ETHOLOGY OF ADULT SIMULIDAE (DIPTERA)

(WITH DISCRIPTION OF A NEW SPECIES FROM NORWAY)

OBSERVATIONS ON SOME FACTORS INVOLVED IN THE HOST-SEEKING BEHAVIOUR OF SIMULIIDS (DIPTERA) IN ONTARIO AND NORWAY

By

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Dedicated

to

those

who

always

search

objectively

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truth

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SCOPE AND CONTENTS:

This study was conducted to elucidate and to compare some factors which influence the host-seeking behaviour of adult female simuliids in two geographically isolated regions. Various observations and experiments were performed with the knowledge of a mechanism inherent in the feeding behaviour of simuliids. This approach has helped to clarify the orientation of simuliids to their hosts and has enhanced the understanding of the transmission of parasites by these flies. Further, it was found valuable to determine whether the behaviour state of simuliids influenced their reaction to visual stimuli.

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TABLE OF CONTENTS

INTRODUCTION

Importance and Feeding Habits of Some Holarctic Black-flies

Among the haematophagous Diptera those belonging to the family Simuliidae have a world-wide medical and economic significance. Simuliids, commonly known as black-flies, affect animals and man both by their bites and as intermediate hosts of various parasites. Although in some tropical regions of the world some species of simuliids are known to transmit the filarial parasite, Onchocerca volvulus Leuckart to man (Blacklock, 1926; Gibson and Dalmat, 1952; Lewis, 1953; Dalmat, 1954), in Europe and North America transmission of pathogens by these flies is restricted primarily to animals, particularly, birds.

In North America at least two simuliid species have been known to transmit the haemosporidian, Leucocytozoon simondi Mathis and Leger, to various species of ducks, often resulting in considerable mortalities (Twinn, 1933; Fallis et al, 1951, 1956; Anderson et al, 1962; Fallis and Bennett, 1966; Khan and Fallis, 1968). Other simuliid species have been found to be vectors of Leucocytozoon smithi (Lavern and Lucet) to turkeys, (S. [illegible]) often causing notable economic losses (Calvin and Richey, 1955). Some black-flies in Ontario have been reported to transmit Ornithofilaria fallisensis Anderson to domestic and wild ducks (Anderson, 1956) and various forms of blood protozoa to a number of other bird species (Fallis and Bennett, 1958; Bennett and Fallis, 1960; Fallis and Bennett, 1960; Bennett, 1961; Fallis and Bennett, 1962).

In other cases the importance of simuliids is not directly associated with their transmission of pathogens. In most parts of the world during periods of outbreak, black-flies make work outdoors virtually impossible for man (Riley, 1887; Jobbins-Pomeroy, 1916; Davies and Peterson, 1956; Davies, Peterson and Wood, 1962; Montshadsky, 1956; Rubtzov, 1956), and cause a marked decline in productivity of livestock (Breev, 1950; Rubtzov, 1956; Anderson and Vaskuil, 1963; Ussova, 1961). In extreme cases, toxemia and excessive anemia through loss of blood from bites of black-flies may result in the death of the host (Millar and Rempel, 1944; Garside and Darling, 1952; Anderson *et al*, 1962; Fredeen, 1969).

Among the simuliids, however, the blood-sucking habit is restricted only to females of certain species; whereas, other black-fly species are known to be autogenous for the first gonotrophic cycle, some even emerging with mature eggs (Rubtzov, 1956; Davies and Peterson, 1956; L. Davies, 1954, 1961) hence obviating the need of a blood meal. Nonetheless, many species of simuliids in Ontario require a blood meal for the second and subsequent gonotrophic cycles, and often the first (Davies *et al*, 1962). The majority of these species obtain blood meals from either birds or mammals; only a few reports exist of simuliids feeding on poikilotherms (Davies and Peterson, 1956; Smith, 1969).

On the basis of their feeding habits, therefore, simuliids in Ontario can be divided into two general groups (Davies and Peterson, 1956; Peterson and Wolfe, 1956; Downe and Morrison, 1957; Davies *et al*, 1962)

Group I: Non-haematophagous species

Twinnia tibblesi Stone and Jamnback
Cnephia (*Greniera*) *abditoides* Wood
Cnephia (*Cnephia*) *dacotensis* (Dyar and Shannon)
Simulium (*Eusimulium*) *baffinense* Twinn

Group II: Haematophagous species

This group comprises a large assemblage of simuliids which are known to feed preferentially on either birds or mammals, and on the basis of such host preferences they have been divided into two subgroups:

A. Ornithophilic species, feeding mainly on birds:

Prosimilium (*Parahelodon*) *decemarticulatum* (Twinn),
Cnephia (*Ectemia*) *invenusta* (Walker), *C.* (*G.*) abdita Peterson
Cnephia (*Cnephia*) *ornithophilia* Davies, Peterson and Wood,
Simulium (*Byssodon*) *rugglesi* Nicholson and Mickel,
and many additional *Simulium* (*Eusimulium*) species.

B. Mammaliophilic species, feeding primarily on mammals:

Prosimulium (*Prosimulium*) *fuscum* Syme and Davies
" " *fontanum* S. and D.
" " *magnum* Dyar and Shannon
" " *mixtum* S. and D.
Cnephia (*Stegopterna*) *mutata* (Malloch)
Simulium (*Psilozia*) *vittatum* Zetterstedt
" (*Hagenomyia*) *longistylatum* Shewell
" " *pictipes* Hagen
" (*Simulium*) *decorum* Walker
" " *tuberosum* (Lundstrum)
" " *venustum* Say
" " *parnassum* Malloch

In northeastern Europe various species of simuliids have been reported as vicious bloodsuckers of man and other mammals (Rubtzov, 1932, 1956;

Montshadsky, 1956; Breev, 1950; Berzina, 1953; Ussova, 1961). On the other hand, in northwestern Europe, specifically in Scandinavia, little is known of the importance of black-flies as pests and as vectors of parasites to animals. A few feeding records of black-flies have been reported from Denmark (Petersen, 1924) and from Norway and Sweden (Carlsson, 1962), but these records appear to be incomplete and often doubtful. Hence, little distinction is made in these reports between mammal-feeding and bird-feeding species. In fact, several *Simulium* (*Eusimulium*) species which would normally be considered as avian feeders, based on studies made in North America (Shewell, 1955; Bennett, 1960; Anderson and DeFoliart, 1961), are reported for Scandinavia to feed probably on mammals. The feeding records of some of the haematophagous simuliids as reported by Petersen (1924) and Carlsson (1962) include the following species:

1. Simuliids reported to feed mainly on mammals:

Prosimulium (*Helodon*) *ferrugineum* (Wahlb.), *P.* (*Prosimulium*) *hirtipes* (Fries), *P.* (*P.*) *nigripes* End., *Cnephia pallipes* (Fries), *C. tridecimata* Edw., *Simulium* (*Eusimulium*) *aureum* Fries, *S.* (*E.*) *angustitarse* (Lundst.), *S.* (*E.*) *bicorne* Dor. & Rubtz., *S.* (*E.*) *costatum* Friedr., *Simulium* (*Schönbaueria*) *pusilla* Fries, *S.* (*Wilhelmia*) *equina* (L.), *S.* (*W.*) *salopiense* Edw., *S.* (*Boophthora*) *erythrocephala* De Geer, *S.* (*Gnus*) *forsi* (Carlsson), *S.* (*Odagmia*) *ornata* Mg., *S.* (*O.*) *monticola* Friedr., *S.* (*Simulium*) *tuberosum* (Lundstr.), *S.* (*S.*) *vulgare* Rubtz., *S.* (*S.*) *argyreatum* Mg. (as *decorum* Walk.) *S.* (*S.*) *morsitans* Edw., *S.* (*S.*) *truncatum* Lundstr. (as *venustum* Say).

2. Simuliids reported by Carlsson (1962) to feed probably on birds:

Simulium (*Eusimulium*) *aureum* Fries, *S.* (*E.*) *latipes* (Mg.). Other simuliids have been reported, judging from their poorly developed mouth parts, as non-haematophagous species (L. Davies, 1954; Carlsson, 1962). These include:

Prosimulium (*P.*) *ursinum* (Edw.)
" " *macropyga* (Lundstr.)
Cnephia (*C.*) *lapponica* (End.)
Simulium (*E.*) *baffinense* Twinn

Little knowledge exists, therefore, of the feeding habits of many of these haematophagous simuliids from Scandinavia. On the other hand, extensive studies made primarily in Canada on the host-seeking and feeding behaviour of some simuliid species have enhanced the understanding of their role as pests and as vectors of haematozoa to various species of birds (Davies and Peterson, 1956; Bennett, 1960; Anderson and DeFoliart, 1961; Bennett, 1963; Lowther and Wood, 1964; Fallis, 1964; Fallis and Smith, 1964; Smith, 1966; Fallis and Bennett, 1966; Fallis *et al*, 1967). A comparative study of some factors affecting the host-seeking behaviour of various species of adult female simuliids in Ontario and Norway was made, therefore, to elucidate further the role of these flies as pests and vectors in these two geographically isolated regions.

Orientation of Haematophagous Flies to their Hosts

In laboratory studies of the orientation mechanism of bloodseeking anopheline mosquitoes Laarman (1955, 1958) indicated that host-seeking consists of a special type of behaviour pattern in which both internal and external stimuli play specific parts. In this connection he considered that several factors acting as external stimuli effect the orientation to a host by these mosquitoes. He divided these factors into:

(a) visual ones, e.g., size, colour, contrasting action, reflection of light, shape.

(b) physical ones, e.g., radiation and convective heat, moisture, sound, surface structure.

(c) chemical ones, e.g., carbon dioxide and a large number of other complex factors generally considered as "odours".

Referring to observations on the behavioural mechanism of other animals (Craig, 1918; Tinbergen, 1942; Dethier, 1947), Laarman (1955) suggested, in addition, that the insect's need for a blood-meal leads to a searching or "appetitive behaviour" which induces the insect to follow a chain of behavioural responses, each being released by a particular stimulus. At the end of this chain of reactions, if undisturbed, the insect will have satisfied its appetite.

Unlike mosquitoes, black-flies do not lend themselves to experimental study of orientation behaviour in the laboratory. Nonetheless, workers studying the host-seeking behaviour of female simuliids under field conditions have adopted similar concepts as those used for mosquitoes under laboratory conditions. Davies (1952) in an investigation of the activity of females of *Simulium venustum* as influenced by meteorological factors considered that flying, attraction, landing, and biting sequentially followed one another. In a detailed account of an analogous phenomenon, Smith (1966) constructed a theoretical hierarchy consisting of a number of behavioural stages considered to act in a sequential fashion in the feeding behaviour of simuliids and tabanids. He divided this hierarchy into six stages, the first four being the following:

1) Appetitive behaviour, 2) Upwind orientation, 3) Near orientation,

and 4) Landing behaviour.

The first stage, appetitive behaviour, is considered to involve the selection by the particular simuliid species of a habitat in which the host is likely to be found. Several investigations on this aspect in North America have revealed that some species of ornithophilic simuliids possess feeding habits inherently associated with host and habitat preferences (Bennett, 1960; Anderson and De Foliart, 1961; Fallis and Smith, 1964). These workers have shown that Simulium rugglesi and S. (E.) euryadminiculum Davies are taken in largest number within a narrow zone near the water's edge than away from water. In his investigation, Bennett (1960) exposed eight pairs of ducks at ground level at approximately 50-ft intervals in a line directed from the edge of a lake into the forest. Most females of S. rugglesi, an average of 83%, were collected in the first 50 ft from the water's edge. Further evidence that S. rugglesi is specifically restricted within a narrow zone of a lakeshore habitat has been provided by Fallis and Bennett (1966) who have shown that the rates of parasitaemias of L. simondi in domestic ducks exposed at water level are greater than in ducks exposed at some elevation above water surface.

Confirmation of habitat and host specificity of simuliids was reported in Wisconsin where many engorged S. rugglesi were collected mainly from domestic and wild ducks at ground level in a marsh habitat (Anderson and De Foliart, 1961). Other ornithophilic species, viz. S. (E.) aureum, S. (E.) johanseni Hart, and S. (B.) meridionale Riley, were collected preferentially in forested areas and were more abundant in lower canopy levels than at ground level on birds other than the Anatidae. Fallis and

Smith (1964), in addition, confirmed earlier reports of habitat and host specificity for *S.* (*E.*) *euryadminiculum* (Davies and Peterson, 1957; Lowther and Wood, 1964), which was shown to frequent entirely river and lake habitats and to be strictly host specific in its host-finding and feeding behaviour. Considering that habitat preference is of notable significance for an understanding of the host-finding behaviour of simuliids, Bennett (1960) divided the ornithophilic simuliids into two major groups. The first group comprised simuliids taken feeding preferentially on anseriform birds by a lake or river habitat, viz. *S. rugglesi*, *S.* (*E.*) *anatinum* Wood (= *Simulium* H of Bennett) and *S.* (*E.*) *euryadminiculum*. The second group comprised simuliids taken feeding preferentially on aboreal avian hosts in the forest habitat at some height above ground level, and these include:

Cnephia (*Ectemia*) *invenusta* (Walker)
Cnephia (*Cnephia*) *ornithophilia* Davies, Peterson and Wood
(= *Cnephia* U of Bennett)
Prosimulium (*Prosimulium*) *decemarticulatum* (Twinn)
Simulium (*Eusimulium*)* *aureum* Fries
" " *croxtoni* Nicholson and Mickel
" " *latipes* Meigen
" " *quebecence* Twinn

Simulium venustum is a ubiquitous species; hence, it is found both by open water and in forest habitats.

Although such a division of ornithophilic simuliids is a practical

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*To delineate these ornithophilic species and their relatives, they will be referred to as *Eusimulium* species throughout the text.

and significant one, Bennett (1960) pointed out that some overlapping of species into the two habitats may occur. Smith (1966), however, contended that habitat preferences are stricter than Bennett (1960) had indicated, since typical lakeshore species, such as S. rugglesi and E. euryadminiculum, are absent from the forest habitat, and typical arboreal simuliids, such as P. decemarticulatum and E. aureum, are not found to any appreciable number either at the lakeshore or at ground level in the forest.

Host and strata preferences also by arboreal simuliids have been considered to be of primary importance in understanding the role of these black-fly species as vectors of a number of haematozoa to woodland birds (Bennett, 1960; Anderson and De Foliart, 1961; Anderson et al, 1962; Fallis and Bennett, 1962). Although host preferences by arboreal simuliids is well documented (Bennett, 1960; Anderson and De Foliart, 1961), a study of stratification preferences by these simuliid species has been pursued only to a limited degree.

After exposing crows at four different heights above ground in a forest habitat, Bennett (1960) observed that arboreal simuliids fed on these birds at several feet above ground level; he reported, however, that no evidence of a preferred vertical strata could be detected between 5 ft and 20 ft. On the other hand, additional observations (Smith, 1966), have revealed that indeed there does exist some degree of preferential stratification by arboreal simuliids from ground level to 35 ft above ground in a forest habitat. In fact, Smith (1966) has observed that individual simuliid species exhibit not only vertical stratification preferences but also a major peak activity in the evening hours. In addition, he has reported observations of vertical movements in the population of some arboreal simuliid species indicating that the preferred strata by these species changed to the higher levels in the forest canopy as the evening progressed. Smith (1966) indicated, however, that although the problem of stratification had not been treated as the principal portion of his research programme, his data, in addition to those of Bennett's (1960), "show the phenomenon of vertical stratification to be far from straightforward and to be in need of a thorough re-examination". On the basis of this evidence, it has been considered opportune to re-examine this problem of vertical stratification of arboreal simuliids in Ontario and to pursue similar investigations on Norwegian simuliids with the hope of providing more definite knowledge in this area of study.

In the second stage, upwind orientation, olfactory stimuli are considered to function, at a distance from the host, as releasers of the host-finding drive which gives rise to a searching behaviour by the insect. Lowther and Wood (1964) hypothesized that the host-finding behaviour of *E. euryadminiculum* involves first the detection of the host-specific air-borne olfactory stimulant from the common loon, *Gavia immer* (Brünnich), and then an upwind orientation toward the source of the odour. This hypothesis was supported by their observation that "many more flies were collected from a loon skin placed on the shore when the breeze was offshore than when it blew off the lake." In addition, Smith (1966) noted that females of *E. euryadminiculum* approached a source of loon uropygial gland extract from downwind and maintained "a downwind orientation as they hovered near the attractant". In a detailed discussion of the role of carbon dioxide as a stimulant of the appetitive behaviour of various insects, Smith (1966) indicated that "carbon dioxide can release an upwind orientation behaviour in all simuliids and tabanids". In this respect, he observed, from an experiment designed to test the discrimination ability of female simuliids between two quantitatively different sources of carbon dioxide, that wind was affecting the discrimination of the two sources of carbon dioxide by S. venustum. Discrimination was noted to be much more pronounced whenever the trap with the larger carbon dioxide source was located downwind with respect to the trap with the lower carbon dioxide source. According to Smith (1966), this seems to indicate that if S. venustum will fly upwind toward both traps, the trap with the higher carbon dioxide source will collect more simuliids partly as a result of its downwind position with respect to the other trap. Although these observations appear to indicate that simuliids under field conditions fly upwind as a response to a wind-borne olfactory stimulus, there is no quantitative evidence which substantiates this behaviour. This lack of direct proof has prompted in the present research the design of experimental procedures for investigating what role wind and a wind-borne stimulus play in the orientation of simuliids to a source of odour under field conditions.

The third stage, near orientation, is thought to consist of direct orientation by simuliids to odour gradients. Laarman (1955) recognized that stimuli may be divided into two main classes according to the mode in which the insect perceives them: (a) those factors which are normal components of the atmosphere and act in the immediate proximity of the host, such as moisture, heat, and carbon dioxide, and (b) those which are derived directly from the host and are perceived at longer distances, such as scents. Odours have been widely recognized as mediators of the host-finding behaviour of blood-sucking insects. Rudolf (1922, see Reeves, 1951) observed that an increase in atmospheric carbon dioxide and ammonia strongly activated female mosquitoes. Reeves (1951) reported that more Culex and Anopheles female mosquitoes were attracted to a trap baited only with dry ice than to a similar trap placed 10 yards away and containing a calf as the only source of odour. He explains, however, that the dry ice reduces temperature and increases relative humidity in the immediate area surrounding the trap.

In field tests, Brown (1951) showed that a water-heated dummy from which a 10% carbon dioxide-air mixture was released from the head at a rate of 2 cc/min attracted 50% more Aedes females than a similarly heated dummy without carbon dioxide. When 100% carbon dioxide was emitted from the head of the dummy, the attractiveness of the body was doubled and that of the head was tripled. Willis and Roth (1952) observed with a large cage olfactometer that a portion of females of Aedes aegypty (L.) were attracted 3 to 4 times more to an air stream containing 10% CO_2 than to a stream of air alone. With a small cage olfactometer, however, they found that A. aegypti was repelled by carbon dioxide at all concentrations. Such a difference in the effect of carbon dioxide has been attributed to the design of the olfactometer, but the possibility that mosquitoes may exhibit physiological states "in which CO_2 may be attractive at one time but not at others" has also been taken into consideration (Willis and Roth, 1952). Laarman (1955) asserted the positive effect of carbon dioxide in eliciting an exploratory behaviour in resting mosquitoes. He noted that when carbon dioxide at approximately 4% was allowed to flow through a cage containing resting Anopheles females, they immediately began to fly about in the cage and gradually accumulated under the carbon dioxide outlet. In addition, Laarman (1955) has shown that carbon dioxide exhaled from the human breath is an important factor in activating mosquitoes. He demonstrated by olfactometer experiments that the higher attractiveness to Anopheles atroparvus van Thiel of human breath over the control air stream disappeared when carbon dioxide was added to the control. Indications exist that the response of mosquitoes to carbon dioxide varies greatly with other conditions. Laarman (1955) has shown with a small cage olfactometer that the response of Anopheles atroparvus to rabbit odour was greatly reduced after the relative humidity was increased to 90%, and indicated that at lower R.H. currents of moist unheated air can effect orientation by A. atroparvus in olfactometers. Clements (1963), however, explains that the most pronounced effect of water vapour is in eliciting mosquitoes to alight. Hence, Brown et al (1951) have reported that Aedes aegypti alighted and probed on an olfactometer outlet emitting warm, moist air, but with warm dry air they rarely alighted and then only momentarily. Brown (1951) indicated further that at air temperatures of 17° - 18° C more Aedes landed on a moistened, warm dummy in the field than on a dry one; whereas, at lower air temperatures of 8° - 13° C the moistened dummy was much less attractive than the dry one.

Laarman (1958) has shown that the reactivity to human arm-air is much lower than to rabbit-air, and explains the difference in terms of (a) "less specific, suitable stimuli in arm-air" and (b) the lower CO_2-content of arm-air which may be difficult for the mosquito to discriminate. He concludes, however, that since the laboratory-bred mosquitoes fed for at least 20 generations on rabbits, they may have developed an adaptation to the host. That some degree of attractiveness of body exudation exists, has been indicated by Haddow (1942) who discovered that *Anopheles gambiae* Giles and *A. funestus* Giles were attracted more to unwashed African children than to washed, and that a larger number of these mosquitoes were attracted into huts due to the presence of dirty clothing. Parker (1948) found that *Aedes aegypti* accumulated on the side of the cage and probed when human armpit sweat was held at some distance away in still air, responding significantly more than to moisture alone. Brown (1951) observed under field conditions that dummies whose clothing was soaked with human sweat from armpits and general body surface were significantly more attractive to *Aedes* than to controls with equally moist clothing. In searching for chemicals attractive to *Aedes aegypti*, Brown and Carmichael (1961) tested several protein hydrolysates by warming them to 37°C and exposing them on filter paper in a cage. Of the 16 samples tested, eleven were found to be significantly more attractive than heated distilled water as controls. Lysine was found to be the most attractive compound to *Aedes aegypti* as well as to *A. stimulans* (Walker) and *Culex pipiens* L. Later investigations (Liptsitz and Brown, 1963) indicated that lysine is one of a group of seven attractive amino acids and that the degree of attractiveness of lysine was directly proportional to its content of adsorbed carbon dioxide. When the amount of adsorbed CO_2 was kept down to less than 2% of the amount possible, its attractiveness disappeared. These same workers found, however, that lysine increased only the number of approaches but not the number of landings by *Aedes aegypti*.

Few workers have directly investigated the role of odour in the orientation of simuliids to a host. Lowther and Wood (1964) were the first to observe that odour from the common loon, Gavia immer, was a probable mediator for the specific attraction of S. euryadminiculum to this host. They observed that the wash and rinse waters from the feathers and skin of the common loon thrown on gravel at the shore of a small lake attracted large swarms of this black-fly species for at least two days after the washing of the host skin. In addition, it was found that the host skin itself still attracted large numbers of E. euryadminiculum 24 days after it had been washed in detergent water. Subsequently, Fallis and Smith (1964) confirmed that the attraction of E. euryadminiculum to the common loon in Ontario was specifically mediated by olfactory stimuli emanating from an ether extract of the uropygial gland of this avian host only. Considering S. rugglesi as a specific duck-feeding fly, Fallis and Smith (1964) also investigated whether the uropygial gland of ducks contained a specific attractant for this simuliid species. They demonstrated that although S. rugglesi was common many fewer flies were attracted to a dead duck as compared to E. euryadminiculum to a dead loon. More S. rugglesi were attracted, however, to a dead duck when CO_2 was emitted slowly beside it. These same workers asserted that the largest number of S. rugglesi was attracted to chloroform or ether extracts of the uropygial gland of duck provided carbon dioxide was emitted beside the extract. The extract and CO_2 alone was reported to attract substantially fewer flies than both in combination. Smith (1966) observed that when a population of simuliids was presented with a choice between two quantitatively different concentrations of carbon dioxide, a larger number of females of S. venustum selected consistently the trap with the higher rate of gas emission. Similarly, Fallis et al (1967) reported that suction fan-traps exposed with increasing concentrations of carbon dioxide from 50 to 800 cc./min. captured correspondingly increasing numbers of *S. venustum* females.

Similar knowledge of the role of odours in effecting the host-seeking behaviour of simuliids, other than for species found in North America, is scarce. Wenk (1965) has indicated that *Wilhelmia equina*, *Boophthora erythrocephala* and *Eusimulium latipes* in southwestern Germany will seek nectar-donor flowers mainly through olfactory rather than visual stimuli. However, olfactory stimuli have been considered less important than visual ones in the orientation of these same simuliid species toward their animal hosts (Wenk and Schlorer, 1963; Wenk, 1965).

It is realized that vision alone or in combination with olfaction also plays a role in near orientation. Some flies, viz. tabanids, may use vision to locate their hosts at a greater distance than other flies, viz. simuliids (Smith, 1966). In fact, Smith (1966) emphasized the importance of visual stimuli in effecting the *landing behaviour* of simuliids while the insect is still flying close to the host, and considered this as the probable final stage in the hierarchy of the host-seeking behaviour. Sippel and Brown (1953) demonstrated that female *Aedes* mosquitoes can detect the presence of a mouse in an airtight box better if the animal is not immobilised and best if the box is perforated to allow exit of the air-borne factors. They considered the sight factor more important than the air-borne factors when the animals are mobile, but less important than the air-borne factors when the animals are anaesthetised. Kennedy (1939) first demonstrated the importance of vision in the orientation of free flying *Aedes aegypti*. Sippel and

Brown (1953) observed that increasing the black and white interface or "contour" of checkered cubes, the number of Aedes females attracted to them also increased. Similarly, Haufe and Burgess (1960) have shown in field tests with a trap consisting mainly of a black and white spirally-striped rotating cylinder, that several species of Aedes flying close to the trap would suddenly orient to the stripes within a maximum distance of about 32 inches from the cylinder. Bracken et al (1962) and Thorsteinson et al (1965) have shown in field tests that those glossy black-coloured silhouettes in greatest contrast to their surroundings were the most effective in attracting various species of female tabanids. The attractivenss of a silhouette was furthermore enhanced by increasing the number of surfaces reflecting light toward flying female tabanids. Hence, regular polyhydra were increasingly attractive as the number of sides was increased, culminating in a sphere as the most attractive. Gjullin (1947) noticed that the colour of clothing affected the rate of attack of several species of Aedes mosquitoes. Darker colours were shown to be more attractive than lighter ones. Similarly, Brown (1951) observed in field tests that several species of female Aedes mosquitoes were attracted more to black clothing than to white at all incident light intensities; only one-quarter to one-tenth as many mosquitoes were observed to alight on the white than on the black. In addition, Brown (1954) confirmed that the attractiveness of a cloth as a landing surface for adult female Aedes was inversely proportional to its brightness. Those cloths with a minimum reflectance in the wavelength range between 475 and 625 mµ were found the most attractive; hence, black, dark blue, and red were attractive, whereas white, green, and yellow were unattractive to female *Aedes* mosquitoes. Similarly, Davies (1951, 1961) observed that the number of simuliids landing on a host is mediated by visual stimuli. He reported from field tests that the number of female *Simulium venustum* landing on several coloured cloths was influenced more by the intensity than by the wave length of reflected light; hence, few flies landed on white cloths with a high intensity of reflected light, whereas more flies landed on dark-blue and dark-green cloths with the lowest reflectance.

The importance of vision has been recognized furthermore in the host-seeking behaviour of several other simuliid species. Wenk (1962, 1965) and Wenk and Schlorer (1963) have shown in field tests that orientation to a host by females of the ornithophilic *Eusimulium latipes* and those of the mammaliophilic species, *Welhelmia equina*, *W. salopiensis*, and *Boophthora erythrocephala*, is specifically mediated by visual stimuli. These workers have asserted that the mammaliophilic simuliids landed on a large-sized, black "horse" silhouette in preference to a small-sized, black "crow" silhouette; the reverse preference was found for the bird-feeding species. The same workers indicated, furthermore, that motion of parts of these silhouettes increased the number of simuliids landing. Similarly, Anderson and De Foliart (1961) have noted that the initial attractancy of a host is influenced by its size and visibility to host-seeking simuliids. They found that camouflaged ducks attracted significantly fewer *Simulium rugglesi* than exposed ducks in the same habitat, and that the number of simuliids attracted to birds of the same species was inversely proportional to the size of the host. These workers have pointed out, however, that, although visibility of a host is an important factor in attracting simuliids, it may not be the only factor influencing selection of a host. In fact, it has been shown (Lowther and Wood, 1964; Fallis and Smith, 1964; Smith, 1966) that olfactory stimuli are important in guiding female simuliids to their hosts; whereas, visual stimuli mediate landing by these flies on their hosts.

Considering the varying degrees of responses primarily to olfactory and visual stimuli by simuliids, Fallis *et al* (1967) have arranged simuliid species into four categories.

1) Species, such as *E. euryadminiculum*, that respond to an odour without the addition of carbon dioxide.
2) Species, such as *S. rugglesi*, that respond to carbon dioxide plus odour, or to carbon dioxide, but not to odour alone.
3) Species, such as *S. venustum*, that respond to carbon dioxide alone.
4) Species, such as *Wilhelmia equina* and *Boophthora erythrocephala*, that respond particularly to visual but not to olfactory stimuli.

These same workers have indicated, however, that "extensive generalizations concerning the relative importance of various stimuli are unwarranted until further work has been done on additional (simuliid) species". The present investigations have been made, therefore, to analyse further the importance of olfactory and visual stimuli as related to the last two stages in the hierarchy of the host-seeking behaviour of various simuliid species both in Ontario and Norway.

At the beginning of the present research it was realized that the manner in which an insect species responds to a particular stimulus is dependent on the physiological state of the insect (Dethier, 1962). Ilse (1937) reported, for example, that hungry cabbage butterflies (*Pieris brassicae* L.) normally prefer to land on red, yellow, blue and violet papers, but not on green; during the egg-laying state, however, this same species distinctly selects green test papers. Similarly, Davies (1949, 1951, 1961) has shown that during the host-seeking state female Simulium venustum Say lands preferentially on dark-blue and dark-red coloured cloths and least on green and yellow coloured ones. During the oviposition state, however, this same simuliid species has been observed in nature to oviposit on emergent (green) vegetation trailing on the water surface (Jobbins-Pomeroy, 1916; Wu, 1931; Davies, 1949; Davies and Peterson, 1956; Davies et al, 1962). In view of these evidences an additional study was made of the preferential selection of a coloured substrate by ovipositing simuliids as related to the existing knowledge (Davies, 1951, 1961) of their colour preference during their host-seeking state.

MATERIALS AND METHODS

Experiments in Algonquin Park, Ontario

A. Description of the General Habitat

During the summer of 1966 and the latter half of the spring of 1967 and 1968, a series of experiments and observations were made at the Wildlife Research Station of the Ontario Department of Lands and Forests in Algonquin Provincial Park. The Park, which constitutes a forested area of 2910 square miles, is situated in a transitional zone between the southern deciduous and northern coniferous forest. The diversity of faunal and floral characteristics of the Park provides an ideal location for a research center for ecological and behavioral studies in a natural environment. The Research Station (45° 35' N, 78° 30' W), is located at an altitude of about 1300 ft above sea level on the North Madawaska River valley which comprises an area of approximately two square miles (Fig. 1).* The center of the Station borders Lake Sasejewun which is a relatively shallow body of water with a surface area of approximately 40 acres. The southern tip of the lake is occluded by a man-made dam which can be used to regulate the water volume of the outfall. The river below the lake has an average width of approximately 20 ft and follows a winding two to three-mile south-westerly course before it empties into Lake of Two Rivers. The entire river course is flanked mainly by speckled alder, *Alnus rugosa* var. *americana* (Regel); whereas, the surrounding land away from the River contains a mixture of deciduous and coniferous trees comprising chiefly: balsam fir, *Abies balsamea* (L.); white spruce,

* **All figures referred to in this section are found in Appendix A.**

Picea glauca (Moench); white pine, *Pinus strobus* L.; tamarack, *Larix laricina* (DuRoi); white birch, *Betula papirifera* (Marsh.); trembling aspen, *Populus tremuloides* Michx.; and sugar maple, *Acer saccharum* Marsh.

Within this general habitat, smaller and more definite localities were selected as suitable sites for various experiments. These localities included:

1. The Forest Canopy

This site (Fig. 1, V) adjoins the western bank of the North Madawaska River and consists of a compact stand of balsam fir and white spruce reaching a maximum height of approximately 40 to 50 ft. The canopy begins at about 3 feet above the forest floor, the latter being covered by herbaceous plants, primarily bracken fern. Here one type of experiment was set-up to investigate the vertical stratification of simuliids.

2. The Forest Clearing

This site (Fig. 1, D) was chosen since it provided an open area in which the influence of wind was minimal, therefore it was considered suitable for collecting simuliids during a series of discrimination experiments. This area was approximately 50 x 50 ft and cleared of trees for the passage of electric and telephone wires to the Wildlife Research Station (WRS). On one side it is bordered by trees and the WRS road and on the other by trees only.

3. Beaver Bog Stream

This is a shallow stream (Fig. 1, O) averaging 3 ft in width which drains a typical small bog lake approximately 50 acres in area. The stream flows along a narrow course for its first 150 ft among a bed of cattail, *Typha latifolia* L., bur Reed, *Sparganium eurycarpum* Engelm. and an assortement of grass, *Glyceria* spp., which abound also in the surrounding swampy terrain. The edges of this section of the stream have an abundance of bur-reed leaves trailing on the water surface, which at times are crawling with ovipositing simuliids, and subsequently provide an excellent substrate for the attachment of larvae and pupae. For the next 30 ft the stream follows a "U" course bordered by recumbent branches of speckled alder; it then emerges into an open area and for an additional 50 ft flows straight eastward toward the WRS road. The last segment of the stream, approximately 30 ft passes under the road and then through bushes of speckled alder before finally joining the North Madawaska River. The water volume of the stream often decreases during a dry summer to approximately one tenth of its capacity in early spring or after a heavy rainstorm.

The upper reaches of the open section of the stream was chosen as the site for experiments on the selection of a coloured substrate by ovipositing simuliids (Fig. 5A). This site, devoid of obstructing vegetation and having an average water current of 1 ft/sec, provided suitable conditions for the oviposition experiments.

4. The Airport

This is a 50-acre area of clear, open, level ground (Fig. 1) which serves as an auxiliary landing field for light aircraft. It is bordered on the north by the North Madawaska R., on the south by the South Madawaska R., on the east by Lake of Two Rivers and on the west by a coniferous forest. The ground is covered by short grass rarely exceeding 6 in. in height because of periodic mowing. Since the site is devoid of tall vegetation, light winds blow unobstructed almost unidirectionally across its wide expanse. Hence, these favourable qualities provided an ideal site for studying the flight activity of simuliids in relation to wind direction.

B. Collecting Methods

1. Vertical Stratification

To study the vertical stratification in the forest, collections of black-flies were made at various levels above the forest floor with the highest collecting point being situated just above the average height of the canopy. In lieu of a tower (Aitken, 1956; Haddow *et al*, 1961) for collecting at various levels, the best alternate method was a modification of the hoist and pulley system utilized by Bennett (1960). For this reason, a 40-ft tall spruce **tree** (Fig. 3) was considered a suitable supporting structure since one side of its trunk had been already cleared of obstructing branches. Its crown was trimmed at the 40-ft level and on it was affixed a "T"-bar with a pulley attached to its extremity at a distance of approximately 3 ft from the trunk. In order to collect beyond the 40-ft level and above the forest canopy, an extension of approximately 10 ft from the decapitated tree-top was constructed. This extension consisted of a durable 15-ft wooden pole, naturally tapering from a diameter of three inches at the base, to about one inch at the top. A "T"-bar with a small pulley dangling from its tip was affixed to the distal end of the extension pole so that the pulley protruded for about 1.5 ft from the side of the pole.

Upon completion, this section of the apparatus consisted of a two hoist-pulley system, one at the 50-ft level and the other at the 40-ft level above the forest floor (Fig. 3).

Collections of simuliids were made with miniature suction fan-traps of acrylic plastic, a modification of the New Jersey Light Trap (Sudia and Chamberlain, 1962) as described by Smith (1966). A brief description of this suction fan-trap reported by Smith (1966 , p. 20) is as follows: "The body of the trap is but six inches in length, with an O.D. of 3-5/8 inches. The traps were equipped with 'Indoperm Elektromotors', type 6V/1000. These small motors can be run on voltages of from three to twelve volts, and at 6 volts they draw an unloaded current of about 150 mA., with a maximum when loaded of about 700 mA. A three-bladed, model-aeroplane propeller (3 inches diameter) was attached to the shaft of the motor. The body of the trap is strengthened with three rings of acrylic plastic just sufficiently large to slip with difficulty over the body (Fig. 2)."

These fan-traps were powered by 6-volt batteries which were recharged periodically. However, since the fan-trap motor under normal operational conditions, sucking in still air at approximately 800 ft/min, draws a current of only 300 mA., these batteries could remain functioning efficiently for several hours especially when two or more were linked together in parallel. A collecting cage fashioned from a cylindrical 1-qt food container of waxed white cardboard was attached at the bottom of each fan-trap and utilized as receptacles for flies sucked into the trap (Smith, 1966; fig. 2). During the series of collections, the cage was easily removed from the trap and replaced with an empty one. After removal each collecting cage was utilized as a holding cage in which simuliids could be maintained alive in the laboratory, if necessary, for some length of time (Smith, 1966; p. 22). The entire unit of fan-trap plus collecting cage weighs approximately 400 gm; hence, it was easily hoisted without undue stress on the pulley system. One such unit was attached on the cord passing over the 50-ft pulley in such a fashion that the unit would be suspended with the open end of the fan-trap facing skyward. Similarly, two other such fan-trap-cage units were attached on the cord suspended from the 40-ft pulley so that they could be hoisted to a height of 25 ft and 12 ft respectively above ground level. Beside each of the three fan-traps was attached the distal end of a red rubber tube with a bore diameter of 5/16 inches. The proximal end of each of the three tubes was inserted onto the outlet of each of three flow meters which were connected to a common source of compressed carbon dioxide contained in a portable 20-lb cylinder resting on the ground at the foot of the tree. Finally, in fully operational condition the entire tree-apparatus consisted of the following: three suction-fan-trap-collecting-cage units, each powered by a mutual 6-volt battery (or more than one battery wired in parallel) by means of electric extension wires, and each with a source of carbon dioxide emission beside it. All three units were hoisted along a mutual vertical line at 12, 25, and 50 ft respectively above ground level. With such an apparatus, hourly collections of female simuliids were made simultaneously at all three levels for various days during June 1966 with a carbon dioxide emission of 150 cc/min beside each suction-trap.

2. Upwind Orientation

Experiments designed to study the orientation by simuliids to wind and to a wind-borne stimulus were begun in the present study in

Algonquin Park in the spring of 1967. It was realized at the beginning that this type of study, conducted under field conditions, necessitated an open space environement in which the wind would remain relatively unidirectional with respect to the site in which experiments were to be performed. Hence the choice was made of the airport site (Fig. 1, W).

(a) Method and apparatus employed in 1967

The choice of the apparatus used in 1967 was primarily fortuitous since its chief part, consisting of a solid ¼-inch thick and 40-inch diameter plywood wheel, was designed for an entirely different type of experiment. It was relized, however, that this wheel could be more profitably employed to set up an experiment presently under discussion. The mounted apparatus is represented diagrammatically in Fig. 2. As it can be seen from this figure, the wooden wheel was nailed firmly on top of a 2-foot high wooden stool which was set on level ground. Sixteen wooden sticks, each 2 x 1/8 x 6 inches, were nailed equidistantly from each other around the circumference of the wheel. The position number of each stick was written in front of it on the surface of the yellowish varnished wheel.

The entire stool-wheel unit was maintained firmly on the ground by inserting through the legs and across the rungs of the stool, a pressurized carbon dioxide cylinder. A flow meter was connected to the cylinder by means of a short 5/16-inch diameter rubber tube. Another similar piece of rubber tube led from the flow meter to the underside of the stool and into a ½-inch hole drilled through the center of the wheel and seat of the stool, so that the distal end of the tube protruded approximately 2 inches above the wheel surface.

Strips 8 inches long by 1.5 inch wide of light brownish-coloured masking tape were coated, on one surface only, with a thin layer of Bird Tanglefoot, a colourless, transparent, odourless, sticky substance. At one end of the coated surface of each of the sixteen strips was written a number corresponding to that of the stick on which the strip was subsequently placed. Prior to every experiment, each Tanglefoot-coated paper strip was placed over the appropriately numbered stick appressed closely to its surface and held firmly in place by an elastic band. The strips were placed on each stick in such a way that one half of the strip, with its number written on it, faced the center of the wheel and the other half faced away from the wheel. Hence, the exposed surface area of each strip coated with Tanglefoot was 12.0 square inches, approximately half of which was on either side of each wooden stick.

Two sets of such collecting strips were prepared in order to facilitate continuous collecting during favourable conditions of black-fly abundance and presence of wind. The prevailing wind direction at the experimental site was determined by observing the position of a sleeve wind-direction device positioned at approximately 300 feet from the apparatus and at a height of 20 feet above ground. During favourable conditions, therefore, collections of female simuliids were made with this wheel apparatus using a carbon dioxide emission of 150 cc/min. At the biginning of each experiment, the wheel was positioned so that the sticks with the lowest and highest numbers (i.e. #1 and #16) faced the prevailing wind direction. Collections of approximately 1-hr duration were made, and at the end of each collection, the Tanglefoot strips from each stick were quickly removed and suspended singly on a line inside a fly-proof cardboard box. During favourable conditions a clean set of Tanglefoot-coated strips were replaced on each stick for another collection. The strips which had been removed previously were then brought back to the laboratory and the number of black-flies caught on the two halves of each strip was assessed and preserved separately in 70% ethanol.

(b) Method and apparatus employed in 1968

During the spring of 1968 a modification was made in the collecting apparatus used in 1967. The principal change consisted of a freely rotating horizontal wheel, which oriented itself automatically to the wind by means of a wind vane. The chief component of the apparatus consisted of a 26-inch diameter front wheel of a bicycle. The lower end of the wheel axle was bolted firmly to the center of a circular plywood disk (1-ft diam by ½-inch thick). Three aluminium rods (each 3 ft long by ½-inch diam) formed a tripod support for the apparatus. The proximal ends of the rods were firmly bolted equidistantly from each other, ½ inch from the periphery of the plywood disk. For stability, the distal ends of the rods were bent outwardly and driven approximately 10 inches into the ground. A metal plate (2 inches square by 3/8 inch thick) was grooved and welded to four upper spokes adjacent to the axle of the wheel. Into a hole in the middle of the plate surface was fastened one end of an aluminium rod (½-inch diam by 4 ft long) which served as a supporting pole for a wind-vane. This rod was held perpendicularly to the plane of the wheel by four nichrome guy wires which were tied through four 1/16-inch holes on the distal end of the rod, and fastened taughtly to the rim of the wheel. A wind-vane consisting of a galvanized sheet-metal cut in a trapezoidal shape, 4 by 8 by 12 inches, was affixed by means of a right angles clamp holder to the distal end of the rod, approximately 3 ft above the wheel surface. The degree of sensitivity of the orientation of the wheel toward any shifting wind direction was adjusted either by changing the distance of the wind vane from the vertical supporting rod or by regulating the pressure on the bearings of the wheel axle by the upper adjusting nut.

Around the upper edge of the rim of the wheel were clamped equidistantly from each other 13 right-angle clamp holders. To each clamp was then affixed a wooden dowling (½-inch diam by 7 inch long). A pressurized carbon dioxide cylinder, coupled to a flow meter, released a measured amount of pure carbon dioxide at the end of a 5/16-inch diameter ruber tube adjacent to the center of the wheel. The apparatus completely mounted is shown in Fig. 4.

An exact replica of this wind-oriented trap was used as a control trap from which <u>no</u> carbon dioxide was released. The two traps were placed at the same site and at approximately 50 ft apart on a line at right angles to the prevailing wind direction.

The black-fly collecting devices, used for this type of trap, consisted of 13 glass test-tubes (each 5/8 inch wide by 6 inch long). Around the neck of each tube was wrapped one layer of ½-inch masking tape on which was written the tube number. The remaining external surface of each tube was coated with an even layer of sticky Tanglefoot. At the beginning of each experiment each of the 13 tubes was inverted over the appropriately numbered rods of wooden dowling clamped around the rim of the wheel, and the carbon dioxide was simultaneously turned on at the specified emission rate, usually 300 cc/min. The average wind speed obtained at the end of each experiment was recorded by a wind meter which was clamped 5 ft above ground to the wind-vane supporting rod and at right angles to the wind direction. At the end of each experiment the test-tubes were removed from each wheel and secured to a peg test-tube rack placed inside a fly proof cardboard box. In the laboratory, the black-flies collected on the sticky surface of each test-tube were counted and preserved in 70% ethanol for later identification.

After a few initial collections with sticky test-tubes, a slight alteration in the collecting method was introduced. The clamps and test-tubes around the periphery of the wheel were replaced with a strip of galvanized sheet metal (3¼ inch wide by approximately 80 inch long), held in place around the rim of the wheel by three clamps and at all points 13 inches from the center of the wheel. The entire length of the outer surface of the strip was divided into 24 numbered equal sections, each 3¼ inches long. This greyish dark outer surface of the strip was coated with a thin layer of sticky Tanglefoot. At the end of each collection, using CO_2 as outlined above, the metal strip was detached from the wheel and brought back to the laboratory where the number of black-flies caught on each 3¼ inch^2 section of the metal strip was determined. No collections were made with this modification on the control wheel.

After a few collections with this modified apparatus, it became desirable to compare the number of female simuliids which might be present farther down-wind from the source of carbon dioxide to that present at the rim of the wheel. To accomplish this, a metal strip of galvanized sheet metal, (3¼ inch wide by 30 ft long) fashioned in the form of an arch with a 15-ft radius from the center of the wheel, was placed down-wind from the wind-oriented trap. The strip was held 3 ft above ground with one surface facing the prevailing wind by means of five supporting posts set firmly into the ground equidistantly from each other. The leeside surface of the strip was then marked into 108 square sections, each 3¼ inch long, and subsequently coated with an even layer of sticky Tanglefoot. At the beginning of each experiment the metal strip surrounding the rim of the wheel was also set in place and the carbon dioxide was switched on. In addition, two similar experiments were made with a 22-ft collecting strip arc having a 10-ft radius from the center of the wheel. The number of simuliids collected on the rim of the wheel was assessed as explained above. Simuliids collected on each section of the collecting-arc were counted directly in the field at the end of each experiment and then removed with **forceps.**

3. Oviposition on Coloured Substrate

In order to examine the effect of colour in the selection of a substrate by egg-laying simuliids, a population of ovipositing black-flies were presented with a number of coloured strips on which either they were allowed to lay eggs or from which gravid females themselves were collected directly.

Six chromatic colours were originally selected by mixing together various pigments of vinyl plastic paint in arbitrary proportions to each other under artificial indoor illumination. The resultant colours were designated red, orange, yellow, green, blue, and purple according to the sensation that they produced on the human eye. Each colour was then diluted with either white or black pigments to a point at which they appeared approximately of equal intensity to the human eye. The matching was done by eye against woollen flannel dyed to Munsell colour specifications (2.5R 7/8, 5YR 7/8, 2.5Y 7/8, 106Y 7/8, 2.5B 7/8, and 2.5P 7/8 respectively).

In addition, four neutral, or achromatic, colours consisting of black, two intermediate greys and white, were selected. The intermediate greys were produced by mixing in various proportions black and white pigments which produced a light-grey and a dark-grey shade with a slightly bluish caste. The matching was done by eye against Munsell colour cards (N1/, N4/, N7/, and N9.6/ respectively).

These ten coloured paints were then each coated individually on 10-inch square sheets of paper towels so as to produce an even layer of paint on one side. After the paint had dried, the other side of the paper towel was evenly covered with the same paint. Hence, all but the central fibres of the paper became throughly permeated with paint, which, after it had dried, resulted essentially in a water impermeable, thin, unicolorous sheet.

The reflectance spectrum of each colour was determined[*] with a spectrophotometer at various wave lengths from 300-750 mµ. The values obtained were based on a standard sample of magnesium carbonate which has an absolute reflectance of about 98% over most of the visible range.

Several sheets of each colour were subsequently cut into strips 10 inches long by 1 inch wide. One strip of each colour was attached at one end by a 5-inch long nichrome wire to sticks planted into the stream bottom. The sticks, and hence the strips, were placed 4 - 5 inches apart, in a line at right angles to the direction of the water flow. To enhance buoyancy of the strips, a thin coating of liquid floor wax

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[*] by courtesy of the Defence Research Board (see Table 44, Appendix C)

was spread on both sides of each strip before it was attached to its respective stick. In this way two sets of floating oviposition strips were exposed simultaneously on the water. One set consisted of four achromatic strips which were placed approximately 10 ft up-stream from the other set of six chromatic strips.

An improvement in the method for attachment of the strips was introduced later in the summer of 1966. This consisted of a 4-ft long by 3-inch wide wooden stick under each end of which was nailed a wooden float. Six nails were inserted at five-inch intervals from each other in a row on the upper surface of the stick. The entire float was allowed to ride freely on the water surface and held stationary by two nichrome wires attached to two sticks planted up-stream into the stream bottom. One end of each oviposition strip was then linked with a 5-inch long nichrome wire to each nail and allowed to float freely on the water surface. A similar float was fashioned for the achromatic strips. This modified floating apparatus maintained all the strips equally above the water surface especially when fluctuations in water volume occurred after short periods of rain.

(a) Natural stream bottom as background

In 1966 gravid female simuliids were allowed to oviposit freely on any strip floating on the water against the natural brownish-coloured stream bottom as background. Oviposition strips containing black-fly eggs in varying proportions were then removed almost daily before noon and were immediately replaced with a set of clean new strips in such a way that their position in relation to each other was changed randomly each day. In order to assess the proportion of the various species of black-flies ovipositing at the experimental site, one yellow oviposition strip was coated on both sides with an even layer of sticky Tanglefoot. This strip was allowed to float freely on the water by attaching one end of it to a stick planted approximately 10 ft downstream from the chromatic strips. Gravid female black-flies which became entangled on the strip surface were collected daily and preserved in vials with 70% ethanol.

(b) Effect of changing the colour of the stream-bed

Subsequently, the question arose as to the effect of the colour of the stream bottom on the choice of the coloured strip on which gravid black-flies preferentially laid their eggs. Hence, the colour of the stream-bed under the strips was changed by stretching on the stream bottom a 4 ft square sheet of *black* vinyl plastic material under each set of chromatic and achromatic strips respectively, (Fig. 5A) and a 4-ft. square sheet of *white* vinyl plastic material under another set of chromatic and achromatic strips respectively placed approximately 10 ft downstream (Fig. The position of the black and the white sheets was alternated daily in order to eliminate possible bias resulting from position effect. Black-fly eggs which were laid on strips floating above the respective black and white stream backgrounds were then collected as explained above.

An assessment of the comparative quantity of black-fly eggs laid on each strip was made during the winter of 1966-67. The egg mass from each strip was identified as belonging to either females of *S. vittatum* Zett., or those of *S. venustum* according to the manner in which the eggs were laid (Wu, 1931; Davies and Peterson, 1956). These two types of eggs were then scraped separately with a fine scalpel and forceps onto individual watch glasses of previously determined weight. The eggs were then allowed to dry completely at room temperature and humidity. Each watch glass with its dried eggs was then weighed periodically with a microbalance until a constant weight was obtained. The net dry weight of the egg mass in each watch glass was then determined and recorded in relation to each coloured strip from which the eggs were obtained.

In the spring of 1968 an alternate method of assessing the preferential selection of a coloured substrate by ovipositing simuliids was introduced. This method was essentially similar to that described above; however, instead of collecting black-fly eggs from each oviposition strip, gravid female simuliids were collected directly from each strip. This was done by coating both sides of each strip with an even layer of sticky Tanglefoot. The strips were then allowed to float on the water over the natural brownish light stream background in the same fashion as described above. The total number of gravid female black-flies caught daily on each strip was assessed and then preserved in 70% ethanol for later identification.

In order to facilitate identification of simuliids from the sticky strips, the Tanglefoot remaining on each specimen was partially removed by immersing the specimens in a solution of 3 parts ethyl acetate and 1 part 70% ethanol for a period of about 4 hr.

4. Comparison of Visual and Olfactory Stimuli

In the spring of 1968 two types of experiments were performed in the forest clearing. One experiment was designed to assess the degree of visual discrimination by various simuliid species between one black and one white suction fan-trap silhouette in relation to the rate of carbon dioxide emission from each. The other experiment was designed to assess the degree of orientation of simuliids to a source of carbon dioxide in the absence of a silhouette.

(a) Experiment 1

Two suction fan-trap cage units were each covered with a 14 x 14 inch piece of soft vinyl plastic, one with white and the other with black. Both units were attached at a distance of 4 ft from each other to a horizontal metal rod suspended 3 ft above ground. The black and white fan-traps, therefore, presented silhouettes differing essentially in reflected light intensities. Each fan-trap was powered by a mutual 6-V car battery. Pure carbon dioxide was released in measurable amounts by means of two gas flow meters, through each of two rubber tubes whose distal end was set beside each fan-trap unit. The black and the white plastic coverings were alternated from one trap to the other for each hourly collection to minimize bias resulting from the position of each trap. Simultaneous collections of black-flies were made initially with 150 cc/min of CO_2 released beside each fan-trap. Subsequently, the volume of CO_2 released from the trap collecting the smaller number of black-flies was increased, without altering the CO_2 output from the other trap. The black-flies collected from each trap were preserved separately in 70% ethanol, and later identified and counted.

(b) Experiment 2

Three suction fan-trap-cage units of the type described on p. 25 were used for this experiment. One unit was wrapped in a 14 x 14 inch piece of soft black vinyl plastic and exposed 3 ft above ground. The second unit was hidden from view by placing it just below ground surface. This was done by excavating, at approximately 10 ft horizontal distance from the exposed fan-trap unit, a 15-inch deep by 12-inch wide hole into the ground. The unit was suspended into this hole from a ½-inch diameter wooden stick such that the mouth of the fan-trap was almost level with ground surface. The surface area of the hole unoccupied by the mouth of the fan-trap was covered with wooden sticks, blending in colour with the surrounding ground, so that only the mouth of the fan-trap remained completely exposed. The third unit, also wrapped in a 14 x 14 inch piece of soft black vinyl plastic, was exposed at 3 ft above ground on a wooden post planted 10 ft from each of the other two units. No carbon dioxide was released beside this third unit. All three fan-trap units were powered by a mutual 6-V car battery. Hourly collections were made simultaneously with all three fan-trap units and the black-flies collected from each trap were preserved systematically in 70% ethanol for later counting.

Experiments in Rendalen, Norway

A. Description of the General Habitat

During the first half of the summer of 1967 and 1968 a series of experiments and observations were made in the environs of Renådalen seter, (61°45' N, 11°38' E) in the Rendalen region of Norway. The topography of the region is mountainous, interspersed with plateaus and valleys of various elevations above sea level (Fig. 6). The ground is richly covered with vegetation which consists primarily of grasses (Gramineae), sedges (Cyperaceae, and Rosaceae, e.g. *Rubus chamaemorus*), shrubs mainly the dwarf birch, *Betula nana* L. and those of the family Ericaceae, of which *Vaccinium* spp. and *Callunia vulgaris* are the most abundant. At higher elevations a gradual transition of ground cover occurs in which lichen, mainly *Cladonia* spp. becomes abundant, especially at and immediately above the tree line. The forest in the lower elevations consists of a heterogeneous growth of coniferous and deciduous trees of which Scot's Pine, *Pinus silvestris* L., and the white birch *Betula verrucosa* L. are dominant. Scot's Pine becomes gradually more predominant but less dense as the elevation increses; hence, at altitudes greater than 2100 ft above sea level, shrubs replace trees and eventually lichen becomes predominant, often as thick spongy mats covering the rocky ground.

Within this general region a more defined area was selected for experiments. This area consists of a plateau-valley of about 2 miles square located at an elevation of approximately 1950 ft a.s.l., just below the tree-line. The eastern and western slopes of the valley are drained by numerous shallow streams having an average width of 2 ft. During late spring and early summer these streams carry an abundance of torrential water from rain and snow-melt down into the Renåa River. The Renåa R. has an average width of approximately 15 ft and flows along the valley bed in northerly direction toward the Mistra River. The water volume of the Renåa R. fluctuates according to that of its tributaries usually reaching in early summer an average depth of approximately 1 to 1.5 ft at its swifter stretches.

Along the course of the Renåa R. were selected two experimental sites (Fig. 6). Site *S* comprises a composite area including a river and a grassland habitat and was selected for stratification and discrimination experiments; site *D* was selected for oviposition experiments. A brief description of these two sites follows.

1. Main orientation site

This site is located on a farmstead (Renådalen saeter) whose focal point is a farm-house and a few adjacent sheds which furnished accommodation for laboratory facilities. Extending for approximately 150 ft from the laboratory to the Renåa R. is a pasture which is grazed in the summer almost daily by 3 to 4 dairy cows from an adjacent saeter. The pasture ground is divided form a north-south direction into two large rectangular sections bordered by a 4-ft high barbed-wire fence. A section of this fence is located approximately 20 ft form the laboratory (Fig. 7) and was used as a supporting structure for some equipment employed in discrimination experiments.

2. Additional orientation sites

Two other sites were selected approximately 150 ft south of the laboratory. One is located on a lichen-covered hill containing a grove of Scot's pine with an average height of 40 ft; vertical stratification experiments and general simuliid collections were made from one such tree. The other site is located beside a pasture 200 ft west of the first site and 200 ft from the west bank of the Renaå River. This site consists of a row of white birch trees with an average height of 30 ft and growing along the edge of a little stream tributary to the Renaå R. The first tree in this row was used for comparative simuliid collection experiments.

In 1968 an additional site was selected on the Renaå River approximately 200 ft west of the laboratory. This site constitutes a segment of the Renaå R. with a rocky river bed approximately 15 ft wide (Fig. 8). In mid-summer the average water depth was one foot with a water speed of 1 ft/sec. The edges of the river are bordered by *Betula verrucosa*, *Salix* spp. abunding in *S. reticulata* and *S. caprea*, and a heterogeneous quantity of grasses primarily of the family Dispacaceae.

3. Oviposition site

This site is situated on the Renaå R. at approximately 150 ft upstream from the remnants of an old wooden dam. The first 140 ft of the stream immediately above the dam forms a lacuna of apparently stationary water approximately 4 ft deep and 15 ft wide, and is flanked on both sides by marshy terrain abunding in *Typha latifolia* and *Sparganium* spp. The next 150 ft upstream adjoining the lacuna consists of a swift water current of 1-1.5 ft/sec flowing over a dark, stony river bed with an average width and depth of 10 ft and 1.5 ft respectively (Fig. 9A). The edges of this segment of the stream abound with reclining shrubs of *Salix* spp., predominantly of *S. caprea* and *S. reticulata*, whose branches and leaves when trailing on the water provided suitable substrate for oviposition by gravid female simuliids.

B. Collecting Methods

Simuliids collected from experiments described below were systematically preserved in 70% ethanol soon after they were collected and were subsequently identified to species with a binocular dissecting microscope. Simuliids collected with sticky Tanglefoot were partly cleaned with a solution of 3 parts ethyl acetate to 1 part 70% ethanol for a period of about 4 hours before they were identified. For each experiment, pure carbon dioxide from a pressurized gas cylinder was used, and a 6-V car battery furnished power simultaneously to all suction fan-traps.

1. Habitat Selection

(a) Comparison of flies from two different species of trees

Simuliids were collected from two different species of trees situated approximately 200 ft from each other and at slightly different habitats as indicated on p. 40. Two black wooden bird models were thinly coated with sticky Tanglefoot; one model was hoisted 20 ft above ground by means of a rope and pulley suspended from a branch of a pine tree, while the other model was elevated by means of a long wooden stick 20 ft above ground among the branches and leaves of a birch tree. At the beginning of each collection CO_2 was released beside each model, by means of a rubber tube connected to a flow meter, at the rate of 200 cc/min. At the end of each collection, simuliids were picked from each model with forceps before the models were re-exposed for another similar collection.

(b) Vertical stratification in a Scot's pine grove

Two white wooden bird-models were coated with sticky Tanglefoot and each was suspended from the same rope 10 ft and 20 ft respectively above ground, by means of a pulley tied to a branch of a pine tree. A

CO_2 rubber-tube outlet was attached 6 inches below each model. At the beginning of each collection, CO_2 was released through each of two flow meters at a rate of 200 cc/min below each model.

(c) Vertical stratification in a river habitat

Simuliids were collected at three different elevations above the water surface and away from the water at the edge of a segment of the Renåa River described on p. 41. A rope was suspended from a pulley attached at the end of a cross-bar which was affixed horizontally on the distal end of a 9-ft wooden pole. The pole was held perpendicular to the water surface by wedging its proximal end among rocks at the east side of the Renåa River. Three white plastic duckling models, each having a surface area of 58 inch^2, were coated with sticky Tanglefoot and suspended from the rope to form a vertical line so that the first model remained at water level (3 inches above water), the second at 4 ft, and the third at 7 ft above water surface respectively (Fig. 8). Carbon dioxide was released through flow-meters at a rate of 100 cc/min at the end of a rubber tube outlet set beside each model. A fourth white plastic duckling model similarly coated with sticky Tanglefoot was exposed without CO_2 at water level approximately 30 ft upstream from the apparatus described above; this model was used as a "control". Each collection was started when CO_2 was switched on simultaneously for all three experimental models. Subsequent collections were made in conjunction with the fourth duckling model, previously employed as a control, placed on land 4 inches above ground level and 30 ft from the other three models on a line at right angles to the Renåa River. Carbon dioxide was similarly released beside this model at 100 cc/min. At the end of each collection the four models were brought back to the laboratory and each was cleaned of flies attached on it before they were re-exposed for another similar collection.

To increase the number of collections made per unit time, the only four available duckling models were replaced by four other models described below. A cylindrical wooden post 4.5 inches in diameter was cut into four 7-inch segments. On the top of each cylinder was inserted a metal hook from which each of the three cylinders was suspended perpendicularly on the rope, at water level, 4 ft and 7 ft respectively above water; the fourth cylinder replaced the duckling model previously exposed on land. Four pieces of flesh-coloured paper each 6.5 x 15 inches in size were coated on one surface with a thin layer of sticky Tanglefoot. Another similar set of paper was prepared and assigned identification numbers distinguishable from the first set. Each sheet of one set of paper was wrapped round the lateral surface of each of the four cylinders and held in place by a paper clip. Simultaneous collections were made as described above with CO_2 released at 100 cc/min beside each cylinder. At the end of each collection the set of paper from each cylinder was replaced by the second set; hence, while a second collection was underway, flies from the first collection were being processed in the laboratory.

2. Comparison of Visual and Olfactory Stimuli

(a) Detection of carbon dioxide

Suction fan-trap-cage units described on p. 25 were suspended from the fence behind the laboratory 4 ft above ground and approximately 10 ft apart. Carbon dioxide was released through flow-meters at various fixed rates beside each fan-trap, excluding the control trap. At the end of each simultaneous collection the position of each fan-trap with the specific CO_2 emission was randomized in relation to each other.

(b) Detection of carbon dioxide in the presence and absence of a silhouette

Collections of black-flies were made with fan-trap-cage units, (three with CO_2: one 4 ft above ground, one at ground level and one underground, and two controls without CO_2 at the 4-ft level and underground) as represented in Fig. 11. Each of the two underground fan-trap-cage units was placed in a hole approximately 12 inches wide by 12 inches deep excavated into the ground such that the unit remained hidden from view, with only the mouth of the fan-trap remaining exposed level with ground surface. Carbon dioxide was released beside each fan-trap, except the controls, at a rate of 200 cc/min. Initially, collections were made simultaneously with only four fan-trap-cage units, excluding that exposed at ground level. Subsequently, it became necessary to make simultaneous collections using four fan-trap-cage units including that exposed at ground level, but excluding the exposed control trap. The position of the underground-control and the underground-CO_2 fan-traps relative to each other was interchanged for each simultaneous collection.

(c) Effect of carbon dioxide in activation and landing

(i) Each of 3 suction fan-trap-cage units was wrapped round the lateral surface with a 15-in^2 black tarpaper whose outer surface was thinly coated with sticky Tanglefoot. Each unit was suspended 4 ft above ground and placed 10 ft apart on 3 fence posts. Carbon dioxide was released beside each unit at 200, 400 and 800 cc/min respectively. Each collection was begun when both CO_2 and the fan-trap motor of the traps were switched on simultaneously. Simuliids collected from each trap were divided into those that were sucked into the cage and those that landed on the Tanglefoot coated paper.

(ii) Two black "cow" model silhouettes were built each consisting of a closed wooden box with dimensions 7 by 7 by 50 inches. Each model was coated with an even layer of sticky Tanglefoot and was held horizontally 22 inches above ground by two pairs of wooden "legs" nailed at either end of the model. A fan-trap-cage unit, with black tar-paper wrapped around the lateral surface, was suspended 6 inches below the "belly" and 12 inches from one end of each model. The two models were placed behind the laboratory on level ground 10 ft from each other, and beside the fan-trap of each model was released CO_2 at 200 cc/min and 800 cc/min respectively. Each collection was begun when both CO_2 and the fan-trap of both models were simultaneously switched on. Simuliids collected from each model were divided into those collected inside the fan-trap and those collected from the body of the model; the latter were in turn divided into those collected from the "belly" and from the sides of the model.

(d) Effect of bird odour in relation to CO_2

Following the stratification experiments at the Renaa River, it became desirable to test at this same site the effect of the uropygial gland extract of domestic ducks in relation to carbon dioxide in attracting female simuliids. The uropygial gland was dissected from each of two freshly dead 4-week old domestic ducklings, Anas boschas L. The extract was prepared by cutting both glands into pieces in a glass jar containing 50 ml of chloroform, and after one hour, each of two Whatman No. 1 filter paper was soaked with 3 ml of the solution and left to dry. Each filter paper was then folded symmetrically twice and pressed within two layers of fine dacron mesh material with an elastic band. The collecting apparatus consisted of three wooden cylinders wrapped with sticky flesh-coloured paper as described on p. 44, and was set up as shown in Fig. 13. Each wooden support was set firmly on the river bottom 10 feet from each other, and a wooden cylinder was suspended from each so that the bottom of each cylinder was approximately 4 inches above water surface. For each of the three collections made, CO_2 was emitted at 100 cc/min beside each of the two cylinders, and the position of the cylinder with CO_2 only, CO_2 + extract, and extract only was changed systematically in relation to each other. The collecting procedure was similar to that described on p. 44.

(e) Detection of a black and a white silhouette

Three suction fan-trap-cage units were used as silhouettes. Each of two units was wrapped round the lateral surface with a 12 inch square black plastic sheet; the other unit was wrapped with a similarly sized white plastic sheet. The traps were suspended 4 feet above ground and 10 feet apart on three fence posts. CO_2 was released at 200 cc/min beside the white and the black suction trap; no CO_2 was released beside the other black trap which was used as a "control".

Similar experiments were made from a Scot's pine tree in a different habitat (see p. 40). One black and one white wooden-bird-model of the type shown in Fig. 11 were coated with sticky Tanglefoot and attached 16 inches apart on a wooden stick. The distal end of a rubber tube, used as a CO_2 outlet, was attached on the wooden stick at the mid-point between the two models. The entire apparatus was hoisted by means of a rope and pulley 20 feet above ground such that the two models at the end of the stick remained parallel to each other. At the biginning of each collection CO_2 was released through a flow-meter at the rate of 200 cc/min.

(f) Effect of size of the silhouette

Four cubic cages of white dacron mesh material were used as silhouettes. Two of these silhouettes were fashioned with a 2-ft cube wooden frame and were designated as large silhouettes; the other two cages which were fashioned with a 0.5-ft cube wooden frame were designated as small silhouettes. The collecting experiments were made on level pasture ground, approximately 30 ft from the east bank of the Renåa R. and directly opposite the site used for the vertical stratification experiment. The experimental apparatus was set up as shown in Fig. 12. One large and one small silhouette were placed on the ground 10 ft apart such that one suction fan-trap-cage unit remained suspended 1 ft above ground on the southerly facing side of each silhouette. A CO_2 outlet was attached beside each fan-trap. The other large and small silhouettes were placed similarly 10 ft apart and 30 ft on a southerly direction away from the first two. A suction fan-trap-cage unit was similarly attached on one side of each silhouette but with no CO_2; these were designated as "control" silhouettes. Simultaneous hourly collections were made with all four silhouettes with an initial CO_2 emission of 100 cc/min from each of the two traps. Subsequently, additional collections were made with the large and small silhouettes placed 5 ft apart and keeping the CO_2 emission at 100 cc/min from each of the two traps. The final collections were made with the large and small silhouettes kept 5 ft apart but with CO_2 emission increased to 200 cc/min for each of the two traps. The distance between the experimental and "control" silhouettes was kept constant at 30 ft throughout the experiment.

3. Oviposition Experiments

Collections of gravid simuliids were made at the Renaa R., site D described on p. 41. Oviposition strips of the same size and colour were used as outlined for the oviposition experiments made in Ontario. The float with the six chromatic strips was placed on the water adjacent to the north shore of the river (Fig. 9A), that with the four achromatic strips was placed adjacent to the south shore. Each strip was coated with sticky Tanglefoot and attached on the respective wooden float as indicated on p.34. Strips with entangled adult female simuliids were removed almost daily in the early afternoon and replaced with new coated strips as described on p. 36.

RESULTS

The experiments reported in the present work were conducted with the knowledge that equivalent traps used in combination under identical conditions and baited with equal CO_2 emissions would collect equivalent numbers of simuliids, a fact which had already been established by earlier investigations (Smith 1966). It is understood, therefore, that the differential attraction of simuliids to combinations of the same type of traps as reported below resulted mainly from the various conditions under which the traps were exposed.

Experiments and Observations in Ontario

1. Vertical Stratification

(a) General flying activity pattern

Preliminary collections with CO_2-baited fan-traps were made in the forest canopy in late spring of 1966 in order to detect the seasonal peak abundance of arboreal black-flies. Subsequently, systematic hourly collections, from mid-morning until late evening were made during a series of six days, namely June 16, 17, 18, 20, 22 and 24. The results of these collections are reported on Table 1 and represented in Figs. 14 to 19. Series A of these figures indicates in general that females of the various simuliid species, collected at all three levels above ground combined, underwent a progressive increase in diurnal flying activity which culminated in early evening. The peak activity* evidently occurred simultaneously for almost all ornithophilic species (Figs. 14A-17A). A few exceptions can be noticed, however, for example *E quebecence* peaked approximately 1.5 hr. after

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*Henceforth *peak activity* will refer to peak abundance in flying activity of ornithophilic simuliid species unless specified otherwise.

and 3 hr before the combined activity peaks on two days (Figs. 15A and 17A respectively) and *E croxtoni* peaked approximately 1 hr later than the average peak (Fig. 16A). The peak activity of the mammaliophilic *S. venustum* occurred, on the other hand, invariably 1 to 3 hr *before* that of the ornithophilic species, with the exception of June 17 (Fig. 15A) on which the peak activity occurred simultaneously for both groups.

The time of this major peak activity varied for each of the six days examined, and it seemed to be related to changes in some meteorological factors. Although diurnal light intensity changes were not measured quantitatively during the course of each collection, it is apparent from these results that on clear sunny days (excluding June 16) the maximum peak activity occurred generally 1 to 1.5 hr after sunset (1930 hours), with the exception of June 17 on which almost all species peaked 1 hr before sunset (Fig. 15A). (Collections for June 22 and 24 were discontinued prematurely due to faulty equipment). The occurrence of the evening peak activity may be related to changes in temperature and relative humidity (RH) (compare Figs. 15A, 16A with Fig. 21). For both June 17 and 18 the maximum peak activity occurred immediately after the daily maximum temperature and minimum RH. However, on June 17 in which a maximum temperature (64°F) and minimum RH (40%) reflected moderate weather conditions, the peak activity occurred approximately 1 hr *before* sunset (Fig. 15A); on June 18, in which a maximum temperature (77°F) and minimum RH (20%) reflected comparatively extreme weather conditions, the corresponding peak activity occurred instead *after* sunset (Fig. 16A). The second case is similar to the results of the remaining three days (Figs. 17 to 19) for which the daily maximum temperature was 72°F, 82°F and 86°F respectively, (no RH records are available for these three days).

Results obtained for June 16 present an interesting case illustrating the influence of weather conditions on simuliid activity. Unlike the clement weather conditions of the other five days, unsettled weather prevailed throughout June 16. The sky was overcast throughout the day and hardly any change in light intensity could be detected by eye; intermittent rain showers occurred from 1300 to 1700 hours with a thunderstorm accompanied by heavy rain from 1530 to 1600 hours. Under these conditions it can be seen from Fig. 14A that the regular major peak activity, which prevailed for the other five days, became subdivided soon after the first rain shower (1315 hours), into a minor peak which was followed four hours later (1640-1740 hours) by a major peak; this major peak in turn declined to a minimum at sunset, but was immediately followed by a third, minor peak at 2015-2115 hours. These three peaks seem to be related to variations in temperature and RH both in time and degree of change (Fig. 21). Corresponding fluctuation patterns were evident also in the activity of S. venustum (Fig. 14A) which showed a major peak 4 hr before the major one for the ornithophilic species, and it was followed by a smaller one 2.5 hr before the third minor peak of the ornithophilic species. Apparently no relationship is evident between these variations in activity and the barogram for this particular day (Fig. 22).

(b) Flying activity pattern at three levels in the forest canopy

To determine whether certain simuliid species were concentrated at various elevations in an open spruce forest, collections were made simultaneously at 12, 25 and 50 feet above the forest floor (Table 1). Most species were concentrated mainly in the forest canopy between the 12- and 25-foot level (Figs. 14B to 19B); only a few species, notably *E. aureum* and *croxtoni*, were found in significant numbers at the 50-foot level. The diurnal activity pattern appeared to be similar at each of the three levels where almost invariably each species showed a simultaneous activity peak. Exceptions to this pattern, however, existed for some species. *P. decemarticulatum* appeared in noticeable numbers from 1030 to 1600 hours at the 12-foot level but not at the 25-foot level (Fig. 14B); on the other hand, at 1900-2000 hours, this species decreased in number at the 12-foot level with a simultaneous increase at the 25-foot level. Also in Fig. 18B, *P. decemarticulatum* appeared to show a similar upward movement between the lower two levels during 1930-2100 hours. Similarly, *croxtoni*, although present in small numbers, revealed (Figs. 14B, 15B) a slight vertical movement in the evening from the two lower levels to the 50-foot level where it peaked during 2015-2115 hours. In Fig. 17B, however, *E. croxtoni* seemed to show during 1800-2100 hours an upward movement from the 12- to the 25-foot level, but during 1900-2100 hours it descended again to the 25-foot level.

The last results may have been affected by inconsistent weather conditions which prevailed on June 20 characterized by a partly overcast sky beginning at 1200 hours, accompanied by a relatively strong wind and culminating in a short rain shower from 1545 to 1645 hours. Under more stable weather conditions, the percent of *E. croxtoni* again seemed to increase from the 12- to the 25-foot level during 1800-2100 hours on June 24 (Fig. 19B) and progressively from the 12- to the 25- to the 50-foot level during 1615-2215 hours on June 18 (Fig. 16B). *E. aureum* also revealed a slight upward movement in the evening (Figs. 15B, 16B and 18B); hence, it can be seen that as the percent of *E. aureum* decreases at the lower two levels, at the 50-foot level it either remains constant (Fig. 15B) or increases (Figs. 16B, 18B). The validity of this vertical movement cannot be proven statistically, however, in view of the relatively small population of each species involved in such activity.

Considering the pattern of activity in terms of population distribution of each species at each level examined, it can be seen from Table 2 that this distribution is rather dissimilar for some days but not for others. This dissimilarity seems to be more pronounced with the ornithophilic species than with the mammaliophilic *S. venustum* which reveals a remarkably consistent pattern of distribution at all three levels for practically each day examined. In spite of these variations in individual distribution patterns, each simuliid species tends toward a general vertical stratification pattern which can be more definitely realized from the total values reported at the bottom of Table 2. These values have been represented in Fig. 20 which indicates more lucidly the relationship in vertical distribution at the three levels above ground. The numbers of each species collected at each level are all significantly different (Table 40)*; hence, they represent a real stratification pattern. *P. decemarticulatum* showed the most pronounced stratification pattern as it was found concentrated almost exclusively around the 12-foot level, while none was taken at 50 feet, just above the canopy. The distribution pattern of *E. aureum* and *croxtoni* are remarcably similar to each

* See Appendix C

other with the greatest number of each species found predominantly around the 25-foot level; these were the only two species found almost in the same proportion at the 12- and 50-foot levels. E. latipes seemed to be equally stratified largely around the 12- to 25-foot level, showing a rapid decrease toward the 50-foot level where only 1.7% of the total was collected. E. quebecense showed a stratification pattern similar to that of E. aureum and croxtoni, as it was found stratified largely around the 25-foot level, but showed a more rapid decrease in number toward the 50-foot level where only 0.8% of the total was collected. S. venustum, the only mammaliophilic species collected in significantly large numbers, was found equally distributed around the 12- to 25-foot level with only a very small proportion (0.4%) collected at the 50-foot level. The significance of the dashed segments appended on the experimentally obtained distribution pattern of each species (Fig. 20) will be discussed in the next section, (see pp. 171-2).

TABLE 1

Simuliidae collected from vertical stratification experiments in the forest using suction fan-traps and carbon dioxide at the Wildlife Research Station, Algonquin Park, Ontario. June, 1966.

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		Eus. aureum		Eus. croxtoni		Eus. latipes		Eus. quebecense		S. venustum *	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
16-V1-66	12	31	3.1	4	0.6			2	0.5			45	8.6
1030-1130	25												
	50			3	0.4			1	0.3			2	0.4
1145-1245	12	23	2.3	6	0.9			1	0.3			51	9.7
	25	3	0.3	16	2.3			2	0.5			44	8.4
	50			10	1.4			1	0.3				
1300-1400	12	55	5.4	6	0.9	1	2.0	1	0.3	1	0.7	50	9.5
	25	7	0.7	17	2.5	3	6.0	1	0.3			64	12.2
	50			5	0.7	1	2.0						
1415-1515	12	14	1.4	2	0.3	1	2.0	5	1.3			57	11.0
	25			1	0.1	1	2.0					28	5.3
	50			1	0.1							1	0.2
1530-1630	12	16	1.6	15	2.3	2	4.0	4	1.1	3	2.2	23	4.4
	25	5	0.4	34	4.9	10	20.0	10	3.0	11	8.2	24	4.5
	50			3	0.4							1	0.2
1640-1740	12	223	22.0	37	5.3	4	8.0	44	11.8	20	15.0	12	2.3
	25	127	12.5	102	14.7	13	26.0	28	7.5	64	47.8	27	5.1
	50			49	7.1	5	10.0	2	0.5			2	0.4
1750-1850	12	188	18.5	42	6.0	1	2.0	51	13.6	8	6.0	21	4.0
	25	60	6.0	41	6.0	3	6.0	23	6.1	4	3.0	34	6.5
	50			60	9.0					1	0.7	1	0.2
1900-2000	12	80	8.0	11	1.6			25	6.7	2	1.5	2	0.4
	25	120	11.8	65	9.4			24	6.4	5	3.7	25	4.8
	50			35	5.0	1	2.0	2	0.5			1	0.2
2015-2115	12	9	0.9	16	2.3			70	18.7	2	1.5		
	25	55	5.4	53	7.6			34	9.1	22	16.4	9	1.7
	50			59	8.5	4	8.0	4	1.1	1	0.7	1	0.2
2130-2230	12							24	6.4				
	25			1	0.1			15	4.0				
	50			1	0.1								
Total		1016		695		50		374		144		525	

* With this species are also included some S. tuberosum and S. verecundum

TABLE 1 (Cont.)

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		Eus. aureum		Eus. croxtoni		Eus. latipes		Eus. quebecense		S. venustum	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
17-VI-66	12			3	1.2			3	1.5			50	3.0
0900-1000	25	1	0.3	13	5.3			3	1.0			71	4.2
	50			6	2.4								
1030-1130	12	1	0.3	2	0.8							47	2.8
	25			3	1.2							38	2.2
	50												
1145-1245	12			1	0.4							41	2.4
	25			3	1.2							42	2.5
	50												
1300-1400	12			3	1.2							54	3.2
	25											47	2.8
	50												
1415-1515	12					1						68	4.0
	25			1	0.4							51	3.1
	50												
1530-1630	12	1	0.3									132	7.8
	25											60	3.5
	50												
1645-1745	12	13	3.5	4	1.1			5	2.4	1	1.0	150	8.8
	25	1	0.3	37	10.3	1		3	1.5			170	10.0
	50			1	0.3								
1755-1900	12	177	47.8	55	15.3	1		47	22.8	1	1.0	229	13.5
	25*	20	5.4	100	27.8			40	19.4			230	13.5
	50			1	0.3								
1910-2010	12	117	31.6	10	2.8			26	12.6	26	24.5	105	6.2
	25	14	3.8	86	23.9	2		24	11.7	39	36.8	109	6.4
	50			2	0.6	1						1	0.1
2020-2120	12	18	4.9	6	1.7			30	14.5	17	16.0	1	0.1
	25	7	2.0	21	5.8			26	12.6	22	20.6	1	0.1
	50			1	0.3	1						1	0.1
2130-2230	12												
	25												
	50			1	0.3								
Total		370		360		7		206		106		1698	

*Estimated numbers

TABLE 1 (Cont.)

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		*Eus. aureum*		*Eus. croxtoni*		*Eus. latipes*		*Eus. quebecense*		*S. venustum*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
18-V1-66	12											136	2.0
0930-1030	25			3	2.6							232	3.3
	50												
1040-1140	12			1	0.9							179	2.6
	25			3	2.6							91	1.3
	50												
1200-1300	12	1	0.4									244	3.5
	25											94	1.4
	50												
1315-1415	12			1	0.9	1	2.6	1	1.5			235	3.5
	25					1	2.6					189	2.7
	50												
1545-1645	12			1	0.9							300	4.3
	25			4	3.4	11	18.2	1	1.5			249	3.6
	50												
1655-1800	12	1	0.4			2	4.1	5	3.5	1	1.5	841	12.0
	25			5	4.3	6	10.4	1	1.5	1	1.5	530	7.6
	50												
1800-1915	12	46	18.9	8	6.8			20	11.0	4	3.0	1092	15.6
	25	5	2.0	9	7.7	8	13.5	10	15.0	2	2.0	946	13.5
	50											1	0.0
1930-2030	12	115	47.1	14	12.0			65	33.3	34	17.4	530	7.6
	25	32	13.1	48	41.0	14	23.0	38	20.0	151	74.0	1013	14.5
	50			3	2.6							7	0.1
2030-2130	12	23	9.4	4	3.4			23	12.4	9	5.3	15	0.2
	25	21	8.6	7	6.0			35	18.4	4	3.0	45	0.6
	50			6	5.1	21	33.8	2	2.0	1	1.5	16	0.2
2145-2255	12												
	25											1	0.0
	50												
Total		244		117		64		201		207		6986	

TABLE 1 (Cont.)

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		*Eus. aureum*		*Eus. croxtoni*		*Eus. latipes*		*Eus. quebecense*		*S. venustum*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
20-V1-66	12	5	1.8	1	0.1	1	1.7	2	1.3	1	1.2	541	7.0
0850-0950	25			6	0.6			1	0.6			792	10.0
	50			2	0.2			1	0.6			3	0.0
1000-1100	12	2	0.7	2	0.2							746	9.5
	25	1	0.4	2	0.2	1	1.7	1	0.6	2	2.4	732	9.3
	50											2	0.0
1110-1200	12											318	4.0
	25					1	1.7	1	0.6			109	1.4
	50												
1210-1310	12											62	0.8
	25											124	1.6
	50												
1315-1415	12	1	0.4									238	3.0
	25					1	1.7			1	1.2	165	2.1
	50											6	0.1
1430-1530	12					3	5.0					377	4.8
	25					4	6.7					165	2.1
	50												
1545-1645	12	2	0.7	1	0.1	1	1.7	9	5.7	10	11.7	408	5.8
	25			30	3.0	2	3.3	8	5.1	13	15.3	371	4.6
	50			8	0.8	2	3.3						
1700-1830	12	54	19.1	19	2.0	3	5.0	12	7.6	14	16.5	766	10.0
	25	1	0.4	71	7.1			4	2.5	17	20.0	705	9.0
	50			13	1.3								
1835-1950	12	74	26.2	71	7.1			16	10.2	4	4.7	503	6.4
	25	18	6.4	152	15.2	2	3.3	18	11.5	21	24.7	469	6.0
	50			98	9.8	11	18.3	3	2.0			10	0.1
2000-2100	12	84	29.8	113	11.3			21	13.4			103	1.3
	25	36	12.8	143	14.3	24	40.0	33	21.0			153	2.0
	50			182	18.2	3	5.0	3	2.0			1	0.0
2120-2200	12	2	0.7	19	1.9			11	7.0			4	0.1
	25	2	0.7	43	4.3	1	1.7	13	8.3	2	2.4	3	0.0
	50			26	2.6							1	0.0
Total		282		1002		60		157		85		7877	

TABLE 1 (Cont.)

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae													
		P. decemarticulatum		*Eus. aureum*		*Eus. croxtoni*		*Eus. latipes*		*Eus. quebecense*		*S. venustum*		*Eus. croxtoni* *latipes* *quebecense*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
22-V1-66	12											152	2.8		
1000-1100	25											116	2.1		
	50					2	11.1					3	0.1	2	1.2
1115-1215	12	1	0.5									192	3.5		
	25			1	0.5					1	1.7	245	4.5	1	0.6
	50											2	0.0		
1230-1330	12											114	2.1		
	25					1	5.6			1	1.7	143	2.7	2	1.2
	50					1	5.6					1	0.1	1	0.6
1340-1450	12	1	0.5					1	1.4			146	2.7	1	0.6
	25	1	0.5			3	16.7			1	1.7	145	2.7	4	2.4
	50														
1500-1600	12					1	5.6	3	4.3	4	6.8	325	6.0	8	4.8
	25			1	0.5							145	2.7		
	50														
1615-1745	12	11	5.1	3	1.4			1	1.4	1	1.7	548	10.1	2	1.2
	25	1	0.5	8	3.8	4	22.2	3	4.3	5	8.5	433	8.0	12	7.2
	50			2	1.0							3	0.1		
1750-1850	12	59	27.2	10	5.0			2	2.8	1	1.7	569	10.5	3	1.8
	25	9	4.1	34	16.0	2	11.1	5	7.2	2	3.4	489	9.0	9	5.4
	50			6	2.8					1	1.7	7	0.1	1	0.6
1900-2000	12	51	23.5	9	4.2			4	5.8			452	10.1	4	2.4
	25	7	3.2	37	17.5	1	5.6	12	17.4	6	10.2	541	10.0	19	11.4
	50			10	5.0							8	0.1		
2015-2115	12	41	19.0	8	3.8			22	31.8	4	6.8	249	4.5	26	15.7
	25	35	16.1	45	21.2			35	50.7	30	50.8	390	7.2	65	39.2
	50			38	18.0	3	16.7	1	1.4	2	3.4	8	0.1	6	3.6
Total		217		212		18		89		59		5426		166	

TABLE 1 (Cont.)

Date time of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		Eus. aureum		Eus. croxtoni		Eus. latipes		Eus. quebecense		S. venustum	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
24-V1-66 0800-0930	12	2	2.0	1	0.6			2	1.8			182	3.8
	25	2	2.0									173	3.6
	50											3	0.1
0945-1045	12											135	2.8
	25											74	1.6
	50												
1055-1155	12											73	1.6
	25					1	2.4					55	1.2
	50												
1200-1300	12											243	5.1
	25									1	0.7	108	2.3
	50											3	0.1
1315-1415	12											209	4.4
	25					4	9.5			1	0.7	116	2.4
	50			1	0.6							3	0.1
1430-1545	12			1	0.6					3	2.2	282	5.9
	25											95	2.0
	50											4	0.1
1550-1830	12	4	4.0	3	2.0	6	14.3	4	3.6	1	0.7	767	16.1
	25			1	0.6	5	12.0	3	2.7	1	0.7	525	11.0
	50											3	0.1
1855-1955	12	38	37.3	18	11.5	5	12.0	11	10.0			588	12.3
	25	2	2.0			8	19.0	13	11.8	3	2.2	344	7.2
	50			7	4.5							6	0.1
2000-2130	12	46	45.0	39	24.8	1	2.4	22	20.0	11	7.9	353	7.4
	25	8	7.8	61	38.9	12	28.6	57	51.9	118	84.8	416	8.7
	50			25	15.9							5	0.1
Total		102		157		42		112		139		4765	

TABLE 2

Total number of female Simuliidae collected from vertical stratification experiments using suction fan-traps and carbon dioxide at the Wildlife Research Station, Algonquin Park, Ontario. Summary of Table 1.

Date of Collection	Elevation in feet of fan-trap above ground level	Species of Simuliidae											
		P. decemarticulatum		*E. aureum*		*E. croxtoni*		*E. latipes*		*E. quebecense*		*S. venustum*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
16-V1-66	12	639	62.9	139	20.0	9	1.8	227	60.7	36	25.0	261	49.7
	25	377	37.1	330	47.5	30	60.0	137	36.6	106	73.6	255	48.6
	50	—		226	32.5	11	22.0	10	2.7	2	1.4	9	1.7
17-V1-66	12	327	88.4	84	23.3	2	28.6	120	55.8	45	42.5	877	51.6
	25	43	11.6	264	73.3	3	42.9	95	44.2	61	57.5	819	48.2
	50	—		12	3.3	2	28.6	—		—		2	0.1
18-V1-66	12	186	76.2	29	24.8	3	9.4	114	56.7	48	23.2	3572	51.1
	25	58	23.8	79	67.5	29	90.6	85	42.3	158	76.3	3390	48.5
	50	—		9	7.7	—		2	0.9	1	0.5	24	0.3
20-V1-66	12	224	79.4	226	22.6	8	13.3	71	45.2	29	34.1	4066	51.6
	25	58	20.6	447	44.6	36	70.2	79	50.3	56	65.9	3788	48.0
	50	—		329	32.8	16	32.0	7	4.4	—		23	0.3
22-V1-66	12	164	75.6	30	14.1	1	5.6	33	37.1	10	17.0	2747	50.7
	25	53	24.4	126	59.4	11	61.1	55	61.8	46	78.0	2647	48.8
	50	—		56	26.4	6	33.3	1	1.1	3	5.1	32	0.6
24-V1-66	12	90	88.2	62	39.5	12	28.6	39	34.8	15	10.8	2832	59.4
	25	12	11.8	62	39.5	30	71.4	73	65.2	124	89.2	1906	40.0
	50	—		33	21.0	—		—		—		27	0.6
Total	12	1630	73.0	570	22.4	35	18.4	604	52.6	183	24.7	14355	52.6
	25	601	27.0	1308	51.4	120	63.2	524	45.7	551	74.5	12805	47.0
	50	—		665	26.2	35	18.4	20	1.7	6	0.8	117	0.4

Fig. 14A Comparison of the abundance of each species of Simuliidae at different times of the day from all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 16, 1966.

⊙——⊙	1016	*P. decemarticulatum*
○——○	695	*Eus. aureum*
△——△	50	*Eus. croxtoni*
⊡——⊡	374	*Eus. latipes*
◇——◇	144	*Eus. quebecense*
×——×	525	*S. venustum*

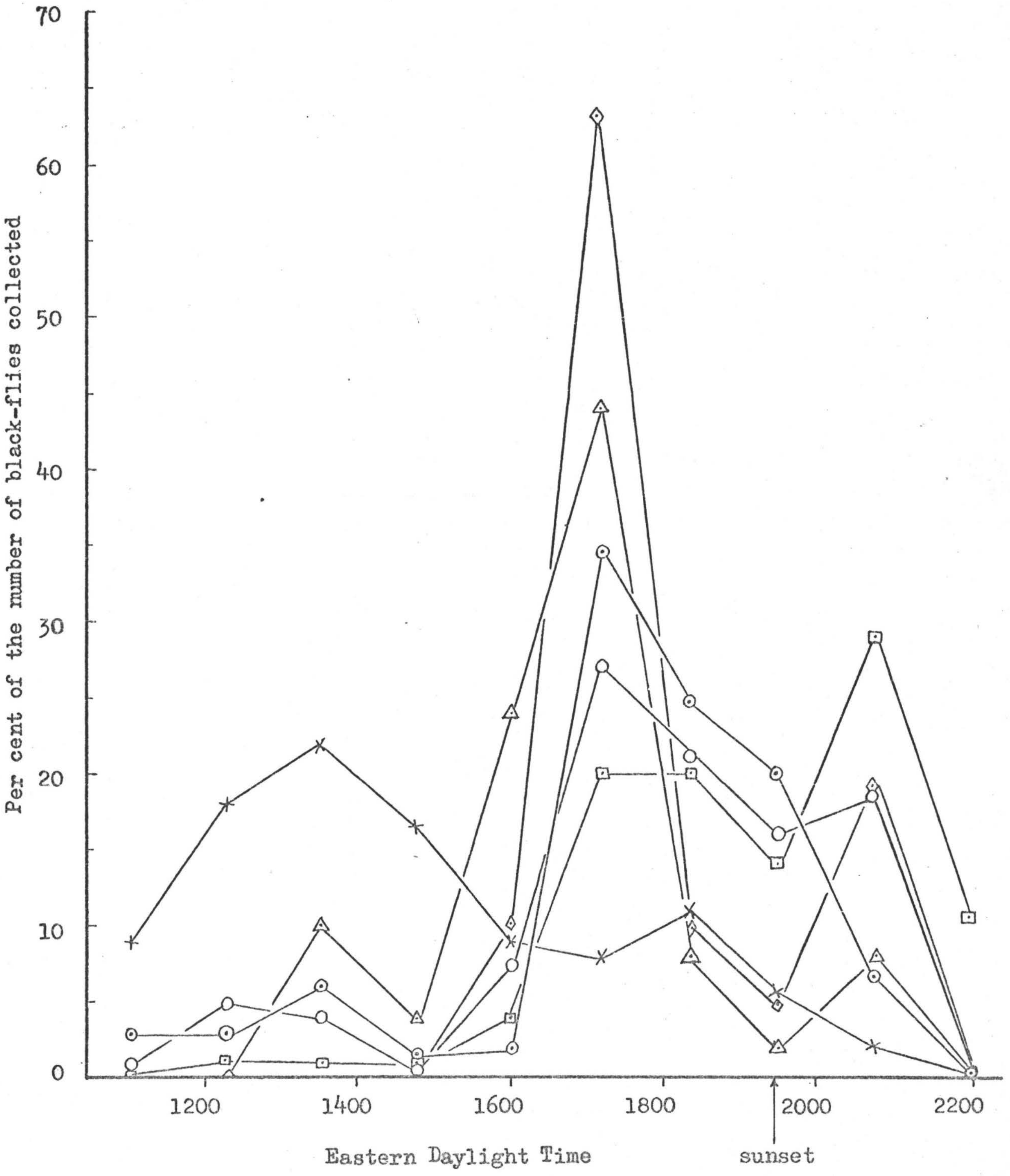

70
60
50
40
30
20
10
0
Per cent of the number of black-flies collected
1200
1400
1600
1800
2000
2200
Eastern Daylight Time
sunset

Fig. 14B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 16, 1966.

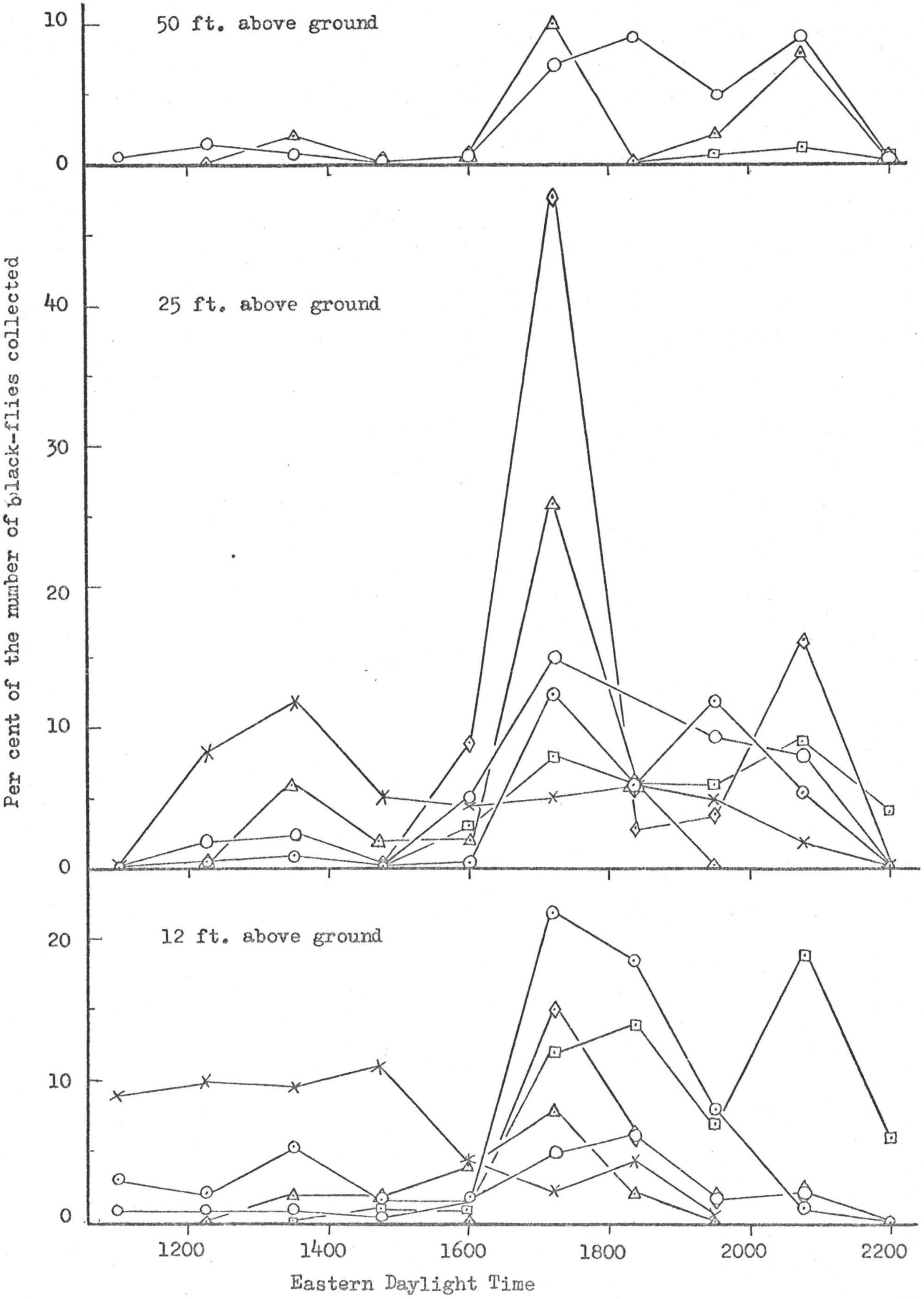

50 ft. above ground
25 ft. above ground
12 ft. above ground
10
0
40
30
20
10
0
20
10
0
Per cent of the number of black-flies collected
1200
1400
1600
1800
2000
2200
Eastern Daylight Time

Fig. 15A Comparison of the abundance of each species of Simuliidae at different times of the day form all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 17, 1966.

⊙————⊙	370	*P. decemarticulatum*
○————○.	340	*Eus. aureum*
△————△	7	*Eus. croxtoni*
⊡————⊡	206	*Eus. latipes*
◇————◇	106	*Eus. quebecense*
×————×	1698	*S. venustum*

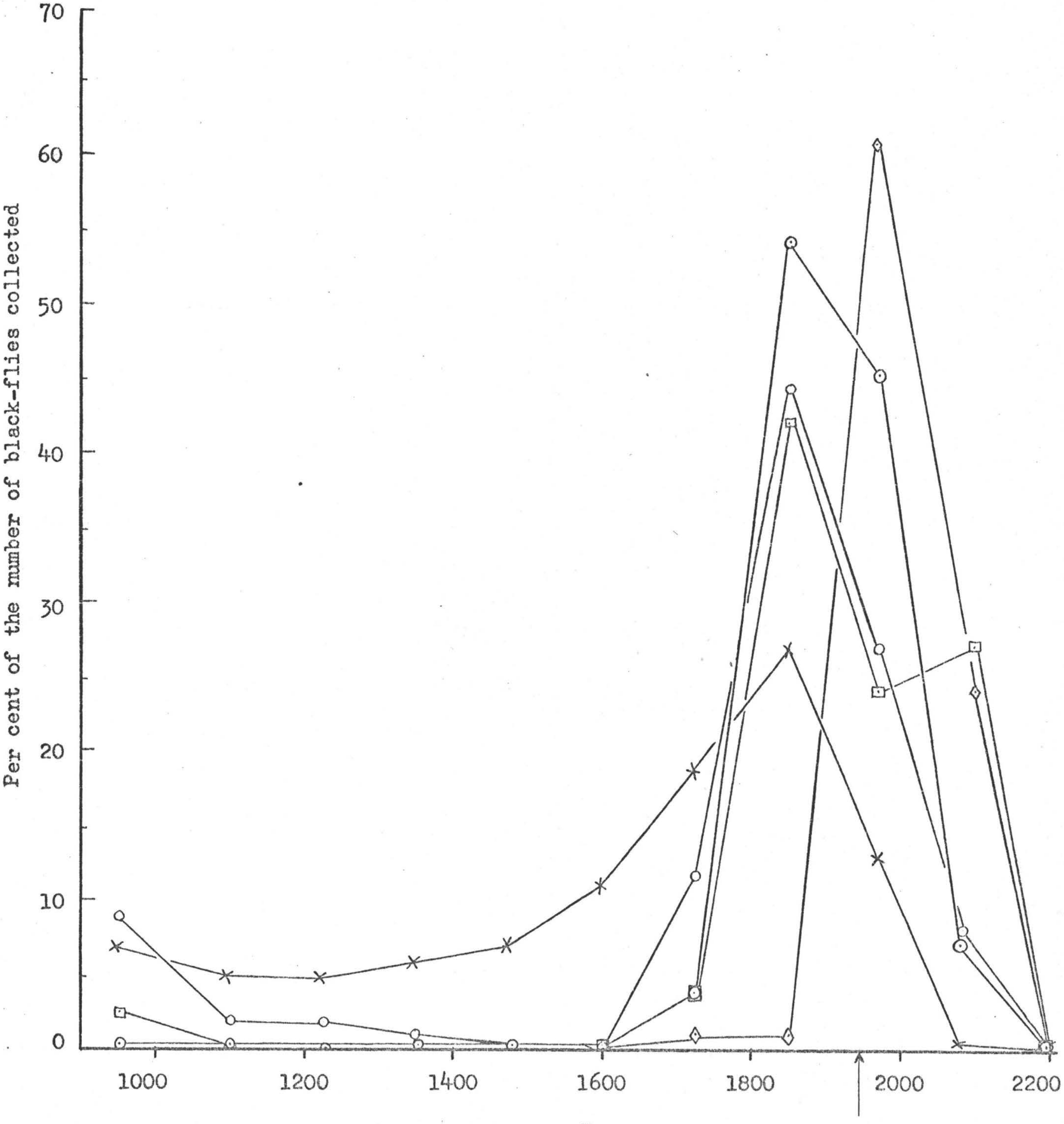

70
60
50
40
30
20
10
0
Per cent of the number of black-flies collected
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time
sunset

Fig. 15B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of the three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 17, 1966.

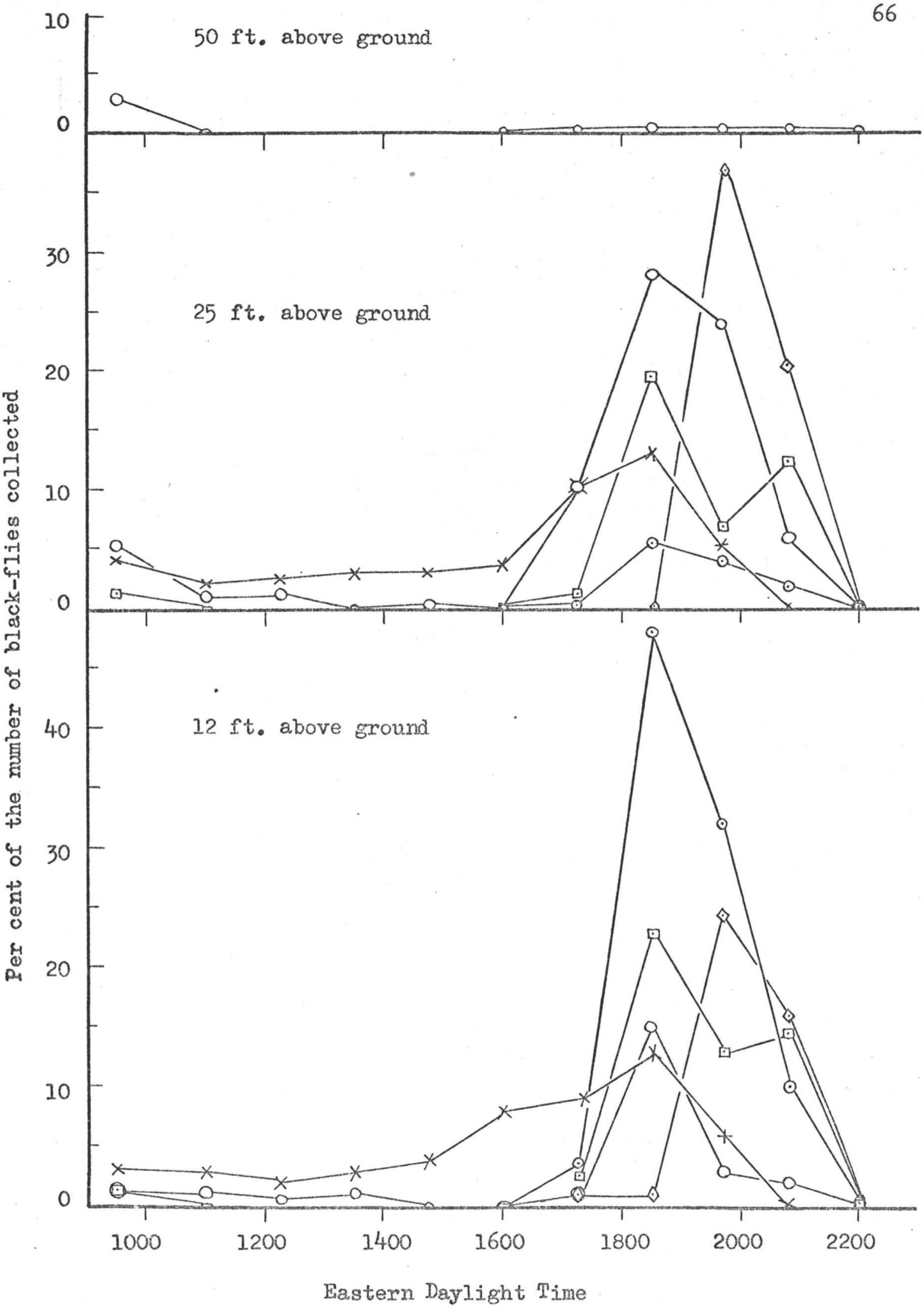

50 ft. above ground
25 ft. above ground
12 ft. above ground
10
0
30
20
10
0
40
30
20
10
0
Per cent of the number of black-flies collected
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time

Fig. 16A Comparison of the abundance of each species of Simuliidae at different times of the day from all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 18, 1966.

⊙——⊙	244	*P. decemarticulatum*
○——○	117	*Eus. aureum*
△——△	64	*Eus. croxtoni*
⊡——⊡	201	*Eus. latipes*
◇——◇	207	*Eus. quebecense*
✕——✕	6986	*S. venustum*

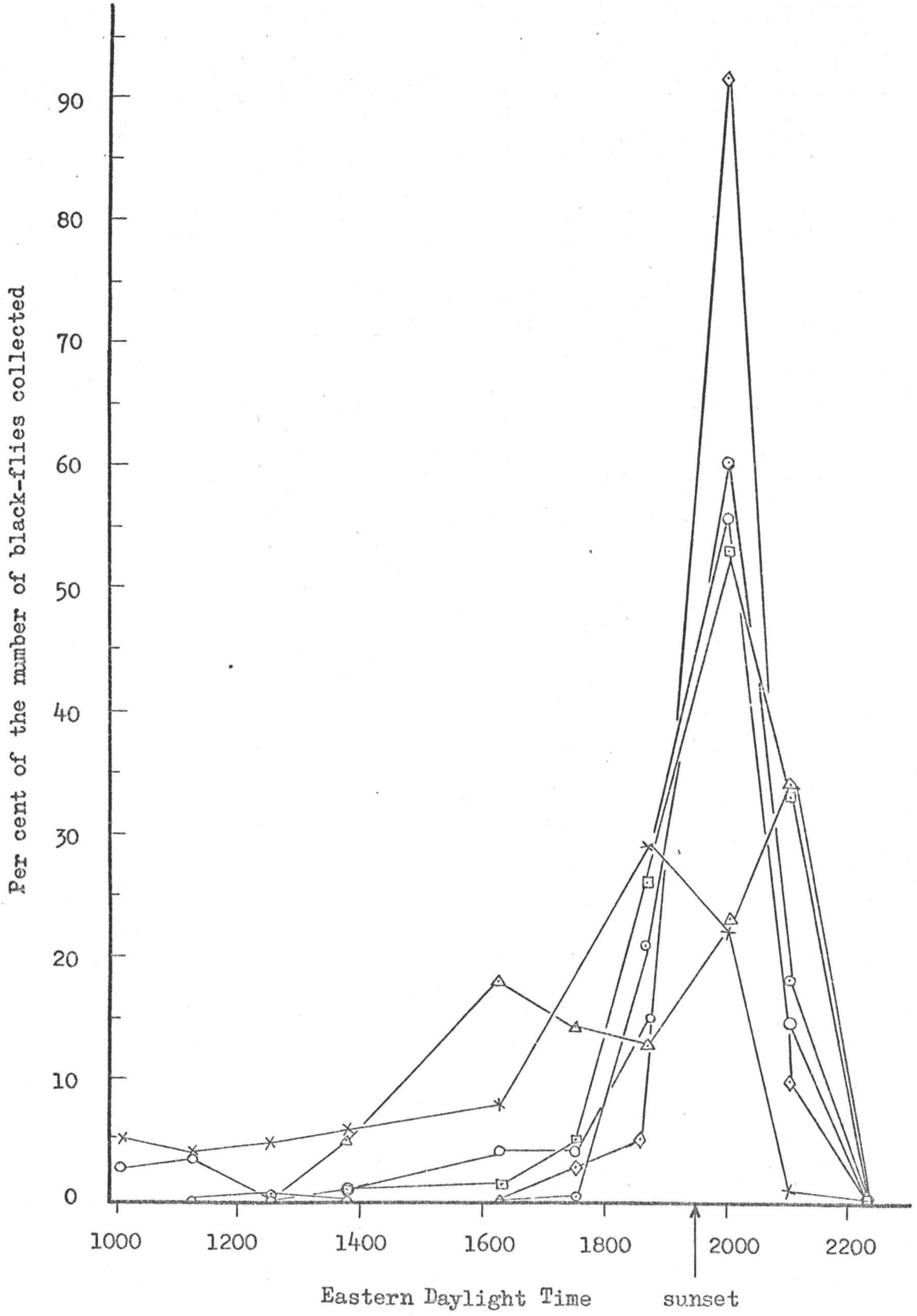

Per cent of the number of black-flies collected
90
80
70
60
50
40
30
20
10
0
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time
sunset

Fig. 16B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 18, 1966.

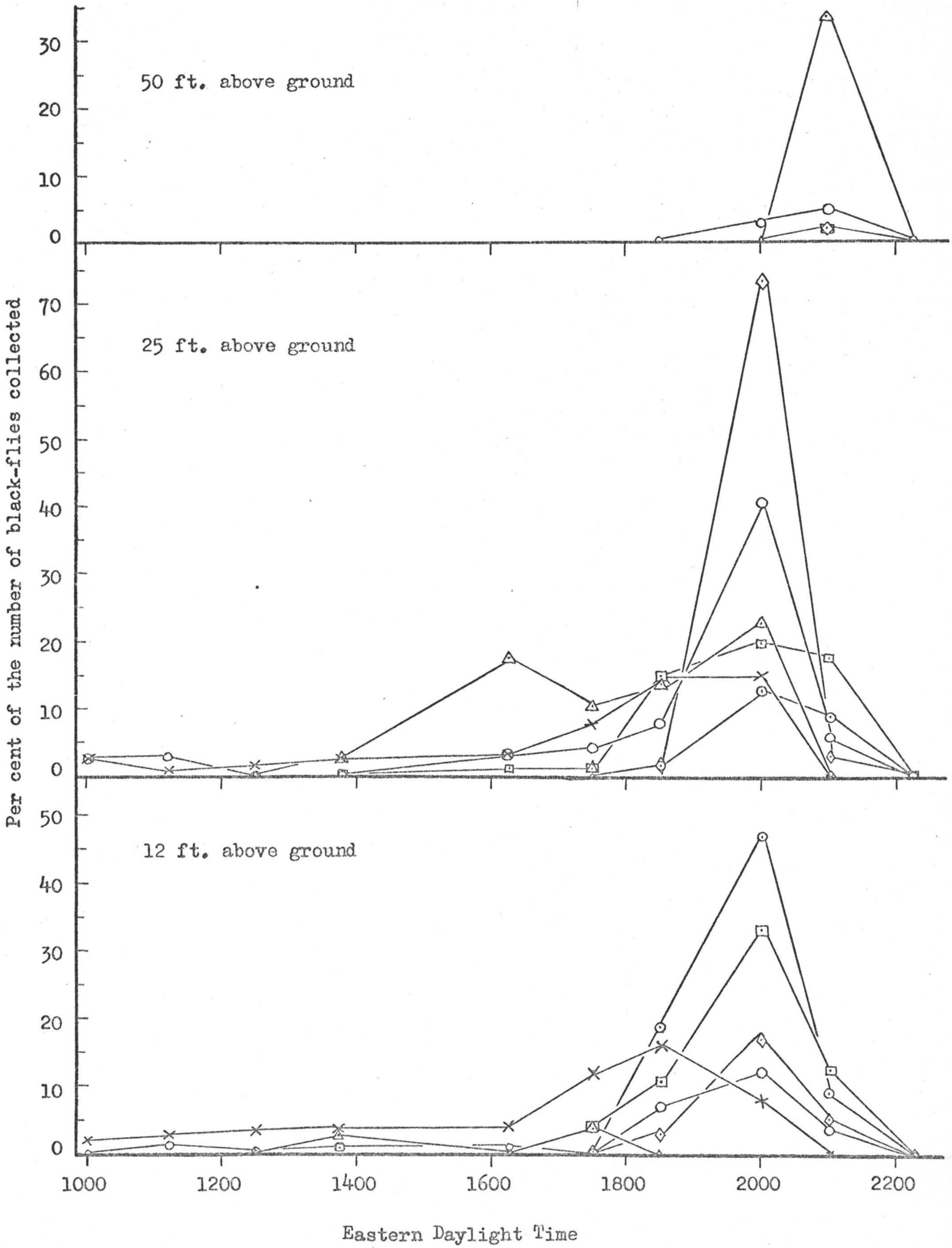

50 ft. above ground
25 ft. above ground
12 ft. above ground
Per cent of the number of black-flies collected
0
10
20
30
40
50
60
70
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time

Fig. 17A Comparison of the abundance of each species of Simuliidae at different times of the day from all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 20, 1966.

⊙——⊙	282	*P. decemarticulatum*
○——○	1002	*Eus. aureum*
△——△	60	*Eus. croxtoni*
⊡——⊡	157	*Eus. latipes*
◇——◇	85	*Eus. quebecense*
×——×	7877	*S. venustum*

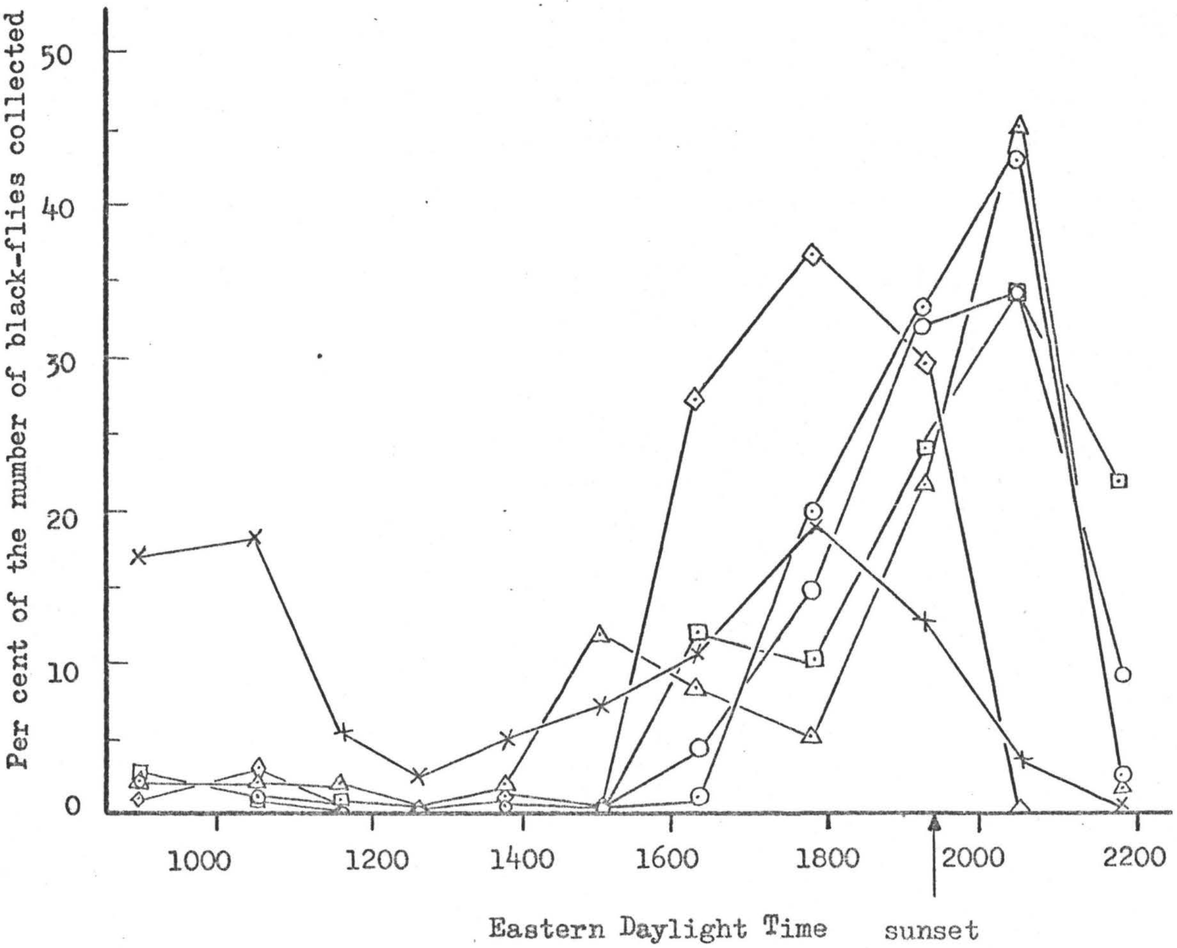

Per cent of the number of black-flies collected
50
40
30
20
10
0
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time
sunset

Fig. 17B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 20, 1966.

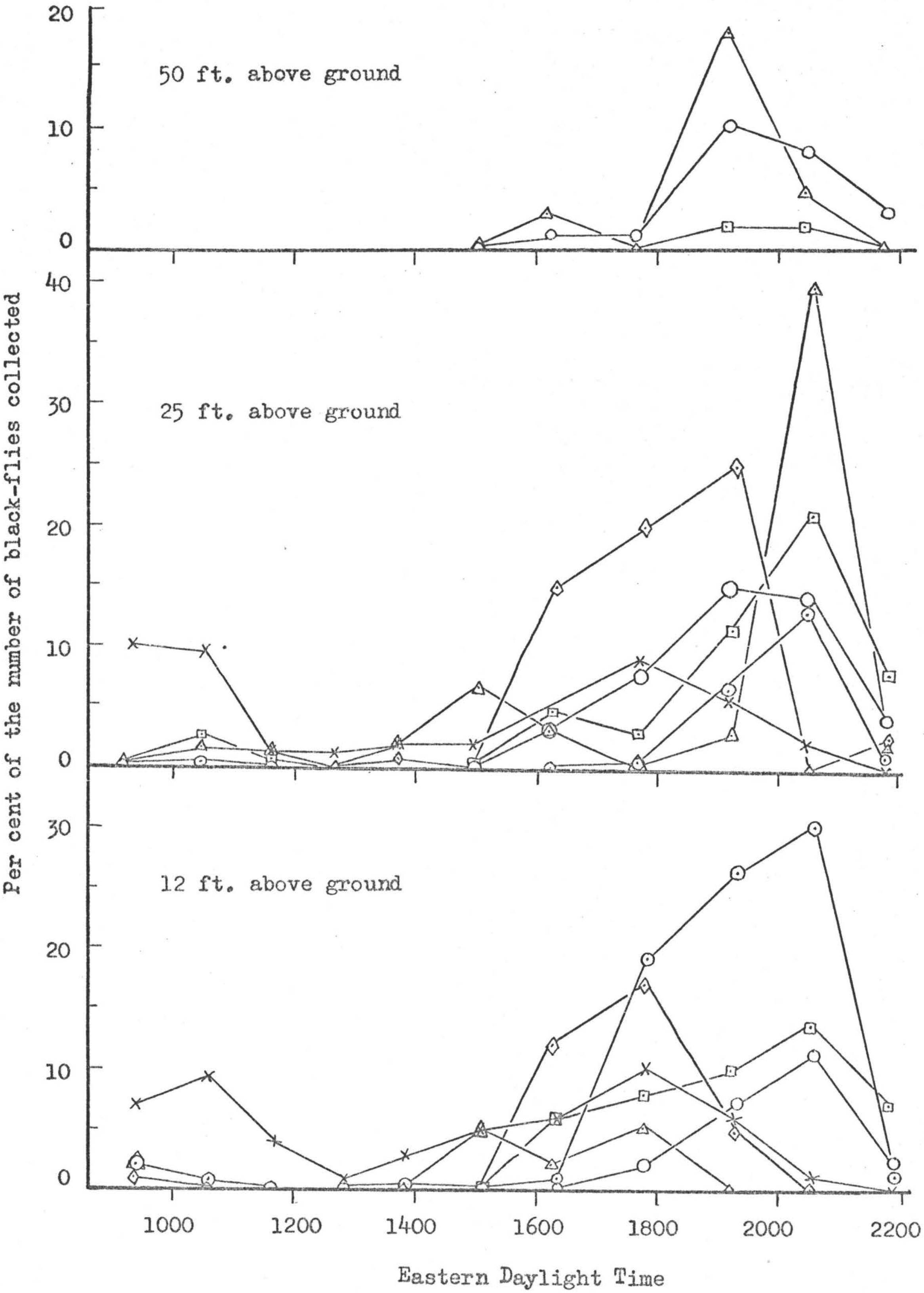

50 ft. above ground
25 ft. above ground
12 ft. above ground
Per cent of the number of black-flies collected
Eastern Daylight Time
20
10
0
40
30
20
10
0
30
20
10
0
1000
1200
1400
1600
1800
2000
2200

Fig. 18A Comparison of the abundance of each species of Simuliidae at different times of the day from all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 22, 1966.

⊙———⊙	217	*P. decemarticulatum*
○———○	212	*S. aureum*
✳———✳	18	*Eus. croxtoni*
	89	*Eus. latipes*
	59	*Eus. quebecense*
×———×	5426	*S. venustum*

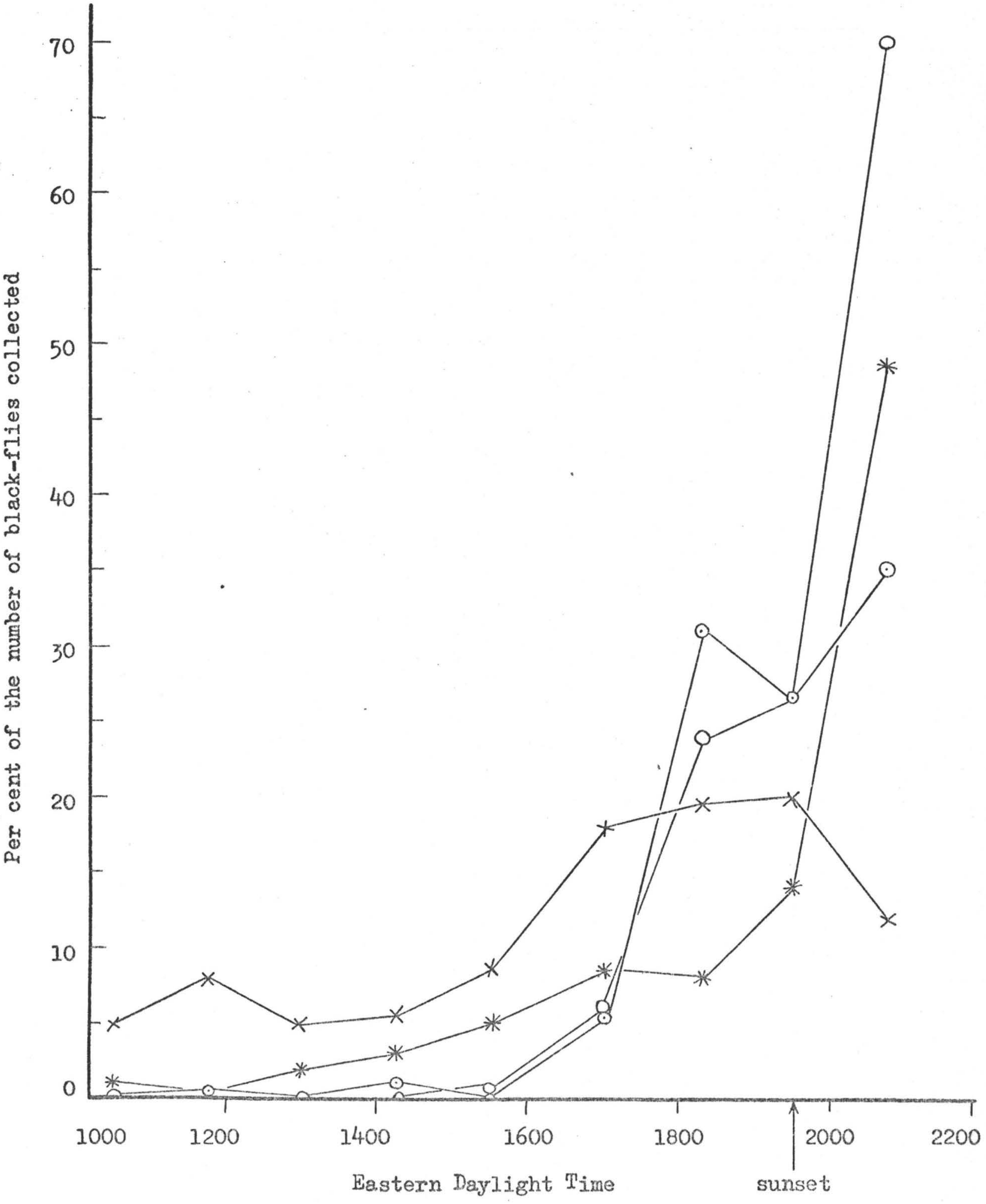

Per cent of the number of black-flies collected
70
60
50
40
30
20
10
0
1000
1200
1400
1600
1800
2000
2200
Eastern Daylight Time
sunset

Fig. 18B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 22, 1966.

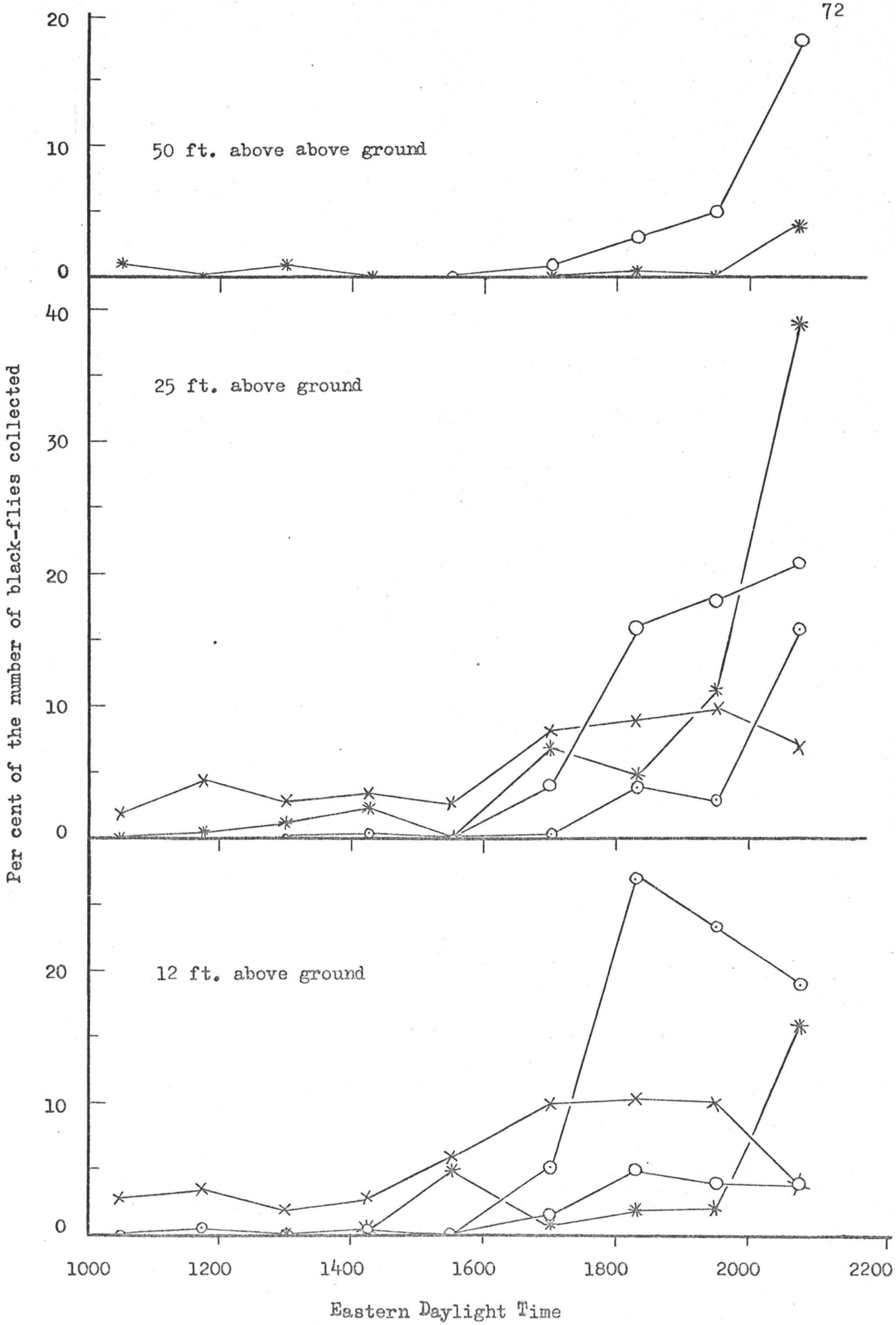

50 ft. above above ground
25 ft. above ground
12 ft. above ground
Per cent of the number of black-flies collected
Eastern Daylight Time
0
10
20
30
40
1000
1200
1400
1600
1800
2000
2200

Fig. 19A Comparison of the abundance of each species of Simuliidae at different times of the day from all three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 24, 1966.

⊙———⊙	102	*P. decemarticulatum*
○———○	157	*Eus. aureum*
△———△	42	*Eus. croxtoni*
⊡———⊡	112	*Eus. latipes*
◈———◈	139	*Eus. quebecense*
×———×	4765	*S. venustum*

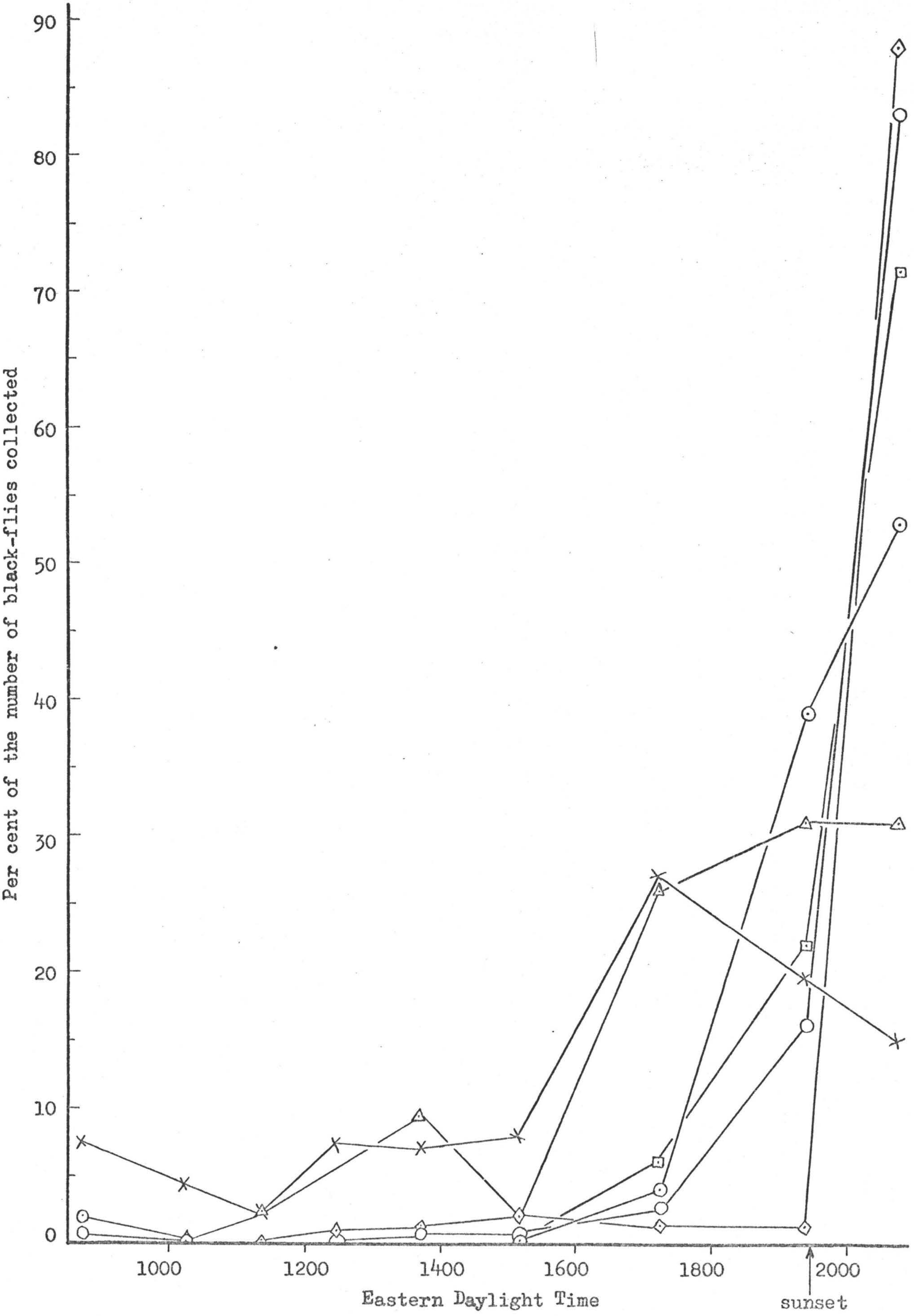

90
80
70
60
50
40
30
20
10
0
Per cent of the number of black-flies collected
1000
1200
1400
1600
1800
2000
Eastern Daylight Time
sunset

Fig. 19B Comparison of the abundance and the time of occurrence of peak activity of each species of Simuliidae during the day at each of three levels above ground in the forest at the Wildlife Research Station, Algonquin Park, Ontario. June 24, 1966.

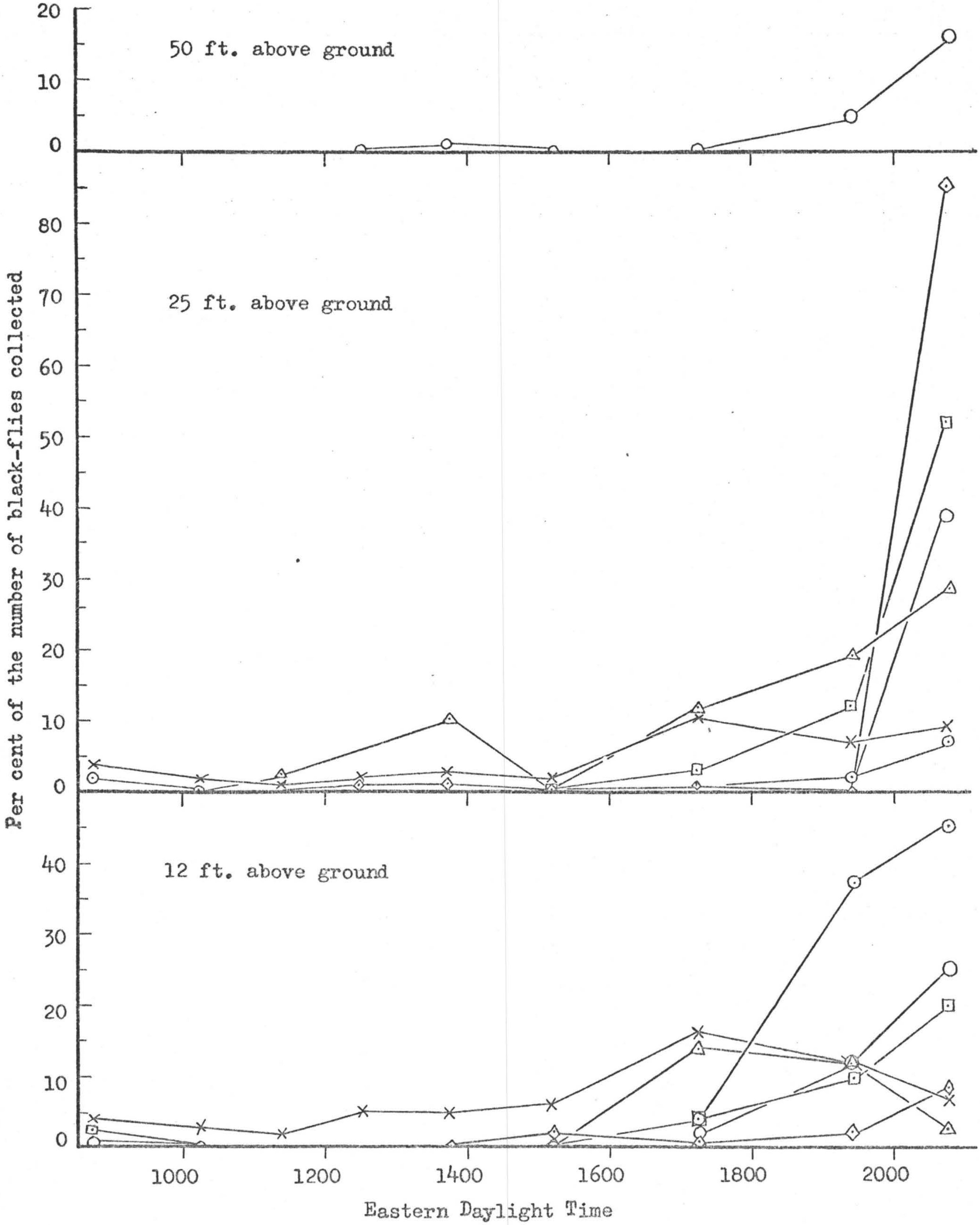
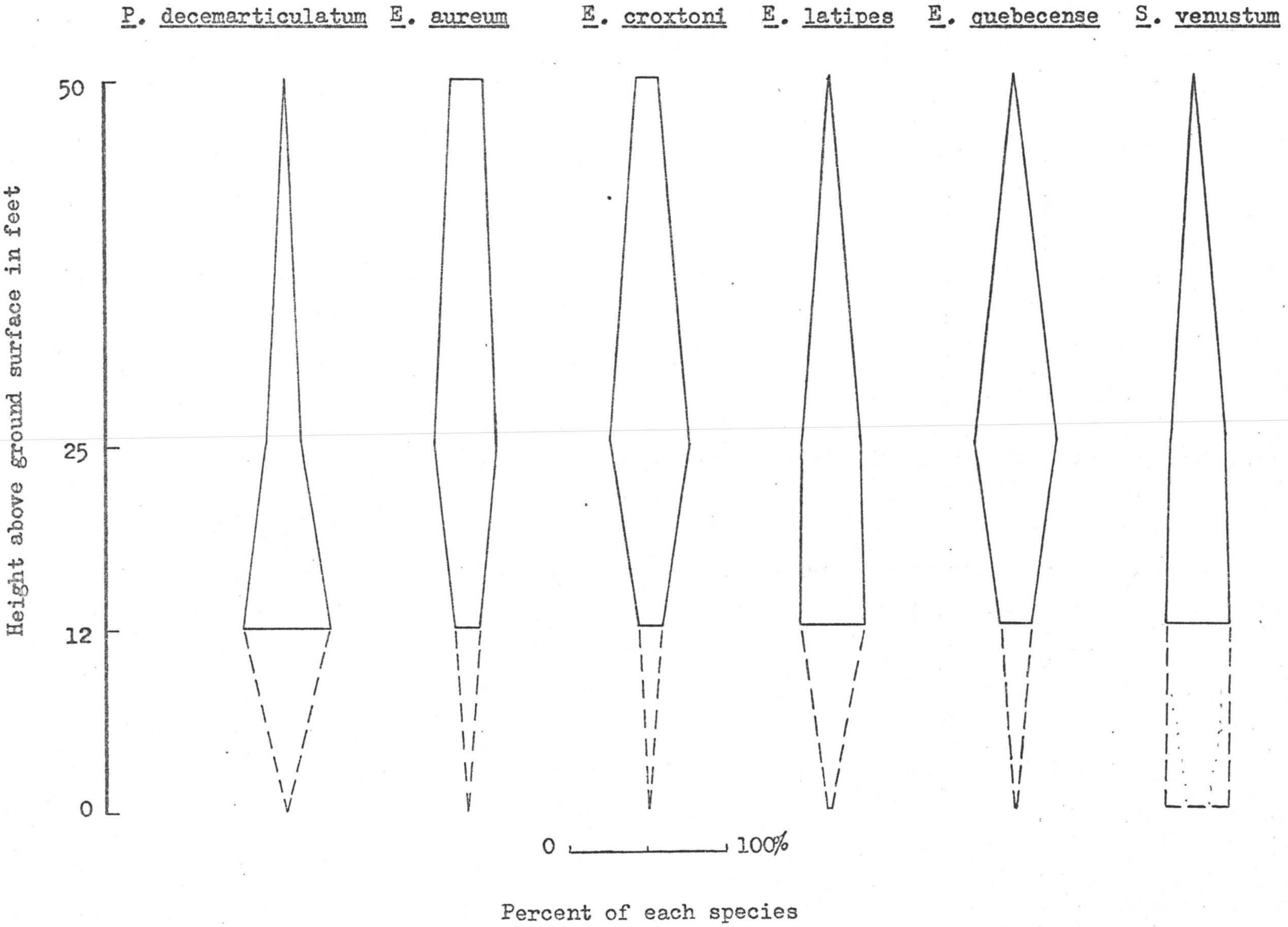

50 ft. above ground
25 ft. above ground
12 ft. above ground
Per cent of the number of black-flies collected
Eastern Daylight Time
0
10
20
30
40
50
60
70
80
1000
1200
1400
1600
1800
2000

Fig. 20 Comparison of the percent of female Simuliidae distributed at three levels above ground surface in the forest at the Wildlife Research Station, Algonquin Park, Ontario. Summer 1966.

Dashed sections indicate the relative proportion of black-flies expected between 0 and 12 feet above ground if simultaneous collections had also been made at ground level.


P. decemarticulatum
E. aureum
E. croxtoni
E. latipes
E. quebecense
S. venustum
Height above ground surface in feet
50
25
12
0
0
100%
Percent of each species

2. Upwind Orientation

(a) Results from spring of 1967

These experiments were designed to test whether the flies approached the CO_2 source equally from all sides or showed a definite upwind orientation. Each collection was made at times when both a noticeable number of black-flies and a wind (or breeze) were present. Although it was realized that the wind was generally unidirectional at any one time, an observer remained at the experimental site approximately 200 feet from the apparatus to watch for any possible change in wind direction during the first two collections (Fig. 23 A-B). Any noticeable change in wind direction was followed by repositioning of the wheel toward the new wind direction. Subsequent collections were made in the absence of the observer at the experimental site. For each test most black-flies were caught on the downwind pegs (Figs. 23A-E) with a progressive decrease in the number of flies on pegs toward the upwind side of the wheel. It is also evident that the larger number of flies were always caught on the downwind surface of each peg than on the corresponding upwind surface. To obtain a clearer picture of the relative distribution of flies round the wheel, the percentage of flies collected from each peg was determined and the results represented in the form of a rosette (Fig. 23 A-E). Generally, these rosettes show a striking preponderance of black-flies on the downwind pegs compared to the upwind ones. However, some collections (Fig. 23 A, C, D), indicate that this preponderance does not result exactly along the prevailing wind direction; rather, a diffuse distribution of flies is represented round the downwind half-sector of the wheel, possibly as a result of slight shifts in wind direction from the path along which the wheel was originally oriented.

(b) Results from spring of 1968

Preliminary collections with the experimental and control wheel (Fig. 24 A-C) indicate that black-flies will not fly upwind in noticeable number in the absence of CO_2. In the presence of CO_2 flies collected from the upwind oriented wheel (Fig. 24 A-C) are predominantly distributed on the downwind half-section of the wheel, as is represented by the rosette-shaped distribution around the wheel. During these collections it became evident that most flies would land on the downwind pegs but that some would penetrate between these and land on the upwind pegs. In order to test whether flies were really penetrating between the "front" pegs and landing on the upwind ones, additional collections were made using a continuous metal strip on the periphery of the wheel which would probably decrease the number of flies entering from the downwind section to the upwind section of the wheel. Two of these collections (Figs. 25A-D) indicate that with this method the number of simuliids flying to the upwind half-sector of the wheel is reduced considerably, the largest number landing on the downwind-facing section and some on the "sides" of the wheel.

This apparatus was further elaborated to test the distance downwind from the source of CO_2 at which flies could detect this wind-borne gas. In addition to the circular strip on the periphery of the wheel, two other metal-strip-arches were placed alternately either at 10 feet or 15 feet from the central source of CO_2. Results of these tests are shown in Figs. 26 A-D.

On the circle are recorded the number of flies collected on each of 24 sections of the sticky metal-strip; on the metal-strip arch are recorded the number of flies collected on each of two adjacent sections of the 54 sections on the "15-ft" arch (Figs. 26 A-B) and of the 38 sections on the "10-ft" arch (Figs. 26 C-D).

Considering the quadrant on the wheel directly downwind from the CO_2 source, it is observed that for the first test (Fig. 26A) the total number of flies collected on this area (63.4 sq. inches) of the sticky metal strip was 68, while on the corresponding section of the arch (730 sq. inches) it was 55. The corresponding numbers for the other three tests were:

112 and 38, Fig. 26 B
207 and 109, Fig. 26 C
580 and 525, Fig. 26 D

Calculations have been made of the relative density of flies in the downwind quadrant of 1, 10 and 15 feet from the source of CO_2 (Table 3) which show that a negligible number of flies were collected at 10 and 15 feet from the source of CO_2 as compared to a distance of 1 foot.

Fig. 23 A-E. Diagrammatic representations showing the number and per cent of female Simuliidae* collected from the inner and outer surface of each stick in relation to the wind direction. Carbon dioxide emission from the center of the wheel at 150 c.c./min. Algonquin Park, Ontario.

*mainly _Simulium venustum_ Say.

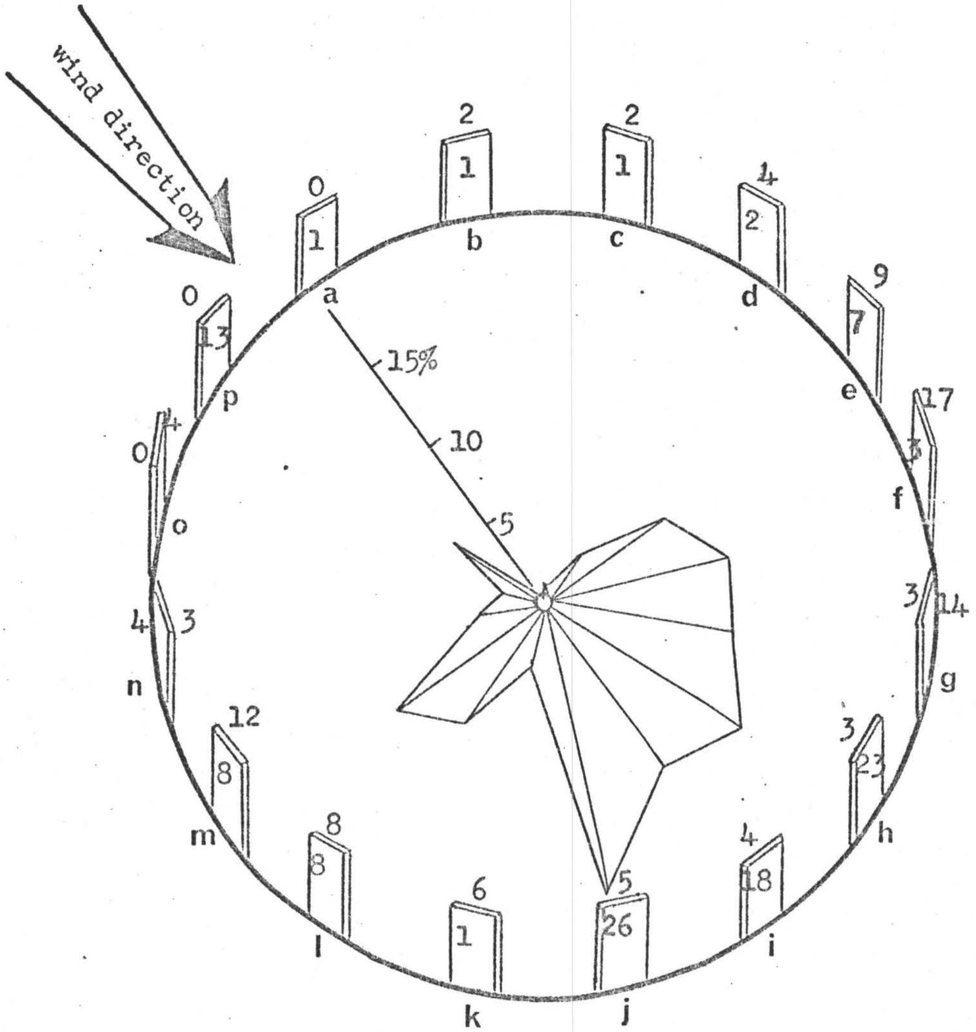


Fig. 23A. June 1, 1967; 1600-1800

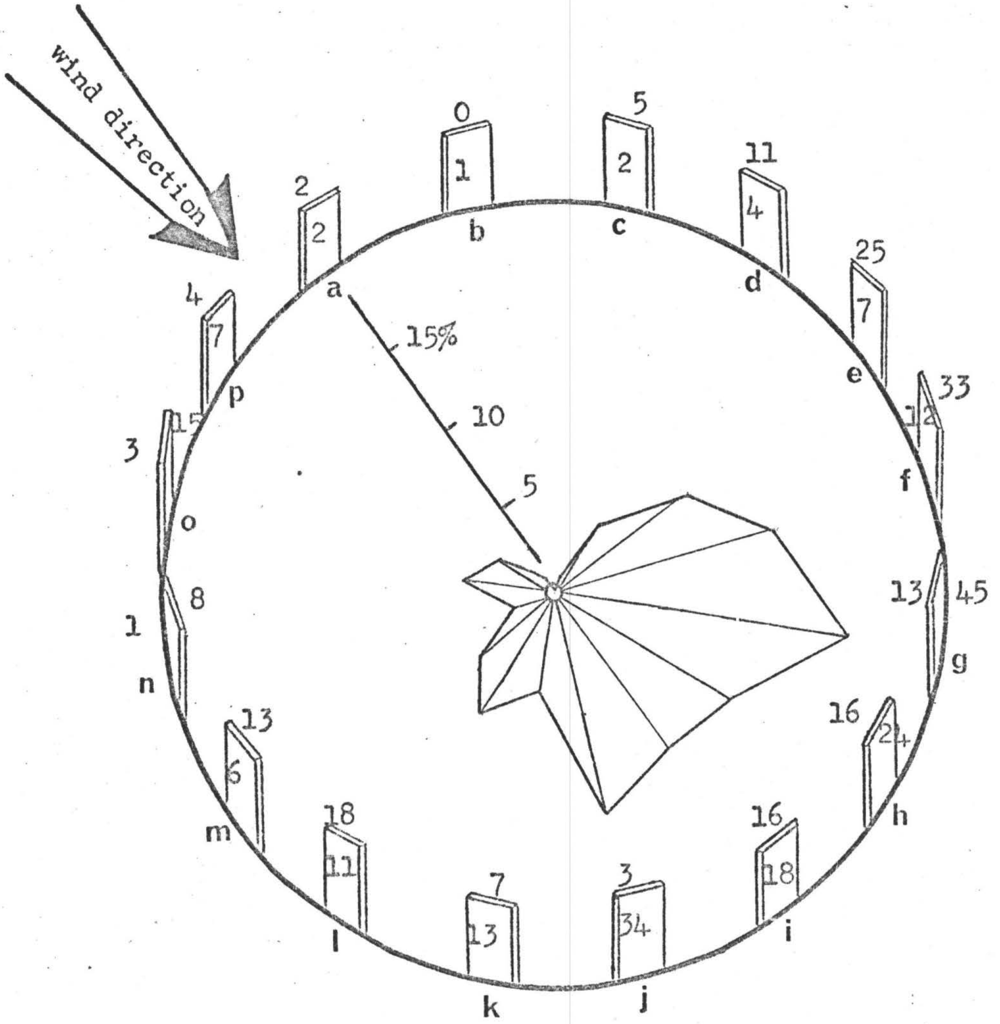


Fig. 23B. June 1, 1967; 1815-1915 EDT

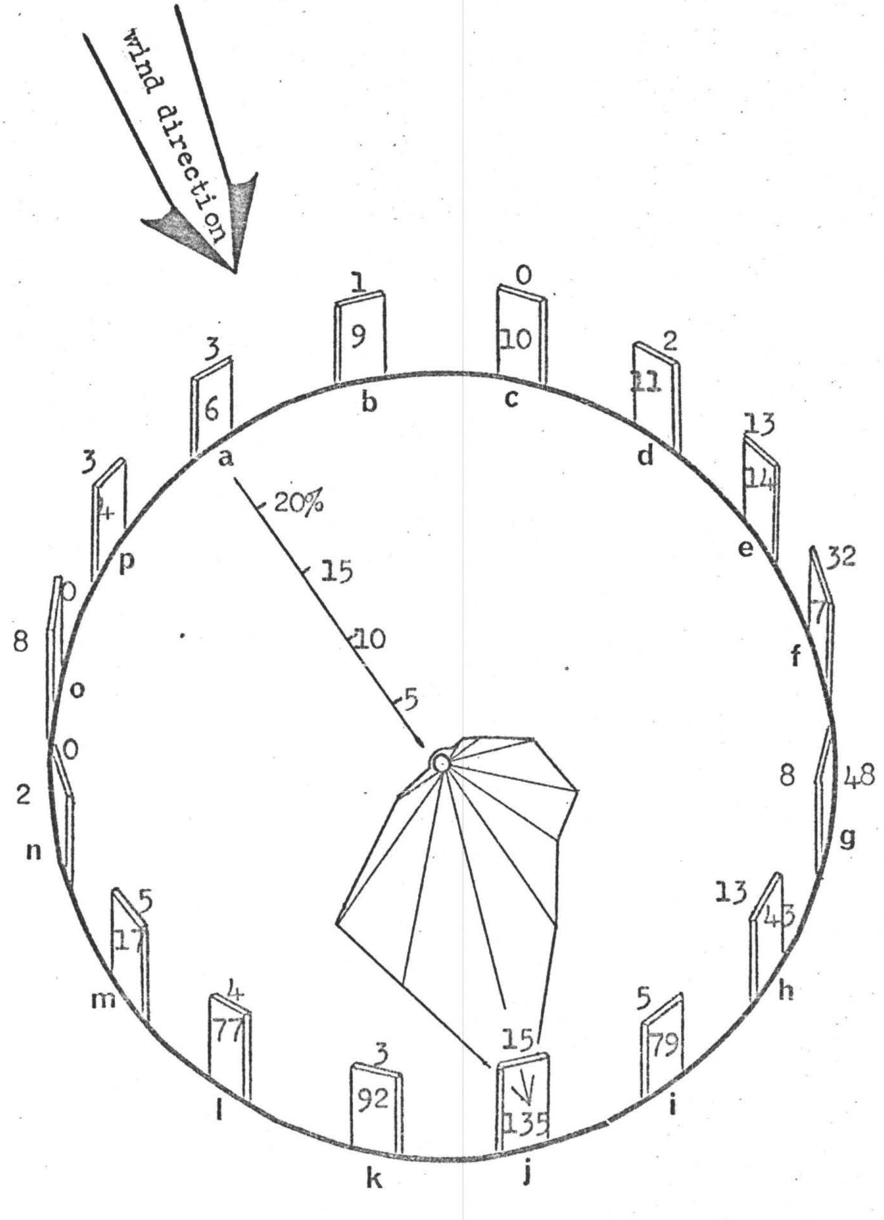


Fig. 23C. June 4, 1967; 1915-2015 EDT

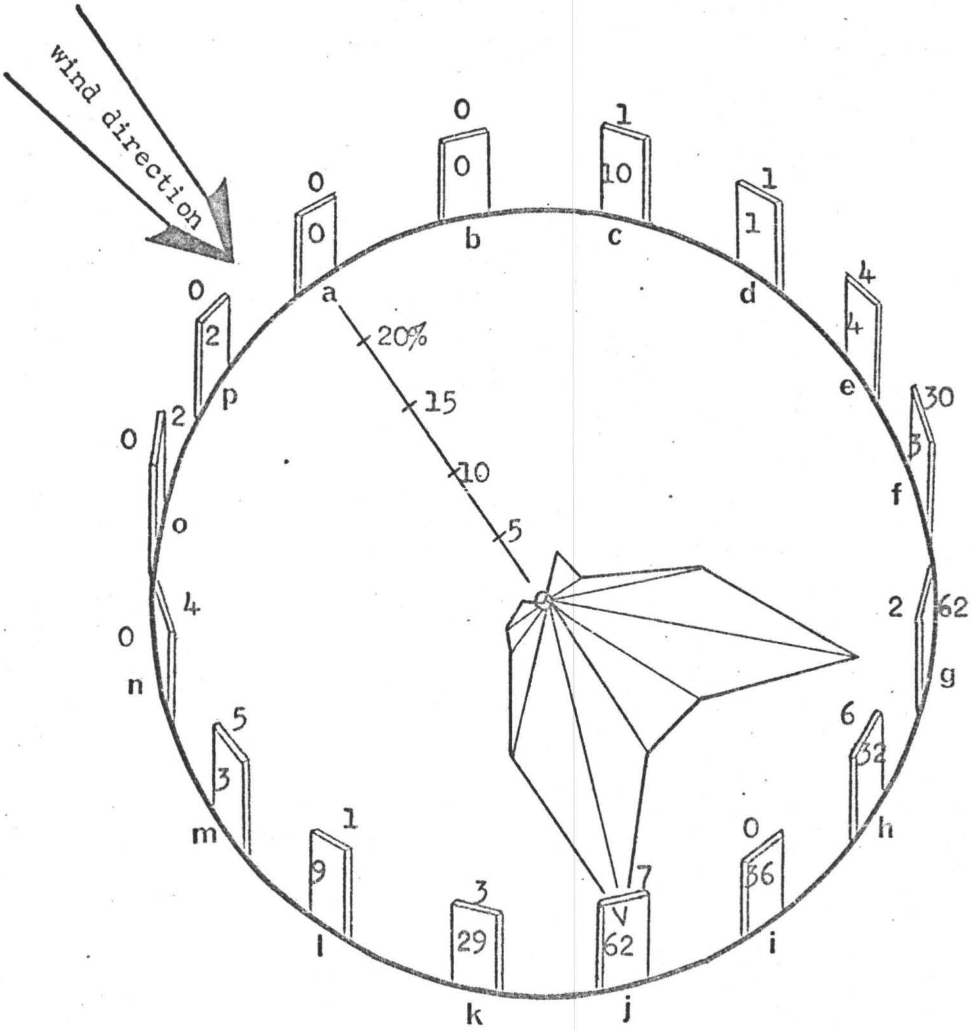


Fig. 23D. June 5, 1967; 1815-1915 EDT

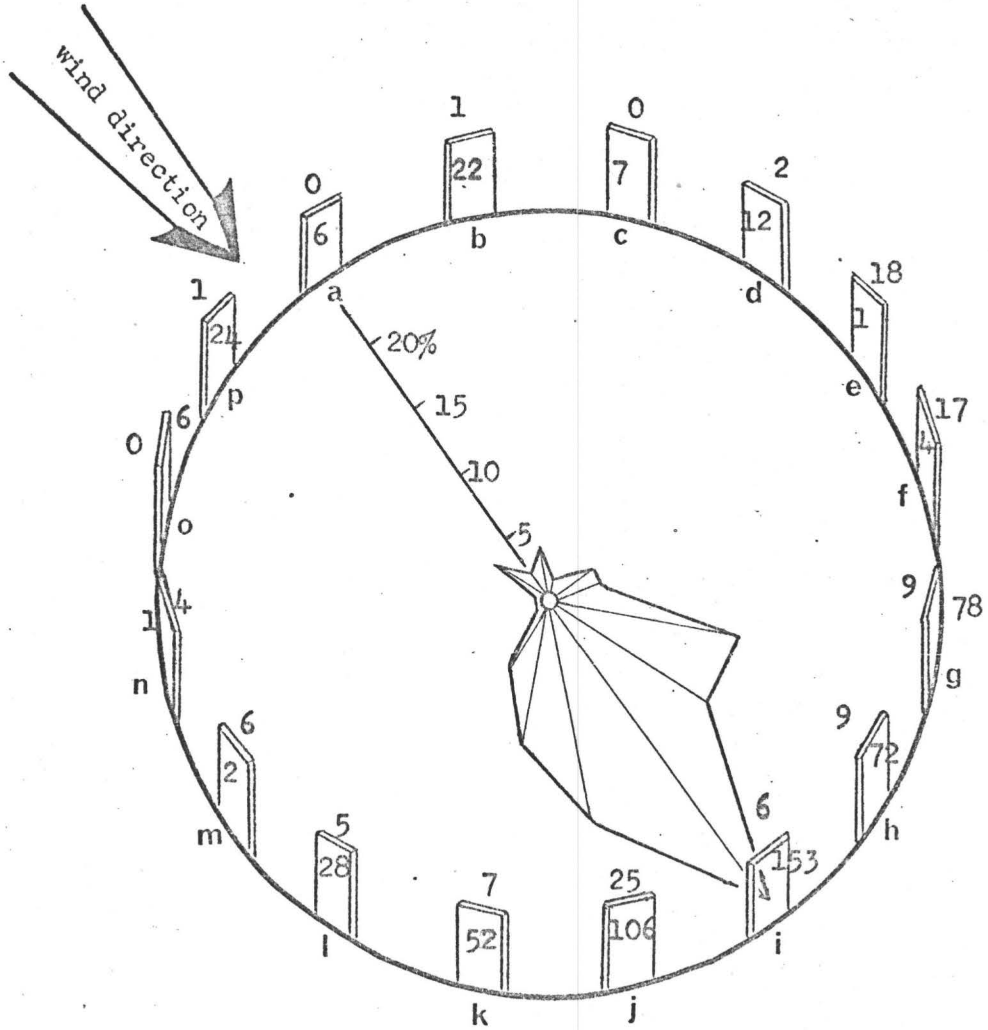


Fig. 23E. June 5, 1967; 1930-2030 EDT

Fig. 24 A-C. Diagrammatic representations showing the number of female Simuliidae collected from each sticky test-tube in relation to the wind direction. Carbon dioxide emission from the center of the wheel at 300 c.c./min. Algonquin Park, Ontario, 1968.

A May 23, 1640-1840 EDT; average wind velocity: 204 ft./min. from the north.

(1) Experimental wheel: 63 *P. fuscum*
54 *Eusimulium* spp.*
38 *S. venustum*

(2) Control wheel without CO_2: 1 simuliid

B May 25, 1645-1845 EDT; average wind velocity: 500 ft./min. from the north.

(1) Experimental wheel: 17 *P. fuscum*
24 *Eusimulium* spp.
79 *S. venustum*

(2) Control wheel without CO_2: 1 simuliid

C May 26, 2045-2145 EDT; average wind velocity: 350 ft./min. from south-west.

(1) Experimental wheel: 1 *P. fuscum*
53 *Eusimulium* spp.
135 *S. venustum*

(2) Control wheel without CO_2:
2 *Eusimulium* spp.
3 *S. venustum*

* include *E. croxtoni*, *latipes*, *quebecense*.

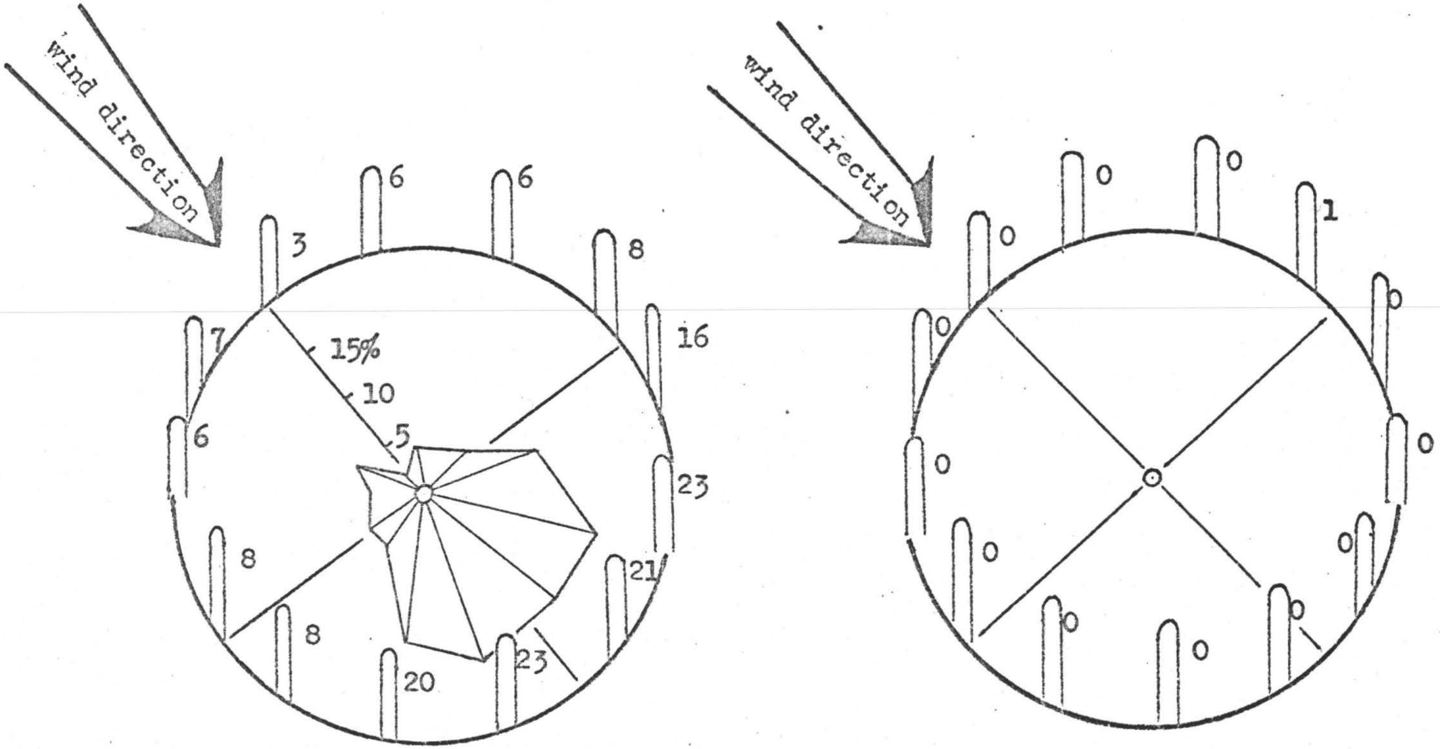

wind direction
3
6
6
8
16
7
15%
10
5
6
23
8
21
8
23
20
wind direction
0
0
0
1
0
0
0
0
0
0
0
0
0
0

Fig. 24A. (1) (2)

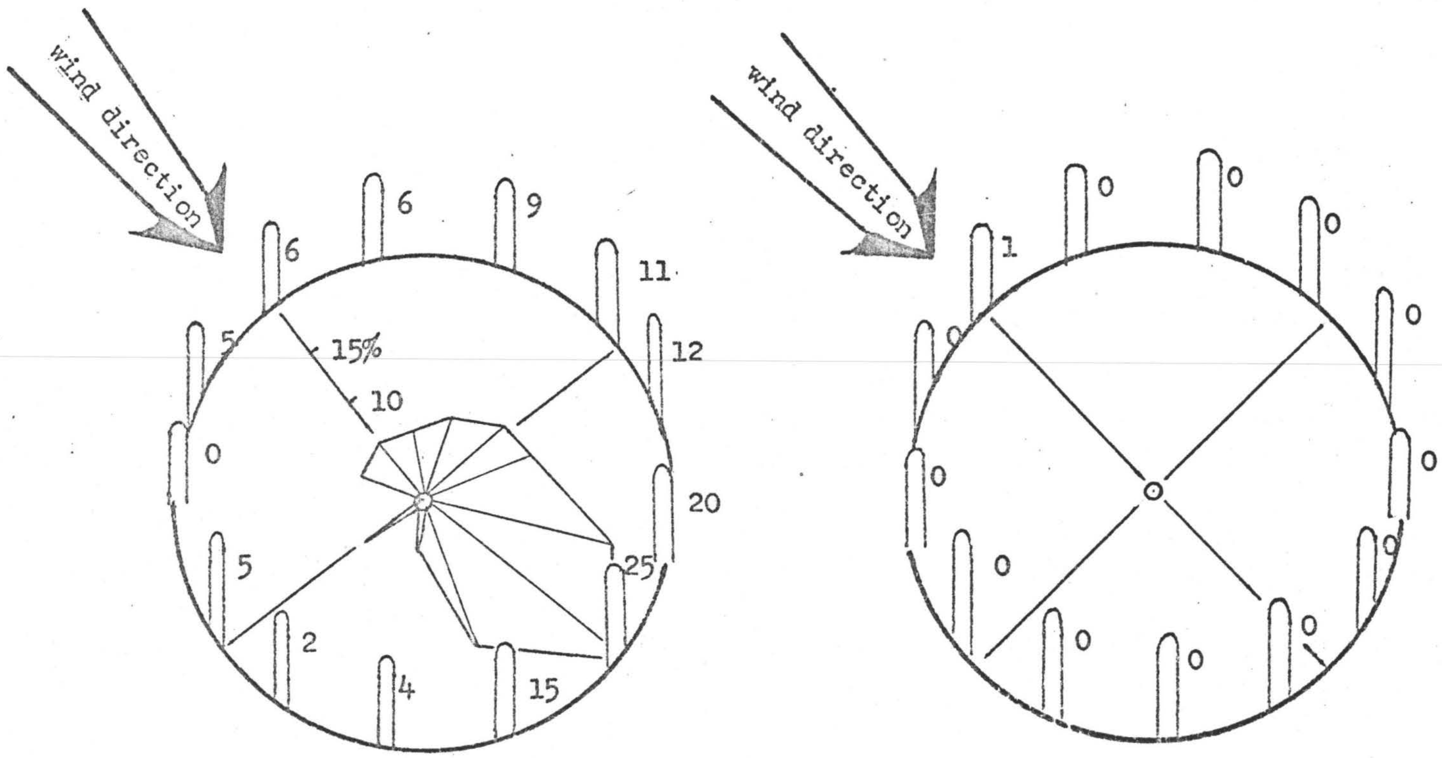

wind direction
6
6
9
11
5
15%
10
12
0
20
5
25
2
4
15
wind direction
1
0
0
0
0
0
0
0
0
0
0
0
0
0

Fig. 24B. (1) (2)

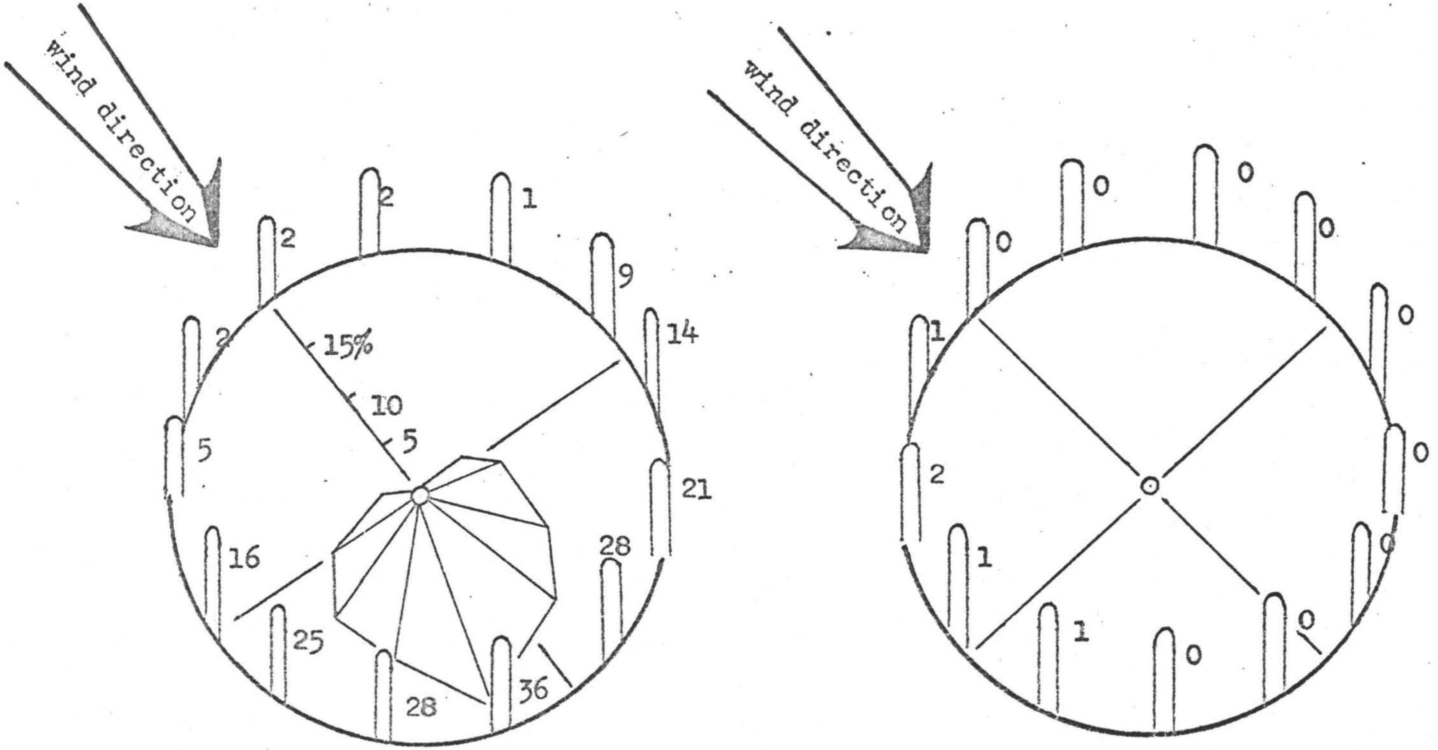

wind direction
2
2
1
2
9
14
5
15%
10
5
21
16
28
25
28
36
wind direction
0
0
0
0
0
0
1
2
1
1
0
0
0

Fig. 24c. (1) (2)

Fig. 25 A-B. Diagrammatic representations showing the number of female Simuliidae collected from each section of the sticky sheet metal strip in relation to the wind direction. Carbon dioxide emission from the center of the wheel at 300 c.c./min. Algonquin Park, Ontario, 1968.

A June 3, 1645-1945 EDT; average wind velocity: 320 ft./min. from the north.

Experimental wheel only:

5	*P. fuscum*
12	*Eusimulium* spp.
5	*Eus. aureum*
151	*S. venustum*

B June 4, 1830-2030 EDT; average wind velocity: 650 ft./min. from the west.

Experimental wheel only:

2	*P. fuscum*
4	*Eusimulium* spp.
211	*S. venustum*

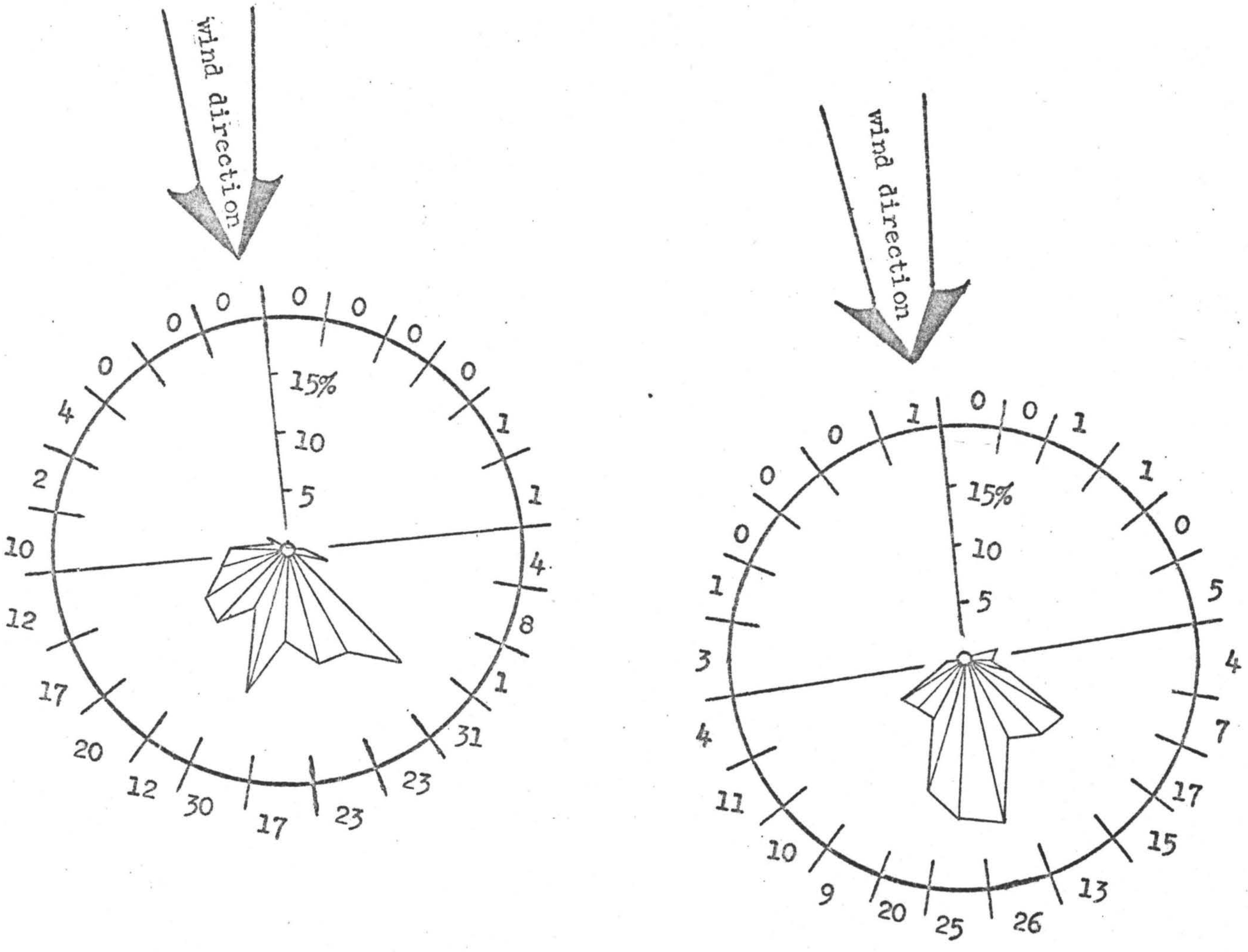

wind direction
15%
10
5
0
0
0
0
0
0
1
1
4
8
1
31
23
23
17
30
12
20
17
12
10
2
4
0
0
wind direction
15%
10
5
1
0
0
1
1
0
5
4
7
17
15
13
26
25
20
9
10
11
4
3
1
0
0
0

Fig.25 B

A

Fig. 26 A-D. Diagrammatic representations showing the number of female Simuliidae* collected from each section of the sticky sheet metal strip in relation to the wind direction. Carbon dioxide emission from the center of the wheel at 300 c.c./min. Algonquin Park, Ontario, 1968.

*mainly *Simulium venustum* Say.

A June 6, 1915-2045 EDT; average wind velocity, from the west at 610 ft./min. Radius of collecting arch 15 feet from the center of the wheel.

B June 7, 1845-2100 EDT; average wind velocity, from the west at 700 ft./min. Radius of collecting arch 15 feet from the center of the wheel.

C June 11, 1900-2030 EDT; average wind velocity, from the south-west at 350 ft./min. Radius of collecting arch 10 feet from center of the wheel.

D June 12, 2000-2200 EDT; average wind velocity, from the west at 444 ft./min. Radius of collecting arch 10 feet from the center of the wheel.

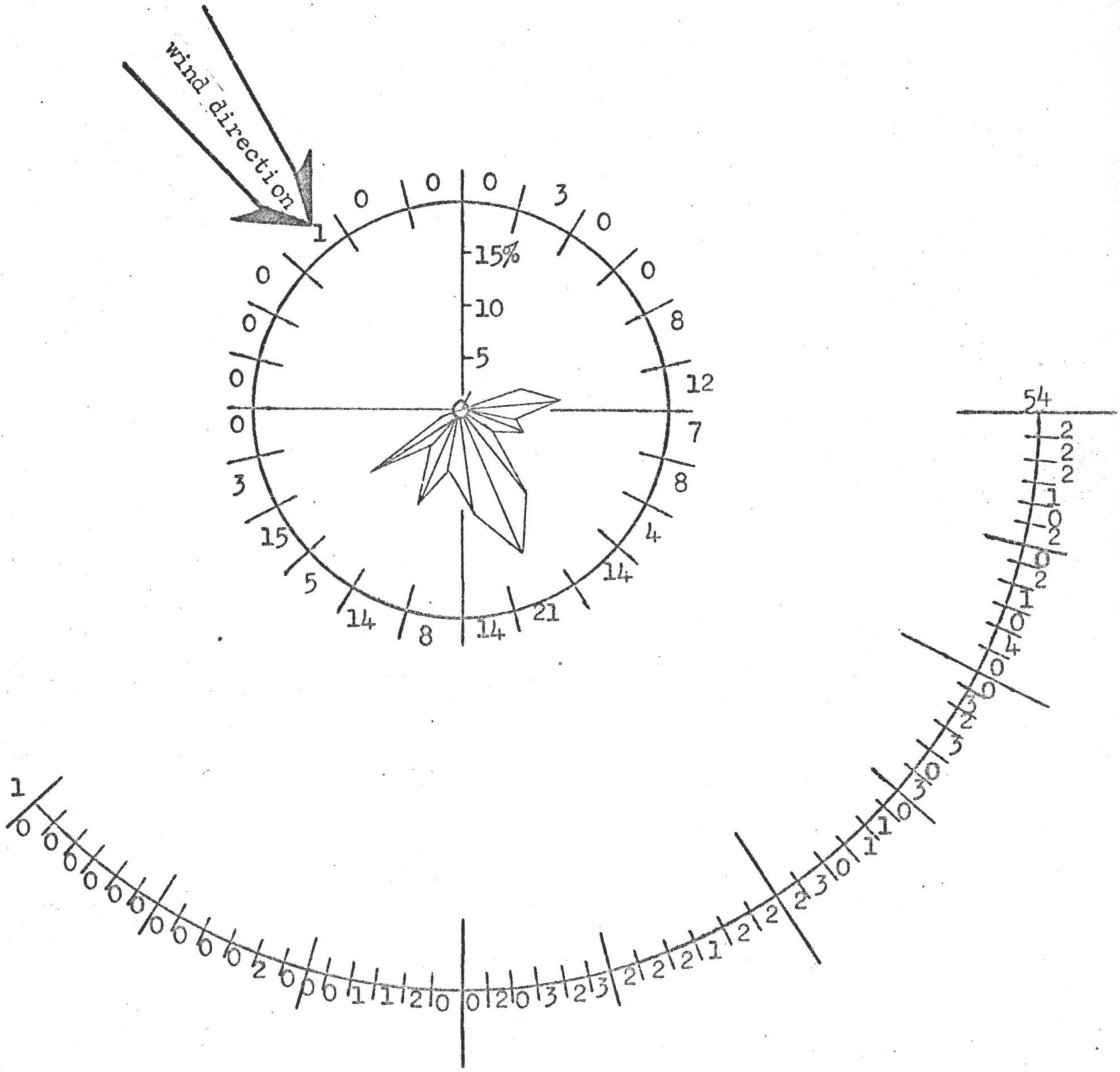

wind direction
15%
10
5
0 3 0 0 8 12 7 8 4 14 21 14 8 14 5 15 3 0 0 0 0 1 0 0
1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 1 1 2 0 0 2 0 3 2 3 2 2 2 1 2 2 2 3 0 1 1 0 3 0 3 2 3 0 0 4 0 1 2 0 2 0 1 2 2 2 54

Fig. 26 A

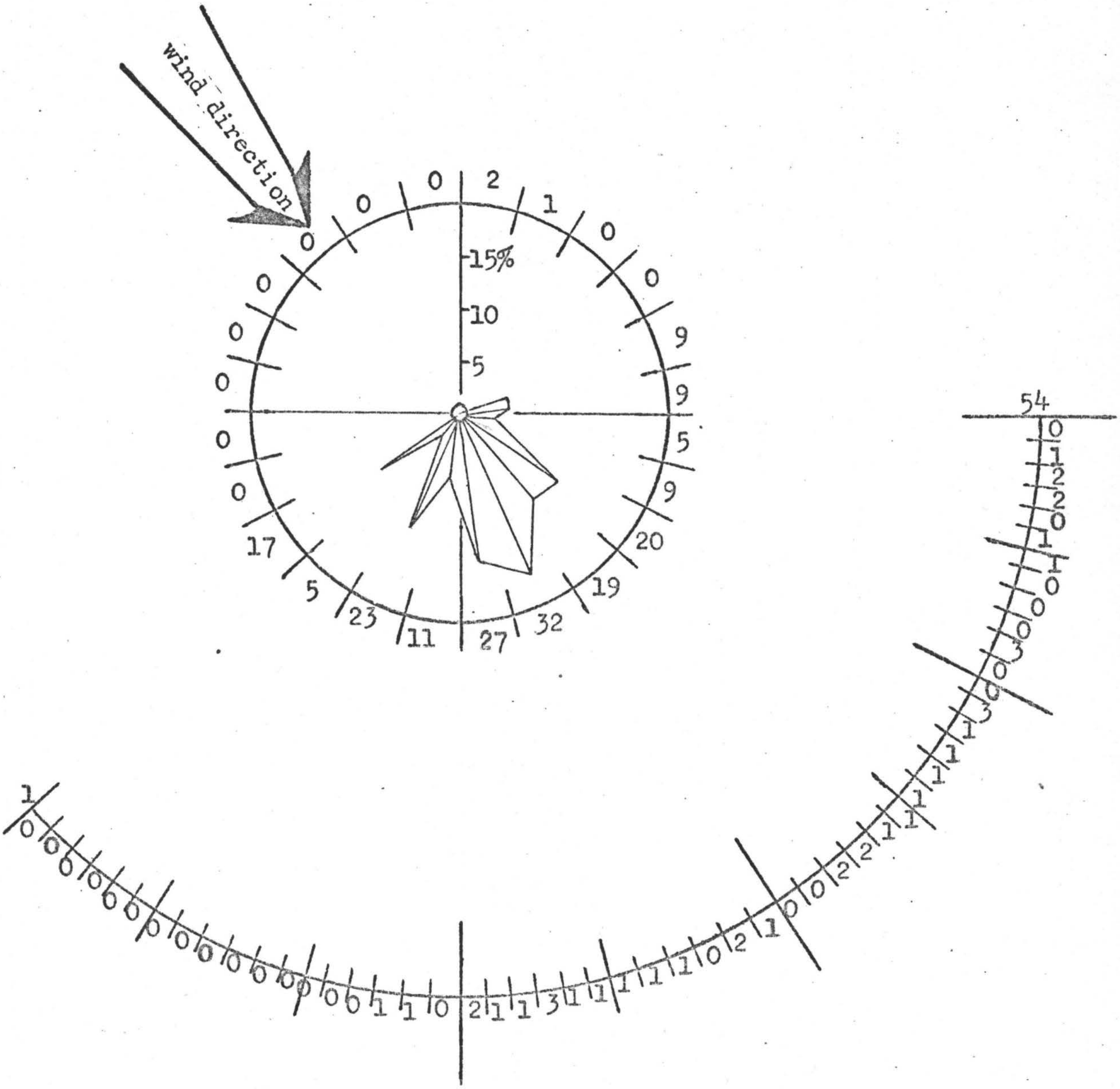

wind direction
15%
10
5
2
1
0
0
9
9
5
9
20
19
32
27
11
23
5
17
0
0
0
0
0
0
0
0
54

Fig. 26 B

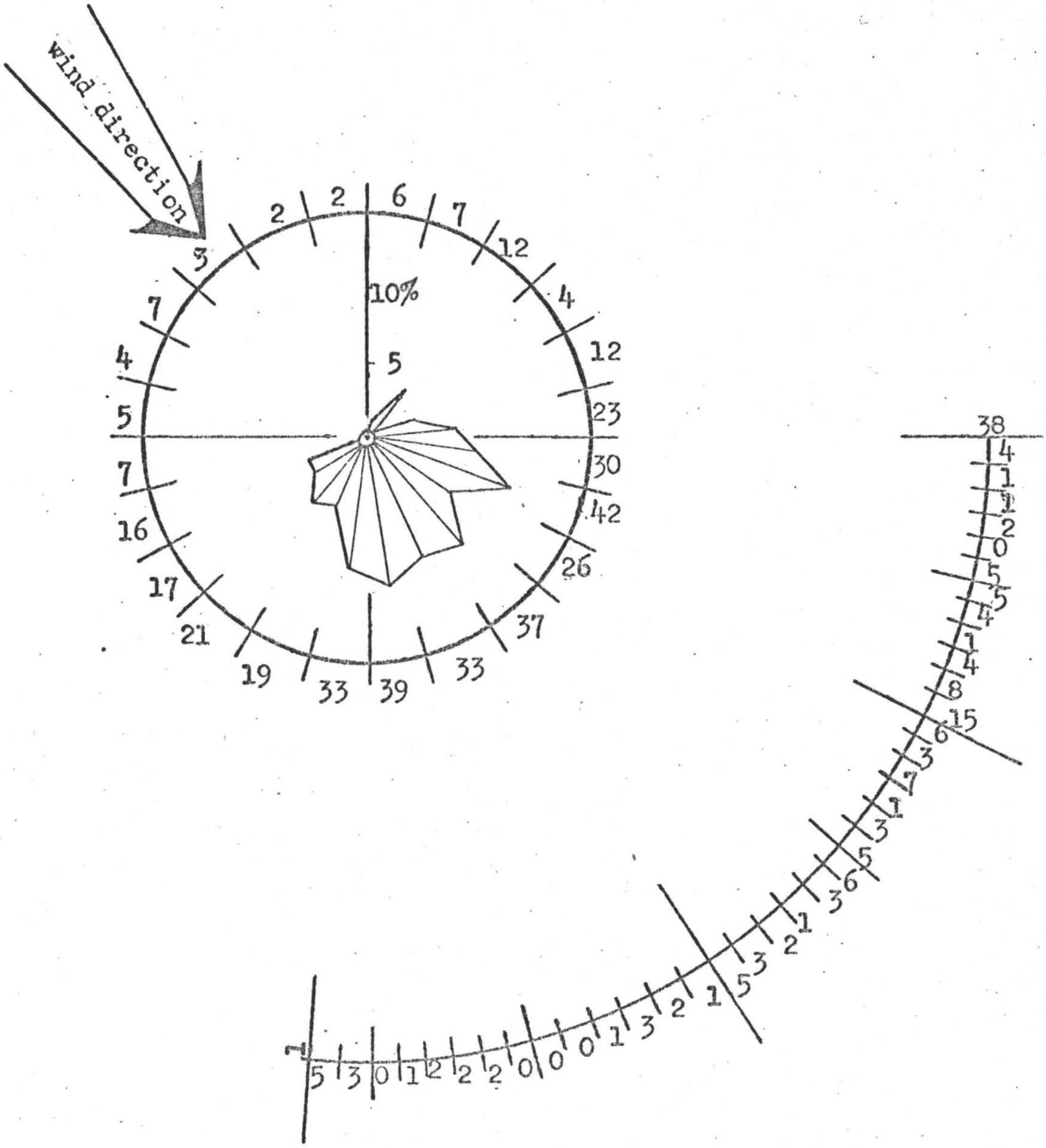

wind direction
10%
5
2
6
7
12
4
12
23
30
42
26
37
33
39
33
19
21
17
16
7
5
4
7
3
2
38
4
1
1
2
0
5
5
4
1
4
8
15
6
3
7
1
3
5
6
3
2
1
3
5
1
2
3
1
0
0
0
2
2
2
1
0
3
5
1

Fig. 26 <u>C</u>

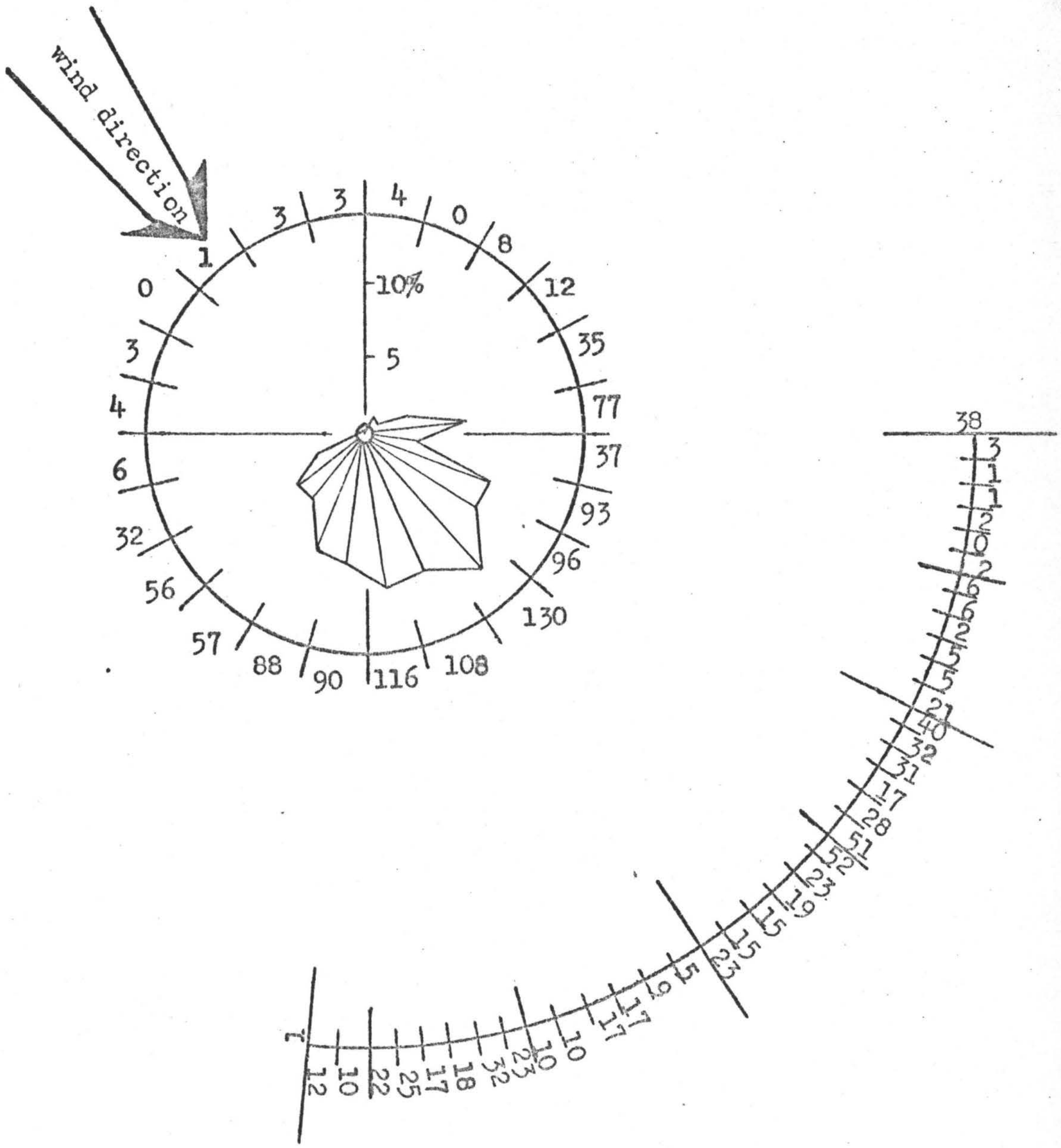

wind direction
10%
5
3
4
0
8
12
35
77
37
93
96
130
108
116
90
88
57
56
32
6
4
3
0
1
3
38
3
1
1
2
0
2
6
6
2
5
5
21
40
32
31
17
28
51
52
23
19
15
15
23
5
9
17
17
10
10
23
32
18
17
25
22
10
12
1

Fig. 26D

TABLE 3

Relative density of female simuliids on the downwind quadrant at various distances from the central source of CO_2, calculated from the results shown in the series of Fig. 26. .

Fig.	No. of flies per square inch		Ratio of flies at 1 and 15 ft and 1 and 10 ft from CO_2
	wheel	arch	
26A	1.0[a]	0.07[b]	14 : 1
B	1.8	0.05[b]	36 : 1
C	3.2	0.14[c]	23 : 1
D	9.2	0.70[c]	13 : 1

Distance from centre : [a] 1 ft, [b] 15 ft, [c] 10 ft.

3. Olfactory and Visual Discrimination

An experiment was conducted to determine the relative importance of the silhouette of a fan-trap and the CO_2 emission in collecting female simuliids. By hiding one trap just below ground surface, the silhouette was avoided. With both visual and olfactory factors combined a larger number of flies were collected than with either alone (Table 4). Indeed, with CO_2 alone in the absence of a silhouette fewer flies were collected (34.3%) than with both in combination (65.4%), and in the absence of CO_2 a silhouette (fan-trap) alone attracted the fewest flies (0.3%).

Another experiment using a black and a white fan-trap was designed to show the relative importance of reflected light and CO_2 emission on the orientation of female simuliids to these traps. A series of collections were made during the first seasonal peak abundance of *P. fuseum*, *Eusimulium* spp. and *S. venustum* (Table 5). In general, it can be seen that the white trap collected significantly fewer flies than the black trap at equal rates of CO_2 emission (Table 6). The gradual decrease in the population of *P. fuseum* during this collecting period makes difficult a clear assessment of the effect of increasing the CO_2 output beside the white (wiith) trap and the attraction of this species to it. Nonetheless, the discrimination ratio between the black and the white trap (number of flies taken in black trap divided by that taken in white trap) seemed to decrease noticeably as the CO_2 output beside the white trap was increased (Table 6); a discrimination equilibrium (discrimination ratio = 1) for *P. fuseum* was reached at "white-trap" CO_2 emission 3 to 4 times that of the black trap. Judging from the gradually decreasing trend of discrimination ratios, this equilibrium point with a larger population of *P.*

fuscum might have occurred more clearly at white-trap CO_2 emission 4 times that of the black trap. *S. venustum*, with an increasing population density during this experimental period, followed a similar trend in discrimintion as that of *P. fuscum* (Table 6). However, *S. venustum* reached its discrimination equilibrium point at white-trap CO_2 emission exactly 3 times that from the black trap; at higher white-trap CO_2 emissions, *S. venustum* was attracted in larger numbers to the white trap as a result of the stronger olfactory sensitivity to the higher volume of carbon dioxide. A definite conclusion on the discrimination behaviour of the *Eusimulium* species is difficult to draw due to the small number collected. However, it appears that olfactory discrimintion between the low and high CO_2 emissions is noticeably less than that of *P. fuscum* and *S. venustum* (Table 6). This can be detected by comparing the higher discrimination ratios of *Eusimulium* species with the ratios of *P. fuscum* and *S. venustum* at the corresponding CO_2 emissions.

TABLE 4

Comparison of the number of female Simuliidae* collected with carbon dioxide without a silhouette and with a silhouette with and without carbon dioxide. Silhouette presented by exposed fan-trap. Carbon dioxide emission at 150 cc./min. beside each trap. Algonquin Park, Ontario.

Date of Collection	Position of Fan-traps		
	Underground	2 feet above ground	
	with CO_2 no silhouette	with CO_2 + silhouette	without CO_2 + silhouette
11-V1-68			
0900 - 1000	263	403	-
1010 - 1110	97	189	-
1815 - 1925	90	164	-
1930 - 2030	58	207	-
12-V1-68*			
1145 - 1330	142	252	2
1700 - 1830	78	292	1
1830 - 1930	106	211	1
1930 - 2200	129	144	-
14-V1-68			
1330 - 1630	67	168	3
1630 - 2030	364	655	5
2030 - 2200	42	196	1
16-V1-68			
1630 - 1830	60	198	-
1930 - 2030	65	73	1
Total	1655	3152	14
%	34.3	65.4	0.3

*Approximately 85% both underground and above ground were *S. venustum* Say. The rest were: 10% *S. decorum* Walk., 3% *Cn. mutata* (Mall.), 1% *P. fuscum* S. & D., 1% *S. tuberosum* (Lund.).

TABLE 5

Simuliidae collected with a black and a white suction fan-trap with different output of carbon dioxide and placed 3 ft. apart and 3 ft. above ground; Algonquin Park, Ontario, 1968.

Collection date	Fan-trap	CO_2 output in cc./min.	Species of Simuliidae		
			P. fuscum	Eusimulium spp.	S. venustum
May 23					
1200-1300	Black	150	61		120
	White	150	3		7
1315-1445	Black	150	25		100
	White	150	6		25
1445-1550	Black	150	73	1	56
	White	300	16		23
1550-1700	Black	150	142		58
	White	300	17		19
1700-1800	Black	150	114	3	65
	White	300	11	1	28
May 26					
1000-1100	Black	150	11	3	70
	White	300	2		14
1115-1315	Black	150	3		54
	White	450	3		12
1900-2000	Black	150	8	34	128
	White	450	10	6	94
2000-2100	Black	150	3	26	114
	White	450	10	6	94
June 3					
1715-1815	Black	150	15	1	281
	White	450	10		196
1830-1930	Black	150	7	15	312
	White	450	3	3	304
1930-2100	Black	150	10	42	358
	White	450	6	2	318
June 4					
1840-1940	Black	150	21	2	96
	White	600	9		303
1945-2030	Black	150	7		402
	White	600	6		563
2045-2145	Black	150		1	87
	White	600	3		119
June 5					
1830-2030	Black	150	9		236
	White	600	6		256
2100-2130	Black	150		15	108
	White	600		3	167
June 7					
1715-1845	Black	150		4	320
	White	600	4	1	392
1845-1945	Black	150	5	1	327
	White	600	4	1	437

TABLE 6

Comparison of the number of female Simuliidae collected with a black and a white suction fan-trap at different pairs of carbon dioxide emissions. Fan-traps placed three feet apart and three feet above ground. Summary of Table 5.

Fan-trap	CO_2 emission in cc./min.	Species of Simuliidae								
		P. fuscum			Eusimulium spp.*			S. venustum		
		No.	Ratio	p**	No.	Ratio	p	No.	Ratio	p
Black	150	86	9.6	<0.001	-			220	6.8	<0.001
White	150	9			-			32		
Black	150	340	7.4	<0.001	7	7.0	0.02	249	3.0	<0.001
White	300	46			1			84		
Black	150	46	1.1	0.20	118	7.0	<0.001	1147	1.0	0.50
White	450	42			17			1118		
Black	150	42	1.3	0.20	23	4.6	<0.001	1576	0.7	<0.001
White	600	32			5			2237		

*Eusimulium spp. include: Eus. croxtoni, latipes, quebecence.

**p represents the probability level of the number of Simuliidae collected with the black and the white suction-trap.

4. Substrate Colour Selection During Oviposition

Prior to this series of experiments it was observed at the experimental site that the major oviposition activity occurred in the period just before and soon after sunset. During this time the vegetation trailing on the water surface of the stream was often teeming with ovipositing black-flies in such large numbers that entire blades of grass (mainly _Typha latifolia_) appeared as floating black ribbons. Eggs were laid on the upper surface of grass blades provided that a thin film of water wetted the edge, or if the blade was partially submerged, eggs were laid at the point where the blade broke the water surface. These same observations were made when the coloured oviposition strips were exposed to ovipositing black-flies. Coloured strips with black-fly eggs were collected, therefore, every morning and replaced by a new set of strips for the next oviposition period. The necessity of making repeated collections is seen in Table 7A, as each collection did not always represent the final average colour preference determined by comparing the weight of eggs lain on each strip. In collections made with a light brownish background (Table 7A), the preference for the four neutral colours, mainly by _S. verecundum_ (Table 9), gradually increased from black showing no attractancy, to white with the highest attractancy of 71%. This pattern of preference is closely related to the quantity of total light reflected from each strip (Table 44)*; the greater the reflectance, the higher the preference. The choice of the chromatic colours, however, seems to be divided into three main spectral ranges: the _yellow-green_ which constitutes an average attractancy peak of 26.0% with yellow appearing slightly more attractive than the green, and the _red-orange_ and _blue-purple_,

* See Appendix C

falling on either side of this yellow-green peak, with an average relative attractancy of 18.5% and 5.5% respectively. This pattern of colour substrate selection does not appear to be specific for S. verecundum, for under identical experimental conditions S. vittatum follows the same trend (Table 8).

The effect of a black stream-background on colour preference appears to be less clear due perhaps to fewer collections (Table 7B); nonetheless, there is a shift in colour preference both in the neutral and chromatic series. In the neutral series, with the black background, light grey appears to be the most attractive (Table 7B) whereas with a lighter background, white was the most attractive (Table 7A). To investigate this background effect more definitely, a comparison between a black and a white artificial stream bottom was made (Table 10). As can be seen these simultaneous collections indicated that the largest number of eggs (95.6%) were laid on all strips floating over a black background as compared with a relatively negligible number (4.4%) laid on the same number of strips floating over a white background.

In the spring of 1968 strips similar to those used in 1966 were coated with sticky Bird Tanglefoot to obtain a more exact account of the simuliid species ovipositing. Collecting gravid female simuliids directly from the sticky oviposition strips (Table 11) did not alter significantly the preference of the chromatic colours as compared to the previous results (Table 7A). The yellow-green range was still the most attractive; by contrast, the preference for the neutral colours appeared to have shifted towards the black, as the black strip collected almost the same number of gravid flies as the white strip.

TABLE 7

Comparison of coloured substrate selection by ovipositing S. verecundum expressed as the weight of eggs laid on each coloured strip exposed on the water of a beaver pond stream, Algonquin Park, Ontario. Summer, 1966. (Numbers represent the weight x 10^{-1} mg of eggs.)

A. Strips floating on natural stream background, brownish light in colour.

Oviposition Date	Colour of Strips											
	Neutral				Sub total	Chromatic						Sub total
	Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple	
15-V1-66			2		2		8	6	62			76
18-V1-66			30		30		60	280	64	28		432
19-V1-66								464	80		10	554
20-V1-66							103	107	22			232
22-V1-66		3			3							
23-V1-66			34	506	540	1197	794	166	547		189	2893
24-V1-66				89	89		103	116	289	91		599
25-V1-66				182	182		320	416			108	844
26-V1-66			183	3	186			58	182	225	21	486
27-V1-66						13			38			51
28-V1-66				33	33			329	128		44	501
29-V1-66								64				64
30-V1-66		7	156		163	4	5	33		71		113
1-V11-66		15	64	717	796	320	224	21	125		104	794
2-V11-66		12		28	40	14		223	54	182		473
5-V11-66						783	599	295	373			2050
6-V11-66		85	222	405	712							
7-V11-66						7	3	113	205			328
9-V11-66			153	495	648			753	101			854
10-V11-66		367	333	711	1411	36	133	64	249			482
11-V11-66			79	224	303							
12-V11-66		66	75	1230	1371	29	22	69	616	197	137	1070
Total	0	555	1331	4623	6509	2403	2374	3577	3135	794	613	12896
%		8.5	20.4	71.1	100	18.6	18.4	27.7	24.3	6.2	4.8	100

TABLE 7

B. Strips floating on black plastic background on stream bottom.

Oviposition Date	Colour of Strips											
	Neutral				Sub total	Chromatic						Sub total
	Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple	
16-V11-66			744	1062	1806	29	465	31	338	615	50	1528
17-V11-66			842	283	1125		384			74	424	882
24-V11-66		34	799	541	1374			25	114	25	19	183
31-V11-66				8	8	8			21	22	35	86
6-V111-66		64	40	260	364							
7-V111-66						8		76				84
Total	0	98	2425	2154	4677	45	849	132	473	736	528	2727
%		2.1	51.8	46.1	100.0	1.7	31.1	4.8	17.3	27.0	19.4	101.3

TABLE 8

Comparison of coloured substrate selection by ovipositing S. vittatum expressed as the weight of eggs laid on each coloured strip exposed on the water of a beaver-pond stream, Algonquin Park, Ontario. Summer, 1966. (Numbers represent the weight x 10^{-1} mg of eggs)

Oviposition Date	Colour of Strips											
	Neutral				Sub total	Chromatic						Sub total
	Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple	
15-V1-66							4		4			8
18-V1-66									6			6
19-V1-66									8			8
20-V1-66							4					4
22-V1-66		2			2					15		15
23-V1-66				25	25	34	15	6	3		12	70
24-V1-66				10	10				26	5		31
25-V1-66				26	26			6			4	10
26-V1-66			24		24			41	9	28	2	80
28-V1-66				10	10			37	9			46
29-V1-66								37				37
30-V1-66			6	3	9					5		5
2-V11-66				14	14							
5-V11-66				12	12	22	19	124	12			177
9-V11-66								8				8
10-V11-66								17	2			19
12-V11-66						3			19	13		35
Total	0	2	30	100	132	59	42	276	98	66	18	559
%		1.5	22.7	75.8	100.0	10.5	7.5	49.3	17.5	11.8	3.2	99.8

TABLE 9

Gravid Simuliidae collected from sticky yellow coloured oviposition strip floating on the water of a beaver-pond stream, Algonquin Park, Ontario. Summer, 1966.

Date of Collection	Species of Simuliidae Eus. aureum	S. tuberosum	S. venustum	S. verecundum	S. vittatum
2-3 July			4	26	6
6 July		3	1	34	5
7-8 July	2	6	3	22	9
9 July	2	4	3	25	3
10 July		2	5	31	1
11 July				2	1
12 July	2	8	2	51	5
17-18 July	1	1	2	54	1
19-24 July				47	2
25-26 July	1			36	
27-28 July		1		39	1
29-30 July	1			22	
31 July				18	
Total	9	25	20	407	34
%	1.8	5.1	4.0	82.2	6.9

TABLE 10

Comparison between a black and a white stream bottom background as affecting the selection of a substrate by ovipositing Simuliidae. Algonquin Park, Ontario, 1966. (Numbers represent the weight x 10^{-1} mg of eggs laid on all neutral and chromatic strips.)

Oviposition Date	Colour of Stream Bottom	
	Black	White
16-V11-66	3334	0
17-V11-66	1971	0
24-V11-66	1557	0
31-V11-66	94	338*
6-V111-66	364	0
7-V111-66	84	0
Total	7404	338
%	95.6	4.4

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*Weight of eggs laid on one white strip only.

TABLE 11

Comparison of coloured substrate selection by ovipositing S. verecundum expressed as the number of gravid female simuliids caught on each coloured strip coated with Tanglefoot, exposed on the water of a beaver-pond stream, WRS, Algonquin Park, Ontario.

Oviposition Date	Colour of Strips											
	Neutral				Sub-total	Chromatic						Sub-total
	Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple	
27-V-68						8	9	7			7	31
28-V-68				21	21	24	38	35	44	8	16	165
31-V-68	2		4	2	8	4		6	14			24
3-V1-68	51	20	5	5	81		6	23			7	36
4-V1-68	12	15	11	10	48	9	8	28	5	5	14	69
5-V1-68	16	9	29	11	65	41	51	72	82	43	11	300
6-V1-68	3	11	4	15	33	5	61	112	37	51	5	271
7-V1-68	16	14	38	19	87	17	68	55	42	61	15	258
8-V1-68	37	13	26	38	114	13	63	29	129	13	8	255
9-V1-68	8	1		7	16	2	36	8	72	10	9	137
10-V1-68	2	3	13	4	22	8	6	26	2	12	12	66
11-V1-68	1	1	1	1	4	6	3	14	14	13	7	57
12-V1-68	3	1		13	16	28	4	48	30	30	14	154
14-V1-68						4	2			1	1	8
15-V1-68						9	2	18	17		7	53
16-V1-68		1			1	8	4	14	9	8	1	44
17-V1-68	1	1		2	4	4	10	4	4	4	3	29
18-V1-68	5	3	1	22	31	11	13	6	13	2	2	47
19-V1-68	3	2	2	2	9	3	3	3	17	6	10	42
Total	160	95	134	172	560	204	387	508	531	267	149	2046
%	28.6	17.0	23.9	30.7	100.2	10.0	19.0	24.8	26.0	13.0	7.3	100.1

TABLE 12

Gravid Simuliidae collected from the yellow coloured oviposition strip floating on the water of a beaver-pond stream, Algonquin Park, Ontario; Spring, 1968.

Oviposition Date	Species of Simuliidae			
	Cn. mutata	*S. venustum*	*S. verecundum*	*S. vittatum*
27-V-68	1	-	6	-
28-V-68	-	-	1	1
28-V-68*	-	-	86	-
30-V-68	-	5	1	-
3-V1-68	1	2	18	2
4-V1-68	-	1	26	1
5-V1-68	1	-	69	2
6-V1-68	-	3	105	4
7-V1-68	-	1	48	6
8-V1-68	-	-	27	2
9-V1-68	-	-	8	-
10-V1-68	-	-	16	10
11-V1-68	-	-	11	3
12-V1-68	-	-	33	15
15-V1-68	-	-	15	3
16-V1-68	-	-	12	2
17-V1-68	-	-	3	1
18-V1-68	-	-	2	4
19-V1-68	-	-	3	-
Total	3	12	490	56
%	0.6	2.4	87.3	10.0

*These female Simuliidae were collected as they were ovipositing on a blade of manna grass, *Glyceria striata* (Lam.), trailing on the water about 10 ft. downstream from the site of the oviposition strips.

TABLE 13

Gravid Simuliidae collected from two "sticky" oviposition strips, one yellow and one green, floating on the water of a beaver-pond stream W.R.S., Algonquin Park, Ontario. Spring 1967.

Date of Collection	Species of Simuliidae						
	P. fuscum	*Cn. mutata*	*S. decorum*	*S. tuberosum*	*S. venustum*	*S. verecundum*	*S. vittatum*
4-V1-67	1	-	-	-	1	7	-
5-V1-67	1	-	-	-	2	17	-
6-V1-67	-	2	-	2	-	16	1
8-V1-67	-	-	-	-	2	8	-
9-V1-67	-	-	-	-	-	2	-
10-V1-67	-	-	1	-	1	9	1
Total	2	2	1	2	6	59	2
%	2.7	2.7	1.4	2.7	8.1	80.0	2.7

Experiments and Observations in Norway

1. Seasonal Occurrence of Some Female Simuliids in the Rendalen Region

Prior to experiments conducted in the summer of 1967, the relative abundance and species composition of the adult female black-fly fauna in the Rendalen region was unknown. Therefore, throughout the summer sweep-net collections were made of simuliids flying around man and each of four dairy cows kept in the pasture at the main experimental site (Table 14A, B). The total number of flies from each collection is not representative of their daily abundance attracted to these hosts since the time spent for each collection was variable, and then only a sample of the total caught each day was identified to species. Among the seven species collected from cows *P. hirtipes* predominated at the beginning of the collecting season and gradually disappeared towards the end of July (Table 14A). *Scho. pusilla* reached its highest abundance in mid-July and was the species most frequently collected from cows (40.2%), while *G. rostratum* and the *Simulium* spp. were more evenly distributed throughout the collecting period.

Some simuliid species were much more common around cows (Table 14A) than around man (Table 14 B). Hence, *P. hirtipes* was rather abundant around cows (26.6%) but formed almost a negligible proportion (0.4%) of flies swept from man during the same period. In the other hand, *Scho. pusilla* was collected in larger proportion from man (66.2%) than from cows (40.2%), and it being the most abundant species from both these hosts suggests that it was the most numerous species in the region during the summer of 1967.

Considering that the abundance of a black-fly species may fluctuate not only within a particular season but also over consecutive seasons, another series of sweep-net collections were made from cattle in 1968 (Table 15). Since these collections were made late in the season, most of the *P. hirtipes* population was missed; nevertheless, in 1968, unlike 1967 (Table 14A) *G. rostratum* was the most abundant (74%) of all the eleven species collected. This change in relative abundance of *G. rostratum* and *Scho. pusilla* can also be seen by comparing the collections made on July 15, 21 and 29 of both years (Tables 14A, 15).

Although *G. rostratum* and *Scho. pusilla* were invariably the predominant species around cows and man, only *Scho. pusilla* often bit man on the exposed upper part of the body, while *G. rostratum* occasionally landed on man but rarely bit. Both of these species and *P. hirtipes*, on the other hand, severely attacked cows on the head , neck, shoulders, front legs and breast, underbelly and udder in such large numbers as to form a compact cover of engorging flies on the skin of the host. Very often these cows were observed to lick flies off their front legs and shoulders and also to stampede across the pasture, undoubtedly to relieve themselves of a dense swarm of flies which could be seen hovering around their heads and shoulders.

TABLE 14

Seasonal distribution of female Simuliidae in the Rendalen Region, Norway, as swept from cows and from man during the summer of 1967.

A. Swept from cows.

Date of Collection	Species of Simuliidae														Total
	P. hirtipes		Scho. pusilla		G. rostratum		S. morsitans truncatum		S. monticola		S. ornatum		S. sublacustre		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
28-V1-67	20	95.2									1	4.8			21
1-V11-67	68	90.7					1	1.3	1	1.3	5	6.7			75
3-V11-67	30	66.7			4	8.9	6	13.3	1	2.2	4	8.9			45
5-V11-67	39	72.2			9	16.7	1	1.9	2	3.7	3	5.6			54
6-V11-67	61	64.2			11	11.6	12	12.6	1	1.1	10	10.1			95
7-V11-67	62	64.0	1	1.0	8	8.2	8	8.2	2	2.6	16	16.5			97
10-V11-67	17	21.3	15	18.8	22	27.5	7	8.8			19	23.6			80
14-V11-67	43	40.6	50	47.2	10	9.4	2	1.9	1	1.0					106
15-V11-67	14	6.5	188	86.6	8	3.7	2	1.0			5	2.3			217
17-V11-67	19	20.2	44	46.8	18	19.1	6	6.4			6	6.4	1	1.1	94
20-V11-67	1	0.8	54	42.9	71	56.4									126
21-V11-67	1	0.8	113	88.3	10	7.8	2	15.6	2	15.6					128
29-V11-67			30	88.2	2	5.9							2	5.9	34
5-V111-67			68	32.3	117	55.5	23	10.9					3	1.4	211
7-V111-67			4	13.8	18	62.1	7	24.1							29
Total	375		567		308		77		10		69		6		1412
%		26.6		40.2		21.8		5.5		0.7		4.9		0.4	

TABLE 14

B. Swept from man.

Date of Collection	Species of Simuliidae														Total
	P. hirtipes		Eus. latipes		Scho. pusilla		G. rostratum		S. monticola		S. morsitans truncatum		S. ornatum		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
26-V1-67	1	5.3									1	5.3	17	89.5	19
6-V11-67							10	55.6			8	44.4			18
7-V11-67							3	13.0			20	87.0			23
8-V11-67					1		2								3
10-V11-67							11	40.7			14	51.9	2	11.8	27
12-V11-67	1														1
13-V11-67					1										1
14-V11-67					17	94.4			1	6.6					18
15-V11-67	1	1.8			53	96.4	1	1.8							55
16-V11-67					142	87.1	16	9.8			1	1.6			159
20-V11-67					28	21.3	99	75.6	2	1.5	1	0.7	1	0.7	131
22-V11-67			1	0.3	267	92.7	14	4.9	1	0.3	2	0.7			285
25-V11-67			2	3.3	31	50.8	28	50.0							61
29-V11-67	1	0.4			205	80.7	48	18.9							254
1-V111-67					26	74.3	9	25.7							35
5-V111-67			1	0.8	39	32.8	73	61.3		6	6	5.0			119
7-V111-67					1	20.0	4	80.0							5
8-V111-67					21	54.0	15	39.5		3	3	7.7			39
Total	4		4		832		333		4		56		20		1253
%		0.4		0.4		66.2		26.5		0.4		4.5		1.6	

TABLE 15

Female simuliids swept from cows in the Rendalen Region, Norway, showing the relative abundance and seasonal distribution of various species around this host during the summer of 1968.

Date of Collection	Species of Simuliidae											Sub-total
	P. hirtipes	*Cn. pallipes*	*Scho. pusilla*	*Gnus rostratum*	*S. monticola*	*S. morsitans*	*S. ornatum*	*S. reptans*	*S. sublacustre*	*S. truncatum*	*S. vulgare-tuberosum*	
12-V11-68	3	1	6	99	2							111
15-V11-68	7	7	18	65	1		1				2	101
16-V11-68	2		2	134			1			1		140
17-V11-68	5		24	94			1		1	1		126
21-V11-68	5	1	3	94								103
23-V11-68			3	113					2	1		119
26-V11-68	1		14	88		5			6		2	116
27-V11-68			11	28		4			5			48
29-V11-68			2	118		4	1	5	6	1		137
5-V111-68			3	76		9		15	7			110
6-V111-68			1	63		27		21	6			118
7-V111-68				48		32	1	14	10			105
11-V111-68			1	56		46		7				110
17-V111-68			1	78	1	7		7	14			108
20-V111-68				80		13	1	6	21			121
Total	23	9	89	1234	4	147	6	75	78	4	4	1673
%	1.4	0.54	5.3	74.0	0.24	8.8	0.36	4.5	4.7	0.24	0.24	

2. Comparison of Olfactory and Visual Stimuli

Of primary interest in the orientation studies of adult simuliids in Norway was the relative importance of olfaction and vision in their host-seeking behaviour. Preliminary experiments were conducted to assess how the emission rate of carbon dioxide, considered as a general host odour, affected the reaction of black-flies to a source of the gas. Several species of simuliids were attracted to fan-traps "baited" with CO_2 and a progressively larger number of these flies were taken with increasing rates of CO_2 emission (Table 16A-C). The control trap, which in the absence of CO_2 was considered to act only as a visual stimulus, caught notably fewer flies than the fan-trap combined with CO_2 (visual and olfactory stimuli). Scho. pusilla and G. rostratum , which were taken in largest numbers, gave the clearest results.

The effect of CO_2 alone, i.e. in the absence of a visual stimulus, was more difficult to determine since even the smallest collecting device (such as the suction fan-trap) exposed beside the CO_2 source would act as a visual stimulus. However, semiquantitative observations were made on July 29 between 2045 and 2100 hours with the following apparatus: two idle fan-traps were suspended 20 feet from each other from a horizontal strand of wire, 4 feet above ground; beside one fan-trap was attached the end of a rubber tube emitting CO_2 but no CO_2 outlet was attached beside the other trap; halfway between the two fan-traps, on the same wire, was suspended only a rubber tube emitting CO_2. From each of the two outlets CO_2 was released at a rate of 800 cc/min. Within seconds of releasing CO_2 a tightly knit swarm of black-flies was seen hovering beside the idle fan-trap with CO_2, fewer flies were flying loosely beside the idle fan-trap lacking CO_2, and almost no flies were seen around the isolated CO_2 outlet. To quantify these observations similar sweep-net collections were made almost simultaneously from each of the three sources; a second set of sweep-collections was made five minutes later. The results clearly confirm that a negligible number of black-flies are attracted to the isolated source of CO_2 as compared to the significantly larger number of flies attracted to a combination of CO_2 and a fan-trap-silhouette (Table 17).

The experiment just outlined above presented limitations resulting mainly from the fact that for each sweep-net collection a proportion of flies attracted to the collector were transferred to each silhouette. This is particularly evident for the first collection (Table 17) which contains undoubtedly flies transferred from around the collector to the silhouettes as the apparatus was being set up. Hence, when compared to the second collection (Table 17) the first collection shows a larger proportion of Scho. pusilla than G. rostratum. To define more clearly, therefore, the role of CO_2 in the absence of a silhouette another experiment was conducted using fan-traps, with and without CO_2, exposed above ground and hidden just below ground surface (for details see p. 45). Individual collections from this experiment are reported in Table 18. It can be seen that the first seven collections were made without a fan-trap exposed at ground level, and these have been summarized on Table 19A. Among the nine simuliid species collected, *Cn. pallipes*, *Scho. pusilla*, *G. rostratum*, and *S. vulgare*[*] were the most numerous, and each of the first three species mentioned were attracted in significantly larger number (see Appendix C, Table 41) to a combination of CO_2 and a silhouette than to CO_2 alone. *S. vulgare* , which was not encountered in 1967, was the only species attracted in significantly larger number to CO_2 alone than to CO_2 plus a silhouette. These results, however, may reflect in addition the influence of vertical stratification preferences exhibited by some species; for instance, *S. vulgare* might have a peculiar flying habit which might restrict it to a ground level stratification.

To test this hypothesis additional collections were made simultaneously (Table 18) with a fifth suction trap exposed at ground level (Fig. 11). A summary of these collections (Table 19B) indicates that *S. vulgare* was indeed stratified at ground level in its flying habit as only negligible numbers were collected at 4 feet above ground compared to a significantly larger number taken at ground level. This behaviour was also manifested by *Cn. pallipes* which seemed to be taken almost exclusively at ground level. However, unlike *Cn. pallipes*, which was taken almost exclusively with CO_2 plus the silhouette, *S. vulgare* was taken in almost equal numbers with CO_2-only (without a silhouette) as with CO_2 in the presence of a silhouette, indicating definitely, therefore, that olfaction plays the predominant role in the orientation behaviour of this species. Both *Scho. pusilla* and *G. rostratum* were attracted more to a combination of CO_2 and a silhouette than to either alone, and this appears to be true in general also for the remaining *Simulium* species (Tables 19A, B).

[*] See Appendix B for determining this species-complex as *S. vulgare* Rubtzov.

The role of CO_2 was further assessed in terms of how relative concentrations of this gas affected the behaviour of simuliids in close proximity to a silhouette. Three fan-traps were each combined with a different CO_2 emission rate and each trap was wrapped in a sticky black plastic material so that flies trapped on the outside could be compared with those sucked into the trap (for details see p. 45). Considering Scho. pusilla, the only species taken in large numbers, (Table 20) fewer flies were taken at low CO_2 concentration (200 cc/min) than at high CO_2 concentration (800 cc/min), but in the former case comparatively more flies were landing on the sticky plastic outside the fan-trap than remained flying around it, and thus taken into the trap. At increasing CO_2 concentrations, however, this trend was gradually reversed so that at CO_2 emission of 800 cc/min comparatively fewer flies were landing on the trap than remained flying around it. This trend is more evident by comparing the ratios of the number of Scho. pusilla remaining flying close to the trap to that landing on the silhouette; these ratios for CO_2 at 200, 400 and 800 cc/min are 0.32, 0.6 and 1.3 respectively.

Results of a similar experiment, described on p. 46, in which a "black cow" model was used as a larger silhouette are reported on Table 21. It can be seen that, in general, comparatively more flies (mainly pusilla and rostratum) were taken landing on the model at low than at high CO_2 emission.

Other experiments concerning the role of host-odours in the orientation behaviour of adult simuliids were conducted in 1968 after collecting a Eusimulium species (near S. dogieli Ussova and S. anatinum Wood)* feeding

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*See Appendix B

on domestic ducklings (Anas boschas) exposed at the edge of the Renåa River. The first blood engorged specimens were collected (with method used by Bennett 1960) on July 12, two to three days after the death of a couple of two-week-old domestic ducklings left exposed on the bank of the Renåa R. Later these two ducklings were observed to carry a heavy infection of a Leucocytozoon sp. in the periferal blood. Subsequent collections of this Eusimulium species (designated as sp. 1) indicated that it was flying most frequently near the water surface (Table 22), and additional collections from other species of birds (Table 23 and 24) indicated further that this fly might feed specifically on aquatic birds, such as ducks (Family Anatidae). To investigate whether olfactory stimuli emanating from the host played an important role in the host-seeking behaviour in this simuliid species, an experiment was conducted evaluating duck uropygial oil, CO_2 and both combined as "attractants" (for details see p. 46). Three sticky collecting cylinders, each with a different odour combination, were exposed over the Renåa R. for a total of 7 hours (Table 25). The total number of each of the eight species collected is reported in Table 26. Considering the two most abundant species, the ornithophilic Cn. pallipes and Eus. sp. 1, many more flies were collected with CO_2 plus the duck uropygial gland extract than with CO_2 only; the smallest number of flies were collected with the extract only. These results are more clearly represented in Fig. 27 which shows that the synergistic effect of CO_2 and uropygial extract is greatest with the duck-feeding Eus. sp. 1 and least with the mammaliophilic S. vulgare.

The influence of vision in the orientation behaviour of simuliids was further assessed comparing black traps and white traps in different habitats. In the grassland habitat a black and a white suction fan-trap were used as two optically contrasting silhouettes as described on p. 47. In general, simuliids were attracted in larger numbers to the black CO_2-trap than to the white CO_2-trap (Table 27). This is clearest for those species taken in largest number, such as *P. hirtipes*, *G. rostratum* and *S. ornatum*. In addition, these three species were attracted in almost equal numbers to the black trap without CO_2 as to the white trap with 200 cc CO_2/min. Results of a similar experiment (Table 28) conducted in the woodland habitat (see p. 47) indicate that *Cn. pallipes*, the only species caught in abundance, is attracted generally more to the black than to the white bird silhouette. This species, however, with a much smaller flying population and with slightly different experimental conditions showed no significant preference for either a black or a white fan-trap silhouette (Table 27). It must be realized that one important difference between these two cases is that *Cn. pallipes* was collected in the former case as it landed on the silhouette and in the latter case while hovering around it. Hence, its preference for either the black or the white silhouette was being measured under two slightly different behavioural phases. Limitations in the experimental procedure may also have influenced the kind of results obtained. In particular, no conscious effort was made to ensure an unbiased relative position of the two silhouettes with respect to wind direction during each collecting period; hence, the silhouette positioned downwind with to the other would naturally attract more flies than the other as a result of the upwind orientation of flies to carbon dioxide.

In other cases this wind effect was taken in consideration when setting up the experiment. During the black and white discrimination experiment whose results are reported on Table 27, a slight breeze was detected during the first collection, (7-VII-67), directed about 30° to the horizontal line formed by the three fan-traps. The three traps were placed with the black CO_2 trap 10 feet between the black control and the white CO_2 trap, the last one being positioned downwind. In this case, although the wind was favouring the white CO_2 trap it collected many fewer flies than the black CO_2 trap, emphasizing, therefore, the inhibitory visual effect on the near orientation to a silhouette reflecting a much higher light intensity. Considering that the difference in number attracted to the black and the white trap (at equal CO_2 emission) was due to opposite visual stimuli received from the two traps, then the ratio of the number attracted to the black as to the white trap could be used as a comparative index of visual sensitivity. With species collected in largest number (Tables 27, 28) this would be (with number from white trap equalling 1): P. hirtipes, 7.1; G. rostratum, 15.4; S. ornatum, 4.7; Cn. pallipes, 2.7. An index of one would indicate zero sensitivity. The index for Cn. pallipes cannot be strictly compared with the others as this species was taken in a different behavioural phase (see above).

TABLE 16

Comparison of the effect of different amounts of carbon dioxide emission in attracting female Simuliidae to suction fan-traps placed at four feet above ground and ten feet apart. Rendalen, Norway, Summer 1967.

A. Fan-traps with CO_2 emission at : 0, 200 and 800 cc./minute

Species of Simuliidae	Date and time of collection												Total*		
	5-VII-67						26-VII-67			29-VII-67					
	1800-2030			1230-1800			1100-1330			1015-1430					
	0	200	800	0	200	800	0	200	800	0	200	800	0	200	800
P. hirtipes	No Collection	5	2	No Collection	12	17	2	1	-	-	67	37	2	85	56
Cn. pallipes		-	-		1	-	-	2	-	-	15	-	-	18	-
Scho. pusilla		-	-		-	-	19	140	526	42	650	1552	61	790	2078
Gnus rostratum		3	2		5	23	43	11	780	13	67	438	56	86	1244
S. monticola		-	1		1	-	-	-	-	-	27	-	-	1	28
S. ornatum		6	2		6	5	1	-	-	-	-	-	1	12	7
Total		14	7		25	45	65	154	1306	55	826	2027	120	992	3413

* Collecting time for traps with CO_2 = 14 hours and 25 minutes.

Collecting time for control trap = 6 hours and 45 minutes.

TABLE 16 (continued)

B. Fan-traps with CO_2 emission at : 200 and 1600 cc./minute

Species of Simuliidae	Date and time of collection															Total*		
	2-VIII-67																	
	1615-1645		1655-1710		1735-1750		1915-1940		1940-1955		2000-2015		2020-2035		1800-2000			
	200	1600	200	1600	200	1600	200	1600	200	1600	200	1600	200	1600	Control NO CO_2	0	200	1600
P. hirtipes	-	-	-	3	-	-	-	16	-	-	-	-	-	-	-	-	-	19
Scho. pusilla	120	716	136	262	355	423	878	1601	211	776	762	699	85	544	42	42	2547	5021
Gnus rostratum	43	163	17	24	207	125	101	65	107	545	248	84	5	121	6	6	728	1127
S. monticola	-	8	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Total	163	887	153	292	562	548	979	1682	318	1321	1010	783	90	665	48	48	3275	6179

*Collecting time for traps with CO_2 = 2 hours and 10 minutes.

Collecting time for control trap = 2 hours.

TABLE 16 (cont.)

C. Fan-traps with CO_2 emission at : 50, 200, 800 and 1600 cc./minute

Species of Simuliidae	Date and time of collection												Total			
	11-VIII-67												75 min.			
	1110-1140				1200-1230				1245-1300							
	50	200	800	1600	50	200	800	1600	50	200	800	1600	50	200	800	1600
C. pallipes	1	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-
Scho. pusilla	-	13	19	70	18	68	61	85	58	68	58	83	76	149	138	238
Gnus rostratum	-	1	12	53	5	18	40	51	23	12	11	47	28	31	63	151
S. morsitans	-	-	-	3	-	1	1	-	-	-	2	-	-	1	3	3
Total	1	14	31	126	13	87	102	136	82	80	71	130	106	181	204	392

TABLE 17

Comparison of the number of female simuliids collected with a sweep-net from CO_2 plus suction-trap-silhouette, CO_2 only, and suction-trap-silhouette only placed 10 feet from each other and 4 feet above ground. CO_2 emission from each source at 800 cc/min. These collections were made at sun-set, July 29, 1967; Rendalen, Norway.

Species of Simuliidae	Condition of collection								
	1st collection			2nd collection			Total		
	CO_2 + silhouette	CO_2 only	silhouette only	CO_2 + silhouette	CO_2 only	silhouette only	CO_2 + silhouette	CO_2 only	silhouette only
Scho. pusilla	70	3	24	9	1	0	79	4	24
G. rostratum	6	1	4	26	2	0	32	3	4
Total	76	4	28	35	3	0	111	7	28

TABLE 18

Female Simuliidae collected with fan-traps, below ground and above ground, with and without carbon dioxide. Rendalen, Norway. Summer, 1968.

Date Time of collection	Position of fan-traps	Species of Simuliidae														
		P. hirtipes	Cn. pallipes	Eus. beltukovae	Eus. bicorne	Eus. curvans	Eus. latipes	Eus. sp.1	Scho. pusilla	Gnus rostratum	S. monticola	S. morsitans	S. ornatum	S. sublacustre	S. truncatum	S. vulgare-tuberosum
22-V11-68	*a		11	6			1									125
1300-1730	*b	no collection														
	*c		91	9					6							4
	*d		42	2		1			7	2						3
	*e															
1730-2115	a		6	4			6									82
	b	no collection														
	c	1	4		1				10	16						1
	d		7						3	18						2
	e															
23-V11-68	a		3				1		1							164
1230-1700	b	no collection														
	c		13						24	33						3
	d		2						5	5						
	e															
1700-2130	a		9	5	1		4		2	10						197
	b	no collection														
	c	5	22	7	7		3		78	168						7
	d	1			1				1	15						
	e															

*a Underground, CO_2 200 cc./min.
b Ground level, CO_2 200 cc./min.
c 4 ft. above ground, CO_2 200 cc./min.
d 4 ft. above ground, no CO_2
e Underground, no CO_2.

TABLE 18 (Cont.)

Date Time of collection	Position of fan-traps	Species of Simuliidae														
		P. hirtipes	Cn. pallipes	Eus. beltukovae	Eus. bicorne	Eus. curvans	Eus. latipes	Eus. sp.1	Scho. pusilla	Gnus rostratum	S. monticola	S. morsitans	S. ornatum	S. sublacustre	S. truncatum	S. vulgare-tuberosum
24-V11-68 1530-2030	a		9	3			1			1						294
	b	no collection														
	c		99	24					12	55						8
	d		22						1	11						1
	e															
25-V11-68 1300-1800	a		1													87
	b	no collection														
	c		22	1			4		18	30						6
	d		2						1	22						
	e															
1800-2130	a															31
	b	no collection														
	c	1	18	1	14		3		11	28				1		5
	d		8							6						
	e															
28-V11-68 1230-1630	a		5			1	2									86
	b		138	15		10	39	1	9	10					1	37
	c	2	5	3		1	2		37	31						
	d						1			2						
	e															
1630-2030	a			1					1							10
	b		221	10	10	19	5		13	30	1				1	20
	c		8	1	27				33	81						1
	d	no collection														
	e	no collection														

TABLE 18 (Cont.)

Date Time of collection	Position of fan-traps	P. hirtipes	Cn. pallipes	Eus. beltukovae	Eus. bicorne	Eus. curvans	Eus. latipes	Eus. sp.1	Scho. pusilla	Gnus rostratum	S. monticola	S. morsitans	S. ornatum	S. sublacustre	S. truncatum	S. vulgare-tuberosum
29-V11-68	a		6													14
1100-1400	b		65						2	7						11
	c	1	2						16	31						
	d		3						1	2						
	e															
1445-1645	a		8													15
	b		66	4			5		23	27				3	1	12
	c	1	1				1		24	44						
	d								1	10						
	e															
1700-1730	a		1	1												14
	b		51	2		1	13		13	57				5	2	42
	c		2	3			1		58	80						
	d		1						1	3						
	e															
1730-1930	a		9				1		3	15		1		1		29
	b		42	6		1	1	1	79	139	2	4	1	5	4	26
	c	1	1				3		83	97				2	2	
	d		3				2		6	8						
	e															
1930-2030	a		1	3	3				2	3						13
	b		32	3	8	1	1		33	60					3	15
	c		2	3	14	1	3		115	184		2	1			
	d								6	14						
	e															

TABLE 19

Comparison of the number of female Simuliidae collected with fan-traps positioned underground and above ground under various conditions. Silhouette presented by exposed fan-trap. Summary of Table 18.

A. Excluding fan-trap at ground level. 30¾ hour collection, from 22 to 25 of July, 1968.

Species of Simuliidae	Positions of fan-traps							Total
	Underground			4 ft. above ground				
	with CO_2 no silhouette		no CO_2 no silhouette	with CO_2 + silhouette		no CO_2 + silhouette		
	No.	%	No.	No.	%	No.	%	
P. hirtipes	0		0	6		0		6
Cn. pallipes	39	10.0	0	269	68.0	83	21.2	391
Eus. beltukovae	18	29.0	0	42	67.8	2	3.2	62
Eus. bicorne	1	4.0	0	23	92.0	1	4.0	25
Eus. curvans	0		0	1		0		1
Eus. latipes	13	56.5	0	10	43.5	0		23
Scho. pusilla	3	1.7	0	159	88.4	18	10.0	180
Gnus rostratum	11	2.6	0	330	78.6	79	18.8	420
S. vulgare	980	96.0	0	34	3.0	6	0.6	1020
Total	1065		0	874		189		2128

TABLE 19 (continued)

B. Including fan-trap at ground level. 16½ hours collection, from 28 to 29 of July, 1968.

Species of Simuliidae	Positions of fan-traps									Total
	Underground			Ground level		4 ft. above ground				
	with CO_2 no silhouette		no CO_2 no silhouette	with CO_2 + silhouette		with CO_2 + silhouette		no CO_2 + silhouette		
	No.	%	No.	No.	%	No.	%	No.	%	
P. hirtipes	0		0	0		5		0		5
Cn. pallipes	30	4.6	0	615	91.5	21	3.1	7	1.1	673
Eus. beltukovae	4	6.2	0	50	77.0	10	15.4	1	1.5	65
Eus. bicorne	3	6.7	0	18	40.0	24	53.4	0		45
Eus. curvans	1	2.9	0	32	91.5	2	5.7	0		35
Eus. latipes	3	3.8	0	64	80.0	10	12.5	3	3.8	80
Eus. sp.1	0		0	2		0		0		2
Scho. pusilla	5	0.9	0	152	28.2	366	68.0	15	2.8	538
Gnus rostratum	18	1.9	0	330	35.3	548	58.6	39	4.2	935
S. monticola	0		0	3		0		0		3
S. morsitans	1		0	4		2		0		7
S. ornatum	0		0	1		1		0		2
S. sublacustre	1		0	13		2		0		16
S. truncatum	0		0	9		2		0		11
S. vulgare	181	52.5	0	163	47.2	1	0.3	0		345
Total	247		0	1456		994		65		2762

TABLE 20

Comparison of different rates of carbon dioxide emission in effecting activation and landing of female Simuliidae when presented with a black suction fan-trap as a silhouette. Activation is measured in terms of the number of Simuliidae taken inside the trap, and landing in terms of the number taken simultaneously on a piece of black "sticky" plastic material wrapped around each trap. Rendalen, Norway, 1967.

Species of Simuliidae	Date and time of collection												Total					
	1.-VIII																	
	1045-1145						1300-1500						3.0 hours					
	Fan-trap with CO_2 in cc./min.						Fan-trap with CO_2 in cc./min.						Fan-trap with CO_2 in cc./min.					
	200		400		800		200		400		800		200		400		800	
	in side	out side	in side	out side	in side	out side	in side	out side	in side	out side	in side	out side	in side	out side	in side	out side	in side	out side
P. hirtipes	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	4	-
Cn. pallipes	1	1	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Scho. pusilla	18	11	43	-	277	419	45	222	48	83	462	143	63	233	51	83	739	562
Gnus rostratum	-	-	-	-	5	4	2	-	1	-	44	-	-	-	1	-	49	4
S. truncatum	-	-	-	-	-	4	-		-	-	-	-	-	-	-	-	-	4
Total	19	12	43	-	282	427	47	222	49	83	510	143	64	234	52	83	792	570

TABLE 21

Comparison of different rates of carbon dioxide emission in effecting activation and landing of female Simuliidae when presented with a silhouette of a sticky black "cow" model. Activation is measured in terms of the number of Simuliidae taken inside a black suction fan-trap suspended six inches below the belly of each model, and landing in terms of the number taken simultaneously on the various parts of each model. The carbon dioxide outlet was placed beside each fan-trap. Rendalen, Norway, July 20, 1030-1230; 1967.

Species of Simuliidae	Carbon Dioxide Emission					
	200 cc./min.			800 cc./min.		
	inside fan-trap	on model*		inside fan-trap	on model*	
		sides	belly		sides	belly
P. hirtipes	-	-	-	7	5	-
Cn. pallipes	-	5	-	-	11	-
Scho. pusilla	94	52	11	211	62	5
Gnus rostratum	4	18	340	30	37	88
S. monticola	-	1	4	-	-	6
S. truncatum	-	1	11	5	3	5
Total	98	77	366	253	118	104

*Almost no simuliids were taken from the back of each model.

TABLE 22

Comparison of the number of female Simuliidae collected after feeding on Pekin ducklings exposed on the Renaa River, Rendalen, Norway, at water level, above water and on land above ground. Summer, 1968.

Date of collection	Species of Simuliidae		
	Eus. sp. 1		*Eus. beltukovae*
	water level	8 ft. above water	on a pine tree 20 ft. above ground
12-V11-68	8		
15-V11-68	50		
16-V11-68	42		
17-V11-68	15		
23-V11-68	20		
24-V11-68 (1430-1830)	*30	**5	4
26-V11-68	5		1
27-V11-68	10		
Total	180	5	5
%	94.7	2.6	2.6

* consist of 5 collections and 15 unfed specimens

** consist of 6 collections and 2 unfed specimens

Simultaneous collections from these three locations were made only on the 24 and 26-V11-68.

TABLE 23

Female Simuliidae collected after feeding on *Turdus pilaris* exposed 20 ft. on a pine tree in the Rendalen Region, Norway. Summer 1967.

Date of collection	Species of Simuliidae			
	C. pallipes	*E. aureum*	*E. bicorne*	*E. beltukovae*
7-V11-67				10
8-V11-67				1
10-V11-67				5
20-V11-67	1			29
1-V111-67		1		10
2-V111-67		1	1	14
10-V111-67		1*	1*	1*
17-V111-67			2	6
Total	1	3	4	76
%	1.2	3.6	4.8	90.5

*Unfed specimens

TABLE 24

Female Simuliidae collected after feeding on *Fringilla montifringilla*, *Turdus pilaris*, *T. philomelos* and *Phoenicurus phoenicurus*, in the Rendalen region, Norway. Summer 1968.

Date of collection	Species of Simuliidae				
	Eus. sp. 1	*E. aureum*	*E. beltukovae*	*E. bicorne*	*E. latipes*
22-V11-68			4		
23-V11-68			19		9
26-V11-68		1	7		
29-V11-68		1	22	10	6
10-V111-68				5	
21-V111-68 *	5		47	2	3
22-V111-68				2	2
Total	5	2	99	19	20
%	3.4	1.4	68.3	13.1	13.8

* All the simuliids in this collection were taken from one *Turdus pilaris* caught in a mist-net at four feet above ground and fifty feet from the Renaa River.

TABLE 25

Collections of female Simuliidae from sticky models with carbon dioxide, carbon dioxide plus uropygial gland extract of Pekin duckling, and extract only; all three at water level on the Renaa River, Rendalen, Norway.

Date Time	Condition of model	Species of Simuliidae						
		Cn. pallipes	Eus. beltukovae	Eus. curvans	Eus. sp.1	Scho. pusilla	Gnus rostratum	S. vulgare
July 26, 1968	CO_2 only	19			56			5
1300 - 1600	CO_2 + extract	31			139			6
	extract only	3			3			1
1630 - 1830	CO_2 only	2			10		2	6
	CO_2 + extract	9	1		91	1		7
	extract only							
1830 - 2030	CO_2 only	3			22			
	CO_2 + extract	16			64			2
	extract only	1		1	2			

TABLE 26 *

Comparison of the number of female Simuliidae collected from sticky models with carbon dioxide, carbon dioxide and extract, and extract only; all three models at water level on the Renaa River, Rendalen, Norway. Summary of Table 25.

Species of Simuliidae	Condition of Models						Total
	CO_2 100 cc./min. only		CO_2 100 cc./min. + extract		Extract only		
	No.	%	No.	%	No.	%	
Cn. pallipes	24	28.6	56	66.7	4	4.8	84
Eus. beltukovae	0		1		0		1
Eus. curvans	0		0		1		1
Eus. sp.1	88	23.3	294	76.0	5	1.3	387
Schö. pusilla	0		1		0		1
Gnus rostratum	2		0		0		2
S. vulgare	11	40.7	15	55.5	1	3.7	27
Total	125		366		11		

* For statistical significance see Table 42, Appendix C

Fig. 27 Comparison of the per-cent of three species of female simuliids collected with three silhouette models each baited with: carbon dioxide only, carbon dioxide + extract from uropygial gland of domestic ducklings, and extract only. All three models were exposed at water-level as indicated on Table 26.

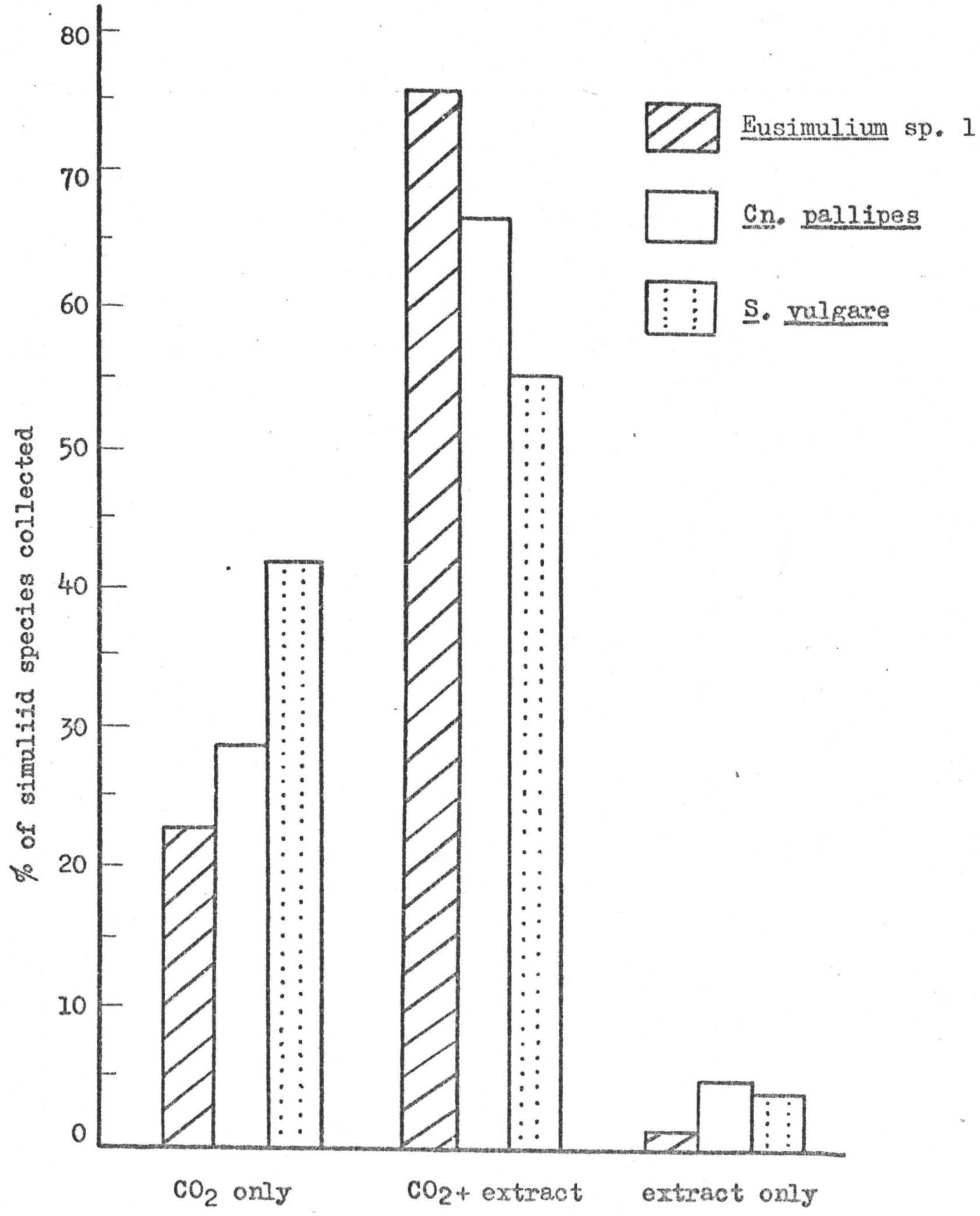

% of simuliid species collected
0
10
20
30
40
50
60
70
80
Eusimulium sp. 1
Cn. pallipes
S. vulgare
CO2 only
CO2+ extract
extract only

TABLE 27

Comparison of the number of female Simuliidae collected with a black and a white suction fan-trap with carbon dioxide emission from each at 200 cc./min. The traps were placed at 10 feet from each other and four feet above ground level. Rendalen, Norway, 1967.

Species of Simuliidae	Date and time of collection									Total		
	7-VII			10-VII			13-VII					
	1300 - 2030			1230 - 2130			1300 - 1630			19 hrs. 30 min.		
	Black	White	Black-con.*	Black	White	Black-con.	Black	White	Black-con.	Black	White	Black-con.
P. hirtipes	242	32	51	71	15	7	38	2	-	355	49	58
Cn. pallipes	11	7	-	8	30	-	14	5	-	33	42	-
Scho. pusilla	11	-	-	9	36	1	28	9	3	48	45	4
Gnus rostratum	813	37	65	35	18	5	3	-	-	851	55	70
S. truncatum	-	-	-	2	3	-	-	-	-	2	3	-
S. monticola	11	1	1	6	16	2	1	-	-	17	17	3
S. ornatum	110	19	18	11	7	4	-	-	-	121	26	22
Total	1198	96	135	144	125	19	84	16	3	1427	237	157

*Black-control fan-trap was exposed without CO_2.

TABLE 28

Comparison of the number of female Simuliidae collected from one black and one white "sticky" bird model placed 16 inches from each other and at 20 feet on a pine tree, *Pinus sylvestris* L. Carbon dioxide emission at 200 cc./min. placed between the models. Rendalen, Norway, 1967.

	Date and time of collection												Total		
Species of Simuliidae	13-VII						14-VII		15-VII				16 hrs. and 35 min.		p
	1130-1445		1450-1730		1745-2030		1100-1615		1230-1500		1515-1630				
	Black	White	Black	White	Black	White	Black	White	Black	White	Black	White	Black	White	Black White
Cn. pallipes	119	31	24	21	39	40	13	12	43	4	66	3	304	111	< 0.001
Scho. pusilla	1	-	-	-	1	-	-	-	-	-	-	-	2	-	-
Eus. aureum	1	-	-	-	1	-	-	-	-	-	1	-	3	-	-
Eus. latipes-beltukovae	5	1	1	3	8	6	-	1	1	5	12	2	27	18	0.2
Total	126	32	25	24	49	46	13	13	44	9	79	5	336	129	< 0.001

3. Effect of Silhouette Size

A series of collections were made to investigate whether simuliids could discriminate between a large and a small silhouette placed at either 5 or 10 feet from each other (see p. 48). The position of the large and the small silhouette was interchanged for each simultaneous collection in order to avoid bias. Results of individual collections are reported on Tables 29A, B, C; no simuliids were collected from the "control" silhouettes. A summary of these collections (Table 30) reveals that some simuliid species showed a definite orientation toward either the large or the small silhouette. In particular, those species collected in relatively large numbers, such as _Cn. pallipes_, _E. bicorne_ and _E. beltukovae_ showed a significant preference for the small silhouette; this was also the case for _Scho. pusilla_ and most of the _Simulium_ spp., particularly _S. vulgare_. On the other hand, _G. rostratum_ was the only species which showed a significant preference for the large silhouette. However, examining these results in their respective parts (ables 31A, B, C), some species reveal obvious variations in their orientation toward either the large or the small silhouette. Initially when the silhouettes were placed 10 feet apart, the orientation toward either silhouette by several simuliid species (Table 31A) was similar to the standard as revealed on Table 30. The result of moving the large and the small silhouettes 5 feet closer to each other indicates that _Scho. pusilla_ and _G. rostratum_ now exhibited no significant preference for either silhouette (Table 31B); whereas, the high preference of _S. vulgare_ for the small silhouette remained unaltered. When the orientation toward either silhouette placed at 10 and 5 feet distance from each other are compared (Table 32), the greatest shift in preference from the large to the small silhouette was shown by G. rostratum, followed next by Scho. pusilla which exhibited a reversed shift of a lesser magnitude. In the final stage of this experiment the quantity of simuliids on the wing decreased considerably in number. Therefore, with the hope of increasing the catch of flies per unit time, the CO_2 emission from each trap was increased from 100 to 200 cc/min, while maintaining the distance between the large and the small silhouettes at 5 feet. A summary of these collections (Table 31C) indicates that Cn. pallipes, E. bicorne and Scho. pusilla retained the original preference for the small silhouette. A significant change, however, occurred with G. rostratum which shifted its preference from the large to the small silhouette, while S. vulgare now showed no significant preference for either silhouette (Table 31C). A comparison of the effect of changing the CO_2 emission from 100 to 200 cc/min while maintaining the intersilhouette distance at 5 feet shows (Table 33) that Scho. pusilla and the Simulium species increase their preference for the small silhouette, while S. vulgare shifted its orientation from the small to the large silhouette.

TABLE 29

Simuliids collected with each of two fan-traps each suspended one foot above ground on one Large and one Small silhouette; Rendalen, Norway.

A. Silhouettes placed 10 ft. apart.
Carbon dioxide at 100 cc./min.

Date time	Size of silhouette	Species of Simuliidae														
		P. hirtipes	*Cn. pallipes*	*Eus. beltukovae*	*Eus. bicorne*	*Eus. curvans*	*Eus. latipes*	*Eus. sp.1*	*Scho. pusilla*	*Gnus rostratum*	*S. monticola*	*S. morsitans*	*S. ornatum*	*S. sublacustre*	*S. truncatum*	*S. vulgare-tuberosum*
31-V11-68 1700-1800	Large		4	1					10	155						4
	Small		3						15	27					1	47
1800-1830	Large		10						8	289		4		1		4
	Small		4						13	61		1	1		1	36
1830-1900	Large		10				1	2	4	220	1	1			1	7
	Small	1	41				1	2	8	32						
1900-1930	Large		3	1	1		1	1	1	36				1		
	Small		32	2				2	6	4	1	1	1			57
1930-2000	Large		5						1	80	1	1				
	Small		41	5	4		2		6	11		1				17
2000-2030	Large		16	2	2		1	1		38		1				
	Small		45	4	7		1		1	1						4
1-V111-68 1100-1200	Large		8						2	14						
	Small		5					2	1	1						53
1415-1515	Large		23	1			1	1	1	6				1		7
	Small		22	1			2	1		3		1				44
1530-1630	Large		2					1	2	6				1		
	Small		20	1			1		3	2						149
1645-1745	Large		10			1			4	10						20
	Small		9				1		5	4		2				16
1800-2030	Large		44				1		1	10						2
	Small		48	2			3			8		2		5		97

TABLE 29 (cont.)

B. Silhouettes placed 5 ft. apart.
Carbon dioxide at 100 cc./min.

		Species of Simuliidae														
Date time	Size of silhouette	H. ferrugineus	Cn. pallipes	Eus. beltukovae	Eus. bicorne	Eus. curvans	Eus. latipes	Eus. sp.1	Scho. pusilla	Gnus rostratum	S. monticola	S. morsitans	S. ornatum	S. sublacustre	S. truncatum	S. vulgare-tuberosum
3-V111-68 0900-1000	Large								1							1
	Small		10						7	1		1				48
1000-1615	Large		4						6	3						2
	Small		7						9	1				9		32
1615-1715	Large		7	1			1		4	4		1		1		4
	Small		5				1	1	3	4						42
1715-1815	Large		1				1		4	5						15
	Small		1	1			1		21	17		1		3		25
1815-2000	Large		5	1			4		86	8						
	Small		9	2	1		5		69	21		2				86
2000-2100	Large		3	3	2		2		1							
	Small		19	3	19		2		7							3
5-V111-68 1600-1700	Large		3						4	2		7		2		7
	Small		6	1					10	3				1		12
1715-1815	Large		1		1				4							1
	Small		2	1			2		2	2		1		4		26
1815-2000	Large		4	2	2		1		1	6		2				3
	Small		13	3	6		1		6	5		3		1		9
2000-2130	Large		1	2	14											
	Small	1	7	2	40	1	1									

TABLE 29 (cont.)

C. Silhouettes placed 5 ft. apart.
Carbon dioxide at 200 cc./min.

		Species of Simuliidae														
Date time	Size of silhouette	*P. hirtipes*	*Cn. pallipes*	*Eus. beltukovae*	*Eus. bicorne*	*Eus. curvans*	*Eus. latipes*	*Eus. sp.1*	*Scho. pusilla*	*Gnus rostratum*	*S. monticola*	*S. morsitans*	*S. ornatum*	*S. sublacustre*	*S. truncatum*	*S. vulgare-tuberosum*
6-VIII-68	Large						1		6	1		1				90
1000-1300	Small								2	1						1
1300-1600	Large		1				2		6	1				1		
	Small		2	1					12	3		4		5		46
1630-1730	Large		2				5		6	6						18
	Small								10	1						15
1730-2030	Large		1							1						7
	Small		6		6		7		41	42		2		11		82
2030-2200	Large				13	1			3	2						
	Small		11	1	21	1										
7-VIII-68	Large		7				2		3	1						3
1000-1300	Small		2	2					9	2				1		10
1600-1830	Large		2				1		6	7				2		12
	Small		5				2		10	4		2		2		2
1830-2130	Large			2			6									
	Small		24	2	17	1	6		1	1		2				5
9-VIII-68	Large		2		21	1	4		2							2
1830-2100	Small		9		61	1	1		2	1		2		3		8
10-VIII-68	Large		3		1		1		1	3						8
1630-2030	Small		6	3	7				8	8		5		5		17
2000-2100	Large		9		1											
	Small		4		7											

TABLE 30

Comparison of the number of female Simuliidae collected from each of two fan-traps one foot above ground beside one *Large* and one *Small* silhouette, including all three parts, *A*, *B*, *C*, of Table 29.

Species of Simuliidae	Size of Silhouette				Total	p*
	Large		Small			
	No.	%	No.	%		
P. hirtipes			1		1	
H. ferrugineus			1		1	
Cn. pallipes	191	31.3	419	68.7	610	< 0.001
Eus. beltukovae	16	30.2	37	69.8	53	< 0.001
Eus. bicorne	56	22.2	196	77.8	252	< 0.001
Eus. curvans	3		4		7	0.2
Eus. latipes	36	47.4	40	52.6	76	0.8
Eus. sp.1	6		10		16	0.5
Scho. pusilla	178	38.3	287	61.7	465	< 0.001
Gnus rostratum	915	72.0	271	28.0	1186	< 0.001
S. monticola	3		1		4	0.5
S. morsitans	17	34.0	33	66.0	50	< 0.001
S. ornatum			2		2	
S. sublacustre	11	18.0	50	82.0	61	< 0.001
S. truncatum	1		2		3	
S. vulgare	217	17.6	989	82.4	1206	< 0.001
Total	1650		2342		3992	

*p represents the probability level obtained from x^2-test of the *number* of each species of Simuliidae collected from the *Large* and the *Small* silhouettes.

TABLE 31

Comparison of the number of female Simuliidae collected from Large and Small silhouettes under various conditions.

A. Silhouettes placed 10 ft. apart; CO_2 at 100 cc./min. 10 hrs. collection from July 31 to August 1, 1968.

Species of Simuliidae	Size of Silhouette				Total	p
	Large		Small			
	No.	%	No.	%		
P. hirtipes			1		1	
Cn. pallipes	135	33.4	270	66.6	405	< 0.001
Eus. beltukovae	5		15		20	0.02
Eus. bicorne	1		11		12	< 0.01
Eus. curvans	1				1	
Eus. latipes	5		11		16	0.1
Eus. sp.1	6		9		15	0.5
Scho. pusilla	34	37.0	58	63.0	92	< 0.001
Gnus rostratum	864	85.0	154	15.0	1018	< 0.001
Simulium spp.	14	43.8	18	56.2	32	0.5
S. vulgare	44	11.0	520	89.0	564	< 0.001
Total	1136		1067		2203	

Simulium spp. include: *S. monticola*, *morsitans*, *ornatum*, *sublacustre*, and *truncatum*.

TABLE 31 (continued)

B. Silhouettes placed 5 ft. apart; CO$_2$ at 100 cc./min. 19¼ hrs. collection from 3 to 5 of August, 1968.

Species of Simuliidae	Size of Silhouette				Total	p
	Large		Small			
	No.	%	No.	%		
H. ferrugineus			1		1	
Cn. pallipes	29	26.8	79	73.2	108	<0.001
Eus. beltukovae	9	41.0	13	59.0	22	>0.2
Eus. bicorne	19	22.4	66	77.6	85	<0.001
Eus. curvans			1		1	
Eus. latipes	9	41.0	13	59.0	22	>0.2
Eus. sp.1			1		1	
Scho. pusilla	111	45.0	134	55.0	245	0.1
Gnus rostratum	29	35.0	54	65.0	83	0.01
S. morsitans	10	55.5	8	44.5	18	0.8
S. sublacustre	3	14.3	18	85.7	21	<0.001
S. vulgare	33	10.4	283	89.5	316	<0.001
Total	252		671		923	

TABLE 31 (continued)

C. Silhouettes placed 5 ft. apart; CO_2 at 200 cc./min. 23½ hours collection, from 6 to 10 of August, 1968.

Species of Simuliidae	Size of Silhouette				Total	p
	Large		Small			
	No.	%	No.	%		
Cn. pallipes	27	28.2	69	71.8	96	< 0.001
Eus. beltukovae	2	18.2	9	81.8	11	0.05
Eus. bicorne	36	23.2	119	76.8	155	< 0.001
Eus. curvans	2		3		5	0.20
Eus. latipes	22	58.0	16	42.0	38	> 0.20
Scho. pusilla	33	25.8	95	74.2	128	< 0.001
Gnus rostratum	22	25.9	63	74.0	85	< 0.001
S. morsitans	1	5.6	17	94.5	18	< 0.001
S. sublacustre	4	12.9	27	87.1	31	< 0.001
S. vulgare	140	42.0	186	58.0	326	0.01
Total	289		604		993	

TABLE 32

Comparison of the discrimination between Large and Small silhouettes, in relation to the distance between them, expressed as the ratio of the number of female Simuliidae. Carbon dioxide emission kept constant at 100 cc./min.

Species of Simuliidae	Distance between silhouettes	
	10 ft.	5 ft.
	Large : Small	Large : Small
Cn. pallipes	0.5	0.4
Eusimulium spp.	0.4	0.4
Scho. pusilla	0.6	0.8
G. rostratum	5.6	0.5
Simulium spp.	0.5	0.8
S. vulgare	0.1	0.1

Eusimulium spp. include: Eus. beltukovae, bicorne, curvans, latipes and sp. 1.

Simulium spp. include: S. monticola, morsitans, ornatum, sublacustre and truncatum

TABLE 33

Comparison of the discrimination between Large and Small silhouettes, expressed as the ratio of the number of female Simuliidae, in relation to the carbon dioxide emission. Distance between silhouettes kept constant at 5 feet.

Species of Simuliidae	Carbon dioxide output	
	100 cc./min.	200 cc./min.
	Large : Small	Large: Small
C. pallipes	0.4	0.4
Eusimulium spp.	0.4	0.4
Scho. pusilla	0.8	0.4
G. rostratum	0.5	0.4
Simulium spp.	0.8	0.1
S. vulgare	0.1	0.8

4. Simuliid Distribution in Various Habitats

The distribution of simuliid species in various habitats was preliminarily considered in Norway in the summer of 1967 and 1968. Simuliids collected from cows in the grassland habitat and from man in open fields and roadways were mainly mammaliophilic species as would be expected (Tables 14, 15). Olfactory and visual discrimination experiments were originally conducted almost at ground level in an arbitrarily chosen grassland habitat from which a heterogeneous quantity of ornithophilic (mainly Cn. pallipes) and mammaliophilic (mainly Scho. pusilla, G. rostratum and S. vulgare) species were collected (Tables 16-21). At the same time, blood engorged simuliids were being collected (using the method employed by Bennett, 1960) from live Turdus pilaris exposed 20 feet in a pine tree, and as can be seen (Table 23) 90.5% of the simuliids collected were E. beltukovae. It was decided, therefore, to see whether collections from a pine tree at heights of 20 feet, among the branches and 10 feet below the branches, would affect the quantity and species composition of simuliids. A series of such simultaneous collections (Table 34) revealed only four species present at 10 and 20 feet above ground. E. beltukovae, the only species collected in significantly large number, was generally more abundant at 10 than 20 feet above ground, as was also the case with Scho. pusilla, the only mammaliophilic species collected.

Another series of collections attempted to assess whether different species of trees in two different habitats harboured the same simuliid species. Four such collections (able 35), using sticky bird models baited with CO_2, revealed almost no difference in the number and quantity of simuliid species collected simultaneously from a birch and a pine tree. E. beltukovae, again collected in largest number, was present in almost equal numbers from both species of trees.

River habitat

Following the collection of blood-fed Eusimulium sp. 1 from domestic ducklings in 1968, an experiment was conducted by the Renåa R. to assess the distribution of this species in this habitat. The experiment consisted essentially of a series of simuliid collections made simultaneously at three levels above water surface and at ground level using CO_2-baited, sticky models (for details see p. 43). During most of these collections, blood-fed simuliids were being taken from domestic ducklings exposed at water level (Table 22) approximately 30 feet up-river (Fig. 8). The first collections were made on July 12, the first day that blood-fed simuliids were taken from domestic ducklings and additional collections were made almsot daily thereafter (Table 36). From a summary of these catches (Table 37) it can be seen that a total of ten simuliid species were collected at all levels, only the last three of these being mammaliophilic species. Also it can be noticed (Table 37) that the quantity of each species collected at any one level varies significantly (Table 43) with the particular species, and for some of these species these variations have been represented more clearly in (Fig. 28). The most striking vertical stratification pattern can be noticed in the duck-feeding Eusimulium sp. 1 of which 96.0% of a total of 1652 specimens (Table 37) were collected at water level, and only a neglibible proportion were collected at 4 and 7 feet above water (1.5%) or at ground level 30 feet away from water (2.5%). *Cn. pallipes* was the second species collected in comparatively large number, comprising a total of 1353 specimens many of which were collected either at water level (38.8%) or at ground level 30 feet away from water (48.5%). By contrast, only an insignificant proportion of the five remaining *Eusimulium* species (Fig. 28) were collected either at water level or 30 feet from water at ground level; the majority of these were collected at 7 feet above water with the exception of *E. curvans* which was collected mainly at the 4-ft level, and *E. bicorne* which was collected in almost the same proportion at both the 4-ft and the 7-ft level.

TABLE 34

Comparison of the number of female Simuliidae collected from two black "sticky" bird models placed at 10 and 20 feet respectively above ground level among the branches of a Scot's pine tree, *Pinus silvestris* L. . Carbon dioxide emission at 200 cc./min. placed six inches below each model. Rendalen, Norway, 1967.

Species of Simuliidae	Date and time of collection														Total 8 hrs. and 40 min.		p
	10-VIII-67																
	1100-1200		1210-1300		1310-1430		1445-1545		1600-1700		1720-1950		2015-2115				
	10'	20'	10'	20'	10'	20'	10'	20'	10'	20'	10'	20'	10'	20'	10'	20'	
Cn. pallipes	3	23	6	9	6	5	1	3	1	3	2	-	1	2	20	45	< 0.01
Scho. pusilla	9	-	21	1	33	8	13	4	4	3	6	3	-	-	89	19	< 0.001
Eus. aureum	-	-	1	-	1	3	1	1	-	-	-	-	-	1	3	5	0.5
Eus. latipes-beltukovae	28	29	28	62	61	53	77	29	72	41	134	85	15	56	405	355	< 0.001
Total	40	52	56	72	101	69	92	37	77	47	142	88	16	59	517	424	< 0.001

TABLE 35

Comparison of the number of female Simuliidae collected from two black "sticky" bird models one exposed on a white birch tree, *Betula verrucosa* L., and the other exposed on a Scots pine tree, *Pinus silvestris* L.. Each model was placed at 10 feet above ground with carbon dioxide emission at 200 cc./min. placed six inches below each model. Rendalen, Norway, 1967.

Species of Simuliidae	Date and time of collection								Total		p
	13-VIII-67								4 hrs. and 30 min.		
	1200-1230		1300-1500		1520-1620		1625-1725				
	Birch	Pine	Birch	Pine	Birch	Pine	Birch	Pine	Birch	Pine	Birch Pine
Cn. pallipes	3	1	2	4	2	4	-	3	7	12	0.2
Scho. pusilla	-	-	6	1	-	-	6	-	12	1	0.01-0.001
Eus. aureum	-	2	4	2	2	2	1	3	7	9	0.8 -0.5
Eus. latipes-beltukovae	2	3	40	18	16	20	30	41	88	82	0.8 -0.5
Total	5	6	52	25	20	26	37	47	114	104	0.5

TABLE 36

Collections of Simuliidae with sticky models and carbon dioxide at three levels above the Renåa River and on land at ground surface, in Norway.

Date (Time)	Position of model	Species of Simuliidae									
		Cn. pallipes	*Eus. aureum*	*Eus. beltukovae*	*Eus. bicorne*	*Eus. curvans*	*Eus. latipes*	*Eus. sp.1*	*Scho. pusilla*	*Gnus rostratum*	*S. vulgare-tuberosum*
12-VII-68 1615-1715	*m1	7						17		10	6
	*m2	1							1	7	1
	*m3	2							1	2	1
	*mc										
2000-2130	m1	2					2			1	
	m2	2						1		2	
	m3	2					1				
	mc										
13-VII-68 1430-2030	m1	5									
	m2			1			2	1			
	m3						8				
	mc										
15-VII-68 1000-1500	m1	2					1	219			8
	m2						5	8	7		15
	m3	2	1	15						2	1
	mc not exposed										
1800-2100	m1									1	3
	m2						9		3		1
	m3			13	2		22		1	1	1
	mc not exposed										
16-VII-68 1630-2030	m1	7						423		1	2
	m2	1	1	2			4	1	8	2	
	m3	7	2	30			18		4	4	
	mc										
1000-1400	m1	13						150			9
	m2		1				2	1		1	1
	m3	11		2			5	2			
	mc							2	1		

TABLE 36 (cont.)

Date (Time)	Position of model	Species of Simuliidae									
		Cn. pallipes	*Eus. aureum*	*Eus. beltukovae*	*Eus. bicorne*	*Eus. curvans*	*Eus. latipes*	*Eus. sp.1*	*Scho. pusilla*	*Gnus rostratum*	*S. vulgare-tuberosum*
17-V11-68											
1030-1530	m1	30	1				1	147		1	
	m2	6	1			1	8	2	4		
	m3	10	5	31		1	16		7	3	
	*m4	71						6			22
1800-2030	m1	9					1	39		1	
	m2			2		1	3				
	m3	4	3	23	3	1	8			1	
	m4	8					1	12	1	5	6
18-V11-68											
1130-1630	m1	15		3	2	2	3	7		13	2
	m2	2		9	2	7	2		5	4	1
	m3	9		15	2	2	5		2		1
	m4	11			1			3			1
1800-2130	m1	62			2		2	5		1	
	m2	10			6	10	5			1	1
	m3	23		7	3	2	3				
	m4	5									
19-V11-68											
1500-2030	m1	12		1		1	1	6			
	m2	3	1	9	1	1	6			1	
	m3	1	1	7	1		11				
	m4	4									4
20-V11-68											
1530-1815	m1	4					1	2		1	
	m2	1			1					1	
	m3	1	1	2						1	
	m4	2						1			1
22-V11-68											
1300-2000	m1	1						37		1	
	m2	1	2	1			7		2		2
	m3		2	2			2				
	m4	1									

TABLE 36 (cont.)

Date (Time)	Position of model	Species of Simuliidae									
		Cn. pallipes	*Eus. aureum*	*Eus. beltukovae*	*Eus. bicorne*	*Eus. curvans*	*Eus. latipes*	*Eus. sp.1*	*Scho. pusilla*	*Gnus rostratum*	*S. vulgare-tuberosum*
24-V11-68											
1100-1200	m1	57						1			5
	m2	31									
	m3	14									
	m4	78									8
1300-1400	m1	78						44			2
	m2	28						3			4
	m3	17									
	m4	7									
1530-1630	m1	61						111			1
	m2	19		2				1	1	1	1
	m3	7		1							
	m4	136						1			10
1630-1730	m1	25						27			
	m2	4		1							
	m3										
	m4	101									2
1800-2000	m1	116						99			
	m2	7						2			1
	m3	8		1					2		
	m4	121						1			2
25-V11-68											
1300-1630	m1	20						74			4
	m2					1		2			1
	m3	2		1					1		
	m4	9						1			18
1645-1800	m1	14						80			1
	m2										
	m3	3	1								
	m4	28									30
1815-2030	m1	12						105			
	m2	2						2	1		
	m3								1		
	m4	8						8			12

*m1 model at water level, CO_2 emission at 100 cc./min.
m2 model at 4 ft. above water, CO_2 emission at 100 cc./min.
m3 model at 7 ft. above water, " " " " "
m4 model on land at ground level and 30 ft. away from water, CO_2 at 100 cc./min.
mc "control" model at water level (no CO_2)

TABLE 37

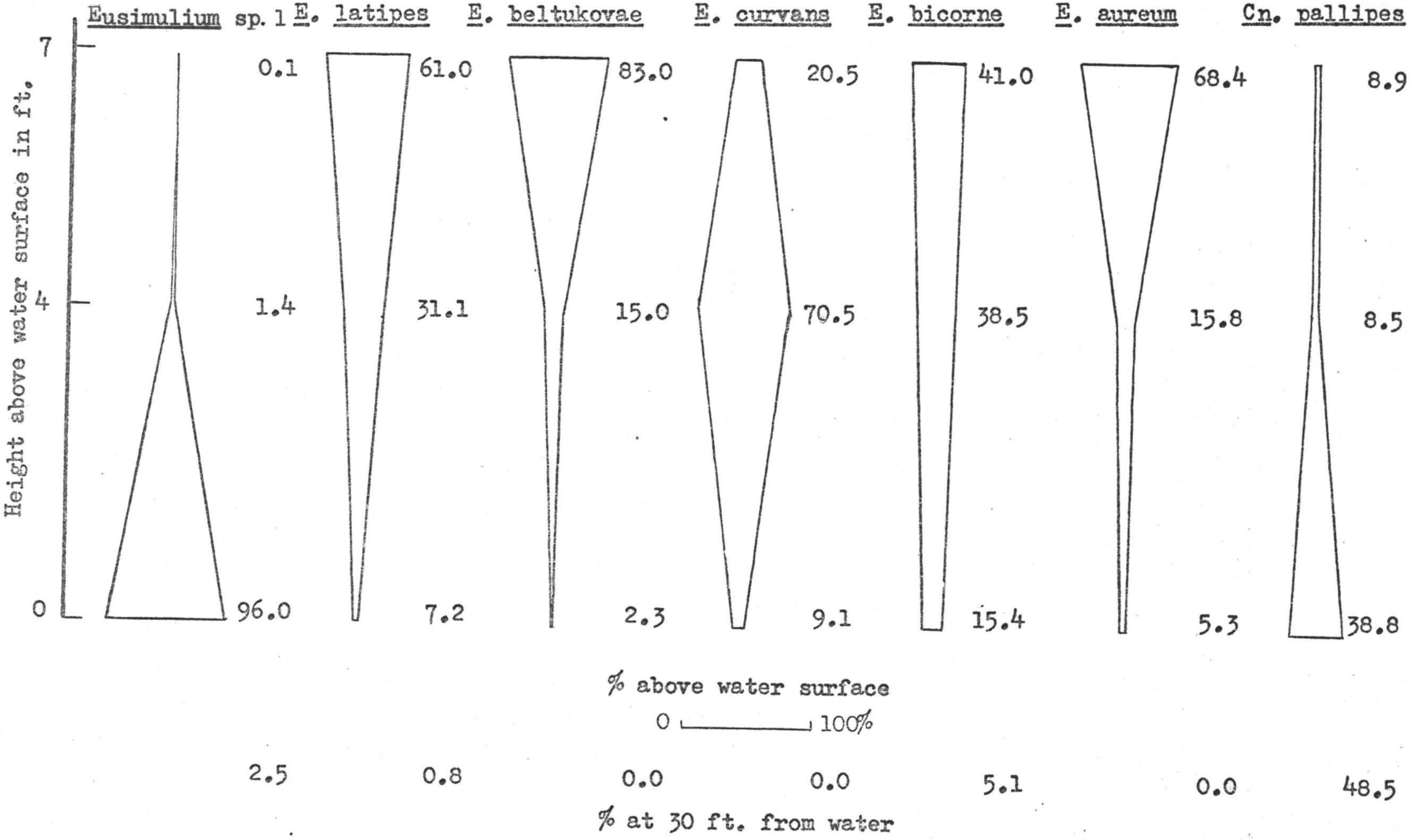
Comparison of the number of female Simuliidae collected with sticky models and carbon dioxide at each of three levels above the Renaa River and on land at ground surface, from 12 to 25 of July, 1968, in the Rendalen Region, Norway. Summary of Table 36.

Species of Simuliidae	Position of Collecting Models								Total	
	*height in ft. above water surface						**ground surface			
	0		4		7		30 ft. from water			
	No.	No./Hr.	No.	No./Hr.	No.	No./Hr.	No.	No./Hr.	No.	No./Hr.
Cn. pallipes	522	8.0	118	1.74	123	1.81	590	10.0	1353	21.6
Eus. aureum	1	0.02	4	0.06	18	0.26	0	0.0	25	0.34
Eus. beltukovae	4	0.06	27	0.40	150	2.20	0	0.0	181	2.66
Eus. bicorne	4	0.06	10	0.15	11	0.16	1	0.02	26	0.39
Eus. curvans	3	0.04	21	0.31	6	0.09	0	0.0	30	0.44
Eus. latipes	12	0.18	53	0.78	104	1.53	1	0.02	170	2.51
Eus. sp.1	1593	23.4	24	0.35	2	0.03	33	0.61	1652	24.4
Scho. pusilla	0	0.0	32	0.47	19	0.28	1	0.02	52	0.77
Gnus rostratum	18	0.26	20	0.29	14	0.21	5	0.09	57	0.85
S. vulgare	43	0.63	29	0.42	4	0.06	116	2.2	192	3.31
Total	2200	32.8	338	5.00	451	7.29	747	14.7		

*Collections above water surface consist of a time period totalling 68 hours.

**Collections at ground surface consist of a time period totalling 54 hours.

Fig. 28 Comparison of the per-cent of the number of female Simuliidae distributed at three levels above water of the Renaa River and on land at ground-level away from water; Rendalen, Norway, 1968.


Eusimulium sp. 1
E. latipes
E. beltukovae
E. curvans
E. bicorne
E. aureum
Cn. pallipes
Height above water surface in ft.
7
4
0
0.1
1.4
96.0
61.0
31.1
7.2
83.0
15.0
2.3
20.5
70.5
9.1
41.0
38.5
15.4
68.4
15.8
5.3
8.9
8.5
38.8
% above water surface
0
100%
2.5
0.8
0.0
0.0
5.1
0.0
48.5
% at 30 ft. from water

5. Substrate Colour Selection During Oviposition

Oviposition experiments were conducted in 1967 on the Renåa river as described on p. 49. The choice of site D (Figs. 6, 9A) was made after finding a large number of willow leaves (Salix spp.) covered with black-fly eggs (Fig. 9B) floating at the river's edge. Oviposition occurred mainly just before and soon after sunset on normal clear days. However at the start of these collections oviposition for the season was well underway and began to decrease soon after the beginning of August. Adult gravid simuliids were collected daily from the four grey and six chromatic strips and were subsequently identified to species (Table 38). A total of five different species comprising 2007 specimens were collected, 98% of which were S. ornatum - the only species showing some pattern of substrate colour selection (Table 39). In the grey series, almost the same number of flies were caught on both the light-grey and the white strip in a proportion of 36.4% and 32.3% respectively, with the black strip being the next highest with 19.2%. The chromatic strips caught a total of 1009 specimens the largest proportion of which were attracted to the yellow strip (25.8%), followed next by the green strip (20.4%); the average attractancy for this yellow-green peak then being 23.1%. The red-orange and the blue-purple, with an average attractancy of 10.2% and 16.7% respectively appear to fall well on either side of the yellow-green peak. Another attempt to repeat this experiment was made at the same site in 1968 using non-sticky oviposition strips with the hope of assessing colour selection in terms of the relative abundance of eggs laid on each strip. However, only an insignificant number of eggs were collected from all oviposition strips combined probably resulting from the scarcity of ovipositing _S. ornatum_ during this particular season.

TABLE 38

Daily collection of ovipositing Simuliidae from each coloured sticky strip exposed on the water of the Renaa River, Rendalen, Norway. Summer 1967.

Oviposition Date	Species of Simuliidae	Colour of Strips											
		Greys				Sub-total	Chromatic						Sub-total
		Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple	
17-V11-67	S. ornatum	29			102	131			123	53	11	17	204
	G. rostratum									1			1
18-V11-67	S. ornatum	13	2	69	36	120			23	39		30	92
	S. morsitans			1		1							
25-V11-67	S. ornatum	9	3	22	5	39	4	6		3	2		15
	G. rostratum			1		1							
	S. vulgare							1					1
26-V11-67	S. ornatum	16	51	98	28	193	18	22	17	20	29	52	158
	G. rostratum		1			1	1						1
	S. vulgare											2	2
	Scho. pusilla							1	1				2
27-V11-67	S. ornatum	46	24	104	45	219	3	20	33	23	32	27	138
	S. vulgare		1			1				1			1
	Scho. pusilla			1		1							
29-V11-67	S. ornatum	2	9	8	30	49	33	9	11	17	20	9	99
	S. vulgare	1	1			2		3			1		4
31-V11-67	S. ornatum	31	4	27	13	75	5	23	33	26	40	24	151
	S. vulgare	1				1				1			1
	Scho. pusilla							2	2	1	1	4	10
1-V111-67	S. ornatum	43	16	33	10	102	23	16	13	21	14	11	98
	S. morsitans		1			1							
	Scho. pusilla		1			1							
2-V111-67	S. ornatum		6	2	4	12	1	1					2
	G. rostratum				1	1		1					1
	Scho. pusilla						1	1					2
9-V111-67	S. ornatum	2	6			8	10	13	8	4	8	11	54

TABLE 39

Comparison of the total number of Simuliidae collected from each sticky coloured oviposition strip exposed on the Renaa River, Rendalen, Norway. Summary of Table 38.

Species of Simuliidae		Colour of Strips													
		Greys				Sub-total	Chromatic						Sub-total	Total	%
		Black	D. Grey	L. Grey	White		Red	Orange	Yellow	Green	Blue	Purple			
Scho. pusilla			1	1		2	1	4	3	1	1	4	14	16	0.7
G. rostratum			1	1	1	3	1	1		1			3	6	0.3
S. morsitans			1	1		2							0	2	0.1
S. vulgare-tuberosum		2	2			4		5		2	1	2	10	14	0.6
S. ornatum	No.	191	121	363	322	997	97	110	261	206	156	181	1009	2007	98.1
	%	19.2	12.1	36.4	32.3	100	9.6	10.9	25.8	20.4	15.4	18.0	100.1		

DISCUSSION

Successive Stages in the Feeding Behaviour

It was indicated (Laarman,1955; Smith,1966) that the feeding behaviour of blood-sucking insects is initiated by an appetitive behaviour, or, as Craig (1918) defined the first phase of the type cycle for many kinds of instinctive behaviours, "an appetite...a state of agitation which continues so long as a certain stimulus,...the appeted stimulus, is present". Craig continued, "when the stimulus is at length received it stimulates a consummatory reaction after which the appetitive behaviour ceases and is succeeded by a state of relative rest". This second phase, culminating in a consummatory reaction, could be considered an integral part of the feeding behaviour of simuliids; in fact, Smith (1966) concludes his theoretical hierarchy*, after the insect has landed on its host, with two final stages, namely, 5) Crawling and Burrowing and 6) Probing and Feeding.

In view of Craig's thesis (1918) it seems appropriate, for the sake of clarity, to include Smith's six stages of the feeding behaviour in simuliids and tabanids within the first two phases of Craig's type cycle of instinctive behaviour, the first phase consisting of finding the host, the second phase feeding on the host.

Phase I. The appetitive behaviour is characterized by the insect's states of "restlessness, varied movements, effort, search" (quote from Craig). This first phase would include the first five stages of Smith's theoretical hierarchy, namely: 1) habitat selection, 2) upwind orientation, 3) near orientation, 4) landing behaviour, 5) crawling and burrowing. Hence, appetitive behaviour

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*Refer to Introduction p. 6

leads not only to habitat selection as Smith (1966) indicated but also to the additional four stages.

Phase II. A consummatory reaction is exhibited by the insect in response to finding the appropriate host (the appeted stimulus). This second phase would include the sixth and final stage of Smith's hierarchy, namely, probing and feeding.

On theoretical considerations, the insect's activity during the feeding behaviour could be followed to completion by appending to Smith's hierarchy two other stages which would correspond to the final two phases of Craig's type-cycle, namely:

Phase III. Cessation of feeding, after the insect has fully engorged, leading to aversion characterized by states of restlessness, trial and effort directed toward flying away from the host.

Phase IV. Physiological state of rest characterized by the insect's inactivity after leaving the host.

It is clear from experiments reported in the present work that only the first four stages in Phase I of the simuliid feeding behaviour have been considered. The field experiments reported herein were designed, however, with no intent of testing the validity of Smith's hierarchy; this hierarchy was considered, instead, as a working model in which were fitted various observations.

Habitat Preferences

1. Horizontal and vertical distribution

Salt (1935, in Laing 1937) has indicated that a parasite cannot find its host unless both animals exist at the same time in the same environment. In this connection Laing (1937), while reporting numerous evidences from the literature of host-parasite relationship, concluded in reference to his own work that "some parasites do first seek a particular environment in which they afterward proceed to seek their host". He demonstrated that three species of parasitic wasps select first a specific habitat and only then begin hunting for a particular host within this habitat. Similar evidences of habitat selection have been reported also among various species of bloodsucking Diptera.

In Uganda, Haddow (1945b) has shown that among 19 different species of adult female mosquitoes, 15 species were found rather abundantly in forest habitats, 3 other species frequented predominantly young banana plantations and a final species was almost equally prevalent in plantations and forests. In Ontario and Wisconsin several simuliid species have been placed in two general groups characterized by the habitat type in which they are most frequently caught feeding on their hosts (see Introduction pp. 7-8). Recently, Smith et al (1970) have shown that several species of female tabanids in Ontario select certain habitat types while in search of a blood meal. Of the 27 most abundant species encountered, the majority, 16 species, were collected preferentially in the forest habitat, whereas only 5 of them were found exclusively in this habitat; 2 species showed a marked preference for the river habitat, while 2 other species were commonly caught in the lakeshore and the river habitat; 3 other species were essentially ubiquitous except for one which was absent from the river habitat.

In the Rendalen region of Norway the female simuliid fauna was studied in each of the three general habitat types: the grassland, the "forest" (consisting essentially of a pine-grove) and the river habitat. The grassland habitat contained the greatest diversity of mammaliophilic and ornithophilic* species while only three ornithophilic and one mammaliophilic species were found in the forest habitat. However, a strict comparison of the number of species found in these two habitats is unwarranted since in the forest habitat collections with host substitutes were made at higher elevations above ground and only in 1967. Hence, the presence of *G. rostratum* in the grassland habitat and its absence from the forest habitat may reflect its peculiarly low-flying habit which may confine it mainly within a few feet above ground. On the other hand, the few ornithophilic species in the forest habitat and their absence from the grassland habitat in 1967 may reflect a general scarcity of these species in that year.

The importance of the flying habit of a particular species in relation to its habitat preferences was further realized in *S. vulgare* which exhibited a remarkably low stratification preference in the grassland habitat. The evidence indicating that more flies of this species were attracted to the underground trap than to the ground-level trap further emphasizes the rather low stratification preference of *S. vulgare* and suggests that this species may feed on burrow-dwelling mammals. In fact, such small mammals as lemmings and voles were frequently seen at the experimental sites.** The ground level

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*These two groups of simuliids are differentiated according to species collected either from cows and man (Tables 14 and 15) or from birds (Tables 22, 23 and 24).

**In Algonquin Park, Ontario, a few simuliids captured from a chipmunk and vole (D. Reidel, unpublished notes) were found to be *S. tuberosum*, a species close to *S. vulgare*. Also, Peterson (1956) caught *S. tuberosum* in Utah, U.S.A., feeding on two species of ground squirrel.

stratification of S. vulgare might also account for its scarcity around cows as judged by collections which were made primarily 3 to 4 feet above ground level. In this same habitat, Cn. pallipes also exhibited a ground-level stratification, although in the absence of a ground-level trap this species might have given the impression of being stratified at higher levels. Similarly, most Eusimulium species were stratified primarily at ground level, whereas Scho. pusilla and G. rostratum were found preferentially at the 4-foot level. In fact, during their peak abundance these two mammaliophilic species were attracted to both man and cows in the form of thick swarms concentrated specifically 4 to 5 feet above ground.

The species composition in the river habitat was rather similar to that of the grassland habitat but with the ornithophilic species predominating in the former. The only three mammaliophilic species were taken in much lower numbers than in the grassland habitat, which suggests a preference by these species for the latter habitat. In fact, of 159 specimens of S. vulgare caught at both water level and ground surface 30 feet from water, 73% were taken away from water. The low stratification of Cn. pallipes above the water surface supports the evidence revealed in the grassland habitat that this species does fly rather low: of the total collected from the river habitat, 39% were taken at water level and 49% at ground level 30 feet from water. This low flying habit may partly account for the scarcity of fed flies of this species collected from live bird-hosts exposed usually several feet above ground; only one fed specimen was taken from Turdus pilaris exposed at a height of 20 feet in a pine tree. It is likely, therefore, considering the abundance of this species taken at such low stratification with CO_2 traps, that Cn. pallipes may feed primarily on some ground-dwelling bird species. In this respect, *Cn. pallipes* closely resembles the case of *S. vulgare*. The *Eusimulium* species, except for *Eus.* sp. 1 were found preferentailly at higher elevations,for a comparatively low percentage of each of these species was collected at both water and ground level. In fact, of all the fed specimens taken from arboreal birds at some height above ground-level consisted primarily of *E. aureum*, *beltukovae*, *bicorne* and *latipes*. However, the evidence of a preferred ground-level stratification by these species in the grassland habitat seems irreconcilable with the preference of a higher level in the river habitat. One reason for this difference could be that the open grassland tends to be comparatively more windswept, hence confining these species to a lower ground-level stratification in this habitat. In fact, flies that were seen as little swarms around the CO_2-traps at 4 feet above ground invariably disappeared at wind speeds above 500 ft/min. In addition, such a difference suggests a less rigid flying pattern by these species which may be modified by changing environmental conditions in the various habitats.

Habitat-specific simuliids, however, may reveal a more rigid flying pattern which consequently restricts their feeding to equally habitat-specific hosts. *S. vulgare* and *Cn. pallipes* may be two cases in point, although the specific host(s) for these two species still remain to be determined. *Eusimulium* sp. 1 provides a better case. This species was generally restricted to the river habitat and almost exclusively just at the water level. It was seldom collected in the grassland or wood-lot habitats and then only in low number, e.g. only 2.5% of the total collection of this species was taken at ground level 30 feet away from the river's edge. Eusimulium sp. 1 was the only species caught feeding on domestic ducklings exposed on the Renaa river, and therefore it was probably the main and only vector of Leucocytozoon sp. which infected these birds soon after they were exposed to this habitat.

Although the habitat preference of Eusimulium sp. 1 is similar to that of S. rugglesi, S. anatinum and S. euryadminiculum in Ontario (see introduction, p. 8), the other ornithophilic species in Rendalen appear to exhibit much less definite habitat preferences than similar species in Ontario. However, the small differences in habitat types in Rendalen especially between the grassland and open "forest" habitats may have contributed to the expression of a ubiquitous distribution of the other ornithophilic species. In fact, the more defined habitat types in Ontario have facilitated the segregation of some ornithophilic simuliids into a group of forest inhabiting (woodland) species (Bennett,1960, Smith,1966). These same workers, in addition, suggested that some of these species may be found seeking a blood meal preferentially at definite elevations above the forest floor.

In the present work it has been shown that some of the arboreal simuliids in Ontario do in fact exhibit a vertical distribution pattern within the forest canopy. However, the significance of making simultaneous collections at ground level was not realized at the time this work was conducted; hence, in order to calculate the relative abundance of each species near the ground, reference was made to similar work conducted previously in the same habitat (Bennett,1960; Smith,1966). Bennett (1960) collected fed simuliids from birds exposed at various elevations above ground and showed that "most aureum, 'latipes' *croxtoni* and *decemarticulatum* were taken above ground in the forest" and that most of these species "feed on birds several feet above ground level". However, the "*latipes*" group which probably included the true *latipes* (s.s.) and *quebecense*, was taken at ground level in comparatively larger number than the other ornithophilic species. Smith (1966) arrived essentially at the same conclusion, stating that "ornithophilic flies (simuliids) of the sylvatic habitat are confined to the upper strata, and are found only rarely at ground level". In his few collections made with CO_2-baited traps exposed simultaneously at 5, 15 and 35 feet above ground, he found that *decemarticulatum*, *aureum*, and *Eusimulium* spp. (*latipes*, *croxtoni* and *quebecense*) were rarely or never taken at the 5-foot level. *S. venustum*, however, was taken consistently at the 5-foot level although only about half as numerous as at the 15-foot level.

Therefore, in the present work the relative percent of most species (with the exception of *E. latipes* and *S. venustum*) that would have been collected at ground-level was considered to approach zero; that of *E. latipes* was, instead considered to be noticeably greater than zero, and that of *S. venustum* approximately half as abundant as at the 12-foot level.

2. Changes in vertical distribution and possible causal factors

When the entire stratification pattern of simuliids in the forest habitat is examined in terms of each daily collection, a slight difference in vertical distribution of the ornithophilic species can be detected. Smith (1966) made a similar observation and proceeded to postulate that such changes in stratification pattern "may vary with the time of day, as a result of movements of the population in response to environmental gradients". The present results indicate that the only significant change that occurred with the time of day was in the degree of flying activity which culminated in an evening peak for each simuliid species and which was related to changes in temperature, relative humidity and with time of sunset. The influence of light intensity in inducing changes in flight activity was emphasized by Wolf and Peterson (1960) who reported that the regular post-dawn and pre-sunset flying activity peak of S. venustum in the forest coincided with the sharp decrease in reflected light intensity to levels below 25 ft-candles; in the morning the activity peak occurred at light intensities of about 15 ft-c, whereas the corresponding peak in the evening occurred at about 5 ft-c. They found no direct relationship with changes in atmospheric pressure, temperature and saturation deficiencies, hence differing from Davies (1952). Wolf and Peterson, however, admitted that the effect of temperature cannot be ruled out entirely as the lower activity peak in the morning, at a higher light intensity, compared to the major peak in the evening, at a lower light intensity "may well be related to the occurrence of lower temperatures after dawn than before sunset". In fact, it may well be that on clear days high or low diurnal temperatures may supersede the effect of light intensity in determining whether the evening peak activity for the ornithophilic species occurs before or after sunset. As it was mentioned earlier, the present results seem to indicate that comparatively high temperatures (and related lower RH) are associated with a peak activity occurring after sunset, and lower temperatures with a peak activity occurring before sunset (doubtless at a correspondingly lower and higher light intensities). It seems, however, that these environmental factors at different intensities affect *S. venustum* differently as compared to the ornithophilic species, because the peak-activity of *S. venustum* was observed to occur, on the average, two hours before that of the ornithophilic species. Wolf and Peterson (1960) asserted further that changes in light intensity induced vertical movements in *S. venustum* in the forest. From sweep collections made at 25 to 30 feet above ground they indicated that black-flies "move vertically toward the top of the forest cover at night and come down in the daytime". The present results indicate no such vertical movements in *S. venustum* as its stratification during the evening was remarkably constant at the 12- and 25-foot levels and only rarely were some specimens collected at the 50-foot level. Some ornithophilic species, as *P. decemarticulatum*, *E. aureum* and *E. croxtoni*, however, seem to show a perceptible vertical movement during the evening peak activity. If vertical movements in the population of these simuliid species do occur as a response to vertical changes in light intensity, then the rather open nature of the particular habitat in which the experiments were conducted may have allowed changes in light intensity over too small a range to effect a meaningful movement in the population of these flies.

Vertical movements in mosquito populations have been shown to occur during their 24-hr biting cycle in some tropical forests. Haddow (1954) has shown that the vertical distribution of *Aedes ingrami* Edwards changes with the time of day; in mid-morning and early afternoon it was found distributed mainly at ground level, but soon after sunset it moved higher in the canopy where it remained throughout the night. *Aedes apicoargenteus* (Theo.) and *A. africanus*

(Theo.) were found confined similarly at ground level throughout the day but moved into the forest canopy just after sunset (Haddow and Ssenkubuge 1965). Haddow (1961) found Mansonia fuscopennata (Theo.) also confined primarily at ground level by day but that it migrated during the evening completely to the top of the forest canopy. He considered that changing light intensities at various levels in the forest was the most important environmental factor influencing such vertical movements.

Orientation of Simuliids to their Hosts

1. Eusimulium sp. 1 feeding on ducks in Norway

From the foregoing account it was implied that preference for a particular habitat-type (and the preferred stratification within it) by biting simuliid species is related to their ability of finding in that habitat the right hosts from which they will ultimately obtain a blood meal; this has been amply documented for ornithophilic simuliids in Ontario (Bennett 1960; Fallis and Smith 1964; Fallis and Bennett 1966; Smith 1966) and in Wisconsin (Anderson and De Foliart 1961). Yet, it is difficult to explain the presence of Eusimulium sp. 1 in relatively large numbers at the Renåa river in which the Anseriforme, the probable host of this simuliid species, were absent. Domestic ducks (Anas boschas) were brought to this site for the first time in the summer of 1968 for experimental purposes, and considering how easily these birds succumbed to Leucocytozoon infection (Eide et al 1969) , it is likely that A. boschas is not the natural host for this fly species. However, since wild ducks (Anas crecca and A. platyrhynchos) were frequently seen in lakes in the Rendalen area, it is possible that these birds may be the natural hosts for Eusimulium sp. 1.

In fact, in Ontario Khan and Fallis (1968) have found that wild ducks (*Anas rubripes* and *A. platyrhynchos*) are considerably more tolerant than domestic ducks (*A. boschas*) to *Leucocytozoon simondi* infection transmitted by *S. anatinum* and *S. rugglesi*. The presence of *Eusimulium* sp. 1 at the experimental site on the Renåa river could be explained therefore by the following factors: (a) *Eus.* sp. 1 could be autogenous for the first gonotrophic cycle, and providing that breeding sites exist along the Renåa river, then each adult generation in the absence of a host will develop only one batch of eggs which would be sufficient to keep the fly population at a low level; (b) *Eus.* sp. 1 may obtain a blood meal from some species of "aquatic" avian host other than the Anseriforme dwelling along the Renåa river; (c) some unknown breeding site of *Eus.* sp. 1 may exist along the Renåa river which is frequented by wild ducks and from which this fly species migrated via the river course to the experimental site. Although no data were obtained in Rendalen to substantiate these three possibilities, circumstantial evidence to support the third possibility exists from work done in Ontario with *S. rugglesi* (Bennett, 1963). With labelling and re-capture experiments Bennett (1963) demonstrated that *S. rugglesi* may fly a minimal distance of 6 miles in 8 days along the water-route of the Madawaska river system. He re-captured P^{32}-marked flies feeding on domestic ducks exposed on a point at the edge of the river approximately 2 miles air distance from a second point on the river where the marked flies were released. However, he considered that due to their rigid habitat preference these flies could have flown back to the re-capture point only via the 6-mile water-route.

2. Role of olfaction in flies orienting to hosts

The above observations raise the question as to what factors are involved in guiding these flies toward their host. Laarman (1955) asserted that odours other than CO_2 are of principal importance in initiating from a distance the host-finding behaviour in female mosquitoes. Considering host specific simuliids, as E. euryadminiculum (Fallis and Smith 1964) there is little doubt that host-odours play a major role in orienting these flies to their host (Lowther and Wood 1964; Fallis and Smith 1964; Smith 1966). Additional observations have indicated that wind together with olfactory stimuli may be another important factor in guiding from a distance E. euryadminiculum and S. venustum females toward the odour source (see Introduction pp. 10-11). In fact, in the present work it has been shown that host-seeking females of S. venustum will fly toward a source of CO_2 against the wind direction only; in the absence of CO_2, wind alone is not sufficient for such upwind orientation.

Kennedy (1939) clearly demonstrated that females of Aedes aegypti, after being stimulated by human breath to take flight in a wind tunnel, flew against the wind and settled at the upwind end of the tunnel. However, with further experimentation he concluded that "flying orientation to a wind-borne scent is not, in a direct sense, easily conceivable. But the activating effect of scent, combined with the visual orientation upwind, would serve as an effective host-finding mechanism for mosquitoes emerging downwind and flying low."

Kennedy demonstrated that free-flying mosquitoes would necessarily orient and fly upwind for they were unable to tolerate images moving from back to front over the compound eyes, the visual equivalent of being swept downwind. Hence, they flew upwind at such a speed as to maintain a constant relation with the background or slightly faster so that images passed over the eyes from front to back. For low wind speeds, mosquitoes attempted to modify their flying speed whenever images passing over their eyes from front to back exceeded a speed of 17 cm/sec. At wind speeds greater than 150 cm/sec (3.3 mph) such modification became impossible, and instead of being swept downwind they would immediately land.

In Algonquin Park, although average wind speeds of up to 700 ft/min (8 mph) were recorded during upwind orientation experiments, it is likely that actual upwind flight by S. venustum females occurred only at much lower wind speeds. In fact, Wolfe and Peterson (1960) observed that flying activity of S. venustum was suppressed at wind speeds higher than 2 mph; however, in Rendalen G. rostratum and Scho. pusilla stopped flying in winds of 500 ft/min (5.6 mph) measured four feet above ground, while in England L. Davies (1956) observed that in female S. ornatum landing was often completely inhibited at average wind speeds greater than 5 mph.

Kennedy (1939) explained further that mosquitoes would fly low since the apparent rate of movement of the background across the eyes would depend on the distance of the insect above this background. Subsequently, Laarman (1955) and Kalmus and Hocking (1960) observed mosquitoes to fly close to the ground while approaching hosts from downwind. The low-flying habit typical of some host-seeking simuliids, as E. euryadminiculum (Davies and Peterson 1957) and S. rugglesi

(Bennett 1960; Fallis and Smith 1964; Smith 1966) in Ontario and *Cn. pallipes*, *S. vulgare* and *Eus.* sp. 1 in Rendalen, may well be related to similar visually compensated upwind orientation.

The maximum distance downwind from which host-seeking simuliids orient to a source of odour is unknown; however, considering CO_2 under conditions reported in the present work, it is doubtful that upwind orientation by *S. venustum* could occur with any precision at greater distances than 15 feet from the source of the gas. In this respect, CO_2 is really a vicinity factor in the sense that it can be perceived only at relatively close distances from its source; by contrast, scents can be perceived by insects in terms of few molecules at distances of up to one mile (Dethier 1947; Wright 1958). The detection of CO_2 only at close proximity to its source is plausible when considering that as a normal component of the environment CO_2 could be sensed only in so far as it forms a diffusing gradient with the CO_2 already existing in the milieu of the insect. This raises the question of how non-host-specific simuliids, which are attracted mainly with CO_2, e.g. *S. venustum* (Smith 1966; Fallis *et al* 1967) and *G. rostratum* and *Scho. pusilla*, reach the vicinity of the odour source at great distances from their breeding sites. These mammaliophilic species have often been noticed to be attracted to man but would not bite near their breeding sites soon after emergence, which suggests the necessity of a pre-biting dispersal flight. This is in close agreement with Colless'(1957) conclusion regarding *Culex annulus* that insects reach the vicinity of the host by a process of random wandering within their particular habitat. On the other hand, Laarman (1965) considered it unlikely for mosquitoes to begin searching for a host without an extrinsic chemical stimulus.

Wright (1958) proposed, however, that flying insects could perceive an odour gradient by virtue of the uneven distribution of odour clouds. Considering that odour clouds tend to be dispersed in a filamentous manner, Wright explained that theoretically an insect could detect the gradient by means of the frequency with which it encountered the filaments of the odour cloud. Increasing frequency of encounter would lead the insect up the gradient, while decreasing frequencies would lead it down the gradient. This mechanism could account for the increase in number of *Cn. pallipes*, *G. rostratum* and *Scho. pusilla* taken with suction-traps baited with increasing rates of CO_2 emission. Increased attraction to traps baited with increasing rates of CO_2 emission has also been shown in *S. venustum* (Smith 1966; Fallis *et al* 1967) and in several mosquito species (Reeves 1953). However, it was shown that although a larger number of *Scho. pusilla* were attracted with higher concentration of CO_2 , the number remaining in flight close to the trap (those drawn into the trap) increased, while the number landing on the silhouette decreased. It is evident then that at higher concentrations of CO_2 a larger proportion of flies remained activated close to the source of the gas than landed on the silhouette. While attraction to an odour is theoretically possible (Wright 1958), the mechanism has not been observed in actual operation in any insect, and therefore many workers have generally recognized that CO_2 functions primarily as an activator in flying insects. Under field conditions it is difficult to test whether CO_2, from a host-substitute, acts as an attractant *per se* because of the difficulty in effectively separating other factors as wind and visual stimuli which exert additional influence in attracting the insect.

3. Interrelation between olfaction and vision in the orientation of flies

A decrease in the effect of vision obtained by separating the suction-trap from the CO_2 source showed that the number of G. rostratum and Scho. pusilla attracted to CO_2 alone at 4 feet above ground was only 1/20 and 1/30 respectively of that attracted to CO_2 plus the suction-trap. The visual stimulus provided by the exposed trap could not have been by itself the more important factor since the trap alone was only 4 times more effective than CO_2 alone in attracting both species together. Similar results were obtained with Cn. pallipes and most Eusimulium species in Rendalen as approximately 1/20 the number of flies were taken with CO_2 alone than with CO_2 in combination with a suction-trap. On the other hand, CO_2 alone appeared to be the most important factor in attracting S. vulgare. In fact, the number of S. vulgare taken with the exposed CO_2 plus suction-trap at ground level was equal to the number taken in the absence of the visible trap, indicating that a visual stimulus associated with CO_2 plays an insignificant role in its host-seeking behaviour. In this respect the behaviour of S. vulgare is quite similar to that of E. euryadminiculum for which has been shown that an olfactory rather than a visual stimulus is important in attracting these flies to their host (Fallis and Smith 1964).

By contrast, both CO_2 alone and in combination with a visual stimulus were found effective in attracting S. venustum, such that the number of flies caught with the combined influence of olfaction and vision was almost double that caught under the influence of olfaction alone. It is possible that in the absence of a silhouette S. venustum and S. vulgare may have located the isolated CO_2 source by relying on visual contact with the ground while maintaining an in-flight upwind orientation toward the CO_2 source, as was pointed out above. Although this may explain, on one hand, the failure of G. rostratum and Scho. pusilla to locate the isolated CO_2 source at 4 feet above ground, it does not explain, on the other, the failure of Cn. pallipes to locate the isolated CO_2 source at ground level and its success in locating one with a visible suction-trap silhouette. It must be considered here that although wind in combination with CO_2 is an important factor in orienting flying simuliids toward the odour source, it is not an indispensible factor for the homing of these flies to the CO_2 source. On many occasions flies of S. venustum and S. vulgare were caught with CO_2 only (traps hidden below ground) during apparently windless conditions, suggesting that these flies may have been attracted to the CO_2 source by flying up along a CO_2 gradient formed by the dissipating gas.

These observations indicate that host-seeking simuliids under field conditons are attracted to CO_2 but their final approach depends in various degrees on a visual stimulus associated with the CO_2 source. The degree of importance of this visual stimulus apparently varies among different species; for species such as S. vulgare it seems of little significance, but it is important for species such as S. venustum, whereas it appears of primary significance for species such as Cn. pallipes, G. rostratum, Scho. pusilla and most Eusimulium species.

The importance of visual stimuli has been emphasized by some workers (Wenk, 1962, 1965; Wenk and Schlorer, 1963; Anderson and De Foliart, 1961) who maintain that the attraction of some simuliid species to their hosts is dependent specifically on visibility and size of the host (see Introduction,

p. 18). In the present work it has been shown that most simuliid species in Rendalen discriminated between a 1/2-foot cubic cage silhouette and one 4 times this size. Generally, G. rostratum was the only species attracted in significantly greater number to the larger silhouette, whereas Cn. pallipes, Scho. pusilla, S. vulgare and E. bicorne were attracted significantly more to the smaller silhouette. Carbon dioxide, however, was necessary for attracting these flies to the silhouettes, and results have indicated that discrimination between the large and the small silhouette depends for some species on the rate of CO_2 emission and the inter-silhouette distance.

Visual stimuli, have been generally recognized to affect landing in simuliids (Davies, 1951, 1961; Fallis and Smith, 1964; Lowther and Wood 1964; Smith, 1966; Fallis et. al 1967). Fallis and Smith have shown that although olfaction is the primary stimulus attracting S. euryadminiculum to its host, "at close range, visual stimuli appeared important, as the flies landed only on certain parts of the bird or on raised objects". It was observed, however, that less host-specific simuliids cannot be attracted by CO_2 (by olfactory stimuli) alone and therefore a visual stimulus may also be important for the final approach to a host or host-substitute. In Rendalen in the summer of 1967 it was realized that apparently identical cows, differing only in colour, attracted in the pasture unequal number of simuliids. Two black cows attracted simuliid swarms consistently two to three times larger than those of the same species attracted to two other cows coloured reddish-yellow; at the same time, many more flies were feeding on the black cows than on the other two cows. Subsequently, it was shown that the number of Cn. pallipes, P. hirtipes, G. rostratum and S. ornatum, in Rendalen, and P. fuscum, S. venustum and some Eusimulium species, in Ontario, approaching a suction-trap was inversely proportional to the quantity of total light reflected from the trap. These results are in agreement with Davies' (1951, 1961) finding that the rate of landing on achromatic coloured surfaces by S. venustum is inversely proportional to the amount of light reflected from the landing surface interposed between the host and the fly. Fallis and Smith (1964) observed, in addition, that landing by E. euryadminiculum is influenced by lightness and colour as flies landed on the dark coloured back, head and neck of a dead loon but not on the white breast feathers.

The interdependence of olfactory and visual stimuli in influencing the final approach to a silhouette was demonstrated for some Eusimulium species, P. fuscum and S. venustum. It was shown that the negative visual response of these flies to a highly reflecting white surface can be changed to a progressively more positive response by increasing the rates of CO_2 emission. Comparing this effect with a standard response to a black surface at constant rates of CO_2 emission, a measure of the relative sensitivity by various species to visual and olfactory stimuli can be determined. Since the differences in reaction to the black and white silhouette (discrimination ratios) by the Eusimulium species were larger than the corresponding ones by P. fuscum and these in turn were larger than those by S. venustum it appears that visual stimuli are of comparatively decreasing importance for these three species in the order mentioned. G. rostratum, P. hirtipes, S. ornatum from Rendalen were listed in a similar decreasing order of visual sensitivity. In addition, the rate at which the discrimination ratio for each species reach the equilibrium point (discrimination ratio = 1) provides a measure of the comparative attraction to CO_2 since the change in discrimination ratios is dependent on the progressive increase of CO_2 emission from the white silhouette. Hence the faster the rate of decrease toward the equilibrium point the greater the response to CO_2 such that in the present work the *Eusimulium* species, *P. fuscum* and *S. venustum* showed a comparatively increasing response to CO_2 in the order listed. The comparatively lesser response to CO_2 by these ornithophilic species is not surprising when it is considered that their attraction to their avian hosts is mediated particularly by host odours (other than CO_2) as in *E.euryadminiculum* and by a combination of these with CO_2 as in *S. rugglesi*, *P. decemarticulatum*, *E. aureum*, *croxtoni*, *latipes*, and *quebecence* (Fallis and Smith,1964). In Rendalen the number of attracted flies landing on a silhouette with CO_2 only was larger for the mammaliophilic *S. vulgare* than for the two ornithophilic *Cn. pallipes* and *Eusimulium* sp. 1. However, by exposing the uropygial gland extract of domestic ducks along with CO_2 , the number of the two ornithophilic simuliids landing increased significantly, compared to the insignificant increase in the number of *S. vulgare*. Of the two ornithophilic species this increase in number was much larger for the *Eusimulium* sp. 1 than for *Cn. pallipes*, evidence supporting the proposal for the possible specificity by this *Eusimulium* species for the Anseriforme. By comparison, an insifnificant number of flies were taken with the uropygial gland extract alone, indicating, therefore, that a synergistic effect by CO_2 and extract was operative in attracting these two ornithophilic species in largest number.

It is conceivable that variations in the number of specific olfactory receptors on the antennae and maxillary palpi among various species of simuliids effect different degrees of response to CO_2 and other host-odours. Willis and Roth (1952) indicated that in female *Aedes aegypti* receptors sensitive to CO_2 are located on the antennae, and from these Steward and Atwood (1963) distinguished three types of chemoreceptors (A_1, A_2, A_3). Subsequently, Daykin et al (1965) assigned the A_1 sensillum the role of CO_2 receptors, and Kellogg (1970) demonstrated that the A_3 sensillum on the maxillary palpi is also a CO_2 receptor. McIver (1969) reported that the number and distribution of these sensilla on the antennae is variable among different species of mosquitoes.

Reaction to Visual Stimuli During Host-seeking and Ovipositing States

In the present work it was shown that a surface reflecting total light at high intensity inhibits the approach of a number of host-seeking simuliid species, a fact which had already been anticipated by Davies (1951, 1961) in his study of the landing behaviour of host-seeking female *S. venustum*. Davies (1961) reported further that the number of flies landing on coloured cloths was related to the wave-length of reflected light such that the attractiveness of coloured cloths reflecting at low intensity was as follows: red-purple, purple and purple-blue were highly attractive; red and blue intermediate; and yellow-red, green-yellow and blue-green less attractive.

In contrast to the behaviour of host-seeking black-flies in relation to reflected light, gravid females of *S. venustum* and *S. vittatum* have often been observed to oviposit on *green* vegetation trailing on the water surface of streams and rivers (see Introduction, p. 20). In the present study this apparent change of response to reflected light in ovipositing flies was explored further.

The most abundant species involved in such egg-laying activity in Algonquin Park during this research was *S. verecundum* Stone and Jamnback rather than *S. venustum*. Adult females of these two species are distinguished by morphological differences of the ovipositor flaps and anal lobes (Stone and Jamnback 1955, Davies *et al* 1962, Stone and Snoddy 1969), and it is possible that these differences may be related to different oviposition behaviour in these two species. In fact, immature stages of *S. venustum* have generally been observed in large masses attached on substrates at shallow depths of streams lacking surrounding vegetation, e.g. below dams or in rapids. This indicates that *S. venustum* may oviposit directly into the water while in flight. In addition, it has been suggested that *S. verecundum* is apt to emerge a little later than *S. venustum* (Davies *et al*, 1962, Stone and Snoddy 1969). But in the present work it was observed that peak oviposition of *S. verecundum* invariably occurred at the same time as the peak biting of *S. venustum*, and the population of biting and ovipositing flies was observed to decrease simultaneously as the season progressed in Algonquin Park. These evidences suggest that these two species coexist both in time and space, differing, however, in oviposition behaviour. It is possible therefore that the communal oviposition on vegetation as reported by a number of authors (see p. 20) may be shown, after closer scrutiny of the species involved, to apply more to *S. verecundum* than to *S. venustum*.

Nonetheless, females of *S. verecundum* and *S. vittatum* have been shown to oviposit preferentially on surfaces reflecting high light intensity than on these reflecting at low intensity. In addition, chromatic surfaces reflecting wavelengths from the middle of the visible spectrum were selected by both these species and *S. ornatum* more frequently than those reflecting shorter wave-lengths; hence, flies oviposited more often on "yellow" and "green" surfaces than on "red", "orange", "blue" and "purple" surfaces. The less defined selection of the sticky achromatic strips by both *S. verecundum* and *S. ornatum* is difficult to explain when realizing that the quantity of reflected light changed only slightly in the presence of a thin layer of Bird Tanglefoot. One explanation might be attributed to a restriction of choice that the Tanglefoot imposed on the gravid flies soon after they landed on these strips. In fact, gravid *S. verecundum* flies were often observed to alight from one non-sticky strip to another before settling down to oviposit. This explanation, however, does not account for the rather consistent order of preference among the chromatic strips with and without Tanglefoot.

Degrees of darkness of the natural stream background may also have contributed to the differences in colour selection by *S. ornatum* and *S. verecundum*. It was shown for *S. verecundum* and *S. vittatum* that substrate preferences for oviposition are relative to the intensity of total light reflected from the stream bottom. By artificially changing the stream background from its natural light-brownish colour to black, these flies tended to shift their preference for the chromatic colours from yellow-green to the orange and blue-purple ends of the spectrum; similarly, under these same conditions their preference among the neutral strips shifted significantly from the brightest surface (white) to the next less bright surface (light grey). In addition, with more pronounced differences in stream background, oviposition was either enhanced with a black stream bottom or suppressed with a white stream bottom. All these variables notwithstanding, the selection of coloured substrates by ovipositing *S. ornatum* in Rendalen was rather similar to that of S. verecundum and S. vittatum in Ontario.

Light intensity has been considered of primary importance in eliciting phototactic reactions in a number of insects such that responses to incident light wave-lengths can be exactly matched by adjusting the intensities of the different spectral regions (Crescitelli and Jahn 1939; Weiss et al 1942). In general, flies can distinguish different shades of green, yellow, orange and near red (Mozakin-Porshnyakov 1969), and in simuliids Davies (1961, unpublished data) noted that by keeping the hue and chroma constant, the frequency of landing on a given coloured cloth by host-seeking S. venustum decreased as the intensity of reflected light was increased. In the present work, although an attempt was made to produce chromatic colours with almost equal intensities, the intensity (reflectance) from 325 to 700 mµ for green and orange turned out to be much lower than for that of the remaining colours (see Appendix C Table 44). Hence, it is possible that the constant preference for "yellow" was influenced to some degree by its greater total reflectance in the 325-700 mu range. However, the fact that other "colours" with almost equal total reflectances as that of yellow and greater than that of green were less attractive than either yellow or green, indicates that the hue (or wave-length) of reflected light appears to be an important factor influencing colour selection by ovipositing simuliids. A number of workers (Weiss et al 1942; Goldsmith 1958b; Burkhardt 1964) have reported that the region of the spectrum from 350 to 490 mµ is the most efficient in eliciting a visual response in many insects. Davies (1951) reported a similar response in biting S. venustum as it landed most frequently on blue cloths with a maximum reflectance-peak at 400 mμ. This maximum response of simuliids for the blue-end of the spectrum apparently shifted during the oviposition state toward the longer wave-lengths of the yellow spectral region. Such colour preference was shown to be directly related to the ratio of the quantity of reflected light from each colour in the 450-700 mμ and 325-450 mμ (ultraviolet-blue) spectral ranges. This indicates that the degree of response to reflected light of various wave-lengths may be dependent on an interplay of the longer and the shorter wave-lengths of the visible spectrum.

SUMMARY

1. Several species of adult female simuliids in Rendalen exhibited various degrees of habitat preferences. These preferences were discussed in relation to similar habits already known of simuliids in Ontario.
2. Vertical and horizontal stratifications were considered an integral part of habitat preference and in Ontario the first was re-investigated in simuliids frequenting the forest habitat. In Rendalen most female simuliids were found to be ubiquitous; *S. vulgare* and *Eusimulium* sp. 1 were the only two notable species restricted preferentially at ground and water level respectively.
3. No direct investigations of host preferences were made in Rendalen. However, most mammaliophilic simuliids were collected in large number and in almost equal proportions from both man and cows; *P. hirtipes* was the only species collected preferentially from cows. Among the ornithophilic simuliids, *E. beltukovae* was the only species caught most frequently feeding on Passeriforme, *Eusimulium* sp. 1 was exclusively the only species caught feeding on *Anas boschas*.
4. Evidences were presented which implicated *Eusimulium* sp. 1 as the probable vector of *Leucocytozoon* sp. to *Anas boschas* in Rendalen. This simuliid species was found to be rather similar to *S. dogieli* and *S. anatinum*, but a few morphological differences indicate that *Eusimulium* sp. 1 is a distinct new species.
5. Most species of simuliids in Rendalen exhibited different degrees of attraction to carbon dioxide with and without a silhouette. A comparison of the responses to these olfactory and visual stimuli was made with other species from Ontario.

Hence: (a) *S. vulgare* was attracted to CO_2 alone and showed an insignificant change in attraction to CO_2 plus a silhouette.

(b) *S. venustum* was attracted to CO_2 alone but a significantly larger number was taken in combination with a silhouette.

(c) *Cn. pallipes*, *G. rostratum*, *Scho. pusilla* and most *Eusimulium* species were attracted to a combination of CO_2 and a silhouette but not to either alone.

(d) *Eusimulium* sp. 1 was attracted to a combination of CO_2 and a silhouette but a significantly larger number was taken with the addition of an extract from the uropygial gland of *Anas boschas*

6. Most species in Rendalen were found to differentiate between a large and a small silhouette such that *S. vulgare* and most *Eusimulium* species were attracted mainly to the small silhouette and *G. rostratum* to the large one.
7. Biting simuliids in both Ontario and Rendalen were attracted significantly more to a silhouette with a low total reflectance of light than to one with a high total reflectance. Ovipositing simuliids instead tended to select substrates with a high total reflectance in preference to those with a low reflectance. The yellow-green spectral range was most frequently selected by ovipositing simuliids in both Ontario and Norway.

REFERENCES *

Aitken, T.G. 1956. Entomological aspects of the Trinidad virus research program. Tenth Intern. Congr. Entomol., 3: 573-580.

Anderson, R.C. 1956. The life cycle and seasonal transmission of Ornithofilaria fallisensis Anderson, a parasite of domestic and wild ducks. Canad. J. Zool., 34: 485-525.

Anderson, J.R. and DeFoliart, G.R. 1961. Feeding behaviour and host preferences of some black-flies (Diptera:Simuliidae) in Wisconsin. Annals Entomol. Soc. Amer., 54: 716-729.

___________ and Vaskuil, G.H. 1963. A reduction in milk production caused by the feeding of black-flies (Diptera:Simuliidae) on dairy cattle in California, with notes on the feeding activity on other animals. Mosquito News, 23: 128-131.

___________, Trainer, D.O. and DeFoliart, G.R. 1962. Natural and experimental transmission of the waterfowl parasite Leucocytozoon simondi M. & L. in Wisconsin. Zoonosis Research, 1(9): 155-164.

Blacklock, D.B. 1926. The development of Onchocerca volvulus in Simulium damnosum. Ann. Trop. Med. Parasit., 20: 1-48. (Abstract seen in Bibliografia de Oncocerciasis to 1945).

* References marked with an asterisk are primarily keys and were used for species identification.

Bennett, G.F. 1960. On some ornithophilic Diptera in Algonquin Park, Ontario, Canada. Canad. J. Zool. *38*: 377-389.

____________ 1961. On the specificity and transmission of some avian tripanosomes. Canad. J. Zool. *39*: 17-33.

____________ 1963. Use of P^{32} in the study of a population of *Simulium rugglesi* (Diptera:Simuliidae) in Algonquin Park, Ontario. Canad. J. Zool. *41*: 831-840.

____________ and Fallis, A.M. 1960. Blood parasites of birds in Algonquin Park, Canada, and a discussion of their transmission. Canad. J. Zool. *38*: 262-273.

Berzina, A.N. 1953. Attack of black-flies on man in nature. Zool. Inst. Acad. Sci. USSR, Parasit. Sympos. XV, 353-386.

Bracken, G.K., Hanec, W. and Thorsteinson, A.J. 1962. The orientation of horse-flies and deer-flies (Tabanidae-Diptera). II The role of some visual factors in the attractiveness of decoy silhouettes. Canad. J. Zool. *60*: 685-695.

Brown, A.W.A. 1951. Studies of the responses of the female *Aedes* mosquitoes. IV. Field experiments on Canadian species. Boll. Entomol. Res. *42*: 575-582.

____________ 1954. Studies of the responses of the female *Aedes* mosquitoes. VI. The attractiveness of coloured cloth to Canadian species. Bull. Entomol. Res. *45*: 67-78.

____________ and Carmichael, A.G. 1961. Lysine and alanine as mosquito attractants. J. Econom. Entomol. 54: 317-324.

____________, Sarkaria, D.S. and Thompson, R.P. 1951. Studies on the responses of the female Aedes mosquito. I. The search for attractant vapours. Bull. Entomol. Res., *42*: 105-114.

Burkhardt, D. 1964. Colour discrimination in insects. Advances in Insect Physiol., *2*: 131-173.

Check: Jones + Ritchy Calvin, M.J. and Ritchey, D.J. (1956) 1955. Biology of the black-flies in Jasper County, South Carolina, and some relationships to a *Leucocytozoon* desease of turkey. J. Econom. Entomol., *49*: 121-123.

*Carlsson, G. 1962. Studies on Scandinavian black-flies. Opuscula Entomologica Supplementum XXI, Lund, Sweden.

Clements, A.N. 1963. *The physiology of mosquitoes*. The Macmillan Company, New York.

Colless, D.H. 1957. Components of the catch curve of *Culex annulus* in Singapore. *Nature*, 180: 1496-1497.

Craig, W. 1918. Appetites and aversions as constituents of instincts. Biological Bull. Woods Hole, *34*: 91-109.

Crescitelli, F. and Jahn, T.L. 1939. The electrical response of the dark-adapted grasshopper eye to various intensities of illumination and to different quantities of light. J. Cell and Comp. Phys., *13*: 105-112.

Dalmat, H.T. and Gibson, C.L. 1952. A study of flight range and longevity of black-flies (Diptera:Simuliidae) infected with *Onchocerca volvulus*. Ann. Entomol. Soc. Amer., *45*: 605-612.

Dalmat, H.T. Ecology of simuliid vectors of Onchocerciasis in Guatemala. Amer. Midl. Naturalist, *52*: 157-196. (1955)

Davies, D.M. 1949. The ecology and life history of black-flies (Simuliidae, Diptera) in Ontario with a description of a new species. Ph. D. Thesis, University of Toronto.

__________ 1951. Some observations on the number of black-flies (Diptera, Simuliidae) landing on coloured cloths. Canad. J. Zool. *29*: 65-70.

Davies, D.M. 1952. The population and activity of adult female black-flies in the vicinity of a stream in Algonquin Park, Ontario. Canad. J. Zool. **30**: 287-321.

___________ 1961. Colour affects the landing of bloodsucking black-flies, (Diptera:Simuliidae) on their hosts. Proc. Entomol. Soc. Ont. **92**: 70-154.

___________ and Peterson, B.V. 1956. Observations on the mating, feeding, ovarian development, and oviposition of adult black-flies (Simuliidae, Diptera). Canad. J. Zool. **34**: 615-655.

___________ ___ ___________ 1957. Black-flies over lakes (Simuliidae, Diptera). Ann. Entomol. Soc. Amer. **50** (5): 514-521.

*___________ ___ ___________ and Wood, D.M. 1962. The black-flies (Diptera: Simuliidae) on Ontario. Part I. Adult identification and distribution with descriptions of six new species. Proc. Entomol. Soc. Ont. **92**: 70-154.

Davies, L. 1954. Observations on *Prosimulium ursinum* Edw. at Holandsfjord, Norway. Oikos, **5** (1): 94-98.

*___________ 1966. The taxonomy of British black-flies (Diptera:Simuliidae). Trans. R. Entomol. Soc. Lond. **118** (14): 413-511.

___________ 1957a. A study of the black-fly *Simulium ornatum* Mg. (Diptera) with particular reference to its activity on grazing cattle. Bull. Entomol. Research, **48**: 407-424.

___________, Downe, A.E.R., Weitz, B. and Williams, C.B. 1962. Studies on black-flies (Diptera:Simuliidae) taken in a light trap in Scotland. II. Bloo-meal identification by precipitin tests. Trans. R. Entomol. Soc. Lond. **114**: 21-27.

Daykin, P.N., Kellog, P.E. and Wright, R.H. 1965. Host finding and repulsion of *Aedes aegypti*. Canad. Entomol. *97*: 239-263.

Dethier, V.G. 1947. *Chemical attractants and repellants*. Philadelphia, Blakiston.

___________ 1962. *The physiology of insect senses*. London, Methuen.

Downe, A.E.R. and Morrison, P.E. 1957. Identification of blood-meals of black-flies (Diptera:Simuliidae) attacking farm animals. Mosquito News, *17*: 37-40.

Eide, A. Fallis, A.M., Brinkmann Jr., A., Allan, T. and Eligh, D. 1969. Haematozoa from Norwegian birds. Årbok for Universitetet i Bergen. Mat.-Naturv. serie No. 6, 3-8.

Fallis, A.M. 1964. Feeding and related behaviour of Simuliidae, (Diptera). Expt. Parasitol. *15* (5): 439-470.

___________, Anderson, R.C. and Bennett, G.F. 1956. Further observations on the transmission and development of *Leucocytozoon simondi*. Canad. J. Zool. *34*: 389-404.

___________ and Bennett, G.F. 1958. Transmission of *Leucocytozoon bonasae* Clarke to the ruffed grouse (*Bonasa umbellus* L.) by the black-flies *Simulium latipes* Mg. and *Simulium aureum* Fries. Canad. J. Zool. *36*: 533-9.

___________ ___ ___________ 1966. On the epizootiology of infections caused by *Leucocytozoon simondi* in Algonquin Park, Canada. Canad. J. Zool. *44*: 101-112.

___________, Bennett, G.F., Griggs, G. and Allen, T. 1967. Collecting *Simulium venustum* females in fan traps and on silhouettes. Canad. J. Zool. *45*: 1011-7.

Fallis, A.M. and Bennett, G.F. 1960. Sporogony of *Leucocytozoon* and *Haemoproteus* in simuliids and ceratopogonids and a revised classification of the haemosporiida. Canad. J. Zool., *39*: 215-228.

Fallis, A.M. and Bennett, G.F. 1962. Observations on the sporogony of *Leucocytozoon* mirande, *L. bonasae* and *L. fringillinarum* (Sporozoa: Leucocytozoidae). Canad. J. Zool., 40: 395-400.

Fallis, A.M., Davies, and Vickers, M.A. 1951. Life history of *Leucocytozoon simondi* M. & L. in their natural and experimental infections and blood changes produced in the avian host. Canad. J. Zool. 29: 305-328.

——————— and Smith, S.M. 1964. Ether extracts from birds and CO_2 as attractants for some ornithophilic simuliids. Canad. J. Zool. 42: 724-730.

Fredeen, J.H. 1969. Outbreaks of the black-fly *Simulium arcticum* Malloch in Alberta. Questiones Entomologicae, 5: 341-372.

Garnett, P. and Hansens, E.J. 1957. Further observations on the effect of biting fly control on milk production on cattle. J. Econ. Entomol. 50: 332-336.

Garside, J.S. and Darling, H.S. 1952. Death of turkeys from attack by *Simulium griseicolle* Becker in the Northern Sudan. Bull. Entomol. Res. 42: 583-584.

Gjullin, C.M. 1947. Effect of clothing colour on the rate of attack of *Aedes* mosquitoes. J. Econom. Entomol. 40: 326-327.

Goldsmith, T.H. 1960. The nature of the retinal action potential, and the spectral sensitivities of ultraviolet and green receptor systems of the compound eye of the worker honeybee. J. Gen. Physiol. 43: 775-799.

Haddow, A.J. 1954. Studies of the biting-habits of African mosquitoes. An appraisal of methods employed, with special reference to the twenty-four-hour catch. Bull. Entomol. Res. 45: 199-242.

Haddow, A.J. 1945b. The mosquitoes of the Bwamba county, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of *Aedes (Stegomyia) simpsoni*, Theo. Ibid., 36: 297-304.

Haddow, A.J., Corbet, P.S. and Gillet, J.D. 1961. Entomological studies from a high tower in Mpanga forest, Uganda. I. Introduction. Trans. Royal Entomol. Soc. Lond., 113: 249-256.

____________ and Ssenkubuge, Y. 1965. Entomological studies from a high steel tower in Zika Forest, Uganda. I. The biting activity of mosquitoes and tabanids as shown by the twenty-four-hour catches. Ibid., 117: 215-243.

Haufe, W.O. and Burgess, L. 1960. Design and efficiency of mosquito traps based on visual response to patterns. Canad. Entomol., 92: 124-140.

Ilse, D. 1937. New observations on responses to colours in egglaying butterflies. Nature (L.). 140: 544.

Jobbins-Pomeroy, A.W. 1916. Notes on five North American buffalo gnats of the genus *Simulium*. U.S. Dept. Agricul. Bull. 329: 1-48.

Kahn, R.A. and Fallis, A.M. 1968. Comparison of infections with *Leucocytozoon simondi* in black ducks (*Anas rubripes*), mallards (*Anas platyhrynchos*), and white Pekins (*Anas boschas*). Canad. J. Zool., 46: 773-780.

Kellogg, F.E. 1970. Water vapor and carbon dioxide receptors in *Aedes aegypti*. J. Insect Physiol., 16: 99-108.

*Knoz, J. 1965. The identification of Czechoslovakian black-flies (Diptera, Simuliidae). Folia, Tomus VI, Opus 5, 1-52 and 425 figures.

Laarman, J.J. 1955. The host-seeking behaviour of the malaria mosquito, *Anopheles maculipennis atroparvus*. Acta Leidensia, 25: 1-114.

____________ 1958. The host-seeking behaviour of Anopheline mosquitoes. Trop. and Geogr. Med., 10: 293-305.

____________ 1965. The plasticity of response patterns in host-seeking mosquitoes. Acta Leidensia, 33/34: 136-138.

Laing, J. 1937. Host-finding by insect parasites. I. Observations on the finding of hosts by Alysia manducator, Mormoniella vitripennis, and Trichogramma evanescens. J. Animal Ecology, 6: 298-317.

Lewis, D.J. 1953. Simulium damnosum and its relation to Onchocerciasis in the Anglo-Egyptian Sudan. Bull. Entomol. Res. 43: 597-644.

Lipsitz, E.Y. and Brown, A.W.A. 1963. Studies on the responses of the female Aedes mosquito. IX. The mode of attractiveness of lysine and other amono acids. Bull. Entomol. Res., 54: 675-687.

Lowther, J.K. and Wood, D.M. 1964. Observations on the specificity displayed by a black-fly, Simulium euryadminiculum Davies, toward its host, the common loon. Canad. Entomol., 96: 911-913.

Mazokhin-Porshnyakov, G.A. 1969. Insect vision. Plenum press: New York.

McIver, S.B. 1969. Antennal sense organs of female Culex tarsalis. Ann. Entomol. Soc. Amer., 62: 1455-1461.

Millar, J.L. and Rempel, J.G. 1944. Live stock losses in Saskatchewan due to black-flies. Canad. J. Comp. Med., 8: 334-337.

Montshadsky, A.S. 1956. Bloodsucking Diptera in the territory of U.S.S.R. and some regularities of their attack on man. Entomol. Rev., 35: 547-559.

Petersen, A. 1924. Contribution to the natural history of Danish Simuliidae. Memoires de l'Academie Royal des Sciences et des Lettres de Danemark, Copenhague, 5: 237-341.

Peterson, B.V. 1956. Observations on the biology of Utah black-flies (Diptera-Simuliidae). Canad. Entomol., 88: 496-507.

*Peterson, B.V. 1970. The Prosimulium of Canada and Alaska (Diptera:Simuliidae). Memoirs of the Entomological Society of Canada, No. 68.

Peterson, D.G. and Wolfe, L.S. 1956. The biology and control of black-flies (Diptera:Simuliidae) in Canada. Proc. X Intern. Congr. Entomol., 3: 551-564.

Reeves, W.C. 1951. Field studies on carbon dioxide as a possible host stimulant to mosquitoes. Proc. Soc. Expt. Biol. Med., 77: 64-66.

____________ 1953. Quantitative field studies on a carbon dioxide chemotropism of mosquitoes. Amer. J. Trop. Med. & Hyg., 2: 325-331.

Riley, C.V. 1887. Simuliidae. in Report of the Entomslogist. Rep. Comm. Agrie. for 1886:

*Rivosecchi, L. 1967. I simulidi degli Appennini. Parasitologia, 9 (3): 129-304.

Rubtzov, I.A. 1939. Factors of outbreaks of the black-flies. Trav. Acad. Milit. Med. Kiroff. Armee Rouge. 19: 177-207. Seen in Rev. Applied Entomol. B, 34: 43, 1947.

____________ 1956b. Nutrition and capacity for blood-sucking in black-flies (Diptera:Simuliidae). Entomological Review, 35: 731-751.

*____________ 1956a. Fauna of USSR insects (Diptera). Black-flies (family Simuliidae). Zool. Inst., Acad. Sci. USSR (N.S. 64) ç (6): 1-860.

*____________ 1964. Simuliidae (Melusinidae). in Die Fliegen der Palearctichen Region, Band III4, No. 14, by Erwin Lindner, Stuttgart.

*____________ and Carlsson, G. 1965. On the taxonomy of black-flies from Scandinavia and Northern USSR. Acta Universitatis Lundensis. Sec. II, No. 18.

Shewell, G.E. 1955. Identity of the black-fly that attacks ducklings and goslings in Canada. (Diptera:Simuliidae). Canad. Entomol., 87: 345-349.

Sippell, W.L. and Brown, A.W.A. 1953. Studies of the responses of females Aedes mosquitoes. V. The role of visual factors. Bull. Ent. Res., 43: 567-574.

Smith, S.M. 1966. Observations on some mechanisms of host finding and host selection in the Simuliidae and Tabanidae (Diptera). M.Sc. Thesis, McMaster University.

__________ 1969. The black-fly *Simulium venustum* attracted to the turtle *Chelydra serpentina*. Entomol. News, 80: 107-108.

__________, Davies, D.M. and Golini, V.I. 1970. A contribution to the bionomics of the Tabanidae (Diptera) of Algonquin Park, Ontario: seasonal distribution, habitat preferences and biting records. Canad. Entomol., 102: in press.

*Stone, A. and Jamnback, H.A. 1955. The black-flies of New York State (Diptera:Simuliidae). N.Y. State Museum Bull., No. 349, 1-144.

*Stone, A. 1963. An annotated list of genus-group names of the family Simuliidae (Diptera). Technical Bulletin 1284, U.S. Dept. Agricult.

*Stone, A. and Snoddy, E.L. 1969. The black-flies of Alabama (Diptera:Simuliidae). Agricult. Expt. Station, Auburn University, Bulletin 390.

Sudia, W.D. and Chamberlain, R.W. 1962. Battery light trap, an improved model. Mosq. News, 22: 126-129.

Tinbergen, N. 1951. The hierarchical organization of nervous mechanisms underlying instinctive behaviour. *In* The study of instinct, Oxford Univ. Press.

1942 ?

Twinn, R.C. 1933. The black-fly *Simulium venustum* Say and a protozoon disease of ducks. Canad. Entomol., 65: 1-3.

*Ursing, B. 1966. Norsk Fargelflora. E.G. Mortensens: Oslo.

*Ussova, Z.V. 1961. *Flies of the Karelia and the Murmansk Region* (Diptera:Simuliidae). Academy of Sciences of the USSR; translated from Russian by Israel Program for Scientific Translations, Jerusalem, 1964.

Vockeroth, J.R. 1966. Pin mounts of alcohol simuliid specimens. Canad. Entomol., 98: 69=70.

Weiss, H.B., Soraci, F.A. and McCoy, Jr. E.E. 1942. The behaviour of certain insects to various wave-lengths of light. J. New York Ent. Soc., 50: 1-35.

Wenk, P. 1962. Zur Wirtsorienterung mammalophiler, einheimischer Simuliden (Diptera). Naturwissenschaften, 49: 165-166.

____________ 1965. Uber die biologie blutsaugender simuliden (Diptera). I. Besamungsrate der weibchen beim blutenbesuch und anflug den blutwirt. Z. Morph. Okol. Tiere, 55: 656-670.

____________ and Schlorer, G. 1963. Wirtsorienterung und kopulation bei blutsaugenden Simuliiden (Diptera). Zeit. fur Tropenmed. und Parasitol., 14: 177-192.

Willis, E.R. and Roth, L.M. 1952. Reactions of Aedes aegypti L. to carbon dioxide. J. Expt. Zool., 121: 149-179.

Wolfe, L.S. and Peterson, D.G. 1960. Diurnal behaviour and biting habits of black-flies (Diptera:Simuliidae) in the forests of Quebec. Canad. J. Zool., 38: 489-497.

Wood, D.M. 1963. An interpretation of the phylogeny of the Eusimulium-Group (Diptera:Simuliidae). with description of six new species. Ph.D. Thesis, McMaster University.

____________ 1963. Two new species of Ontario black-flies (Diptera:Simuliidae). Proc. Entomol. Soc. Ont., 93: 94-98.

____________, Peterson, B.V. Davies, D.M. and Gyorkos, H. 1963. The black-flies (Diptera:Simuliidae) of Ontario. II. Larval identification with descriptions and illustrations. Proc. Entomol. Soc. Ont., 93: 99-129.

Wright, R.H. 1958. The olfactory guidance of flying insects. Canad. Entomol., 90: 81-89.

Wu, Y.F. 1931. A contribution to the biology of Simulium. Michigan Acad. Sci., Arts & Letters. 13: 543-599.

APPENDIX A.

Additional Figures

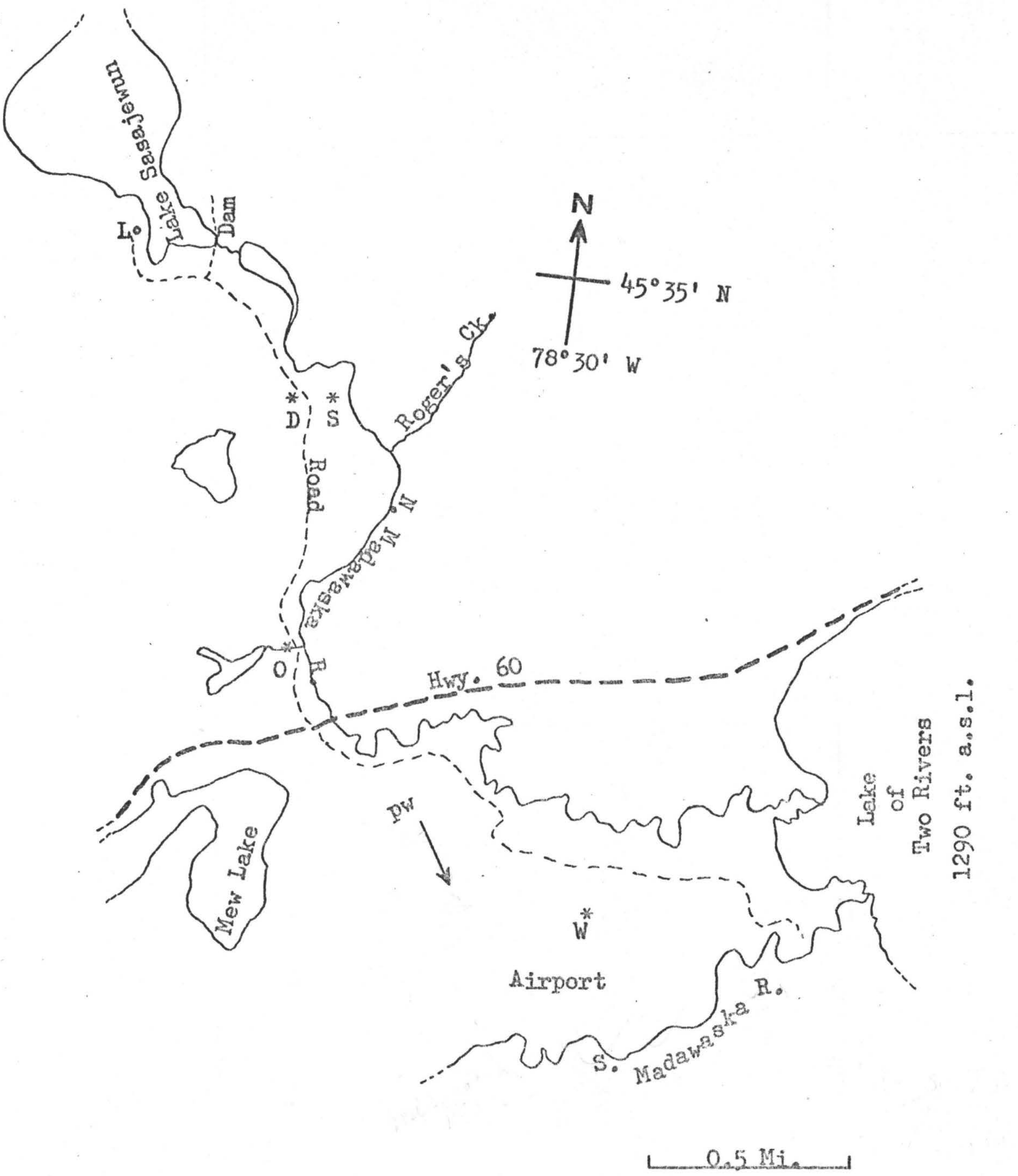


Fig. 1 Map of the area surrounding the Wildlife Research Station of the Ontario Department of Lands and Forests, Algonquin Park, Canada. Localities where experiments were conducted are indicated with an asterisk:

D = forest clearing; S = forest canopy; O = the beaver pond stream; W = airport; L = laboratory; pw = prevailing wind.

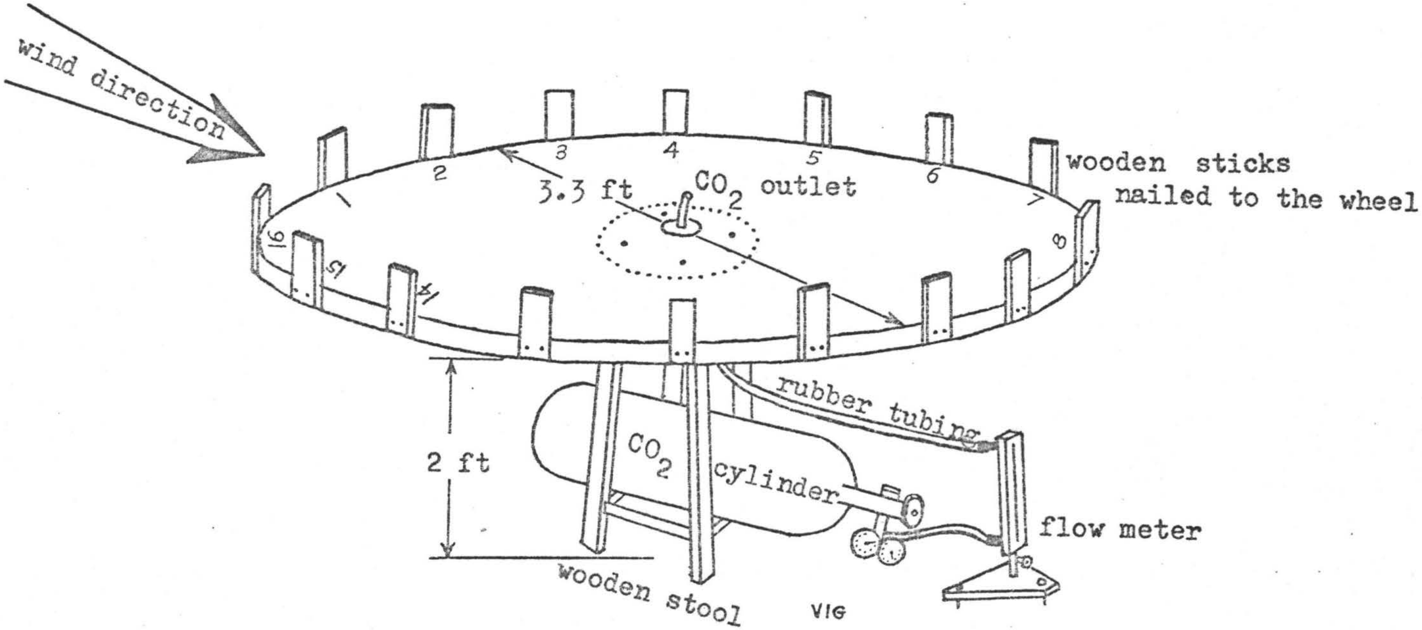


Fig. 2 Diagrammatic representation of the experimental apparatus designed to study the upwind orientation of female Simuliidae in Algonquin Park, Ontario. Spring 1967.

Fig. 3 Vertical stratification apparatus used at the Wildlife Research Station, Algonquin Park, showing: the 40-foot spruce tree with the 10-foot pole extention affixed at its top; two suction-fan-traps at the 12- and the 25- foot levels respectively, each trap is suspended from one of the two ropes passing on a pulley at the 40- and the 50- foot levels.

Fig. 4 Upwind orientation fly-trap used in Algonquin park in 1968, showing: the CO_2 cylinder and flow-meter on the ground; the tripod system holding horizontally a 26-inch bicycle wheel surrounded by sticky glass test-tubes inverted onto wooden dowlings; wind-meter and wind-vane clamped on vertical supporting rod.

Fig. 3

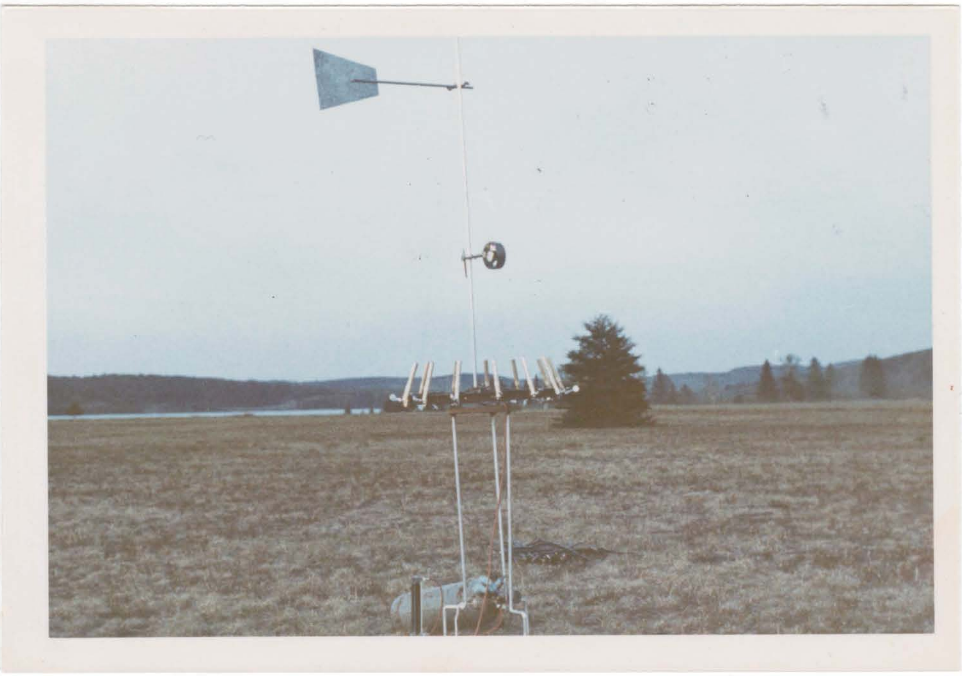


Fig. 4

Fig. 5A Oviposition strips floating on the watwr surface and on artificial black bottom of the beaver bog stream, WRS, Algonquin Park. Chromatic strips are shown in the (back-) foreground, the neutral strips in the background.

Fig. 5B Oviposition strips floating on the water surface and on artificial white bottom of the beaver bog stream, WRS, Algonquin Park.

Fig. 5A

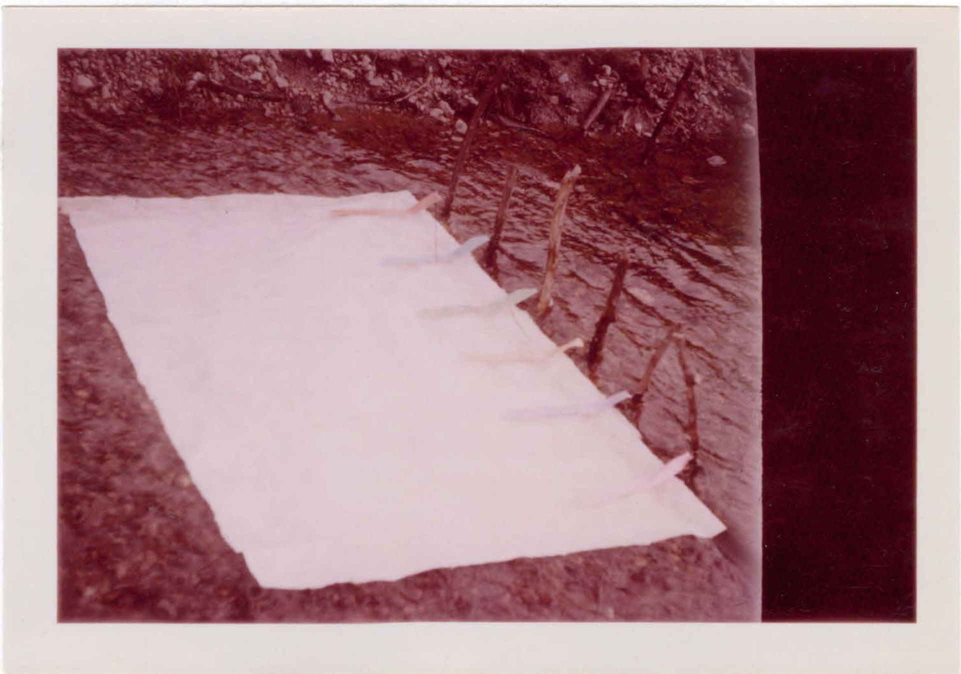


Fig. 5B

Fig. 6 Map of the Rendalen Region in Norway.
The topography of the land is illustrated indicating the elevation in meters above sea-level in relation to the collecting sites S and D where experiments were performed. (sjoen = lake)

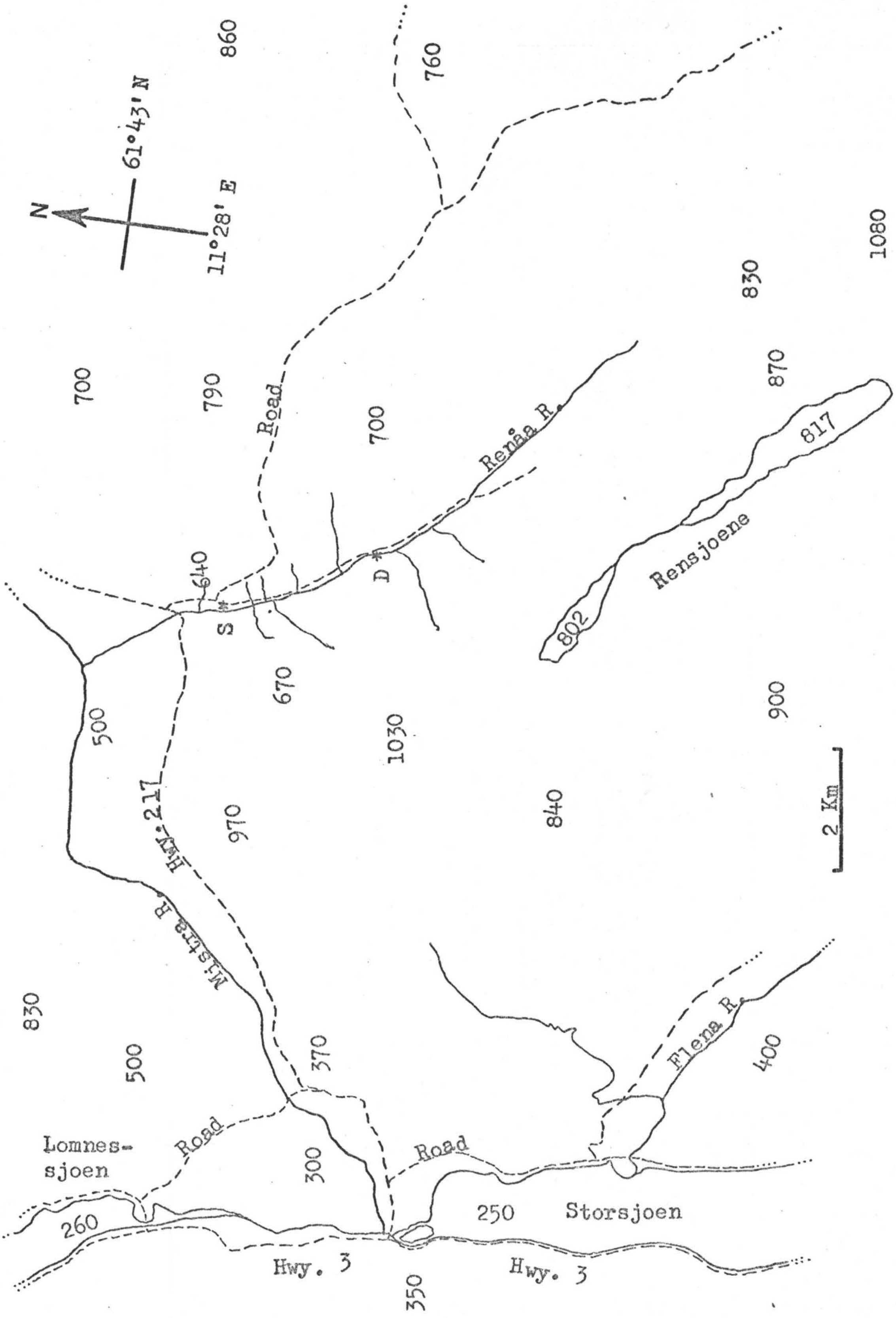

N
61°43' N
11°28' E
860
760
1080
830
870
817
Rensjoene
802
900
700
790
Road
700
Renåa R.
640
S
D
670
1030
500
Hwy. 217
970
840
2 Km
Mistra R.
830
500
370
Flena R.
400
Lomnes-
sjoen
Road
300
Road
260
250
Storsjoen
Hwy. 3
Hwy. 3
350

Fig. 7 Main orientation site, indicated at S in Fig. 6, showing: the grassland (pasture) habitat surrounded on the background by a barbed-wire fence which was used as support for some equipment employed in CO_2-silhouette discrimination experiments.

Fig. 8 The river habitat at the Renåa river adjacent to the pasture, showing: in the foreground, a 4-foot long cage for holding domestic ducks, and a duck in each of two smaller cages resting on two white boards, while collecting fed simuliids; in the middle background, the vertical stratification apparatus with a 9-foot vertical pole and 3 CO_2 sticky white-plastic-duckling-models suspended at ¼, 4, and 7 feet respectively above the surface of the water.

Fig. 7

Fig. 8

Fig. 9A Oviposition site on the Renaa river showing sticky oviposition strips floating on the water surface.

Fig. 9B Masses of S. ornatum eggs deposited on leaves of Salix spp. and Typha latifolia contained in a 4-inch Petri dish. These were collected from the edge of the Renaa river at the oviposition site.

Fig. 9A

Fig. 9B

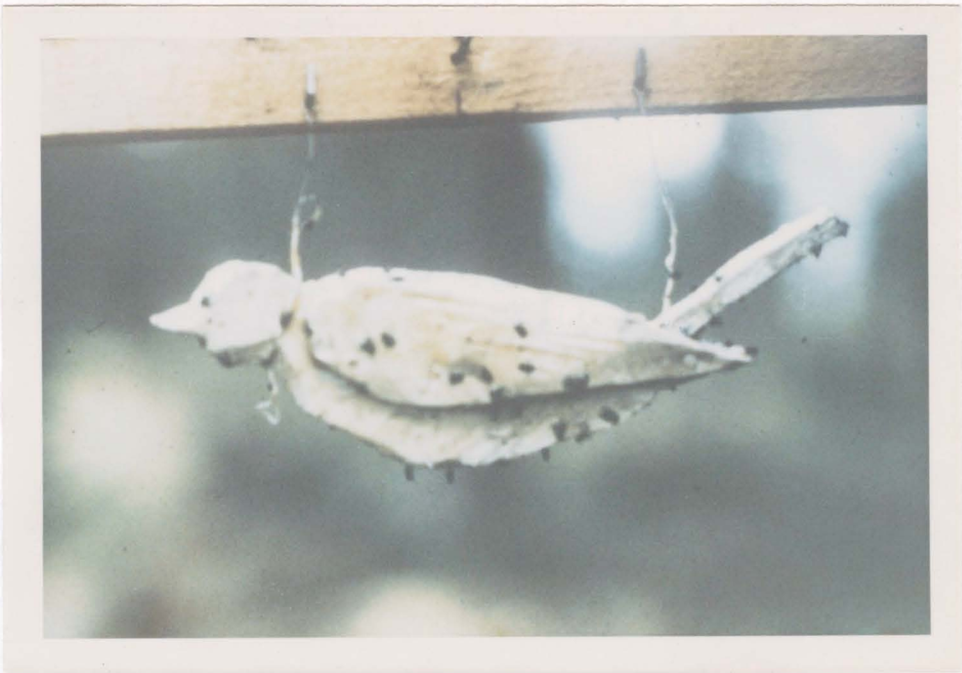


Fig. 10. White wooden bird-model used in relation to a similar black model in visual discrimination experiment. Simuliids are shown as black dots stuck on the Tanglefoot coated surface of the 6-inch long model.

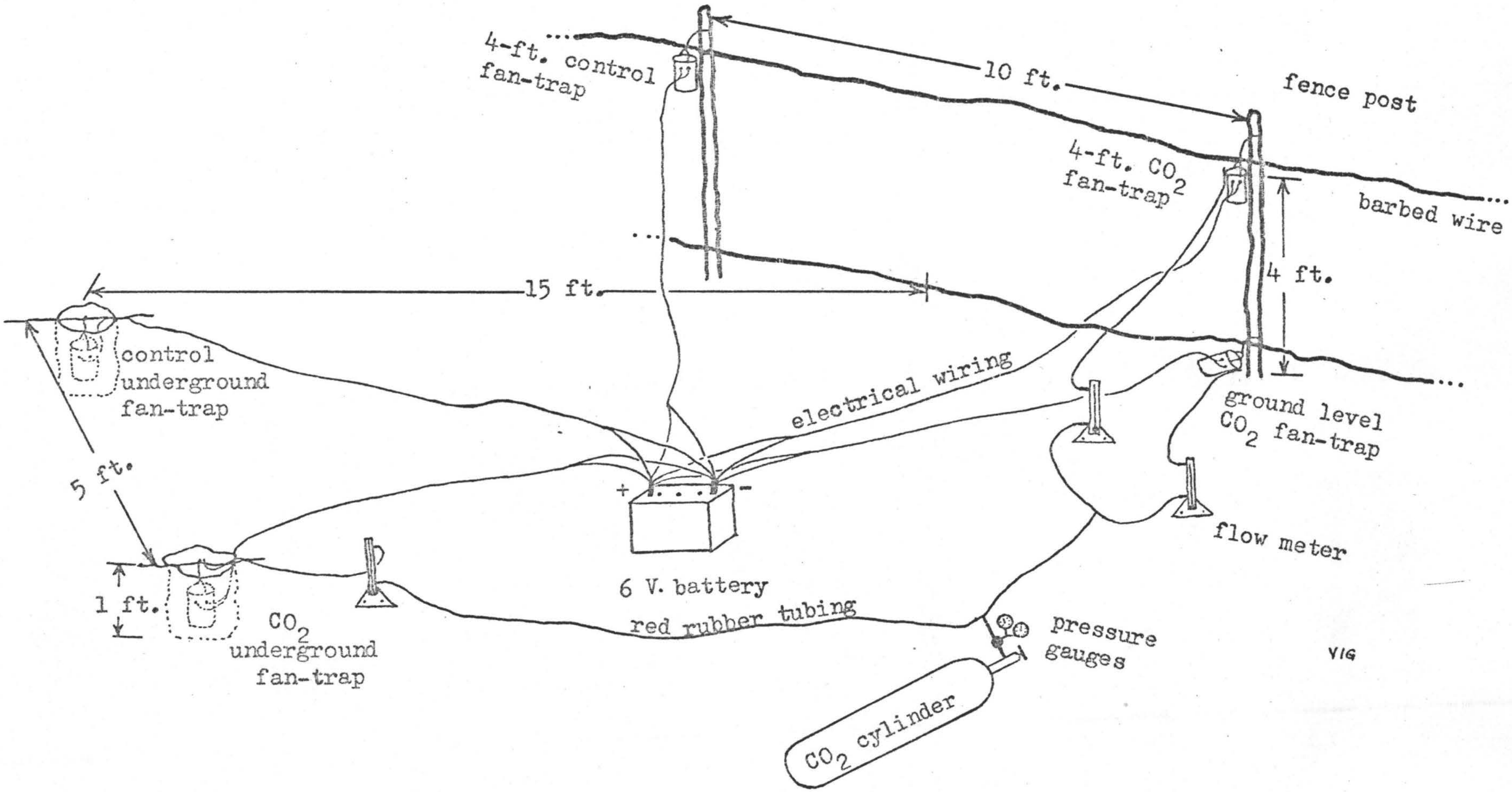


Fig. 11 Diagrammatic representation of the experiment designed to investigate the role of vision and olfaction of some simuliid species in locating a silhouette with and without carbon dioxide; Rendalen, Norway.

Fig. 12 Diagrammatic representation of the experiment designed to investigate the discrimination between a Large and a Small silhouette by some species of female simuliids at the main experimental site; Rendalen, Norway.

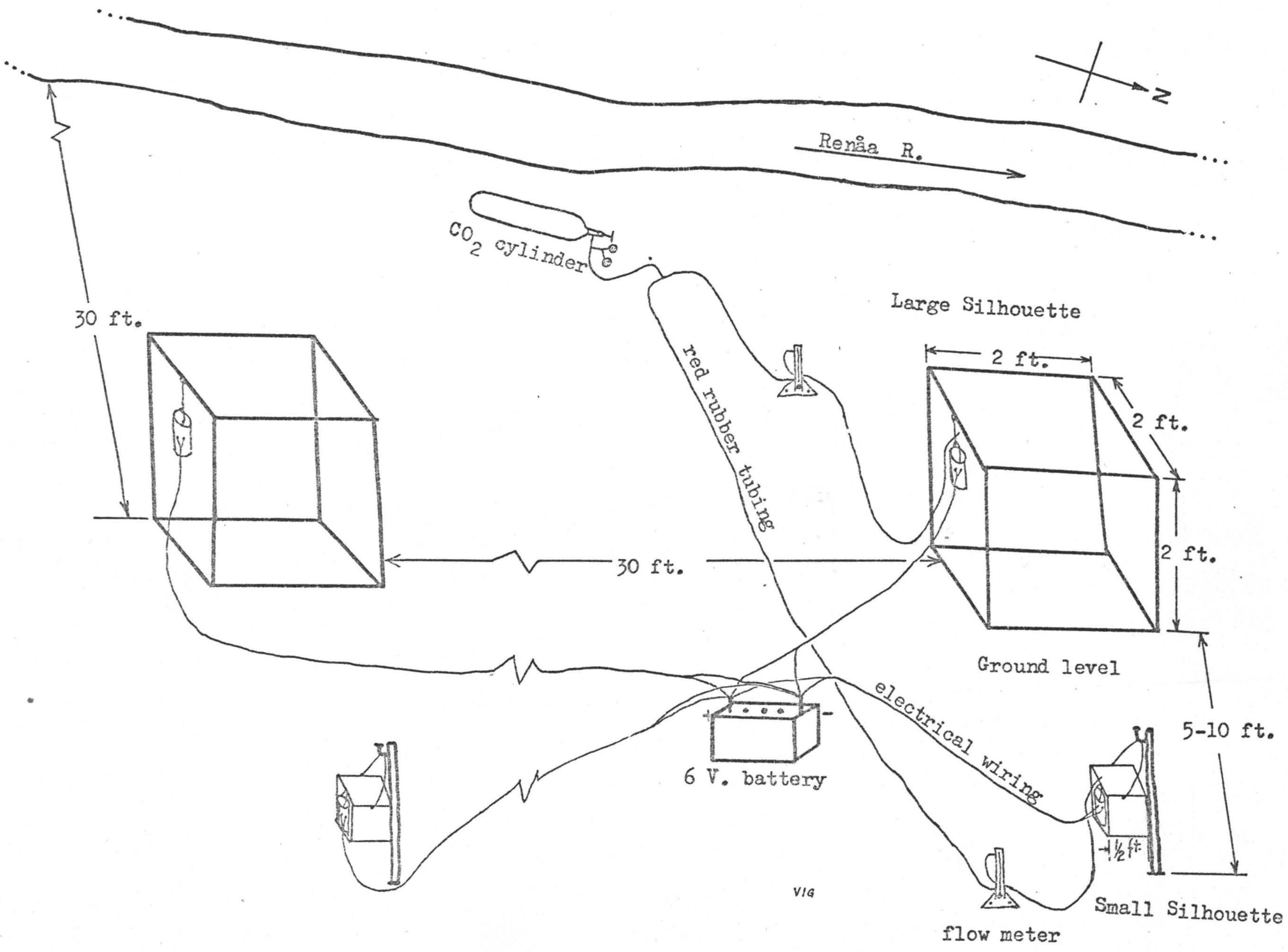
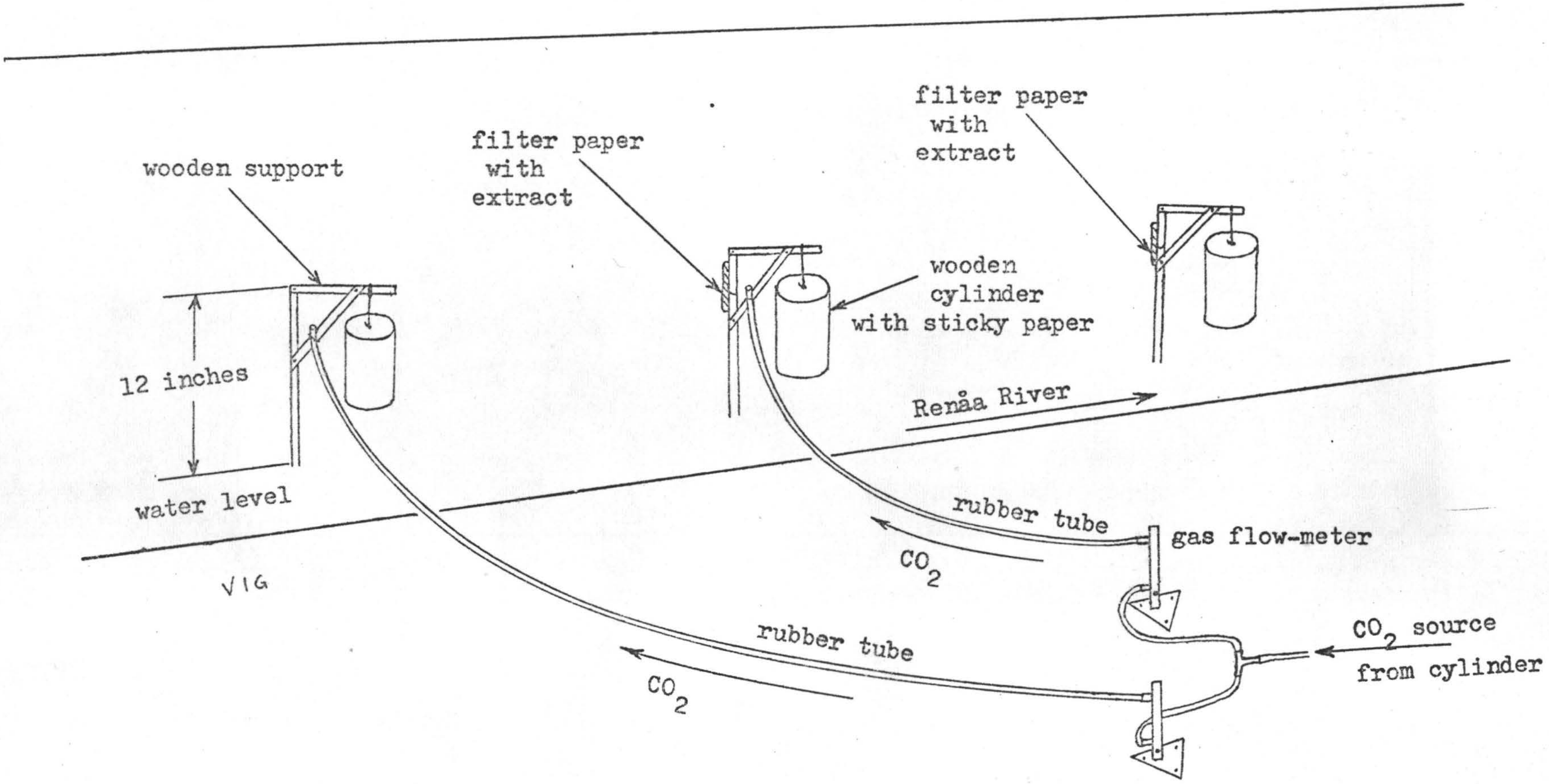

N
Renåa R.
CO$_2$ cylinder
30 ft.
red rubber tubing
Large Silhouette
2 ft.
2 ft.
2 ft.
V
V
30 ft.
Ground level
electrical wiring
5-10 ft.
6 V. battery
½ ft.
V/G
flow meter
Small Silhouette

Fig. 13 Diagrammatic representation of the experiment designed to investigate the attraction of female simuliids to carbon dioxide and uropygial gland extract of domestic ducklings, separately and in combination, on the Renåa river.



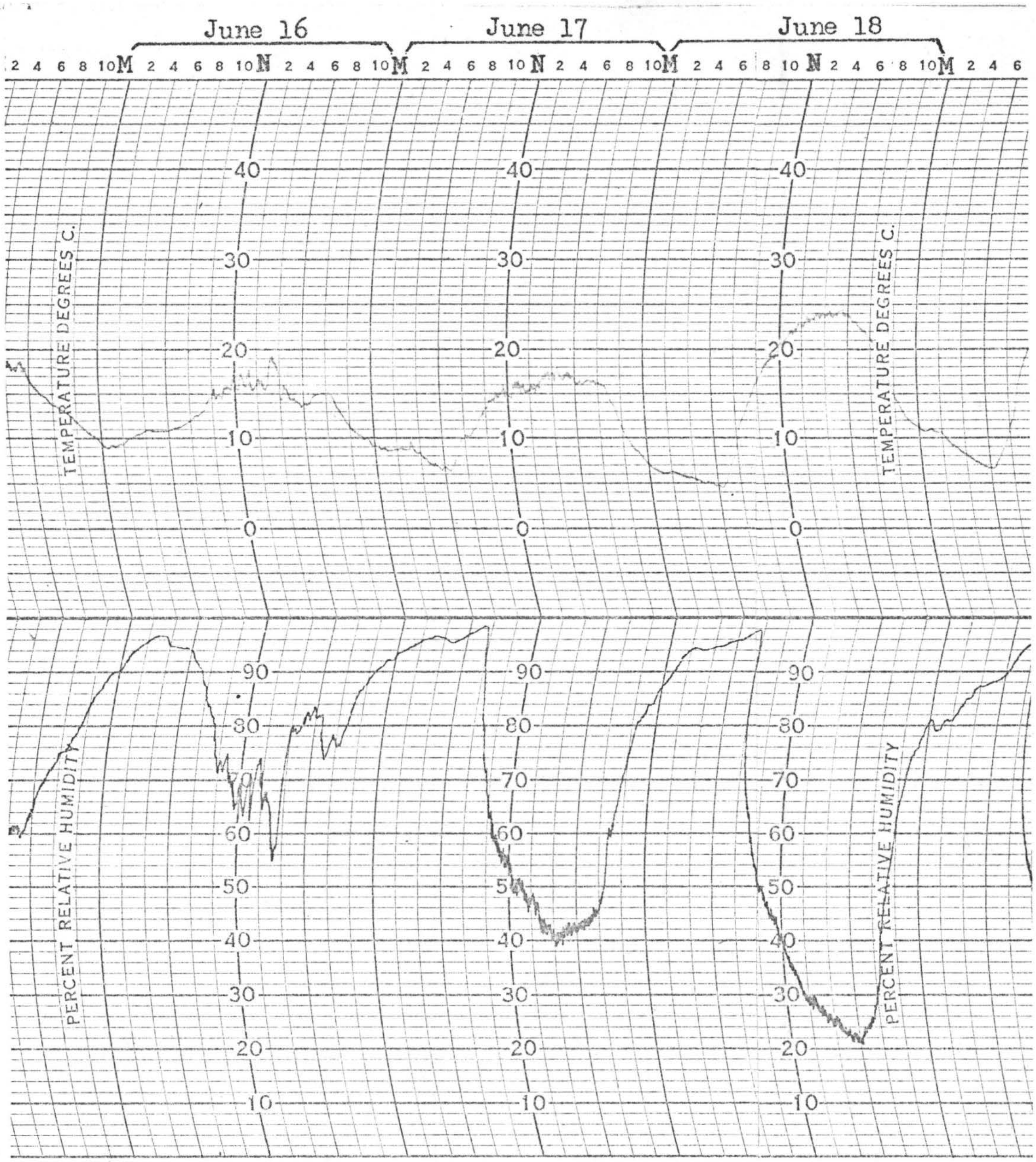


Fig. 21 Hygro-thermograph record for June 16, 17 and 18, 1966 taken at the Wildlife Research Station, Algonquin Park.

(M=midnight; N=noon)

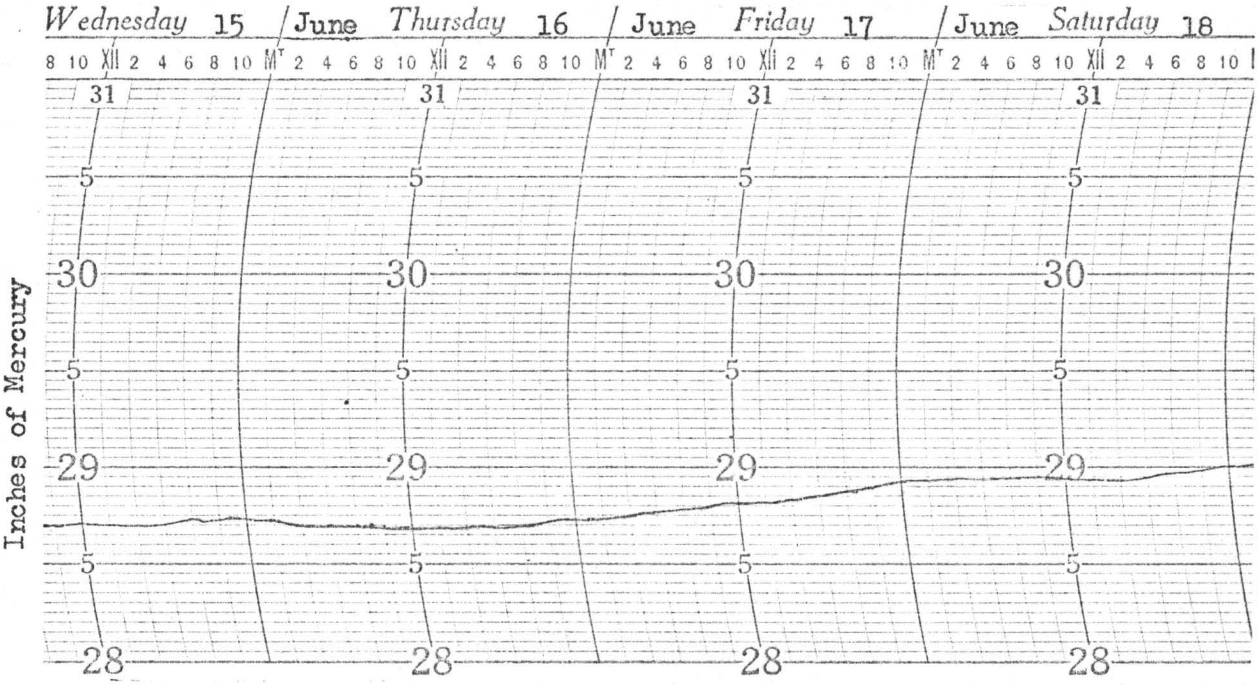


Fig. 22 Barogram for June 15, 16, 17 and 18, 1966, recorded at the Wildlife Research Station, Algonquin Park, Ontario.

APPENDIX B.

Notes on Identifications

Notes on Identifications

General considerations

The various simuliid species collected in the present work were identified with keys as indicated in the References section. Although specimens from Ontario were identified with little difficulty, those from Norway, especially the *Eusimulium* group, presented relatively greater difficulty. Consequently, the *Eusimulium* species collected in Norway in 1967 were placed in various groups, e.g. *E. latipes-beltukovae*, and only in the 1968 collection were these segregated and identified to species. The majority of the *Simulium* species collected with the CO_2-baited traps in 1968 were originally identified as the comlex *S. vulgare-tuberosum* because of the difficulty of separating the two morphologically identical species, *S. vulgare* Rubtzov and *S. tuberosum* (Lundstrom). However, L. Davies *et al* (1962) have caught *S. tuberosum* (Lundstr.) feeding frequently on man and cattle in Scotland, but *S. vulgare-tuberosum* was rarely if ever caught feeding on these hosts in Norway. These evidences, together with the now-known very low flying habit of this species-complex, point to *S. vulgare* Rubtzov as the likely species comprising this morphological complex.

Of the duck-feeding *Eusimulium* sp. 1 only adult females were collected in 1968, and these could not be identified as belonging to any described simuliid species. However, based on morphological characters of the female, this species has been associated with each of the following three related groups: *annulum* (Lundstr.) of Rubtzov, 1964; *hellichia* End. of Ussova, 1961; ***rivuli*** **Twinn**, of Wood, 1962. In this respect, females of *Eusimulium* sp. 1 have been compared to *S. dogieli* Ussova and *S. anatinum* Wood but they differ from these in some morphological features (Figs. 29-35). Because of these differences a description of the female of this species is given below, and its obvious diagnostic features have been compared with those of *S. dogieli* Ussova to which it is more closely related morphologically and ecologically (see Ussova 1961, pp. 77-80) than to *S. anatinum* Wood

The description of this simuliid species is based on specimens preserved for about 12 months in 70% ethanol and from others which were then removed from this preservant and pinned using the method of Vockeroth (1966). The species name is derived from the type locality, Rendalen region, from which the female specimens were collected.

Figures 29-35 were prepared from a female specimen after it was cleared with 10% KOH for about 24 hours at room temperature; the various parts of this specimen were then reproduced using the method of Wood *et al* 1963, p. 103.

Description of *Simulium* (*Eusimulium*) *rendalense* new species

Female: Small (2.3-3.0 mm) dark-brown covered with short silvery hairs.

Head: Frons narrow (0.07-0.08mm wide at its narrowest part, 0.12-0.16mm long). Clypeus and frons grey pollinose with recumbent silvery hair. Antennae light-brown (0.4-0.5mm long) densely covered with short silvery hair; Palps. segment 3 twice as long as wide (0.10-0.11 mm long; 0.04-0.05 mm wide), nearly the lenght of the fourth segment but one-half that of the fifth.

Thorax: Scutum dark brown with recumbent short silvery hair. Scutellum dark brown with long silvery hair. Halteres white. Pleuron light brown. Pleural tuft and hair on pronotum and proepisternum silvery. Precoxal bridge well developed. Base of costa with golden hairs, the rest covered with spinules interspersed among fine dark hairs. Stem vein, dorsal surface of radius and ventral surface of subcosta with dark hair. Ventral surface of radial sector with a double row of fine dark hair.

Coxa and legs brown, with silvery hair. Tarsi covered with dark hair interspersed with spinules. Hind tibia 5 times longer than wide (0.6-0.7 mm long; 0.12-0.14 mm wide). Metatarsus of hind leg almost 6 times longer than wide (0.50-0.58 mm long; 0.08-0.1 mm wide) with a small calcipala about 1/3 the width of the segment at distal end. Base of second segment of tarsus of hind leg light-coloured; pedisulcus shallow, with transverse ridges and usually covered with brownish hair. Claw with large thumb-like basal lobe.

Abdomen dark-brown, covered with short fine silvery hair. Fork with long thin stem (0.14-0.20 mm long) and width between arms 0.06-0.08 mm. Anal plates triangular (0.09-0.11 mm long; 0.06-0.07 mm wide) covered with long hair at the posterior margin. Cerci rounded apically (0.06-0.07 mm long; 0.06-0.07 mm wide) uniformly covered with long dark-brown hair.

S. (E.) dogieli Ussova

Redrawn from Ussova 1961

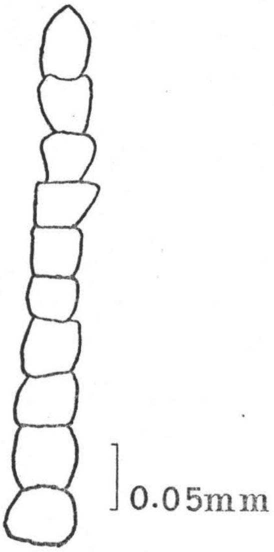


Fig. 29

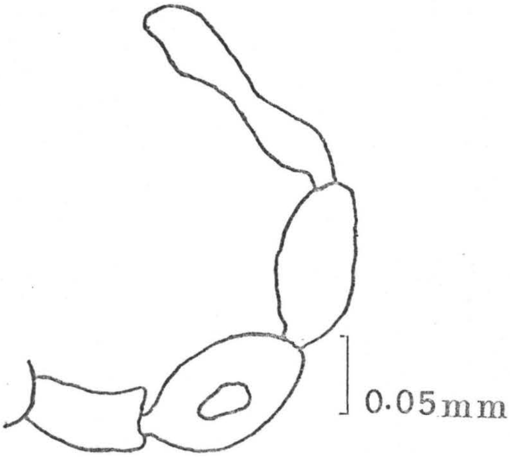
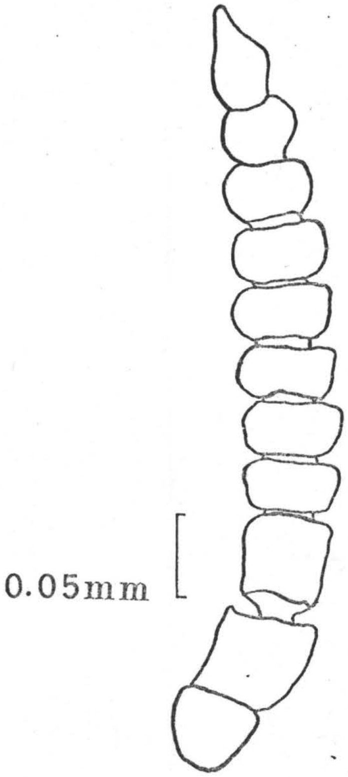
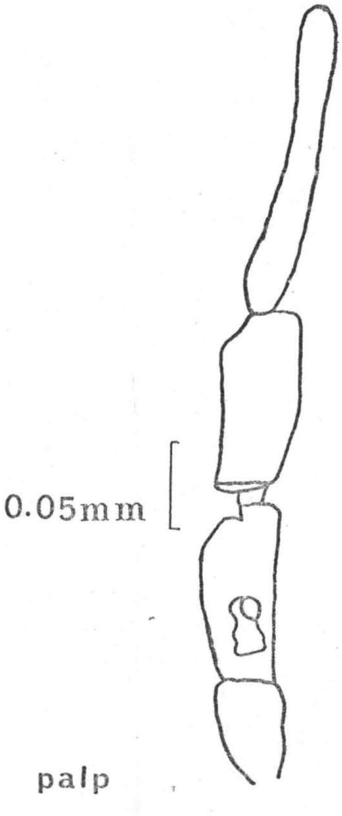


Fig. 30

S. (E.) rendalense new species



antenna



palp

S. (E.) dogieli Ussova

Redrawn from Ussova 1961

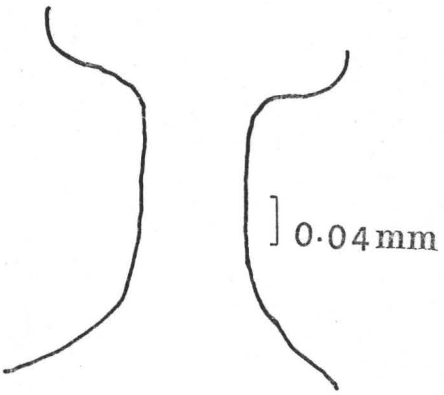


Fig. 31

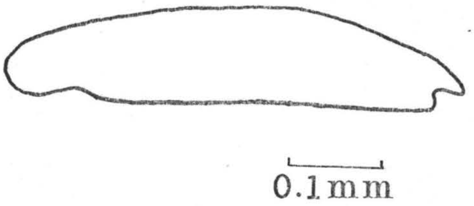


Fig. 32

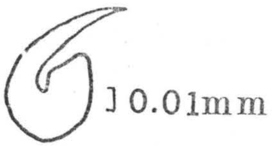
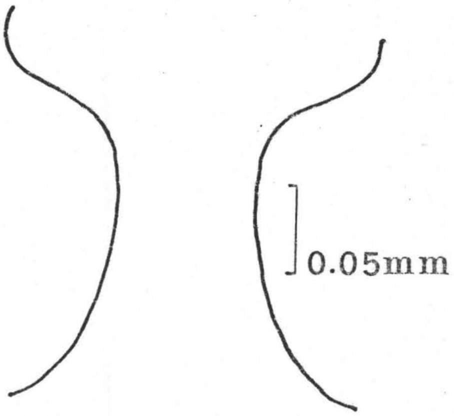
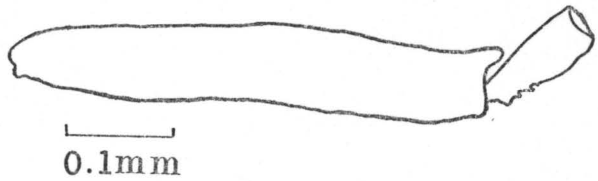


Fig. 33

S. (E.) rendalense new species



frons



metatarsus of hind leg

tarsal claw

S. *(E.)* *dogieli* Ussova

Redrawn from Ussova 1961

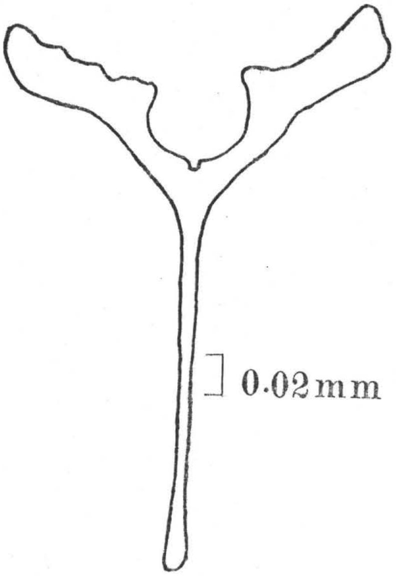


Fig. 34

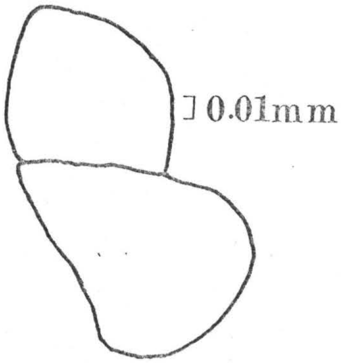
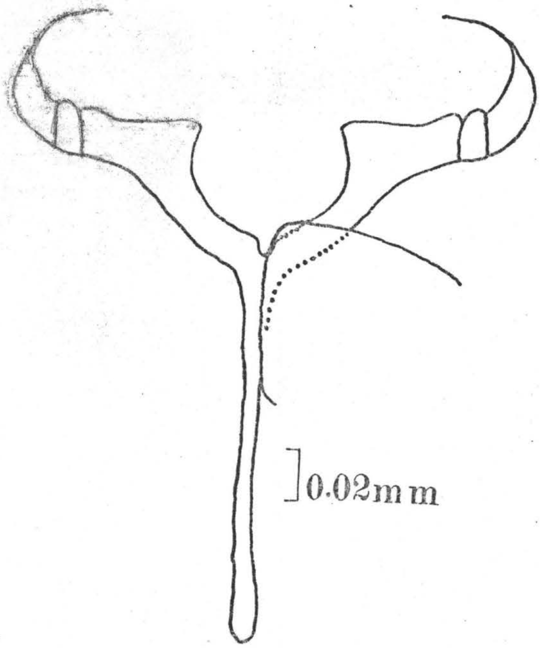
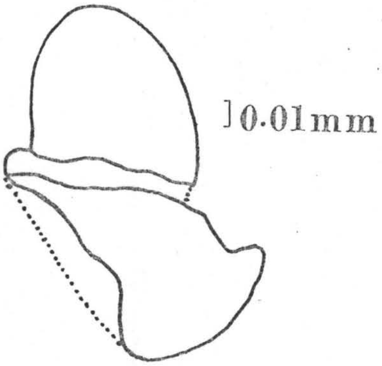


Fig. 35

S. *(E.)* *rendalense* new species



genital fork



cercus and anal lobe

APPENDIX C.

Additional Tables

TABLE 40

Correlation of the distribution of Simuliidae at the three levels above ground in the forest, calculated from the total number of each species reported at the bottom of Table 2.

Species of Simuliidae	*Probability Values		
	p^a	p^b	p^c
P. decemerticulatum	< 0.001	< 0.001	< 0.001
E. aureum	< 0.001	0.02 - 0.01	< 0.001
E. eroxtoni	< 0.001	1.0	< 0.001
E. latipes	0.02 - 0.01	< 0.001	< 0.001
E. quebecense	< 0.001	< 0.001	< 0.001
S. venustum	< 0.001	< 0.001	< 0.001

*p^a - Between 12 and 25 ft. levels.

p^b - Between 12 and 50 ft. levels.

p^c - Between 25 and 50 ft. levels.

TABLE 41

Correlation of the number of Simuliidae collected under various conditions as reported on Table 19, A and B.

Species of Simuliidae	Probability values*		
	p^a	p^b	p^c
P. hirtipes	0.02 - 0.01	0.02 - 0.01	-
Cn. pallipes	<0.001	<0.001	<0.001
Eus. beltukovae	<0.001	<0.001	<0.001
Eus. bicorne	<0.001	0.2 -	<0.001
Eus. curvans	-	<0.001	<0.001
Eus. latipes	<0.001	<0.001	<0.001
Scho. pusilla	<0.001	<0.001	<0.001
Gnus rostratum	<0.001	<0.001	<0.001
Simulium spp.	<0.001	<0.001	<0.001
S. vulgare-tuberosum	<0.001	<0.001	0.5

* p^a with a silhouette, with and without CO_2 at 4ft. above ground.

p^b with a silhouette and with CO_2, at ground level and 4ft. above ground.

p^c with CO_2 underground and at ground level.

TABLE 42

Correlation of the number of female Simuliidae collected with sticky models under various conditions as reported in Table 26.

Species of Simuliidae	*Probability values		
	p^a	p^b	p^c
Cn. pallipes	< 0.001	< 0.001	< 0.001
Eus. sp.1	< 0.001	< 0.001	< 0.001
S. vulgare-tuberosum	0.5 - 0.2	< 0.001	0.01-0.001

*p^a between models with CO_2 only and CO_2 + extract.

p^b between models with CO_2 + extract and extract only.

p^c between models with CO_2 only and extract only.

TABLE 43

Correlation of the distribution of the number of female Simuliidae collected from each model compared to that at water level as reported in Table 37.

Species of Simuliidae	*Probability values		
	p^a	p^b	p^c
Cn. pallipes	<0.001	< 0.001	0.5 -
Eus. aureum	0.2	< 0.001	0.8
Eus. beltukovae	< 0.001	< 0.001	0.2
Eus. bicorne	0.1	0.1	0.1
Eus. curvans	0.01	0.5 - 0.2	0.2
Eus. latipes	< 0.001	< 0.001	< 0.001
Eus. sp.1	< 0.001	< 0.001	< 0.001
Scho. pusilla	< 0.001	< 0.001	0.8
Gnus rostratum	0.8 - 0.5	0.5 - 0.2	0.01 - 0.001
S. vulgare-tuberosum	0.1	< 0.001	< 0.001

*p^a Between 0 and 4 ft. above the river.

p^b Between 0 and 7 ft. above the river.

p^c Between 0 ft. above water and at ground level 30 ft. from the river.

TABLE 44

Reflectance spectra taken from twelve samples of coloured oviposition strips. The values are expressed as per-cent reflectance as compared to a standard sample of magnesium carbonate which has an absolute reflectance of about 98% over most of the visible range.

Colour	Wavelengths in mµ																Average mµ			Ratio
	325	350	375	400	425	450	475	500	525	550	575	600	625	650	675	700	325-700	325-450	450-700	$\frac{450-700}{325-450}$
Black	4.5	4.1	3.2	3.5	3.5	3.4	3.4	3.2	3.2	3.0	3.1	3.1	-	4.0	-	3.5	3.6	3.9	3.3	0.8
Dark Grey	5.2	5.0	6.3	15.8	17.6	16.0	14.0	14.8	13.9	13.0	12.9	12.0	-	11.6	-	11.1	11.7	10.3	13.3	1.3
Light Grey	5.5	5.1	7.2	31.0	41.2	39.5	38.0	36.0	35.1	34.0	33.8	32.2	-	31.7	-	29.9	27.1	19.4	34.5	1.8
White	6.1	6.0	7.2	35.2	86.0	90.9	91.0	90.0	90.0	89.6	89.4	88.9	-	90.0	-	90.2	63.8	34.0	90.0	2.6
Red	6.5	6.9	10.0	35.1	45.0	42.9	40.4	38.2	40.0	33.1	38.0	63.9	-	85.2	-	86.6	38.5	21.8	52.0	2.4
Orange	5.1	5.0	6.0	10.0	10.0	10.0	9.8	13.9	20.0	20.1	23.0	44.0	54.1	58.3	61.2	62.0	24.6	7.4	34.2	4.6
Yellow	5.0	4.8	5.0	12.0	12.3	12.1	12.4	21.1	43.9	46.5	52.7	58.2	61.7	65.0	68.0	71.0	32.8	8.1	46.6	5.8
Green	6.3	6.0	7.0	15.0	16.9	16.9	17.8	28.8	51.5	42.0	32.5	26.5	23.8	24.0	25.0	25.9	22.0	10.7	28.6	2.7
Blue	6.8	6.3	8.2	26.1	42.4	47.9	59.9	63.6	55.0	44.1	34.7	28.0	23.5	23.1	24.0	26.2	31.0	20.7	39.1	1.9
Purple	7.2	7.0	8.9	29.9	46.0	42.8	38.9	34.9	31.0	29.0	28.1	31.9	35.0	37.8	42.1	47.0	30.0	21.3	36.2	1.7
White + tf*	3.9	3.7	6.9	30.7	88.6	92.0	91.5	91.1	90.8	90.5	90.1	89.9	91.0	89.9	90.0	90.0	66.8	-	-	-
Yellow + tf	3.3	3.3	4.8	10.5	11.0	11.0	11.4	17.0	43.7	45.8	50.9	58.1	61.0	63.5	66.2	69.0	31.4	-	-	-

*tf = strip sample coated with an even layer of Tanglefoot.