HOST-SEEKING ACTIVITY OF
TABANIDS (DIPTERA: TABANIDAE)

SEASONAL DISTRIBUTION, DIURNAL PERIODICITY AND PHYSIOLOGICAL AGE OF HOST-SEEKING TABANIDS (DIPTERA: TABANIDAE)

by

DAVID ALEXANDER TROUBRIDGE, B.Sc.

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AUTHOR: David Alexander Troubridge, B.Sc. (McMaster University)

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Host-seeking activity, for most tabanid species, reached a maximum in mid-afternoon. The diurnal periodicities of *Chrysops vittatus* and *C. univittatus*, however, were bimodal, with activity peaks in the morning and late afternoon. Air temperature and rainfall were the meteorological parameters having the greatest influence on the diurnal activity pattern.

Host-seeking activity began at 13°C and reached a maximum at temperatures between 26 and 28°C. The effect of solar radiation on activity varied with the air temperature.

Physiological age studies showed that few females completed two gonotrophic cycles. *Tabanus reinwardtii* was proven to be autogenous. Autogeny is suspected for *C. niger*. *C. cuclux*, *C. cincticornis*, *T. quinquevittatus* and *Hybomitra lasiophthalma* are thought to be capable of facultative autogeny. Other species (*C. moechus*, *C. vittatus*, *C. univittatus*, *T. similis*, *T. lineola*, *C. aberrans*, *H. epistates* and *C. callidus*) were anautogenous.

Parous females formed a greater percentage of the host-seeking population in the afternoon than in the morning.

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I. INTRODUCTION

The Tabanidae, the deer flies and horse flies, are known primarily for their voracity as blood suckers. Because of their blood-feeding habits, tabanids are of some medical importance and many species have been shown to be involved or implicated in the transmission of disease (Ofsufjev, 1937; Leclerq, 1952; Pechuman, 1972). Of perhaps greater significance, at least in North America, are the economic losses sustained when livestock are exposed to the attacks of large numbers of these flies (Stone, 1938; Tashiro and Schwardt, 1949; Teskey, 1960; Shemanchuk and Depner, 1972). As pests of man, tabanids, although generally of less importance than mosquitoes or black flies, can at times be a serious deterrent to outdoor activities (Hocking, 1952; Gojmerac and Devenport, 1971; Pechuman, 1972).

Since blood-feeding is the activity which has resulted in the unpopular reputation held by the Tabanidae, this phase of their life cycle has received the most attention. The first point is that, as in mosquitoes and black flies, it is only the females which take blood, the protein of which is used for the development of the eggs. However, it is known that females of some species do not always require a blood meal (Thomas, 1971).

Much previous research has dealt with the method of host-finding. Olfaction is of considerable importance in long-range orientation to the host and carbon dioxide is known to attract host-seeking females in large numbers (Defoliart and Morris, 1967; Bennett and Smith, 1968; Roberts, 1971). Visual stimuli have been shown to assist females in locating a suitable host at shorter range (Hansens, 1947; Bracken _et_ _al_., 1967; Bracken and Thorsteinson, 1965; Thorsteinson _et_ _al_., 1965; Granger, 1970).

Other aspects of tabanid behaviour, associated with host-seeking and blood-feeding, have been less thoroughly examined. There are few references to the diurnal periodicity of host-seeking or biting in tabanids (Miller, 1951; Sasakawa _et_ _al_., 1968, 1969; Polyakov, 1968; Roberts, 1969) and most are based on rather limited data. Furthermore, the conclusions reached to not always agree and authors differ as to which factors they consider responsible for the diurnal cycle.

Of considerable medical significance, in terms of potential disease transmission, is a knowledge of the physiological age structure of the population of biting flies. Physiological age, in the present sense, is the number of gonotrophic cycles completed by a female i.e. the number of batches of eggs laid. Generally speaking, one blood meal is required for each gonotrophic cycle, and since a pathogen can be transmitted only if more than one blood meal is taken, then the disease-transmitting potential of a species can be seen to depend on the longevity of the females, as measured in terms of physiological age. Seasonal studies on the physiological age structure of tabanid populations have been carried out in Alberta (Thomas, 1971) and for Hybomitra lasiophthalma (Macquart) in Wisconsin (Morris and Defoliart, 1971).

The objectives of this thesis were divided into three major sections:

1. to determine the diurnal cycle of host-seeking activity and account for this cycle in terms of meteorological parameters.
2. to examine the effect of meteorological parameters on mean daily tabanid host-seeking activity.
3. to examine the changes in the physiological age structure on both a seasonal and a diurnal basis.

II. MATERIALS AND METHODS

A. Location

The area chosen for the study in 1972 was a deciduous wood located two miles south of Caledonia, in Haldimand County, Ontario. It contained many wet areas suitable for tabanid breeding. These included a number of small ponds, both permanent and temporary, one large stream with a small tributary and numerous marshy areas.

Potential hosts for Tabanidae in the immediate area were few. The only large mammals present in the wood were a few white-tailed deer, two being seen during the summer. None of the fields adjacent to the wood were used for grazing although cattle and horses were available to the tabanids at greater distances. Other mammals in the wood, such as foxes, rabbits or groundhogs, may serve as hosts, although little is known about the role of these animals in this capacity.

B. Description of Traps

The traps used for collecting host-seeking female tabanids were designed to ensure portability, rapid assembly, and minimum time for removal of the specimens (Fig. 1). The traps were a modification of the Manitoba fly trap (Thorsteinson, et al., 1965), being pyramidal instead of conical and using carbon dioxide as an attractant rather than a visual target.

The legs and cross-pieces consisted of 1" x 1" lumber and the square platform at the top of ½" plywood. The legs formed an angle of approximately 60° with the ground. They were joined to the platform by screws inserted through the top of the platform. For this purpose, the upper ends of the legs were cut at an angle of 30°. The ends of each cross-piece were similarly cut and into each end a finishing nail was partially driven. The finishing nail, protruding from the end, was inserted into a corresponding hole in the leg, half-way from the top, thus making the cross-pieces removable. The lower ends of the legs were cut at a sharp angle to facilitate insertion into the ground.

A single piece of white netting, cut to the shape of the trap, was held in place along the legs and cross-pieces with thumbtacks, so that no gaps occurred where the ends of the netting met and where it touched the bottom of the platform. A strip of black cloth, 9" in width, was fitted below the netting. Without this, a large number of tabanids flew in circles about the trap without entering.

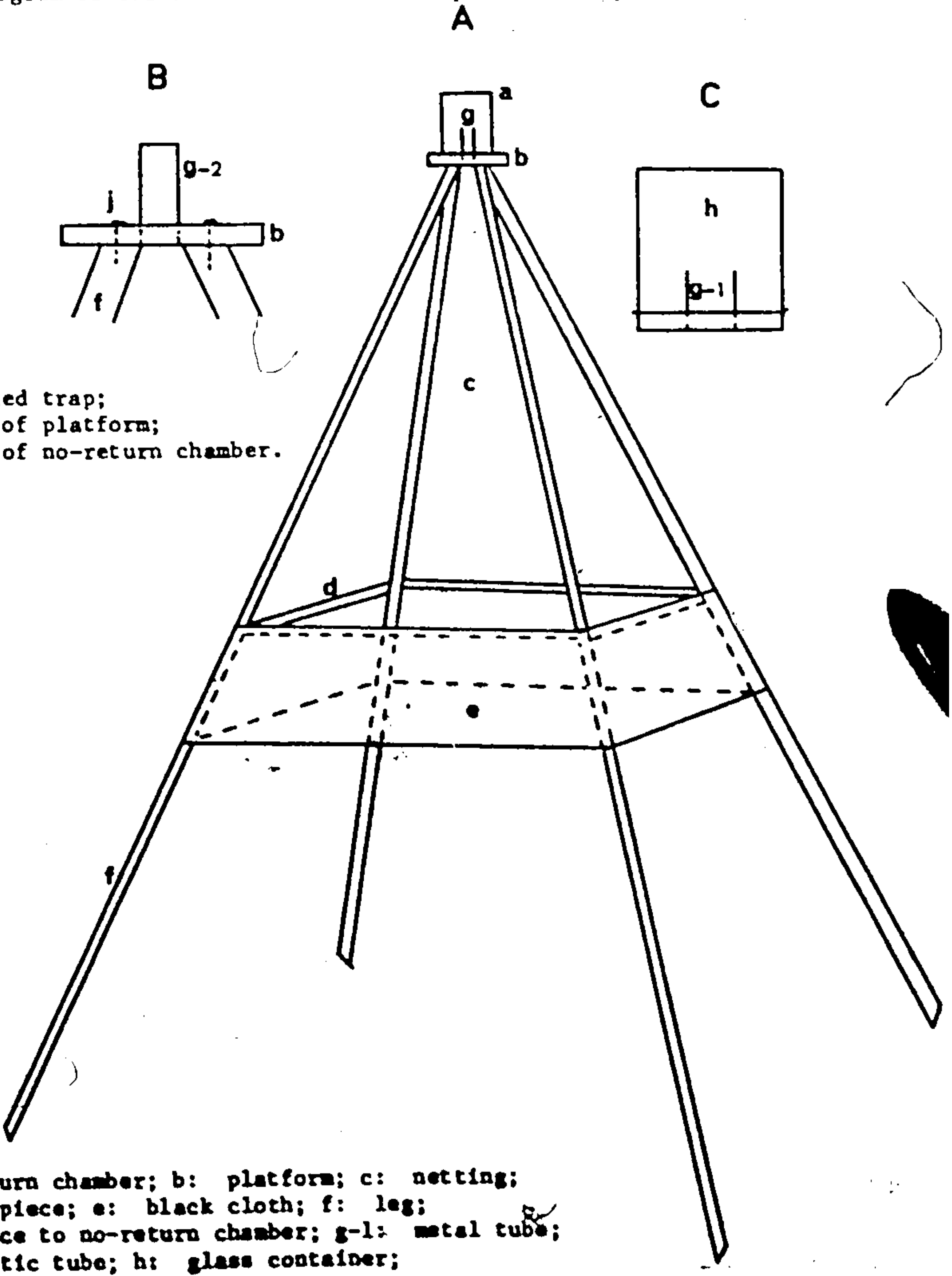
The "no-return" chamber was an inverted glass jar, 3½" in diameter and 4" high with a 1" circular hole cut in the centre of the screw-on, metal lid. Above the lid (on the inside) was welded a piece of metal tubing, 1½" long and 1" in inside diameter. A 2½" section of plexiglass tubing (1" outside diam., 3/4" inside diam.) was inserted firmly into a 1" hole in the platform with the bottom of the tube flush with the bottom of the platform. The inverted "no-return" chamber slipped onto this tube. When the chamber was removed, its opening was covered with a piece of tape so that no flies escaped. Two chambers were used for each trap, so that, when one was removed, it was replaced immediately by another.

Not all flies entered the "no-return" chamber and it was sometimes necessary to go beneath the trap and manually collect these additional flies.

The traps could be quickly moved to a new location by loosening the screws at the top and removing the cross-pieces. Once this was done, the legs came together and the trap was easily carried in one hand.

The carbon dioxide was supplied from gas compressed in 20 lb. cylinders, the release being controlled with a step-down regulator and an adjustable flowmeter. The gas was emitted through a rubber tube at a rate of approximately 400 ml/min into the centre of the trap at the level of the cross-pieces.

FIG. 1. Diagram of carbon dioxide-baited trap used to capture female tabanids.



A: assembled trap;
B: detail of platform;
C: detail of no-return chamber.

a: no-return chamber; b: platform; c: netting;
d: cross piece; e: black cloth; f: leg;
g: entrance to no-return chamber; g-1: metal tube;
g-2: plastic tube; h: glass container;
j: screw for attachment of leg to platform.

C. Trap Locations

The carbon dioxide traps were located in the wood at four sites (sites A, B, C and D) and the traps at those sites were designated as traps A, B, C and D respectively.

Site A was an elongated clearing containing a pond and marshy areas. The trap was located on the east side of the clearing. Trap B was located in a small damp opening 25 yd. inside the edge of the wood and approximately 200 yd. south-west of trap A. Trap C was located on higher and drier ground than the other three traps and was not in an open area. It was about 150 yd. north-west of trap B. Trap D was approximately 200 yd. west of trap C in a large clearing containing a small pond.

Not all traps were operated simultaneously. Traps A, B and C were used together in June and the first half of July. Towards the end of this period, few tabanids were being caught in traps B and C and their use was discontinued. A trap was erected at site D, and beinning 20 July, traps A and D were used concurrently. Flies were removed from the traps at one- or two-hourly intervals during the day. All times mentioned are Eastern Standard Time.

D. Netting Collections

Tabanids were also captured by netting them as they flew about the observer. Such collections were made while walking from site A to site D and back, and were terminated after 15 min. of collecting time. Care was taken to conduct the netting at least 15 yd. from any trap in operation at the time. The first part of the netting route was slightly different when traps A, B and C were being used together, than at other times.

E. Handling of Adults

Tabanids were killed by freezing in a deep freeze and stored there until they were to be identified and aged (see below). Each no-return chamber containing trapped flies was placed directly into the freezer and after 15 min., when the flies were immobilized, they were transferred to labelled storage tubes and left in the freezer.

Flies captured during netting collection were pinched while still in the net, transferred to the labelled storage tubes and also deep-frozen.

F. Physiological Age of Females

One measure of the physiological age of a female tabanid is defined as the number of gonotrophic cycles completed by the female i.e. the number of batches of eggs which have been laid. A female which has yet to oviposit is termed nulliparous or a nullipar. After one gonotrophic cycle, the female is uniparous, or a unipar, and after two cycles, biparous, or a bipar. A parous individual is one which has completed one or more gonotrophic cycles, the number of cycles being unspecified.

Physiological age is determined by examining the fly's ovaries. In many cases, a parous individual can be distinguished by the presence of one or more retained mature oöcytes. However, as this occurs only in certain females (Lewis, 1960; Raybould, 1967; Thomas, 1972), it cannot be used exclusively.

The presence of a sac-shaped distension in the ovariole is another indication that the fly is parous. After an oviposition, the follicular tube is distended and remains so for one to two days. A female whose ovarioles have this feature are said to be parous and in the sac stage. As this is a temporary condition, it is, in itself, of only limited value. However, after the follicular tube has contracted to its original size, a small dilatation remains. This dilatation contains a follicular relic or "yellow body," which consists of the remains of nurse cells and follicular epithelium (Detinova, 1962). Moreover, a relic is formed, after each oviposition, anterior to the previous relic, and so the physiological age of the female may be obtained by counting these relics. This was discovered by Polovodova in 1947 (see Detinova, 1962) working with a mosquito, <u>Anopheles</u> <u>maculipennis</u> Mg., but has since been applied to

Tabanidae (Raybould, 1967; Thomas, 1971).

G. Ovarian Stages

Ovarian stages mentioned in the text refer to the state of development of the follicles in the ovary. The classification is that of Christophers (1911) and Mer (1936) but the numbering is that of Dr. S. M. Smith (personal communication):

Ovarian Stage	Characteristics
IA	follicle consists of 16 undifferentiated cells
IB	oöcyte distinguishable from nurse cells but no yolk present
IIA	fine yolk granules visible about nucleus of oöcyte
IIB	oöcyte occupies up to ½ of follicle, yolk present throughout oöcyte
IIIA	oöcyte occupies 1/2 - 3/4 of follicle
IIIB	oöcyte occupies 3/4 of follicle
IVA	oöcyte occupies 9/10 of follicle, follicle beginning to elongate
IVB	follicle approaches shape of mature egg, but is not chorionated
V	mature egg, chorion added.

The classification of Christophers (1911), although developed for use with mosquitoes, is applicable to tabanids

(Detinova, 1962) and has been used, with minor modifications, mainly in the numbering of the stages, by several persons working with Tabanidae (Raybould, 1967; Rockel, 1969; Thomas, 1971).

H. Examination of Ovaries

Physiological age and ovarian stage were determined by examining the ovaries under a dissecting microscope. The ovaries were exposed by pulling away the two terminal abdominal segments of the female. The ovaries were then removed and examined in saline containing a small amount of detergent to reduce adhesion.

I. Measurement of Meteorological Parameters

Air temperature and relative humidity were recorded continuously by means of a Serdex hygro-thermograph (Bacharach Industrial Instrument Co., Pittsburgh, U.S.A.), which was set up in the wood near site A.

Total solar radiation, in langleys, was measured continuously with a recording pyreheliograph (Belfort Instrument Co., Baltimore, U.S.A.). This was placed outside the wood so that it was not shaded at any time during the day.

Wind speed was recorded with a hand anemometer (Casella, London) both inside and outside the wood.

These data were supplemented by written observations and by atmospheric pressure and total rainfall data from the meteorological station at Mount Hope Airport, approximately 10 mi. from the study site.

III. RESULTS

A. Seasonal Pattern of Abundance

Twenty-one species of Tabanidae were collected in 1972 at the experimental site near Caledonia (Table I). Of these, Chrysops cincticornis (Walker), C. moechus (Osten Sacken), C. univittatus (Macquart) and C. vittatus (Wiedemann) accounted for 87.9% of the total number collected.

During the summer, two periods of peak abundance were observed, one in mid-June and a second at the end of July (Table I). The June peak was due primarily to C. cincticornis. Hybomitra lasiophthalma (Macquart), H. epistates (Osten Sacken), C. cuclux (Whitney) and C. indus (Osten Sacken) were also common species in June. The peak in late July resulted from the many C. vittatus and C. univittatus. C. moechus attained maximum abundance in mid-July. The number of Tabanidae collected, whether in CO_2-baited traps or in netting collections decreased rapidly after the first week in August and few were found at the end of that month.

Two females of Tabanus sulcifrons (Macquart), from CO_2-baited traps, and two males of Stonemyia rasa (Loew), collected from vegetation, appeared late in August.

TABLE I

Number of Each Species Collected Each Week at Caledonia in 1972, Arranged According to Seasonal Occurrence

	DATE													
	June					July				August				
	5-11	12-18	19-25	26-2	3-9	10-16	17-23	24-30	31-6	7-13	14-20	21-27	28-4	TOTAL
Chrysops cuclux (Whitney)	17	55	14	3		1								90
C. cincticornis (Walker)	130	298	147	46	6	3		1						631
C. indus (Osten Sacken)	3	12	18	3		3		1						40
Hybomitra illota (Osten Sacken)	1	2	6		1		1							11
H. epistates (Osten Sacken)	2	7	27	8	2	6	8	1	2					63
H. lasiophthalma (Macquart)	2	42	40	8	4									96
C. niger (Macquart)		1	9											10
C. callidus (Osten Sacken)		4	9	4	2	15	15	11	3	1				64
Tabanus similis (Macquart)		1	4	3	8	3	7	7	1					34
C. moechus (Osten Sacken)			11	56	33	129	92	64	56	16	2			459
C. frigidus (Osten Sacken)			1	1			1		1					4
C. vittatus (Wiedemann)			1	6	1	105	333	681	485	100	55	14	1	1781
C. univittatus (Macquart)			1	2	2	22	156	469	291	64	23	3		1033
T. atratus (Fabricius)			1					1	1					3
T. lineola (Fabricius)						1	12	5	9	1	1	1		30
T. quinquevittatus (Wiedemann)						2	23	16	10	4	1	1		57
C. aberrans (Philip)						1	5	6	12	2	1			27
T. reinwardtii (Wiedemann)						1	2		1					4
H. sodalis (Williston)							2							2
T. sulcifrons (Macquart)											1	1		2
Stonemyia rasa (Loew)												2		2
TOTAL	155	421	289	140	59	292	658	1263	872	188	84	22	1	

FIG. 2. Relative seasonal abundance of *C. vittatus* females as determined by netting collections; smoothed using a 5-point moving mean.

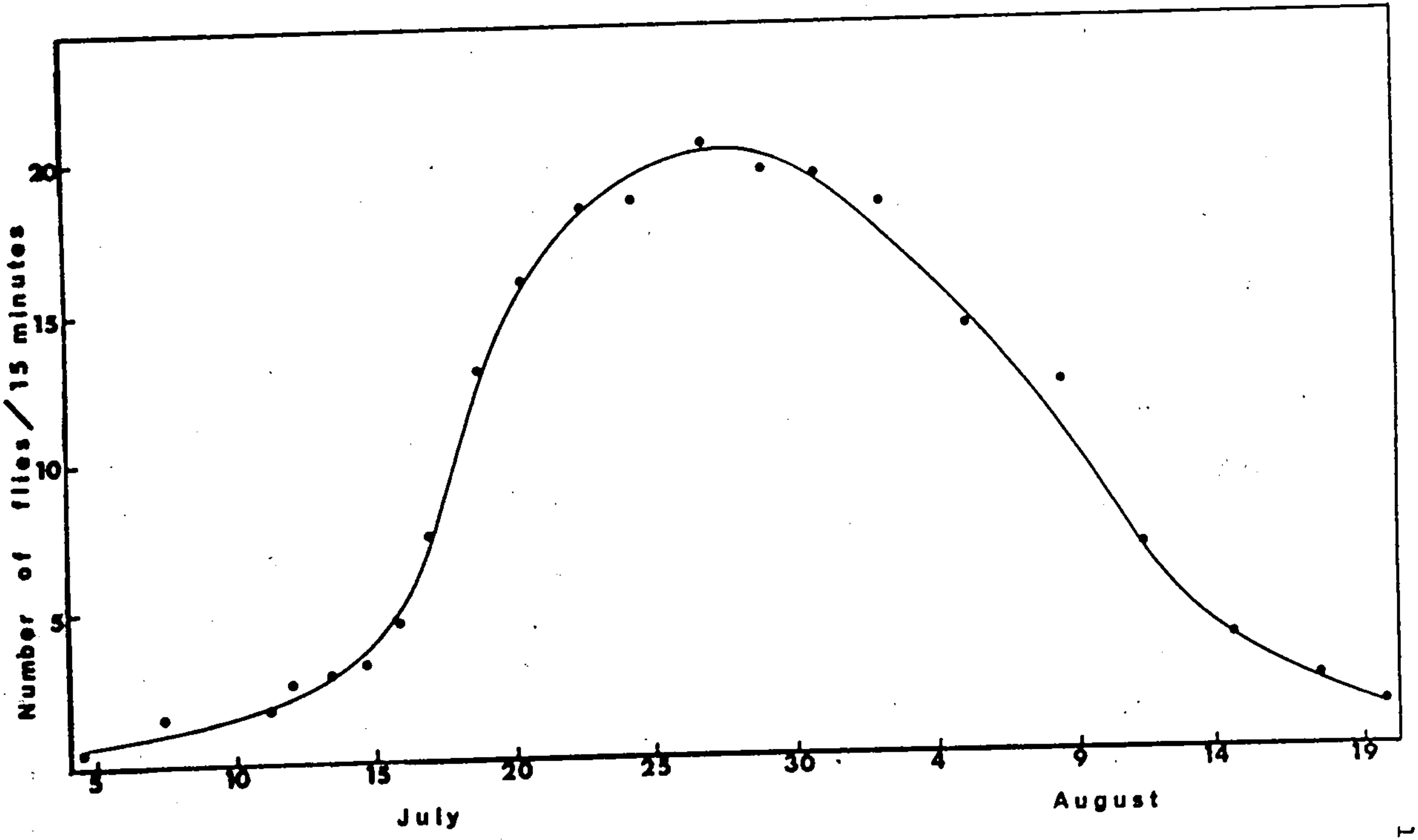
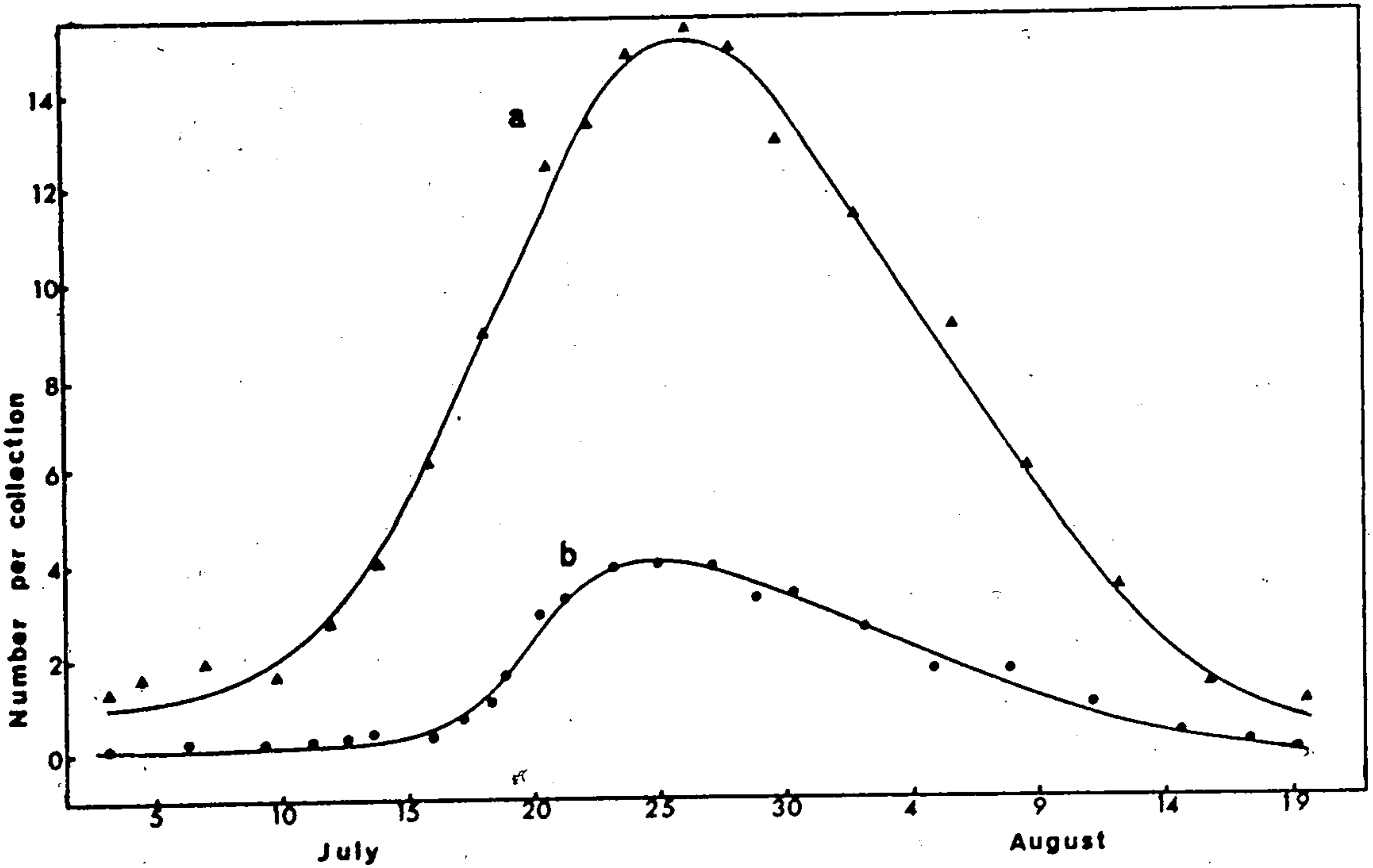


FIG. 3. Relative seasonal abundance of *C. univittatus* females as determined by trap collections (a) and by netting collections (b); curves smoothed using a 5-point moving mean. Length of collections 2 hours in a, 15 minutes in b.



For the two most abundant species, *C. vittatus* and *C. univittatus*, an attempt was made to establish the seasonal changes in population size (Figs. 2 and 3). These seasonal abundance curves were calculated by using a five-point moving mean, each point consisting of five consecutive two-hour collections. To provide consistency, only collections at temperatures between 19°C and 29°C, and between 0800 and 1600 hr. were included.

Two curves of relative seasonal abundance were drawn for *C. univittatus*, one based on trap collections (Fig. 3a) and a second based on netting collections (Fig. 3b). Only netting collections were used to calculate the curve for *C. vittatus*, as few females of this species were caught in the traps (Table XIV).

In a later section, these curves are used as a means for comparing activity on different days.

B. Diurnal Pattern of Activity

1. General

Tabanids captured in the CO_2-baited traps were removed at regular intervals, of either 1 hr. or 2 hr. duration. These data were analysed to determine the diurnal pattern of activity.

In instances where it was desirable to combine data for different days, the data had to be transformed in a way that avoided any bias resulting from more flies occurring on some days than others. Such transformations were performed as follows: for any day in which there were "n" collection periods (of either 1 hr. or 2 hr. duration) the number of flies (x) caught in any collection period (t) was divided by $\bar{x}$ where $\bar{x} = \frac{\Sigma xt}{n}$. Thus for each day, there are "n" values of $x/\bar{x}$, each corresponding to a particular collection period.

The diurnal activity pattern was found to vary somewhat from day to day throughout the summer, but a mean pattern was established using all collecting days between 14 June and 18 August (Table II).

Activity was generally highest between 1000 and 1600 hr., although on certain days, most flies were caught between 0800 to 1000 hrs. or in the period 1600 to 1800 hrs. Activity was negligible between 0600 and 0800 hrs. However, such early morning collections were not made after the middle of July. On four days when evening collections were made, activity decreased markedly after 1800 hrs.

However, the mean pattern shown in Table II was found to be misleading, as the diurnal pattern was observed to differ during different periods of the summer. Two periods, 14-28 June and 17-31 July, were selected and the diurnal activity patterns for each period compared (Table III).

In June, the greatest activity was always observed between 1000 and 1600 hrs. On neither of the days on which

TABLE II

Mean Diurnal Activity Pattern of Total Tabanidae taken in CO_2-Baited Traps from 14 June to 18 August, 1972

	Time (hours)						
	0600-0800	0800-1000	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000
number of collections (N)	8	31	34	34	33	10	4
mean $x/\bar{x}$	0.03	0.87	1.07	1.14	1.15	0.97	0.52

TABLE III

Mean Diurnal Activity Pattern of Total Tabanidae taken in CO_2-Baited Traps in the Last Half of June* and of July, 1972

		Time (hours)					
		0800-1000	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000
14-28 June	N	6	6	6	6	2	2
	mean $x/\bar{x}$	0.56	1.47	1.50	1.41	0.93	0.38
17-31 July	N	9	11	11	11	3	2
	mean $x/\bar{x}$	1.04	0.89	0.85	1.14	1.49	0.67

*Few days in June provided flies because many days were too rainy.

collections were made after 1600 hrs. did activity increase after this time. In July, by contrast, activity tended to be depressed around noon. Activity in July was greatest between 1400 and 1800 hr. and, in addition, there was frequently, but not always, an earlier peak between 0800 and 1000 hrs.

2. Diurnal Activity Pattern of Individual Species

The seasonal differences in the diurnal activity pattern, apparent in Table III, reflected specific differences since the species composition in the two time periods was quite dissimilar (Table IV).

Warm days, (T>25°C) when different species were most active, were used to examine their activity patterns.

C. cincticornis, mainly a June species, was most active between 1000 and 1600 hr., with few flies active before 0900 hr. Activity gradually decreased after 1600 hr (Table V). On the two days when maximum seasonal activity occurred, an early peak in numbers was observed between 1000 and 1100 hr., followed by lower numbers between 1100 and 1300 hr. (Table V a and b). Activity increased again after 1300 hr., especially on 14 June.

The activity patterns of C. cuclux and C. indus during June were similar to that of C. cincticornis except that they tended to maintain their afternoon level of activity

TABLE IV

Species Composition of CO_2-Baited Trap Collections in June as Compared to that in July, 1972

14-28 June		17-31 July	
Species	**% of Total**	Species	% of Total
C. cincticornis	61.8	C. univittatus	67.1
H. lasiophthalma	12.0	C. moechus	11.1
C. cuclux	7.9	T. quinquevittatus	5.8
H. epistates	5.8	C. vittatus	5.1
C. indus	4.1	T. lineola	2.8
C. moechus	2.5	C. callidus	2.4
Other (7 spp.)	5.9	Other (10 spp.)	5.6

TABLE V

Diurnal Change in Numbers of Tabanids in CO_2-Baited Traps during Selected Days in June, 1972

(a) 14 June; maximum air temperature 30°C

Time (hours)	08-09	09-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19
C. cincticornis	0	16	40	9	19	35	27	40	36	15	11
C. cuclux	0	3	3	0	4	5	3	2	7	7	2
C. indus	0	0	0	0	3	1	1	0	2	1	3
H. lasiophthalma	1	3	5	0	4	5	1	2	1	5	1
H. epistates	0	0	0	0	1	3	1	1	1	0	0
Other (4 spp.)	0	0	0	0	2	2	0	1	2	0	0
TOTAL	1	22	48	9	33	51	33	46	49	28	17

(b) 19 June; maximum air temperature 28.5°C

Time (hours	06-07	07-08	08-09	09-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20
C. cincticornis	0	0	1	9	28	9	10	12	16	7	5	4	2	0
C. cuclux	0	0	0	1	2	1	0	2	4	0	0	1	0	0
C. indus	0	0	0	1	2	3	3	1	1	1	0	2	2	0
H. lasiophthalma	0	0	5	2	5	4	3	3	3	3	0	0	0	0
H. epistates	0	0	0	2	6	3	1	1	6	1	0	3	1	0
Other (7 spp).	0	0	0	0	7	3	1	7	3	1	0	3	0	0
TOTAL	0	0	6	15	50	23	18	26	33	13	5	13	5	0

.....continued.....

TABLE V (continued)

(c) 20 June; maximum air temperature 27.5°C

Time (hours)	06- 07	07- 08	08- 09	09- 10	10- 11	11- 12	12- 13	13- 14	14- 15	15-* 16
C. cincticornis	0	1	1	4	5	6	6	12	3	6
H. lasiophthalma	0	1	1	3	1	1	1	0	0	4
Other (8 spp.)	0	2	0	0	3	2	2	8	3	4
TOTAL	0	4	2	7	9	9	9	20	6	14

*Rain beginning 1545 hr.

into the late afternoon and early evening (Table V a and b).

Both H. epistates and H. lasiophthalma were most active between 1000 and 1600 hrs. H. lasiophthalma, however, became active earlier in the day than H. epistates, and in fact usually earlier than all the other June species (Table V). On 19 June, a high level of activity of H. lasiophthalma was observed between 0800 and 0900 hrs. (Table Vb).

The diurnal activity pattern of C. univittatus differed from that of the species which comprised the June complex. The latter species were most active from late morning until the middle or late afternoon. By contrast, on warm days, C. univittatus was more active between 0800 and 1000 hr. than between 1000 and 1400 hr. (e.g. 21 July, Table VIb). This was a consistent pattern, the only notable exceptions being 24 and 31 July, when high numbers continued until noon (Table VI c and d). However, on 24 July, no collecting was done in the early morning (0800-1000 hr.). Generally, a second peak occurred from 1600 to 1800 hr. (Table VI c, d). Thus, C. univittatus had a distinct bimodal activity pattern.

C. moechus was most active in the middle of the day (Table VI) and in this respect was similar to the species which were most abundant in June.

The other species taken in the traps in July were never numerous enough on any one day for a clear diurnal pattern to be distinguished. Some trends, however, were

TABLE VI

Diurnal Change in Number of Tabanids in CO_2-Baited Traps during Selected Days in July, 1972

(a) 11 July, maximum air temperature 27.5°C

Time (hours)	07-08	08-09	09-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18
C. moechus	0	0	3	5	4	6	7	3	1	3	1
Other (6 spp.)	0	0	4	1	1	1	2	1	2	2	0
TOTAL	0	0	7	6	5	7	9	4	3	5	1

(b) 21 July; maximum air temperature 30°C

Time (hours)	0800-1000	1000-1200	1200-1400	1400-1600
C. univittatus	24	6	8	11
C. moechus	1	0	2	6
C. vittatus	5	2	3	0
T. quinquevittatus	4	1	3	2
Other (6 spp.)	3	3	5	4
TOTAL	37	12	21	23

.....continued.....

TABLE VI (continued)

(c) 24 July; maximum air temperature 28.5°C

Time (hours)	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000
C. univittatus	27	19	19	42	27
C. moechus	0	4	3	1	1
C. vittatus	2	1	2	1	1
T. quinquevittatus	0	1	0	2	2
Other (6 spp.)	5	0	7	6	1
TOTAL	34	25	31	52	32

(d) 31 July; maximum air temperature 27°C

Time (hours)	0800-1000	1000-1200	1200-1400	1400-1600	1600-1800
C. univittatus	20	23	15	21	36
C. moechus	2	3	4	1	3
C. vittatus	0	4	1	0	3
T. quinquevittatus	0	3	2	0	2
Other (7 spp.)	2	3	3	5	1
TOTAL	24	34	25	27	45

apparent after compiling the total seasonal collections for these species (Table VII). *H. illota* (Osten Sacken) was included in Table VII although it was caught mainly in June. Most females of this species were taken in the early afternoon. *C. callidus* (Osten Sacken) and *T. lineola* (Fabricius) were most often trapped in the early and middle afternoon. There was some indication, from trap collections, that *C. vittatus* and *T. quinquevittatus* (Wiedemann) might have a bimodal distribution similar to that of *C. univittatus*.

Since *C. univittatus* was the dominant species in trap collections in the last half of July (Table VI), and was the only species with a clearly bimodal pattern of activity, the overall activity pattern in July (Table III) is accounted for by the behaviour of this species.

C. vittatus was caught mainly (95%) in netting collections and its diurnal activity pattern was examined using these data (Table VIII). On warm days, a high level of activity was always observed in the early morning (0800), followed by lower levels at 1000, 1200 and 1400 hrs. Activity increased again at 1600 hrs. and reached a peak at 1800 hrs. On 24 July, the number of *C. vittatus* caught at 2000 hr., although less than at 1800 hr., was still greater than the number caught at 1200, 1400 or 1600 hrs. (Table VIII). This bimodality in the activity pattern of *C. vittatus* was also observed in Algonquin Park in 1971 (Table VIII) also by netting collections.

TABLE VII

Number of Tabanids Caught at Different Times of the Day; All 1972 Seasonal Data Employed*

	Time (hours)					
	0800-1000	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000
T. similis	6	8	10	5	4	0
T. lineola	4	5	9	12	0	0
T. quinquevittatus	11	17	11	11	5	2
H. illota	0	2	8	0	1	0
C. callidus	2	8	17	15	4	0
C. aberrans	4	5	0	3	2	1
C. vittatus	21	16	17	13	6	1

*Fewer collections were made between 1600-2000 hr. than at other times of the day.

TABLE VIII

Diurnal Change in Number of *C. vittatus* caught in Netting Collections on Warm Days Near Caledonia in 1972 and in Algonquin Park in 1971

Date	Time (hours)												
	08	09	10	11	12	13	14	15	16	17	18	19	20
July 21	50		12		7		8		10				
July 24			61		33		19		30		92		45
July 31	61		12		7		10		28		48		
July 29*	4	7	7	8	7	3	4	5	-	10	1	8	0
Aug. 10*	62		21		9		19			17			
Aug. 18*		56				24		33		45		32	

*Algonquin Park 1971.

3. Effect of Weather Conditions on Diurnal Activity Pattern

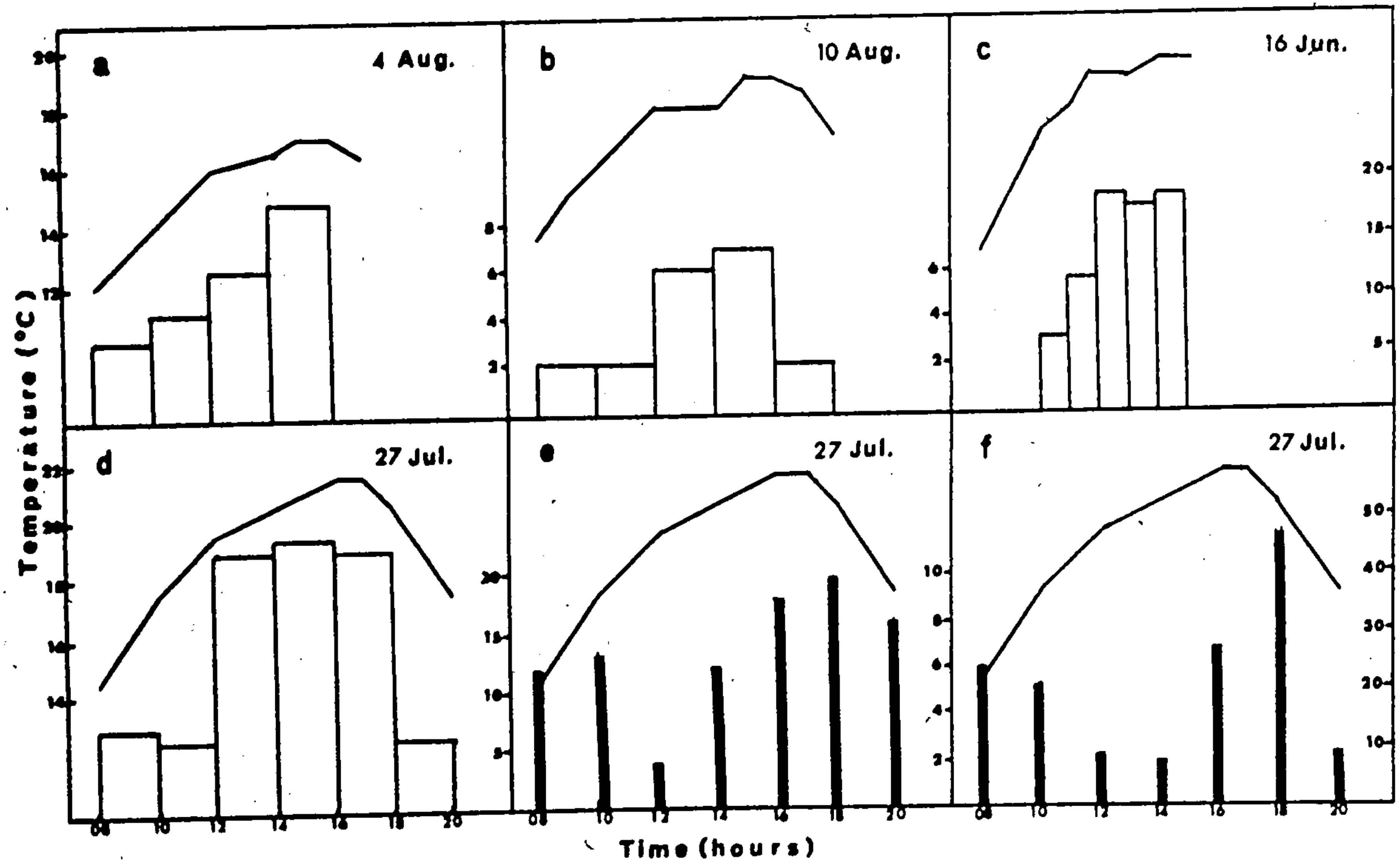
As the diurnal pattern showed differences from the "usual" pattern on certain days, the weather conditions that might be responsible for these activity patterns were examined.

a) Air Temperature. To see whether or not air temperature influenced the diurnal activity pattern as such, the activity patterns on days of low air temperature (<20°C) and on days of very high air temperature (>29°C) were compared with the "usual" pattern.

On cool days, the number of tabanids caught in CO_2-baited traps increased during the day as the air temperature rose (Fig. 4a,b,c,d), with tabanid activity reaching a maximum at the highest temperature.

The effect of low temperature on the activity patterns of *C. vittatus* and *C. univittatus* was a suppression of the morning activity peak. On 4 and 10 August, when the air temperature at 0800 hr. was 12°C and 13.5°C respectively, no morning peak was observed in either species, either by trap collections or netting collections. However, on 27 July, a slightly warmer day (14.5°C at 0800 hr.), the diurnal patterns of *C. vittatus* and *C. univittatus*, as reflected by netting collections showed an initiation of bimodality with a small morning peak in activity for both species (Fig. 4e,f).

FIG. 4. Change in numbers of tabanids during the day on cool days. a-d, total trap collections; e, *C. univittatus*, netting collections; f, *C. vittatus*, netting collections.



By contrast in the traps, few _C. univittatus_ were caught until after 1200 hrs. and no _C. vittatus_ during the whole day.

There was no indication of a reduction in tabanid activity at very high temperatures, at least on a diurnal basis. The activity of _C. vittatus_ and _C. univittatus_ was reduced in the afternoon when the temperature was at a maximum, but this appeared to result from an inherent bimodal diurnal pattern. Nor were other species adversely affected by high temperatures _per se_, e.g. Tables Va, VIb. In fact, _C. moechus_ was generally most active at the hottest time of the day e.g., 11, 21 and 24 July (Table VI a,b,c).

b) _Relative Humidity_. On a particular day, the effect of relative humidity on the activity pattern was difficult to ascertain because of the relationship of the changes in relative humidity with the changes in air temperature. No examples were found where an increase in one of these variables did not coincide with a decrease in the other. Thus, if high activity was observed as the temperature was rising, it could also be said that high activity occurred as the relative humidity was decreasing.

c) _Solar Radiation_. On days when it is sunny or when there is an even amount of cloud cover during the day, the changes in the amount of solar radiation during the day follow a regular pattern. This pattern was, in general, not paralleled by the changes in activity of different species. However, it was thought that a sudden increase in cloud cover might have some disruptive influence on the diurnal activity pattern. Although a number of instances of this type were recorded, many were associated with storm activity; these were not considered. On only one day (14 June) did an increase in cloud cover result in a significant change in activity. On 14 June, a short period of clouding coincided with a sharp reduction in the number of tabanids caught in CO_2-baited traps (Table IX).

On cloudy days, the cloud cover occasionally broke up for a period of time, resulting in an increase in solar radiation. However, these instances were not found to be coincident with significant changes in tabanid activity.

The diurnal activity pattern on cloudy days did not appear to differ from that found on sunny days.

d) Precipitation. Few tabanids were caught when it was raining. Most of these were caught in netting collections.

Tabanid activity was observed to increase before rain began, e.g. on 20 June, and 1 August (Table X a,b). On 1 August, rain was not heavy and tabanids were caught when it was raining. Activity was high immediately after the rain had stopped on 2 August (Table Xc).

TABLE IX

Changes in the Level of Tabanid Activity when Solar Radiation Decreased, 14 June, 1972. Solar Radiation Measured in Langleys; Flies Collected in CO_2-Baited Traps.

	Time (hours)						
	0800-0900	0900-1000	1000-1100	1100-1200	1200-1300	1300-1400	1400-1500
C. cuclux	0	3	3	0	4	5	3
C. cincticornis	0	16	40	9	19	35	27
H. lasiophthalma	1	3	5	0	4	5	1
Other (6 spp.)	0	0	0	0	6	6	2
Total	1	22	48	9	33	51	33
Total langleys/hr.	15	35	55	35	72	69	63

TABLE X

Tabanid Activity Before and After Periods of Rain

(a) 20 June. Rain began at 1545 hr.

	Trap Collections									
	06-07	07-08	08-09	09-10	10-11	11-12	12-13	13-14	14-15	15-16
C. cincticornis	0	1	1	4	5	6	6	12	3	6
H. lasiophthalma	0	1	1	3	1	1	1	0	0	4
C. callidus	0	0	0	0	0	0	0	1	1	2
Other (7 spp.)	0	2	0	0	3	2	2	7	2	2
TOTAL	0	4	2	7	9	9	9	20	6	14

(b) 1 August. Light rain began at 1500 hr.

	Trap Collections				Netting Collections				
	08-10	10-12	12-14	14-16	08	10	12	14	16
C. univittatus	20	5	7	4	4	0	1	0	3
C. vittatus	0	0	2	2	58	21	5	10	8
C. moechus	0	0	7	2	2	0	0	2	2
Other (5 spp.)	2	2	2	0	1	0	0	0	0
TOTAL	22	7	18	8	65	21	6	12	13

.....continued.....

TABLE X (continued)

(c) 2 August. Rain stopped at 0930 hr.

	Trap Collections			Netting Collections			
	10-12	12-14	14-16	10	12	14	16
C. univittatus	13	1	11	17	1	3	5
C. vittatus				57	11	9	13
C. moechus				3	4	1	1
Other (2 spp.)	1	0	0	3	0	0	0
TOTAL	14	1	11	80	16	13	19

4. Discussion

Two distinct types of diurnal activity pattern were found to occur. A bimodal periodicity was followed by *C. vittatus*, *C. univittatus* and possibly *T. quinquevittatus*. The remainder of the species had a single peak of activity in the afternoon.

These two patterns were similar to those found by other workers. The three species studied by Sasakawa *et al.* (1968) in Japan all had a bimodal pattern. Polyakov (1968) in Russia found a unimodal pattern, but did not distinguish between species. Roberts (1969) found the greatest activity from 0800-1000 hrs. but his collections stopped at 1600 hrs.

In none of the above studies were species differences noted. This may be because they were of short seasonal duration (1-8 days) and hence not all species in the area were examined. Miller (1951), however, found that two contemporal species had different activity patterns. *H. affinis* (Kirby) had two peaks of activity (0600-0900 hrs., 1800-2100 hrs.) whereas *H. septentrionalis* (Loew) had one (1200-1800 hrs.).

There are two possible reasons for the observed activity patterns. The first is that the activity of the females is controlled by an intrinsic diurnal rhythm. The second is that the females actively seek out a host or respond to host stimuli only within certain ranges of one or more meteorological parameters. This possibility is discussed first.

Stone (1930) states that the adults are lovers of sunlight, warmth and moisture. The first of these, sunlight, did not appear to have much influence on the diurnal activity pattern as such. Since the amount of solar radiation reaching the earth changes during the day according to a regular pattern, the importance of this factor on activity can be judged by examining the symmetry, about noon, of the diurnal activity pattern.

The mean diurnal pattern for the summer (Table II) showed no symmetry about noon. The species which had a unimodal pattern of activity did not generally show peak activity at noon. Most often, activity was higher in the afternoon than in the morning. This was most apparent in June e.g. Table V. *C. vittatus* and *C. univittatus*, the species which had bimodal activity patterns, were often least active at noon, although occasionally the time of least activity was slightly later in the day e.g. 24 July (*C. univittatus* Table VIc, *C. vittatus* Table VIII). Numbers of females of these two species could still be caught at dusk (2000 hrs.). In Algonquin Park in 1971, *C. vittatus*, *C. univittatus*, *C. shermani* (Hine) and *C. montanus* (Osten Sacken) were still active for a short time after sunset.

Sasakawa *et al*. (1968,1969), found that the bimodal periodicity observed on sunny days was damped on cloudy days. This was not observed in the present study. However, the study area used by Sasakawa et al. was a large open pasture where the flies were not shaded from the sun's radiation, as they were in the wood used in the present study.

Mean patterns of activity were disrupted by storm activity (Table X). Activity increased somewhat prior to the commencement of rain and was high immediately after rain had stopped. Similar occurrences have been reported elsewhere (Olsufjev, 1937; Tashiro and Schwardt, 1949). From studies on black flies (Davies, 1952), it seems possible that the increased activity may result from the rapid changes in atmospheric pressure which normally accompany the approach and passage of a storm front.

Air temperature exerted the greatest influence on the diurnal activity pattern. For most species, C. vittatus and C. univittatus excepted, the greatest activity occurred in the middle of the afternoon when the air temperature was at a maximum, and least in the early morning, when the temperature was lowest. The effect of air temperature was most apparent on cool days, when maximum activity coincided with maximum temperature. This was true even for C. vittatus and C. univittatus, the morning peak of these two species being absent or reduced on cool days.

The influence of relative humidity on the diurnal pattern could not be determined because of its inverse relationship with air temperature. Although these two variables should be considered together when discussing the diurnal activity pattern, temperature would seem to be the more important if one considers the altered patterns, especially of C. vittatus and C. univittatus, occurring on cool days.

Although wind speeds in excess of 15 m.p.h. are known to cause a considerable reduction in activity (Olsufjev, 1937; Hansens, 1947; Tashiro and Schwardt, 1949), this was not observed in the present study, due to the sheltered nature of the wood.

If all species had a unimodal pattern of activity, the conclusion would be that the observed patterns of activity were primarily due to the diurnal changes in air temperature (and relative humidity). This was the explanation given by Polyakov (1968). Conversely, if all species had a bimodal pattern, solar radiation might be considered the major controlling factor. Sasakawa et al. (1968) felt that this was the case.

However, in this study, two distinct types of diurnal activity pattern were found. This might be due to marked physiological differences between species having different patterns. These differences would presumably result in different optimum values of temperature and other meteorological parameters. However, this proposal is considered unlikely as such differences would have to be great to cause the completely opposite patterns which were observed. In this case, the possibility that activity is strictly a function of any one meteorological factor, or of a combination of factors, is ruled out.

Thus it would seem that each species must have a particular intrinsic diurnal rhythm of host-seeking activity. Circadian rhythms are known to be involved in many types of mosquito activity, including host-seeking (Clements, 1963). In the Tabanidae, the close association of some activities with a particular time of day suggests that circadian rhythms may be important. The swarming of males at dawn has been frequently reported (see Bailey, 1948) and the exact time of this occurrence seems to be controlled by a response to low light intensity (Corbet and Haddow, 1962). That mating takes place for only a short period of time in the early morning is also known (Hine, 1906; Anderson, 1971).

The diurnal rhythms reported here, in connection with host-seeking activity, appear to be largely exogenous, in that they vary somewhat from day to day, according to meteorological conditions. Of these, air temperature appears to have the greatest influence.

C. Effect of Atmospheric Parameters on Day-Day Activity

1. Results

During the summer, it was found that average daily activity often varied considerably between consecutive days. An attempt was made to relate these differences to changes in meteorological factors.

The presence or absence of rain was a major factor affecting activity, which was much reduced during rains. When it was not raining, air temperature was the most important variable.

Tabanids were caught in CO_2-baited traps at temperatures as low as 13.5°C and as high as 31°C. Traps were operated when the air temperature was less than 13.5°C but 31°C was the maximum air temperature in the wood during the summer of 1972.

The minimum temperature, at which host-seeking activity occurred, varied for different species (Table XI). In general, species of the genus Chrysops, were found to be active at lower temperatures than those of Tabanus or Hybomitra. Three species of Chrysops were taken in CO_2-baited traps when the air temperature was 13.5°C, whereas no Hybomitra or Tabanus was caught at temperatures less than 16°C. Species of Chrysops common in June (C. cincticornis, C. cuclux, C. indus) were not found at temperatures as low as were the

TABLE XI

Mean, Minimum and Optimum Temperatures (°C) at which Different Species Caught in CO_2-Baited Traps over the Period 0800-1600 hr.

	N	Minimum Temp.	Mean Temp.	Optimum Temp.
C. cincticornis	370	17.5	25.0	28.0
C. cuclux	38	16.0	25.5	27.5
C. indus	23	16.0	26.7	27.5
C. niger	10	25.5	26.8	-
C. callidus	42	17.0	25.8	-
C. moechus	210	13.5	24.2	26.0
C. vittatus	68	13.5	24.4	26.5
C. univittatus	575	13.5	23.0	26.5
C. aberrans	13	16.0	23.1	-
H. lasiophthalma	80	18.5	24.3	27.0
H. epistates	54	20.5	25.9	26.0
H. illota	9	16.0	26.2	27.5
T. similis	30	19.5	24.5	-
T. quinquevittatus	50	16.5	24.4	26.5
T. lineola	30	20.0	26.4	26.0

major species of Chrysops in July and August (C. moechus, C. vittatus, C. univittatus).

The optimum temperature for each species was estimated to be the temperature at which the greatest number of females were caught in a single two-hour period (Table XI). This estimate could not be made for some of the less common species as they were never caught in significant numbers. For the rest of the species, however, the optimum temperature ranged from 26.0°C to 28.0°C. Also included in Table XI is the mean temperature of collection for each species. This is simply the average air temperature at which the individuals of a particular species were caught.

Species of Chrysops were taken in both trap collection and netting collections. However, at low temperatures, relatively more females were caught by the latter method. This was reflected in the fact that the mean temperature of collection was lower for flies taken in netting collections (Table XII).

Curves of activity versus temperature were drawn for the two most numerous species, C. univittatus (Fig. 5) and C. vittatus (Fig. 6). Since data for these curves were taken from days extending over a period of three or more weeks, consideration had to be given to the changes in abundance during this time. This was done by using the curves of seasonal abundance (Figs. 2 and 3). For any

TABLE XII

Mean Temperature (°C) at which Different Species of *Chrysops* Caught in CO_2-Baited Traps and in Netting Collections from 0800-1600 hr. over the Period 11 July to 25 August, 1972

	CO_2 Traps		Netting Collections	
	N	Mean T.	N	Mean T.
C. callidus	30	25.7	10	24.8
C. moechus	167	25.0	138	22.7
C. vittatus	65	24.4	1399	22.4
C. univittatus	572	23.0	224	22.1
C. aberrans	13	23.1	10	22.4

FIG. 5. C. univittatus: activity versus air temperature.

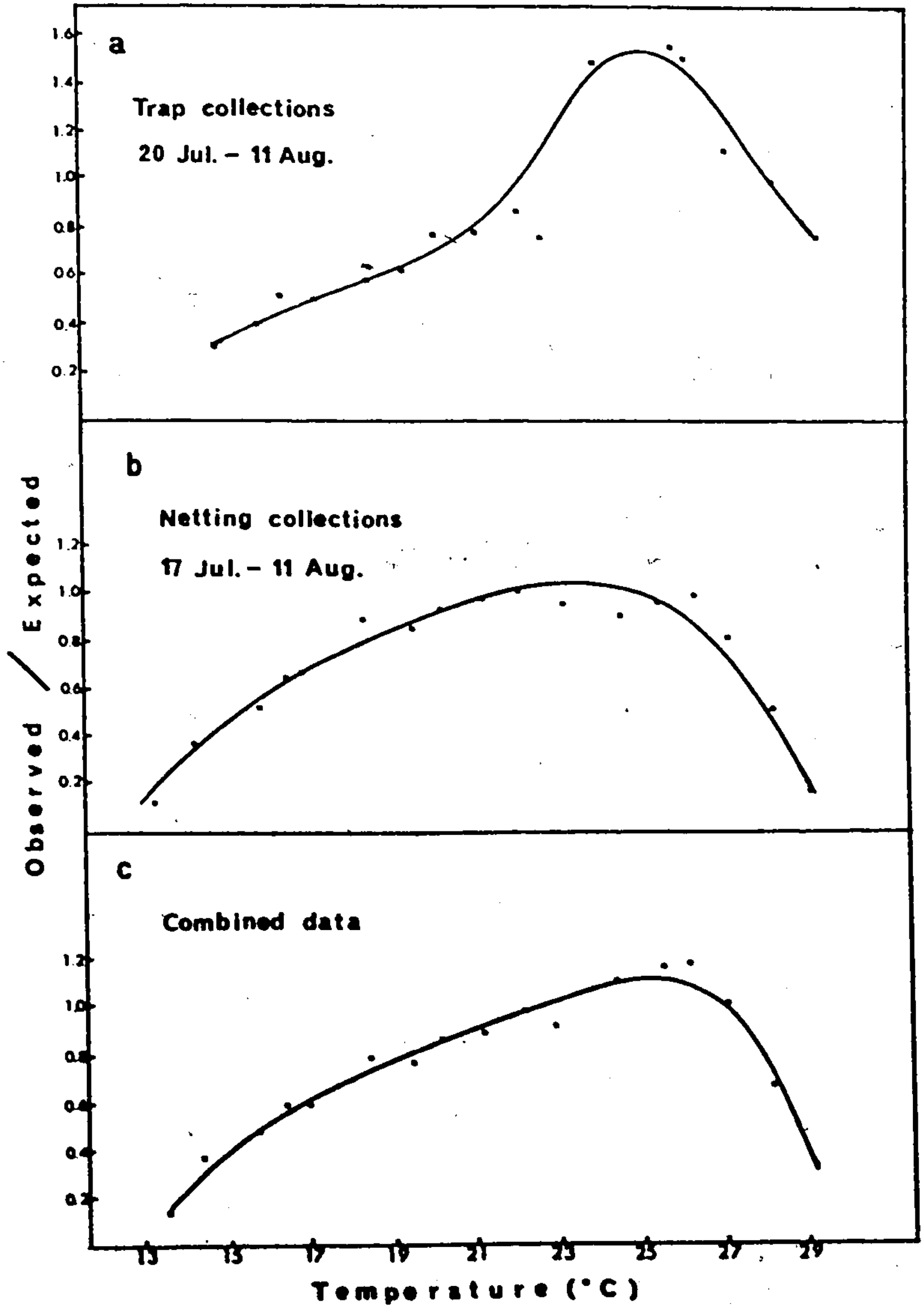
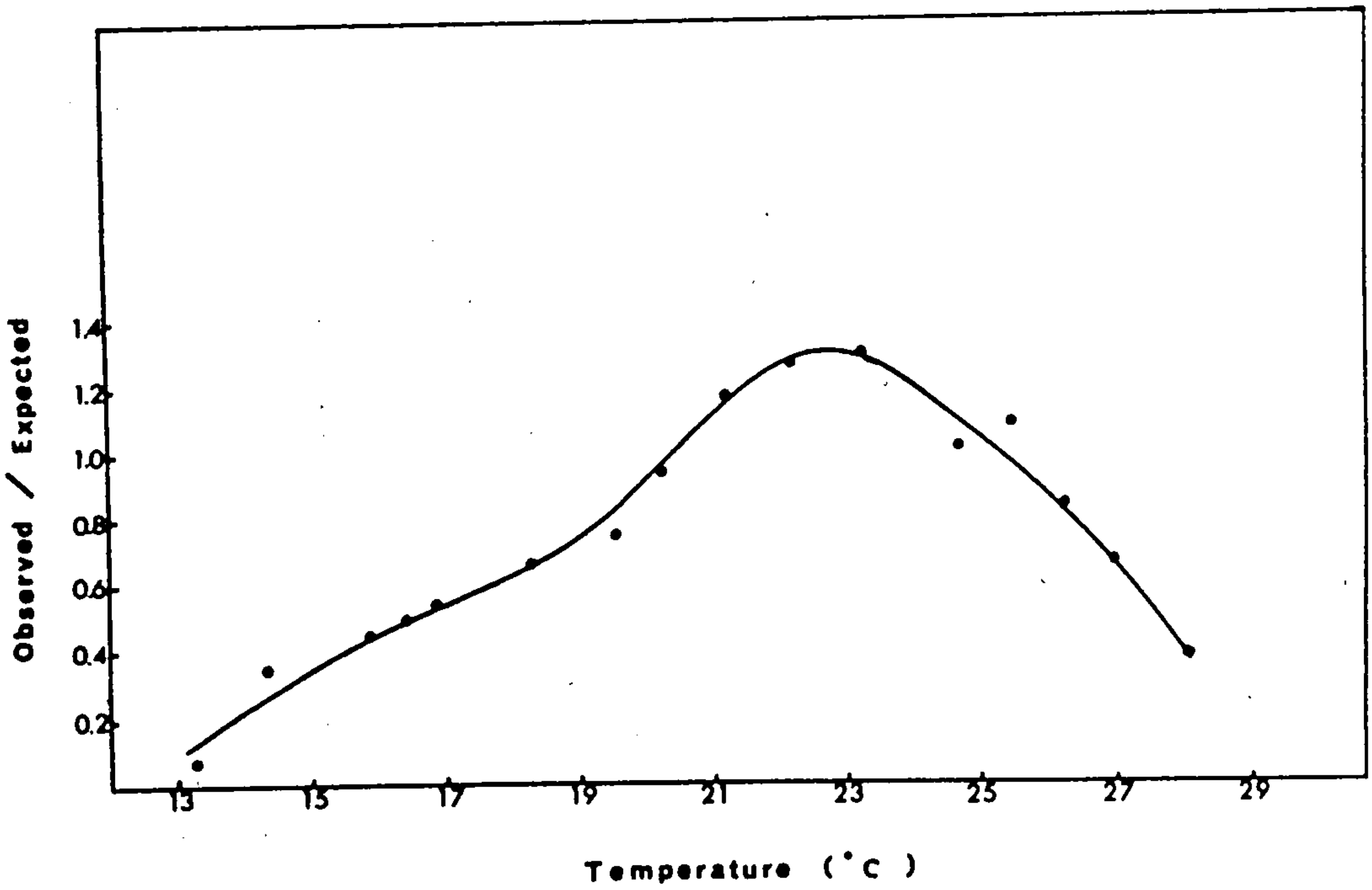


FIG. 6. _C._ _vittatus_: activity versus air temperature; netting collections.



collection on a particular date, the number of flies captured (observed) was divided by the expected number for that date as obtained from Fig. 2 or Fig. 3. The resulting number was termed the observed/expected value (obs./exp.).

As activity varies not only with temperature, but also with time of day, solar radiation and other environmental factors, inconsistencies were expected to be considerable. To reduce some of the inconsistency involved, only collections made between 0800 and 1600 hr. were used and the highest obs./exp. value and the lowest at each point on the graphs were excluded. Also, collections were only drawn from that part of the flight season when reasonable numbers of flies were available. A three-temperature moving mean was employed.

Air temperature had a more pronounced effect on the number of C. univittatus caught in the traps (Fig. 5a), than on the number caught in netting collections (Fig. 5b). Activity, as measured by trap collections, reached a peak at temperatures between 24 and 26°C. However, netting collections showed little change in activity over a wide range of temperature. In both cases, activity declined at temperatures greater than 26°C.

Activity of C. vittatus, as measured by netting collections, was greatest at approximately 23°C.

Because the mean air temperature varied from day to day, the real effect of different degrees of cloudiness on activity was difficult to ascertain. If the air temperature rose above 25°C, activity was generally high whether the sky was clear or clouded.

However, some difference in response to light conditions was noted between the two subfamilies, Chrysopinae (Chrysops) and Tabaninae (Hybomitra, Tabanus). A period of twelve days from late July to early August was selected to examine this difference. During this time, the ratio of Chrysopinae to Tabaninae in the total population remained relatively constant.

For each day, the mean number of Chrysopinae and Tabaninae per hour and the percentage of Tabaninae in the total tabanid population were plotted against temperature and light (Fig. 7). Light is expressed at the length of time that the total radiation exceeded 1.0 langley. This was found to be a good indication of the brightness of a particular day.

A number of trends are evident in Fig. 7. Although both groups increased in number as the temperature rose, the Tabaninae increased at a greater rate, as indicated by the larger percentages of the Tabaninae at higher temperatures. The number of Tabaninae increased also with light in a given temperature range. In the Chrysopinae, there was some indication that this occurred at lower temperatures, but not at higher temperatures. Thus in July and August, light and temperature had a greater effect on the activity of the

FIG. 7. Activity of Chrysopinae and Tabaninae at different levels of light and temperature on days between 20 July and 4 August. Each point represents trap collections from 0800-1600 hr. except those marked *, when a shorter interval (up to 2 hr. shorter) was used because of rain. a = number of Tabaninae/ total X 100; b = no. Chrysopinae/hr.; c = no. Tabaninae/ hr.

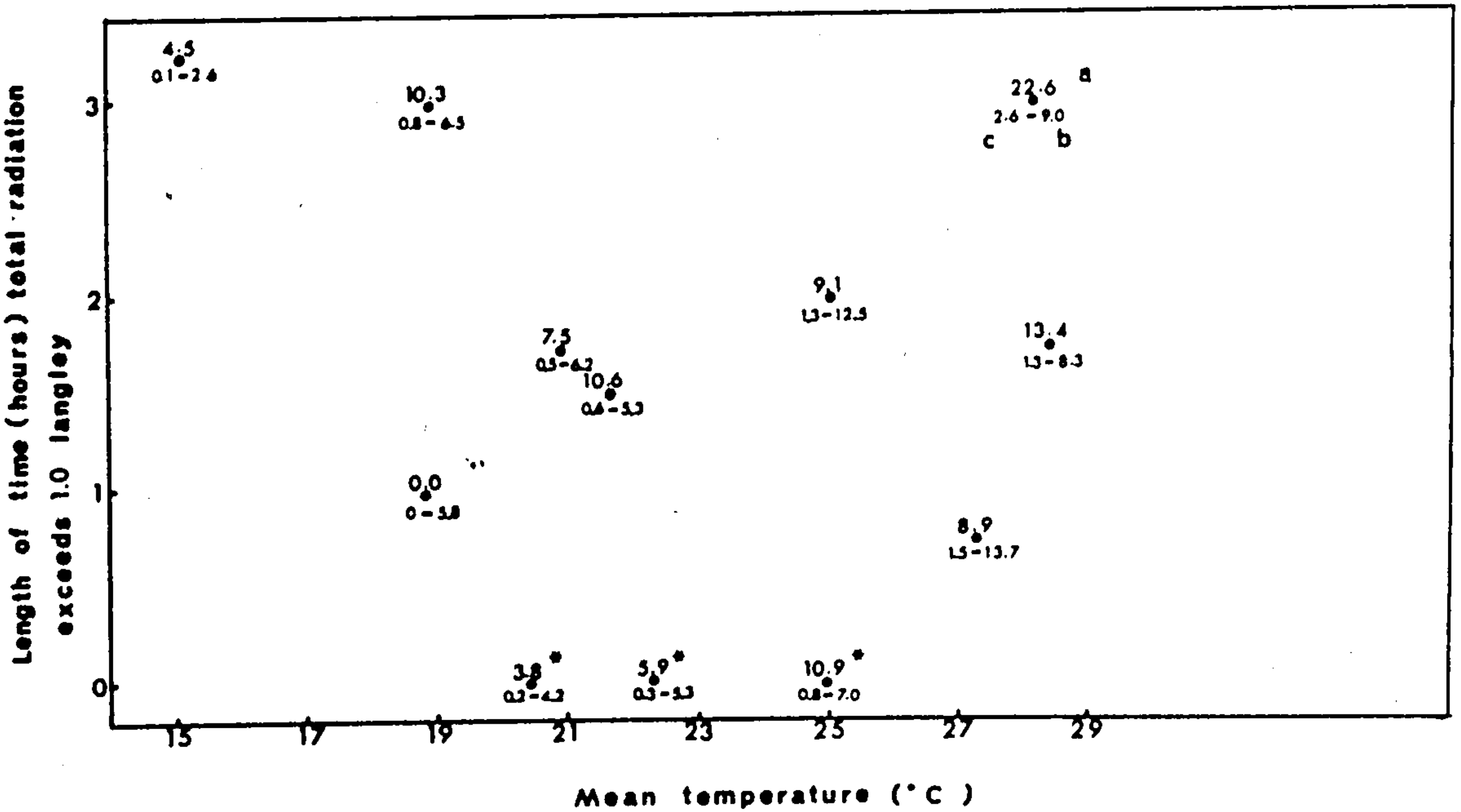
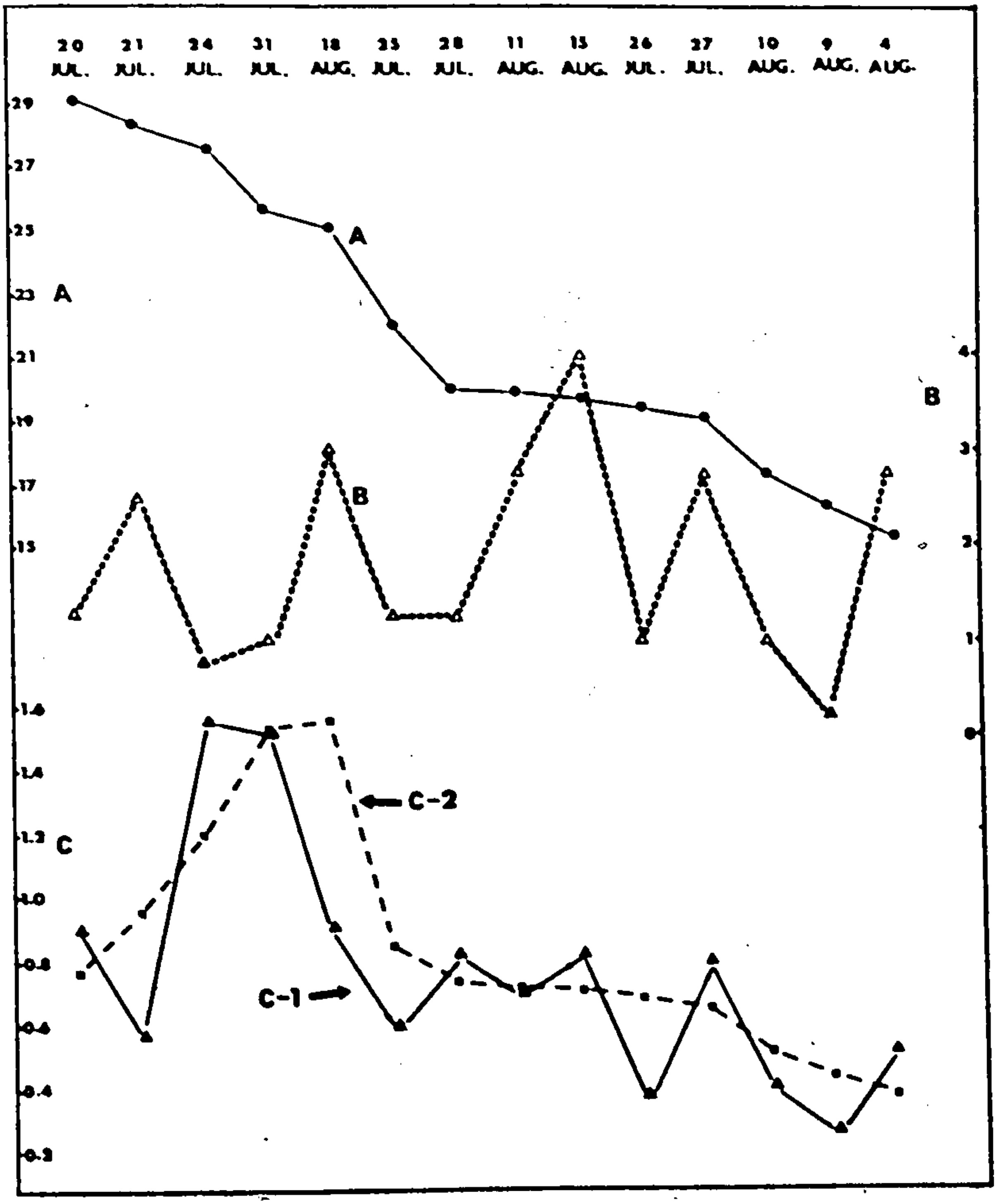


FIG. 8. Activity of C. univittatus (CO_2 traps) between 1000-1400 hr. at different levels of air temperature and solar radiation on days between 20 July and 18 August. Days on which it rained not included.



A = mean air temperature; B = length of time (hrs.) total radiation exceeded 1.0 langleys; C = obs/exp. value; C-1 = activity on each date; C-2 = activity expected according to mean air temperature.

Tabaninae than of the Chrysopinae. This appeared to be the case in June as well, but the rapidly changing population, both in size and composition, and the low number of suitable days (when it was not raining) precluded a more detailed analysis.

The effect of different levels of light on the activity of C. univittatus was examined (Fig. 8). In Fig. 8 are plotted values for temperature, solar radiation and activity (obs./exp.). Also plotted, for comparison with activity, is the obs./exp. value predicted by the graph of activity versus temperature (Fig. 5a) from the mean temperature for each day.

On warm days (mean temperature >25°C), the activity of C. univittatus was depressed during conditions of bright sunlight and increased when it was cloudy. However, at low temperatures (<19°C), the reverse occurred, activity being highest on bright days. Thus it appeared that the way light affected activity varied with the air temperature.

2. Discussion

Most types of insect activity are not regulated by a single environmental factor, but by a combination of factors (Uvarov, 1931). Since there is interaction between these variables, a considerable quantity of data is needed to determine the effect of different sets of environmental conditions on activity. If activity is to be examined on a day-to-day basis, then for each of the days involved in such an analysis, the size of the available population must be known; otherwise, activity on different days cannot be compared. This difficulty can be compensated for by comparing daily activity to a curve of seasonal abundance. In this way, widely separated days in the same season or even days in different seasons can be employed in the same analysis.

However, there can be problems in setting a seasonal abundance curve. Since these curves are to be the basis for further analysis, they must be reliable; also, the mean number of individuals per unit of collecting time should be enough that large inconsistencies do not result when observed/ expected values are calculated.

In the present study, for instance, it would have been desirable to produce and utilize seasonal abundance curves for each species and for the family as a whole. This, however, was not possible. It was found necessary to change the arrangement of CO_2-baited traps mid-way through the summer, as, in July, traps B and C were catching few flies and the total of traps A, B and C was insufficient for analysis. After the introduction of trap D, it was found that the species composition of the catches in this trap was markedly different from that of the other traps and so it was difficult to relate the catches in the two trap combinations (A+B+C, A+D) well enough to permit the drawing of a total seasonal abundance curve.

Among the individual species, seasonal abundance curves were drawn for the two most numerous, C. vittatus and C. univittatus.

Actual data showing the effect of environmental parameters on the mean daily activity of tabanids are scarce. However, there are many statements in the literature concerning this relationship. Most of these recognize the importance of air temperature (e.g., Stone, 1930; Schwardt, 1936; Olsufjev, 1937; Hansens, 1947; Tashiro and Schwardt, 1949; Miller, 1951; Davies, 1959; Polyakov, 1968; Sasakawa, 1969; Thomas, 1970; Pechuman, 1972). Fewer mention light intensity or solar radiation (e.g. Stone, 1930; Miller, 1951; Sasakawa et al., 1969; Pechuman, 1972). The implication is that temperature has a greater effect on activity than light intensity or solar radiation.

Chvála et al. (1972) state that, although light intensity is important, it is not as decisive as temperature.

Since air temperature and solar radiation both act on the body temperature of the individual fly, it should be expected that their effects on activity would be interrelated. It was possible to show this for C. univittatus (Fig. 8). At air temperatures above 25°C, high levels of solar radiation depressed activity. At lower air temperatures, when body temperature was also presumably lower, activity was higher than the mean level only on bright days.

The depressing effect of increased light at high temperatures was not entirely expected considering that the study area was well shaded. However, the traps themselves were located in open areas where the flies would have been exposed to the sun's radiation and so these areas may have been avoided. In connection with this, Barrass (1960) noted that, as the air temperature rose, fewer Haematopota insidiatrix (Austen) landed on the unshaded side of a vertical black cloth screen. Also, in the present study, on one afternoon when it was particularly hot (29°C) and sunny, two female C. univittatus were found resting on the undersides of leaves in a tree which was in the open and only fifteen yards from trap D. The oöcytes of both were in ovarian stage IIB and no evidence of a previous blood meal was found. That these two individuals needed a blood meal and yet were not responding to a nearby host stimulus (CO_2) suggests that flying in the open had or would have raised their body temperatures to intolerable levels, although the increased rate of water loss at high temperatures, especially when flying (and hence respiring at a greater rate), may be the critical factor. This was the only occasion on which tabanid females were observed resting on vegetation.

On the other hand, when the air temperature was low, solar radiation had a positive influence on the activity of C. univittatus by raising the body temperature to levels more suitable for host-seeking activity.

Solar radiation and air temperatures affected the two subfamilies, Tabaninae and Chrysopae, somewhat differently. These differences, summarized below, are apparent in Fig. 7. Although activity in both groups increased with air temperature, this increase was greater in the Tabaninae. Whereas Chrysopine activity declined after 28°C, this did not occur among the Tabaninae. Tabanine activity increased with the level of solar radiation throughout the temperature range, but this was the case with the Chrysopinae only at lower temperatures. In both groups, however, temperature had a more pronounced effect on activity than had solar radiation.

There are two possible reasons for these differences. One is that the optimum body temperature of the Tabaninae is higher. However, this does not seem to be borne out by the estimates of optimum air temperature given in Table XI. The second possibility may be discussed considering physical differences between the two groups.

The Tabaninae are considerably larger than the Chrysopinae and therefore have a smaller surface area to volume ratio. One result of this is that their body temperature is more stable. On a cool day, then, it would take a tabanine longer, utilizing solar radiation and heat from the air, to attain a body temperature suitable for flight. This is in agreement with the finding that species of Chrysops were active at lower temperatures than were species of Tabanus or Hybomitra (Table XI). Conversely, since the Tabaninae do not heat up as fast, they could remain active at high temperatures for a longer time than the Chrysopinae. However, at high air temperatures, water retention is probably a more important consideration. Again the Tabaninae would have an advantage due to the smaller surface area to volume ratio. Since the rate of water loss, relative to volume, is less for the Tabaninae, they can keep flying, and thus respiring at a higher rate, for a longer time than the chrysopines before the amount of water lost (through the spiracles) becomes critical.

The relationship of activity to air temperature was described for two species, C. univittatus (Fig. 5) and C. vittatus (Fig. 6). The activity of C. vittatus reached a peak at 23°C, after which it declined. This temperature (23°C) does not agree with the optimum temperature as estimated in Table XI (26.5°C). The reason for this difference may be found in the way in which the two figures were derived. The optimum temperature given in Table XI was the air temperature at the time when the greatest number was caught in CO_2-baited traps. Atmospheric conditions in general were probably close to being ideal at that time. However, Fig. 6 was based on the results of netting collections, and since it is a mean curve, the effects of variables other than air temperature on the curve are much reduced. The main reason for the difference is believed to be the differential effect of air temperature on the two types of collection. This is discussed later.

The greatest activity of _C_. _univittatus_, based on trap collections, occurred at 25°C (Fig. 5a). This is reasonably near the figure of 26.5°C given in Table XI.

Estimates of the optimum temperatures of other species were fairly consistent, all being between 26 and 28°C (Table XI). This range is generally in agreement with optimum temperatures given elsewhere: Tashiro and Schwardt, 1949 (22 to above 30°C); Miller, 1951 (20-23°C); Polyakov, 1968 (25-28°C); Sasakawa _et_ _al_., 1969 (25-26°C); Chvála _et_ _al_., 1972 (25°C).

The lowest temperatures at which individual species were caught in CO_2-baited traps are listed in Table XI. According to Pechuman (1972), _C_. _indus_ is more tolerant of low temperatures than other species of _Chrysops_. However, this could not be fully confirmed in the present study due to the small number of this species captured. Activity for three species (_C_. _moechus_, _C_. _vittatus_, _C_. _univittatus_) began at about 13°C. For most species, however, activity did not begin until the air temperature had reached 16°C or higher. Other estimates of the minimum air temperature for activity in temperate regions vary somewhat: Olsufjev, 1937 (13-16°C); Hansens, 1947 (rarely active below 15.5°C); Tashiro and Schwardt, 1949 (little activity below 22°C); Polyakov, 1968 (15-16°C); Thomas, 1970 (rarely active below 18°C); Chvála et al., 1972 (13°C). In the Russian arctic, however, activity begins at 11°C (Polyakov, 1968).

The July species of Chrysops [C. moechus, vittatus, aberrans (Philip), univittatus] seemed to be more tolerant of low temperatures than the June species (C. cuclux, cincticornis, indus). This was shown by the differences in both minimum temperature and mean temperature of collection (Table XI). However, this difference is at variance with Jamnback's theory (Jamnback, 1969). He feels that since the June species are more darkly coloured than the July species (C. indus and C. univittatus are exceptions to this rule), they should be able to absorb more heat from the sun, allowing them to be active at lower air temperatures. Although no data were given, this line of reasoning seems quite logical and no reason can be given for the apparent contradiction reported here, unless it is that this study was made in a shaded locality.

With species of Chrysops which were commonly caught by both collecting methods, it was found that at low air temperatures, relatively more females were caught by netting than with CO_2-baited traps. This is shown by a comparsion of the mean temperature of collection for each species by each of the two methods (Table XII). For C. univittatus, an examination of the graphs of activity versus temperature based on the two collecting methods (Figs. 5a,b) shows a similar difference. The number caught in netting collections varied little over a wide range of air temperature, whereas with trap collections, a distinct peak was present at 25°C.

A comparison of the two types of collection is in order at this time. In both types of collection, both a visual stimulus and an olfactory stimulus were presented to the flies. The visual stimulus presented by the traps was stationary and so could be seen only by flies in the immediate area. This was especially so as the important part of this target was the narrow strip of black cloth, which was put below the netting so that the flies would more readily enter the trap (see section on construction of traps in MATERIALS AND METHODS). The remainder of the trap was white, which is unattractive to tabanids (Bracken et al., 1962, 1965). In the netting collections, however, a larger, moving visual stimulus was presented to flies in a much greater area of the wood.

Both the trap and observer had an associated, attractive, chemical gradient around them which allows host-seeking females to locate the potential host. However, since the observer did not remain in one place during the netting collections, it is probable that the ability of the females to locate the source by means of this chemical gradient was considerably reduced. The traps, on the other hand, were stationary, and females following the CO_2 gradient would be brought into visual range of the traps.

Thus the netting collections primarily employed a visual stimulus and the trap collections an olfactory stimulus. Since, at low air temperatures, relatively more Chrysops females were captured by netting, it would seem that the temperature threshold for a fly to respond to a visual stimulus may be less than that for a response to an olfactory stimulus. Some behavioural observations presented in the following section support this theory.

D. Behavioural Observations

During the course of this investigation, a number of additional, often qualitative observations were made relating to tabanid host-seeking behaviour. Some of these have bearing on the results discussed in previous sections; others are independent. These observations are presented and discussed in this section.

1. Distribution of Species within Study Area

Many species of Tabanidae are found to have definite habitat preferences and can be classified according to these preferences (e.g., riverine, sylvan, riparine), whereas others are essentially ubiquitous (Smith et al., 1970). Of the species they discussed which were also found in the wood at Caledonia, *H. epistates* was classified as being essentially ubiquitous, *C. cuclux* as exclusively sylvan, *C. cincticornis*, *C. niger* (Macquart), *C. univittatus*, *C. vittatus* and *H. lasiophthalma* preferentially sylvan, *C. indus* riverine and *H. illota* riparine.

However, the wood at Caledonia was fairly uniform in nature, the only major disruptive feature being a stream and this was more than 200 yds. from the nearest trap (D). In spite of this, there were distinct differences between the catches in different traps (Table XIII). As all four traps were never operated simultaneously, Table XIII has been divided into two parts, one comparing the catches in traps A, B and C and the other comparing A and D.

No species was caught in the greatest numbers in trap B. This may have been due to its proximity to the edge of the woods. If the wind was northerly, as it frequently was, the carbon dioxide emitted at this trap would pass through only a small area of wooded habitat before entering an open field where there were, presumably, fewer tabanids.

TABLE XIII

Number of Females Caught at Different Trap Sites near Caledonia, Ontario in 1972

Species	Trap*				
	A	B	C	A	D
C. cuclux	36	11	10		
C. cincticornis	251	80	129		
C. indus	27	2	5		
H. illota	6	1	1		
H. lasiophthalma	33	10	49		
H. epistates	24	8	22	3	2
C. niger	6	1	3		
C. callidus	21	2	0	9	5
T. similis	6	7	6	1	11
C. moechus	69	6	7	22	53
C. vittatus	4	2	2	35	20
C. univittatus	4	1	2	64	576
T. quinquevittatus	6	2	1	11	29
C. aberrans	1	0	0	3	11
T. lineola	2	0	0	8	16

*Traps A, B and C were used simultaneously until the middle of July, after which traps A and D were operated together.

Sites A and D, where there were ponds and large clearings, were the preferred areas of most species. Trap D, which was in a slightly larger clearing than trap A and was further back into the wood, generally caught more tabanids than trap A, most notably for _C_. _univittatus_ and _T_. _similis_. _C_. _callidus_ and _C_. _vittatus_ were the only species which showed the opposite trend.

The reasons for the different distributions apparent in Table XIII cannot be stated with certainty. However, three possibilities present themselves. One is that the observed distributions are related to larval habitat, as the larva of many species have distinct habitat preferences (Teskey, 1969). A second is that females of different species may seek out particular areas in their search for a blood meal. This may be related to the habits of their preferred host. The third possibility, which would explain the greater number of females captured at sites A and D, is that female Tabanids tend to remain in the vicinity of areas where requirements other than a blood meal can be fulfilled. Sites A and D offered both water (ponds) and carbohydrates (nectar from flowers) which sites B and C did not.

2. _Host Preferences_

Some indication of host preferences was provided by a comparison of the number of each species caught by each of the two collecting methods (Table XIV). However, as netting collections were not made on a regular basis in June, the species caught on days when both types of collection were made was also tabulated (Table XV).

Few females of *Tabanus* or *Hybomitra* were caught about man during the summer; most females preferred the non-descript host imitated by the CO_2-baited traps. Species of *Chrysops*, however were captured by both methods. The most important species attacking man was *C. vittatus*. Relatively few females of this species were caught in the traps. Pechuman (1972) also found *C. vittatus* to have a preference for humans. *C. cuclux*, *C. cincticornis*, *C. moechus* and *C. univittatus* were also important pests of man during the summer.

However, *C. cuclux* and *C. cincticornis* appeared to favour the dog as a host animal. When a dog (black labrador retreiver) and the observer were present at the same time, the dog attracted more females of these two species. They were often observed to feed on the dog, generally about the neck or on the undersides. Females of other species of *Chrysops* were seldom attracted to the dog; nor were females of *Tabanus* or *Hybomitra* seen about the dog. However, it is probable that these other species will occasionally feed on dogs as feeding on dogs by different species has been reported elsewhere: Miller, 1951 [*H. affinis* (Kirby), *H. septentrionalis* (Loew)]; Davies, 1959 (*C. montanus*).

TABLE XIV

Number of Females of Each Species Caught in CO_2-Baited Traps and by Netting in 1972

Species	Method of Capture	
	CO_2 Trap	Netting
C. cuclux	70	20
C. cincticornis	570	61
C. indus	38	2
H. illota	10	1
H. epistates	63	
H. lasiophthalma	92	3
C. niger	10	
C. callidus	48	16
T. similis	33	1
C. moechus	213	246
C. frigidus	4	
C. vittatus	75	1706
C. univittatus	724	309
T. atratus	1	
T. lineola	30	
T. quinquevittatus	57	
C. aberrans	15	12
T. reinwardtii	4	
H. sodalis	2	
T. sulcifrons	2	

TABLE XV

Number of Females of Each Species Caught in CO_2-Baited Traps and by Netting in 1972 on Days when Regular Collections were made by Both Methods

Species	Method of Capture	
	CO_2 Trap	Netting
C. cuclux		1
C. cincticornis	24	21
C. indus	1	2
H. illota	1	
H. lasiophthalma	5	1
H. epistates	19	
C. callidus	28	15
T. similis	21	1
C. moechus	171	205
C. frigidus	2	
C. vittatus	70	1669
C. univittatus	693	290
T. atratus	1	
T. lineola	30	
T. quinquevittatus	57	
C. aberrans	15	12
T. reinwardtii	4	
H. sodalis	2	
T. sulcifrons	2	

As foxes were numerous in the woods, these may serve as hosts for *C. cuclux* and *C. cincticornis* and possibly other species as well.

3. Attacking Behaviour

While netting collections were being made, observations were made on the behaviour of female tabanids as they were attempting to obtain a blood meal from the observer. The remarks made here are restricted to species of *Chrysops*.

Females generally spent up to 30 sec. or longer flying in circles about the upper part of the observer before attempting to land. When a number were circling at the same time, they generally flew in the same direction and were often grouped closely.

Females generally landed only on the exposed parts of the body, i.e. the arms and head. *C. vittatus* restricted its landing to the head region, especially favouring the hair on top of the head. Other species were less restricted than *C. vittatus* in their landing pattern. *C. univittatus* landed, with approximately equal frequency, in the hair, on the arms, on the front of the neck and on the back of the neck, especially behind and below the ears. Pechuman (1972) feels that the preferred areas of this species are the cheek and the back of the ear. *C. callidus* most frequently landed on the arms. Blickle (1955) also noted that landing patterns differed between species.

The behaviour of C. univittatus was distinct from other Chrysops species when attempting to obtain a blood meal from man. It was an extremely quiet flyer so that it was seldom heard unless close to the ears. Its small size and dark colour made it difficult to see and unless one were watching for it, it would probably be unobserved in flight. Also, it seemed to land more quickly than other Chrysops species when it reached the host. In addition, it landed very gently, so that, unless it was seen, it went unnoticed until the mouthparts penetrated the skin. These characteristics presumably enhance its success in obtaining a blood meal. Pechuman (1972) in fact, states that "humans are more likely to be bitten by this species than by any other."

On cool days, when the air temperature was less than 16°C, it was noted that Chrysops females were sluggish, flying weakly and landing quickly with little or no circling. Also, normal landing patterns were lost, and the flies landed on any part of the body on clothing, even on the net or its handle. These observations indicate that host stimuli are recognized even at air temperatures barely above the minimum for flight. Under these conditions, it is doubtful that long range host-seeking would occur.

Another observation was that, regardless of temperature, the flies landed more quickly in the early morning and in the evening than at other times of the day. This was also true of cloudy periods as against sunny periods in the middle of the day. As this behaviour was not associated with any sluggishness, it may be that, under conditions of lower light intensity, a visual stimulus causes a more vigourous response than when the light intensity is high.

It was noted that, during early morning collections (at, or before, 0800 hr.), flies were often aggregated in small sunlit clearings along the collection route. This was especially noticeable on cooler days. This behaviour would seem to be an attempt by the flies to increase their body temperature by seeking out areas which are exposed to the direct rays of the sun.

E. Physiological Age of Host-Seeking Females

During the summer, females captured in CO_2-baited traps and in netting collections were dissected and the ovaries examined for changes in the physiological age structure of each species, both on a seasonal and a diurnal basis.

1. Seasonal Changes

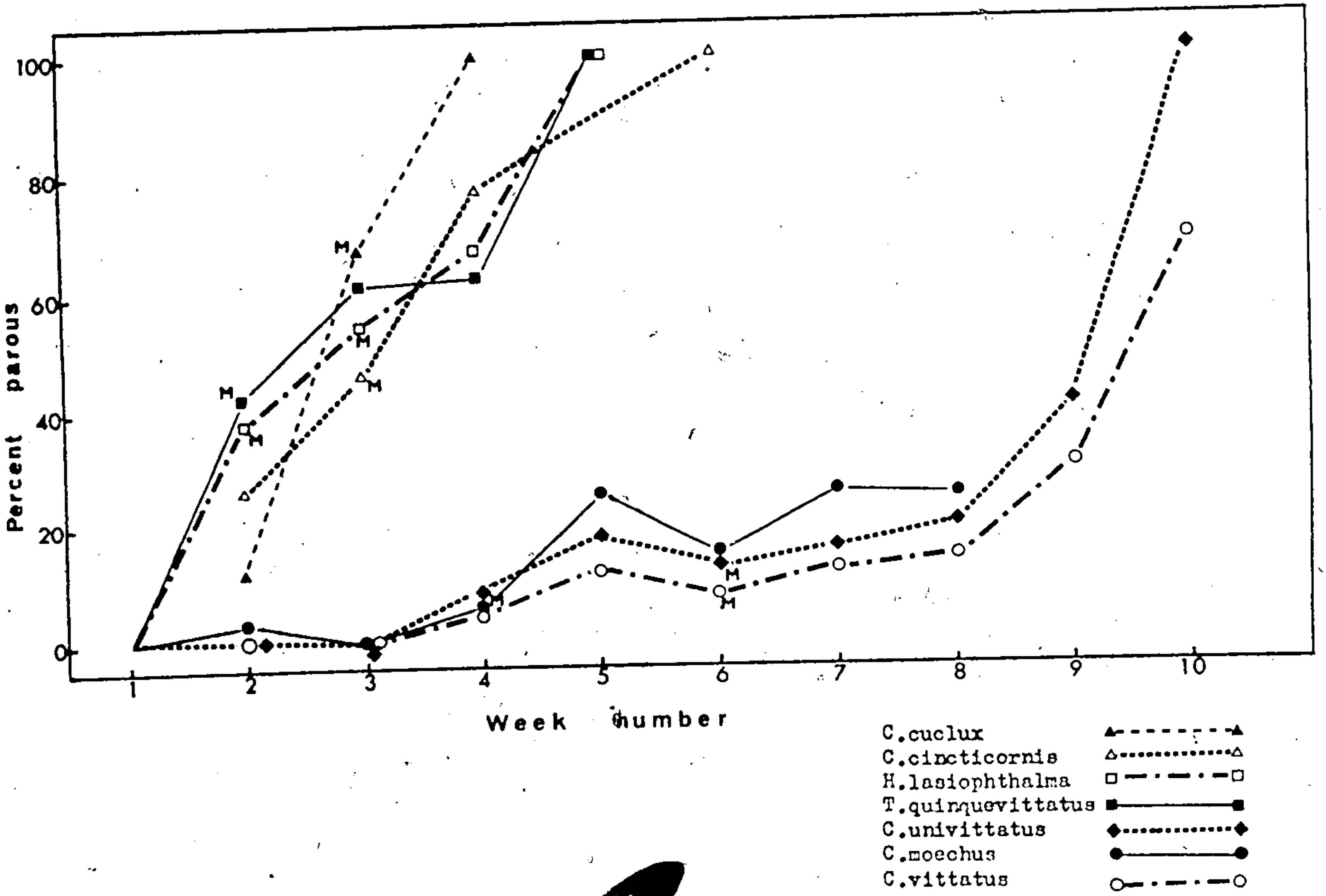
Nulliparous females formed most of the population of each species at the beginning of the flight season, with two exceptions. All ten specimens of C. niger were caught during a seven-day period, nine of them on two consecutive days (19, 20 June). However, nine of the ten, including the first (14 June) were uniparous, the other being nulliparous. All three females of T. reinwardtii (Wiedemann) examined from trap collections were parous. One additional female of T. reinwardtii was found resting on a path. It was also parous and its oöcytes were in an advanced stage of development (ovarian stage IVB). A few females of T. reinwardtii were reared from late larvae or pupae and maintained on sugar and water only, and proved to be autogenous. After ten days, all had oöcytes developed to stage IVa or IVb and one deposited her infertile eggs in the container in which it was being kept.

For all other species, the percentage of parous flies increased during the summer. However, the rate of this increase differed among the species.

For one group of species e.g. C. cuclux, C. cincticornis, H. lasiophthalma and T. quinquevittatus, the percentage of the population which was parous increased rapidly and 100% parity was observed three or four weeks after the first appearance (Fig. 9). H. illota appeared to follow the same pattern.

Species in a second group, however, e.g. C. moechus, C. univittatus and C. vittatus, maintained a low level of parity throughout much of their flight season. C. vittatus

FIG. 9. Percentage of females which were parous versus time after first appearance (week 1). M. indicates week of greatest abundance.



and C. *univittatus* were found to be mostly parous only in the last part of August, when only a few flies were present. For C. *moechus*, at no time were more than 26% of captured females parous (Fig. 9). This group also includes C. *callidus*, T. *lineola* and C. *aberrans* and probably H. *epistates* and T. *similis* (Macquart) as well.

When C. *moechus*, C. *univittatus* and C. *vittatus* were most abundant, less than 15% of the females were parous. By contrast, in the first group (C. *cuclux*, etc.), at least 40% of the females examined were parous during the week of greatest abundance.

Biparous females were uncommon, accounting for less than 1% of the females examined during 1972. However, relatively greater numbers of biparous females were found in some species than in others (Table XVI). Few females of H. *illota* were caught, but three of ten were biparous. On the other hand, of 943 C. *vittatus* females examined, only two were biparous and for C. *univittatus*, only one of 632 was biparous. Most biparous females belonged to species of the C. *cuclux* group.

Biparous females were always found late in the flight season (Table XVII). The relative change in numbers of nulliparous, uniparous and biparous females of C. *cincticornis* during the flight season in shown in Fig. 10.

The age composition of each species was summarized

TABLE XVI

Age Composition of Female Tabanids Examined in 1972

Species	Number				Percentage		
	ex.	nul.	uni.	bi.	nul.	uni.	bi.
C. cuclux	71	27	42	2	38.0	59.2	2.8
C. cincticornis	470	197	260	13	41.9	55.3	2.8
C. indus	37	28	7	2	75.7	18.9	5.4
H. illota	10	3	4	3	30.0	40.0	30.0
H. epistates	61	46	15	0	75.4	24.6	0
H. lasiophthalma	88	46	41	1	52.3	46.6	1.1
C. niger	10	1	9	0	10.0	90.0	0
C. callidus	56	43	13	0	76.8	23.2	0
T. lineola	22	18	4	0	81.8	18.2	0
C. moechus	331	287	44	0	86.7	13.3	0
T. similis	31	21	10	0	67.8	32.2	0
C. vittatus	943	826	115	2	87.6	12.2	0.2
C. univittatus	632	526	105	1	83.2	16.6	0.2
T. quinquevittatus	48	21	26	1	43.8	54.2	2.1
C. aberrans	25	21	4	0	84.0	16.0	0
T. reinwardtii	3	0	3	0	0	100.0	0
C. frigidus	3	1	2	0	33.3	66.7	0
H. sodalis	2	1	1	0	50.0	50.0	0
T. atratus	1	1	0	0	100.0	0	0
T. sulcifrons	1	1	0	0	100.0	0	0

NOTE: ex. = examined; nul. = nulliparous, uni. = uniparous;
bi. = biparous.

TABLE XVII

Change in Physiological Age Structure of Females in the weeks Following Their First Appearance (1 = week of first appearance)

Species are arranged according to seasonal occurrence. a = number of females examined, b = number of nullipars, c = number of unipars, d = number of bipars.

		1	2	3	4	5	6	7	8	9	10
C. cuclux*	a		17	36	14	3		1			
	b		15	12							
	c		2	24	14	1		1			
	d					2					
C. cincticornis*	a		54	228	139	39	6	3		1	
	b		40	124	32	1					
	c		14	104	106	29	5	2		1	
	d				1	9	1	1			
C. indus	a	3	11	16	3		3		1		
	b	3	11	12			2				
	c			4	2		1		1		
	d				1						
H. illota	a	1	2	5		1		1			
	b	1	1					1			
	c		1	3							
	d			2		1					

.....continued.....

TABLE XVII (continued)

		1	2	3	4	5	6	7	8	9	10
H. epistates	a	2	6	37	8	2	6	8	1	1	
	b	2	6	23	3	2	4	5		1	
	c			4	5		2	3	1		
H. lasiophthalma	a	2	38	39	6	3					
	b	2	24	18	2						
	c		14	21	4	2					
	d					1					
C. niger	a	1	9								
	b		1								
	c	1	8								
C. callidus	a	3	8	2	2	14	13	10	3	1	
	b	3	6	2	2	11	9	9	1		
	c		2			3	4	1	2	1	
T. similis	a	2	4	3	8	3	5	6			
	b	2	4	1	7		3	4			
	c			2	1	3	2	2			
C. moechus	a	10	32	27	96	62	47	39	16	2	
	b	10	31	27	90	46	40	29	12	2	
	c		1		6	16	7	10	4		
C. vittatus	a	1	3	1	71	231	251	218	100	54	13
	b	1	3	1	67	204	232	191	85	38	4
	c				4	27	19	27	14	16	8
	d								1		1

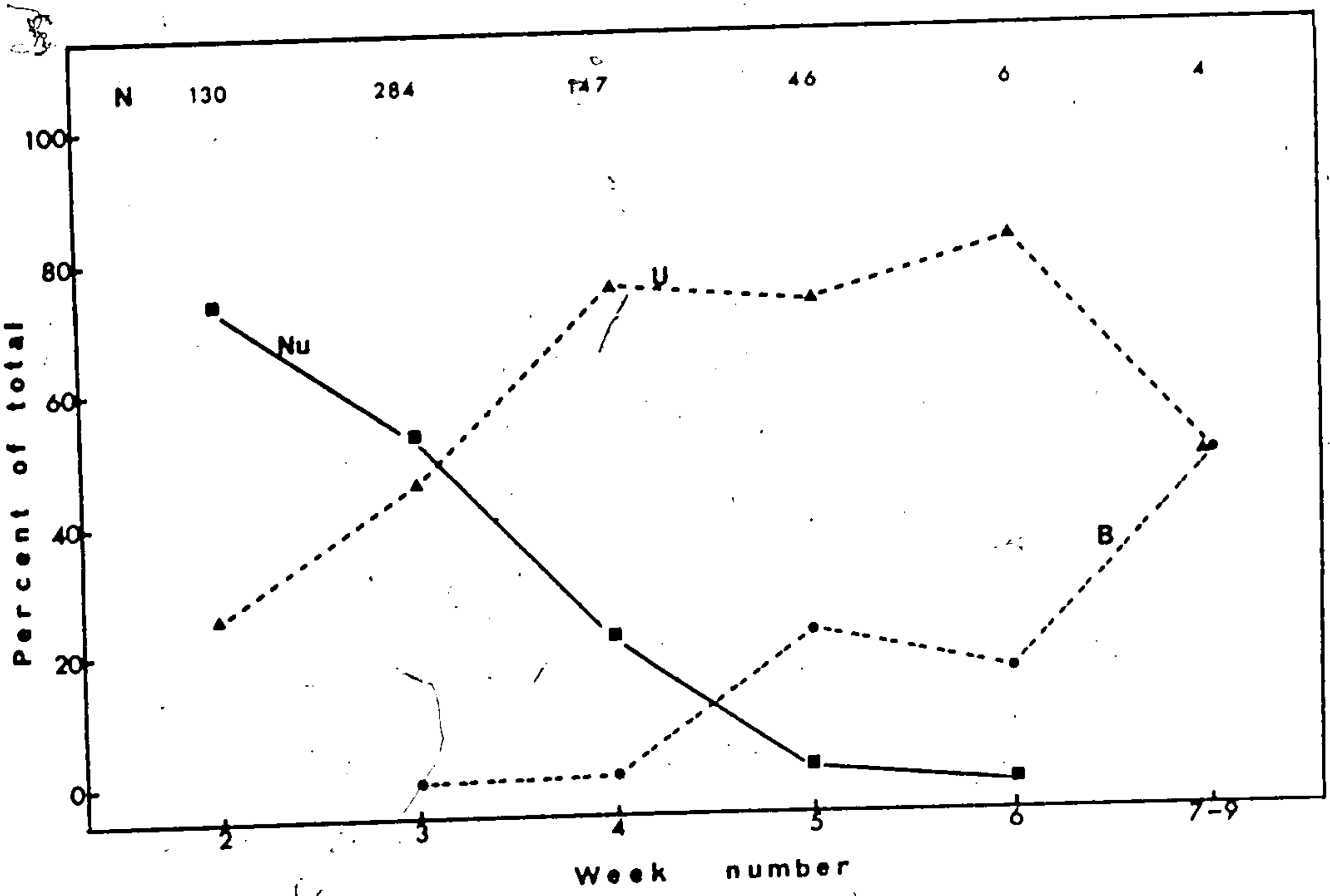
......continued.....

TABLE XVII (continued)

		1	2	3	4	5	6	7	8	9	10
C. univittatus	a	1	1	2	13	111	231	184	64	22	3
	b	1	1	2	12	91	201	154	51	13	
	c				1	20	30	30	13	9	2
	d										1
T. lineola	a	1	8	4	6	1	1	1	1		
	b	1	7	3	6	1					
	c		1	1			1	1	1		
T. quinquevittatus	a	2	19	13	8	4	1	1			
	b	2	11	5	3						
	c		8	8	5	4	1				
	d							1			
C. aberrans	a	1	5	6	10	2	1				
	b	1	5	5	8	1	1				
	c			1	2	1					

*First week missed.

FIG. 10. C. cincticornis: change in physiological age structure with time. N = number examined; Nu = nulliparous; U = uniparous; B = biparous.



on a seasonal basis (Table XVI) and on a weekly basis (Table XVII).

2. Diurnal Changes

An examination of the physiological age data for females caught at different times of the day showed that, for most species, the age composition changed insignificantly during the day (Table XVIII). Data from 1600 to 2000 hrs. was omitted from the table since collections after 1600 hr. were made only on certain days and these were unevenly distributed throughout the season. Only *C. callidus* and *C. cincticornis* showed a significant difference in age composition between the morning and afternoon (Table XVIII), relatively more parous flies being caught in the afternoon. The same trend was observed for *C. cuclux*, *H. lasiophthalma* and *T. quinquevittatus*, although it was not significant.

However, on certain days, such as 14 June, when *C. cuclux* and *H. lasiophthalma* were relatively numerous, the number of parous flies increased progressively during the day (Table XIX).

The number of uniparous *C. cincticornis* females was found to increase from the morning to the afternoon on 14 June (Table XIX), and the number of biparous females showed a similar increase on 27 June (Table XX).

TABLE XVIII

Percentage of Population Formed by Parous Females in Morning (0800-1200 hr.) and Afternoon (1200-1600 hr.)

	0800-1200 hr.		1200-1600-hr.		X^2	Significance of Difference
	No. examined	% parous	No. examined	% parous		
C. univittatus	288	19.4	256	14.8	2.01	-*
C. moechus	169	15.4	129	13.2	0.29	-
C. vittatus	641	11.7	276	12.3	0.07	-
T. quinquevittatus	27	55.6	15	66.7	0.14†	-
C. callidus	16	0.0	35	34.3	18.41†	.005>p>.0025
H. epistates	24	33.3	30	23.3	0.26†	-
H. lasiophthalma	37	40.6	44	50.0	0.72	-
C. cuclux	13	61.5	29	75.9	0.34†	-
C. cincticornis	150	58.0	198	70.2	4.09	.05>p>.025

*Difference not significant at 5% level.

†Yates' correction for continuity applied.

TABLE XIX

Change in Numbers of Nulliparous (N) and Parous (P) Females* during the Day (14 June)

		Time (hours)		
		0800-1200	1200-1600	1600-1900
C. cuclux	N	5	5	5
	P	1	9	11
H. lasiophthalma	N	9	8	2
	P	0	3	5
C. cincticornis	N	43	37	38
	P	6	32	28

*All parous females on 14 June uniparous.

TABLE XX

Change in Numbers of Uniparous (U) and Biparous (B) Females* of C. cincticornis During the day (27 June)

	Time (hours)		
	0700-1000	1000-1300	1300-1600
U	9	11	4
B	0	4	3

*No nulliparous C. cincticornis were caught on 27 June.

TABLE XXI

Retention of Mature Eggs by Parous Females in 1972

Number of parous females (a), number with relict eggs (b), mean number of relict eggs in those having relict eggs (c), range (d), percentage of parous females having one or more relict eggs (e).

	a	b	c	d	e
C. cuclux	44	15	5.0	1-12	34.1
C. cincticornis	273	27	1.7	1-6	9.9
C. indus	9	0			0.0
H. illota	7	0			0.0
H. epistates	15	1	3	3	6.7
H. lasiophthalma	42	8	4.3	1-15	19.0
C. niger	9	0			0.0
C. callidus	13	1	1	1	7.7
T. lineola	4	1	3	3	25.0
C. moechus	47	1	2	2	2.1
T. similis	10	2	9.5	4-15	20.0
C. vittatus	117	4	11.0	1-41	3.4
C. univittatus	106	7	1.4	1-3	6.6
T. quinquevittatus	27	4	3.0	1-8	14.8
C. aberrans	4	1	2	2	25.0

3. Retention of Mature Eggs by Parous Females

While dissecting flies to check for physiological age, a number of females were found with relict eggs. Records were kept to compare different species during the summer as to the degree of this incompleteness in oviposition. For each parous female, the presence or absence of relict eggs and the number of relict eggs was recorded (Table XXI). It was found that this occurrence was much more common in some species than in others. More than one third of parous *C. cuclux* females retained one or more mature oöcyte. When many relict eggs were found in a particular female, most of them tended to be contained in one ovary.

4. Discussion

a) *Seasonal Changes*. Before interpreting the present results, some discussion of the question of autogeny is warranted. In the case of the Tabanidae, or other haematophagous Diptera, autogeny is the ability of the female to produce mature oöcytes without the necessity of a blood meal. Anautogency, on the other hand, means that a blood meal is required before egg development can proceed to completion. A particular species may be autogenous only for the first gonotrophic cycle or it may be autogenous for more than one cycle.

A number of North American species of Tabanidae have been shown to be autogenous for at least one cycle:

C. atlanticus (Pechuman) and T. nigrovittatus (Macquart) (Rockel, 1969; Anderson, 1971); C. aestuans (van der Wulp) and C. fulvaster (Osten Sacken) (Cameron, 1926); C. fuliginosus (Wiedemann) (Rockel, 1969); C. mitis (Osten Sacken) and T. reinwardtii (Cameron, 1926; Thomas, 1971); C. frigidus (Osten Sacken); Atylotus "A", C. nubiapex (Philip), H. frontalis (Walker) and H. itasca (Philip) (Thomas, 1971).

Other species appear to be anautogenous: T. lineola (Rockel, 1969; Schwardt, 1936); T. atratus (Fabricius) (Schwardt, 1930); C. discalis (Williston); C. excitans (Walker); C. furcatus (Walker); H. epistates, H. illota and H. typhus (Whitney) (Thomas, 1971).

However, proof of autogeny of anautogeny for a particular species in one locality does not necessarily mean that this will be true in another area if one considers the complications among some of the mosquitoes (see Spielman, 1971). In Alberta, Haematopota americana (Osten Sacken) was autogenous in one locality but anautogenous in another (Thomas, 1971).

Direct proof of autogeny is obtained only when a female (usually one reared from a larva or pupa) completes the development of its eggs without having taken a blood meal. Indirect evidence for autogeny, however, may be gained by examining the physiological age of females captured while seeking a blood meal. If only parous females are caught, then there is good reason to suspect that the species in question is autogenous. If the species is anautogenous, both parous and nulliparous females will be captured. Both Thomas (1971) and Anderson (1971) found agreement in the conclusions (autogenous or anautogenous) arrived at by using each of these two methods.

Intermediate between obligatory autogeny and obligatory anautogeny is a third condition, facultative autogeny. Females exhibiting facultative autogeny are capable of producing eggs with or without a previous blood meal. Such females will take a blood meal if the opportunity presents itself and develop eggs as an anautogenous female would. However, if a blood meal is not procured after a number of days, autogenous ovarian development occurs. This is known among certain species of mosquitoes (Corbet, 1967) and Rubtzov (1958) considers it to be common among the Russian species of black flies. <u>Haematopota</u> <u>americana</u>, in Alberta, may exhibit facultative autogeny (Thomas, 1971).

For a species which is facultatively autogenous, field collections of host-seeking females would contain both parous and nulliparous individuals and so in this respect, would appear similar to an anautogenous species.

In the present study, at least one species was autogenous. Females of <u>T</u>. <u>reinwardtii</u>, reared from larvae and maintained on a diet of sugar and water, produced mature eggs; eggs were deposited by one female. Although few females were captured in CO_2-baited traps, all were parous. Autogeny in *T. reinwardtii* has previously been reported in Saskatchewan (Cameron, 1926) and Alberta (Thomas, 1971). Thomas (1971) suggested that this species may be autogenous for two or more gonotrophic cycles because while larva were abundant, no adults were collected. However, this may not be the case in all localities since at Caledonia, four females were caught in CO_2-baited traps and of the three which were dissected, all were uniparous and had oöcytes in stage IIB of development. Also, the author, and Davies (personal communication) have found females of this species is barns near Caledonia and Hamilton, Ontario. Thus it is possible that a blood meal is required by at least some females of this species before a second cycle may be completed.

There is evidence that *C. niger* is also autogenous. All but one female of this species caught in CO_2-baited traps were parous and no blood was seen in their guts. That the females were uniparous means that they were autogenous for the first cycle only. There are no previous statements of either autogeny of anautogeny for *C. niger*.

As nulliparous females constituted a significant percentage of the population of all other species (Table XVI), these species cannot be considered to be autogenous. In each case, the first females caught were nulliparous, after which parous females appeared and gradually formed an increasingly greater portion of the population (Table XVII). The rate of this increase, however, varied among the species (Fig. 9).

For the purpose of this discussion, the species can be divided into three groups. The first, consisting of *T. reinwardtii* and *C. niger* has already been discussed. The division of the remainder of the species into two groups was based on similarities and differences, between the species, in physiological age structure and seasonal changes in physiological age structure. Thus the second group is made up of *C. cuclux*, *C. cincticornis*, *H. lasiophthalma*, *T. quinquevittatus* and probably, *H. illota*. The third group includes *C. moechus*, *C. vittatus*, *C. univittatus*, *C. callidus*, *T. lineola*, *C. aberrans* and likely *H. epistates* and *T. similis*. The position of *C. indus* is uncertain.

The first differences between species in the two groups are seen in Table XVI. A much higher percentage of females were parous in species of group two (47.7-70.0%) than in species of group three (12.4-32.2%). Also, most biparous females were of group two species.

In group two, all females were parous four to six weeks after first appearance (Fig. 9). (It should be noted at this time that the beginning of emergence of C. cuclux and C. cincticornis preceeded trapping operations, but it is felt that the time span involved was no more than one week.) In group three, however, 100% parity was seldom reached. When group two species were at their peak abundance, more than 40% of the females were parous, but in group three, this figure was generally less than 20% (Fig. 9; Table XVII).

In summary, the difference between the two groups was that relatively more females of group two species were able to develop and deposit eggs than females of group three species. The question now is, what allowed group two to be more successful than group three? It cannot be related to taxonomic divisions as both groups contained species of all three genera. It is possible that some species are more successful in obtaining a blood meal than others. However, this does not seem a likely explanation for the difference between the two groups as all species were exposed to the same host population. Also species of Tabanus and Hybomitra, which generally restrict themselves to feeding on large mammals, are found in each group.

Because the species within each group were quite similar and because the two groups were distinctly different, it is the author's opinion that physiological differences are involved and that females of group two species are capable of facultative autogeny. This would certainly account for the relatively greater numbers of uniparous flies in group two. Group three species, then would be obligatory anautogenous and the lower number of parous flies would reflect the difficulties involved in obtaining a blood meal.

If this hypothesis is correct, then since group two species require a blood meal for a second batch of eggs while group three species require one for the first batch, and assuming that the chances of obtaining a blood meal are the same for both, the ratio of bipars to unipars in group two should equal the ratio of unipars to nullipars in group three. However, a contradiction arises here in that there were more unipars compared to nullipars in group three than bipars to unipars in group two (Table XXII). This contradiction may be explained in the light of Thomas' (1971) finding that there was greater survival between successive age classes in anautogenous species than in autogenous species. If the females of species considered here to be capable of facultative autogeny developed their eggs autogenously, their chances of survival would be reduced. Also, it is not known whether or not the chances of survival decrease with age; biparous females would be expected to be older temporally, as well as physiologically.

However, a decisive test of this hypothesis, that certain species are capable of facultative autogeny, requires that rearing studies be done.

TABLE XXII

Ratio of Unipars to Nullipars and Bipars to Unipars Among Females of Species Caught in 1972

(N = number of females examined)

	N	$\frac{\text{unipars}}{\text{nullipars}}$ X 100	$\frac{\text{bipars}}{\text{unipars}}$ X 100
Group 2 Species*			
C. cuclux	71	155.5	4.8
C. cincticornis	470	132.0	5.0
H. lasiophthalma	88	89.1	2.4
T. quinquevittatus	48	123.7	3.9
Group 3 Species*			
C. moechus	331	15.3	0
C. univittatus	632	20.0	1.0
C. vittatus	943	13.9	1.7
C. callidus	56	30.2	0
T. lineola	22	22.2	0
C. aberrans	25	19.1	0
H. epistates	61	32.6	0
T. similis	31	47.6	0

*See text.

b) Diurnal Changes. For certain species, the number of uniparous females increased from the morning until the afternoon. This was shown for *C. cuclux*, *H. lasiophthalma* and *C. cincticornis* (Table XIX) and *C. callidus* (Table XVIII). These observations parallel those of Duke (1960) with *C. silacea* (Austen) except that there, the increase in parous fly activity in the afternoon coincided with a decrease in the number of nulliparous flies. At Caledonia, no similar decrease in the number of nulliparous flies was observed.

The same pattern was noticed with biparous *C. cincticornis* on 27 June (Table XX). On this date, however, the number of uniparous females did not increase during the day. This is of some significance as it indicates that an increase in uniparous flies during the day is not necessarily a regular occurrence. It is possible that the relative absence of uniparous *C. cincticornis* in the morning of 14 June and the total absence of biparous females on the morning of 27 June is related to oviposition and post-oviposition activities. There is some evidence that this is the case as most of the uniparous females on 14 June and more than half of the biparous females on 27 June were in the sac stage, indicating recent oviposition. However, the ovaries of most of the uniparous females on 27 June were past the sac stage so that they had probably oviposited on the previous day or before.

c) Retention of Mature Eggs. Data on the retention of mature eggs by parous females are shown in Table XXI. This occurred from 0-34.1% of the time for different species. This range is in agreement with data presented by other authors: Lewis, 1960 [14% for *C. bicolor* (Cordier)]; Raybould, 1967 (11% for *C. bicolor*); Thomas, 1972 (6-28% for 12 spp.); Morris and Defoliart, 1971 (30% for *H. lasiophthalma*).

In general, egg retention was more common in species considered capable of facultative autogeny than anautogenous species. Egg retention was slightly more common in biparous females (16.0%) than in uniparous females (9.7%).

IV. SUMMARY

A. Diurnal Activity Pattern

Most tabanid species had a unimodal periodicity, the greatest number of flies being active between 1000 and 1600 hr. (E.S.T.). The activity patterns of *Chrysops vittatus* and *C. univittatus*, however, were bimodal, with peaks in the morning and in the late afternoon. The diurnal rhythms of host-seeking activity were largely exogenous, as they could be altered under different sets of meteorological conditions.

Activity was increased before and after a storm. Solar radiation appeared to be important in raising the body temperature of tabanids prior to flight in the early morning. On cool days, activity was controlled mainly by air temperature.

B. Effect of Meteorological Parameters on Day-Day Activity

The main factors affecting activity on a given day were air temperature and solar radiation. Of the two, air temperature was the more important. The optimum temperature for tabanid host-seeking activity was between 26 and 28°C and no activity was observed at temperatures less than 13°C. Curves of activity versus temperature were drawn for *C. vittatus* and *C. univittatus*. The effects of air temperature and solar radiation were found to be interrelated. This was demonstrable for *C. univittatus*; activity varied directly with the level of solar radiation at low air temperatures and inversely at high air temperature.

A comparison between the *Chrysopinae* and the *Tabaninae* was made. On hot, sunny days, the Tabaninae were relatively more active than the Chrysopinae, but if it was cool or cloudy, the Chrysopinae were the more active group. These differences were considered to be related to size differences between flies in the two subfamilies.

C. Physiological Age Studies

The physiological age of captured females was summarized on both a seasonal and a weekly basis. Of all females captured, 24.8% were uniparous and 0.9% biparous, the remainder being nulliparous. It is possible that some females may complete three cycles.

T. reinwardtii was shown to be autogenous, but possibly for only the first gonotrophic cycle. There was evidence that *C. niger* is also autogenous, but again, only for the first cycle. It was suggested that *C. cuclux*, *C. cincticornis*, *H. lasiophthalma*, *T. quinquevittatus* and *H. illota* were capable of facultative autogeny and the reasons for this viewpoint were discussed. Other species (*C. callidus*, *H. epistates*, *T. lineola*, *T. similis*, *C. aberrans*, *C. moechus*, *C. univittatus*, *C. vittatus*) were considered to be anautogenous.

Among certain species (*C. cuclux*, *C. cincticornis*, *H. lasiophthalma*, *C. callidus*), parous females were more active in the afternoon than in the morning. In the case of *C. cincticornis*, this was felt to be because of oviposition activities in the morning.

The incidence of mature egg retention in parous females varied from 0 to 34.1% among the species. It was slightly more prevalent in biparous females (16.0%) than in uniparous females (9.7%).

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