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Activities and physiological states of male and female *Tabanus sackeni*.
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Abstract Male and female *Tabanus sackeni* Fairchild (Diptera: Tabanidae) were collected on a road, dipping at pools of water on a road, and at UV-light traps; females were also caught in Malaise traps. Most males at UV-light traps were collected just before sunrise. Most females at UV-light traps were collected in the evening and most had recently taken a bloodmeal. Malaise-trapped females showed a distinct crepuscular peak of host-seeking activity. Crop volumes were variable in these host-seeking females; many had large-volume crops. Crop volumes were small in individuals of both sexes collected dipping or on the road. Many dipping females were gravid. By examining how physiological states and the behavior of individuals changed according to trap type, we are able to make inferences about the timing and importance of a number of unobserved activities. A link between uptake of water and sugar feeding was apparent and we postulate that mating takes place in the early morning, just before sunrise.

Introduction

Female Tabanidae are important pests of humans and livestock, and vectors of several diseases of man and other animals throughout the world. Historically, studies of their biology have focused on the host-seeking and blood-feeding behaviors, and the physiological ages of females in populations (e.g. Magnarelli and Stoffolano 1980), but recently there has been increased interest in the importance and role of carbohydrate feeding in both sexes (e.g. Kniepert 1980; Magnarelli 1985). A bloodmeal is required for oogenesis by many species of Tabanidae (anautogeny; Wilson 1967); carbohydrates are used to fuel flight (Hocking 1953). For females, flights are essential for dispersal, host searching, and oviposition. In some species, males utilize energy-costly hovering flights as a prelude to mating (e.g. Wilkerson *et al.* 1985).

There have been few studies of Tabanidae that have examined physiological states and carbohydrate use by both sexes during a variety of activities. Because flight is so important to Tabanidae, and carbohydrates are essential for flight, carbohydrate usage is an important aspect of adult survival and fitness. The primary difficulty lies in sampling individuals that are in physiological states other than host seeking,

The purpose of the present paper is to examine the interactions among physiological states, carbohydrate reserves, activities, and sex, in order to better understand the biology of 1 species of tabanid, viz. *Tabanus sackeni* Fairchild. *Ta. sackeni* is found throughout eastern North America and reaches its northern limit in southwestern Ontario (Pechuman *et al.* 1983). We trapped both sexes of *Ta. sackeni* throughout the day and night and in a variety of physiological states. By examining how these states and the behavior of individuals changed according to trap, we were able to make inferences about the timing and importance of a number of unobserved activities. This approach could be exploited in the study of cryptic components of the behavior of other biting flies.

Materials and Methods

Study area. Rondeau Provincial Park (RPP) (UTM: 17 MS 28; 42°10' N; 81°90' W) is a cuspate sand spit jutting into Lake Erie, Ontario. It contains a large (*ca.* 1100-ha) remnant Carolinian forest with numerous seasonal ponds (sloughs).

Most of our work was carried out along a dirt road leading to a small clearing in an oak-pine woodland in the center of RPP (UTM: 17 MS 302 828; ‘the clearing’) and at a cottage along a beach (UTM: 17 MS 305 815; ‘the cottage’). About 400 white-tailed deer (Cervidae; *Odocoileus virginianus* Zimmerman) (A. Woodliffe, Ontario Ministry of Natural Resources, personal communication), a known host for *Ta. sackeni* were present in RPP during the study.

Collections. Ta. sackeni were collected using a variety of trap types on daily visits to the 2 sites during late July and August of 1985 and 1986. Both sexes were collected during the day using a black-plastic sheet on the road (PVC trap; Kniepert (1979) first described this trap and called it a 'Foil' trap — its shiny black surface mimics a pool of water) and during the night using a 15-W ultraviolet lamp placed in front of a white sheet (1.5×2 m) at 1 m above ground level (UV-light trap). Females were collected during the day using Malaise (Roberts 1971) and Manitoba (Thorsteinson *et al.* 1964) traps. Malaise and Manitoba traps worked passively (they retained flies that were trapped) whereas the PVC traps and UV-light traps were manned (an observer collected flies that came to the traps). We operated a single Malaise trap in the clearing for 4 consecutive 24-h periods in August 1986. It was emptied at least 3 times between 0500 and 1800 (all times are EST): early in the morning (0500–0700), at mid-day (1000–1200), and in the early evening (1600–1800). Between 1800 and 2000, when fly activity was at a peak, the trap was emptied every 20 min. In addition, a Malaise trap was run for 4 consecutive 24-h periods, and 2 Manitoba traps were run for 8 consecutive 24-h periods at locations up to 4 km from the clearing, to ensure that the patterns of activity being observed in the clearing were not site- or trap-specific.

We operated UV-light traps for 7 trap nights in 1985 and 15 trap nights in 1986. They were turned on before sunset (*ca.* 1900) and run continuously until after sunrise (*ca.* 0600) at the clearing and/or the cottage sites. Flies that landed on the sheet were collected continuously from sunset until *ca.* 2300. A light was usually left on after 2300 (during heavy rainfall it was disconnected) but no collections were made until *ca.* 0300. Flies collected from the sheet at 0300 could have been on the sheet since 2300 and so were not included in any analyses. From *ca.* 0300 hours until sunrise, flies that landed on the sheet were continuously collected.

2 PVC traps were operated in the clearing for 8 d in 1985 and 1 day in 1986. *Ta. sackeni* adults landed on and beside the traps, on damp roads and at the edges of nearby puddles. The behavior of the various individuals appeared identical, so all were collected and used as part of the sample from the PVC trap. They were collected during the period 0700–1600, but the duration and times of collecting varied each day.

All flies collected were placed into a Plexiglass cage (2.5×2.5×16 cm, with 2 screened sides) to be held for dissection. Those not dissected immediately after collection were placed (without access to water) in a cooler with ice, or a refrigerator at 4°C, within 30 min of collecting. Individuals not dissected within 4 h were discarded.

Dissections were done using watchmaker's forceps under stereoscopic microscopy, usually at ×60. 3 variables were assessed in both males and females: crop-volume; refractive index of crop contents; and the amount of fatbody. 3 additional variables were assessed for females: the ovarian stage; parity (using the presence of follicular dilatations (Detinova 1962)); and the gut contents. In 1986 we noted the presence or absence of sperm in the spermathecae of most females, and the ovarioles in each ovary of 22 females were counted.

Individuals to be dissected were immersed in a physiological saline (Hagedorn *et al.* 1977) containing a drop of liquid detergent. The ventral surface of the abdomen was torn open near the thorax, and torn down the side. The ventral diverticulum (crop) was grasped at the point where it joins the esophagus, and pulled out intact. Its surface was dried by blotting lightly with bibulous paper.

Crop-volume was assessed visually and assigned to an open-ended series of categories as follows: 0 (nothing visible); 0–0.5 µl (some liquid); and further categories that increased from 0.5 µl by 1-µl increments. These visual assessments were tested occasionally by measuring actual crop-volumes using microcapillary tubes. The refractive index of crop contents was measured using a temperature-compensated refractometer (Reichert, Model 10423). This index can be used as a relative measure of the combined concentration of the sugars sucrose, fructose and glucose in liquids (Inouye *et al.* 1980). Crops containing >1.5 µl of liquid were assessed as follows. The blotted crop was pierced with a 2-µl microcapillary tube and *ca.* 1 µl was drawn into the tube by capillary action. The fraction of the tube containing crop fluid was recorded. The tube was then filled with distilled water and the refractive index of the resulting solution was measured and converted to a refractive index of undiluted crop fluids.

The amount of fat body was assessed visually and assigned to one of four categories: 0 = no fat; 1= some fat; 2 = much fat; and 3 = obese. Gut contents were assessed visually and assigned to 1 of 4 categories: no blood; small amount of blood in midgut; half-digested blood; and recently blood-fed (a large amount of uncoagulated blood).

Analysis. Log-linear models were fitted to the multiway tables of data using a forward-selection technique (Fienberg 1980). In order to increase expected frequencies in cells of sparse tables, most variables were collapsed into 2 or 3 states. The maximum probability of a type-1 error was set at 1% for each stage of the selection procedure so that the table-wise type-1 error rate would not exceed 5%.

Crop-volume was collapsed into 3 categories: <0.5 µl fluid; 0.5–2.5 µl fluid; and >2.5 µl fluid; the amount of fatbody was collapsed into 2 categories: little or no fat; and much fat; ovarian state was collapsed into 2 categories: resting stage or earlier (I, II); and beyond the resting stage (III, IV, gravid); and gut-contents was collapsed into 2 categories: blood present; and blood absent. We amalgamated 2 variables, viz. time-of-day and trap-type, because they are complementary (Malaise traps catch flies only during the day and UV-light traps work only at night). The resulting synthetic variable, 'activity', contained the following 5 categories: host-seeking before 1700; host-seeking after 1700 (the division was made at 1700 hours because there was a distinct change in the intensity of activity after this time); at PVC trap or sitting on the road (dipping); at UV-light traps before 2300 (evening period); and at UV-light traps after 0300 hours (morning period).

Log-linear models were fitted using the TABLES procedure in SYSTAT (Wilkinson 1986). The effects of sex and crop-volume on the refractive index of crop contents was tested using a 2-way ANOVA using the MGLH procedure in SYSTAT (Wilkinson 1986). All means are reported ± 1 SE.

Results

Activities

Adults dipping. Both sexes were observed 'dipping' as described by Jones (1922) and Blickle (1955); individuals in flight briefly touched the surface of pools of water 1 or more times, then flew away. Dipping was commonly observed in 1985; there was little rain during late July and early August and there were few areas of standing water in RPP (at London, ON, 100 km NE of RPP, 64.3 mm of rain fell between 9 July and 12 August; Environment Canada). All but the largest sloughs were dry. In 1986, rain was more frequent (153 mm fell between 9 July and 11 August at London, ON; Environment Canada) and most sloughs contained water; dipping was only rarely observed. We suspect that the activity was equally prevalent in 1985 and 1986, but because there was more open water in 1986, dipping was distributed over a larger area and, consequently, more difficult to observe.

Dipping occurred predominantly on sunny days. We suspect that there were daily differences in the frequency and intensity of dipping but our sample sizes were too small to adequately assess these. 47 males and 63 females were observed dipping; of these, 27 males and 36 females were collected for dissection.

Host-seeking females. No males were collected in Malaise or Manitoba traps. No females were collected in Malaise traps at night and few were collected during most of the day. However, capture rates increased markedly *ca.* 2.5 h before sunset (*ca.* 1700), peaked just before sunset, and then declined rapidly to zero after sunset (Fig. 1). 287 females were collected in Malaise and Manitoba traps; 205 of these were dissected.

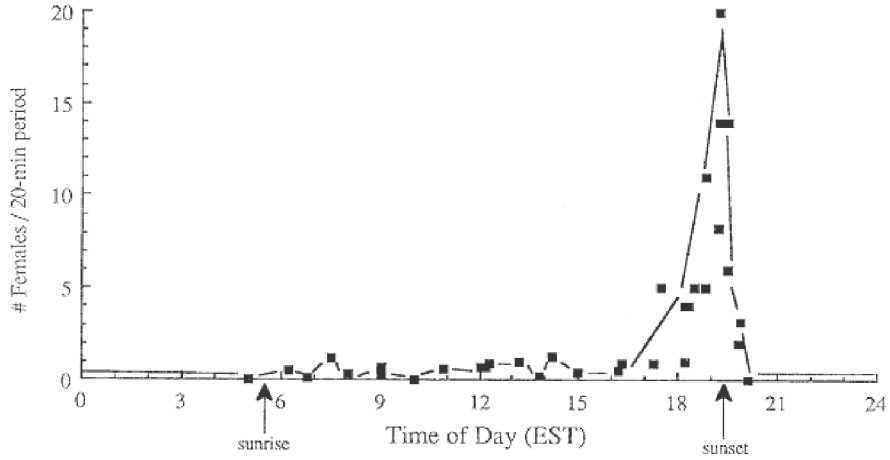

Fig. 1. Number of female *Tabanus sackeni* collected in a Malaise trap over a 4-d period. Data have been converted to a rate (number/20-min period).

Adults at UV-light traps. Males and females were collected at UV-light traps in both 1985 and 1986, but with less success in 1986. The number of individuals collected was strongly related to the mean ambient temperature during the collecting period. As ambient temperature increased, the numbers of individuals we captured increased logarithmically (Fig. 2a, b). 99 males and 54 females were collected in UV-light traps; of these, 84 males and 50 females were dissected.

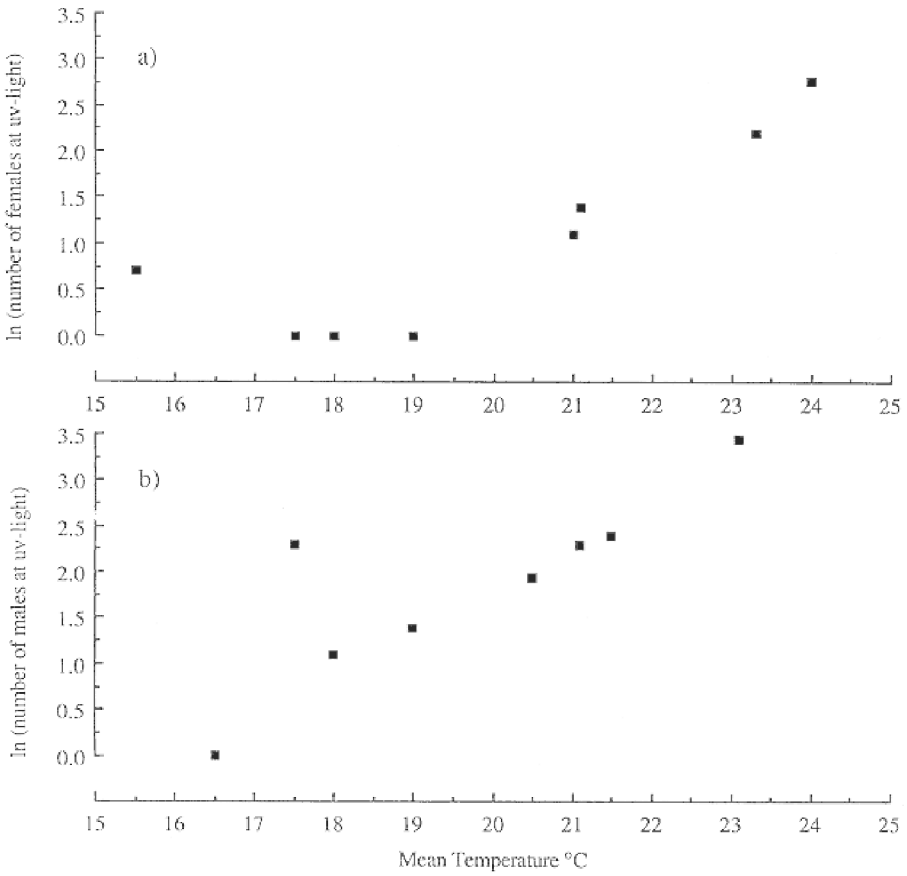

Fig. 2. (a) ln (no. female *Tabanus sackeni*) at UV-light trap in evening (time period of major activity) *vs.* mean temperature over the evening period. Spearman's rank correlation coefficient = 0.83, $P < 0.05$. (b) ln (no. male *Tabanus sackeni*) at UV-light trap in morning (time period of major activity) *vs.* mean temperature over the morning period. Spearman's rank correlation coefficient = 0.82, $P < 0.05$.

Physiological state

Summaries of physiological variables by activity are presented for males and females in Table 1. In order to gain a broader understanding of how physiological variables changed across activities, by sex, and in relation to each other, we proceeded with a series of contingency-table analyses. Multi-way patterns of change are more informative than a series of 2-way analyses. However, as the dimensionality of a table increases, the number of cells increases exponentially, and tests quickly become less robust (Fienberg 1980). We were forced in some instances to explore tables of lower dimensionality than we had hoped.

Table 1. Percentage occurrence of male and female *Tabanus sackeni* in various physiological states at all trap-types / times in Rondeau Provincial Park, Ontario.

	Activity and time (hours EST)*				
	Dipping	Host-seeking		At uv light-trap	
	06.00–17.00	06.00–17.00	17.00–21.00	19.00–23.00	03.00–06.00
Females					
Ovaries					
I–II	28	98	100	70	69
III–IV	25	0	0	27	31
Gravid	47	2	0	3	0
N	36	64	139	37	13
Gut content					
bloodfed	25	3	1	78	46
N	36	64	141	37	13
Crop (μl)					
<0.5	75	62	46	32	69
0.5–2.5	22	23	26	62	23
>2.5	3	15	29	5	8
Mean	0.47±0.14	0.96±0.21	1.91±0.23	1.16±0.15	0.64±0.29
N	36	61	140	37	13
Males					
Crop (μl)					
<0.5	70	–	–	19	53
0.5–2.5	26	–	–	75	34
>2.5	4	–	–	6	13
Mean	0.56±0.17	–	–	1.45±0.25	1.10±0.18
N	27	–	–	16	68
Effort† (h)	17	42	16	51	42

* Activities, time periods, and ovarian-state categories are explained in the text. Sunrise in August ranged from 0521–0552; sunset ranged from 1947–1903.

† Effort is the approximate number of trap-hours in both 1985 and 1986.

We were initially interested in how 2 energy variables, crop-volume (exogenous energy) and fatbody (endogenous energy) were related to activity and sex. Understanding differences in energy utilization between sexes, and across activities, as well as understanding sexual differences in activity patterns, is central to the understanding of the biology of the flies. A loglinear model was fitted to the 4-way table: sex × activity × crop-volume × fatbody. Because males do not host-seek, and none was collected in the Malaise traps, the appropriate cells in the table were treated as structural zeros (Everitt 1977).

The model that best fitted the table contained 2-way interactions between sex and activity and between crop-volume and activity, and all 1st-order terms. The effects of the interaction terms were elucidated by examining the corresponding 2-way tables and tables of standardized residuals.

The interaction of sex × activity was due to a differential response to UV-light traps between the sexes. Males were captured at UV-light traps predominantly during the morning period, whereas females were captured predominantly during the evening period (Table 1). The distinct segregation of the behavior of the sexes, especially the strong tendency for males to be found at the light in the morning, indicates that the UV-light trap does not attract all subsets of the population equally, and that there is a strong temporal component to the efficacy of the trap.

The interaction of crop-volume × activity was due to different proportions of individuals in each of the 3 crop-volume categories among the activities. Standardized residuals indicated that 3 cells contributed to the significant *G*-value: more individuals of both sexes had medium crop-volumes in evening UV-light-trap catches than was expected (under the null hypothesis of independence of all effects); fewer had large crop-volumes when dipping than was expected; and more females with large crop volumes were collected in evening Malaise catches than was expected (Table 1).

There were no interactions involving the variable fatbody. Fatbody undoubtedly varies throughout the season as the mean age of the population increases and individuals deplete their fat reserves. Our method for coding the variable was possibly too crude, and/or our samples were not distributed through the season in such a way as to detect these changes. We omitted this variable from further analysis.

Female physiological states and activity

Next, we examined the relationship among gonotrophic state (ovarian state, gut-contents and parity), energy state and activity in the females. However, in order to produce a table of sufficiently small dimensionality (i.e. with adequate cell frequencies and marginal totals) we were first forced to restructure several variables.

We first examined the variables gut-contents and ovarian state. Blood is utilized by the females for ovarian development, so a high concordance between the 2 variables was expected, and found. Therefore, we created a synthetic variable, 'gonotrophic state', from the 2 variables. Females were divided into 3 categories: those with ovaries in the resting stage but with no blood in the gut (host-seeking females); those with ovaries in the resting stage (stage I or II) and with full, recent bloodmeals; and those with ovaries developed beyond stage II (most had partially digested bloodmeals). Inasmuch as host-seeking females are almost always in the same gonotrophic state (viz. ovaries in the resting stage, no blood in the gut) little additional information could be gained by including them in an analysis; they were therefore dropped from the table. Most of the remaining individuals had small or medium crops; consequently, the crop-volume variable was restructured to form a binary variable indicating presence (>0.0 µl) or absence of fluid in the crop. Finally, we eliminated parity from the analysis because parous state does not markedly influence the behavior of anautogenous female Tabanidae (Magnarelli and Anderson 1981; Leprince and Lewis 1986).

A model containing 2 interactions, activity × crop-volume and activity × gonotrophic state, fit the resulting 3-way table. The activity × crop-volume interaction was expected, given the first analysis. The activity × gonotrophic state interaction indicates that females dipping and at UV-light traps are gonotrophically distinct. Females dipping usually have developing ovaries, but are not recently blood-fed, whereas females at UV-light traps in the evening are usually recently blood-fed. Females collected at UV-light traps in the morning are more likely to be in a host-seeking state (*see* Table 1).

The effects of crop-volume and sex on refractive indices of crop contents were tested using a 2-way ANOVA. There were no significant effects, indicating that the sugar concentration of the crop contents was independent of the volume. Individuals with larger amounts of fluid in the crop therefore contained larger energy reserves.

The mean number of ovarioles in 22 females was 256 ± 36.3 (range 194–317).

Discussion

Little was known of the biology of *Ta. sackeni* prior to these studies (Pechuman 1981). In spite of gaps that remain (we observed no mating or oviposition) we can postulate a life history for *Ta. sackeni* by examining observed patterns of physiological change and behavior and deducing when and where certain events are occurring. Many studies of biting flies are compromised by the inability to trap individuals in behavioral states other than host-seeking. The techniques we used to explore the biology of *Ta. sackeni* enabled us to detect changes in behavior and physiological state through time and by sex that would otherwise have gone unnoticed.

Host seeking

Malaise traps intercept flight, and direct insects upward into a collecting chamber. Hollander and Wright (1980) found correlations between the biting activity of female Tabanidae on a host and the number of females collected in Malaise traps, suggesting that Malaise traps are intercepting flight-activity associated with host seeking. The physiological data from the present study support this association; no males were collected in Malaise traps and virtually all the females collected had resting-stage ovaries, were not blood-fed, and hence were in a host-seeking physiological state. Furthermore, recently blood-fed females were frequently collected at UV-light traps after sunset implying that successful host-seeking had recently occurred. Female *Ta. sackeni* are host-seeking during a short window of activity in the hour containing sunset. The crepuscular-activity peak was found at 4 sites using 2 types of trap and so cannot be attributed to trap type or location.

If host-seeking activity occurred at night, the Malaise trap did not detect it. Inasmuch as host-seeking Tabanidae rely considerably on visual cues to detect hosts (Allan *et al.* 1987), it is unlikely that active host seeking occurs after 1 h past sunset, the time of the last catches in the Malaise trap. The few females collected in the Malaise trap during the day may indicate that some females can be stimulated into appetitive flight outside the sunset window, perhaps by the presence nearby of a host.

The crepuscular-activity peak of female *Ta. sackeni* parallels a behavior pattern of white-tailed deer in southern Ontario. At dusk, deer move from forest cover to openings near edge habitats (D.R. Voigt, Ontario Ministry of Natural Resources, personal communication), a behavior that would increase their detectability by tabanids. A host-searching strategy that restricts activity to a brief period when an encounter with a host is enhanced will decrease the amount of active time, and therefore energy, required by the fly to obtain a bloodmeal, and may therefore increase the probability of successful oogenesis.

Mean crop-volume was highest in host-seeking females, but nevertheless, many host-seeking females had little or no fluid in the crop. Females need carbohydrates to fuel flight (Hocking 1953), and for survival during oogenesis (Lall 1970; Magnarelli and Stoffolano 1980). If it is true that tabanids do not convert carbohydrates to fat or glycogen (Auroi and Briegel 1985), then females with small crop-volumes (and thus small stores of carbohydrates for flight) before, during or after host-seeking, may be at a disadvantage as compared with females with large crop-volumes.

Magnarelli and Anderson (1981) postulated 2 strategies for carbohydrate acquisition and usage: ‘(1) a large intake of nectar and a slow release of sugars from the crop to provide energy or (2) intermittent ingestion of small sugar meals throughout the flight period and immediate metabolism’. The large crop volumes of some host-seeking female *Ta. sackeni* rules out (2) as the sole strategy. If all host-seeking females in the population took a large carbohydrate meal (strategy 1), we would expect to see a larger, and earlier diel peak in crop-volume within the population than was observed.

At UV-light traps

Most female *Ta. sackeni* found at UV-light traps in the evening were recently blood-fed or had ovaries developed beyond the resting stage, with a partially digested bloodmeal; few females in a host-seeking state were found. Biting Diptera, after blood feeding, seek resting sites in which to complete oogenesis. The presence of recently blood-fed female *Ta. sackeni* at UV-light traps suggests a positive phototaxis when seeking such resting sites. After feeding at sunset, a positive phototaxis would cause females to be attracted to the upper canopy of the forest, where light from the sky is strongest; UV-light traps may act to divert this behavior. Females with partially digested bloodmeals that are disturbed while resting, would also be attracted to the UV-light traps when seeking a new resting site. The few males that were found at UV-light traps in the evening may also have been searching for resting sites in the canopy. Bowden (1977) lists several canopy-inhabiting, crepuscular Tabanidae that are also attracted to lights.

Many male *Ta. sackeni* were found at UV-light traps in the hours just before sunrise, indicating that an activity associated with sunrise was being diverted, or prematurely elicited by UV-light traps. There are interesting parallels between the behavior of *Ta. sackeni* at UV-light traps and an African tabanid, *Tabanus thoracinus* Palisot de Beauvois. Corbet (1964) found a pronounced peak in the number of male *Ta. thoracinus* at UV-light traps just before sunrise and immediately prior to the time when males hovered above the forest canopy (Corbet and Haddow 1962).

Mating in Tabanidae is often associated with aggregations of males (Wilkerson *et al.* 1985). Although we were unable to find male aggregations in *Ta. sackeni,* we speculate that *Ta. sackeni* is mating at aggregation sites in the canopy at sunrise as *Ta. thoracinus* appears to do. Males and females may be attracted to UV-light traps in anticipation of sunrise. For 2 mornings in 1985, a UV-light trap was operated in RPP *ca.* 5 m above ground and 2 m below the top of the canopy in synchrony with a UV-light trap at ground level. Both traps collected the same number of male *Ta. sackeni,* which suggests that males can be active at both levels.

Female *Ta. thoracinus* captured at lights before sunrise were more likely to be nulliparous; some were uninseminated (Corbet 1964). The only 3 uninseminated female *Ta. sackeni* we collected were at UV-light traps during the morning period, further strengthening the association between mating, the morning, and attraction to lights. There are no data on physiological states of most species of Tabanidae that are attracted to lights.

Tabanidae are less active at lower temperatures (Pechuman 1981), which may partially explain the low number of *Ta. sackeni* at UV-light traps during cooler periods. Similarly, there is a strong link between ambient temperature and the onset of aggregation in three other species of Tabanidae studied at RPP (Taylor 1987). The absence of males at UV-light traps on cool mornings may reflect a delayed onset of aggregation, and a subsequent failure to respond to the UV-light traps when ambient light levels rose after sunrise. This could provide a clue to the exact timing of aggregation in ideal thermal conditions. For example, Corbet and Haddow (1962) found *Tabanus insignis* Loew hovering above the forest canopy before sunrise, but 15–20 min later than *Ta. thoracinus* and *Chrysops centurionis* Austen. All 3 species were present in the same area, engaged in the same behavior. In direct contrast to *Ta. thoracinus* and *Ch. centurionis,* however, *Ta. insignis* was only rarely collected at UV-light traps (Corbet 1964). Perhaps by the time *Ta. insignis* males were physiologically ready to aggregate, the UV-light trap was not effective because ambient light levels were too high.

Dipping

Tabanidae 'dip' at pools of water along roads and in streams, as noted for *Tabanus sulcifrons* Macquart by Hine (1906). Jones (1922) gave a detailed description of the dipping behavior, describing individuals as coming down from a height to dip or to make a series of dips before flying up again out of sight. Because dipping is associated with the behavior of individuals that probe the damp road as well as the edges of puddles, and even sit on top of the puddles, it seems likely that water uptake is the principal purpose of the activity.

Female *Ta. sackeni* collected dipping had small crop volumes and had ovaries developed past the resting stage. Kniepert (1984) found a similar situation with female *Tabanus bromius* L. That both sexes of *Ta. sackeni* were found at water, and the females were in a range of gonotrophic states, suggests that in a variety of physiological states there is a common need for water., In addition, a link between water uptake and carbohydrate feeding is suggested by the generally low crop-volumes found in individuals dipping.

In male *Hybomitra epistates* (Osten Sacken), dipping occurs immediately after the cessation of aggregation (hovering) in the morning (Taylor and Smith, unpublished observations), at a time when crop volumes are small (Taylor 1987). If male *Ta. sackeni* hover or expend energy in a mating aggregation as speculated, crops will be depleted in the morning and dipping may be necessary to imbibe water needed for carbohydrate feeding (see below). Males and females of *Chrysops atlanticus* Pechuman feed on nectar frequently in the morning, before and immediately after mating (Magnarelli *et al.* 1979).

The sources of carbohydrates used by Tabanidae have long been questioned. Adults are found feeding on flowers, but not frequently enough to account for the large carbohydrate reserves commonly found in crops (Magnarelli *et al.* 1979). Several species are known to feed on aphid honeydew (Hine 1906; Magnarelli *et al.* 1979; Kniepert 1980). Dried honeydew was abundant on the leaves of most trees around the study area in August of 1985 and 1986 and we observed some species of Tabanidae (but not *Ta. sackeni*) feeding on it. We concur with Magnarelli *et al.* (1979) and Kniepert (1980) that aphid honeydew may be an important source of nectar for Tabanidae. During periods of light rain, or high humidity, liquids with high sugar contents will absorb water from the air (Crane 1975; Corbet *et al.* 1979). In these periods, adult Tabanidae could take advantage of the aqueous honeydew, and feed frequently. Conversely, during periods of drought or low humidity, honeydew would be viscous, and therefore more difficult to imbibe. During these times, successful feeding would depend on first finding water, which could be used to dilute dried honeydew or nectar. Corbet *et al.* (1979) showed that floral nectars were concentrated at lower humidities. Some nectaries that were apparently dry were repeatedly probed by empidid flies. They speculate that these flies (and other insects) may spit into the nectaries to liquify dried sugars. A similar situation in *Ta. sackeni* would offer a ready link between carbohydrate needs and water uptake.

The decrease in prevalence of nectar-feeding through the year in populations of Tabanidae described by Kniepert (1980), and the slightly higher prevalence of nectar feeding in parous females described by Leprince and Lewis (1986) have been usually interpreted with respect to the physiological status of the flies. For example, Kniepert (1980) showed seasonal changes in nectar-positivity rates for 4 species of Tabanidae. He proposed that individuals that emerge early in the season are the principal nectar-feeders and that the peak of nectar feeding occurs 1 wk prior to blood feeding in the females. An alternative hypothesis is that environmental conditions are an important factor in determining the availability of nectar resources and observed seasonal changes in nectar-positivity rates are due to variation in the availability of nectars through the season.

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