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A study was undertaken to investigate the general behavior and reproductive activity of an adult population of Lestes vigilax at an impoundment in piedmont North Carolina. The study was conducted from July through October, 1971 with observations being made daily, weather permitting. These observations were made with regard to time of day, temperature and light intensity.

Lestes vigilax is a late summer species in this locality. Emergence took place in July and August with the adults flying until the first of October. Following emergence the teneral damselflies flew to the woods and remained there for a maturation period of undetermined length. Studies on interaction and reproductive behavior were made with the mature adults during the mornings while they were flying. It was found that the males made random approaches to other males in a primitive territorial maneuver. During these approach flights, threats and contacts were made; a threat being simply an approach while actual physical touching constituted a contact. The mates achieved tandem with the females without courtship display. Following tandem achievement one-half of the observed pairs experienced a pre-copulation rest period. The remaining pairs began copulation immediately. This copulation took place while the pair was perched on the vegetation bordering the lake. After copulation oviposition followed, usually immediately. Oviposition took place on or in floating sprigs of Elodea near the center of the lake. The female, in tandem with the male, always oviposited on the surface; they never descended beneath the water. Following oviposition, the pair broke tandem and returned to the shore.

A STUDY OF BEHAVIORAL AND REPRODUCTIVE PATTERNS OF ADULT *LESTES VIGILAX* HAGEN (ODONATA: LESTIDAE)

by

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Approved by

Paul E. Lutz

This thesis has been approved by the following committee of the Faculty of the Graduate School at The University of North Carolina at Greensboro.

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March 25, 1972
Date of Examination

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Adult odonates are quite common and familiar insects during the spring and summer, since this is their flight period. The adult stage is extremely important as it is the feeding and reproductive stage. They feed mostly during their teneral phase of life as they are maturing. Adults occasionally feed during the reproductive period, but this is mainly for sustenance and not development (Corbet, 1962).

A few adult behavior studies have been done on representatives of this order. These studies were concerned with such things as territoriality, oviposition and general behavior. Pajunen (1963) studied the threat display of resting dragonflies and found that as a flying male approaches, a resting male will raise up on its legs until the abdomen is elevated in the air. Females of Ischnura verticalis displayed a similar response to approaching males (Bick, 1966). The female raised her abdomen and added a vigorous fanning of the wings. Kaiser (1969) discovered that males of Aeschna cyanea displayed a time-regulated territorial behavior at their mating place. Johnson (1962a) studied Calopteryx maculatum and found that the male selected the oviposition site, achieved tandem with a female, copulated and then returned to the oviposition site and guarded the female while she laid her eggs. In adults of Enallagma civile, Bick and Bick (1963) found there was no courtship display by either sex. While the male was the active partner in seizure and copulation, the female controlled ovipositing activity. Archilestes grandis also showed no

courtship display (Bick and Bick, 1970). Hetaerina americana was studied by Bick and Sulzbach (1966) and they found that oviposition occurred beneath the water with the female staying submerged three to five minutes. With Ischnura verticalis, Grieve (1937) found definite courtship patterns and that oviposition was initiated anywhere from a few hours to several days after mating. These reports offered valuable information even though they dealt with species other than those of the genus Lestes.

In the genus Lestes studies have been made by Bick (1961) on Lestes disjunctus australis where he found that the teneral period lasted 13 days and the behavior of the female attracted the male. He also observed that the males remained with the females during oviposition and that they oviposited well above the waterline. Gower and Kormondy (1963) found that the male of Lestes rectangularis did not stay with the female during oviposition. Bick and Hornuff (1965) studied Lestes unquiculatus and found that the lack of courtship behavior and territoriality characteristic of recent groups led them to believe Lestes unquiculatus to be a primitive species. Lutz (1968) found that larvae of Lestes eurinus had a two-month emergence period which was temperature-dependent. Corbet (1956) stated that Lestes sponsa adults oviposited from July to September. Lestes eurinus was studied again by Lutz and Pittman (1968). They found that the adults of Lestes eurinus oviposited in June and July in tandem above the water level. The male was dominant in selecting the oviposition leaf, while the specific site on the leaf was chosen by the female. Specific

details on the location, duration and mechanisms of oviposition are poorly known in the zygopterans.

Very little is known about the general biology of adults of Lestes vigilax. With the availability of a newly emerging population of Lestes vigilax at a nearby lake, I undertook a study of the adult behavior of this species. I studied their intra- and interspecific non-reproductive behavior and their reproductive activities. All observational studies were related to time of day, ambient temperature and light intensity.

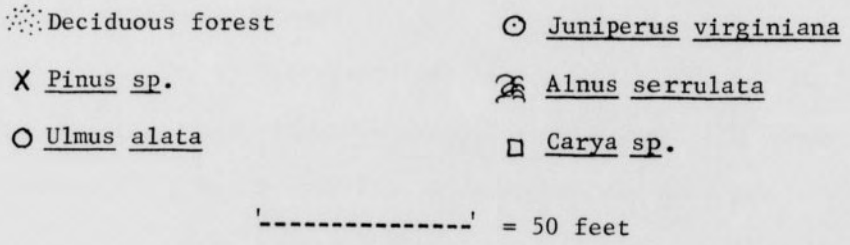
MATERIALS AND METHODS

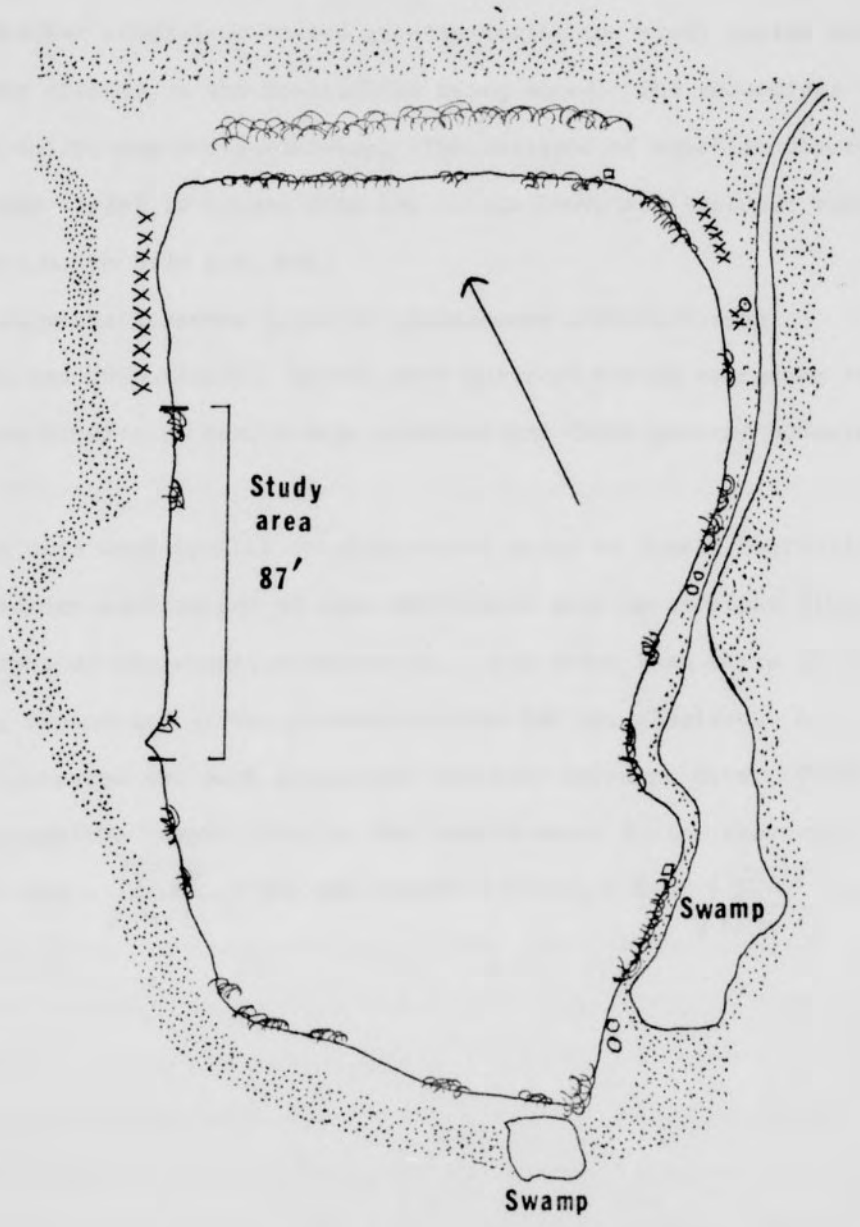
This investigation was conducted at a small impoundment near McConnell Road (N. C. No. 3000) in southeast Greensboro, Guilford County, North Carolina. The lake covered an area of approximately three acres. It was bordered on all sides by woods consisting of oaks, hickories, beeches, dogwoods, other hardwoods and conifers with sedges and bushes on the immediate shore. There were two small swamps in the immediate vicinity which may have accommodated some of the reproductive activity but a substantially large amount was observed to occur at the lake's edge. The lake itself had a fairly large growth of Elodea canadensis with many floating sprigs upon or in which the damselflies oviposited. A path of one meter was cut around the lake several meters from the water line to facilitate the observational rounds during the research. Adults of Lestes vigilax frequented most of the shore line, but only one side was used for the study area. This study area was chosen because of its accessibility and because there was a relatively large number of adults at this site. Figure 1 is a diagram of the lake and surrounding area with the study area being indicated.

Data were collected in the summer of 1971 with the majority being recorded during the months of August and September. Observations on times of emergence, pre-copulation, copulation, and oviposition, as well as frequency and nature of interactions and normal daily habits were recorded. Time of day, temperature and light intensity were noted

Figure 1

Diagram of the lake and its immediate surroundings;
the study area is indicated on
the western side.




Study
area
87′
Swamp
Swamp

using a watch, a centigrade thermometer and a Cassen light meter, respectively. Durations of observed events were measured with a stopwatch. Weather conditions varied greatly during the study period with the various effects on the damselflies being noted. The recordings were made daily, weather permitting. The duration of specific observation periods varied in length from one to six hours and included times from 5:30 a.m. to 6:30 p.m. EDT.

Twenty-six separate pairs of adults were studied during copulation and oviposition. Larvae were observed during emergence and interaction studies on adults were recorded and their general behavior observed.

The data were treated to statistical tests of linear regression and correlation coefficient to show that there were no straight lines on the graphs as the abscissa increased. This means that there is a non-linear dependency of the ordinate values for the abscissa. A table was prepared for each graph that contains averaged data. These tables include the sample size, n; the sample mean, $\bar{x}$; the standard deviation, S.D., $\sqrt{\frac{\Sigma d^2}{n-1}}$; and the standard error, S.E., $\sqrt{\frac{\Sigma x^2}{N(N-1)}}$.

RESULTS

Lestes vigilax is a late summer species. I observed emergence in July and August. With this species having about a two-month emergence period, the emergence could have begun about the first of July. The adults flew until the first of October. This could be compared to a species like *L. disjunctus* which I observed to have emerged late in April to early May. Adults of *L. disjunctus* were disappearing as those of *L. vigilax* were appearing. This fact probably enabled the adults to occupy quite similar niches at different times of the year.

The larvae of *L. vigilax* crawled out of the water, up onto emergent sedges and grasses and clung approximately 2.5 to 20 cm above the waterline. The larval skin split down the back and the head emerged first. Slowly the adult crawled out of its larval skin. As the wings emerged from their wing sheaths they were folded tightly and were greenish-yellow in color. As the process of emergence continued the wings unfolded accordian-fashion. While the damselflies were clinging to the vegetation drying out, the wings became transparent and the body began to darken into the future adult colors. These larvae, upon emerging, were termed teneral adults. After drying out for approximately 1.75 hours, they flew short, shaky flights from the water's edge into the woods. The entire process of emergence took from 2.5 to 3.5 hours. The earliest time they were seen to begin the process of emergence in the morning was 7:10 a.m. EDT and the latest

was 10:45 a.m. EDT. The odonates were sexually immature following emergence and remained in the woods for an undetermined maturation period.

At the end of the maturation process, the adults returned to the lake, this time flying in strong, even sprints. Generally the damselflies lighted on vegetation from 2.5 to 35.0 cm above the waterline. But occasionally they would fly to the higher branches of the bushes on the shore. Usually they would light with their backs to the water and their wings extended at a 45° angle from the body. A few were seen with the wings folded; however, these were believed to be teneral. They emerged from the woods in the morning when the sun emerged over the trees on the opposite shore and the light struck the shoreline of the study area. The earliest time adults were seen on the wing was 7:10 a.m. EDT. Adults of Lestes vigilax flew from the woods to the lake in the early morning and stayed at the lake until approximately 10:30 a.m. when they returned to the woods for the remainder of the day. However, a few exceptions to the statement were noted. The damselflies usually would appear at sunrise unless there was a) a heavy mist, b) a heavy cloud cover, c) rain, or d) the temperature was below the threshold for flight. Individuals of Lestes vigilax would stay in the woods when there was a heavy fog or mist on the lake, waiting until later in the day when the fog or mist would dissipate. A heavy cloud cover or rain could keep the odonates in the woods all day. They would appear only when there was a warm, mostly clear day. Figure 2 and Table I illustrate the frequency of adults in the study area compared to ambient temperatures. During the study

Figure 2

Numbers of adults of Lestes vigilax present in the study area as a function of temperature.

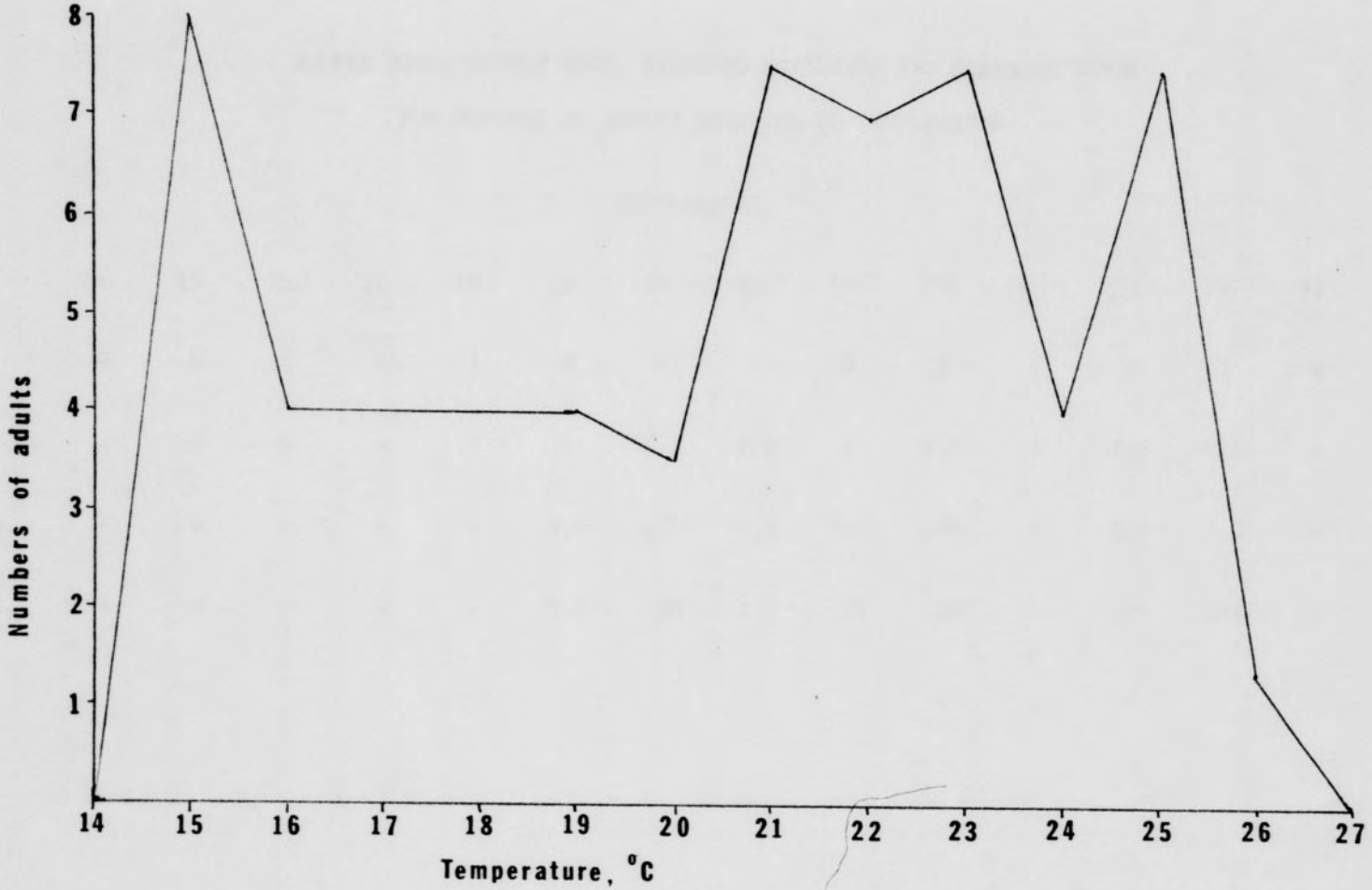

Numbers of adults
8
7
6
5
4
3
2
1
14
15
16
17
18
19
20
21
22
23
24
25
26
27
Temperature, °C

TABLE I

SAMPLE SIZE, SAMPLE MEAN, STANDARD DEVIATION AND STANDARD ERROR FOR NUMBERS OF ADULTS COMPARED TO TEMPERATURE

	TEMPERATURE, °C.													
	14	15	16	17	18	19	20	21	22	23	24	25	26	27
n	0	1	1	1	1	2	2	2	3	2	1	5	3	0
$\bar{x}$	-	-	-	-	-	4	3.5	7.5	7	7.5	-	7.4	1.3	-
S.D.	-	-	-	-	-	1.4	.70	4.9	1.0	.70	-	1.7	1.2	-
S.E.	-	-	-	-	-	1.0	.50	3.5	.57	.50	-	.74	.66	-

period I observed that the threshold temperature for flying was 15°C. Below this temperature they would remain in the woods, but at 15°C or above they would fly to the lake and light on the vegetation around the edge. There was usually a brief period of resting before the males would patrol the banks in search of females. As the temperature rose, there was an increase in the population size with the peak occurring at approximately 20-23°C. A rapid decline occurred from 25-26°C., this being the temperature when they returned to the woods. The warmer the day, the more activity there was until the thermal level of 25-26°C was reached. Then activity for all practical purposes ceased.

Figure 3 and Table II depict the adult population activity compared to time of day. In correlating observational data with time, (EDT), there was an increased activity from 7:30 - 9:30 a.m. After 9:30 a.m. there was a sharp decrease in numbers of adults. During the time of the present study, 10:30 a.m. was the latest any adults were seen. This I attribute to the fact that in late August by 10:30 a.m. the temperature was reaching the maximum tolerant level. Light intensity data were taken during these observations. There seemed to be no real correlation with the data, as activity occurred whether the light intensity was quite low or high. This leads to the conclusion that activity is a function of temperature and time of day and not of light intensity.

The damselflies flew up and down the shoreline with no regular patterns or no regular time limits of flying and resting. Some odonates fly regular patterns known as patrols where they protect their territories from invasion by other dragonflies. This patrolling

Figure 3

Numbers of *Lestes vigilax* adults present in the study area as compared to time of day.

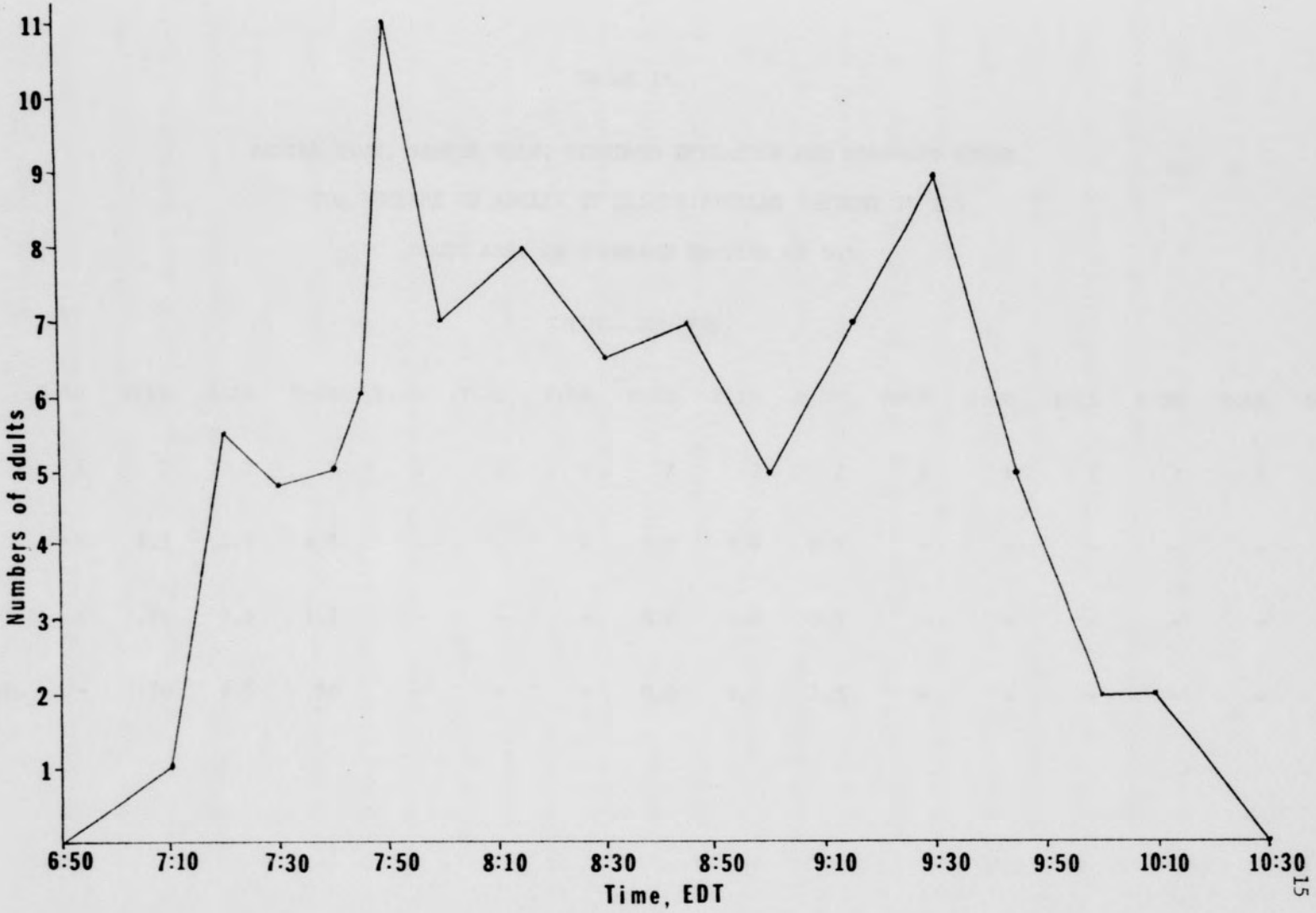

Numbers of adults
11
10
9
8
7
6
5
4
3
2
1
6:50
7:10
7:30
7:50
8:10
8:30
8:50
9:10
9:30
9:50
10:10
10:30
Time, EDT

TABLE II

SAMPLE SIZE, SAMPLE MEAN, STANDARD DEVIATION AND STANDARD ERROR FOR NUMBERS OF ADULTS OF LESTES VIGILAX PRESENT IN THE STUDY AREA AS COMPARED TO TIME OF DAY

TIME, AM, EDT

	7:10	7:15	7:20	7:30	7:40	7:45	7:50	8:00	8:15	8:30	8:45	9:00	9:15	9:30	9:45	10:00
n	1	2	2	3	1	1	1	2	2	2	1	1	1	1	1	1
$\bar{x}$	-	3.5	5.5	4.7	-	-	-	7.0	8.0	6.5	-	-	-	-	-	-
S.D.	-	.70	3.5	1.2	-	-	-	0.0	0.0	3.5	-	-	-	-	-	-
S.E.	-	.50	2.5	.66	-	-	-	0.0	0.0	2.5	-	-	-	-	-	-

as such, however, was not present with Lestes vigilax. Adults of Lestes vigilax flew only in search of food or a mate. The adults made random approaches toward other small approaching damselflies. The food usually consisted of smaller damselflies, flies, mosquitoes, and other small insects. One Lestes vigilax male was observed eating an Argia violacea adult. Once the odonates were mature, they sought mates and subsequently reproduced. Only on one occasion was a Lestes vigilax adult seen to come in contact with a species (Libellula incesta) other than its own. This Lestes-Libellula contact probably represented an extreme form of behavior related to survival rather than that concerning reproduction. When a male sighted another Lestes vigilax male or female, he flew directly toward the approaching damselfly. If it happened to be a female, the male would attempt to achieve the tandem position. If the approaching individual was another male, usually either a threat or a contact resulted. Flying toward and close to another Lestes vigilax male constituted a "threat." When this happened the two odonates usually flew in separate directions. At times, however, they touched one another. This physical touching constituted a "contact." While in contact some other species I observed flew in repeating circles around each other. One flew above the other and then they exchanged positions. Others flew straight up together for several meters before breaking apart. Yet others, including Lestes vigilax, came together, made contact and broke apart immediately. In general, contacts were much less frequent than threats. Figure 4 and Table III show the frequency of contacts compared to ambient temperatures. Generally the higher the temperature the greater the number of contacts were observed.

Figure 4

Numbers of contacts observed in relation to ambient temperatures.

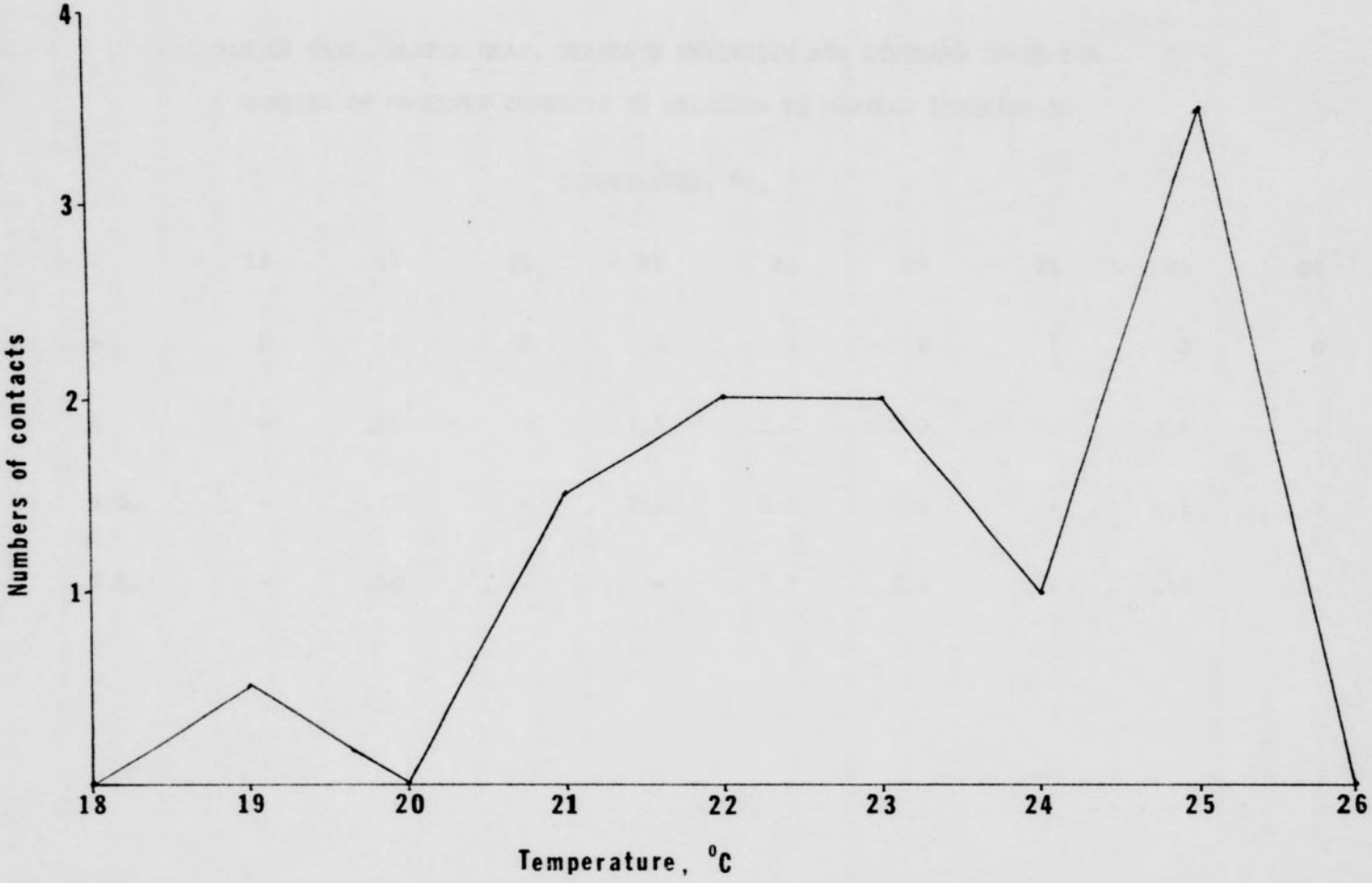

4
3
2
1
Numbers of contacts
18
19
20
21
22
23
24
25
26
Temperature, °C

TABLE III

SAMPLE SIZE, SAMPLE MEAN, STANDARD DEVIATION AND STANDARD ERROR FOR NUMBERS OF OBSERVED CONTACTS IN RELATION TO AMBIENT TEMPERATURE

	TEMPERATURE, °C.								
	18	19	20	21	22	23	24	25	26
n	0	2	0	2	3	2	1	5	0
$\bar{x}$	-	.50	-	1.5	2.0	2.0	-	3.4	-
S.D.	-	.70	-	2.1	1.0	1.4	-	1.1	-
S.E.	-	.50	-	-	5.7	1.0	-	.50	-

However, at 26°C the incidence of contacts dropped to zero. Above this temperature the contacts were nil and the incidence of observed flying was almost at zero. These odonates were definitely an early morning, cool temperature species.

Figure 5 and Table IV represent the average number of threats made by adults of Lestes vigilax as a function of temperature. Generally, there were more threats than contacts. Physical contact was less common than flying in close proximity to each other and then going separate ways (threats). There were 34 contacts made during the observation period as compared with 47 threats. The number of threats increased with the temperature in a pattern similar to that of the contacts; activity diminished at 24°C and became almost non-existent at 26°C.

When females flew to the lake, they tended to light on sedges and grasses the same as the males; however, they seemed to stay longer in one location than the males. As a male approached a female, he would light dorsally on her thorax in a semi-hovering state. He bent his abdomen tightly in a ventral arc and clasped the female behind the head with his superior and inferior abdominal appendages. The two achieved full tandem as the male flew upward and the female followed. They usually flew to a stalk and the male grasped it with his legs. Sometimes the female would grasp the stalk and at other times she merely would hang below the male free of the vegetation. Other males occasionally approached at this time. But the two never terminated the tandem position. If the attack was serious enough, the pair flew to another stalk. If, however, the second male was not too aggressive,

Figure 5

Numbers of threats observed when compared to ambient temperatures.

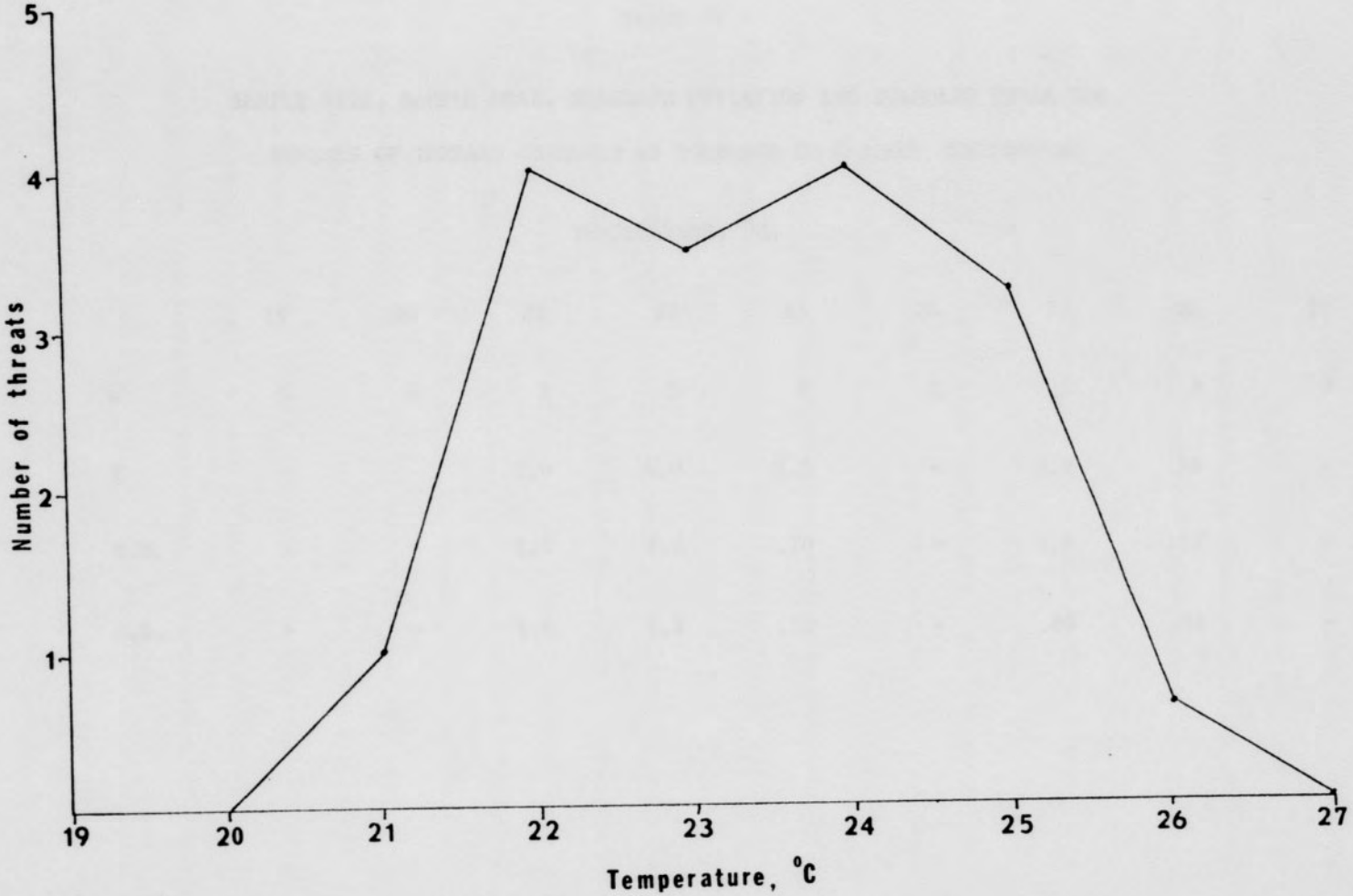

5
4
3
2
1
Number of threats
19
20
21
22
23
24
25
26
27
Temperature, °C

TABLE IV

SAMPLE SIZE, SAMPLE MEAN, STANDARD DEVIATION AND STANDARD ERROR FOR NUMBERS OF THREATS OBSERVED AS COMPARED TO AMBIENT TEMPERATURE

	TEMPERATURE, °C.								
	19	20	21	22	23	24	25	26	27
n	0	0	2	3	2	1	5	3	0
$\bar{x}$	-	-	1.0	4.0	3.5	-	3.2	.66	-
S.D.	-	-	1.4	2.0	.70	-	1.8	.57	-
S.E.	-	-	1.0	1.2	.50	-	.80	.33	-

the pair remained stationary. The average time for this pre-copulation was 4.38 minutes. One male was observed trying to achieve tandem with a teneral female. After a few unsuccessful attempts she flew into the woods, and he remained at the lake. The earliest observed time of copulation was 6:30 a.m. EDT.

After the pre-copulation period the female would curl her abdomen under her thorax and holding her abdomen with her legs, would unite with the male in a heart-shaped arrangement. The point of contact was the first abdominal segment of the male and between the ninth and tenth abdominal segments of the female. This was the sperm transfer position. Never was a second male seen to approach the pair during this stage of the reproductive activity. During copulation the male arched his abdomen dorsally in a seemingly regular rhythm. This could possibly be linked with the transfer of sperm. After this transfer was completed, the male and female would close up the heart by straightening his abdomen. There was a rapid beating of the males wings and they would achieve the pre-copulation position by going from the heart-shape position to the free-hanging position by the female. The length of copulation was recorded from the time the sperm transfer position was achieved until this position was terminated and the female was in the pre-copulation position. The average time for sperm transfer was 16.13 minutes. Copulation occurred in a range of ambient temperatures ranging from 19-25°C. In comparing this stage to temperature it was seen that the greater the temperature, the greater the duration of copulation; conversely, the lower the temperature, the faster they copulated. Figure 6 and Table V illustrate the average length of

Figure 6

Average length of copulation compared

to temperature.

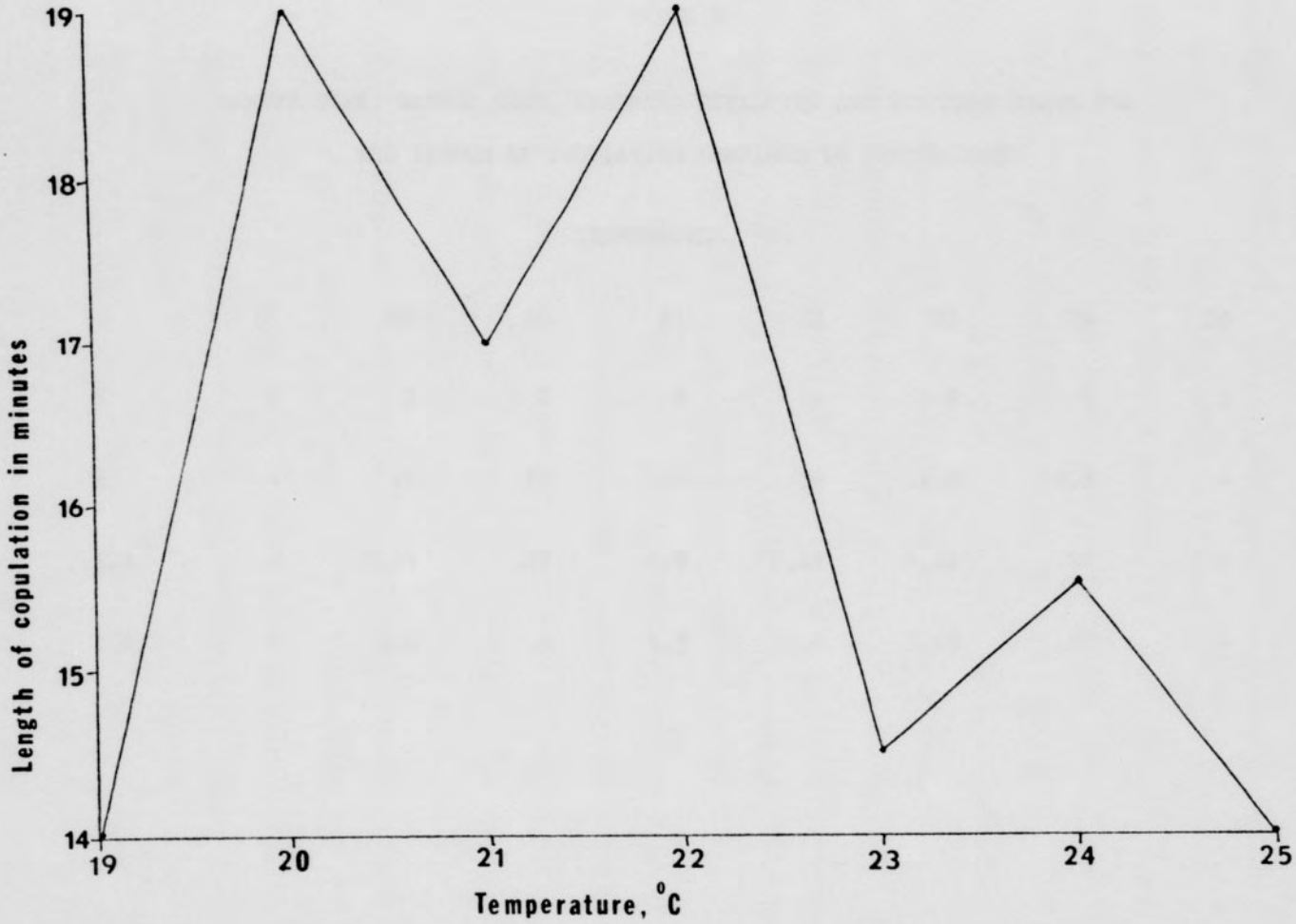

Length of copulation in minutes
19
18
17
16
15
14
19
20
21
22
23
24
25
Temperature, °C

TABLE V

SAMPLE SIZE, SAMPLE MEAN, STANDARD DEVIATION AND STANDARD ERROR FOR THE LENGTH OF COPULATION COMPARED TO TEMPERATURE

	TEMPERATURE, °C.								
	18	19	20	21	22	23	24	25	26
n	0	3	2	6	4	8	2	1	0
$\bar{x}$	-	14	19	17	19	14.6	15.5	-	-
S.D.	-	5.35	.87	4.8	5.35	9.85	.30	-	-
S.E.	-	3.1	.6	1.9	2.6	3.48	.21	-	-

copulation in minutes compared to temperature. As was seen in Figure 2 the period around 20-23°C was a very active period with large numbers appearing, a high incidence of flying and several pairs in tandem and copulating. With the increased temperature there was a decrease in activity, and hence there followed a decrease in mating. As they were resting after copulation other males approached again at times. Sometimes the heterosexual pair flew as a result of the intruding male, while at other times the pair remained in tandem in the same location.

After sperm transfer the pair did one of three things. They might a) fly immediately toward the center of the lake and begin ovipositing, b) rest and then fly lakeward to oviposit, or c) fly lakeward to oviposit, be approached by a second male while over the lake and return to shore, rest, and later to initiate oviposition. When they flew lakeward to oviposit, they flew over the lake about 10-15 cm above the water and eventually would light on a sprig of Elodea and oviposit. During oviposition they both held their wings at approximately a 45° angle with the male being in front of the female on the sprig. Whether this oviposition was endophytic or exophytic cannot be stated with certainty due to the inaccessibility of the eggs or oviposition sites. However, comparing the abdominal movements of the female of Lestes vigilax with that of known endophytic species, such as Lestes disjunctus and L. eurinus, the author would hypothesize that Lestes vigilax is also an endophytic species.

The male of Lestes vigilax remained with the female during oviposition. As the pair moved up and down the sprig, the female seemed to initiate the movements. Even when they flew from one plant

to another, the female appeared to initiate all movements. The pair flew to several sprigs during the course of oviposition, the average number of trips being 6.96 per pair. The average for total oviposition time was 10.91 minutes. Figure 7 summarizes the reproductive activity of Lestes vigilax compared to time. For each of the 26 pairs observed in the entirety of reproduction, the durations of pre-copulation, copulation and oviposition times are given. The average for each again was 4.38 for pre-copulation, 16.13 for copulation and 10.91 for oviposition.

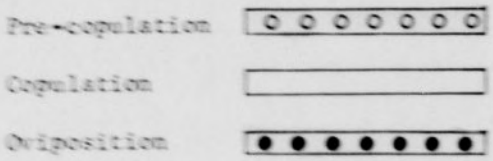
After oviposition the pair flew back to the shore and rested. Sometimes they stayed in tandem and at other times they terminated tandem and the female returned to the woods. This also was an opportune time for other males to approach her. All adults of Lestes vigilax would return to the nearby woods by 10:30 a.m. EDT.

The adults of Lestes vigilax flew from July to the first week in October. After this time no more individuals were ever sighted and it was believed that all had died.

Figure 8 represents a typical day in the summer. The activity of adults of Lestes vigilax is compared to temperature, light intensity and time of day. However, there was insufficient data to plot specific light intensities, but general trends could be seen. Adult activity of Lestes vigilax increased to around 8:40 to 9:00 a.m. EDT, plateaued from 9:00 to 10:00 a.m., then began decreasing around 10:00 a.m., ending finally 10:30 a.m. As stated earlier, Lestes vigilax is an early morning species with no activity observed in the afternoon.

Figure 7

Durations of pre-copulation, copulation and oviposition periods for each of the 26 pairs studied.



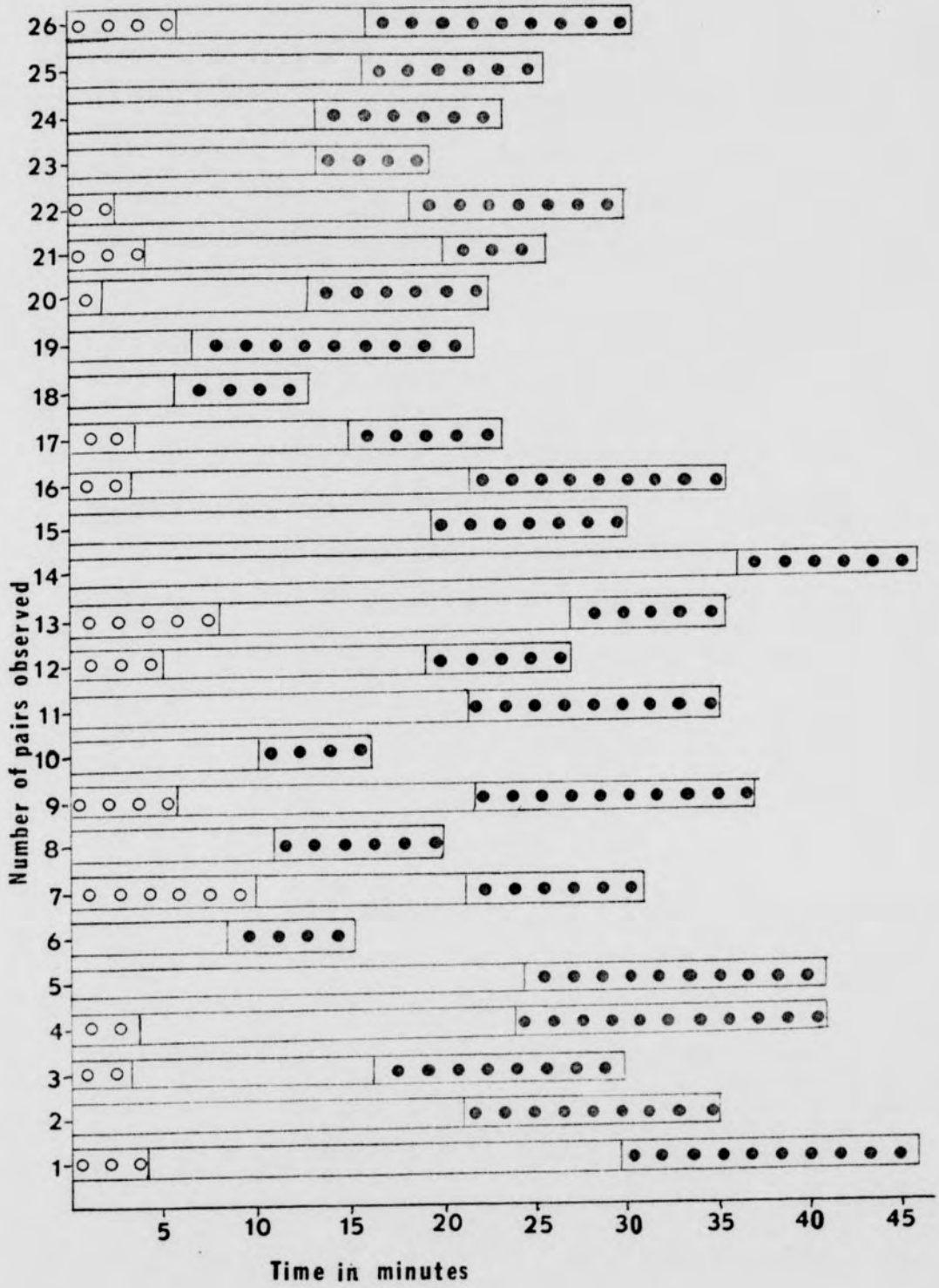
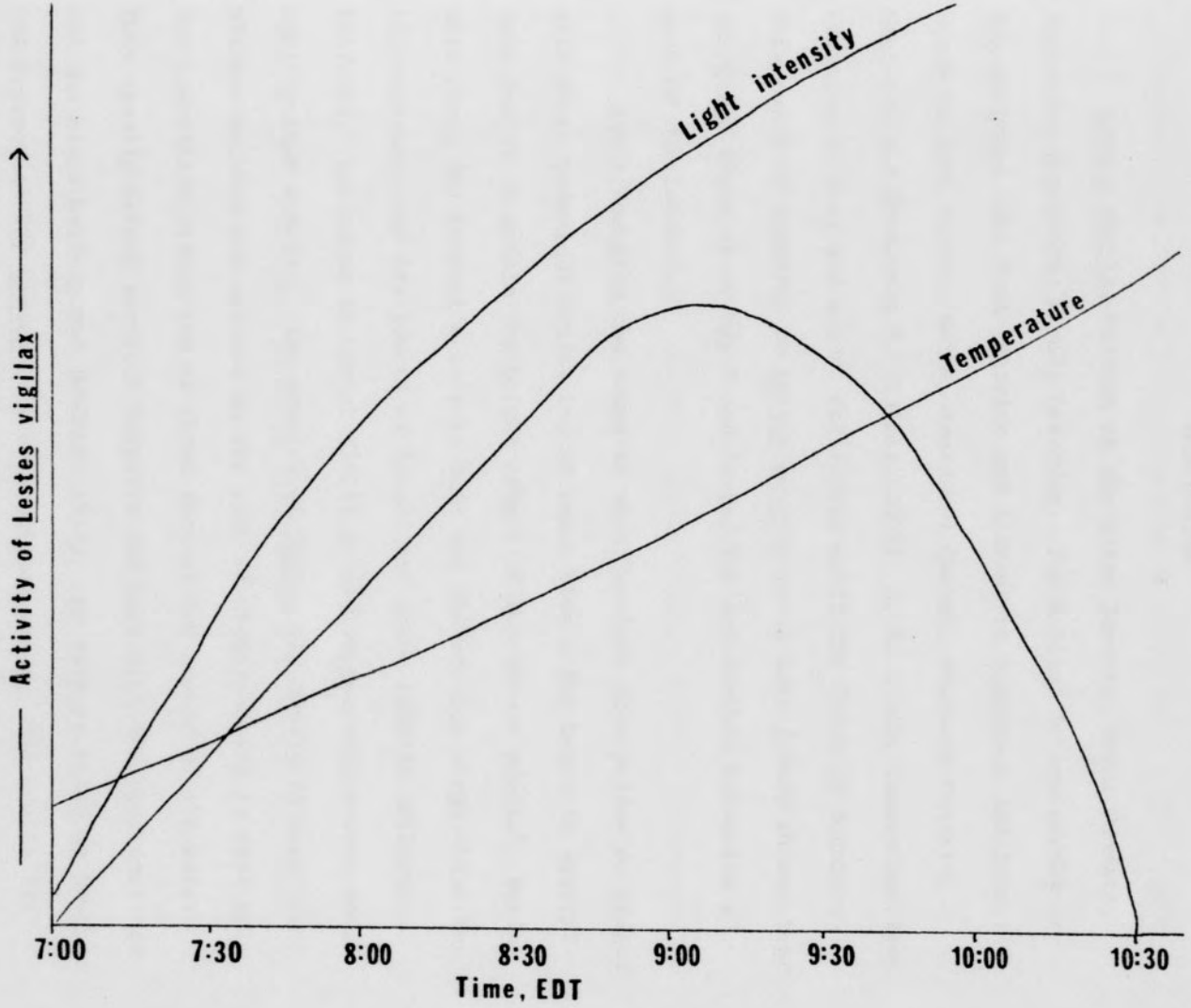

Number of pairs observed
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
5
10
15
20
25
30
35
40
45
Time in minutes

Figure 8

A typical day showing activity of adults of *Lestes vigilax* in relation to time, temperature and light intensity.


Light intensity
Temperature
Activity of Lestes vigilax
7:00
7:30
8:00
8:30
9:00
9:30
10:00
10:30
Time, EDT

DISCUSSION

Lestes vigilax belongs to the Class Insecta, Order Odonata, Sub-order Zygoptera, Family Lestidae. Its habitat is any marshy or bog-margined lake from "Florida and Alabama to Tennessee and Iowa, north to Nova Scotia, Maine, southwest Quebec, southern Ontario, Michigan and Minnesota." (Walker, 1953) It is a late summer species, emerging in July and August and flying until the first of October. This could be compared to *Lestes eurinus* which Lutz (1968) showed that emergence began about May 1 and lasted for two months, climaxing a year of development.

After emerging the imago is of a "uniform pale yellow or tinged with blue, brown, or white, and it takes from a few hours to several days for it to attain the bright colors of the mature adult." During this time, the teneral's body is soft and flabby, its wings shine as if varnished, and its powers of flight are quite limited (Wilson, 1917-18). According to Corbet (1962) males, in general, mature more rapidly than females. The species of *Lestes* fly mostly in open places--marshes and meadows on the edge of woods--coming to rest on low vegetation within two or three feet of the ground or the water. They usually select vertical supports and rest with the body inclined and the wings half-spread (Walker, 1953). As authenticated by Needham and Heywood (1929) *Lestes* is a cosmopolitan genus. The adults fly little over open water but seek the seclusion of marshes or the closer vegetation of reed-choked streams. As mentioned earlier, adults of

Lestes perch with half-spread wings. Johnson and Westfall (1970) have used this knowledge descriptively in comparing Lestes with other odonates. Other damselflies, according to them, usually fold the wings together over the body if not flexing them back and forth in some behavioral display. Clear, petiolated wings separate lestids from calopterygids, while large body size and spread-wing perching habit distinguish the group from most coenagrionids.

Some species of odonates exhibit territoriality. Johnson (1964a) states the origin of this practice is related to evolutionary changes which occurred in the odonate breeding pattern. Some species are able to recognize by sight conspecific individuals at a distance but not the sex. Thus, random approach flights seem to be extended to all dragonflies of the same size. This appeared to be the case with Lestes vigilax. Random approaches were made to other Lestes adult males flying nearby. These were recorded as the contact and threat data cited in the results. But this type of "territoriality" is rather primitive, and most odonates have evolved more advanced techniques. The next step, slightly more advanced than these random approaches, was displayed by Lestes unquiculatus and reported by Bick and Hornuff (1965). Here, their most frequent event was a shift of perch site for no detectable reason. When a male reached a perch, he occupied it only momentarily; when he shifted it was usually for more than 1 meter, so that during one 20 minute episode a male usually moved around one entire margin of the pond. This frequent shifting gave the impression of consistent and random cruising among or just above the vegetation. In contrast to this, adults of Angia apicalis successfully

defend their territory and seldom shift the perch. Individuals frequently darted out from their perch and quickly returned to the same place in a maneuver considered effective in maintaining territory (Bick and Hornuff, 1965). About as advanced as the above is a display recorded by Pajunen (1963) where at the approach of a flying male, the resting male suddenly raises his wings clearly above the normal position, flaps them vigorously a few times and simultaneously raises his body until it is at an angle of 30-45° to the normal position. The change of posture is effected by the legs, the bending of the abdomen having little significance. All movements are sudden and brisk, and the original attitude is resumed after one to two seconds. There is no appreciable orientation to the approaching male. Kormondy (1961) states that "the spacing of males (in territoriality) appears independent of localization, but the degree of spacing appears density-dependent. Signalling is ambivalent and occurs by chase, challenge, mere presence or display. Territoriality may function in sexual selection and dispersal. It is proposed that territorial-induced dispersal may be significant in obliterating crowding effects in a restricted breeding area, lessening interference with oviposition and populating newly opened or reopened areas." Kaiser (1969) reported that males of Aeschna cyanea display time-regulated territorial behavior at their mating place. Johnson (1961) also found that Hetaerina americana and H. titia displayed a sophisticated territorial behavior. This territoriality is far more advanced than the random approaches of Lestes vigilax, and the odonates exhibiting these phenomena are likewise far more advanced. Lestes is one

of the most primitive of dragonflies in terms of territoriality; Figure 9 illustrates the general primitive condition of Lestes.

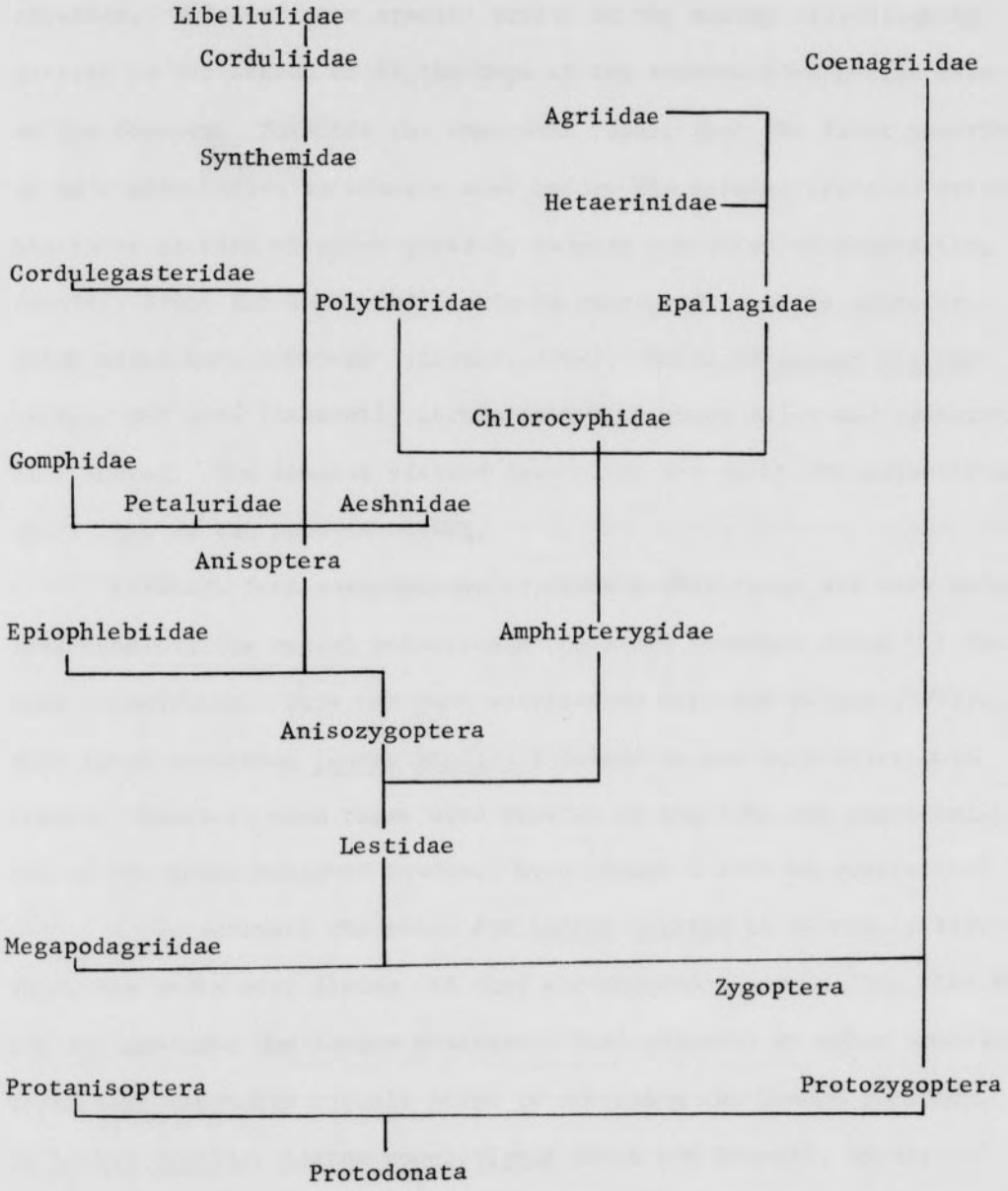
There are two main stages in the life of an average damselfly --teneral feeding and reproduction. Occasionally a third stage--post-reproductive--will be seen. Most of the tenerals are active only in sunshine. According to Walker (1953) "when the feeding period is in full swing dragonflies are very sensitive to changes in the intensity of sunlight. When the sun is momentarily overcast they seem to disappear as though by magic. The Zygoptera simply come to rest in the grass or sedges." The behavioral patterns for Lestes vigilax adults, however, did not conform to this statement. I observed activity when the light intensity was low as well as high. The majority of feeding occurs during this teneral stage of the adult odonate. Adults of Lestes vigilax according to Garmon (in Wilson, 1917-18) eat Diptera and Nematocera. They have also been observed feeding on smaller damselflies. As Kennedy (1950) stated, "dragonflies are predatory insects and occupy the same niche in the insect world as that occupied by hawks and owls in the bird world. They are at the peak of a pyramid of numbers."

Newly emerged adults of Lestes disjunctus australis left the water for a mean of 13 days and were reproductive on the day of return (Bick, 1961). For the sexes to meet effectively, they must coincide in time as well as in space. "The seasonal restriction of emergence will ensure that most of the annual population of males and females become mature at about the same time, while the diurnal rhythm of flight activity will result in both sexes visiting the mating site

Figure 9

Hypothetical dendogram of the Odonata

(redrawn from Corbet, Longfield & Moore, 1960).


Libellulidae
Corduliidae
Coenagriidae
Agriidae
Synthemidae
Hetaerinidae
Cordulegasteridae
Polythoridae
Epallagidae
Chlorocyphidae
Gomphidae
Petaluridae
Aeshnidae
Anisoptera
Epiophlebiidae
Amphipterygidae
Anisozygoptera
Lestidae
Megapodagriidae
Zygoptera
Protanisoptera
Protozygoptera
Protodonata

together. Males of some species arrive at the mating site slightly earlier in the season or in the days of the reproductive period than do the females. This has the important result that the first severity of male interaction is usually over before the females begin to arrive. The early arrival of males probably reduces predation of ovipositing females, since the latter will only be attracted to those sites at which males have survived" (Corbet, 1962). Males of Lestes vigilax visited the pond frequently interacting with other males and occasionally mating. The females visited less often but spent the majority of their time at the pond in mating.

Although from observations it appears that there are more males than females, the actual male:female sex ratio averages about 1:1 for most damselflies. This has been verified by Parr and Palmer (1971). When first observing Lestes vigilax I seemed to see more males than females; however, soon there were females at the lake and practically all of the males achieved tandem. Even though I have no statistical data I would estimate the ratio for Lestes vigilax to be nearly 1:1. While the males were flying, if they encountered a female they flew to her and achieved the tandem position. Some odonates of other species go through courtship rituals prior to achieving the tandem position. In Lestes vigilax, Lestes unquiculatus (Bick and Hornuff, 1965), Archilestes grandis (Bick and Bick, 1970) and Enallagma civile (Bick and Bick, 1963) there was no sexual courtship display by either sex. The movement of the females of Lestes dryas, Lestes sponsa, and Lestes disjunctus australis (Bick, 1961) was a stimulus for the male's approach. The females of Calopteryx maculatum (Johnson, 1962a) accepted the advance

of the male by remaining with her wings closed, while he hovered over her with beating wing. Definite courtship patterns were also observed in Ischnura verticalis according to Grieve (1937). The male and female of Lestes vigilax showed no courtship signs of any kind. The male approached the female and achieved tandem while the female remained perched on the vegetation. The females of Archilestes grandis showed no refusal signs; they were simply absent from the reproductive area or escaped by rapid flight. By contrast, a female Ischnura verticalis (Bick, 1966) flexed her abdomen ventrally, and vigorously fanned her wings to ward off approaching males. Lestes vigilax females likewise showed no refusal signs. They simply flew away or were not available at the lake to achieve tandem.

Before the males achieve tandem, according to Borror and DeLong (1971) he must transfer sperm from the genital opening on the ninth segment to the reproductive structures on the second segment; this is done by bending the abdomen downward and forward. This action has been observed by Johnson (1961) for Hetaerina americana and H. titia. Once this has been accomplished, the male joins with a female in the tandem position. Before copulation commences, Lestes vigilax adults occasionally would spend a period of resting or perching while in tandem. I have termed this period the pre-copulation period. Exactly one-half of the observational couples exhibited a pre-copulation resting period. No references could be found in the literature for precisely this type of behavior. Johnson (1962a) stated that after tandem was achieved in Calopteryx maculatum the pair flew to the oviposition site which the male had previously selected. After again inspecting the site, they

would return to her perch and begin copulation. Bick (1961) found that for Lestes disjunctus australis, once tandem was achieved, copulation followed almost immediately. This was the case I found with fifty percent of Lestes vigilax adults.

The average time of copulation for Lestes vigilax was 16.13 minutes. Table VI shows recorded durations of total copulation times for a variety of Odonata. My observations seem to agree with the data obtained on other species of Lestes. Bick and Sulzbach (1966) observed that in Hetaerina americana the female's legs straddled or gently touched her abdomen without grasping it, while most males pumped rhythmically for at least part of the period. The same results were observed for Lestes vigilax. During the entire copulation time the pair formed a heart-shaped tandem. The male was the active partner in seizure and copulation, but the female controlled the movements during oviposition.

In adults of Lestes vigilax oviposition followed copulation either immediately or after a short delay. The Calopteryx maculatum male upon breaking tandem led the female back to the oviposition site where she began depositing the eggs (Johnson, 1962a). But with Ischnura verticalis, it is different. Oviposition data were studied by Grieve (1937) and it was discovered that it might begin within a few hours after mating or not for several days thereafter. This is quite different from my observations and those of Johnson. The male of Lestes vigilax stayed with the female during oviposition. This is also true for Calopteryx maculatum (Johnson, 1962a), Lestes sponsa (Macan, 1964), and Lestes dryas and Lestes disjunctus australis (Bick,

TABLE VI

RECORDED DURATIONS OF TOTAL COPULATION TIMES FOR A VARIETY OF ODONATA

Libellula quadrimaculata	Corbet, *et al.* (1960)	3 seconds
Hetaerina americana	Johnson (1961)	3.1 minutes
Hetaerina titia	Johnson (1961)	3.7 minutes
Calopteryx maculatum	Johnson (1962a)	5.0 minutes
Hetaerina titia "tricolor"	Johnson (1961)	5.0 minutes
Orthetrum cancellatum	Corbet, *et al.* (1960)	5.0 minutes
Lestes barbarus	Nielsen *	6.0 minutes
Lestes disjunctus australis	Bick (1961)	6-19 minutes
Lestes vigilax	O'Briant (this study)	16.13 minutes
Enallagma civile	Bick and Bick (1963)	18.7 minutes
Lestes viridis	Loibl (1958) +	21-36 minutes
Sympetrum striolatum	Corbet, *et al.* (1960)	24 minutes
Lestes unquiculatus	Bick and Hornuff (1965)	25.0 minutes
Lestes sponsa	Loibl (1958) +	26-47 minutes
Lestes dryas	Loibl (1958) +	47-75 minutes

* From Corbet (1962)

+ From Bick and Hornuff (1965)

1961). However, in Lestes rectangularis (Gower and Kormondy, 1963) the male did not stay with the female during oviposition.

If the species happens to be an endophytic species on floating vegetation (as I am hypothesizing that Lestes vigilax is), it becomes highly vulnerable to attack by fishes, frogs and newts. Corbet et al. (1960) state that the habit these zygopterans have of ovipositing in tandem may cut down on the female mortality rate, by increasing the speed of take-off and acceleration. For species which oviposit under water, tandem could also be advantageous were she to become waterlogged. The males also stay with the females to protect them from attack by other males. If the male does not remain in tandem with the female while she is ovipositing, he usually hovers or flies overhead to protect her and comes down to join her when she has finished ovipositing. Table VII summarizes oviposition times for several odonates.

Walker (1953) says that the genus Lestes "oviposits on vegetation bordering on or emergent from the water where it lives during the season of flight. Corbet (1962) agrees with this as it pertains to Lestes dryas. In fact, heavy damage has been done to the more exposed stems of an American iris, Iris veriscolor, by Lestes dryas. Oviposition in woody material along the shore is recorded by Bick and Bick (1970) for Lestes viridis and Lestes barbarus. Lutz and Pittman (1968) found that adults of Lestes eurinus oviposited in an emergent plant. But Corbet (1962) states that Lestes sponsa oviposits under water and down to a depth of 30 cm.

I found that Lestes vigilax oviposited on the surface of the water on or in sprigs of Elodea canadensis. Fischer (1964) gave

TABLE VII

RECORDED DURATIONS OF TOTAL OVIPOSITION TIMES FOR A VARIETY OF ODONATA

Lestes disjunctus australis	Bick (1961)	6-209 minutes
Lestes vigilax	O'Briant (this study)	10.91 minutes
Calopteryx maculatum	Johnson (1962a)	10-30 minutes
Hetaerina americana	Bick and Sulzbach (1966)	27.0 minutes
Enallagma civile	Bick and Bick (1963)	46 minutes
Aeschna cyanea	Corbet, *et al.* (1960)	48 minutes
Lestes unquiculatus	Bick and Hornuff (1965)	99 minutes

Elodea canadensis as one of the favored sites of Lestes oviposition. In June and July I observed Lestes disjunctus to oviposit on sedges above the waterline and to continue ovipositing as they backed down into the water. It appears that the genus Lestes is more diversified than was once thought. In areas of high density there exists the danger of plants being damaged or even killed by excessive oviposition. This has been exemplified by Lestes dryas Corbet (1962). He reports such damage as the galls which form at the sites of injury as being easily recognized. However, damselflies which oviposit above the waterline have eliminated most of the risks of attack by fishes, newts and frogs. But the advantages of ovipositing on floating vegetation as stated by Corbet are that the eggs are automatically insured against all but extreme desiccation, and it helps to keep a more constant temperature for the eggs. When adults descend under water to oviposit the eggs, they form an air bubble around their thoracic spiracles. Another element which Corbet (1962) thinks may play an important role here is the hydrophobe surface caused by the waxy pruinescence which develops on the thorax and distal part of the abdomen of certain species of Angia and Lestes. Accordingly, Lestes vigilax females never developed this pruinescence and they did not oviposit under water.

Death usually occurred during the reproductive period (Corbet, 1962). On occasion a few individuals may outlive it and enter the third adult age-phase--the post-reproductive. During this phase the colors become duller, the gonads regress and visits to the breeding site cease. According to Kennedy (1950) the adult life is usually 2-4 weeks.

Among several species of damselflies there exists chromatic sexual dimorphism. Johnson (1964b) discussed the phenomenon genetically. He says that dimorphism is sex controlled in expression. Through breeding data he was able to state that it is governed by a single allelic gene pair. Females with the male-like pattern (andromorphic) are homozygous recessive, and the females with the different pattern type (heteromorphic) are heterozygous and homozygous dominant. The color change in individuals was thought to have something to do with maturity. Grieve (1937) discovered that oviposition never occurred before the color change, but usually directly after; hence, color change is more or less coincident with sexual maturity. Johnson (1962b) states that where sexual dimorphism in color patterns is not strongly marked, the pattern in one sex, usually the male, becomes partly obliterated by means of a whitish exudate, pruinescence. This type of sexual dimorphism is probably important in species recognition. Since Lestes vigilax does not express sexual dimorphism strongly, there is little difference in the two except the male pruinescence which comes with age. This could be the reason that when the male is searching for a female with which to reproduce, he approaches any zygopteran which is small and of the same color. Bick and Bick (1965) noted that Angia apicalis reacted sexually more frequently to brown than the other normal female colors. The blue-tipped abdomen they also found aided in sex recognition along with the dorsal and lateral thoracic colors. Johnson (1962a) stated that for Calopteryx maculatum the white stigma on the female's thorax was thought to guide the male in alighting on the female's thorax. Clearly, sexual dimorphism is important in reproduction.

Corbet (1962) states that the most important single factor determining the pattern of adult activity is the daily fluctuation of temperature. The characteristic diurnal rhythms of flight, feeding and reproduction all appear to be under strong exogenous control by temperature, and the selection of sites for resting or feeding similarly appear to be dictated by the protection they offer from cold and wind. He found their activity to be limited by high as well as low temperatures. I found the limits for Lestes vigilax to be 15-26°C. Lutz and Pittman (1970) are the only other investigators who have given data for other species.

SUMMARY

1. Lestes vigilax is a late summer species, emerging in July and August and flying until the first of October. Following emergence, the odonates were sexually immature and remained in nearby woods for a maturation period of undetermined length.

2. Mature adults began flight in the morning when the temperature was at least 15°C. They flew until approximately 10:30 a.m. EDT or until a temperature of 26°C was reached. During this flying period interactions occurred between individuals in addition to reproduction activities.

3. Adults of Lestes vigilax made random approaches to other L. vigilax adults. If they flew toward each other, this was termed a threat. However, if physical touching resulted, then the move was termed a contact. During the observational period, there were 34 contacts made compared to 47 threats.

4. When a male approached a female, tandem was usually achieved with reproduction following. One-half of the tandem pairs observed a precopulation rest period for an average time of 4.38 minutes.

5. The remaining odonates began copulation immediately upon achieving tandem. The average time for copulation for the 26 pairs studied was 16.13 minutes.

6. After copulation, they did one of three things:

   a) flew immediately toward the center of the lake and began ovipositing

b) rested and then flew lakeward to oviposit, or

c) flew lakeward to oviposit, were approached by a second male while over the lake and returned to shore to rest, later to continue oviposition.

The average time for actual oviposition was 10.91 minutes.

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