Mitchell, William H. The Influence of Environmental Conditions on the Daily Activities of Enallagma geminatum (Kellicott), Enallagma signatum (Hagen) and Enallagma civile (Hagen) (Odonata: Zygoptera). (1973) Directed by: Dr. Paul E. Lutz Pp. 67.

A field station was established on the farm pond of the North Carolina Agricultural and Technical State University to study some environmental impacts upon the activity cycle of three species of Enallagma. Sites of observation were established to determine activities in association with terrestrial and aquatic segments of the station.

The activity cycle of the three species was observed to contain periods of perching, patrolling, mating and ovipositing. Perching was the one single event that dominated the time span for all three species. All other activities were conducted in decreasing frequency.

During the study it was determined that each species had a definitive time of day when each phase of the activity cycle was to be conducted. Several of these events were so definitive that they could be used in a general taxonomic identification of the species. In conjunction with the time of day, environmental temperature was closely associated with the initiation of events occurring during the day. Cloud cover was the least effective in differentiating activities of the three species. It can be concluded that cloud cover is ineffective as a single factor, but when coupled with time of day and temperature, the composite environmental effect has profound effect on the activities of the three species of Enallagma.

THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON THE DAILY ACTIVITIES OF *ENALLAGMA GEMINATUM* (KELLICOTT), *ENALLAGMA SIGNATUM* (HAGEN) AND *ENALLAGMA CIVILE* (HAGEN) (ODONATA: ZYGOPTERA)

by

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APPROVAL SHEET

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INTRODUCTION

Behavioral studies have been classically conducted on larger vertebrates and under controlled laboratory conditions. Contemporary behavioral research has gradually shifted from the laboratory to the natural environment of the research organism. In attempts to study a given individual in its natural environment, other organisms often better suited for such investigations have frequently been utilized.

Members of the Order Odonata have been used as behavioral study subjects by many observers. The Odonata are generally found to exist in large populations in a wide variety of aquatic habitats. The Suborder Zygoptera has been described by Needham and Heywood (1929) and Walker (1953) to be composed of numerous small genera and one which is very large, Enallagma. The genus Enallagma is composed of 38 species in North America and in excess of 70 in the world, thus defining it as one of the largest genera in the Odonata. This genus is further sub-divided into four groups (I, II, III and V) based primarily upon subtle anatomical modifications of the terminal abdominal appendages. Members of the genus Enallagma have been described as being very common, based upon their large numbers of species and the diverse conditions under which they are found to exist.

Behavioral patterns of adult Odonata have been reported by Corbet (1962), Bick and Bick (1965) and Johnson (1964) to be influenced by two environmental factors: time of day and temperature. Lutz and Pittman (1970) reported that the level of cloud cover exerts a positive effect on many of the Odonata. In a study conducted by Lutz and Pittman (1970) a preferential period of species arrival was established for a community of Odonata. Bick and Bick (1963) and Bick and Hornuff (1966) reported a positive preference of arrival time for both males and females of E. aspersum and E. civile.

Time of arrival at the habitat is the prelude to a series of behavioral responses. Corbet (1962) reports that the normal behavioral response of an odonate is significantly dependant upon the thermal conditions of the environment. It was reported by Bick and Hornuff (1966) that insignificant differences existed in the reproductive behavior of E. exsualans and E. aspersum (representing groups I and III, respectively) when observed under the same thermal conditions.

The present study was initiated to enhance information presently available regarding time of day and temperature as it affects selected zygopteran forms. The study was further designed to expand the sparse knowledge concerning cloud cover and its effect on the normal adult activities. Three species (representing Groups I, II and IV) of Enallagma were selected as study organisms to determine

if significant levels of intrageneric behavior exist. Those species representing groups I, II, and IV were E. geminatum, E. signatum and E. civile, respectively.

MATERIALS AND METHODS

During the summer of 1968, observations were made on three species of damselflies of the genus Enallagma inhabiting a farm pond of the North Carolina Agricultural and Technical State University. The study site was located on the eastern edge of the city of Greensboro, North Carolina, at a distance of 2.75 miles from the center of town on N. C. #3000.

The pond was constructed in the early 1950's as a biological station and watering facility for livestock pastured in the immediate area. Water level in the pond was maintained by runoff from its watershed and from several springs at a maximum depth of 4 m by an overflow pipe in the southern end of the pond; this is illustrated in Figure 1. The southern boundary of the pond was an earthen dam extending 80 m in an east-west direction. The dam also served as an access route to the livestock barns in the area. The impounded water extended in a northeasterly direction for 150 m into drainage lines from the watershed. It was perpendicular to the linear length that the pond attained a maximum width of 80 m.

The study site was highly productive and supported a varied flora. The dominant plants were of the submerged and floating forms; Elodea canadensis and Potamogeton sp. constituted approximately 90% of the rooted aquatic vegetation. Several large stands of Typha latifolia, Juncus sp. and Cyperus sp. were present.

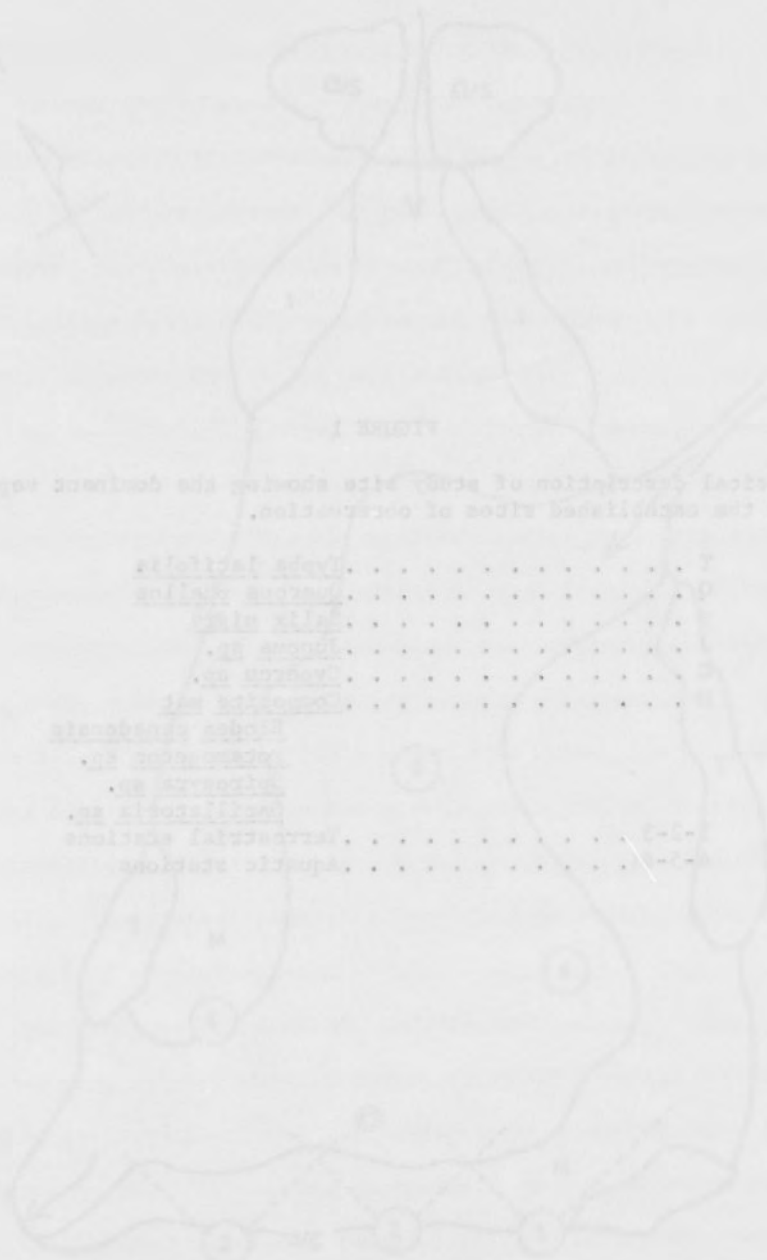
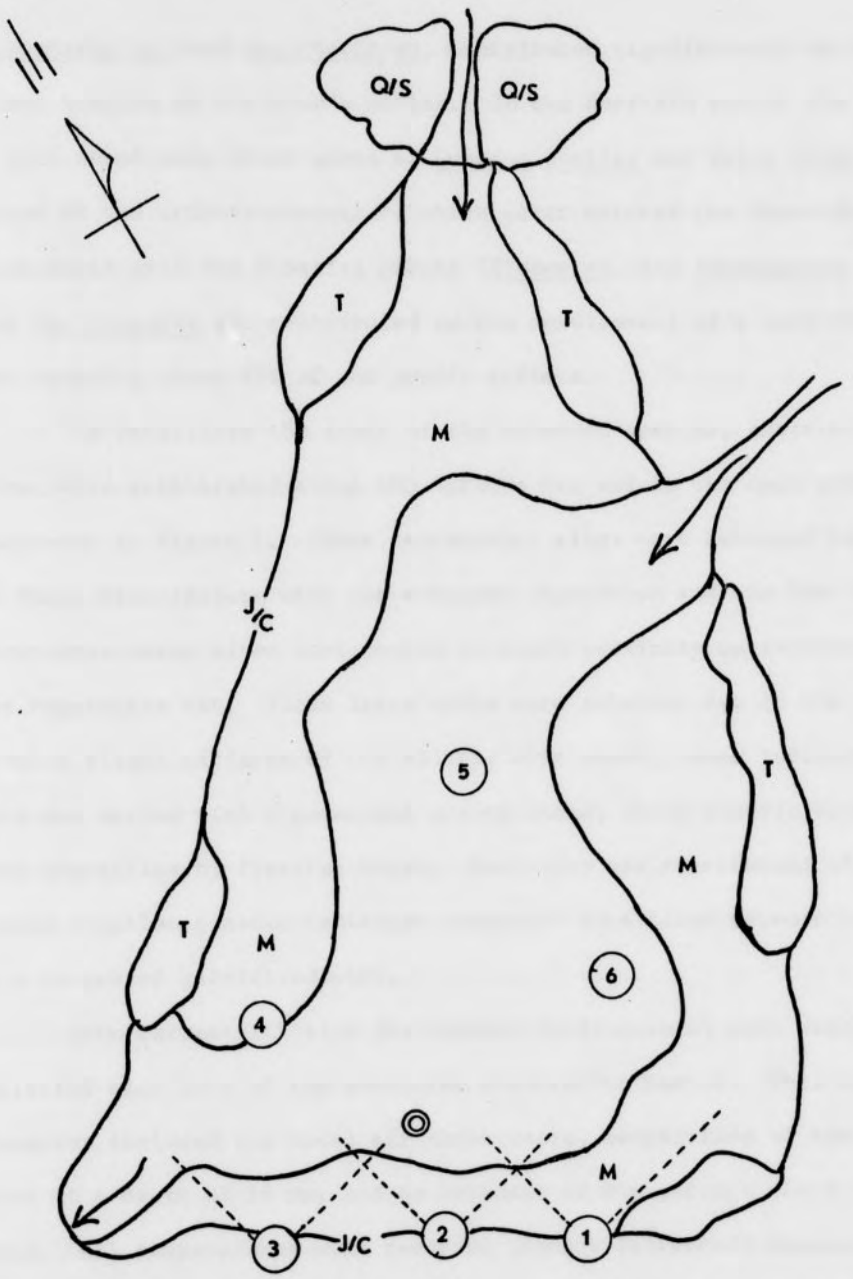


FIGURE 1

Physical description of study site showing the dominant vegetation and the established sites of observation.

T . . . . . .*Typha latifolia*
Q . . . . . .*Quercus phellos*
S . . . . . .*Salix nigra*
J . . . . . .*Juncus sp.*
C . . . . . .*Cyperus sp.*
M . . . . . .*Composite mat*
Elodea canadensis
Potamogeton sp.
Spirogyra sp.
Oscillatoria sp.
1-2-3 . . . . . .Terrestrial stations
4-5-6 . . . . . .Aquatic stations


Q/S
Q/S
T
T
M
J/C
5
T
M
T
M
6
4
M
3
J/C
2
1

Eleocharis sp. and Sagitteria sp. contributed significantly to the plant biomass at the pond's margin. In the northern end of the pond, a well-developed, mixed stand of Quercus phellos and Salix nigra were found in the primary channel by which water entered the impoundment. Associated with the floating plants (Elodea sp. and Potamogeton sp.) and Oscillatoria sp. contributed to the development of a very dense mat covering about 75% of the pond's surface.

To facilitate the study of the selected species, observation sites were established along the earthen dam and in the open water as indicated in Figure 1. Three terrestrial sites were selected because of their associations with the emergent vegetation and the land mass. Three open-water sites were chosen in close proximity to sections of the vegetative mat. These later sites were selected due to the extensive flight patterns of the animals over water. Each terrestrial site was marked with a permanent ground stake, while aquatic sites were identified by floating bouys. Each bouy was constructed of a sealed 1-gallon plastic container connected to a fired ceremic block by a length of galvinized wire.

From terrestrial site #2, certain environmental data were collected each hour of the scheduled observation period. This information included the local air temperature, temperature of the water at a depth of 15 cm, and an estimate of the percent cloud cover. All temperatures were recorded using a Fahrenheit thermometer and later converted to a Centigrade scale for reporting. Cloud cover was estimated on a relative percent scale with "0" being clear and "10"

being total overcast. From the study site, no consideration was given to the altitude of the cloud cover. The cloud cover data were supplemented with a light meter reading. The environmental data collected at the study site were correlated with those of the National Oceanic and Atmospheric Administration, ne: Environmental Sciences Services Administration at the Greensboro-High Point-Winston Salem airport. Some slight differences for the same time period of observation were found. An average thermal error of +2.93°C was noted while an error of -2.63 was found in cloud cover estimates. These differences reported can be attributed to the distance and the physical conditions of each of the recording stations. The study site was approximately twelve miles east of the official NOAA station.

In addition to hourly collections of environmental data, the primary concern was that of the activities of the adult insects as affected by the local climatic conditions. During periods of observation, the sites were toured regularly on a 30-minute schedule. During the three-month period of observation, (June, July and August) ten consecutive day-long sessions were utilized each month. The day-long sessions prevailed from the time of initial morning flight activity until all activity was terminated in the evening. Data obtained from these sessions permitted greater flexibility in the scheduling of future observations. Additional observations were scheduled which permitted detailed study of the activities of a given species at a given time of day.

The two general types of observation sites were visited alternately on successive periods of initial observation. Each site was visited for 10 minutes, thus permitting complete coverage of all stations in one hour. Data collected from each station were later combined to give a total mosaic of activity of a given species at a given time of day. All data were recorded as occuring at various local times, Eastern Daylight Savings Time (EDT).

During the rotation of the observational schedule, a field of vision was established which permitted an approximate 5 degree overlap of the adjacent station. The alignment of the stations provided observations along a given line and at a given depth of field. Terrestrial observation sites extended from the margin of the pond across the mat and out into the open water. The depth of field from each of the terrestrial sites averaged 15 m.

The aquatic sites were toured by means of a 2.5 m fiberglass boat. From the floating stations, observations were established in 360 degrees, using a 15 m radius as the maximum depth of study. Using the boat as a platform, many of the observations were recorded at a minimal distance of 15 cm.

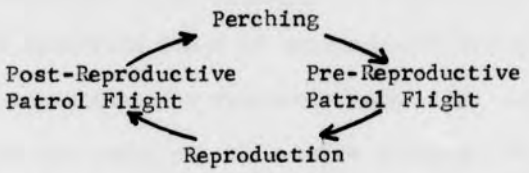
Definitive species identification was based primarily upon distinctive coloration patterns which enabled me to identify quickly and accurately a given organism into its correct specific classification. In order to obtain qualitative detail regarding the activities of the insects, the use of a pair of binoculars (7x35) permitted study from a distance which did not deter the normal activities. The

minimal distance from which the instrument could be used effectively was approximately 2.5-3 m. Beneath this level, the unaided eye was found to be very satisfactory.

To facilitate a more objective comparison in reporting the activity patterns of each of the species, the quantitative data have been converted to percentages. This particular method of reporting was elected to present the activities of the small population of E. civile on an equivalent basis with that of E. geminatum and E. signatum. In all graphic representations E. geminatum is reported by a solid (_____) line, E. signatum by a broken (_ _ _ _ _) line and E. civile by a sequence of dots (.....), respectively.

RESULTS

PERCHING. Members of the genus Enallagma were observed to express interesting behavioral patterns when influenced by varied environmental conditions. Information collected from approximately 10,500 observations made during a three-month study permitted the relative grouping of adult activity as follows:



When extreme environmental conditions were encountered, the activity patterns of the adults were observed to vary. By further analysis of the data, it was observed that certain conditions were apparently favored by the adult. Those criteria were valuable in establishing the preferential environmental limits of each species.

Adult males of each species arrived daily at the study site between 0900 and 1000 hours EDT. During this time period, an order of species arrival was determined. Adults of Enallagma geminatum arrived at the study site earlier and in larger numbers than those of Enallagma signatum or Enallagma civile. The two large populations of E. geminatum and E. signatum dominated the study site at mid-day and late afternoon, respectively. The small population of E. civile was present at the study site and apparently unaffected by either of

the dominant forms. In several areas the small population provided only minimal data for the development of conclusive statements concerning its behavioral patterns and environmental requirements.

Based upon the rate of population increase, and the time of peak perching activity, E. geminatum was designated as the "early" and E. signatum the "late" species. E. civile was identified as an "all day" species, in that it generally arrived early and persisted until the departure of E. signatum in the early evening. The relative arrival and departure times of each species are reflected in Figure 2.

The selection of a favorable perch site was the initial objective of the adult of all species irrespective to the time of arrival. The more desirable sites were invariably located near the edge of the vegetative mat, while secondary sites were established away from the mat's edge. In those instances where the mat was completely surrounded by water, perch sites were located along the perimeter. There was no discernible preference for perch site materials between the species. A random distribution of sites was established on stems, flower heads, twigs and the mat's surface with indifference.

As the population density of each species increased during the day, perch sites were observed within 4-6 cm of each other. Perching dominated the daily activity of a large segment of each population. Each species expressed a definitive period when perch frequency was most evident as shown in Figure 2.

An examination of the total activity pattern of these animals indicated that perching dominated all other activities. By further

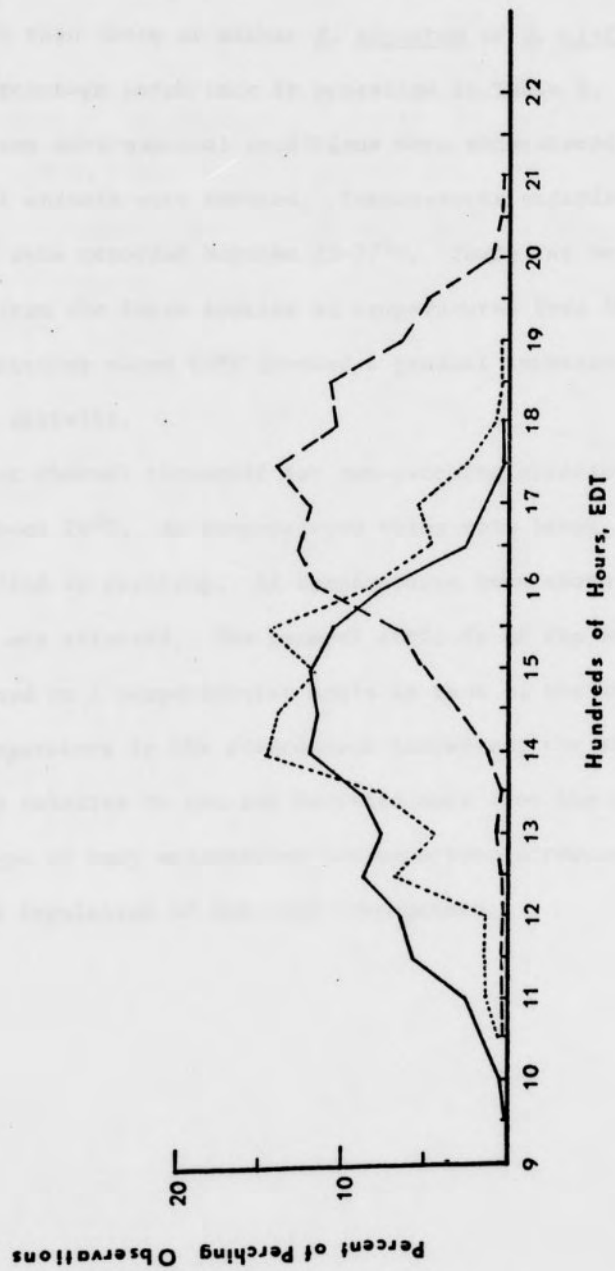
FIGURE 2

Perch rate frequency as distributed during the daily period of observation.

E. geminatum = _____(N=4,052)

E. signatum = _ _ _ _ _ _ _ (N=3,962)

E. civile = ...(N= 234)



the daily period of

N=4,052)

N=3,962)

N= 234)

comparison of the three species, adults of E. geminatum spent more time on the perch than those of either E. signatum or E. civile. A comparative percentage perch rate is presented in Table 1.

When extreme environmental conditions were encountered, activities of all animals were reduced. Temperatures experienced during the study were recorded between 23-37°C. There was no flight activity from the three species at temperatures less than 23°C. Increasing temperatures above 23°C invoked a gradual increase in the level of species activity.

An apparent thermal threshold for non-perching activity was observed to be about 24°C. At temperatures below this level, all activity was limited to perching. As temperatures rose above 24°C, the body posture was affected. The general attitude of the insect's body was positioned at a perpendicular angle to that of the sun's rays. As the temperature in the environment increased, the angle of the animal's body relative to the sun deviated more from the perpendicular. This type of body orientation may have been a response necessary for the regulation of the body temperature.

TABLE 1

Percentage of the Total Activity Spent in Perching by Each of the Three Species of *Enallagma*.

Species	Total No. of all observations	No. of perching observations	Percent Perching
E. geminatum	4,671	4,052	86.75
E. signatum	5,367	3,962	73.82
E. civile	527	234	44.40
All Species	10,565	8,248	78.07

At one point (24-25°C) in the temperature range all three species were observed to exhibit a common response with regard to perching frequency. From the data collected, the perching frequency was observed to increase slowly between 23-28°C and then drop suddenly as shown in Figure 3. It is concluded that this thermal peak is associated with the attainment of conditions necessary for the initiation of other phases of the activity cycle.

As the environmental temperatures exceeded 28°C adults of the three species reacted somewhat differently. The small population of E. civile expressed the highest level of thermal resistance with only a slight increase in perch frequency when temperatures were in excess of 32°C. The large population of E. geminatum was observed to decrease it's perching rate between 28-31°C in preference to other activities. Temperatures in excess of 31°C produced a general increase in perching. From this evidence it may be concluded that E. geminatum is hyper-responsive to elevated temperatures. The frequency of perching of E. signatum was observed to increase up to 33°C. Temperatures in excess of 34°C induced an appreciable drop in perching. This drop may be associated with the elevated levels of other activities conducted by this species in the late afternoon. This further identifies a response to elevated thermal changes common to this species.

The degree of cloud cover at a given time is based upon an estimate of clouds present, irrespective of type and altitude. For this estimate values extending from zero to ten were utilized.

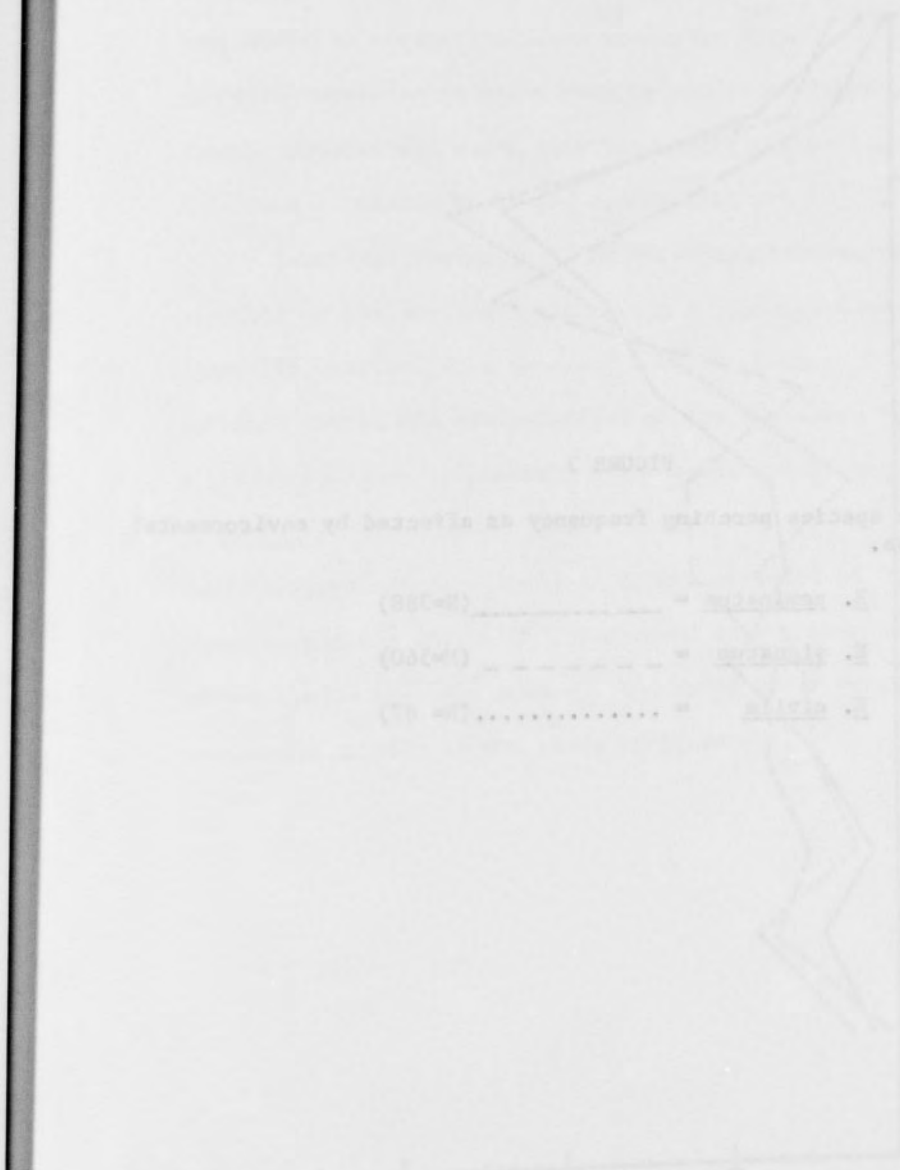
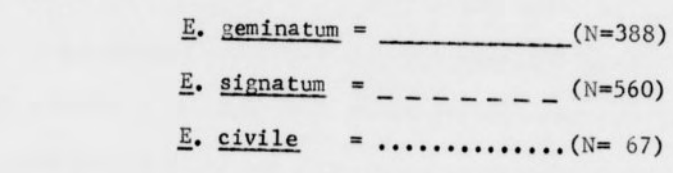


FIGURE 3

Comparative species perching frequency as affected by environmental temperatures.

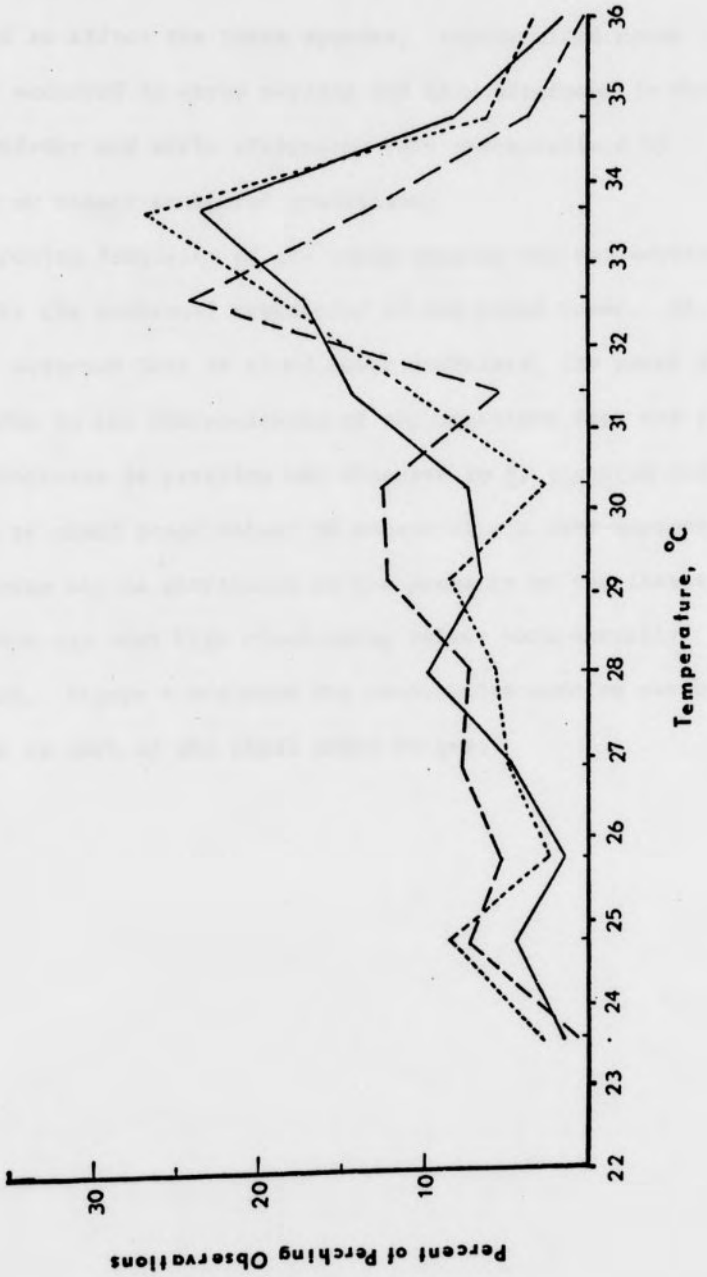


s affected by environmental

(N=388)

(N=560)

.(N= 67)



Cloud cover was the most changeable of the environmental factors considered to affect the three species. Higher cloud cover estimates occurred in early morning and late afternoon in this study. Mid-day and early afternoons were characterized by cloudless or widely scattered conditions.

Perching frequency of the three species was not adversely affected by the continual transition of the cloud cover. It was generally observed that as cloud cover increased, the perch frequency declined due to the disappearance of the organisms from the pond. A slight increase in perching was observed in E. signatum and E. civile as cloud cover values in excess of six were encountered. This increase may be attributed to the presence of the insects later in the day when high cloud cover values were normally encountered. Figure 4 presents the comparative species perching percentage at each of the cloud cover values.

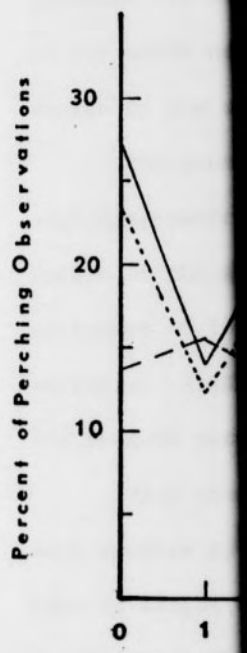
FIGURE 4

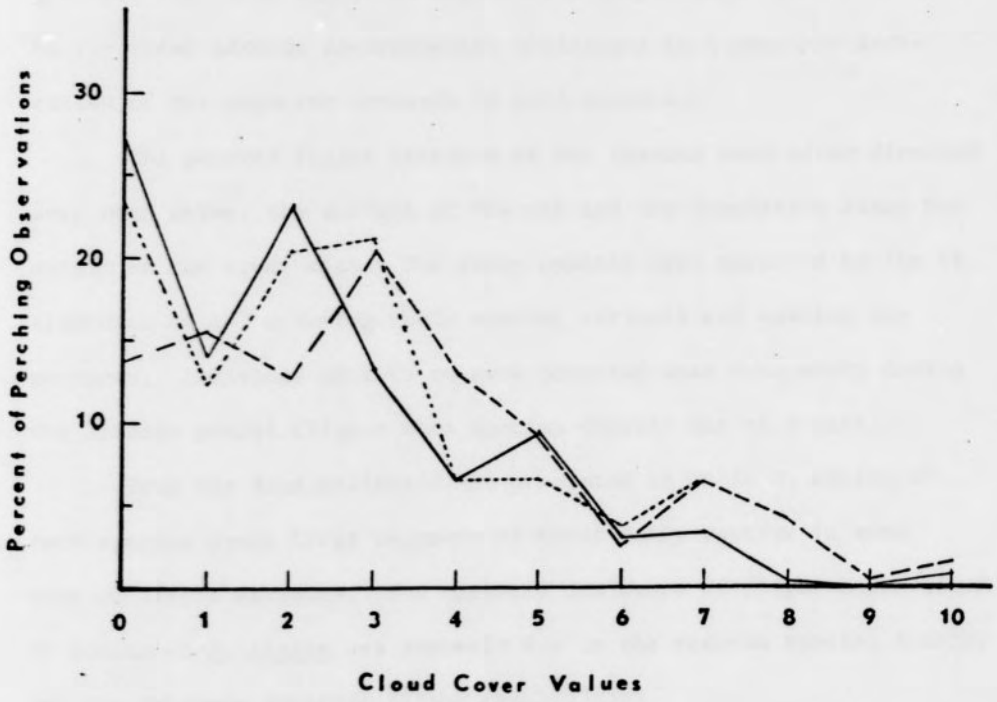
Comparative perching frequency of the three species of Enallagma at the respective cloud cover values.

E. geminatum = _____(N=3,918)

E. signatum = _ _ _ _ _ _ _ (N=3,788)

E. civile = ...(N= 277)





pecies of Enallagma

=3,918)

=3,788)

= 277)

PATROL FLIGHTS. The flight patterns of the Enallagma adults expressed minor differences between the three species. The typical flight pattern of Enallagma sp. is a smooth fluttery motion capable of traversing short distances. Of the three species adults of E. civile were observed to fly with minimal expenditure of effort. Frequently, adults of E. civile flew when climatic conditions had grounded all other Zygoptera and smaller Anisoptera. This ability to fly under adverse environmental conditions is a possible indication of the superior strength in this species.

The general flight patterns of the insects were often directed over open water, the surface of the mat and the vegetation along the margin of the study site. The three species were observed to fly at altitudes of 1-3 m during their morning arrivals and evening departures. Altitudes of 2-15 cm were observed most frequently during the insects patrol flights when species density was at a peak.

From the data collected and presented in Table 2, adults of each species spent large segments of their daily routine in some type of flight activity. The elevated incidence of flight experienced by adults of E. civile was probably due to the reduced species density and the inherent superior flight capabilities.

The flight capabilities of the insects were often used as an integral tool in the expression of many of their behavioral activities. Many of the flight responses were initiated due to population shifts. The response flight patterns of the individual organism were most often directed over the vegetative mat or the open water at altitudes of 2-15 cm.

TABLE 2

Percentage of the Total Activity Spent in Patrolling by each of the Three Species of Enallagma.

Species	Total no. of all observations	No. of patrolling observations	Percent Patrolling
E. geminatum	4,671	389	8.33
E. signatum	5,367	559	10.42
E. civile	527	85	16.13
All Species	10,565	1,033	9.78

Most adults were observed to conduct periodic patrol flights in the area of the perch. The patrol flight followed an elliptical pattern of 1-3 m from the perch site. These flights were apparently initiated due to the intrusion of a member of the same or different species. When an intruder approached a perch site, the occupant exhibited a defensive gesture defined as a "wing warning." The gesture was described as an elevation of the wings, which moved them slightly toward the head in a fluttering motion. If the warning was not recognized, the occupant directed a frontal attack on the intruder or abandoned the perch site. If the intruder was forced from the area by the aggressive act, the original occupant executed a short patrol flight and then reoccupied its perch or one in the immediate area. When associated with aggressive defense of the perch site, patrol flights were most evident during the period of the greatest species density. The aggressive acts were most frequently directed against members of the same species; however, identical responses were observed against members of different species.

Those aggressive acts among the species of Enallagma sp. were observed to be either interspecific or intraspecific. The respective pattern of aggression provided the identification of the two participants, one active, the other passive. From the aggressive acts recorded, E. geminatum was shown to be the most aggressive of the three species. Table 3 presents limited data reflecting the inter- and intraspecific responses of the three species.

TABLE 3

Frequency of Aggressive Conflicts Between Three Species of *Enallagma*.

	Passive member		
Active Member	*E. geminatum*	*E. signatum*	*E. civile*
E. geminatum	22	30	4
E. signatum	3	92	-
E. civile	-	-	8

Patrol activity represents a broad area of flight responses and can, therefore, be divided into several categories: a) defense of a perch site, b) isolation of a female for reproductive purposes and c) selection of resting sites following reproductive activities. A distribution of total patrol activity is reported in Figure 5 as recorded during the observational periods.

During the day when the population of a given species increased to a maximum, an increase in the male-female activity was observed. As the females of each species arrived at the study site, they were subsequently pursued by one or more males until a tandem relationship had been established. The three species in this study failed to present any distinctive characteristics in their respective modes of tandem establishment.

When the tandem relationship had been established, the flight pattern of the pair was not obviously affected by the physical union. The female of each couple occupied the trailing position and was, therefore, capable of exerting significant control on the rate and direction of flight. In this position the female was observed to determine the site of perching, copulation and oviposition. From the in-flight attitude of the pair, it was apparent that the female of each exhibited the greater flight strength. The superior strength of the female was also evidenced in her ability to break away from undesirable males and to escape from all males following oviposition.

Post-reproductive patrol was a common event occuring in the final 25% of each day's activity. This activity was unique to the

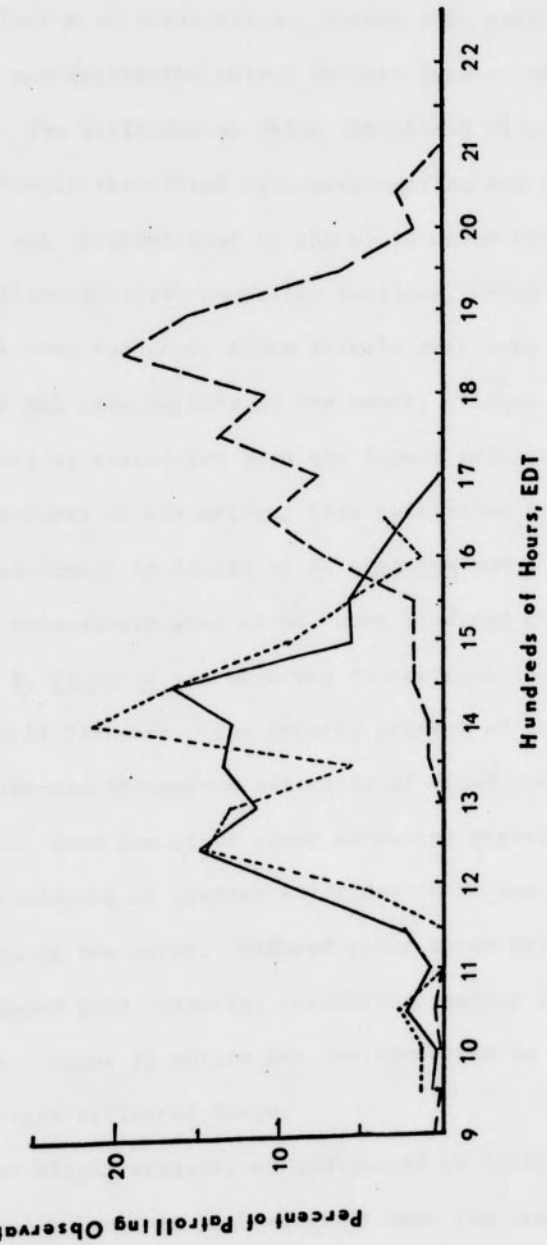
FIGURE 5

Comparative species patrol frequency as distributed during the period of daily observation.

E. geminatum = _____(N=389)

E. signatum = _ _ _ _ _ _ _ (N=559)

E. civile = ...(N= 85)



ted during the

males of each species, due to the early departure of all females following their completion of oviposition. During this period there were extensive non-aggressive patrol flights between males of the same species. The altitudes at which the patrol flights were executed were closely associated with water motion and cloud cover estimates. It was observed that as the cloud cover estimates increased, all patrolling activity generally declined. When high cloud cover estimates were recorded, those animals that were flying were within 2-4 cm of the calm surface of the water. Flight at this low altitude could be associated with the insect tracking its mirror image on the surface of the water. This particular type of patrol flight was most common in adults of E. signatum and E. civile, both of which patrol extensively when cloud cover readings are generally elevated. E. signatum was observed to continue this pattern of solitary flight until darkness. The general pattern of patrol flight activity as affected by various estimates of cloud cover is presented in Figure 6. When low cloud cover estimates prevailed, patrol flights were conducted at greater altitudes so as not to fly into the rough surface of the water. Reduced cloud cover may be associated with increased wind velocity, thereby increasing the activity of the water. Water in motion was not conducive to the formation of an in-flight reflected image.

The patterns of flight activity as influenced by local temperatures were shown to exhibit peak activity near the upper limits of the animal's thermal resistance. Activity was observed

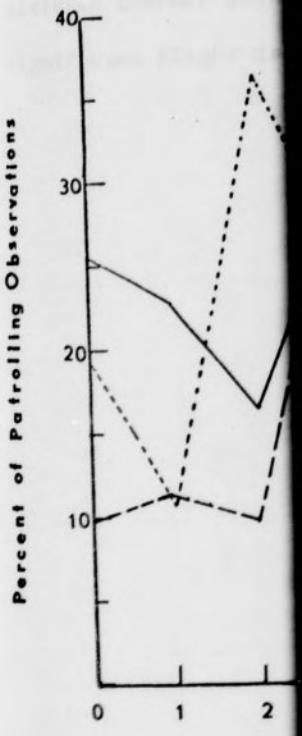
FIGURE 6

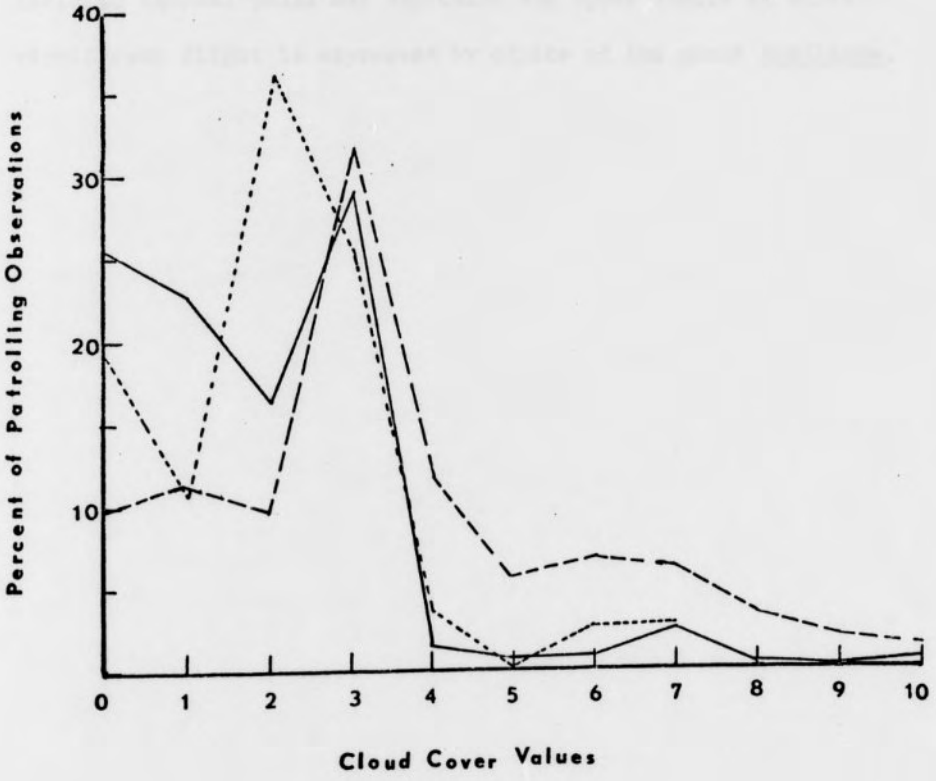
Comparative species patrol frequency as affected by cloud cover values.

E. geminatum = _____ (N=541)

E. signatum = _ _ _ _ _ _ _ (N=554)

E. civile = ... (N= 83)

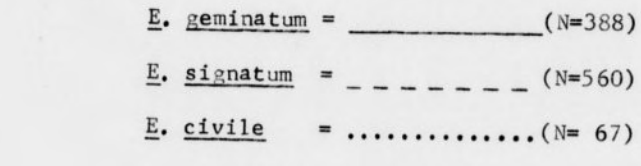


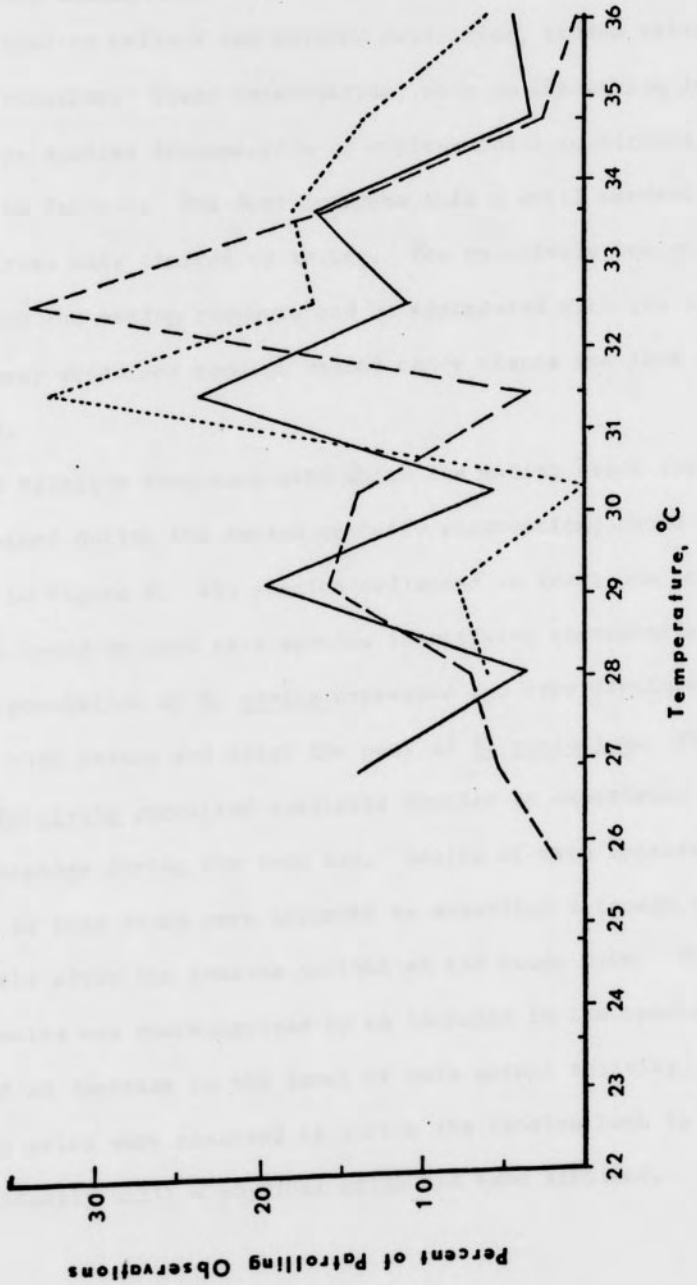

Percent of Patrolling Observations
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
Cloud Cover Values

to reach a peak for all species in the narrow thermal band between 31-33°C, as shown in Figure 7. From the data it was evident that E. geminatum and E. civile were more sensitive to higher temperatures than E. signatum. Temperatures in excess of 34°C invoked a complimentary decline in frequency of flight for all species. This isolated thermal point may represent the upper limits at which significant flight is expressed by adults of the genus Enallagma.

FIGURE 7

Comparative species patrol frequency as affected by environmental temperatures.





by environmental

MATING ACTIVITIES. Mating activities of the individual species were described to reflect two primary activities, tandem relationships and sperm transfer. Those observations, made on the mating frequencies of the three species irrespective of environmental conditions, are reflected in Table 4. The data indicate that a small percent of all the activities were limited to mating. The relatively low values computed for the mating response can be associated with the isolation in which many organisms conduct reproductive events and thus go unobserved.

The relative frequency with which the mating event occurred was determined during the period of daily observation; these data are shown in Figure 8. All species reflected at least one primary peak which could be used as a species identifying characteristic. The small population of E. civile expressed two very distinct peaks occurring both before and after the peak of E. geminatum. The dual peaks of E. civile permitted available females to experience possible multiple matings during the long day. Adults of each species of Enallagma in this study were observed to establish a tandem relationship shortly after the females arrived at the study site. The arrival of the females was characterized by an increase in the species population and an increase in the level of male patrol activity. Those patrolling males were observed to pursue the females both in groups and individually until a physical union had been attained.

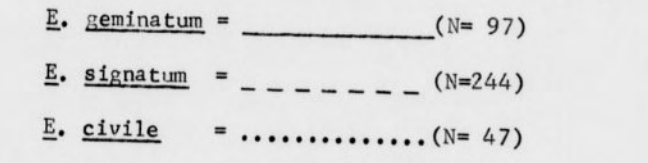
TABLE 4

Percentage of the Total Activity Spent in Mating by Each of the Three Species of *Enallagma*.

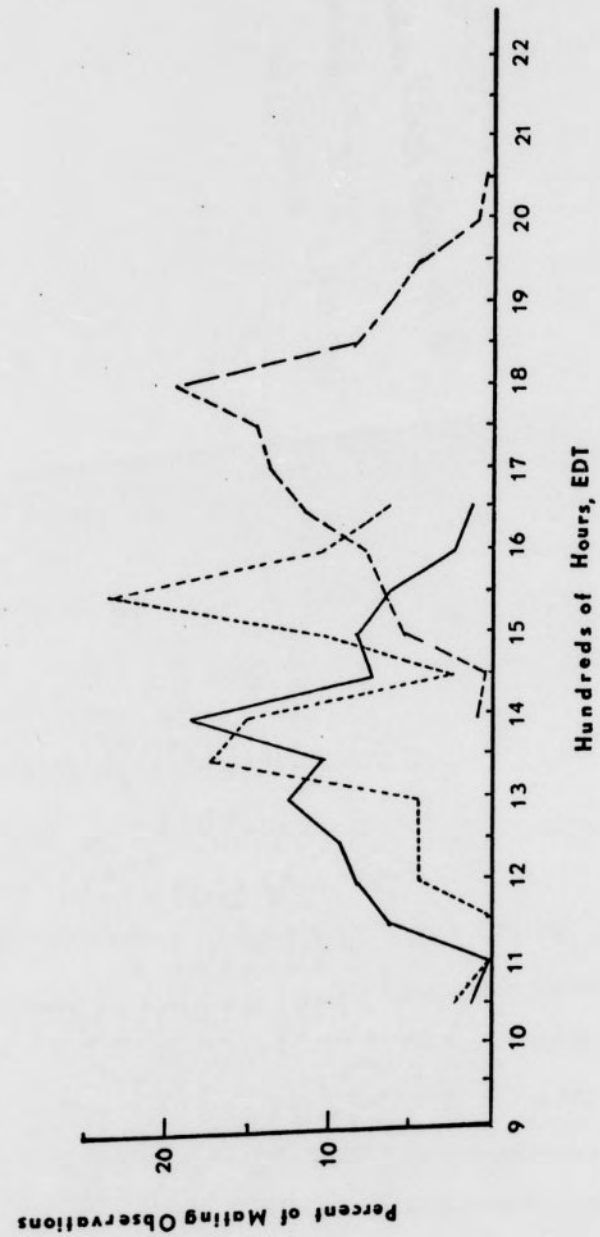
Species	Total No. of all observations	No. of mating observations	Percent Matings
E. geminatum	4,671	97	2.08
E. signatum	5,367	244	4.55
E. civile	527	47	8.92
All Species	10,565	388	3.67

FIGURE 8

Mating frequency as a function of time of day.



of day.


Percent of Mating Observations
20
10
9
10
11
12
13
14
15
16
17
18
19
20
21
22
Hundreds of Hours, EDT

The initial union established by the pair was considered as being non-sexual, as the reproductive structures were not utilized. The tandem union was attained by the male flying over and slightly ahead of the female. Then by flexing the appendages on the terminal abdominal segment, union was attained by grasping the posterior edge of the female's prothorax. In the final analysis the female was the determining factor in the establishment of the union. As previously described, the females generally expressed a flight strength superior to that of the male. Those females unwilling to establish a tandem union presented several evasive maneuvers. Rapid changes in flight direction and altitude were the two most frequently evidenced techniques used to evade possible tandem. In other conditions the female merely out-distanced those males pursuing. On several occasions a female was observed to terminate an undesired tandem union by initiating a series of rapid changes in flight direction resulting in the dislodging of the male.

When an acceptable pair had been united, they flew short exploratory flight patterns in search of a favorable perch site. Observations indicated that a favorable perch site was one which permitted both members of the pair to rest on the site without termination of the physical union. In the maintenance of the perch site, the physical union was not terminated due to the extreme flexion of the abdomen of the male. On other occasions the pair was observed to show only the female on the perch site while the male fluttered

its wings to maintain either a horizontal or vertical posture. The type of perching apparently placed severe stress on the male as well as the physical union.

The tandem union was frequently attacked by males of the same species in an attempt to terminate the union and to achieve tandem themselves. These aggressive acts were directed towards the pair while they were perched and while in-flight. During the in-flight attacks, the pair attempted to out-distance the aggressor. In most instances the pair was forced to separate with the female escaping or establishing an immediate tandem with the original or the aggressor male. When single males attacked a perched pair, both male and female extended a wing warning to the aggressor. In most situations this gesture was adequate in deterring further advances by the intruder. In situations where the pair became airborne, the aggressor quickly developed the advantage which usually resulted in the termination of the tandem union.

When a pair was permitted to continue the mating sequence, an isolated area was selected by the stronger flying female to conduct the copulatory phase of the sequence. Adults of all species were observed to engage in the pre-copulatory act. The abdomen of the male was severely flexed so as to bring the head of the female and his terminal abdominal segment in contact with the ventral surface of his lower thoracic segment. From observing many reproductive pairs, this gesture apparently does not precede each copulation. Many pairs were observed to move directly from tandem flight to perch site

where copulation followed immediately. Upon a more detailed examination of the gesture, it was noted that the genital opening of the male are on the 9th abdominal segment. Due to the extreme flexion of the abdomen, these openings are brought into contact with the copulatory structures located on the 2nd thoracic segment. The contact between these two areas was concerned with the transfer of spermatozoa prior to copulation. In those events where the gesture was not observed to preclude copulation, it must be assumed that gametes had been transferred at a previous time. During extensive copulation, the male was observed to bring together his ninth and second abdominal segments presumably to replenish the supply of gametes on the copulatory structures.

Copulation represents that phase of the mating sequence in which sperm were deposited into the genital opening of the female. Union of the opposed sex systems was accomplished by the female flexing her abdomen anteriorly between her thoracic appendages until it attained union with the copulatory structures of the male. During the process of gamete deposition, the female perched on a surface while the male most frequently held the tip of the female's abdomen with his thoracic appendages to insure continued sexual union.

Those individuals that were observed to maintain an extended presence at the study site were subjected to a wide range of fluctuating environmental conditions. Light intensity, as associated with an estimate of cloud cover, introduced a regulatory effect on the mating activities as shown in Figure 9. The early populations of

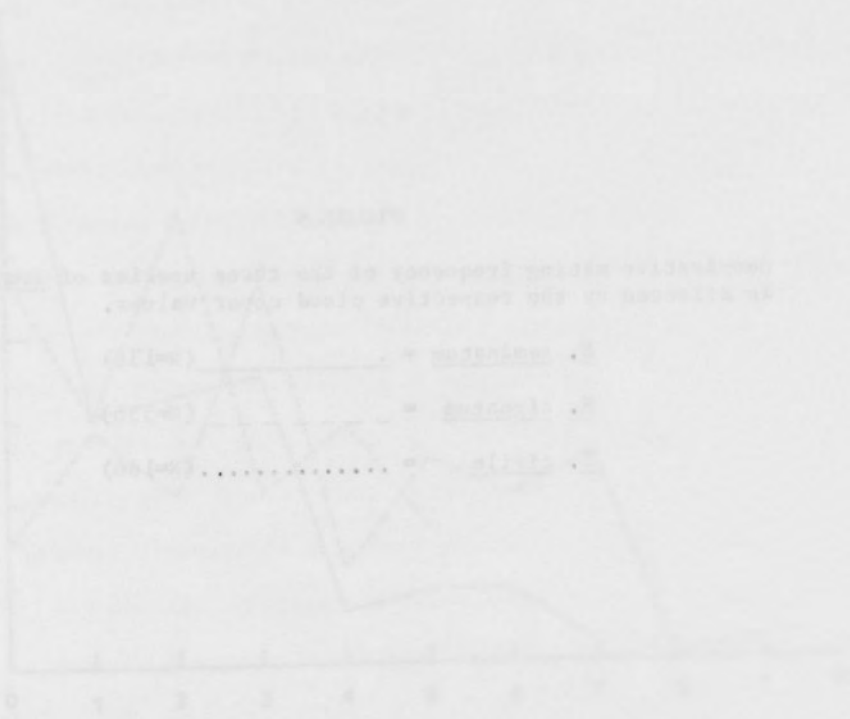


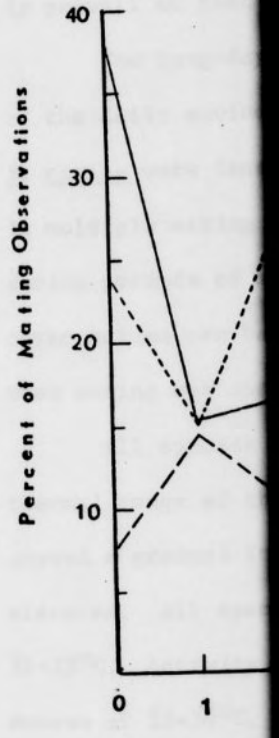
FIGURE 9

Comparative mating frequency of the three species of Enallagma as affected by the respective cloud cover values.

E. geminatum = _____ (N=136)

E. signatum = _ _ _ _ _ _ _ (N=556)

E. civile = ... (N=166)

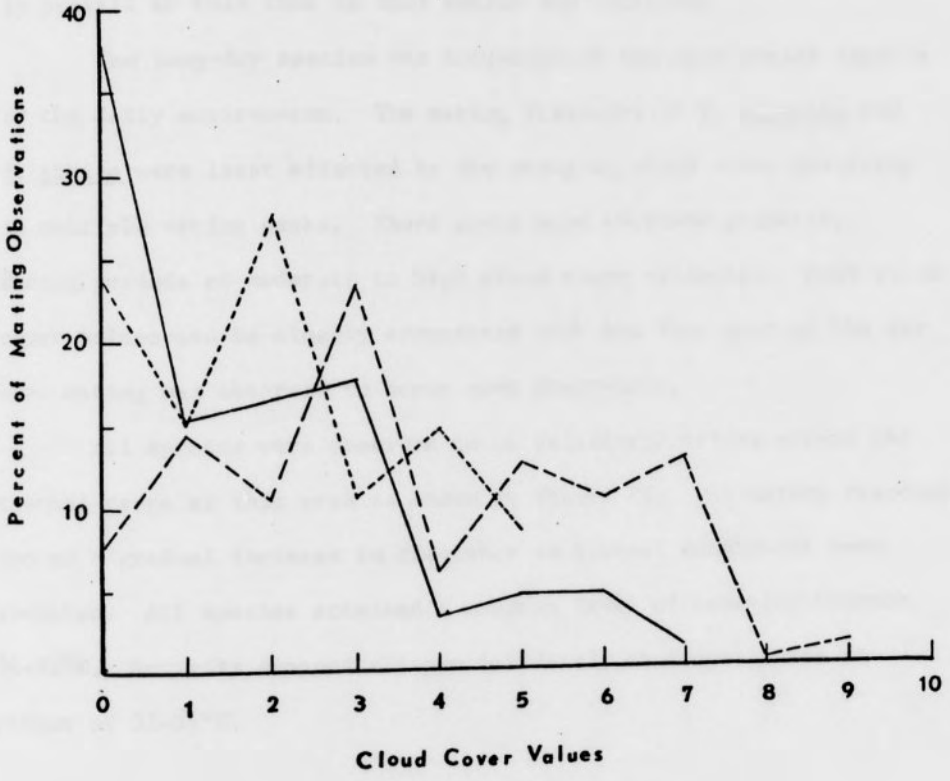


species of Enallagma
values.

(N=136)

(N=556)

(N=166)



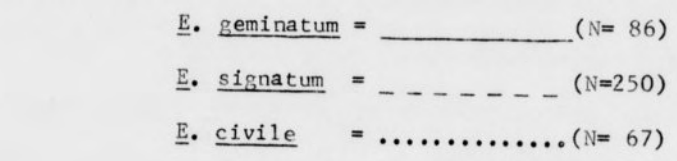
E. geminatum and E. civile expressed a preference for the early cloudless condition as a time to conduct mating activities. Mating frequency in E. geminatum declined as cloud cover estimates increased. The dominant mating peak expressed by E. geminatum at 1400 hours can be closely associated with the near cloudless conditions that generally prevail at that time in this season and latitude.

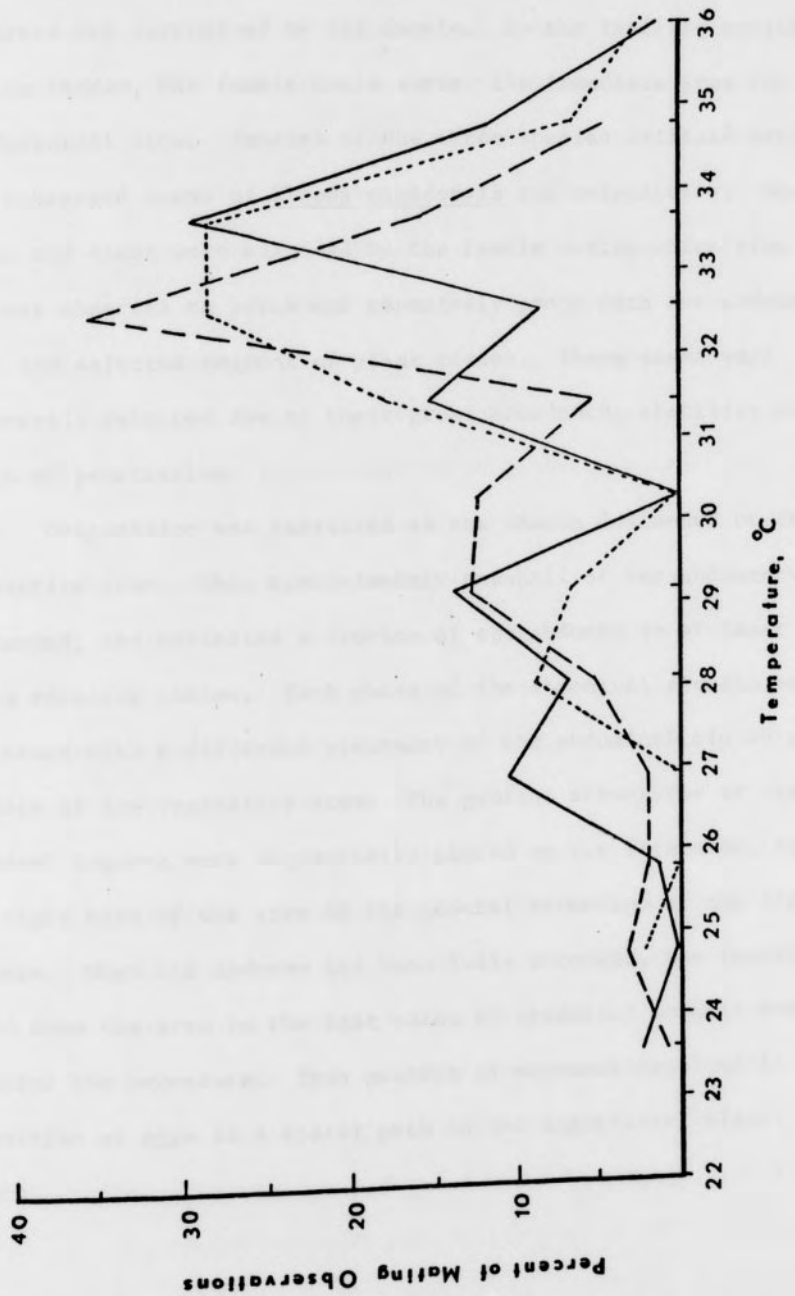
The long-day species was subjected to the most varied aspects of the daily environment. The mating frequency of E. signatum and E. civile were least affected by the changing cloud cover resulting in multiple mating peaks. Those peaks were observed primarily during periods of moderate to high cloud cover estimates. High cloud cover values can be closely associated with the late hour of the day when mating was observed to occur most frequently.

All species were observed to be relatively active across the thermal range of this area as shown in Figure 10. The mating response showed a gradual increase in frequency as thermal conditions were elevated. All species attained a maximum level of activity between 32-33°C. Activity dropped off precipitiously at temperatures in excess of 33-34°C.

FIGURE 10

Comparative species mating frequency as affected by environmental temperatures.





cted by environmental

= 86)

=250)

= 67)

OVIPOSITION. The site at which oviposition initially occurred was determined by the female. In the trailing position of the tandem, the female could survey the immediate area for a preferential site. Females of the three species utilized mainly the submerged stems of Eloeda canadensis for ovipositing. Many areas and stems were examined by the female during which time she was observed to perch and repeatedly probe with her abdomen into the selected segment of plant tissue. Those stems were apparently selected due to their great abundance, stability and depth of penetration.

Oviposition was initiated as the female descended on the vegetative stem. When approximately one-half of her abdomen was submerged, she exhibited a flexion of the abdomen in at least three relative phases. Each phase of the abdominal flexion was concerned with a different placement of the abdominal tip on the surface of the vegetative stem. The genital structures of the terminal segment were sequentially placed on the left side, top and right side of the stem by the general extension of the flexed abdomen. When the abdomen had been fully extended, the female moved down the stem to the last point of abdominal contact and repeated the procedure. This pattern of movement resulted in the deposition of eggs in a spiral path in the superficial plant tissue.

To further insure the desired placement of her eggs, females of E. civile often submerged to a depth of 6-8 cm. The practice of total submergence was not exhibited by the other species. Males of E. civile terminated the tandem union when the terminal one-third of their abdomen was drawn into the water by the submerging female. During the period of the female's submergence, the male assumed an aggressive defense posture in the immediate area. Other males entering the area were promptly attacked and expelled from the area. When the female emerged from the water, tandem was immediately re-established by the original male. This temporary termination of the tandem union may represent the initial evolutionary step necessary to insure the liberation of the female to oviposite independently of the male association.

The frequency with which oviposition occurred was determined by the time of day that the adults of each species were most abundant. During those periods dominated by individual species a relative frequency at which oviposition occurs was computed. The data reported in Table 5 reflect an interesting comparison between the small population of E. civile and the two dominant populations.

Each species was identified by its response activity to a relative time span. The peak of oviposition for each species is reported in Figure 11. The two day-long species had dual activity peaks in contrast to the one presented by E. geminatum. This pattern of oviposition activity can be associated with the two species not being adversely affected by the declining environmental conditions common in the final one-third of each day.

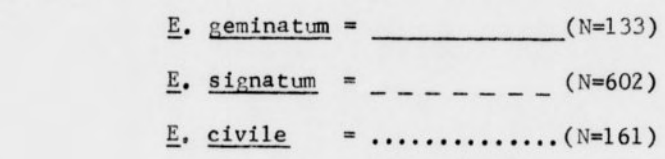
TABLE 5

Percentage of the Total Activity Spent in Oviposition by each of the Three Species of Enallagma.

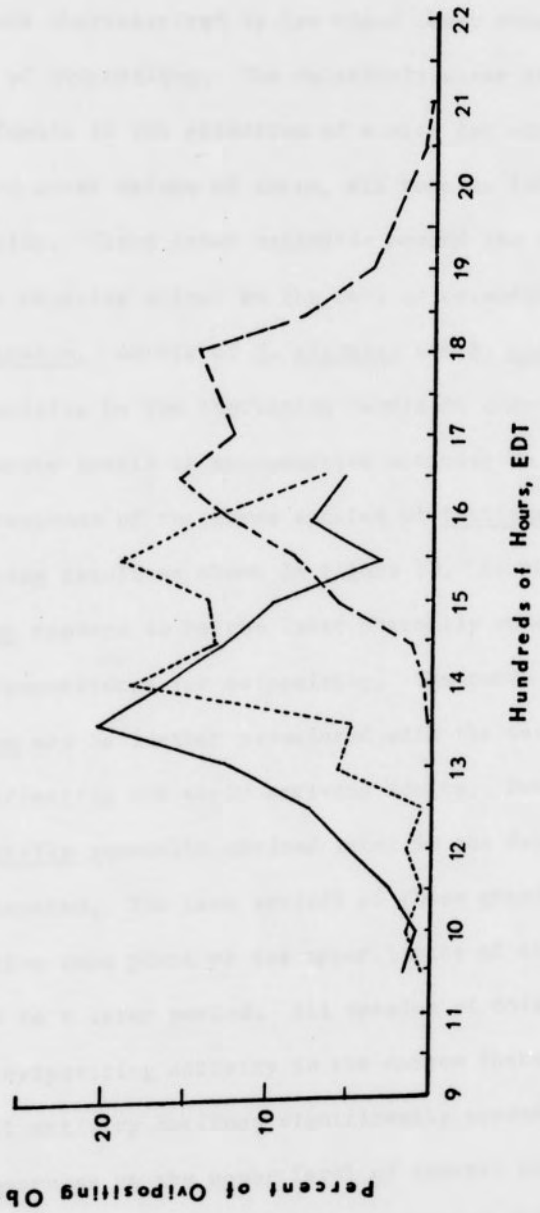
Species	Total no. of all observations	No. of all ovipositions observed	Percent Ovipositions
E. geminatum	4,671	133	2.8
E. signatum	5,367	602	11.22
E. civile	527	161	3.55
All Species	10,565	896	8.48

FIGURE 11

Comparative species ovipositing frequencies as affected by time of day.



affected by time



Cloud cover was observed to exert a very definite effect upon the number of females undergoing oviposition. Figure 12 presents those periods characterized by low cloud cover values and elevated levels of ovipositing. The relatively clear sky may be of value to the female in the selection of a site for egg deposition. At cloud cover values of three, all species indicated an increase in activity. Cloud cover estimates beyond the level of three had an extreme negative effect on the rate of ovipositing as expressed by E. geminatum. Adults of E. signatum and E. civile were apparently least sensitive to the increasing levels of cloud cover, thus permitting moderate levels of reproductive activity to continue.

The thermal response of the three species of Enallagma presents an interesting result as shown in Figure 13. Of the three species, E. geminatum appears to be the least thermally sensitive regarding specific temperatures for ovipositing. The three activity peaks of E. geminatum may be further associated with the varied thermal conditions affecting the early arriving adults. Females of E. signatum and E. civile generally arrived later in the day when temperatures were elevated. The late arrival of these gravid females demand that oviposition take place at the upper limits of the thermal range or be deferred to a later period. All species of this study reflect substantial ovipositing activity in the narrow thermal range between 32-34°C. All activity declines significantly beyond the 34° point, inferring a nearness to the upper level of thermal tolerance.

Figure 14 presents the summary of the comparative activities of the three species irrespective of the environmental conditions.

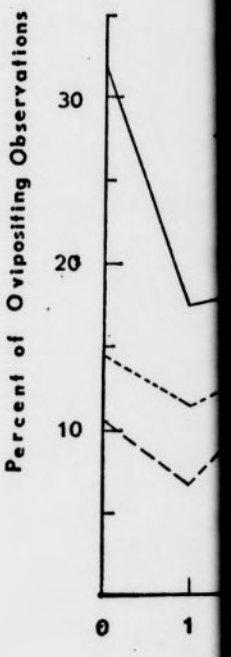
FIGURE 12

Comparative frequency of ovipositing as affected by cloud cover values.

E. geminatum = _____(N= 91)

E. signatum = _ _ _ _ _ _ _ (N=232)

E. civile = ...(N= 47)



by cloud cover values.

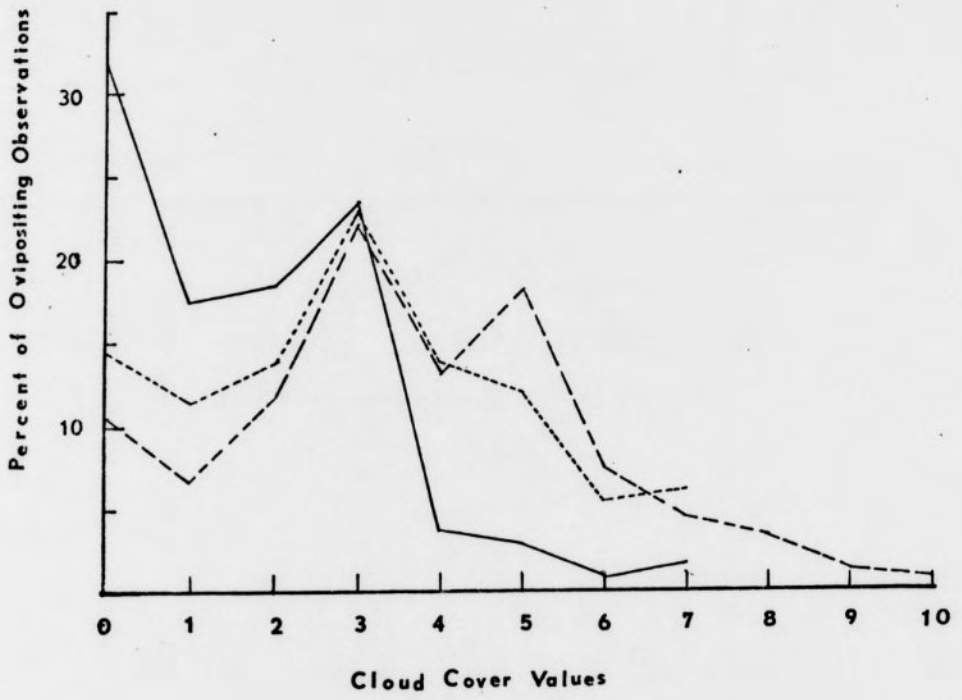


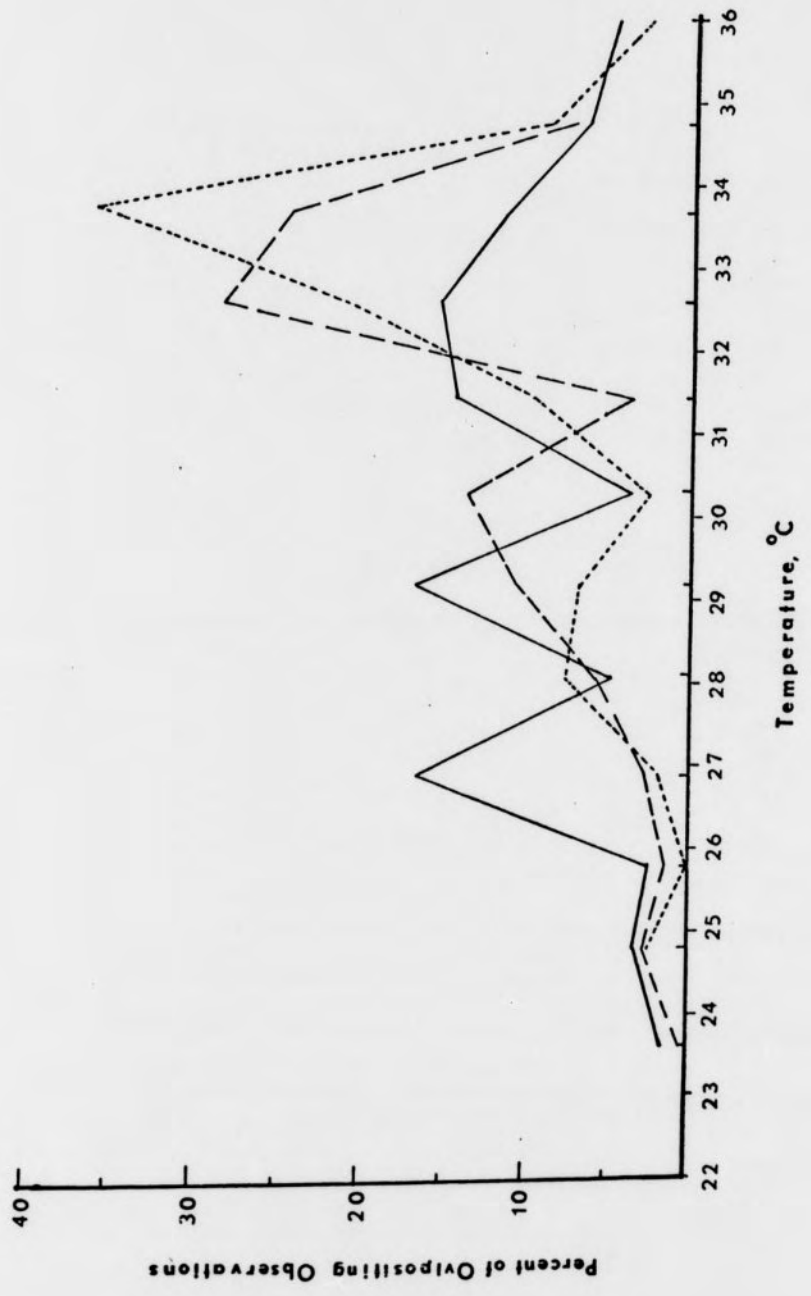
FIGURE 13

Comparative species oviposition frequency as affected by environmental temperatures.

E. geminatum = _____(N=126)

E. signatum = _ _ _ _ _ _ _ (N=586)

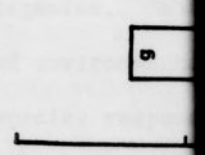
E. civile = ...(N=158)



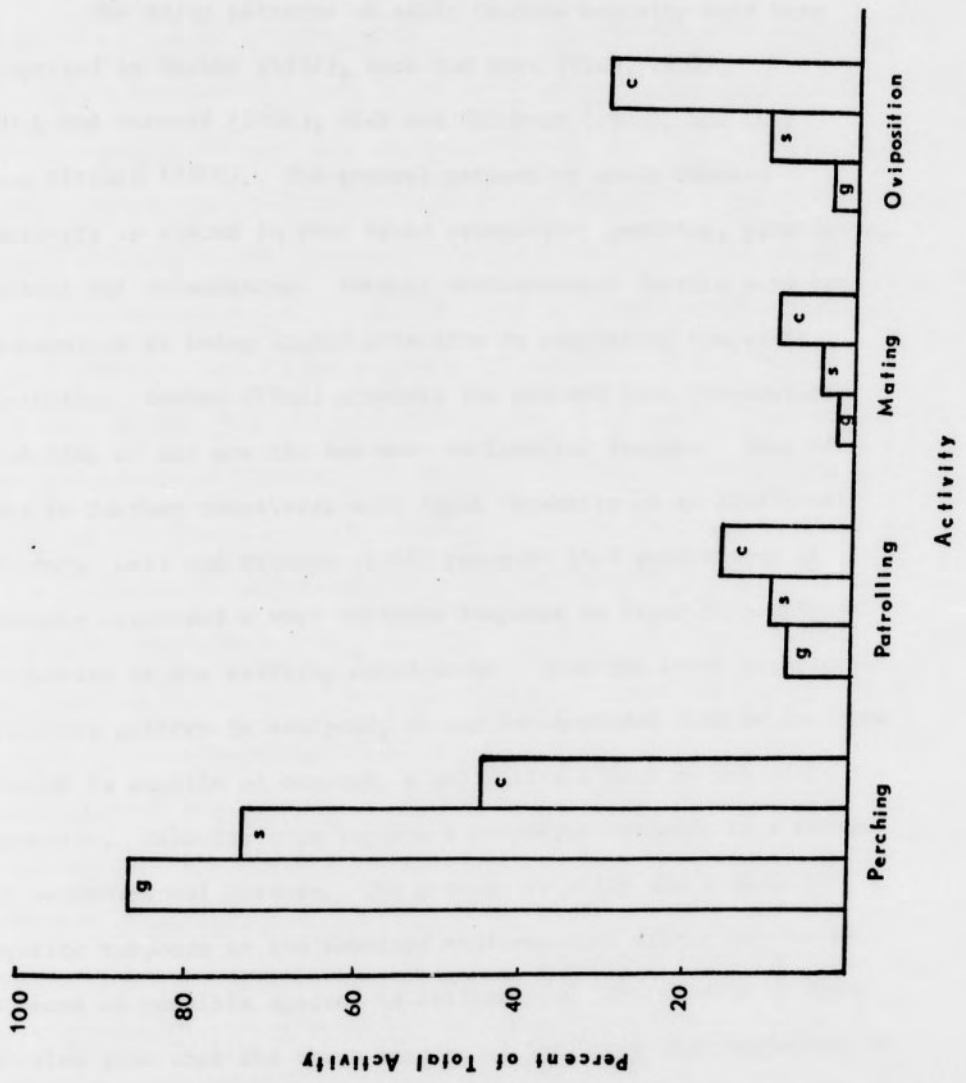
ed by environmental

FIGURE 14

Comparative events in the activity day of the three species of Enallagma.



species of


Percent of Total Activity
100
80
60
40
20
g
s
c
Perching
Patrolling
Mating
Oviposition
Activity

DISCUSSION

The daily patterns of adult Odonata activity have been reported by Corbet (1962), Bick and Bick (1963, 1965), Bick and Hornuff (1966), Bick and Sulzbach (1966), and Lutz and Pittman (1970). The general pattern of adult Odonata activity is placed in four broad categories: perching, patrolling, mating and ovipositing. Several environmental factors have been recognized as being highly effective in regulating the adult activity. Corbet (1962) presents the concept that temperature and time of day are the two most influential factors. Time of day is further correlated with light intensity as an additional factor. Lutz and Pittman (1970) reported that populations of Odonata expressed a very definite response to light intensity as regulated by the shifting cloud cover. When the total behavioral response pattern is analyzed, it can be concluded that no isolated factor is capable of exerting a definitive effect on the adult organism. Behavior thus becomes a composite response to a series of environmental factors. The pattern by which the individual species responds to the combined environmental effect may become a means of possible species identification. The results of this problem show that the three species of Enallagma show variation in their respective response patterns to a series of changing environmental conditions.

It was determined by extensive observations that each of the species of Enallagma arrived at the study site at definite periods of the day. Based upon their respective times of arrival, the duration of their presence and the time of departure: E. geminatum was designated as the early species, E. signatum the late species and E. civile the long-day species. The arrival and departure times for E. geminatum (0930 and 1800 hours, respectively) and E. signatum (1030 and 2100 hours, respectively) compliment the times recorded by Lutz and Pittman (1970) for the same species at a study site on the northwest side of Greensboro. The period when E. civile was present at the site extended from 1030 to 1930 hours, this period is comparable to that recorded by Bick and Bick (1963) in their work on the same species in Oklahoma.

During those periods when each species was present at the site, the dominant activity was that of perching. The early perch freqency of each species is indicative of an increasing population, which is composed primarily of sexually mature males. When the perch frequency of each species is examined, it can be concluded that each species exhibits a particular response to a series of additional factors which result in the initiation of other phases of the activity cycle. Those conditions that possibly initiate the decline in the perching frequency are: increased population of males, elevated environmental temperatures, shifting cloud cover and the arrival of gravid females in the area.

Of all the factors listed as causing the decline in perching, temperature is concluded to be the most effective. The effect of a particular thermal point apparently affected all species in a similar manner. Perch rate declined and patrol flights were initiated when the environmental temperatures reached 23-24°C. Maximum patrol flight by the genus Enallagma does not attain a peak until a temperature of 29°C has been reached. All three species were observed to conduct the major aspect of their patrol flight activity between 23-29°C. It is at the upper thermal limit that flight activity is reduced in preference to the initiation of other activities.

Flight activity can be further correlated with the thermal changes that occur in the environment. Extensive patrol flight activity was not initiated until temperatures were favorable for each species. E. geminatum and E. civile showed extensive flight patterns by 1200 hrs. and continue until 1430 hrs. It is apparent during this period that desirable thermal conditions existed for the species. E. signatum was observed to follow its flight patterns at a different period of the day when its population dominated the area and environmental temperatures had been somewhat reduced. Based upon the lateness with which E. signatum flies, the species may be more responsive to the higher temperatures than either of the other species.

The flight responses of the Enallagma are conducted within limits that preclude the initiation of other events in the activity

cycle. Flight of the three species is divided into three categories: pre-reproductive flight, tandem (reproductive) flight and post-reproductive flight. Of the three species, E. civile was observed to express its flight patterns over a larger area and under more adverse environmental conditions. The extended flight capabilities of this species was apparently influenced by the small size and density of the population. E. signatum as the late species was least affected by the shifting environmental conditions in the expression of its flight capabilities. It can be concluded that each species must prefer a certain combination of environmental factors, but are not adversely affected if those preferred factors are not present.

When an examination is made of the mating frequencies of Enallagma, it can be noted that time of day and cloud cover showed a very definite relationship. All three species showed an elevated frequency of mating as temperature increased to the upper thermal limits of the species. The mating expression of E. civile, as reported by Bick and Bick (1963) in their work in Oklahoma, supports the mating time of the present study by an additional thirty-minute period. E. signatum, the late species was indifferent to cloud cover and elevated temperature, but this may be justified by the generally declining environmental conditions that were present when the population was at its most active time. Those forms that arrived at the study site late in the afternoon must conduct their normal activity cycle under conditions that afford little compromise.

Cloud cover and thermal conditions are incapable of exerting species identifying response characteristics in the three species of Enallagma. Each species was observed to express oviposition under the prevailing conditions of the time of day when each population is at its peak. Time of day can be further correlated with the species population peaks, and thusly be used as a behavioral identifying characteristic. Each species was observed to oviposit at very definite periods of the day. Upon a clear examination of the three species, both of the late species, E. civile and E. signatum were observed to express twin peaks of ovipositing. These dual peaks may be associated with a large population of gravid females that arrive at the study site in waves to insure the availability of a mate.

SUMMARY

The activity cycle of the three species was observed to contain periods of perching, patrolling, mating and ovipositing. Perching was the event in which all species were observed to spend the greater percentage of their time. All other phases of the cycle were conducted with decreasing progression.

Perching and environment. All species expressed a positive time period for arrival and departure from the study site. Each species could be identified by its time schedule. All species expressed an elevated incidence in the perch frequency as the environmental temperature attained 33°C. Above 33°C all three species expressed a dramatic decline in their perching. When low cloud cover values were recorded, the perch frequency of each species was found to be elevated. The three species were observed to respond similarly to variant temperatures and cloud cover values, thus complicating the identification of a species differential.

Patrol and environment. The frequency of patrolling for each species reflects the preference for a particular time period. Patrol flights were observed between 23-33°C with the highest incidence occurring between 31-33°C. Minor differences were found to exist between the patrol frequency of the three species when subjected to identical cloud cover values. E. signatum was observed to patrol less than the other species when cloud cover values were low. When cloud cover values were elevated, a more extensive patrol pattern was expressed by E. signatum.

Mating and environment. Each species was capable of being identified by a definitive period when mating activities occurred. Unlike the other species of the study, E. civile was observed to express two such mating peaks. E. geminatum and E. civile show a preference for mating activities when cloud cover values existed between 0-3. For this study, E. signatum was observed to mate with relative indifference to the estimate of cloud cover. Each of the three species was observed to show an elevated frequency of mating between 32-34°C. At higher thermal reading the frequency of mating abruptly declined.

Oviposition and environment. The frequency of species oviposition was reflected in a time period that is unique for each. It is apparent that E. geminatum was more sensitive to the higher cloud cover values than either of the other species in that oviposition occurs most frequently at the lower cloud cover values. E. signatum and E. civile expressed their thermal preference for oviposition at the upper end of the thermal scale 32-34°C. E. geminatum was least affected by temperature in that oviposition was observed to occur across the thermal range.

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