SOME ASPECTS OF HOST ORIENTATION AND SPECIES DISTRIBUTION OF TABANIDAE (DIPTERA) IN MANITOBA

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ABSTRACT

by

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The attractiveness of colored spheres was compared in the field for several tabanid species. Black and red spheres were highly attractive to all species. Two species, *Hybomitra illota* O.S. and *Chrysops mitis* O.S., were also attracted by grey and white spheres. The attractiveness of grey and white spheres for the other species decreased rapidly with increasing reflectance. Green and yellow spheres were unattractive for all species.

The effect of surface texture on the attractiveness of black horizontal cylinders was investigated. Glossy black cylinders were more attractive than matte cylinders; rugose cylinders were less attractive than smooth cylinders whether glossy or matte.

The phototactic responses of tabanids to light of different wave lengths at equal intensities were determined. Tabanids responded maximally at 405 mµ, the shortest wave length tested, and again at 515 mµ. The response fell off rapidly toward the red region of the spectrum.

Two-dimensional objects attracted only small numbers of tabanids. Three-dimensional objects which presented convex curvature in the vertical plane were two or three times more attractive than other silhouettes. Interpretations of these results are presented.

A black horizontal cylinder (height=diameter=41 cm) was more attractive to tabanids than smaller cylinders and equally attractive as the larger cylinders tested. The conjointness of the black area is important; if it is disjoint, as in a pattern of black and white stripes, it is much less attractive.

Neither the motion of a body, nor its surface temperature, significantly influenced its attractiveness under the field conditions of the experiments.

The seasonal and geographic distribution of Tabanidae in southern Manitoba was studied on the basis of captures of tabanids in Manitoba fly traps. One species of *Atylotus*, one of *Haematopota*, two of *Tabanus*, four of *Chrysops* and eleven of *Hybomitra* were captured. The seasonal and geographical distribution of each species is described.

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CHAPTER I

INTRODUCTION

The Tabanidae are a family of the suborder Brachycera (Diptera) of which some 335 species have been identified in North America. Several common names such as "horse flies", "deer flies", "bulldogs", "gadflies" and "greenheads" have been given them but, of these, only the names "horse flies" and "deer flies" are officially recognized by the Entomological Society of North America. While representatives of the family are found generally throughout the continent, the populations are highest where areas of moist soil occur, since this is the typical larval habitat.

The females of most species attack mammals to obtain a blood meal. Attacks of these flies on domestic cattle are often severe and are considered of economic importance since the annoyance of the attacks prevents the animals from grazing. While it is commonly believed that a blood meal is necessary for the development of the ovaries of the female fly there is no critical evidence for this.

It is known that aggregations of female tabanids are often found in automobiles or buildings. Taxonomists take advantage of this phenomenon to collect female specimens. The aggregations found in these structures occur as a result of the flies entering an open door or window and being apparently attracted to a closed window they are unable to escape. Arrival of the flies at the building or automobile may be a result of either random or orientated flight.

If there is no orientation then the insects encounter the structure simply because it intercepts their random flight path. The size of the aggregation produced in this manner would be entirely dependent on the amount of air space occupied by the object and no other property. The data to be presented later clearly indicate that this is not the case and we must accept the alternative that the insects orientate to certain structures or objects and are attracted by them.

Orientation implies perception of the object. The senses that might mediate perception of an object by horse flies include gustatory, tactile, olfactory, sonic, thermal, moisture and visual. The first two, gustatory and tactile, cannot pertain since they involve contact with the object and so could not contribute to orientation from a distance. Of the others, visual perception would seem likely since horse flies have well-developed eyes morphologically. Also, assessment of the visual properties of an object would permit orientation at some distance since horse flies are strong fliers and have an appreciable flight range.

If an object is to be perceived visually, it must produce a different visual imput to the insect's eye than its surroundings. It can do this by reflecting light quantitatively or qualitatively in a different manner than the background. It follows that if the object reflects light in exactly the same manner as the background no discrimination is possible and therefore no visual orientation is possible. It must be remembered, however, that the visual contrast offered by an object against the background as seen by man or as measured by instruments is not necessarily that which it provides to the insect eye. Furthermore, while orientation implies perception, perception does not necessarily imply orientation.

It is pertinent to consider what behaviour pattern of horse flies is being represented by their orientation to objects. Two possibilities may be suggested: (1) the object serves as a swarm marker, and (2) the object simulates a host. With regard to the first it may be said that swarms usually occur above objects, whereas if a sticky black or red object is provided for horse flies they become entangled on it in large numbers. The second hypothesis is more likely, since only females are captured on such objects and only they feed on blood. It will be assumed, therefore, that objects simulate hosts and when tabanids orient to them they are engaged in host-seeking behaviour.

The host orientation of Tabanidae has not been extensively studied and mention of it has usually occurred in connection with taxonomic surveys or economic reports. In some instances traps have been used to assess adult population densities but little investigation of behavioural mechanisms has been carried out. The study of orientation behaviour of adult tabanids is difficult to conduct under laboratory conditions due to space limitations. Field observations are hampered by the fact that the observer himself is a significant component in the perceptual field.

A device for the successful trapping of aggregations of flies about an object was developed by Thorsteinson (1958). By providing a visual target and altering its physical properties it was possible to investigate the influence of these properties on the orientation of tabanids in an objective manner.

The properties of an object that affect visual perception and attraction are most extensively investigated in this thesis. Some attention has also been given to the possible importance of thermal factors. Throughout the study it has been kept in mind that the orientation behaviour of all species may not be the same. Where possible, species have been identified and individual variations in behaviour compared.

The thesis is based chiefly on field data obtained from investigations carried out during the summers of 1960 and 1961. In 1960, experiments were conducted in a semi-wooded swampy area ten miles east of St. Laurent, Manitoba, about sixty miles northwest of Winnipeg. The drought during these years apparently reduced the populations of horse flies in this area. In 1961 experiments were conducted in the vicinity of Beaver Creek on the west shore of Lake Winnipeg, 120 miles north of Winnipeg, where permanent swamps support large numbers of tabanids.

The thesis is divided into chapters, each dealing with a single topic or topics best considered together. Chapter VII deals with the seasonal and geographical distribution of Tabanidae in southern Manitoba. It presents data obtained from the results of a survey based on the operation of the Manitoba fly trap in widely separated locations in the province. Literature and the methods of investigation pertinent to the subject matter are given at the beginning of each chapter. Discussion of results is also included in each chapter and the summary and conclusions make up Chapter VIII.

CHAPTER II

THE ORIENTATION OF TABANIDAE TO OBJECTS OF DIFFERENT COLOR AND REFLECTANCE

Review of the Literature

The importance of the reflectance of objects for insect vision has been studied in many insects but true color vision has been confirmed in only a few. Von Frisch (1914) demonstrated color vision of the bee and this has been confirmed more recently by Daumer (1956). In addition to the wave lengths seen by man the bee also is capable of perceiving ultraviolet radiation. Mazokhin-Porshnyakov (1959) determined the ultraviolet reflection of several flowers and showed how it could play a significant role in the orientation of bees and other insects to these objects. Weiss (1946) made an extensive review of the literature and concluded that the intensity of reflected light was more important in evoking behavioural reactions than the wave length.

The importance of reflectance and color in the orientation of mosquitoes to hosts has been studied by Gjullin (1947) and more extensively by Brown (1954). These authors found that the colors black, blue and red were the most attractive and yellow and white the least attractive. Generally, they found that the attractiveness of an object was related inversely to the intensity of reflected light but apparently not in a simple quantitative way to the wave length. Brown (1954) found no correlation between ultraviolet reflection nor infra-red radiation and attractiveness. Sippell and Brown (1953) noted also that enamel surfaces were more attractive to the female Aedes mosquito than were matte surfaces of the same color.

Davies (1951) made observations on the number of black flies landing on different colored cloths. His results were similar to those of Brown (1954) except that dark green was attractive to black flies whereas Brown (1954) stated that his dark green was unattractive to Aedes. Hocking and Richards (1952) also observed the landing rates of black flies on clothing fabrics of different color. They found that black flies were attracted to blue serge more frequently than other colors and also found no correlation between attractiveness and ultraviolet reflection. Peschken (1960) found that black flies were attracted to dark colors during host orientation behaviour but found that when the flies were seeking substrates in the water at dusk for oviposition, higher reflecting colors, notably green and yellow, were the most attractive.

Harris (1938) stated that the tsetse fly depends on "sight and visual impression for the location of its food." He constructed a trap which apparently simulated the host and was highly effective for the capture of the tsetse. A modified version of this trap was constructed by Morris and Morris (1949). These workers found that a light brown or khaki covering was slightly superior to black and that a rough surface was superior to a smooth surface. They found also that the trap was more effective in sunny situations, presumably because here it provided more contrast to the surrounding vegetation. Barrass (1960a) found that the tsetse prefers to settle on the darker of two screens and on the sunny rather than the shady side. Waterhouse (1948) observed that the house fly, Musca domestica L. prefers to rest on red or black surfaces.

The importance of the color and reflectance of objects for the orientation of Tabanidae has received little systematic investigation. Philip (1931), Hansens (1952), Tashiro and Schwardt (1953) and Bromely (1952) have noted that dark cattle were more readily attacked by tabanids than white cattle. Philip (1931) observed that tabanids tended to investigate any dark object in the field and that they were attracted in large numbers to a motor car. Snow (1957) and Pechuman (1961) mention that vehicles are excellent for trapping female tabanids. Pechuman (1961) states further that darker vehicles appear to be more effective for this purpose.

Hansens (1947) observed that "greenheads" (Tabanus nigrovittatus Marq.) were attracted to dark colored objects in larger numbers than to light ones. He employed 2 $ft.^2$ shingles painted black and covered with sticky material to trap this species. Brown and Morrison (1955) assessed tabanid populations by noting their landing rates on tents of black cloth. Miller (1951) obtained data for the diurnal activity of horse flies by leaving the door of a dark green shed open for fifteen minutes of every hour and collecting the flies that entered. Barrass (1960b) showed that the tabanid Haematopota insidiatrix Aust. settled on black screens more frequently than on lighter-colored screens and that the attractiveness of a screen was reduced if a white area was superimposed upon part of it. A trap for the population estimation of European tabanid species was designed by Skuffin (1951). This consisted of a wooden frame covered with a blanket. Skuffin (1951) stated that a dark blanket or "any other color" was suitable for the cover. Trojan (1956) however used a similar device and mentions the use of black material for the trap cover.

From reviewing the literature it appears that generally the intensity of reflected light is more important than color of objects for the orientation of biting flies. Ultraviolet reflection from objects has not been found to be a significant factor in the orientation of either mosquitoes or black flies to objects under photoptic conditions.

The orientation of Tabanidae to spheres of different color and reflectance (St. Laurent, 1960)

Methods and materials. Paint pigments were obtained from the Sherwin-Williams Paint Company in Winnipeg. The pigments obtained were black, violet, blue, red, green, yellow and white. The company also provided the spectrophotometric characteristics of these pigments and these are listed in Table I. The color characteristics were obtained by means of a color-eye spectrophotometer and all readings

TABLE I

SPECTROPHOTOMETRIC CHARACTERISTICS (REFLECTANCE VALUES) OF THE VARIOUS PIGMENTS USED IN THIS STUDY (SHERWIN-WILLIAMS PAINT CO.)

Colour and pigment no.	White 6631	Black 7055	Green 78G9	Yellow 80G25	Blue 76G18	Red 86G28	Violet 76G20
Wave length millimicrons							
220-330	9.45-11.25		3.70-5.95	2.90-6.00	3.00-7.65	2.95-7.20	3.95-7.70
400	52.20	1.95	1.95	2.29	1.21	1.43	30.01
433	81.76	1.90	2.20	2.62	1.15	1.51	34.79
467	85.07	1.93	4.44	2.98	1.15	1.76	26.87
500	86.93	1.93	16.41	12.45	1.14	1.96	18.32
533	88.17	1.95	15.55	53.49	1.20	1.86	15.09
567	88.39	1.95	8.97	81.46	1.17	3.48	14.89
600	88.32	1.93	6.30	84.13	1.16	13.59	16.59
633	88.17	1.95	4.37	82.92	1.16	50.28	27.72
667	88.22	1.94	3.54	84.97	1.18	71.00	41.76
700	88.68	1.95	3.26	85.18	1.18	77.73	42.03
Tot. brightness or reflectivity*	835.91	19.38	66.99	492.49	11.70	224.60	268.07

*Does not include ultraviolet reflectance 222-330 mµ.

are relative to magnesium oxide which is the absolute reference standard for reflectance comparisons.

It will be noted that none of the pigments approach spectral purity. This is especially true of the violet which shows a maximum reflectivity at 433 mμ and at 700 mμ with a low point at 533 mμ. Furthermore, the total reflectance of the blue pigment is actually lower than that of the black, although readings of the Weston light meter (Model 756) show the black to be of lower reflectance than the blue. In any case the spectral characteristics of both blue and black are so close that they may best be considered equivalent and this unfortunately leaves a gap in the color series in the blue region.

A series of greys was now prepared to match the reflectance of each color. This was done by mixing appropriate portions of the black and white pigments, painting the resultant mixtures on a suitable surface and comparing their reflectance to the color in question by the Weston light meter. The final mixture was painted on the actual sphere and readings were taken in a dark room under the illumination of a 200 watt flood lamp set at 45 degrees from a point on the surface of the sphere at a distance of 1 meter. The sensing element of the meter was placed 31 cm from the same point on the sphere and the readings noted in foot candles. The results of this procedure are entered in Table III under the reflectance column. Here the reflectance of the white sphere is taken as 100 per cent and the other readings are relative to it. The grey shades are designated by the color whose reflectance they match followed by a vertical stroke superscript. For example the grey corresponding to the red in reflectance is designated grey (red'). All of the pigments had the same oil base and when dry presented a glossy surface.

The reflectance of ultraviolet light for the pigments was also determined by the Sherwin-Williams Paint Company. Apparently ultraviolet light decomposes the oil vehicle of the paint resulting in strong absorption of U.V. The company overcame this by mixing the pigments with volatile aliphatic hydrocarbons and measured the U.V. reflectance after the vehicle had evaporated. This preparation insured the maximum reflectance of U.V. The highest per cent-reflectance under these conditions was 5.95 for the yellow and 11.25 for the white. Since these determinations were done under optimum conditions it can be assumed that under the field conditions of the experiments the U.V. reflectance was much lower, inasmuch as the oil base absorbs most of the ultraviolet. Therefore the data do not provide information about the influence, if any, of U.V. on visual orientation of horse flies to objects.

Spherical shapes were used in this experiment in the form of a polystyrene balloon inflated to 56 cm. in diameter. Two coats of the paint were applied to each and the spheres were then suspended from the tripod of a Manitoba fly trap.

The center of the sphere was about 76 cm. from the ground. Twelve traps were used to accommodate the painted spheres which included each color, a grey sphere of corresponding reflectance. and one black and one white. The traps were positioned on the periphery of a circle 15 meters in diameter and 3 meters from each other. The positioning of the traps is illustrated in Figure 1.

The different spheres were changed in the trap positions according to a random distribution table and each new set of positions was considered a replicate. A replicate was considered complete when about 70 flies were captured in the trap supporting the black sphere. The time required for the completion of a replicate varied from one to four days during the population peak up to a week during August when the numbers of flies began to decline. At the termination of each replicate the flies were removed, counted and classified to species. Eleven replicates were completed and the five species which were captured in the highest number were analysed separately after the data were transformed by the formula log x + 1 to obtain a more normal distribution (Snedecor, 1961).

Results. The numbers of the individual species captured and the per cent of each of the total is presented in Table II. In the complete experiment 2,745 specimens of Tabanidae were captured with Hybomitra illota O.S. making up the greater part of this number. The remainder included, in

Figure 1. Traps supporting spheres of different color and reflectance at St. Laurent, Manitoba, 1960.

TABLE II

TOTAL CAPTURES OF TABANID SPECIES IN TRAPS WITH SPHERES OF DIFFERENT COLOR AND REFLECTANCE AT ST. LAURENT, MANITOBA, 1960

Species	Total for species	Per cent of all captures
Hybomitra illota O.S.	1989	72.46
Tabanus similis Marq.	243	8.85
*Hybomitra frontalis** Walk.	178	6.48
Hybomitra epistates O.S.	104	3.79
Hybomitra lasiophthalma Macq.	102	3.72
Hybomitra nuda McD.	25	.91
Hybomitra liorhina Philip	29	1.06
Chrysops aestuans Wulp.	70	2.55
Atylotus incisuralis Macq.	1	.04
Unidentified	4	.15
Total	2745	

*includes subspecies *H. frontalis septentrionalis* order of number, *Tabanus similis* Marq., *Hybomitra frontalis* Walk. (which also included the subspecies *H. frontalis septentrionalis*), *H. epistates* O.S., *H. lasiophthalma* Marq., *H. nuda* McD., *H. liorhina* Philip, *Chrysops aestuans* Wulp. and *Atylotus incisuralis* Macq.

The transformed means together with the least significant differences are presented in Table III for the five predominant species captured in this experiment. There was no significant difference among the captures of all species in traps with the black, blue, grey (blue') and the red sphere and all species were captured in traps with these spheres in relatively high numbers. None of the species were captured in significant numbers in traps with the yellow or green spheres. For four of the species, traps with the red sphere captured significantly more flies than traps with the grey (red') sphere. However, for *H. illota* there was no significant difference between captures in traps with these two spheres.

H. illota was captured in nearly equally high numbers in all traps with the grey and white spheres. Traps with the grey (green') and the grey (violet') were the only ones, with the exception of yellow and green, that captured significantly fewer numbers of *H. illota* than the black. None of the traps with grey or white spheres captured significantly more of the other species than traps with the colored spheres which matched their reflectance. A graphic illustration of this difference

TABLE III

TRANSFORMED MEANS* OF CAPTURES OF TABANIDAE IN TRAPS WITH COLOURED SPHERES

Colour	Reflectance**	T. illota O.S.	T. similis Macq.	H. frontalis Wlk. (complex)	H. epistates O.S.	H. lasiophthalma Macq.
Black	6.0	1.28	0.52	0.34	0.51	0.36
Blue	9.0	1.40	0.73	0.50	0.46	0.35
Grey (Blue')	9.0	1.29	0.73	0.41	0.50	0.26
Green	17.0	0.32	0.03	0.11	0.00	0.00
Grey (Green')	18.0	0.91	0.19	0.10	0.03	0.13
Red	34.0	1.09	0.43	0.34	0.21	0.26
Grey (Red')	33.0	1.04	0.05	0.03	0.08	0.00
Violet	35.0	0.78	0.07	0.00	0.00	0.00
Grey (Violet')	39.0	0.91	0.05	0.05	0.05	0.00
Yellow	75.0	0.08	0.00	0.00	0.00	0.03
Grey (Yellow')	70.0	1.16	0.10	0.00	0.00	0.05
White	100.00	1.17	0.03	0.00	0.00	0.00
L.S.D.(01)		0.37	0.25	0.25	0.16	0.23

* log x + 1 transformation

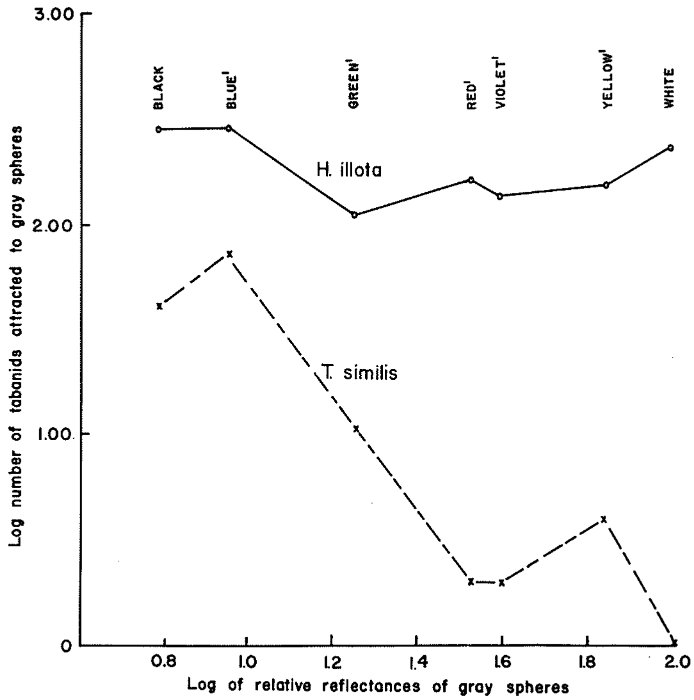
** measured with Weston light meter, Model 756, expressed as percentage of reflectance of white sphere.

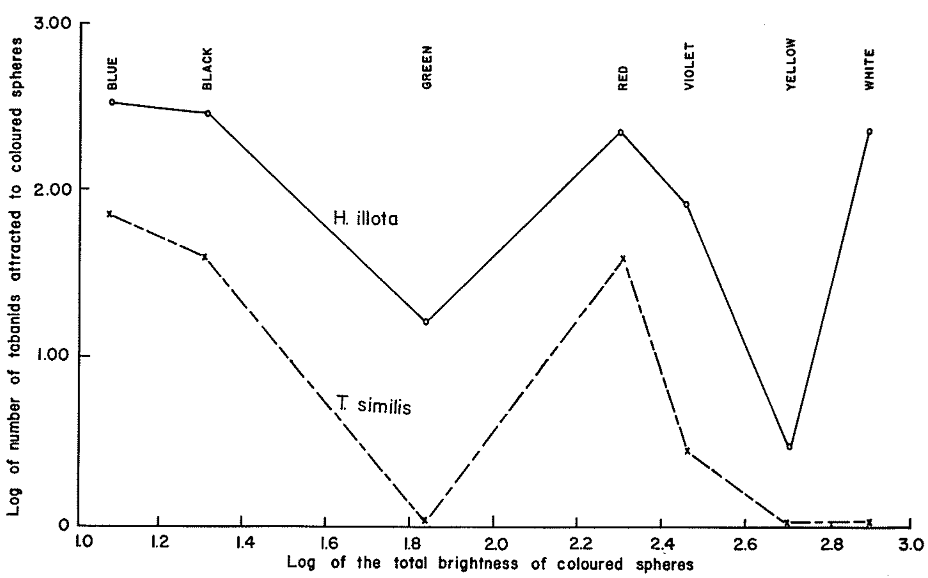
in behaviour is presented in Figure 2a. Captures in traps with the grey spheres and the black and white spheres are compared for *H. illota*, the exceptional species, and *T. similis* which is typical of the other predominant species. With respect to color, the captures in traps bearing the colors were similar for all species except that white was attractive to *H. illota* but not to the others. Captures for the same two species in traps with the colored spheres and the black and white spheres are shown in Figure 2b.

Discussion. As pointed out in the introduction, the visual perception of an object depends on the fact that it reflects light in a different manner than the background. All of the objects (as will be shown later) had a reflectance, as measured by a Weston light meter, equal to or greater than the background. The phenomenon of physiological brightness must also be considered and it is possible that to the horse flies some of the objects appeared darker than the background. Within the terms of this concept it may be conjectured that the most attractive objects, e.g., black, blue and red, may have been physiologically darker than the background. Von Frisch (1950) has shown that the bee does not distinguish yellow from green nor red from black or dark grey. Although no precise data are available pertinent to physiological brightness in tabanids, this factor must be taken into account as an alternative to explanations that involve color vision.

Figure 2a. Log total captures of *H. illota* and *T. similis* in traps with spheres of different reflectance.

Figure 2b. Log total captures of *H. illota* and *T. similis* in traps with spheres of different color including black and white.


3.00
2.00
1.00
0
BLACK
BLUE'
GREEN'
RED'
VIOLET'
YELLOW'
WHITE
H. illota
T. similis
Log number of tabanids attracted to gray spheres
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Log of relative reflectances of gray spheres


3.00
2.00
1.00
0
BLUE
BLACK
GREEN
RED
VIOLET
YELLOW
WHITE
H. illota
T. similis
Log of number of tabanids attracted to coloured spheres
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
Log of the total brightness of coloured spheres

For most species only those objects which were of low reflectance were attractive. Although red was of relatively high reflectance, orientation to this object can be explained by the fact that it might be physiologically darker and therefore similar to black to the horse fly. <u>H. illota</u>, on the other hand, appears to orientate to some objects that are of appreciably higher reflectance than the background. However, although yellow and green are of high reflectance they are not attractive to this species. It may be said that although these two colors are of high reflectance they do not present sufficient contrast with the background for <u>H. illota</u> since they are in the same color range as the green vegetation. It might be possible, however, to provide contrast for these colors by presenting them on a background of different color.

<u>Orientation of Tabanidae to spheres of different color and reflectance presented on backgrounds of different color and reflectance (Beaver Creek, 1961)</u>.

<u>Methods and materials</u>. The purpose of this experiment was: (1) to confirm the results in 1960, (2) to study the behaviour of additional species and their reactions to objects of different color, and (3) to see if the pattern of orientation to colored objects could be influenced by providing backgrounds of different color and reflectance.

The following backgrounds were selected: (1) a highly reflectant background on the beach at Beaver Creek, (2) a predominantly green background provided by vegetation in a clearing in the bush also at Beaver Creek, and (3) a black background provided by an area of fresh summerfallow located in the Washow Bay area about twenty miles south of Beaver Creek.

The reflectance of these backgrounds was determined by a Weston light meter held 31 cm from the surface. Measurements were taken at the same time of a cardboard surface which was taken as a standard and the reflectances of the different surfaces were expressed as ratios of the readings taken on this surface. The surfaces presented by the terrain at the beach and summerfallow locations were relatively flat and reasonably consistent reflectance data could be obtained. The grass and plants at the bush locations made reflectance readings difficult. The meter was held 31 cm from these surfaces and about 20 readings were averaged.

Attempts were made to measure the reflectance of the spheres in sunlight. Such determinations were difficult since the glossy surface of the paints produced a highlight image of the sun which was often picked up by the light meter and the resulting readings were very high. Determination of reflectances of the spheres was, therefore, made indoors using flood lamps with the standard surface as a control.

The mean reflectances for the three backgrounds and for the colors green, red, yellow and black and white are presented in Table IV.

In view of the methods used the reflectance comparisons are not precise. However, the relative reflectances of the colored spheres as compared to the background provide a basis for interpreting the data.

Spheres painted with the colors red, green and yellow, the greys corresponding to them in reflectance and the black and white were tested with the Manitoba fly trap on each of the backgrounds just described. The pigments were of the same stock as those used in 1960. Positioning of the traps was done in a similar manner as in the previous year except at the beach location where space restrictions necessitated placing the traps in a straight line about three meters from the water edge. The tabanid populations were higher in these areas than at St. Laurent and regulation of the total numbers captured in each replicate was more difficult than before. Attempts were made to terminate the replicates after approximately 500 flies had been taken in the trap fitted with the black sphere but this number was often exceeded. Eight replications were completed in each location and the spheres were interchanged after each replicate so that each was tested once in every position. At the beach location the grey (red') sphere was lost after the

TABLE IV

MEAN RELATIVE* REFLECTANCES IN FOOT CANDLES OF COLORED SPHERES AND BACKGROUNDS

Sphere color	Reflectance (ft-C)	Background	Reflectance (ft-C)
Black	645	Bush	630
Green	793	Beach	1500
Red	992	Summerfallow	620
Yellow	1824		
White	2618		

*Readings expressed as ratios of the reflectance, measured in sunlight, from a manilla pasteboard surface.

third replication and so the captures in traps assigned this sphere color were not considered in the analysis.

Results. The numbers captured, in integers and in per cent of the total, for the various species in the three locations are shown in Table V. Representatives of sixteen species were captured. This compared with only seven species in the experiment at St. Laurent in 1960. The predominant species in all three locations was H. epistates. H. illota, H. lasiophthalma and H. affinis (Kirby) are also well represented in the captures at each location.

The log of the mean of the total captures for H. epistates, H. illota and C. mitis O.S. on each background are plotted in Figure 3 against the log of the total reflectance of the pigments (Table I). Points joined by a solid line represent the log of the mean of the total captures in traps with the black, grey and white spheres. The circles represent the log of the mean of the total captures in traps with the green, red and yellow spheres in that order.

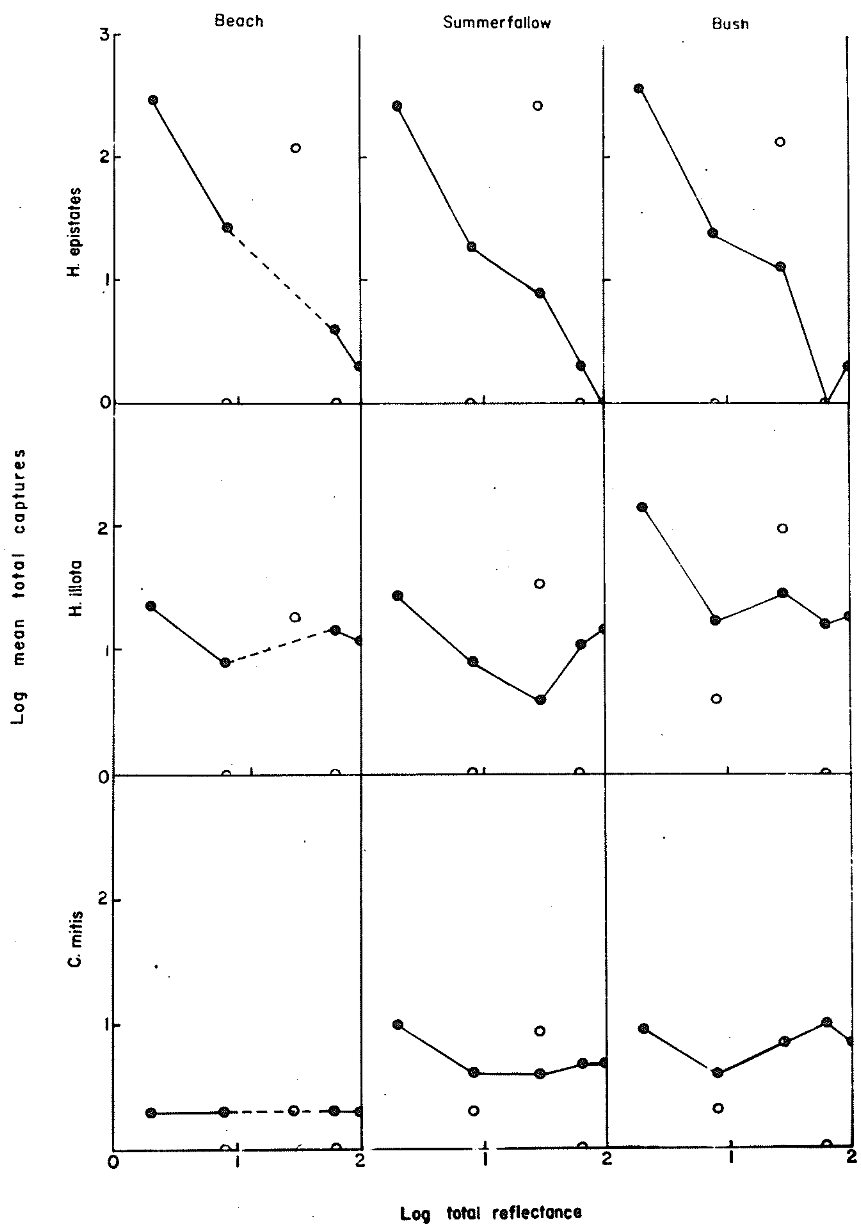
The results for H. epistates are typical for most of the species. This species was captured in highest numbers in traps with black and red spheres but the captures fell off rapidly for traps in the grey and white spheres as the reflectance of these increased. Very few captures of this species occurred in traps with yellow and green spheres. The curves are the same for each background and are similar to the curve

TABLE V

TOTAL CAPTURES OF TABANID SPECIES IN TRAPS WITH DIFFERENT COLORED SPHERES ON DIFFERENT BACKGROUNDS AT BEAVER CREEK, 1961

Species	Total for species			Per cent of total captures		
	Beach	Summer-fallow	Bush	Beach	Summerfallow	Bush
Hybomitra affinis (Kirby)	1171	752	325	11.9	8.9	2.7
Hybomitra arpidi (Szil.)	126	42	492	6.3	.6	4.2
Hybomitra epistates (O.S.)	3736	4252	4439	38.0	50.2	37.5
Hybomitra frontalis (Wlk.)	24	323	2	.2	4.0	0.07
Hybomitra illota (O.S.)	642	757	2640	6.5	8.9	22.3
Hybomitra lasiophthalma (Macq.)	1379	1072	650	14.0	12.7	5.5
Tabanus marginalis Fabr.		13	5	0.0	.2	0.0
Hybomitra metabola (McD.)	791	29	1482	8.0	.3	12.5
Hybomitra nuda (McD.)	1361	89	1160	13.8	1.1	9.8
Hybomitra trepida (McD.)	18	17	10	.2	.2	.1
Hybomitra typhus (Whitn.)	169	575	10	1.7	6.8	.1
Hybomitra zonalis (Kirby)	320	68	77	3.3	.8	.7
Tabanus similis Macq.	1	40			.5	0.0
Chrysops aestuans Wulp.	6	95	10	.1	1.1	.1
Chrysops excitans Wlk.	10	9	166	.1	.1	1.4
Chrysops mitis O.S.	72	289	361	.7	3.4	3.1

Figure 3. Log mean of total captures in traps with spheres of different color and reflectance of H. epistates, H. illota and C. mitis on three backgrounds; beach, summerfallow and bush. Solid points traps with black, greys and white. Circles traps with the colors green, red and yellow in order of increasing reflectance.



Beach
Summerfallow
Bush
H. epistates
H. illota
C. mitis
Log mean total captures
Log total reflectance
0
1
2
3

shown for T. similis in Figure 2a. The curves obtained for H. illota and C. mitis are also the same on each background and similar to the curve shown for H. illota in Figure 2b. Captures for these two species in traps with grey and white spheres did not fall off with increasing reflectance. Captures for these two species were very low in traps with the yellow and green spheres.

For a more detailed inspection of the data, the transformed means with the least significant differences for the captures in traps with the different spheres for each background for H. epistates, H. affinis, H. illota and Chrysops mitis are presented in Table VI.

There is no significant difference between captures in traps with the black and red spheres for any of the species with the exception of H. epistates at the beach location. Here captures in traps with the red sphere are significantly lower than captures in traps with the black. A similar result occurs for this species in the bush location although the difference here is not significant. Possibly red is physiologically brighter for H. epistates than for the other species.

The captures of H. illota in traps bearing red spheres were significantly higher than captures of this species in traps with grey (red') spheres on both the summerfallow and bush locations. This result differs from that obtained for

TABLE VI

TRANSFORMED MEANS OF CAPTURES OF FIVE TABANID SPECIES IN TRAPS WITH COLORED SPHERES AT THREE LOCATIONS PRESENTING BACKGROUNDS OF DIFFERENT COLOR AND REFLECTANCE

Color	*H. illota*			*G. mitis*			*H. epistates*			*H. affinis*			*H. lasiophthalma*		
	Beach	Summer fallow	Bush	Beach	Summer fallow	Bush	Beach	Summer fallow	Bush	Beach	Summer fallow	Bush	Beach	Summer fallow	Bush
Black	1.208	1.361	2.013	.259	.740	1.045	2.409	2.418	2.723	1.829	1.451	1.292	1.753	1.591	1.635
Red	1.145	1.448	1.745	.392	.791	.867	1.918	2.432	2.320	1.886	1.602	1.159	1.615	1.649	1.286
Grey (Red')		.594	.968		.359	.904		.883	.923		.391	.421		.606	.259
Green	.335	.060	.480	.100	.219	.481	.339	.308	.301	.201	.038	.167	.129	.038	.179
Grey (Green')	.810	.876	1.056	.410	.467	.756	1.215	1.189	1.138	1.034	.420	.376	.833	.708	.542
Yellow	.000	.000	.270	.000	.076	.230	.050	.043	.000	.000	.000	.000	.000	.000	.000
Grey (Yellow')	.967	.997	.915	.513	.460	.988	.670	.458	.216	.762	.135	.050	.728	.232	.167
White	1.015	1.117	.961	.506	.540	.934	.404	.365	.304	.117	.038	.050	.329	.075	.050
LSD 01	.286	.421	.434		.351	.369	.562	.334	.635	.356	.335	.425	.523	.369	.523
05	.212	.315	.325		.263	.273	.420	.250	.475	.267	.251	.315	.388	.276	.390

this species at St. Laurent in 1960 where no significant difference could be shown between these two traps. Furthermore, while no significant difference could be shown between captures of this species in traps with black and white spheres at the beach or summerfallow locations, the black sphere attracted significantly more _H. illota_ than the white sphere in the bush location. In every case, however, including the results of the previous year, higher numbers of _H. illota_ were captured in traps with the black or red sphere than with the white sphere. Why the difference is significant only at the bush location is not yet explained.

The numbers of _C. mitis_ captured at the beach location were too few to permit analysis. At the other locations this species was captured in traps with spheres of all colors except green and yellow. The behaviour of this species with respect to orientation to colored objects appears similar to that of _H. illota_.

Discussion. It was suggested previously that while _H. illota_ orientated to some spheres of higher reflectance than the background, its failure to orientate to yellow or green spheres might be explained by the presumption that these colors do not provide a color contrast, against the vegetation, for this species. The changes of the background color presented in this experiment did not, however, increase the orientation to green or yellow spheres of this species nor of _C. mitis_, a species with similar behaviour. It is concluded that the backgrounds offered did not produce sufficient contrast for these colors to evoke orientation responses of these species. The failure of H. illota and C. mitis to orientate to yellow and green spheres could be explained in teleological terms since these colors represent "vegetation" rather than host animals.

Investigations on the effect of the surface texture of objects on their attractiveness to Tabanidae.

The surface of an object may be glossy or matte, smooth or rugose. All of the objects used so far in this investigation were glossy and smooth. Since for the majority of the species, objects of low reflectance were most attractive, one might expect that objects which present matte rugose surfaces would reflect the least light and might be the most attractive. The observations of Sippell and Brown (1953) referred to in the review of the literature showed, however, that an enamel (glossy) surface was more attractive for the mosquito, Aedes than a matte surface.

Methods and Materials. The objects used in this experiment were cylinders (height = diameter = 46.5 cm) suspended horizontally from the Manitoba fly trap. These were constructed by wrapping corrugated cardboard around a suitable frame. Four black surfaces were prepared: glossy smooth, glossy rugose, matte smooth and matte rugose. The black paint used in the color experiments was used for the glossy surfaces. For the matte surfaces black blackboard paint was used. To provide a rugose surface the cylinders were covered with jute sacking and painted heavily with two coats of enamel or matte paint as required. The experiment was conducted at Beaver Creek in a clearing in the bush. Four replications were completed with positional changes after each replicate.

Results and discussion. The results are presented in Table VII along with the transformed means (based on transformation of the data to logarithms) and the least significant differences. Captures in traps with the glossy black cylinder were significantly higher than captures in traps with the matte cylinder and very significantly higher than captures in traps with rugose cylinders. Traps with the matte cylinder and the glossy rugose cylinder did not capture significantly different numbers but traps with the matte cylinder captured significantly more horse flies than traps with the matte rugose cylinder.

It appears, therefore, that an object with a glossy surface is more attractive to horse flies than an object with a matte surface and that rugosity as presented in this experiment reduces the attractiveness of either glossy or matte surfaces. A further experiment was carried out to confirm

TABLE VII

CAPTURES OF TABANIDAE IN TRAPS WITH HORIZONTAL CYLINDERS HAVING DIFFERENT SURFACE TEXTURES

Surface texture	Replicate				Total	Transformed means*
	1	2	3	4		
Glossy smooth	4054	5402	3822	3960	17,238	3.630
Matte smooth	1730	757	910	850	4,247	3.001
Glossy rugose	685	386	588	1290	2,949	2.826
Matte rugose	468	34	190	980	1,672	2.368

*Means based on logarithms of variates (log x)

$L.S.D._{.05}$ for transformed means = 0.499

the comparison of the glossy and matte surfaces, compare the effectiveness of a highly polished metallic surface with white and to see if the attractiveness of a black surface could be increased by placing highly reflectant spots on it.

Cylinders of the same size as those of the previous experiment were used. A glossy and a matte cylinder was prepared as before. A third cylinder was covered with aluminum foil. A fourth was painted matte black and 36 bright aluminum discs, each 6 cm in diameter, were pasted randomly over the cylinder. A fifth cylinder was painted white using the same enamel paint used in the color experiments. The experiment was conducted in the same area as the former and five replications were completed, the positions of the cylinders being changed for each replicate.

The results of this experiment are presented in Table VIII along with the transformed means and the least significant differences. Captures in traps with the glossy black cylinder were significantly higher than captures in traps with the matte cylinder and very significantly higher than captures in traps with the other cylinders. Traps with the white cylinder captured highly significantly more flies than traps with the shiny aluminum cylinder. More than half of the flies captured in traps with the white cylinder were _H. illota_ and _C. mitis_ which have already been shown to orientate with higher frequency than other species to the white spheres. It appears that a highly polished surface

TABLE VIII

CAPTURES OF TABANIDAE IN TRAPS
WITH HORIZONTAL CYLINDERS
HAVING DIFFERENT SURFACES

Surface	Total	Transformed means *
Glossy black	11,304	3.352
Matte black	5,869	2.996
Matte black with silver spots	1,213	2.221
White	1,681	2.512
Silver	50	0.936

*Based on transformation of captures to logarithms.

LSD_{01} for transformed means = .402
LSD_{05} for transformed means = .287

alone is not attractive to Tabanidae.

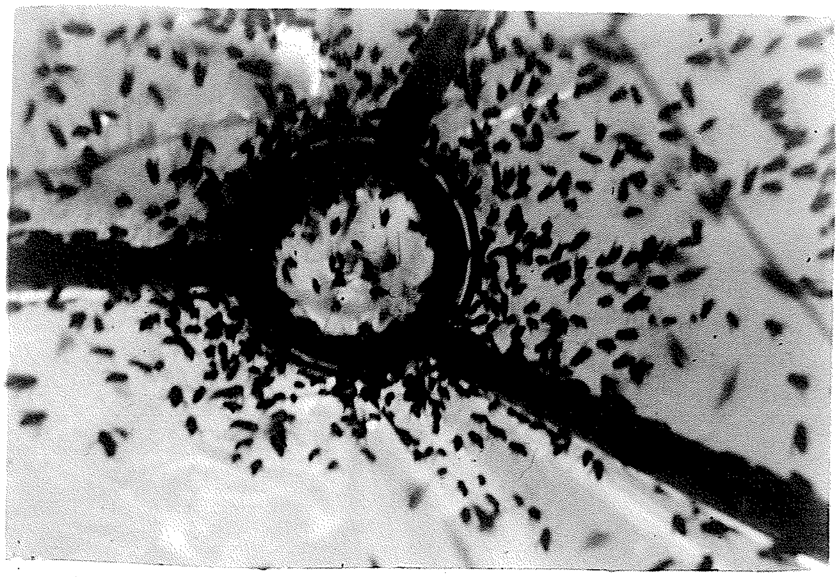
Providing shiny metallic spots on the matte black cylinder had the effect of reducing the attractiveness of this object very significantly as compared with the matte black cylinder. This will be further discussed in Chapter IV.

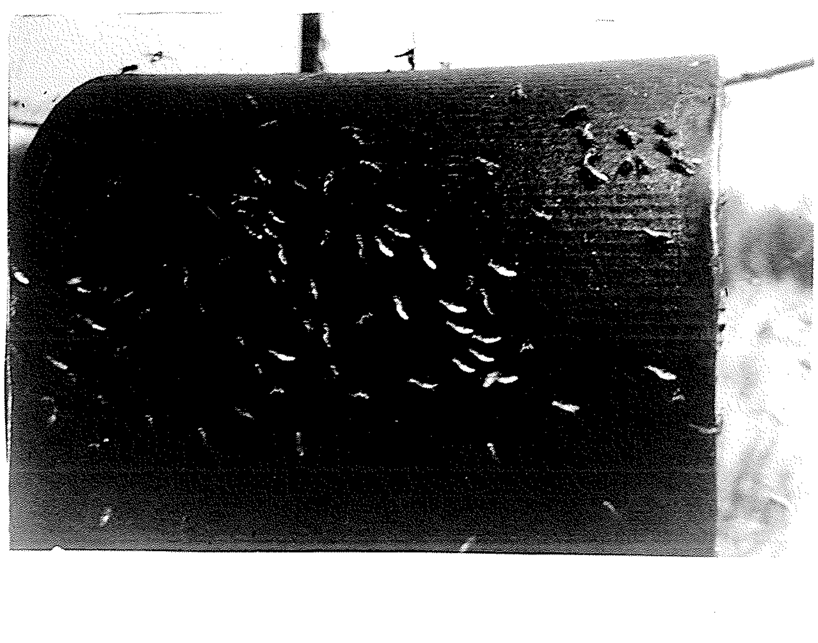
Investigation of the possible influence of "fly factors".

It will be noted from Table VII that very large captures occurred in the traps bearing the glossy black cylinder. It was observed that the horse flies tended to settle on this cylinder in larger numbers than on the other three less attractive ones. This behaviour is illustrated in Figure 4b. It was observed also that a certain amount of fluid, either feces or regurgitated nectar, fell on this object from flies that were in the canopy of the trap (see Figure 4a). Although the flies were not observed to attempt feeding on this deposit there was little doubt that it had some locomotor-inhibiting effect, since a freshly prepared cylinder was scarcely settled on at all. By inducing the flies to settle on the object one would think that this arrestant would actually reduce the numbers captured in the canopy above it. However, the presence of an aggregation of settled flies on the cylinder might serve as an additional visual attractant, causing more flies to orientate to the object than if the aggregation was not present.

Figure 4a. The interior of the canopy of a Manitoba Fly Trap which had a glossy black horizontal cylinder suspended from it.

Figure 4b. A glossy black cylinder showing tabanids resting on it.





In a preliminary experiment a freshly painted glossy black cylinder which had had no exposure to flies was compared with the glossy black cylinder used in the experiment on surface properties. The total captures in two replications were 5,026 for the "contaminated" compared with 4,175 for the new cylinder. It appeared, therefore, that the cylinder that had been exposed to flies was in some way more attractive than the fresh one. Another possibility is that the paint on the freshly painted cylinder had some repellent effect.

An experiment was conducted to test for the effects of the hypothetical "fly factor" and exposure to sunlight on the attractiveness of cylinders to horse flies. Three cylinders were painted enamel black at the same time. One cylinder was exposed to flies by suspending it in a trap at Beaver Creek for four days. The second was exposed to the sun for the same period where no flies were present and the third was placed indoors. The three were then suspended in traps at Beaver Creek. Four replications were completed; the positions of the cylinders were changed after each replicate. The experiment extended through a period of ten days.

The results are presented in Table IX. In total captures the contaminated cylinder was more effective than those which had not been exposed to flies. The cylinder exposed to sunlight attracted more flies than the cylinder that had been kept indoors. There was no significant difference among the

TABLE IX

NUMBER OF TABANIDAE COLLECTED IN TRAPS WITH GLOSSY BLACK CYLINDERS TREATED IN DIFFERENT WAYS

Replicate	Exposed to flies and sunlight	Exposed to sunlight	Not exposed
1	1285	865	984
2	183	165	179
3	687	722	447
4	136	99	35
Total*	2291	1851	1645

*No significant differences among treatment.

treatments, however. It is concluded that existence of a "fly factor" is not demonstrated. Furthermore, while there may be some repellent effect in a freshly painted surface, this is not a serious source of error in the other experiments since all of the objects used were painted at the same time.

CHAPTER III

THE PHOTOTACTIC BEHAVIOUR OF TABANIDAE IN RESPONSE TO LIGHT OF DIFFERENT WAVE LENGTHS

Review of the Literature.

The relative sensitivity of insects to different regions of the spectrum has been the subject of numerous investigations. Only some of the more recent works will be reviewed here. Cameron (1938) made an extensive review of the literature paying particular attention to methods. He concluded that while the quantitative results of different methods were not comparable, there was generally good agreement as to the qualitative aspects of phototactic behaviour. He found that for the house fly, *Musca domestica* L., ultraviolet light at 365 mμ was more stimulating than any other part of the spectrum examined. Stimulation fell off rapidly toward higher wave lengths and no other maximum was observed.

Weiss (1943) studied the reactions of 14,000 insects which included 19 species of Coleoptera, two of Hymenoptera and one each of Hemiptera and Diptera to different wave lengths at equal intensities. He found that, in the range of wave lengths between 365 mμ and 740 mμ, two peaks of maximum response occurred consistently; a maximum peak at 365 mμ and a lower peak at 402 mμ. Stermer (1959) investigated the spectral sensitivity of seven species of stored-product insects to nine wave bands of radiation between 290 mμ and 600 mμ.

Generally, two maxima were obtained, one peak at 500 mμ and another between 334 mμ and 365 mμ. One species, the rice weevil, Sitophilus oryzae L. responded nearly equally to all wave lengths between 334 mμ and 546 mμ.

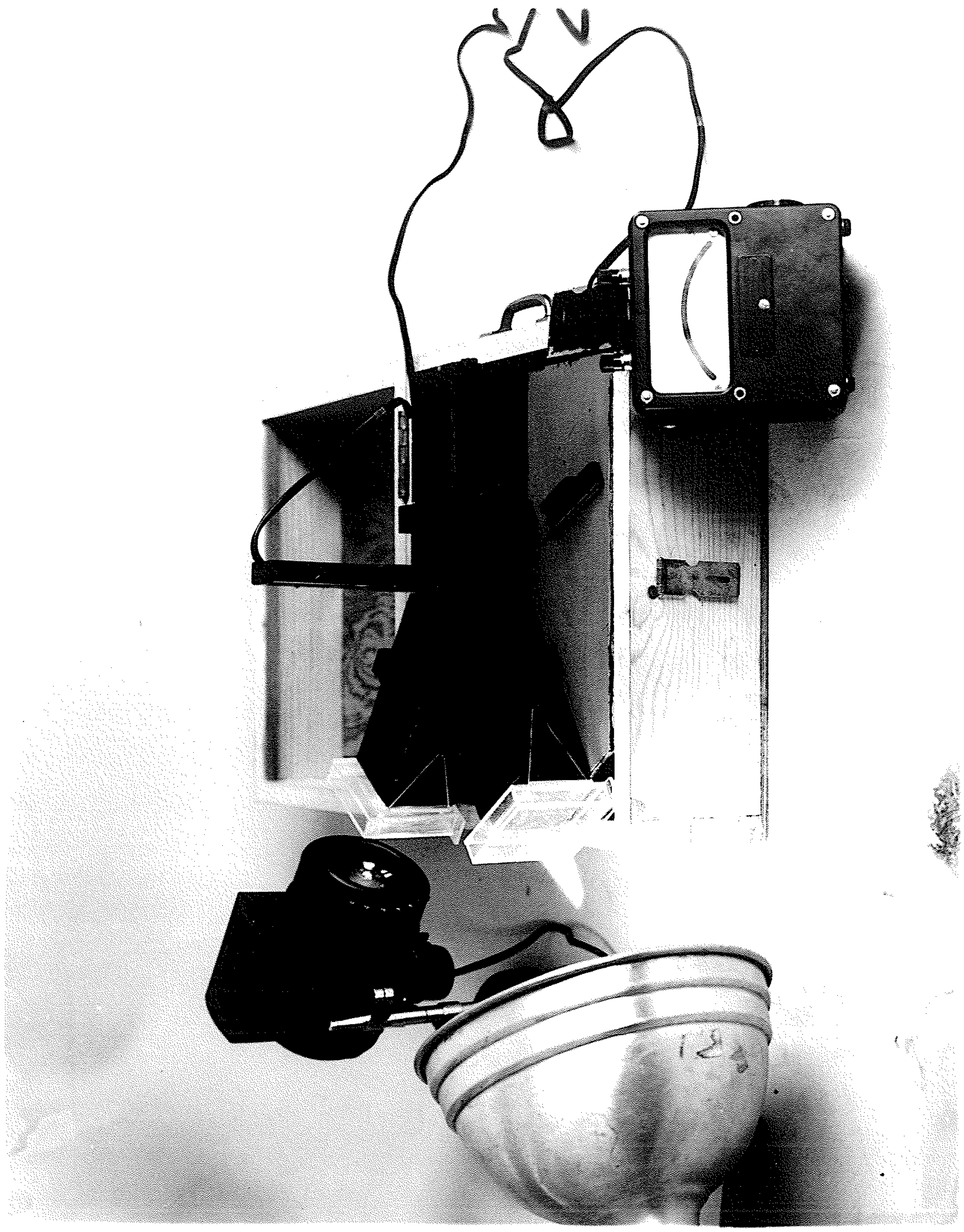
Fingerman (1952) investigated the responses of six color mutants of Drosophila melanogaster Meig. Of the wave lengths investigated, 366 mμ evoked the maximum response. The position of the second maximum varied from 440 mμ for the eyetype "apricot" to 560 mμ for types "sepia" and "brown". Fingerman and Brown (1952) also demonstrated a "Purkinje Shift" in the compound eye of D. melanogaster. In the vertebrate eye this is the overall shift of the sensitivity of the eye to shorter wave lengths caused by a shift from cone to rod vision. Dorner and Mulla (1961) studied the responses of the eye gnat, Hippelates collusor (Townsend), to light of different wave lengths. Using one technique, two peaks were found, one at 440 mμ and one at 550 mμ. The second technique yielded only one peak at 550 mμ. These authors noted that the intensities used in the technique giving two peaks was about one thousand times greater than in the technique giving only one peak and interpreted this to be another example of a "Purkinje Shift" described by Fingerman and Brown (1953). It might be noted in this connection that Schneider (1956) using very low intensities determined the spectral sensitivity of Calliphora erythrocephala (Meig.) and found only a single peak at 480 mμ.

Ballard (1958) made a study of the response of Stomoxys calcitrans L. to wave lengths of light at two intensity levels. He used a "Y" tube method similar to that of Fingerman and Brown (1953) and used filters to obtain light of different wave lengths. He found that at low intensity both sexes responded maximally in the region of 365 to 465 mμ and again at 640 mμ. At the higher intensity level the males showed peaks at 390, 440, 515 and 640 mμ whereas the response of the female slowly decreased from 365 to 575 mμ and increased to a peak again at 640 mμ. The peak at 640 mμ had not been demonstrated previously in studies of other insects.

So far as could be determined, no studies on spectral sensitivity have been carried out for tabanid species. The object of this study was to determine this sensitivity and to see if the information obtained could be related in any way to the behavioural data observed in the field.

Methods and materials. The apparatus used in this study is illustrated in Figure 5. The "Y" tube was constructed from one-quarter inch plywood and the interior dimensions were 5 cm wide by 4.5 cm high. The base and the arms of the tube were removable. When the base and arms were in place the base was 16 cm long, the arms 16.5 cm long. The base and arms could be closed individually by metal shutters. The central portion of the tube into which the base and arms fitted

Figure 5. The "Y" tube used for studying the responses of tabanids to lights of different wave lengths at equal intensities.



was fixed to a baseboard which in turn fitted snugly into a case. A slot was provided at the base of the arms which accommodated the sensing element of a Weston light meter, Model 756. The inside of the tube was painted with flat black blackboard paint. The distal end of one arm was closed by a color filter inserted between the end of the arm and a piece of perspex which was held in place by rubber bands. The distal end of the other arm was closed by a piece of perspex only. The filter window was illuminated by a Westinghouse 200 watt frosted bulb. The unfiltered window was illuminated by a Westinghouse 60 watt microscope bulb. A water filter constructed from perspex was placed in front of each light source to absorb heat radiation. Each light source was in series with a rheostat which permitted intensity adjustments. The filters (Klett Manufacturing Company) transmitted wave bands approximately 30 mμ wide.

The method of testing the flies was as follows. Twenty flies were placed in each of the six available bases and permitted to dark adapt for a period of thirty minutes. The filter was put in place and the intensity of light transmitted through it was brought to four foot candles. This light was then cut off by use of the shutters and the control light brought to the same intensity. The sensing element of the light meter was then removed and a cover placed over the slot. After both shutters in the arms had been removed the base was put in place and its shutter was removed. After three minutes the base shutter and the arm shutters were replaced. The flies found in the base and in both arms were counted and in half of the replicates the flies were killed and identified to species.

Twelve spectral bands were provided by the filters. Each replicate consisted of the investigation of the responses of twenty flies per filter color. Ten replicates were completed. Previous to experiments with the filters, 200 flies were put through the apparatus in groups of twenty with white lights in both arms adjusted to four foot candles. No inherent bias was found in the apparatus.

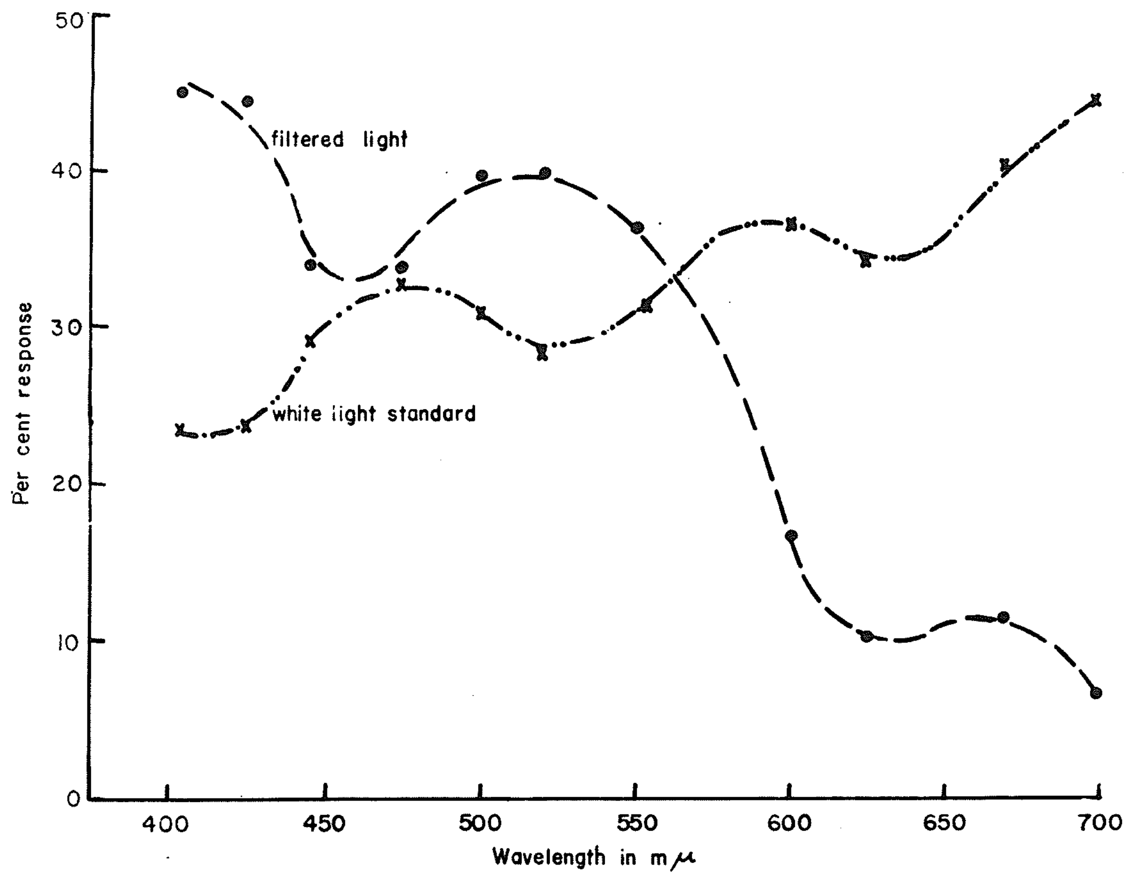
The flies for the first three replicates were captured at Beaver Creek. For the remaining replicates the flies were captured at the Hecla Island Ferry Dock, which is about 30 miles south of Beaver Creek.

Results and discussion. The species representation in the five replicates for which species determinations were made was as follows: *H. frontalis* 77 per cent, *H. typhus* 11 per cent, *H. epistates* 6 per cent, *H. arpadi* 2 per cent and several other species less than one per cent each. The predominant species in the first three replicates were *H. typhus* and *H. epistates*. In the last seven replicates the predominant species was *H. frontalis*. The data were inadequate to detect differences in behaviour among the species. In the main the data represent the behaviour of the predominant species, H. frontalis.

The number of flies responding to the filtered light and the control light expressed as a percentage of the total number of flies tested with each filter is plotted against the wave length in Figure 6. The flies responded maximally at 405 mμ, which was the shortest wave length available, and at 525 mμ. It is possible that the curve at 405 mμ represents part of a higher peak which might be found in the ultraviolet region. Analysis of the numbers in the filter and control arm indicated no significant difference in the response to filtered light between 405 and 550 mμ and the control, although at 525 mμ the difference is very close to significance at the 5 per cent level. For other regions of the spectrum examined there was a significant difference between the numbers in the control arm and the filter arm.

The results are very similar to those reported by Weiss (1943) as being a rather typical response of insects to light. It is significant that no peak was found in the 640 mμ region of the spectrum as was found by Ballard (1958) for the biting fly, Stomoxys calcitrans L. Lack of response in this area for the horse flies lends support to the postulate that horse flies may be "red-blind" and that red objects may be physiologically darker to them than grey objects of the same reflectance as suggested in Chapter II by the interpretation of the attractiveness of colored spheres.

Figure 6. The response of tabanids to light of different wave lengths and a control white light at equal intensities in the "Y" tube apparatus.



50
40
30
20
10
0
Per cent response
filtered light
white light standard
400
450
500
550
600
650
700
Wavelength in mμ

CHAPTER IV

THE ORIENTATION OF TABANIDAE TO OBJECTS OF DIFFERENT SHAPE AND SIZE

Review of the Literature

The problem of form discrimination has been studied critically for bees. Von Frisch (1950) showed that complex forms with irregular outlines were preferred and that this attraction is interpretable in terms of optomotor stimulation. Tinbergen and Kruyt (1937) observed that objects with three dimensions served to orient a species of sphecid wasp, *Philanthus triangulum* Fabr. to its nest more effectively than flat ones. These authors also determined that larger objects were better than small ones for this orientation.

The tsetse fly trap employed by Morris and Morris (1949) was essentially a horizontal cylinder which according to the authors best simulated a host animal. They concluded that curvature of the trap in the vertical plane was an important factor in its attractiveness to the tsetse fly. The trap constructed by Skuffin (1951) also presented such curvature although the author makes no mention of the possible significance of this property in the attractiveness of the trap to horse flies.

The relation of the size of an object to orientation has been studied for the male of the butterfly, *Argynnis paphia* L. by Magnus (1956). As the size of a dummy female butterfly was increased, its attractiveness to the male increased in a linear manner, the largest dummy being more attractive than one which was the actual size of the female. Magnus (1956) also noted that the shape of the dummy was not an important factor in its attractiveness to the male.

The purpose of the present investigation was to determine the relative attractiveness of objects of different shape to tabanids and to determine the size of an object which is maximally attractive.

The attractiveness of objects of different shape to Tabanids

Methods and materials. The forms tested were a sphere, hemisphere, plane circle, cube, plane square, tetrahedron, plane equilateral triangle and two cylinders, one suspended horizontally, the other vertically. The diameter of the sphere was 60 cm and the surface area of the three-dimensional shapes was the same as that of the sphere. The surface area of each side of the two-dimensional objects was equal to one-half that of the sphere. The cylinders were 33 cm in diameter, 53 cm in length.

The objects were constructed by covering wooden frames with corrugated cardboard with the exception of the hemisphere which was custom made from perspex and the sphere which was a polystyrene balloon as used in the experiments in Chapter II. All objects were painted with two coats of black enamel paint and covered with tanglefoot to trap the flies. The objects were suspended from a steel wire, "clothesline" fashion, one meter apart with their centers about 75 cm from the ground. The two-dimensional objects were tethered to the ground to prevent excessive oscillation in the wind but permitted to twist about the vertical axis. The position of the objects relative to each other was randomized for each replicate. The earlier replicates were terminated when about 70 flies had adhered to the most attractive form. Later in the season the population of horse flies declined and the numbers per replicate had to be reduced. The captured flies were removed after each replicate and the tanglefoot replenished as required. This experiment was conducted at St. Laurent in 1960.

Results and discussion. The captures of horse flies are presented in Table X. The sphere was clearly more attractive than any other shape in the series and captured three times as many horse flies as the cube. The horizontal cylinder captured twice as many horse flies as the cube whereas the vertical cylinder captured about the same number as the cube. The differences among these more attractive silhouettes can be discussed more effectively after considering the other comparisons available in Table X.

The lowest captures were obtained with the two-dimensional objects (plane circle, square and equilateral triangle).

TABLE X

CAPTURES OF TABANIDAE ON OBJECTS
OF DIFFERENT SHAPE

Object	Replicate						Total	Trans-formed means*
	1	2	3	4	5	6		
Sphere	86	71	90	50	59	30	386	7.97
Horizontal cylinder	84	53	28	35	25	20	245	6.27
Vertical cylinder	54	21	15	20	18	13	141	4.80
Cube	30	24	13	9	18	21	115	4.42
Hemisphere	30	26	15	3	6	7	87	3.71
Tetrahedron	22	8	5	3	9	4	51	2.49
Plane circle	16	2	3	4	3	5	33	2.42
Plane square	5	3	3	3	6	5	25	2.26
Plane Equil. Triangle	2	1	1	1	2	3	10	1.62
Totals	329	209	173	128	146	108	1093	

*Means based on transformation of variates: ($\sqrt{x_i + 1}$)

L.S.D.$_{.01}$ for transformed means = 1.30

These presented a full silhouette in only two directions and were practically invisible in two directions at any moment. On the other hand, being sensitive to air displacement, they gyrated even in a slight breeze so that the silhouettes "scanned" the field in all directions over a period of time. If this gyration were an effective substitute for the continuous scanning of all directions simultaneously, the plane square should have captured as many flies as the cube which was, however, four times aseffective. Similarly the tetrahedron scans all directions and is five times as attractive as the plane equilateral triangle which scans in only two directions simultaneously.

On the other hand the sphere attracted ten times as many horse flies as the corresponding plane figure, the circle. This difference appears too large to account for solely in terms of simultaneous scanning. Apparently the convex curvature of the sphere contributes appreciably in some way to its high attractiveness to horse flies. This is clearly confirmed by comparison of the numbers of horse flies captured by the sphere and the cube which scan all directions in the field but obviously not with equal effectiveness.

If horse flies are attracted to a sphere with equal frequency from all directions it would be expected that the hemisphere would be approximately half as attractive since the numbers attracted to the plane side of the hemisphere should be relatively small (cf., the data for the plane circle). The hemisphere, however, attracted only one-quarter as many flies as the sphere, strongly suggesting that the curved surface of a hemisphere free to turn in the wind is scanning in the wrong direction about half of the time. As yet no direct observations are available on the approach direction of horse flies to the objects although it has been observed that larger numbers are captured on the sunny side of a stationary black object covered with tanglefoot. Furthermore, any optical characteristic peculiar to a spherical surface presumably provides a much more conspicuous cue for visual orientation on the sunny side than on the shady side. Therefore, the postulate is tentatively adopted that the orientated approach to the most attractive objects is most frequently from the sunny side.

One cylinder is nearly twice as attractive as the other although they are identical apart from the fact that one is suspended horizontally, the other vertically. The high captures by the sphere and the horizontal cylinder strongly suggest that some characteristic of a surface curved in the vertical plane contributes to attractiveness for horse flies and this characteristic becomes ineffective in the case of a vertical cylinder which is curved only in the horizontal plane.

It has already been established that a horizontal cylinder with a matte surface is not as attractive as a horizontal cylinder with a glossy surface (see Table VII). Furthermore, positional error in an experiment with forms at Beaver Creek (to be discussed later) was apparently due to shading of trap positions; those in shaded situations captured fewer flies than those in sunny positions. It is difficult to avoid the inference that horse flies orientate in some way to the light reflected from the black surfaces and that some curved surfaces are more favourable to such orientation.

The illuminated side of a glossy black sphere presents a highlight which is an indistinct image of the sun. This image can be seen from any elevation on the sunward side of a glossy black sphere located in sunlight. This remains true even while the sphere gyrates. Neither of these statements can be made without restriction for any of the other objects tested.

When a horizontal glossy black cylinder is exposed broadside to the sun, a horizontal series of images is visible from the sunward side from any elevation provided it is not viewed too obliquely. Whenever one of the plane ends of the cylinder faces the sun it should be no more attractive to flies than the plane circle. Whether or not the horse flies orientate specifically to these solar images, ineffectual scanning by the ends of the cylinder must account in large part for the lower captures on this object as compared to the sphere.

A characteristic of the vertical cylinder is that no image of the sun can be seen from the sunward side except from the ground almost below the cylinder. When the sun is low, however, this image might be seen from a greater distance. (Discussion of this effect with respect to species that may fly early and late in the day will be discussed in a later experiment.) There is, however, a broad diffuse vertical band somewhat brighter than the vertical margins of the cylinder on either side. In this experiment the vertical cylinder is no more attractive than the cube and apparently this pattern is no more attractive than the plane side of the cube which presents a uniformly illuminated surface to approaching flies.

The possibility must be considered that the horse flies are not orientating to the reflected image of the sun as such, but to a plane or degree of polarization of some of the reflected light. At "Brewster's angle" the light reflected is totally polarized, the degree of polarization fading off gradually on either side. If this effect provides the orientation cue the interpretation remains otherwise the same. For example, on the sunward side there is no angle of approach for a horse fly such that some part of the surface of a glossy sphere does not reflect totally polarized light toward it. In short, if either the sun's image or a beam of completely polarized light provides an orientation cue the actual experimental data for the attraction of horse flies to the various shapes are in agreement with expectations.

It may be argued that all the other colored objects discussed in Chapter II reflect the sun's image and polarize light in the same way yet most of them are unattractive as compared to the black or red spheres. To explain this apparent discrepancy it is only necessary to add one additional postulate, _viz._, that the sun's image or the cone of polarized light must be seen in a field (the rest of the silhouette) not physiologically brighter than the background to be exceptionally attractive. However, the exceptional case of the attractiveness of the white sphere for _H. illota_ and _C. mitis_ is not included in this tentative explanation.

It might be added that traps with a horizontal cylinder covered with shiny aluminum foil captured very few flies but traps with a white cylinder captured a considerable number, especially of _H. illota_ and _C. mitis_, (cf. Table VIII, Chapter II). This would lend some support to the postulate that polarized light might be the orientation cue since the silver surface would elliptically polarize light, whereas the white surface would plane polarize it. However, the other species are not attracted to a white object. An extension of this comparison to the majority of species would require testing a copper cylinder with a grey of equal reflectance.

Further experiments were conducted at Beaver Creek in 1961 to confirm the results of 1960 and to determine if there is any species variation in the attractiveness of different shapes. The forms used were as follows: a sphere (51 cm diameter), a horizontal and vertical cylinder (height = diameter = 41.6 cm), a cube, and a form made up of two plane square surfaces at right angles to each other, hereafter called the vane silhouette. Each form was suspended in a Manitoba Fly Trap. A sixth trap was operated as a control without a silhouette object. Six replications were completed and the position of each form was changed after each replicate.

The results of this experiment are presented in Table XI. There was again no significant difference between captures in traps with the cube and traps with the vertical cylinder. In this experiment, although the sphere attracted more horse flies than the horizontal cylinder, the difference is not statistically significant. The cube attracted significantly more flies than the vane silhouette. Although this figure scans in four directions simultaneously it captured only one third as many flies as the cube. It is curious that two square planes at right angles should be relatively no more effective than one. With the exception of the sphere, the ratios of attractiveness of the other forms are in good agreement with those of the previous year. The capture of only three flies in the trap without a form indicates that some silhouette must be present for the trap to be effective.

TABLE XI

CAPTURES OF TABANIDAE IN TRAPS WITH OBJECTS OF DIFFERENT SHAPE

Object	Total	Transformed mean *
Sphere	2602	2.522
Horizontal cylinder	2369	2.493
Vertical cylinder	1111	2.092
Cube	1116	2.056
Vane silhouette	351	1.572
No silhouette**	3	0.000

*Based on transformation of captures to logarithms.

**Not included in analysis.

L.S.D.$_{.01}$ for transformed means = .448
$_{.05}$ for transformed means = .324

It was observed that the proximity of some tall trees shaded some of the trap positions from the sun at different periods of the day. Presumably for this reason traps in certain positions were more effective than others. Since the experiment was conducted early in the season there was a large variation in the abundance of different species. This combined with the positional error made the determinations of species preferences for the different shapes unreliable.

A second experiment in 1961 was conducted at Beaver Creek in a larger clearing in the bush where no shade fell on any of the traps throughout the day. It was conducted at the peak of the horse fly season and was completed within two days so that little variation in species abundance could occur. The sphere, horizontal and vertical cylinder, and the cube were tested in four replications with the positions of the shapes changed after each replicate. The arrangement of the traps with the different silhouette forms is shown in Figure 7. Specimens captured were classified to species.

The total captures for six of the predominant species in traps with the different forms are presented in Table XII. Considering the totals for all species, captures in traps with the cube were relatively low as compared with the previous results, although the difference between captures in traps with this form and captures in traps with the vertical cylinder are not significantly different. Captures in traps

Figure 7. Manitoba Fly Traps with a sphere, horizontal cylinder, vertical cylinder and a cube at Beaver Creek, 1961.

TABLE XII

CAPTURE OF SOME INDIVIDUAL SPECIES OF TABANIDAE IN TRAPS WITH OBJECTS OF DIFFERENT SHAPE

Object	*H. epistates*	*H. lasiophthalma*	*H. illota*	*H. affinis*	*H. arpadi*	*H. typhus*	Others	Total	Transformed mean*
Sphere	3083	508	461	377	255	215	308	5207	3.109
Horizontal cylinder	933	368	256	188	128	111	182	2166	2.678
Vertical cylinder	553	112	135	57	7	27	114	1005	2.285
Cube	164	50	73	44	8	27	83	449	1.971

*Based on transformation of captures to logarithms.

$L.S.D._{.01}$ for transformed means = .469
$_{.05}$ for transformed means = .310

with the sphere were also somewhat higher relative to captures in traps with the horizontal cylinder than in previous experiments. The ratio of captures in traps with the vertical cylinder and the horizontal cylinder were again 1 to 2 as before.

For _H. epistates_, the ratios of total captures in traps with the vertical cylinder and traps with the cube were about 3 to 1. This species was also the most numerous. It will be noted that the less abundant the species the closer the captures in traps with these two forms approaching a one to one ratio. Although there are no data on the daily activity of the different species, it is possible that the more numerous species, as estimated by the captures, are active for a longer period of the day. When the sun is low on the horizon the sun's image on the vertical cylinder would now be visible at a greater distance from the cylinder than when the sun is higher in the sky. This may account for the larger number of captures in traps with the vertical cylinder as compared with the cube for the more abundant species. In any event the ranking of attractiveness of the different forms is similar for all of the species, confirming both of the earlier experiments.

Investigations to determine the size of object maximally attractive to tabanids

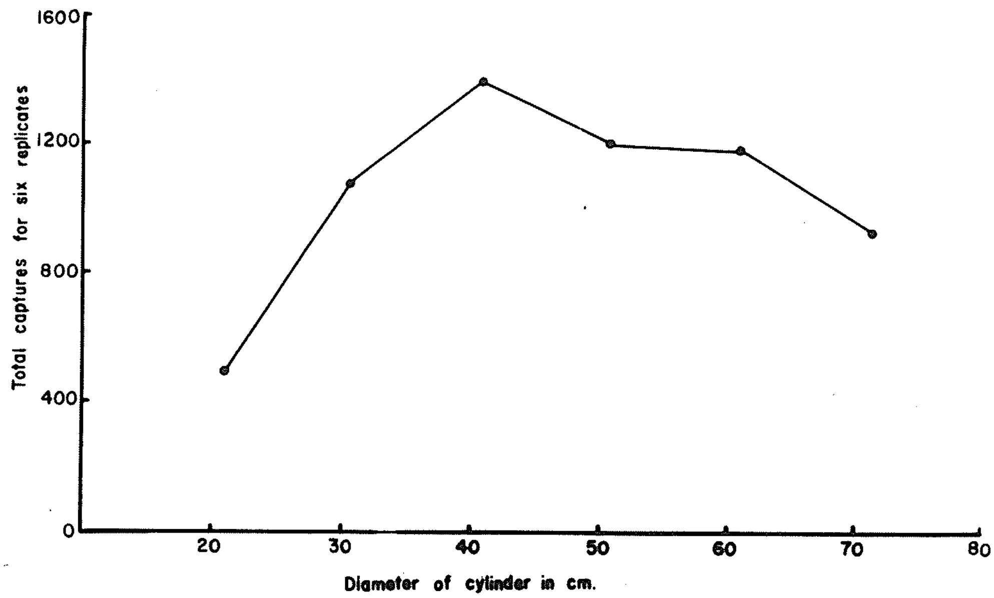
Methods and materials. Six cylinders were constructed from corrugated cardboard so that the diameter and height were equal. The smallest cylinder had a diameter of 20.5 cm and the diameter of the others increased arithmetically by 10.24 cm. The cylinders were given two coats of black enamel paint and were covered with tanglefoot. They were then suspended from a suitable support so that the center of each was 70 cm above the ground. The cylinders were positioned on the periphery of a circle approximately three meters from each other. The position of the cylinders relative to each other was randomized in each replicate and six replicates were completed. After each replicate the flies were removed, counted and the tanglefoot replenished as required.

Results and discussion. The logarithms of the total captures are plotted against the diameter of the cylinders in cm in Figure 8a. The curve shows that the cylinder 41 cm in diameter captured the largest number of flies and that the total captures for larger cylinders fall off slightly. Analysis of the results showed that captures on the smallest cylinder were significantly lower than on the larger ones but there was no significant difference among captures on the other five.

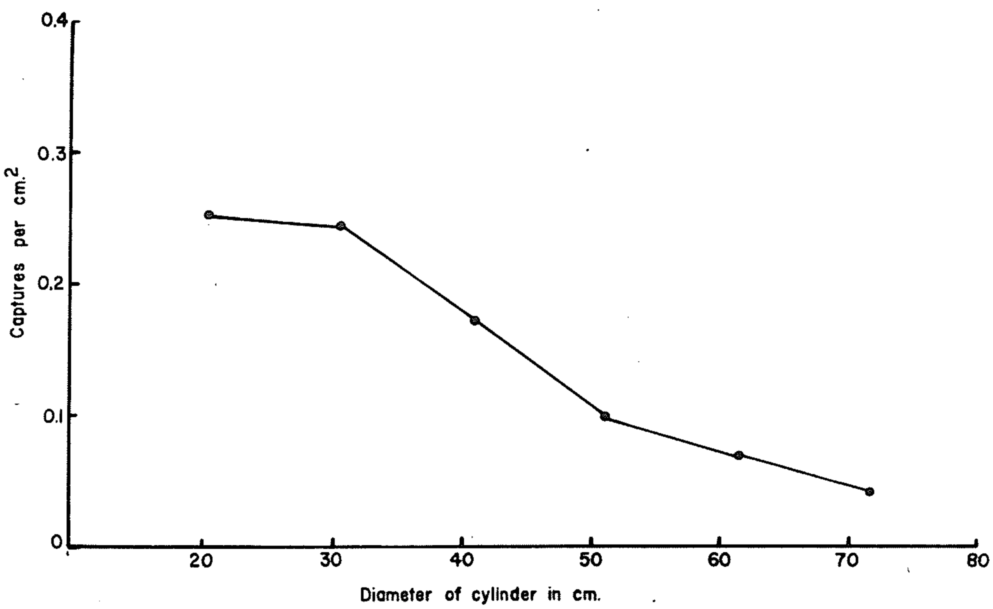
In Figure 8b the logarithms of the total captures are plotted against the surface area of the cylinders. Considering the attractiveness of the cylinders with respect to surface area, the smaller two cylinders were the most attractive. The point at which this relationship breaks down as the area

Figure 8a. Total captures of Tabanids on sticky black horizontal cylinders (diameter=height) of different size plotted against the diameter of the cylinder.

Figure 8b. Total captures of Tabanids on sticky black horizontal cylinders (diameter=height) of different size plotted against the surface area of the cylinder.



1600
1200
800
400
0
Total captures for six replicates
20
30
40
50
60
70
80
Diameter of cylinder in cm.



0.4
0.3
0.2
0.1
0
Captures per cm.2
20
30
40
50
60
70
80
Diameter of cylinder in cm.

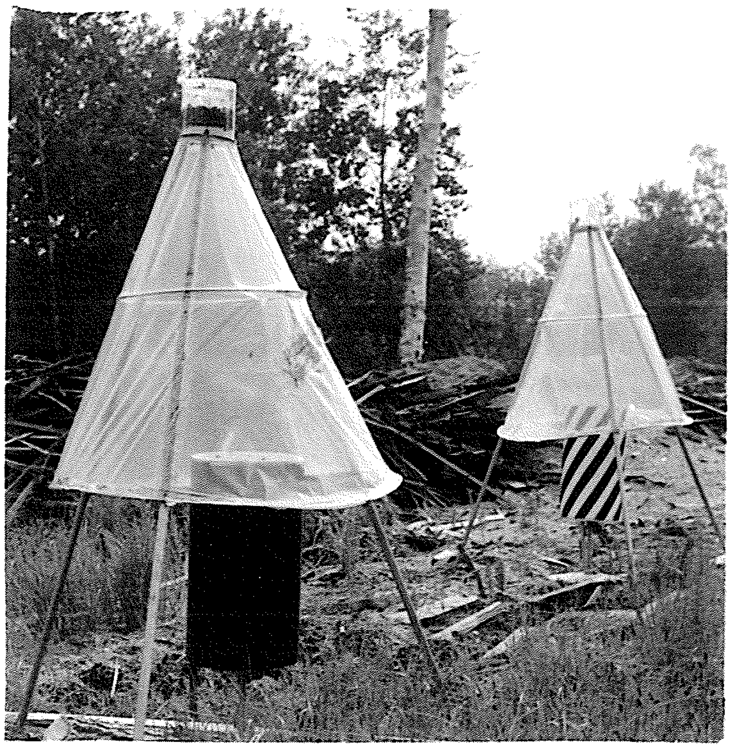
decreases was not reached with the sizes used in the experiment. It appears from Figure 8b, however, that the effectiveness of the cylinders per unit area was leveling out at the smallest size.

It must be remembered that this experiment gives an indication of the size of the cylinder that is maximally alighted on or struck by tabanids. It gives no unequivocal indication of which size evokes maximal orientation from a distance. At greater distances it is possible that the larger objects or even the entire group of objects provide a visual imput that evokes orientated flight toward them. At short range, however, the object that attracts a given horse fly might be different than the one that attracted it from a greater distance. In other words, the maximal size may depend on the distance the horse fly is from the object.

There is evidence that reduction of the area of black on an object reduces its attractiveness to tabanids if it is done in a manner that breaks up the conjointness of the figure (Barrass 1960b). A confirmation of this is a byproduct of this investigation.

A vertical cylinder striped black and white was compared with a solid black cylinder of the same size as illustrated in Figure 9. The total captures in the trap with the solid black cylinder were, in two replicates, 1498 as compared with 35 for the striped cylinder. Thus, by reducing the area

Figure 9. Manitoba Fly Traps over vertical cylinders, one completely black, the other striped black and white at Beaver Creek, 1961.



of black on the vertical cylinder by one-half, its attractiveness was reduced 32 times. Referring to the experiment in Chapter II (Table VIII), where shiny aluminum discs were placed on a matte black cylinder, captures in traps with this object were reduced by almost six times as compared with captures with a solid matte black cylinder, although the discs covered only one-ninth of the area of black. In the experiment with solid black cylinders of different size just described, the smallest cylinder captured one-half as many tabanids as the one next larger in the series and its surface area was just less than one-half that of the larger. It appears, therefore, that the conjointness of a black figure is an important factor in its attractiveness to tabanids.

CHAPTER V

INVESTIGATIONS ON THE INFLUENCE OF MOTION OF OBJECTS ON THEIR ATTRACTIVENESS TO TABANIDAE

Review of the Literature

The effect of motion of objects on their attractiveness to horse flies was noted by Philip (1931). This author stated that almost any moving object will cause them to hesitate for investigation in passing and refers also to the "habit of females following trains." Frost and Pechuman (1958) state that, ". . . They [horse flies] frequently follow moving objects such as automobiles and trains keeping pace with them . . . ." These authors observed also that moving objects seemed more subject to attack by horse flies. Barrass (1960) reported the settling of the tabanid, Haematopota insidiatrix Aust. on cloth screens as they were being carried through the bush.

The importance of motion of objects for the orientation of the mosquito, Aedes agypti (L.) has been demonstrated by Sippell and Brown (1953). An active mouse in an air tight transparent box was approached more frequently than an anaesthetized mouse in a similar container. A black canister moved to and fro was about twice as attractive as a stationary one to Aedes agypti. Haufe and Burgess (1960) used a revolving cylinder with black and white stripes to attract mosquitoes into a trap in the field. Magnus (1956) showed that a striped drum which was designed to simulate the female was more attractive to the male when rotated. These observations in the literature refer to orientation from relatively short distances.

It might be stated that while horse flies follow moving objects this may not indicate an optomotor response. It is perhaps better described as an example of menotaxis (Fraenkel and Gunn, 1940) in that the insect maintains a constant position relative to the object.

Methods and materials. Two experiments were conducted. In the first, a moving object was provided as follows. A laundry tub approximately 60 cm in diameter and 40 cm deep was inverted and its bottom fixed at the center to the hub of a front wheel bicycle assembly. The axle of the assembly was screwed into a length of pipe which in turn was welded to a suitable base. The tub itself was painted black. Four white anemometer cups, 15 cm in diameter, were fastened to the sides of the tub. Two such devices were constructed. Each was placed on top of a larger inverted laundry tub (also painted black) to elevate the rotating tub to the level of the canopy of a Manitoba fly trap which was placed over both. In alternating replicates one tub was tethered, then the other. Ten replicates of this experiment, which was carried out at Lake Francis in 1960, were completed.

A second experiment was carried out at Beaver Creek in 1961. A string saddle was constructed for each of two glossy black spheres. Each sphere was suspended by means of the saddle from a Manitoba fly trap. One of the spheres was tethered by wiring three of the strings of the saddle to the three legs of the trap. Complete immobility of the tethered sphere was possible by this method whereas the untethered sphere was nearly always in motion, even in slight breezes. After each replicate the tethered sphere was released and the free one tethered. Twelve replicates were completed.

Results and discussion. The results of the first experiment are shown in Table XIII. Analysis of the data showed no significant difference between the captures although somewhat fewer flies were captured in the traps over the rotating tub.

The results of the second experiment are presented in Table XIV. Here again analysis of the data showed no significant difference between captures in traps over the stationary and free sphere although more flies were captured in the trap fitted with the stationary sphere. It is evident that motion as presented by these objects under field conditions did not increase their attractiveness to horse flies.

TABLE XIII

CAPTURES OF TABANIDAE IN TRAPS OVER A STATIONARY AND ROTATING BLACK TUB AT LAKE FRANCIS, 1960

Black tub	Replicate number										Total*
	1	2	3	4	5	6	7	8	9	10	
Stationary	3	60	31	19	10	18	34	14	9	14	212
Rotating	4	65	17	14	5	9	18	23	5	14	174

*No significant difference between treatments

TABLE XIV

CAPTURES OF TABANIDAE IN TRAPS OVER
TETHERED AND FREE SPHERES
AT BEAVER CREEK, 1961

Sphere	Replicate Number												Total*
	1	2	3	4	5	6	7	8	9	10	11	12	
Tethered	2646	1615	1135	1426	2223	327	1266	175	245	140	215	153	11,566
Free	1978	1531	643	1379	1525	265	757	172	113	221	319	185	9,086

* No significant difference between treatments

CHAPTER VI

INVESTIGATIONS ON THE EFFECT OF THE SURFACE TEMPERATURE OF OBJECTS ON THEIR ATTRACTIVENESS TO TABANIDAE

Review of the Literature

The importance of the temperature of objects for their attractiveness to tabanids was noted by Philip (1931). He stated that, "heat seems to be the chief attraction as they [horse flies] seek the warmest parts of the car," and that, "tires recently heated by running are more attractive than those that have cooled or stood for some time." Pechuman (1961) stated in this connection that, "the attraction appears to be a thermotactic response to the warmth radiated by the surface."

Experiments with other biting flies have shown that thettemperature of bodies is an important factor in their attractiveness. Peterson and Brown (1951) showed that objects at temperatures from 100 to 120° F. were more attractive to *Aedes agypti* than similar objects 20° cooler. Bodies heated to 130° F. were repellent. Laarman (1955) showed that for *Anopheles maculipennis atroparvus* either moisture or heat is necessary to evoke alighting and that heat is the more important factor. Krijgsman (1930) and Krijgsman and Windred (1930) found that *Stomoxys calcitrans* L. and *Lyperosia exigua* were attracted to heat under the conditions of his experiments.

Methods and materials. Two steel barrels, 34 cm in diameter and 44.5 cm deep, served as the attracting objects for this experiment. A hole was cut in the side of each of the barrels and each was placed horizontally in a wooden stand under a Manitoba Fly Trap. Both the barrels and the stands were painted glossy black. One barrel was filled with water and the other was filled with a mixture of water and ice which was maintained throughout each replicate. The surface temperature of each barrel was monitored by a "banjo" thermocouple connected to a YSI tele-thermometer Model 44. The temperature in the canopies of the traps, 60 cm above the barrels, and the ambient temperature was monitored by air thermocouples connected to the same instrument. The experiment was replicated three times with the position of the cool and warm barrels changed after each replicate. The apparatus is illustrated in Figure 10.

Results and discussion. The captures in the traps for each replicate, the mean temperature in the canopy, surface of the barrels and the ambient air are presented in Table XV. Analysis of the captures showed no significant difference at the 5 per cent level between the captures in traps over the warm and cool barrel although the captures were always higher in the trap over the warm barrel.

The results of this experiment indicate that a warm body is not appreciably more attractive to horse flies than a cool one under the field conditions of the experiments. There

Figure 10. Manitoba Fly Traps over barrels; one filled with water, the other with a mixture of water and ice.

TABLE XV

CAPTURES OF TABANIDAE IN TRAPS OVER WARM AND COOL BLACK ENAMEL BARRELS

Replicate	Captures*	Mean Surface Temp. °C.	Mean Canopy Temp. °C.	Mean Ambient Temp. °C.
1 - cool barrel	265	10.3	28.7	28.0
1 - warm barrel	345	30.9	31.1	28.0
2 - cool barrel	271	11.5	28.8	28.3
2 - warm barrel	390	31.4	29.8	28.3
3 - cool barrel	153	11.0	30.4	28.0
3 - warm barrel	191	31.0	31.8	28.0

*No significant difference between treatments.

is some evidence from the data of the experiments described in Chapter II that support this finding.

1. Measurements of the surface temperature of the red and black spheres showed that the black sphere was 4° C. higher than that of the red. With only one exception (that of _H. epistates_ at the beach location), there was no significant difference between captures in traps supporting red and black spheres.
2. The surface temperature of the white spheres were from 7 to 10°C. lower than that of the black. However, for two species, _H. illota_ and _C. mitis_, the black and white spheres were almost equally attractive.
3. The surface temperature of the matte black rugose horizontal cylinder was 6.4°C. higher than that of the glossy black cylinder yet the latter was highly significantly more attractive.

It may be concluded that the surface temperature of a body is not as significant a factor as visual factors in the attraction of horse flies to objects at the unknown distances in the field from which the horse flies orientate to them.

CHAPTER VII

THE SEASONAL AND GEOGRAPHICAL DISTRIBUTION OF TABANIDAE IN SOUTHERN MANITOBA AS DETERMINED BY CAPTURES IN MANITOBA FLY TRAPS

Review of the Literature

The seasonal and graphical distribution of Tabanidae in Manitoba has received little attention from previous authors. Cameron (1926) and Curran (1927) described a few species from several areas of the province. Miller (1951) made an extensive survey of tabanids at Churchill in northern Manitoba and described the seasonal distribution of some species of *Tabanus* (*Hybomitra*) and *Chrysops*. McAlpine (1961) collected horse flies in the Ninette and Brandon areas of Manitoba during 1958. He observed that larvae of *H. frontalis* (Wlk.) are found mainly in acid soils and *H. pediontis* McA. in alkaline sloughs and ponds. He collected several species of *Chrysops* and a large number of species of *Tabanus* (*Hybomitra*).

Elsewhere in Canada, a seasonal distribution survey of tabanids was made by Davies (1959) in Algonquin Park, Ontario. He collected 2,712 females of *Chrysops* species, 278 females of 13 *Tabanus* and *Hybomitra* species and one species of *Stonemyia*. The same author found that *H. trepida* McD. and *H. epistates* (O.S.) constituted about one-half of the population of horse flies during the summer. *Chrysops* vittatus Weid, C. montanus O.S. and C. wiedemanni (=univittatus Marq.) made up over one-half of the population of the Chrysops genus. H. nuda (McD.) and H. lasiophthalma (Macq.) were the early species appearing late in May and disappearing at the end of July.

Judd (1958) studied the seasonal distribution of horse flies in the Byron Bog in southwestern Ontario. H. minuscula Hine comprised 90 per cent of the tabanid population; the remainder included nine species. H. zonalis (Kirby) appeared earliest, being taken on July 17 and a species of Atylotus remained the longest, persisting to August 26.

Teskey (1960) collected 28 specimens of Tabanidae on farms near Guelph and Erin, Ontario. He found that H. lasiophthalma comprised about 50 per cent of the population in this area. He noted also that the horse fly activity extended from May to the middle of September. Tabanus quinquevittatus Weid. had the longest season commencing in early July and persisting into September. Of the genus Chrysops, C. inda O.S. was the most numerous and the earliest species, appearing in late May. The late summer species were C. vittatus and C. univittatus (=macquarti Philip), the latter making up about 50 per cent of the Chrysops population in one specific locality. This author also observed that over 80 per cent of the tabanid bites on livestock were inflicted by Tabanus and Hybomitra species.

The distribution of European Tabanidae in the

Kampinos Forest near Warsaw has been studied recently by Trojan (1956). However, none of the species reported in this paper has been found in Manitoba. Pechuman (1957) provided classification keys and occurrence records for Tabanidae in New York and Pechuman et al (1961) published a similar work for the Tabanidae of Ontario. These three papers also list numerous references to earlier investigations of various aspects of horse fly occurrence and distribution.

In an M.Sc. thesis (Bracken, 1960), I reported the occurrence and seasonal distributions of Tabanidae taken in various forms of the Manitoba fly trap placed in the Whiteshell, La Salle, Raeburn and Lake Francis areas. One of the features of these data was the large number of different species taken in the forested Whiteshell area compared with the relatively few species taken in the Parkland areas of Raeburn and Lake Francis. Twenty-four species were captured in the Whiteshell. Of these, ten were Chrysops, eleven Hybomitra, two Tabanus and one Haematopota. Only one species of Chrysops, C. aestuans Wulp., was captured at La Salle and Raeburn where it comprised 50 per cent of the total tabanid population. Relatively smaller numbers of this species were found at Lake Francis but the species was not taken in the Whiteshell region. T. similis Macq. made up about 35 per cent of the horse fly population at La Salle and Lake Francis but was not captured in the Whiteshell. On the other hand _Hybomitra typhus_ (Whitn.) made up about 47 per cent of the captures in the Whiteshell but was not taken in the other three regions. Pechuman (1961) identified twenty-six species from Whiteshell collections. He stated that a number of the Whiteshell species are eastern forms probably reaching their extreme western range at this point and this accounts for their occurrence in Manitoba collections.

It was evident from this data that the occurrence of tabanid species was very variable in Manitoba even in adjacent areas. During the summer of 1961, a survey was conducted with the following objectives: (1) to determine the species distribution of horse flies occuring in southern Manitoba, (2) to study the seasonal distribution of the various species in this area. It was hoped also that some evidence could be obtained to determine whether there was any relationship between the general soil type of an area and its tabanid fauna.

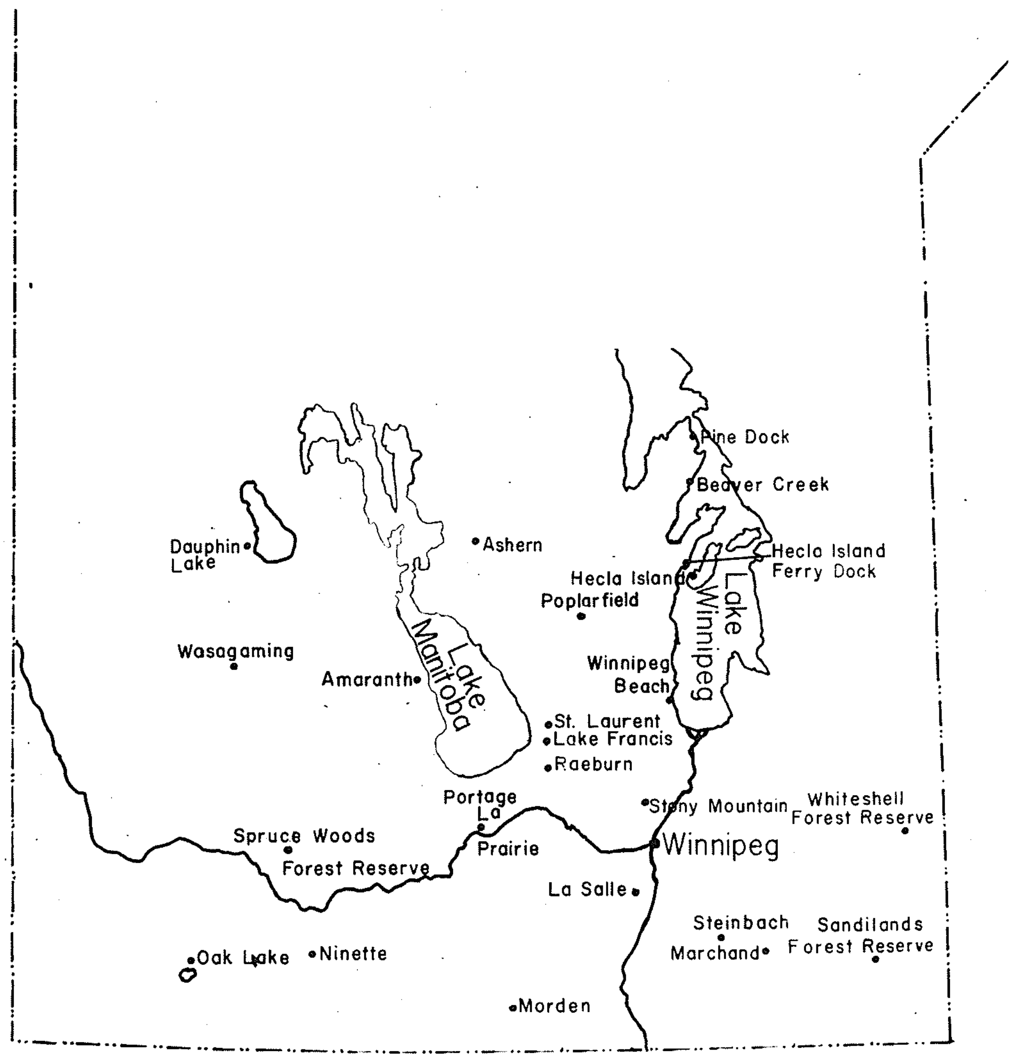
Methods and materials. The relative numbers of the various species were estimated by means of traps, the trap captures were taken as indices of the population densities of the species. This assumption is open to criticism but no other method provides so much information over a large area in a short time. The data are presumably no more subject to bias than other methods and provide at least a first approximation.

The traps used for this study were the same as those used in the behavioural investigations. The attracting object was a sphere painted with black enamel, inflated to 61 cm in diameter, or in some traps a black enamel cylinder suspended horizontally was used. The traps were set up in various localities in Manitoba during the last week of May and the first week of June 1961. It was intended originally to have the traps serviced weekly but this was not always possible. The captured specimens were classified according to the key for the Tabanidae of Ontario by Pechuman et al (1961). A representative sample of the classified specimens was then sent to Dr. Pechuman for verification and correction.

A map showing the locations of the traps is shown in Figure 11. Since tabanids are usually more abundant in areas where the soil is moist the individual traps were located on or near swamps, bogs, ditches, dugouts or sloughs. Attempts were made to locate the traps in sheltered areas and to protect them from cattle by fencing where necessary. The traps situated far from Winnipeg were usually serviced by a local farmer or agricultural research worker. However, optimum locations and servicing arrangements were not realized for all traps.

Results and discussion. Of the twenty-one trap locations only six yielded sufficient information to give an

Figure 11. Map of Manitoba showing the positions of Manitoba Fly Traps during the summer of 1961.



Pine Dock
Beaver Creek
Dauphin Lake
Ashern
Hecla Island Ferry Dock
Hecla Island
Poplarfield
Lake Winnipeg
Wasagaming
Amaranth
Lake Manitoba
Winnipeg Beach
St. Laurent
Lake Francis
Raeburn
Portage La Prairie
Stony Mountain
Whiteshell Forest Reserve
Spruce Woods Forest Reserve
Winnipeg
La Salle
Steinbach
Sandilands Forest Reserve
Marchand
Oak Lake
Ninette
Morden

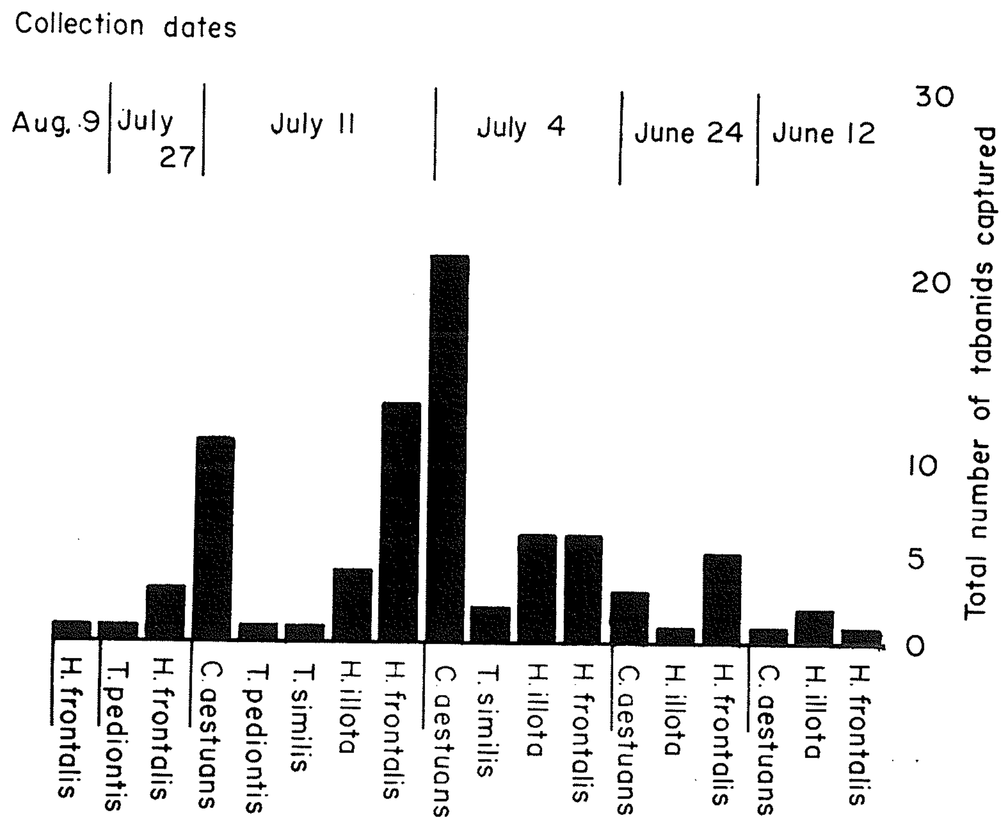
indication of the relative abundance of different species. The captures of individual species as a percentage of the total captures of horse flies in the traps are presented in Table XVI. Data from a trap at St. Laurent in 1960 are also included in this table. The seasonal distribution of the more prominant species at these six locations is plotted in Figures 12 to 17 inclusive. Low captures in traps in the other locations were often due to poor location, poor servicing or damage to the trap by wind or animals. The species captured in traps at these locations is noted in Table XVII.

The genus _Atylotus_ is represented by only one species, _incisuralis_ Wlk. This species was captured at Oak Lake and Steinbach. In previous years it was also captured at Raeburn and Lake Francis (Bracken, 1960). It has been captured only in parkland areas of the province.

Haematopota americana O.S. was the only species of the genus _Haematopota_ captured. It had been captured previously in the Whiteshell area (Bracken, 1960). It was found only in the Beaver Creek area in this survey.

The genus _Tabanus_ was represented by only two species in the captures, _marginalis_ Fabr. and _similis_ Macq. _T. marginalis_ was found in small numbers in the Beaver Creek area whereas _T. similis_ was relatively common in parkland areas such as St. Laurent.

Figure 12. The seasonal distribution of Tabanid species at Ninette, Manitoba, 1961.



Collection dates
Aug. 9
July 27
July 11
July 4
June 24
June 12
Total number of tabanids captured
0
5
10
20
30
H. frontalis
T. pediontis
H. frontalis
C. aestuans
T. pediontis
T. similis
H. illota
H. frontalis
C. aestuans
T. similis
H. illota
H. frontalis
C. aestuans
H. illota
H. frontalis
C. aestuans
H. illota
H. frontalis

Figure 13. The seasonal distribution of Tabanid species at Dauphin Lake, Manitoba, 1961.

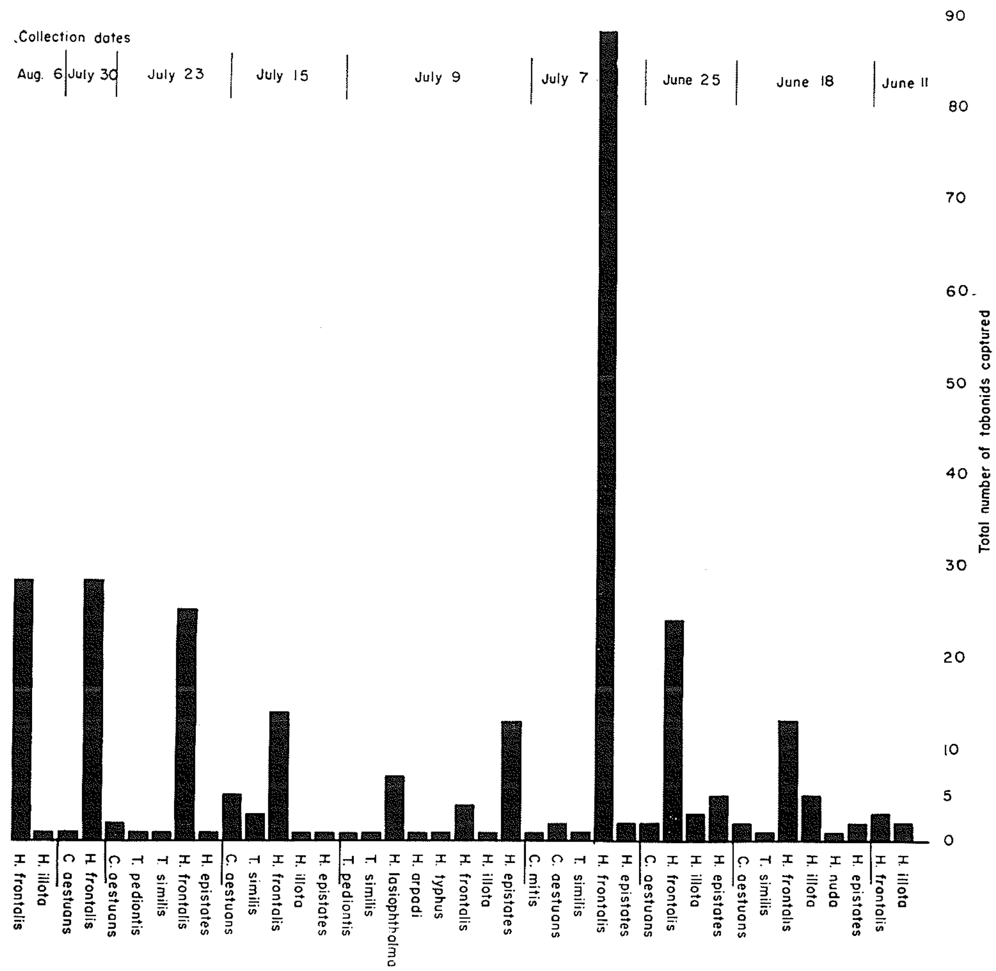

Collection dates
Aug. 6
July 30
July 23
July 15
July 9
July 7
June 25
June 18
June 11
Total number of tabanids captured
90
80
70
60
50
40
30
20
10
5
0
H. frontalis
H. illota
C. aestuans
H. frontalis
C. aestuans
T. pediontis
T. similis
H. frontalis
H. epistates
C. aestuans
T. similis
H. frontalis
H. illota
H. epistates
T. pediontis
T. similis
H. lasiophthalma
H. arpadi
H. typhus
H. frontalis
H. illota
H. epistates
C. mitis
C. aestuans
T. similis
H. frontalis
H. epistates
C. aestuans
H. frontalis
H. illota
H. epistates
C. aestuans
T. similis
H. frontalis
H. illota
H. nuda
H. epistates
H. frontalis
H. illota

Figure 14. The seasonal distribution of Tabanid species at Spruce Woods, Manitoba, 1961.

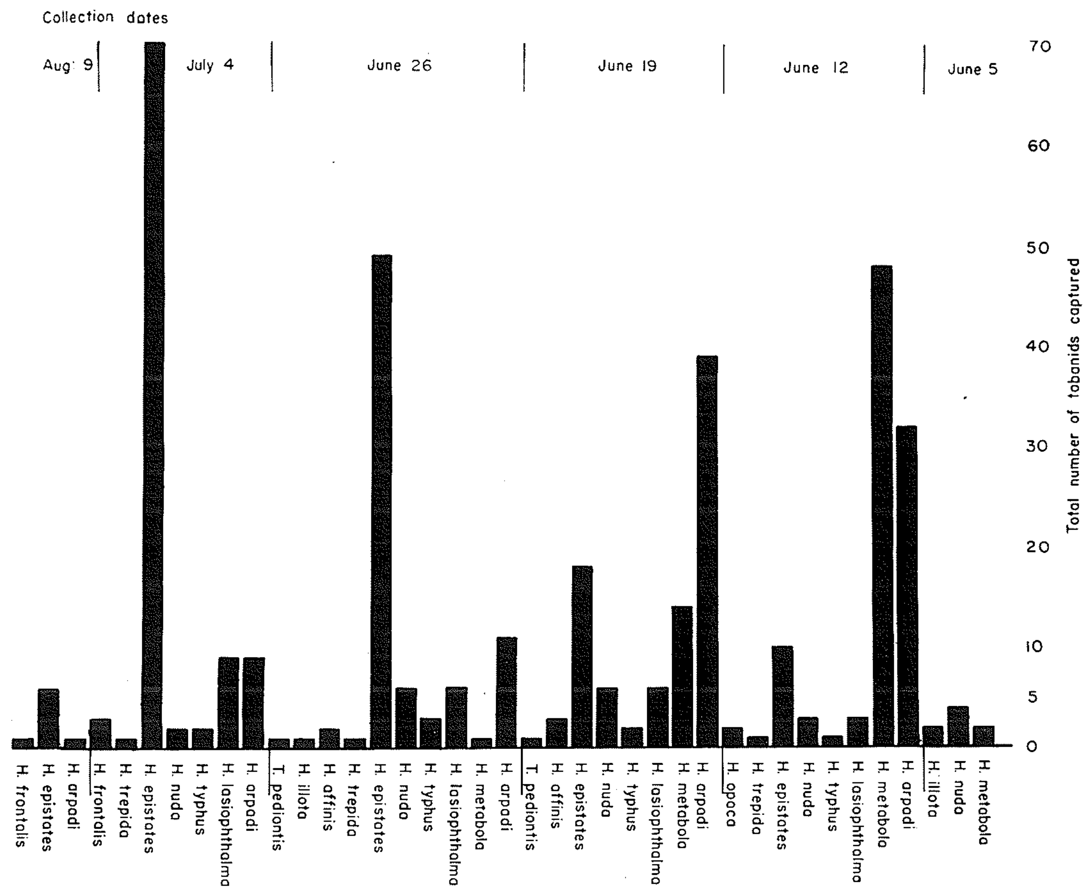

Collection dates
Aug. 9
July 4
June 26
June 19
June 12
June 5
Total number of tabanids captured
0
5
10
20
30
40
50
60
70
H. frontalis
H. epistates
H. arpadi
H. frontalis
H. trepida
H. epistates
H. nuda
H. typhus
H. lasiophthalma
H. arpadi
T. pediontis
H. illota
H. affinis
H. trepida
H. epistates
H. nuda
H. typhus
H. lasiophthalma
H. metabola
H. arpadi
T. pediontis
H. affinis
H. epistates
H. nuda
H. typhus
H. lasiophthalma
H. metabola
H. arpadi
H. opaca
H. trepida
H. epistates
H. nuda
H. typhus
H. lasiophthalma
H. metabola
H. arpadi
H. illota
H. nuda
H. metabola

Figure 15. The seasonal distribution of Tabanid species at Sandilands, Manitoba, 1961.

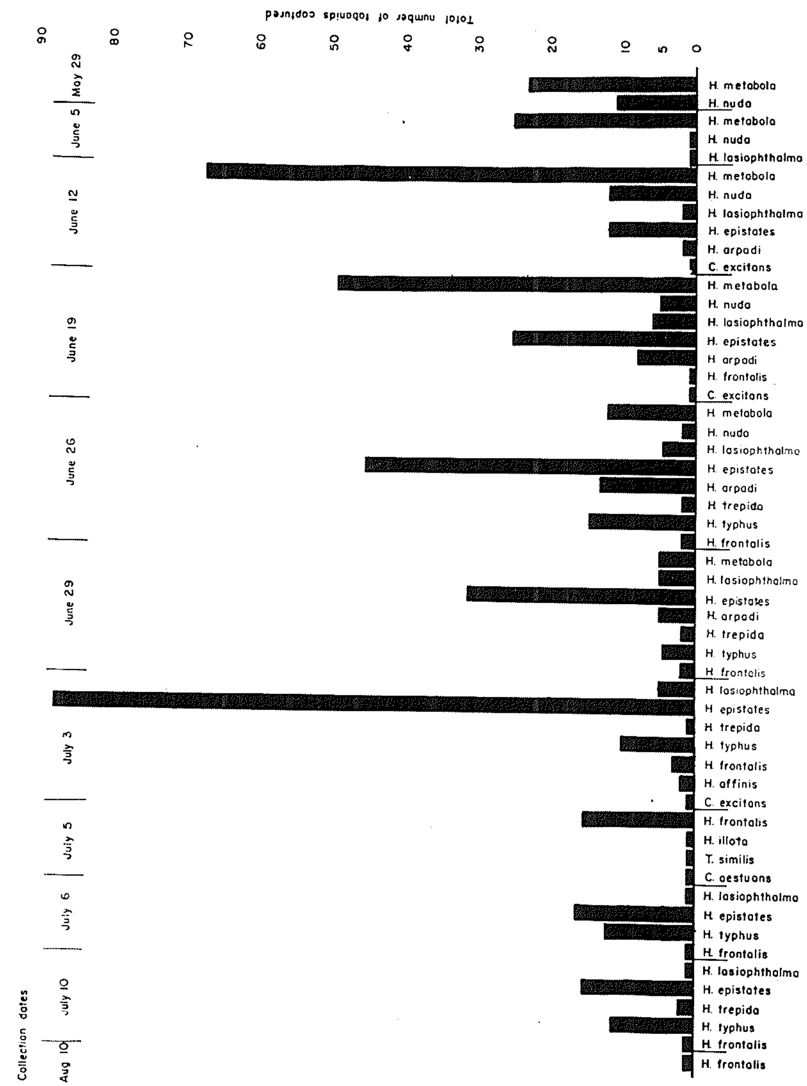

Total number of tabanids captured
0
5
10
20
30
40
50
60
70
80
90
H. metabola
H. nuda
H. metabola
H. nuda
H. lasiophthalma
H. metabola
H. nuda
H. lasiophthalma
H. epistates
H. arpadi
C. excitans
H. metabola
H. nuda
H. lasiophthalma
H. epistates
H. arpadi
H. frontalis
C. excitans
H. metabola
H. nuda
H. lasiophthalma
H. epistates
H. arpadi
H. trepida
H. typhus
H. frontalis
H. metabola
H. lasiophthalma
H. epistates
H. arpadi
H. trepida
H. typhus
H. frontalis
H. lasiophthalma
H. epistates
H. trepida
H. typhus
H. frontalis
H. affinis
C. excitans
H. frontalis
H. illota
T. similis
C. aestuans
H. lasiophthalma
H. epistates
H. typhus
H. frontalis
H. lasiophthalma
H. epistates
H. trepida
H. typhus
H. frontalis
H. frontalis
May 29
June 5
June 12
June 19
June 26
June 29
July 3
July 5
July 6
July 10
Aug 10
Collection dates

Figure 16. The seasonal distribution of Tabanid species at Wasagaming, Manitoba, 1961.

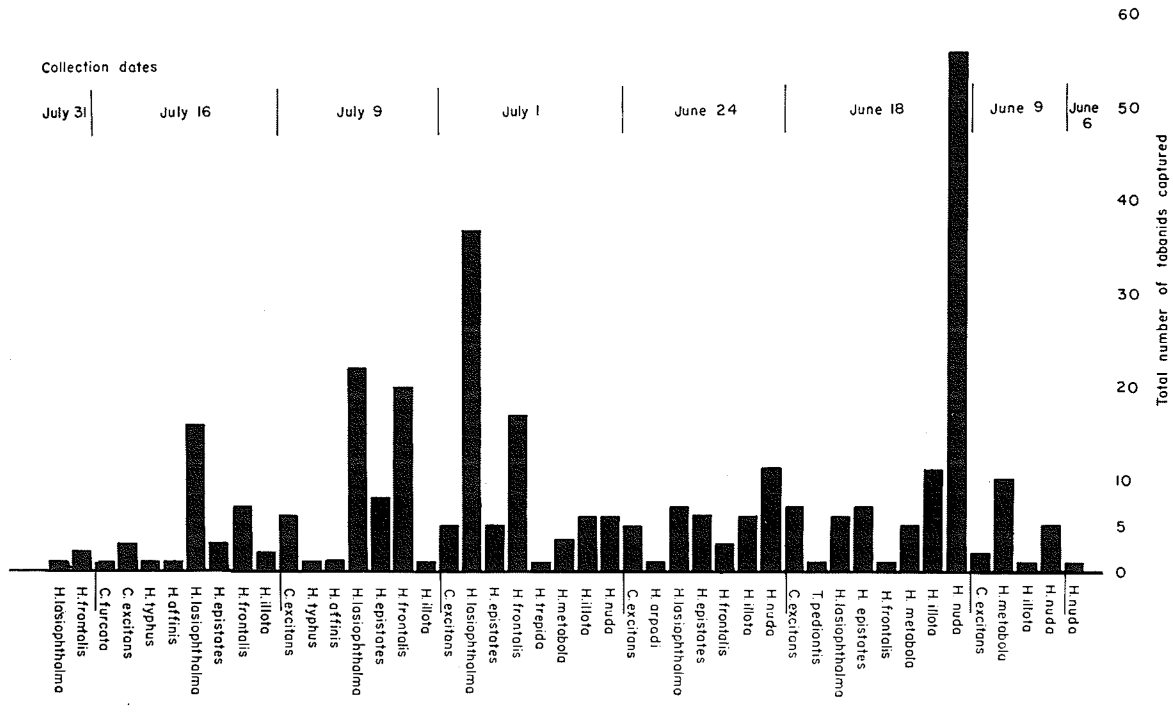

Collection dates
July 31
July 16
July 9
July 1
June 24
June 18
June 9
June 6
Total number of tabanids captured
0
5
10
20
30
40
50
60
H.lasiophthalma
H.frontalis
C.furcata
C.excitans
H.typhus
H.affinis
H.lasiophthalma
H.epistates
H.frontalis
H.illota
C.excitans
H.typhus
H.affinis
H.lasiophthalma
H.epistates
H.frontalis
H.illota
C.excitans
H.lasiophthalma
H.epistates
H.frontalis
H.trepida
H.metabola
H.illota
H.nuda
C.excitans
H.arpadi
H.lasiophthalma
H.epistates
H.frontalis
H.illota
H.nuda
C.excitans
T.pediontis
H.lasiophthalma
H.epistates
H.frontalis
H.metabola
H.illota
H.nuda
C.excitans
H.metabola
H.illota
H.nuda
H.nuda

Figure 17. The seasonal distribution of Tabanid species at Beaver Creek, Manitoba, 1961.

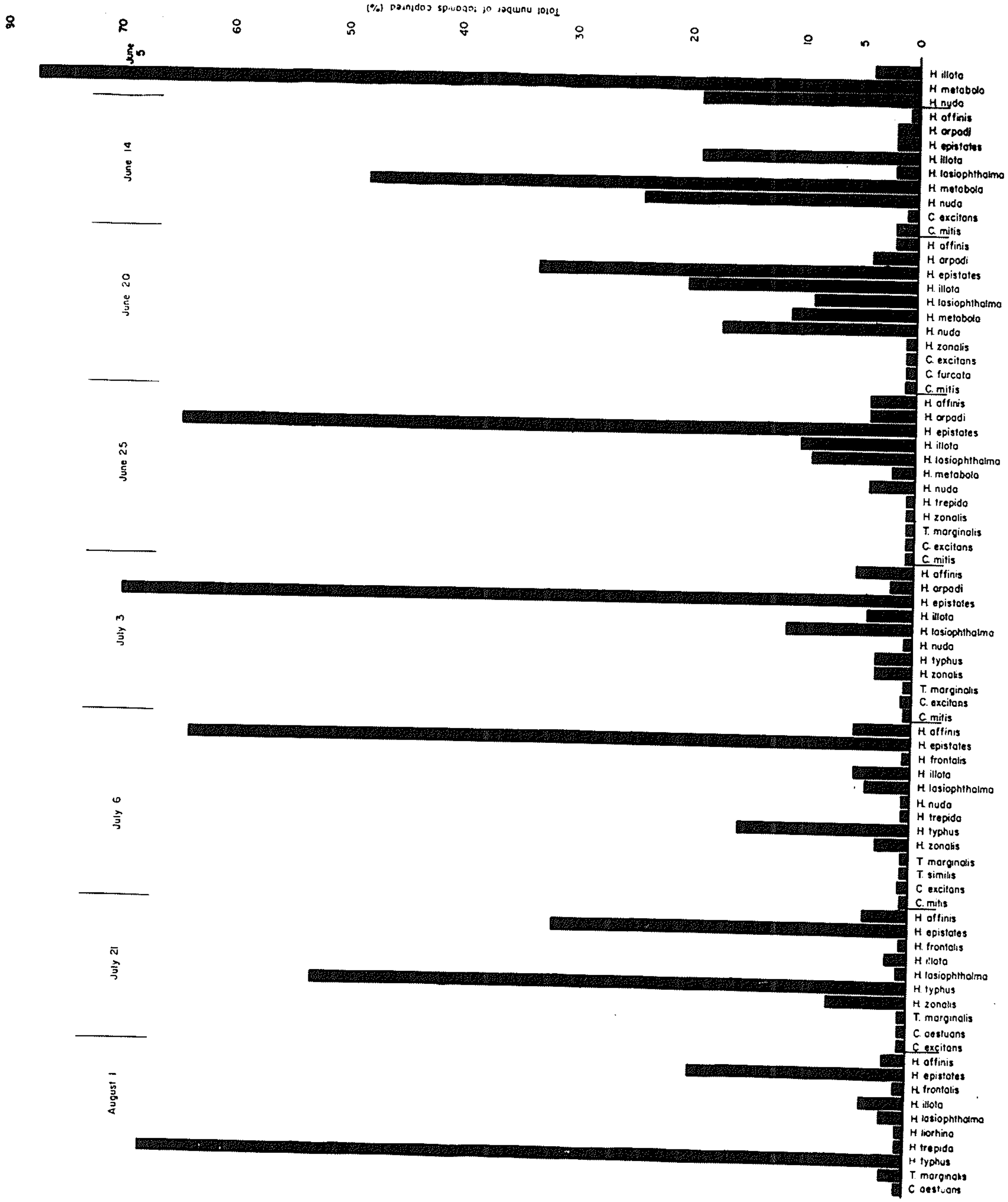

Total number of tabanids captured (%)
90
70
60
50
40
30
20
10
5
0
June 5
H illota
H metabola
H nuda
June 14
H affinis
H arpadi
H epistates
H illota
H lasiophthalma
H metabola
H nuda
C excitans
C mitis
June 20
H affinis
H arpadi
H epistates
H illota
H lasiophthalma
H metabola
H nuda
H zonalis
C excitans
C furcata
C mitis
June 25
H affinis
H arpadi
H epistates
H illota
H lasiophthalma
H metabola
H nuda
H trepida
H zonalis
T marginalis
C excitans
C mitis
July 3
H affinis
H arpadi
H epistates
H illota
H lasiophthalma
H nuda
H typhus
H zonalis
T marginalis
C excitans
C mitis
July 6
H affinis
H epistates
H frontalis
H illota
H lasiophthalma
H nuda
H trepida
H typhus
H zonalis
T marginalis
T similis
C excitans
C mitis
July 21
H affinis
H epistates
H frontalis
H illota
H lasiophthalma
H typhus
H zonalis
T marginalis
C oestuans
C excitans
August 1
H affinis
H epistates
H frontalis
H illota
H lasiophthalma
H liorhina
H trepida
H typhus
T marginalis
C oestuans

TABLE XVI

RELATIVE ABUNDANCE OF SPECIES OF TABANIDAE CAPTURED IN MANITOBA FLY TRAPS IN SEVEN LOCALITIES OF SOUTHERN MANITOBA IN 1961

Species	St. Laurent*	Ninette	Wasa-gaming	Sandi-lands	Spruce Woods	Dauphin Lake	Beaver Creek
Chrysops aestuans Wulp	3	41		<1		4	<1
Chrysops excitans Wlk.			8	<1			1
Chrysops furcatus Wlk.			1				<1
Chrysops mitis O.S.							<1
Haematopota americana O.S.						1	<1
Hybomitra affinis (Kirby)							3
Hybomitra arpadi (Szil.)				<1	1		2
Hybomitra epistates (O.S.)			<1	4	23	<1	46
Hybomitra frontalis (Wlk.)	1		8	39	40	8	<1
Hybomitra illota (O.S.)	3	37	15	4	1	76	10
Hybomitra lasiophthalma (Macq.)	9	15	8	<1	<1	4	6
Hybomitra liorhina (Philip)	5		32	4	7	2	<1
Hybomitra metabola (McD.)	1						11
Hybomitra nuda (McD.)			5	32	16		8
Hybomitra opaca (near) (Coq.)	64		22	5	6	<1	
Hybomitra pediontis McA.					<1		
Hybomitra trepida (McD.)		3	1	1	<1	1	<1
Hybomitra typhus (Whitn.)			1	1	<1		10
Hybomitra zonalis (Kirby)			1	9	2	<1	2
Tabanus marginalis Fabr.							<1
Tabanus similis (Macq.)	16	4		1		2	<1
Total captures	341	78	360	588	382	315	7351

*The results for this area are from 1960.

Note: Figures refer to the per cent of the total captured.
<1 indicates a species was present in very small numbers.

TABLE XVII

OCCURRENCE OF SPECIES OF TABANIDAE IN CAPTURES OF TRAPS IN DIFFERENT LOCATIONS IN MANITOBA IN 1961

Species	Amaranth	Ashern	Hecla Island Ferry Dock	Marchand	Morden	Oak Bluff	Oak Lake	Pine Dock	Portage la Prairie	Poplar-field	Steinbach	Stony Mountain	Teulon	Winnipeg Beach
Atylotus incisuralis (Wlk.)							+				+			
Chrysops aestuans Wulp			+		+	+	+		+					
Chrysops mitis O.S.			+											
Tabanus similis Macq.				+			+		+		+			
Hybomitra arpadi (Szil.)								+						
Hybomitra epistates (O.S.)	+		+	+				+			+		+	
Hybomitra frontalis (Wlk.)	+		+	+			+		+	+	+		+	
Hybomitra illota (O.S.)	+	+	+	+			+		+	+	+	+	+	
Hybomitra lasiophthalma (Macq.)	+			+			+			+	+		+	+
Hybomitra metabola (McD.)		+	+	+				+		+			+	
Hybomitra nuda (McD.)		+	+	+				+		+	+	+	+	+
Hybomitra trepida (McD.)				+										
Hybomitra typhus (Whitn.)				+				+						

Four species of the genus *Chrysops* were captured. Of these *C. aestuans* Wulp. was the most abundant and made up 40 per cent of the total captures at Ninette. This species was most frequently captured in parkland areas. It made up about 40 per cent of the total captures in traps at Raeburn and La Salle in previous years (Bracken, 1960). The other three species, *C. excitans* Wlk., *C. furcatus* Wlk. and *C. mitis* O.S., were captured in relatively small numbers in forested areas such as Beaver Creek, Wasagaming and Dauphin Lake.

Hybomitra was better represented than the other genera in the captures. The distribution of representatives of this genus will be summarized briefly.

H. affinis (Kirby) and *H. arpadi* (Szil.) were captured in traps located in forested areas such as Sandilands, Spruce Woods Forest Reserve and at Beaver Creek.

H. epistates (O.S.) is widespread throughout the area studied and is very numerous in some locations. It constituted 40 per cent of the total captures in the Sandilands, Spruce Woods Forest Reserve and Beaver Creek. Although it is more numerous in forested areas it also occurs in parkland areas such as St. Laurent.

H. illota (O.S.) is also widespread throughout the area studied and does not appear to be more abundant in one area than others.

H. lasiophthalma Macq. is similar to *H. illota* in its distribution. It generally makes up a small part of the population but was relatively abundant at Wasagaming and in Riding Mountain National Park.

H. liorhina Philip appears to be limited in distribution and abundance. Only a few specimens were captured in this survey at Beaver Creek. In 1959, however, it made up 6 per cent of the total captures in traps at Lake Francis (Bracken, 1960).

H. metabola (McD.) was captured only in the bush areas where a greater part of the trees were evergreens. It was captured at Wasagaming, Beaver Creek, Sandilands and comprised about one-third of the captures in the Spruce Woods Forest Reserve.

H. nuda (McD.) was captured most frequently in wooded or partially forested areas. Its population density was extremely variable in different locations but was very abundant at St. Laurent in 1960 where it made up 64 per cent of the captures. This result may seem contradictory to the results shown for the behavioural experiment in Table II, Chapter II. This experiment was not set up until the second week of June when the abundance of *H. nuda* was already declining. In this area *H. nuda* appeared early and was very abundant for about four days during the last week in May.

H. typhus (Whitn.) was captured in areas where evergreen forest prevailed and was common at Beaver Creek. This species was found in large numbers in the Whiteshell area in 1959 (Bracken, 1960). Pechuman (1961) stated that this species had not been previously reported for Manitoba. However, from the results of this survey it appears to be well established in the Beaver Creek area and was also captured at Marchand.

H. trepida (McD.) was found only at Beaver Creek in this survey. This species was also captured in the Whiteshell area in 1959 (Bracken, 1960).

Only one specimen of *H. opaca* (near) Coq., was captured and that was found in the Spruce Woods Forest Reserve. McAlpine (1961) identified specimens of *opaca* (=opacus) from collections at Whitewater Lake in the Sandilands Forest Reserve in 1958.

The seasonal distributions of tabanid species in six localities are illustrated in Figures 12 to 17. For convenience the season will be divided into three periods, beginning with the setting up of the traps during the last week of May and ending on the 14th of August.

1. May 29 to June 14: *H. metabola* was the first species on the wing and its numbers built up quickly in the space of a few days. *H. nuda* and *H. illota* also appeared early, *nuda* began to decline in numbers

toward the second week of June. However, *H. illota* was still increasing in abundance during this time.

2. June 15 to June 30: The numbers of *H. metabola* and *H. nuda* rapidly declined. *H. epistates*, *H. lasiophthalma* and *H. frontalis* appeared and increased rapidly in numbers where they occurred. *C. aestuans* became abundant in parkland areas during this period.
3. July 1 to August 15: *H. typhus* appeared in this period and became the prevalent species by mid July where it occurred. It declined rapidly in numbers toward the end of the month. *H. frontalis* reached its highest numbers during this period. Most of the species had disappeared by the end of the first week in August except *H. frontalis* which was still relatively abundant.

The local distribution of Tabanidae

The intrinsic flight range of horse flies is considerable (Hocking, 1953), but whether they actually disperse over large areas is another question. This is a significant problem in surveys where distribution of species is based on the captures of adult flies, as the adults conceivably may range long distances from their larval habitat. In principle, larval surveys would be a more reliable method of studying the correlation between soil type and prevalent tabanid species of an area. However, the time and labor required by this method are prohibitive for a short term study.

During the summer of 1961 preliminary investigations were initiated to study the dispersion of horse flies in relation to meteorological conditions by releasing adult flies tagged with P^{32}. Eight trap lines were set up radiating from a central release point. There were four traps one-quarter mile apart in each line, the first trap one-quarter mile from the release point. The number of tagged flies recaptured were insufficient to yield significant results. However, since the vegetation of the four square mile area sampled by the traps varied from bush to cultivated plain, the specimens captured in the traps were identified as to species to see if certain species occurred more frequently in certain locations within the area. The occurrence of the different species, represented as the per cent of the total captures for each trap, are presented in Table XVIII for the east and north-west trap line together with a short description of the surroundings of each trap. The results do not reveal any preference of the species found in the area for either forested or open cultivated locations.

Trap number		.zona-lis	T.margi-nalis	T.simi-lis	Total
(1) E $\frac{1}{4}$ m.				5	562
(2) E $\frac{1}{2}$ m.		3		1	930
(3) E $\frac{3}{4}$ m.	(	1		7	180
(4) E 1 m.	(	1	1	11	880
(5) NW $\frac{1}{4}$ m.	N			1	842
(6) NW $\frac{1}{2}$ m.	O			5	650
(7) NW $\frac{3}{4}$ m.	O:			5	222
(8) NW 1 m.	S	1		2	735

*The i

Note:

CHAPTER VIII

SUMMARY

The aggregations of Tabanidae on and near certain inanimate objects in the field are interpreted in terms of visual orientation. This orientation is assumed to be an expression of host orientation behaviour.

The orientation of tabanids to objects of different color and reflectance was studied by evaluating captures in Manitoba fly traps fitted with painted spheres. The colors red, yellow, green, blue and violet were compared with a series of greys matched for reflectance with these colors and with black and white. Spheres of low reflectance, viz. black, blue and the dark grey corresponding to blue in reflectance were attractive to all species. Red spheres were also attractive to all species although the grey corresponding to it in reflectance was not. The attractiveness of red spheres is explained by postulating that tabanids may be red blind so that red is physiologically darker. The light greys and white were unattractive for most of the species, attractiveness decreasing with increasing reflectance. Green and yellow spheres were unattractive for all species. Presentation of the spheres on natural backgrounds of different color and reflectance did not change the results appreciably. Considering the phenomenon of physiological brightness, it was concluded that most of the tabanid species studied orientate to objects that are not physiologically brighter than the background.

Two species, _Hybomitra illota_ and _Chrysops mitis_, orientated to all of the spheres except yellow and green in all experiments. Apparently these species orientate to any object that contrasts with the background by reflecting more or less light, provided the color of the object does not simulate vegetation.

Rugose black cylinders were less attractive than smooth black, whether glossy or matte. Glossy black cylinders were more attractive than matte black cylinders. However, a very highly reflecting surface provided by covering a cylinder with shiny aluminum foil was unattractive.

The phototactic responses of tabanids to light of different wave lengths at equal intensities was investigated using a "Y" tube apparatus. Horse flies responded maximally at the shortest wave length tested, 405 mμ and again at 515 mμ. The response fell off rapidly toward the red region of the spectrum. Lack of response of tabanids to red light lends support to the hypothesis that horse flies are red blind and agrees with the interpretation given above of the behavioural data obtained in the field.

The orientation of tabanids to variously shaped forms including a sphere, plane circle, cube, plane square, tetrahedron, plane equilateral triangle, horizontal and vertical cylinder was studied. The three-dimensional objects were more attractive than the two-dimensional objects and this was related hypothetically with the magnitude of the angle of field scanned at any instant. Of the three-dimensional objects, those presenting curvature in the vertical plane, i.e., the sphere and horizontal cylinder, were more attractive than the other forms. It is postulated that the orientation of horse flies was influenced by solar images or to the plane of the polarized light reflected from the surfaces.

The influence of the size of an object on attractiveness to tabanids was determined by suspending black horizontal cylinders coated with tanglefoot in the field. The diameters and length of each were equal. Attractiveness increased with size from 20.5 cm to 41 cm diameter but was constant in the range 41 cm to 71.7 cm. A black cylinder was 32 times as attractive as a cylinder of the same size with equal black and white stripes. The conjointness of the black surface of a figure more strikingly affects its attractiveness to horse flies than its size.

When a rotating black tub with white conical vanes was compared with a similar stationary silhouette, horse flies were attracted to either in nearly equal numbers. The same result was obtained when a stationary sphere was compared with a freely suspended sphere. Motion of an object does not, therefore, increase its attractiveness to horse flies under the conditions of the field experiments.

The effect of the surface temperature on the attractiveness of objects to horse flies was investigated by comparing captures in traps over a black enamelled barrel containing warm water and a similar barrel containing water and ice. Although captures were higher in traps over the warm barrel the differences were not statistically significant. Other data from the investigations of the attractiveness of objects of different color to tabanids support this finding. Heat, therefore, did not play a significant role in the attraction of horse flies to the trap silhouettes under the field conditions of the experiments.

The seasonal and geographic distribution of Tabanidae in southern Manitoba was studied on the basis of captures of tabanids in the Manitoba fly trap placed in various locations in the province. In the area studied one species of _Atylotus_, one of _Haematopota_, two of _Tabanus_, four of _Chrysops_ and eleven of _Hybomitra_ were captured. Some species, notably _Hybomitra affinis_, _H. arpadi_, _H. metabola_ and _H. typhus_ were captured only in forested regions whereas others, such as _Tabanus similis_, _Chrysops aestuans_ and _Hybomitra frontalis_ were most abundant in parkland areas. However, collections in traps over a limited area of four square miles, which consisted of both forest and parkland vegetation, did not reveal differences in species abundance in the two types of vegetation.

Hybomitra metabola and *H. nuda* were the earliest species, appearing in the last week of May. The majority of the species were prevalent in the last two weeks of June and the first two weeks of July. *Hybomitra typhus* and *H. frontalis* became prevalent during the latter part of July. *H. typhus* disappeared within the first week of August. *H. frontalis* alone persisted to the second week of August.

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TABLE XVIII

THE NUMBER AND SPECIES OF TABANIDAE CAPTURED OVER VARIOUS TYPES OF SOIL AND VEGETATION

Trap number	Description of immediate area surrounding trap	H.americana	C.aestuans	C.mitis	H.affinis and H.arpadi	H.epistates	H.frontalis	H.illota	H.lasiophthalma	H.nuda	H.typhus	H.zonalis	T.marginalis	T.similis	Total
(1) E $\frac{1}{4}$ m.	Virgin tamarack and spruce bush; deciduous shrubs; wet peat.		1		2	61	8	20	2		1			5	562
(2) E $\frac{1}{2}$ m.	Same as above	1			1	66	4	22	1	1		3		1	930
(3) E $\frac{3}{4}$ m.	On road allowance; surrounded by summerfallow of mixed black and peat soil; near evergreen bush and semi-bog.		1		1	57	10	21	1		1	1		7	180
(4) E 1 m.	On road allowance; summerfallow to north and grain field to south; permanently wet, drainage ditch near by.		1	1	4	55		22	5			1	1	11	880
(5) NW $\frac{1}{4}$ m.	Native grass meadow*		1	1	3	79	6	6	3					1	842
(6) NW $\frac{1}{2}$ m.	On border of grain field and native grass meadow*		3	1	3	68	2	17	1		4			5	650
(7) NW $\frac{3}{4}$ m.	On summerfallow of peat* and black soil mixture.				1	63	8	20	3					5	222
(8) NW 1 m.	Same as above*				2	78	5	9	2			1		2	735

*The immediate area in this section was not suitable for tabanid breeding.

Note: Varieties expressed as per cent of total for each species.

Date of collections - July 7, 1961.