.34 | 20.6-30.6 | 33-68 |
| *H. microcephala* | 1400-1500 | 2.48-2.72 | 26.1-30.0 | 44-53 |
| *H. pechumani* | 1100 | 3.05 | 27.2 | 58 |
| *H. sodalis* | 0800-1700 | 1.42-3.29 | 20.0-28.9 | 43-73 |
| Sub-total | 0700-1900 | 0.39-3.39 | 15.6-31.7 | 33-89 |
| *T. atratus* | - | - | - | - |
| *T. catenatus* | 1000-1600 | 2.23-3.26 | 22.2-28.3 | 43-62 |
| *T. lineola* | 0800-1800 | 0.87-3.29 | 20.6-30.0 | 38-76 |
| *T. quinquevittatus* | 0700-1900 | 0.25-3.39 | 20.0-30.0 | 38-91 |
| *T. similis* | 0600-1900 | 0.31-3.36 | 17.2-31.7 | 39-84 |
| Subtotal | 0600-1900 | 0.25-3.38 | 17.2-31.7 | 38-91 |
| TOTAL | 0600-1900 | 0.25-3.39 | 15.6-31.7 | 33-91 |

h Eastern standard time

* Solar radiation ($MJ/m^2$)

°C Temperature °C

RH Relative humidity %

Table 19. Wing length and number of ovarioles of *Tabanus* females from southwestern Quebec 1980-81

| Species | # | Wing length (mm) X ± SD | Ovarioles Y ± SD |
|---|---|---|---|
| *T. atratus* | 1 | 20.5 | 592 |
| *T. catenatus* | 1 | 18.9 | 610 |
| *T. lineola* | 17 | 10.41 ± 0.61 | 515.65 ± 76.07 |
| *T. quinquevittatus* | 126 | 9.44 ± 0.50 | 250.91 ± 37.56 |
| *T. similis* | 32 | 11.24 ± 0.47 | 602.94 ± 60.92 |

Table 20. Comparison of wing length and potential fecundity of *Tabanus* females collected in 1980 and 1981

| Species | Years | # | Wing (mm) X ± SD | Ovarioles Y ± SD |
|---|---|---|---|---|
| *T. lineola* | 1980 | 9 | 10.06 ± 0.54 | 474.67 ± 78.67 |
| | 1981 | 8 | 10.81 ± 0.42 ** | 561.75 ± 39.55 ** |
| *T. quinquevittatus* | 1980 | 62 | 9.45 ± 0.51 | 246.81 ± 36.65 |
| | 1981 | 64 | 9.43 ± 0.48 n.s. | 254.88 ± 38.28 n.s. |
| *T. similis* | 1980 | 8 | 11.36 ± 0.51 | 584.25 ± 62.34 |
| | 1981 | 24 | 11.20 ± 0.45 n.s. | 609.17 ± 60.47 n.s. |

\# Number of specimens dissected

n.s. not significant

** significant at .01 level

## V GENERAL DISCUSSION AND FUTURE AREAS OF RESEARCH

Male aggregation sites are unique in that they permit observations on several species in limited time and space. At the top of Mount Rigaud, males were more abundant and usually had a longer seasonal distribution than females of the same species. Males of tabanid species avoided competition by having different seasonal distributions and peaks of abundance, different diurnal patterns of activity and behaviors (hovering, waiting). Hovering is not necessarily characteristic of all members of the genus *Hybomitra* since *H. microcephala* males waited instead of hovered. Incidence of nectar meal was related to male behavior; in hovering males it was twice that of waiting males.

Pollen analysis was useful in determining the species of flowers visited by male tabanids. Most common or abundant pollen or pollenia found on *H. sodalis* males came from nectariferous plants with large inflorescences. These flowers probably facilitate the collection of nectar while providing a landing platform for male tabanids. Further studies should compare the pollen found in the diverticula (where the nectar meal is stored) with the pollen found on the fly to further define the flowers visited versus the ones providing nectar.

Future research projects should take advantage of the fact that hovering males are large, easy to collect, and active during a much longer period than waiting males. A precise topography of Mount Rigaud summit coupled with marking and capture-recapture methodology might help to characterize preferred hovering sites of different species. An hourly record of males collected and climatic factors would help to define (1) the diurnal pattern of male activity in relation to climatic factors, (2) the time spent by males on the summit and (3) the frequency of their visits to the summit. An understanding of the effect of climatic factors on male diurnal activity and detailed description of hovering sites might help to locate male aggregation sites in flatland areas.

The diurnal pattern of male activity of *C. fuliginosus* has been correlated with temperature and male attitude (head up and head down position; Catts and Olkowski 1972). Additional studies on Mount Rigaud could verify if a similar attitude is taken by males of other *Chrysops* species.

Anautogeny prevailed in horse fly females collected in the present study. Most *Hybomitra* and *Tabanus* species are obligatory blood feeders. They should be considered as pests of humans and livestock. No more than one gonotrophic cycle was detected by ovarian dissection although there was evidence of the start of a second based on the presence of fresh blood in parous females of anautogenous species. Laboratory rearings are required to determine if there is a correlation between the number of ovariole sheath dilatations and the number of gonotrophic cycles completed. If only one dilatation develops after more than one gonotrophic cycle, it would mean that ovarian dissection is not reliable for evaluating the number of completed gonotrophic cycles. Determining the mean number of gonotrophic cycles completed by females of different species would help to define the mean number of blood meals taken by females and consequently their importance as pests. It could also determine the mean egg production by females of different species by adding the number of eggs laid after each gonotrophic cycle.

Egg-sac dilatations of the ovariole sheath of tabanids is an indication of recent oviposition (Thomas 1972). Information on egg-sac dilatations has not been systematically recorded in most tabanid ovarian studies and there is a need for this information. Further laboratory studies should consider the time required by the ovariole sheath to contract and form a distinct yellow body. Confirmation of the work of Thomas (1972) might provide more credibility for estimations of oviposition

periods based on ovariole sheath dilatations.

Further ovarian studies might consider the recording of sperm presence, a factor largely overlooked in preceding studies. Insemination generally occurs prior to blood feeding but did not seem to be a prerequisite to host-seeking behavior in this study. The higher incidence of sperm in pars compared to nullipars is perhaps related to their being older and having greater chances of being intercepted by a male. The proportion of unmated parous females could give an indication of the proportion of unfertilized egg masses in the field. The evidence presented in section 4.5 (*H. epistates*) may indicate that sperm presence could be useful in predicting population fluctuations. Sperm presence could become an important variable in studies of tabanid population dynamics.

Based on the high incidence of sugar in the diverticula of horse flies, it is suggested that sugars are essential dietary nutrients during their entire adult life. The high incidence of sugar meals in tabanids suggests that it provides the energy to fuel their basic metabolic activities. Evaluation of the incidence of sugar feeding using the anthrone test should be performed on the diverticula of tabanids instead from whole insects to prevent contamination from crushed insect body parts.

The proportion of blood fed horse flies was very low (3%) in southwestern Quebec. This might indicate that a very high number of specimens would be required to obtain significant results in a study of the host range of different species by serological analysis.

Carbon dioxide increased by almost 6-fold the number of horse flies collected in Canopy traps. Carbon dioxide would be an advantage in studies where large number of specimens are required for biological studies or pathogen screening. The attractiveness of carbon dioxide to nullipars and pars was shown to vary from year to year in most species; sometimes the pattern of attraction of pars and nullipars differed from year to year for the same species. Trends were more stable for the two most abundant species *H. lasiophthalma* and *T. quinquevittatus*. It is suggested that the interpretation of the attractiveness of carbon dioxide to parous and nulliparous tabanid females should be made with caution, especially if it is based on less abundant species and one sampling season.

The number of ovarioles was found to differ drastically between *Tabanus* species, suggesting that different reproductive strategies might be used by different species. Number of ovarioles and wing length were useful characters for intra, interspecific, and seasonal comparisons. It is believed that populations in different geographical areas could also be compared using these parameters. In future studies, comparison of the number of ovarioles and the number of eggs produced would help to define the proportion of active ovarioles and assess the validity of physiological age determination based on ovariole examination.

## VI LITERATURE CITED


Alverson, D.R. and R. Noblet. 1977. Activity of female Tabanidae (Diptera) in relation to selected meteorological factors in South Carolina. J. Med. Entomol. 14: 197-200.

Anderson, J.R., W. Olkowski and J.G. Hoy. 1974. The response of tabanid species to $CO_2$-baited insect flight traps in northern California (Diptera: Tabanidae). Pan-Pac. Entomol. 50: 255-68.

Anwyl, R. 1972. The structure and properties of an abdominal stretch receptor in *Rhodnius prolixus*. J. Insect Physiol. 18: 2143-53.

Auroi, C. 1982. Physiological age of tabanid (Diptera) populations in Switzerland. J. Med. Entomol. 19: 281-84.

Bailey, N.S. 1948. The hovering and mating of Tabanidae: a review of the literature with some original observations. Ann. Entomol. Soc. Am. 41: 403-12.

Baribeau, L. and A. Maire. 1983a. Latitudinal distribution of Quebec Tabanidae. Mosq. News 43: 7-13.

Baribeau, L. and A. Maire. 1983b. Spatial distribution of Tabanidae (adults and larvae) in two bogs of southern Quebec. Mosq. News 43: 24-29.

Baribeau, L. and A. Maire. 1983c. Abundance and seasonal distribution of Tabanidae in a temperate and in a subarctic locality of Quebec. Mosq. News 43: 135-43.

Bidlingmayer, W.L. and D.G. Hem. 1973. Sugar feeding by Florida mosquitoes. Mosq. News 33: 535-38.

Blickle, R.L. 1959. Observations on the hovering and mating of *Tabanus bishoppi* Stone (Diptera: Tabanidae). Ann. Entomol. Soc. Am. 52: 183-90.

Bosler, E.M. and W.J. Hansens. 1974. Natural feeding behavior of adult saltmarsh greenheads, and its relation to oogenesis. Ann. Entomol. Soc. Amer. 67: 321-24.

Burnett, A.M. and K.L. Hays. 1974. Some influences of meteorological factors on flight activity of female horseflies (Diptera: Tabanidae). Environ. Entomol. 3: 515-21.

Cameron, A.E. 1926. Bionomics of the Tabanidae (Diptera) of the Canadian prairie. Bull. Entomol. Res. 17: 1-42.

Catts, E.P. 1970. A Canopy trap for collecting Tabanidae. Mosq. News 30: 472-74.

Catts, E.P. and W. Olkowski. 1972. Biology of Tabanidae (Diptera): mating and feeding behavior of *Chrysops fuliginosus*. Environ. Entomol. 1: 448-53.

Chagnon, G. and O. Fournier. 1943. Les tabanides du Québec. Nat. Can. 70: 49-84.

Chapman, J.A. 1954. Studies on summit-frequenting insects in western Montana. Ecology 35: 41-49.

Christopher, S.R. 1911. The development of the egg follicle in anophelines. Paludism 2: 73-79.

Chvala, M., L. Lyneborg and J. Moucha. 1972. The horse flies of Europe (Diptera, Tabanidae). Entomol. Soc. Copenhagen. 500pp.

Colless, D.H. and W.T. Chellapah. 1960. Effects of body weight and size of blood-meal upon egg production in *Aedes aegypti* (Linnaeus) (Diptera, Culicidae). Ann. Trop. Med. Parasitol. 54: 475-82.

Dale, W.E. and R.C. Axtell. 1975. Flight of the salt marsh Tabanidae (Diptera), *Tabanus nigrovittatus, Chrysops atlanticus* and *C. fuliginosus*: Correlation with temperature, light, moisture and wind velocity. J. Med. Entomol. 12: 551-57.

Davies, D.M. 1959. Seasonal variation of tabanids (Diptera) in Algonquin Park, Ontario. Can. Entomol. 91: 548-53.

DeFoliart, G.R., R.O. Anslow, R.P. Hanson, C.D. Morris, O. Papadopoulous and G.E.

Sather. 1969. Isolation of Jamestown Canyon serotype of California encephalitis virus from naturally infected *Aedes* mosquitoes and tabanids. Amer. J. Trop. Med. Hyg. 18: 440-47.

Detinova, T.S. 1962. Age-grouping methods in Diptera of medical importance. Wld. Hlth. Organ., Geneva. 216 pp.

Downes, J.A. 1969. The swarming and mating flight of Diptera. Annu. Rev. Entomol. 14: 271-98.

Engelman, F. 1970. The physiology of insect reproduction. Pergamon Press. New York. 307pp.

Freeman, T.N. 1953. Interim report of the distribution of the tabanids obtained in the northern insect survey. Defence Res. Board EP Tech. Report 4: 1-35.

Friend, W.G. 1978. Physical factors affecting the feeding responses of *Culiseta inornata* to ATP, sucrose, and blood. Ann. Entomol. Soc. Am. 71: 935-40.

Friend, W.G. 1981. Diet destination in *Culiseta inornata*: effect of feeding conditions on the response to ATP and sucrose. Ann. Entomol. Soc. Am. 74: 151-54.

Friend, W.G. and J.G. Stoffolano, Jr. 1983. Feeding response of the horsefly, *Tabanus nigrovittatus*, to phagostimulants. Phys. Entomol. 8: (in press).

Friend, W.G. and J.G. Stoffolano, Jr. 1984. Feeding responses of the horsefly, *Tabanus nigrovittatus* to physical factors, ATP analogues and blood fractions. (unpublished).

Golini, V.I. and R.E. Wright. 1978. Relative abundance and seasonal distribution of Tabanidae (Diptera) near Guelph, Ontario. Can. Entomol. 110.: 385-98.

Hines, J.S. 1906. Habits and life histories of some flies of the family Tabanidae. USDA. Bur. Entomol. Tech. Series 12, Part II. 19-36.

Hocking, B. 1953. The intrinsic range and speed of flight of insects. Trans. R. Entomol. Soc. London. 104: 223-345.

James, H.G. 1963. Larval habitats, development, and parasites of some tabanids (Diptera) in southern Ontario. Can. Entomol. 95: 1223-32.

Kniepert, F.-W. 1980. Blood feeding and nectar feeding in adult Tabanidae (Diptera). Oecologia (Berl.) 46: 125-29.

Krinski, W.L. 1976. Animal disease agents transmitted by horse flies and deer flies (Diptera: Tabanidae). J. Med. Entomol. 13: 225-75.

Lall, S.B. 1969. Phagostimulants of haematophagous tabanids (Diptera). Entomol. Exp. Appl. 12: 326-36.

Lall, S.B. 1970a. Feeding behavior of haematophagous tabanids (Diptera). J. Med. Entomol. 7: 115-19.

Lall, S.B. 1970b. Carbohydrate meals of haematophagous tabanids (Diptera). J. Med. Entomol. 7: 127-30.

Laird, M., A. Aubin, M.M. Chance, F.J.H. Freeden, W.O. Haufe, H.B.N. Hynes, D.J. Lewis, I.S. Lindsay, D.M. McLean, G.H. Surgeoner, D.M. Wood and M.D. Sutton. 1979. Biting flies of Canada: Health effects and economic consequences. Natl. Res. Council Canada. Publ. 19248. 157pp.

Lane, R.S. and J.R. Anderson. 1982. The reproductive life history and blood meal sources of *Chrysops hirsuticallus* (Diptera: Tabanidae). J. Med. Entomol. 19: 157-63.

Lane, R.S. and J.R. Anderson. 1983. Multiple autogeny and burrow oviposition by a marine horse fly (Diptera: Tabanidae). J. Med. Entomol. 20: 212-13.

Lane, R.S., J.R. Anderson and C.B. Philip. 1983. Biology of autogenous horse flies native to coastal California: *Apatolestes actites* (Diptera: Tabanidae). Ann. Entomol. Soc. Am. 76: 559-71.

Lavigne, R.J., M.H. Bloom and W.A. Neys. 1968. Adult behavior of *Tabanus reinwardtii* and *Chrysops fulvaster* (Diptera: Tabanidae). Sci. Monogr. 12 Ag. Exp. Stat., Univ. Wyoming, Laramie, Wyoming. 1-37.

Leprince, D.J. and D.J. Lewis. 1982. Seasonal distribution of adult horse flies and deer flies (Diptera: Tabanidae) at lac Boivin, Granby, Quebec. Ann. Entomol. Soc. Quebec 27: 94-99.

Leprince, D.J. and D.J. Lewis. 1983. Aspects of the biology of female *Chrysops univittatus* (Diptera: Tabanidae) in southwestern Quebec. Can. Entomol. 115: 421-25.

Leprince, D.J., D.J. Lewis and J. Parent. 1983. Biology of male tabanids aggregating on a mountain summit in southwestern Quebec. J. Med. Entomol. 20: 608-13.

Lewis, D.J. and G.F. Bennett. 1977. Biting flies of the eastern Maritime Provinces of Canada. I. Tabanidae. Can. J. Zool. 55: 1493-503.

Lewis, D.J. and D.J. Leprince. 1981. Horse flies and deer flies (Diptera: Tabanidae) feeding on cattle in southwestern Quebec. Can. Entomol. 113: 883-86.

Lutta, A.S. 1970. Slepni (Diptera, Tabanidae) Karelii, 313 pp., Leningrad. (in Chvala *et al.* 1972).

Maddrel, S.H.P. 1963. Control of ingestion in *Rhodnius prolixus* Stal. Nature (Lond.) 198: 210.

Magnarelli, L.A. 1976. Physiological age of Tabanidae (Diptera) in eastern New York State, U.S.A. J. Med. Entomol. 12: 679-82.

Magnarelli, L.A. and J.F. Anderson. 1979. Oviposition, fecundity, and fertility of the salt marsh deer fly, *Chrysops fuliginosus* (Diptera: Tabanidae). J. Med. Entomol. 15: 176-79.

Magnarelli, L.A. and J.F. Anderson. 1980a. Feeding behavior of Tabanidae (Diptera) on cattle and serologic analyses of partial blood meals. Environ. Entomol. 9: 664-67.

Magnarelli, L.A. and J.F. Anderson. 1980b. Parasitism of *Tabanus nigrovittatus* immatures (Diptera: Tabanidae) by *Trichopria* sp. (Hymenoptera: Diapriidae). J. Med. Entomol. 17: 481-82.

Magnarelli, L.A. and J.F. Anderson. 1981. Sugar feeding by female tabanids (Diptera: Tabanidae) and its relation to gonotrophic activity. J. Med. Entomol. 18: 429-33.

Magnarelli, L.A. and J.F. Anderson and J.H. Thorne. 1979. Diurnal nectar-feeding of salt marsh Tabanidae (Diptera). Environ. Entomol. 8: 544-48.

Magnarelli, L.A. and L.L. Pechuman. 1975. Ovarian studies of *Tabanus quinquevittatus* (Diptera: Tabanidae). J. Med. Entomol. 11: 687-90.

Magnarelli, L.A. and J.G. Stoffolano. 1980. Blood feeding, oogenesis, and oviposition by *Tabanus nigrovittatus* in the laboratory. Ann. Entomol. Soc. Am. 73: 14-17.

Matthysse, J.G., D.E. Mock and H.R. Netherton. 1974. Seasonal flight period and relative abundance of Tabanidae (Diptera) near Ithaca, New York. Ann. Entomol. Soc. Am. 67: 158-66.

Mer. G.G. 1936. Experimental study on the development of the ovary in *Anopheles elutus* (Dipt. Culic.). Bull. Entomol. Res. 27: 351-59.

Miller, B.R., K.O. Kloter, B.J. Beaty and L.A. Magnarelli. 1983. Nonreplication of Jamestown Canyon and Keystone (California group) viruses in tabanids (Diptera: Tabanidae). J. Med. Entomol. 20: 214-15.

Miller, L.A. 1951. Observations on the bionomics of some northern species of Tabanidae (Diptera). Can. J. Zool. 29: 240-63.

Mullens, B.A. and R.R. Gerhardt. 1979. Feeding behavior of some Tennessee Tabanidae. Environ. Entomol. 8: 1047-51.

Pechuman, L.L. 1964. A list of Tabanidae (Diptera) of Quebec. Can. Entomol. 96: 1495-96.

Pechuman, L.L. 1981. The horse flies and deer flies of New York (Diptera: Tabanidae) (2nd ed.). Search (Ithaca) 18: 1-68.

Pechuman, L.L. and J.J.S. Burton. 1969. Seasonal distribution of Tabanidae (Diptera) at Texas Hollow, New York in 1968. Mosq. News 29: 216-20.

Philip, C.B. 1963. Records of Tabanidae from Labrador and Newfoundland. Opusc. Entomol. 27: 230-36.

Robert, A. 1958. Les tabanides du parc Mont Tremblant. Ann. Entomol. Soc. Quebec. 4: 25-32.

Roberts, R.H. 1965. A steer-baited trap for sampling insects affecting cattle. Mosq. News 25: 281-85.

Roberts, R.H. 1969. Biological studies of Tabanidae: a preliminary study of female tabanids attracted to a bait animal. Mosq. News 29: 236-38.

Roberts, R.H. 1970. Tabanidae collected in a Malaise trap baited with $CO_2$. Mosq. News 30:52-53.

Roberts, R.H. 1971. Effect of amount of $CO_2$ on collection of Tabanidae in Malaise traps. Mosq. News 31: 551-58.

Roberts, R.H. 1972a. Relative attractiveness of $CO_2$ and a steer to Tabanidae, Culicidae, and *Stomoxys calcitrans* (L.). Mosq. News 32: 208-11.

Roberts, R.H. 1972b. The effectiveness of several types of Malaise traps for the collection of Tabanidae and Culicidae. Mosq. News 32: 542-47.

Roberts, R.H. 1975. Relationship between the amount of $CO_2$ and the collection of Tabanidae in Malaise traps. Mosq. News 35: 150-4.

Roberts, R.H. 1976. The comparative efficiency of six trap types for the collection of Tabanidae (Diptera). Mosq. News 36: 530-35.

Roubaud, E. 1929. Cycle autogène d'attente et générations hivernales suractives inapparentes chez le moustique commun, *Culex pipiens* L. C. R. Acad. Sci. Paris 188: 735-38.

Shemanchuk, J.A. 1978. A bait trap for sampling the feeding populations of blood-sucking Diptera on cattle. Quaest. Entomol. 14: 433-39.

Smith, S.M., D.M. Davies, and V.I. Golini. 1970. A contribution to the bionomics of the Tabanidae (Diptera) of Algonquin Park, Ontario: seasonal distribution, habitat preferences, and biting records. Can. Entomol. 102: 1461-73.

Spielman, A. 1971. Bionomics of autogenous mosquitoes. Annu. Rev. Entomol. 16: 231-48.

Stoffolano, J.G. Jr. 1983. Destination of the meal and the effect of a previous sugar or blood meal on subsequent feeding behavior in female *Tabanus nigrovittatus* (Diptera: Tabanidae). Ann. Entomol. Soc. Am. 76: 452-54.

Surcouf, J.M.R. 1908. Les tabanides de France et des pays Limitrophes. Encyc. Entomol. Sér. A5, Paris. Lechevalier. 261pp.

Tashiro, H. and H.H. Schwardt. 1949. Biology of the major species of horseflies of central New York. J. econ. Entomol. 42: 269-72.

Tashiro, H. and H.H. Schwardt. 1953. Biological studies of horse flies in New York. J. econ. Entomol. 46: 813-22.

Teskey, H.J. 1960. Survey of insects affecting livestock in southwestern Ontario. Can. Entomol. 92: 531-44.

Teskey, H.J. 1969. Larvae and pupae of some eastern North American Tabanidae (Diptera). Mem. Entomol. Soc. Canada 63: 1-147.

Teskey, H.J. 1979. Suborder Brachycera. In Danks, H.V. (ed.): Canada and its insect fauna. Mem. Entomol. Soc. Canada. 108: 405-07.

Thibault, J. and P.P. Harper. 1983. Les peuplements de taons (Diptères; Tabanidae) d'une forêt des basses-Laurentides: inventaire, phénologie, activité et habitats. Nat. Can. 110: 27-36.

Thomas, A.W. 1972. Physiological age structure of adult tabanid populations (Diptera: Tabanidae) in Alberta, Canada. J. Med. Entomol. 9: 295-300.

Thomas, D.J. 1980. New records for some Canadian horse flies and deer flies (Diptera: Tabanidae). Entomol. News 91: 59-60.

Thompson, P.H. 1967. Abundance and seasonal distribution of the Tabanidae (Diptera) of the Great Swamp, New Jersey. Ann. Entomol. Soc. Am. 60: 1255-60.

Thompson, P.H. 1969. Collecting methods of Tabanidae. Ann. Entomol. Soc. Am. 62: 50-57.

Thompson, P.H. and L.L. Pechuman. 1970. Sampling populations of *Tabanus quinquevittatus* about horses in New Jersey, with notes on the identity and ecology. J. Econ. Entomol. 63: 151-155.

Thorsteinson, A.J., G.K. Bracken and W. Hanec. 1965. The orientation behavior of horse flies and deer flies (Tabanidae, Diptera). III. The use of traps in the study of orientation of tabanids in the field. Entomol. Exp. and Appl. 8: 189-92.

Townes, H. 1962. Design for a Malaise trap. Proc. Entomol. Soc. Wash. 64: 253-62.

Troubridge, D.A. and D.M. Davies. 1975. Seasonal changes in physiological age composition of tabanid (Diptera) populations in southern Ontario. J. Med. Entomol. 12: 453-57.

Van Handel, E. 1972. The detection of nectar in mosquitoes, Mosq. News 32: 458.

Wellington, W.G. 1974. Changes in mosquito flight associated with natural changes in polarized light. Can. Entomol. 106: 941-48.

Winn, A.F. and G. Beaulieu. 1932. A preliminary list of the insects of the Province of Quebec. Part II. Diptera. Revised and supplemented by C.E. Petch and J.B. Maltais. Suppl. 24th Rep. Qué. Prot. Plant.: 3-100.

Wright, R.E., R.O. Anslow, W.H. Thompson, G.R. DeFoliart, G. Seawright and R.P. Hanson. 1970. Isolation of LaCrosse virus of the California group from Tabanidae in Wisconsin. Mosq. News 30: 600-03.