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A community of adult Odonata, composed of 15 species, was studied from 7 August 1975 until 17 November 1975 at a small pond in piedmont North Carolina. Studies were made on adult behavioral patterns including flight, reproductive, and perching activity in relation to ambient temperature, light intensity, and time of day. The frequencies of intra- and inter-specific interactions were recorded for the most abundant species.

Most species initiated their flying periods by mid-day and terminated them by 1900 hrs with considerable variation among the species. Perching activity varied inversely with the incidence of mid-morning to afternoon flight period for most of the libellulids. A general reduction in the total flight period was observed for most species as the photoperiod gradually decreased throughout the study period. Maximum reproductive behavior in a given day occurred near the middle to latter part of the patrolling period. Minimal temperature thresholds for activity ranged from 20 - 26°C in August compared to 16 - 24°C in September. A diurnal cycle of attendance at water for most female Odonata occurred at a higher temperature and at a later time of day than for their male counterparts.

Intraspecific interactions, usually between males, were much more common than interspecific interactions. Threat behavior was much more prevalent during August when relative numbers of individuals in the community were high.

EFFECTS OF SOME ECOLOGICAL FACTORS ON A LATE SUMMER COMMUNITY OF ADULT ODONATA

by

James Marshall Cheshire

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Paul E. Lutz
Thesis Advisor

APPROVAL PAGE

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

Thesis Adviser Paul E. Lutz

Committee Members Robert E C

Robert H. Stavn

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To Dr. Bruce M. Eberhart, Head, and to the faculty and staff of the Department of Biology, I wish to express my appreciation for their continued support and encouragement.

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INTRODUCTION

Community studies on adult odonate behavior have been conducted by only a few investigators. Most American, British, and European investigators have concentrated on specific adult behavior (i.e., reproductive and territorial) within the suborders Anisoptera or Zygoptera. The British investigators Corbet, Longfield, and Moore have been most instrumental in reporting various aspects of odonate behavior and development for British species. Their work has been concerned mostly with the ecology of African and British dragonfly fauna in relation to larval growth, seasonal regulation, classification, and specific adult behavior of individual species. In Corbet (1962) adult behavior has been related to various environmental factors such as temperature and time of day, but unfortunately there have been very little guantitative data gathered to support many of his findings. Only a few of these British studies have viewed a community of adult odonates inhabiting a specific pond and dealt with community population densities (Moore 1951a, b, 1952, 1953).

Most of the European investigators have studied specific adult odonate behavioral patterns for individual species. Pajunen (1962a, 1962b, 1963, 1964a, 1966) with the use of cinephotography has been able to distinguish between aggressive and sexual behavior in a few specific odonates. Pajunen (1962b) also observed that anisopteran species of colder climates were behaviorally different than others found in warmer climates. These conclusions were based on numerous observations which showed that colder climate anisopteran males, for example, displayed only sexual attacks, and warmer climate species were typically agressive in behavior. Buchholtz (1951, in Pajunen, 1962b) working with three closely related species of Agrion, also correlated climate with several behavioral patterns that directly influenced territorial changes within the three species. The investigations of Kaiser (1974) suggest that intraspecific aggression for adult Aeschna cyanea was time-dependent and not bound to a limited area of defense. This would imply that individuals of the same species may occupy identical territories, but not at the same time during the day.

The majority of American investigators have concentrated their studies on the reproductive and territorial behavior of individual species. A few of these studies have related physical factors to adult behavior (Jacobs 1955, Bick and Bick 1961, 1963, Johnson 1961, 1962a, b, c, 1963, Bick and Sulzbach 1966, and Lutz and Pittman 1968). Jacobs (1955) reported a correlation between mating peaks and environmental conditions such as temperature, storms during hot humid cloudy weather, and unfavorable weather. Reduction in mating frequencies of Perithemis tenera was observed by Jacobs (1955) when temperatures were greater than 33°C. It was suggested by Mitchell (1962) that dispersal in the damselfly Ischnura verticulis was regulated by storm-induced wind currents.

The work of Lutz and Pittman (1970), Green (1974), and Ubukata (1973, 1974, 1975), are the only recent studies that have dealt with the community dynamics of adult Odonata and have related physical factors to adult behavior. Green (1974) attempted to show that each species in the community had a characteristic time of arrival at the pool and that initial territorial behavior was activated by temperature. The factor governing this attendance at the pool was thought to be a requirement of a certain minimum temperature before territorial activity begins. Lutz and Pittman (1970) studied a community of adult odonates and were the first to show how temperature, light intensity, and time of day were related to adult flight and reproductive activity. The observations of Ubukata (1975) demonstrated that all activity at the pond for Cordulia genea amurensis was "suppressed completely by cool air temperatures lower than 5.8°C or ordinary rain, while only lowered by the strong reduction of illumination or slight rain. The suppression by neither high temperature (28.8°C) nor strong wind (force of wind = 5) was recognized." It is important to note that these observations made by Ubakata represent periods of maximum population density midway through the study period. Ubakata (1974) also noted a 3.5 month shorter dragonfly season in Horainuma than that of Satusuma Pennisula, and attributed this reduction in dragonfly season to severe climatic conditions.

The present study was undertaken to show experimentally the separate and combined effects of temperature, light intensity, and time of day on adult behavioral patterns for a community of adult Odonata. Such a study has never been done on a late summer community of adult Odonata. I wanted to understand better the ecology and behavior of such a community.

MATERIALS AND METHODS

A community of adult Odonata was studied at a small pond located in rural Guilford County, North Carolina (Latitude 36° 02′N, Longitude 79° 55′E) about 4 km east of Jamestown. The pond, partially surrounded by an oak-hickory forest, had a surface area approximately 0.8 ha with numerous rushes, sedges, and grasses comprising the marginal emergent vegetation. Free floating algal mats with rooted aquatic vegetation were particularly dominant during late summer. A physical description of the entire pond and study area is presented in Figure 1.

The study area was divided into four stations located on the southwestern side of the pond; they had a combined shoreline of approximately 44 m. Each station consisted of both a land and water component. During the morning hours water and land at Stations 1, 2, and 4 were in full sunlight. At Station 3 the land component received much lower light intensities until mid-day. The land portions of Stations 1 and 2 had a reduced light intensity beginning in the early afternoon. Stations 3 and 4 were affected little by shading from surrounding trees until late afternoon.

Observations of adult behavior were made hourly at each station and included data on all species present, the inter- and intra-specific adult behavior, time of day, ambient temperature, light intensity, and cloud cover. After these parameters were recorded, I moved frequently from station to station recording any significant adult odonate activity. Deviation from this procedure occurred during early and late periods of the day when observations were recorded every 15-30 min. at each station.

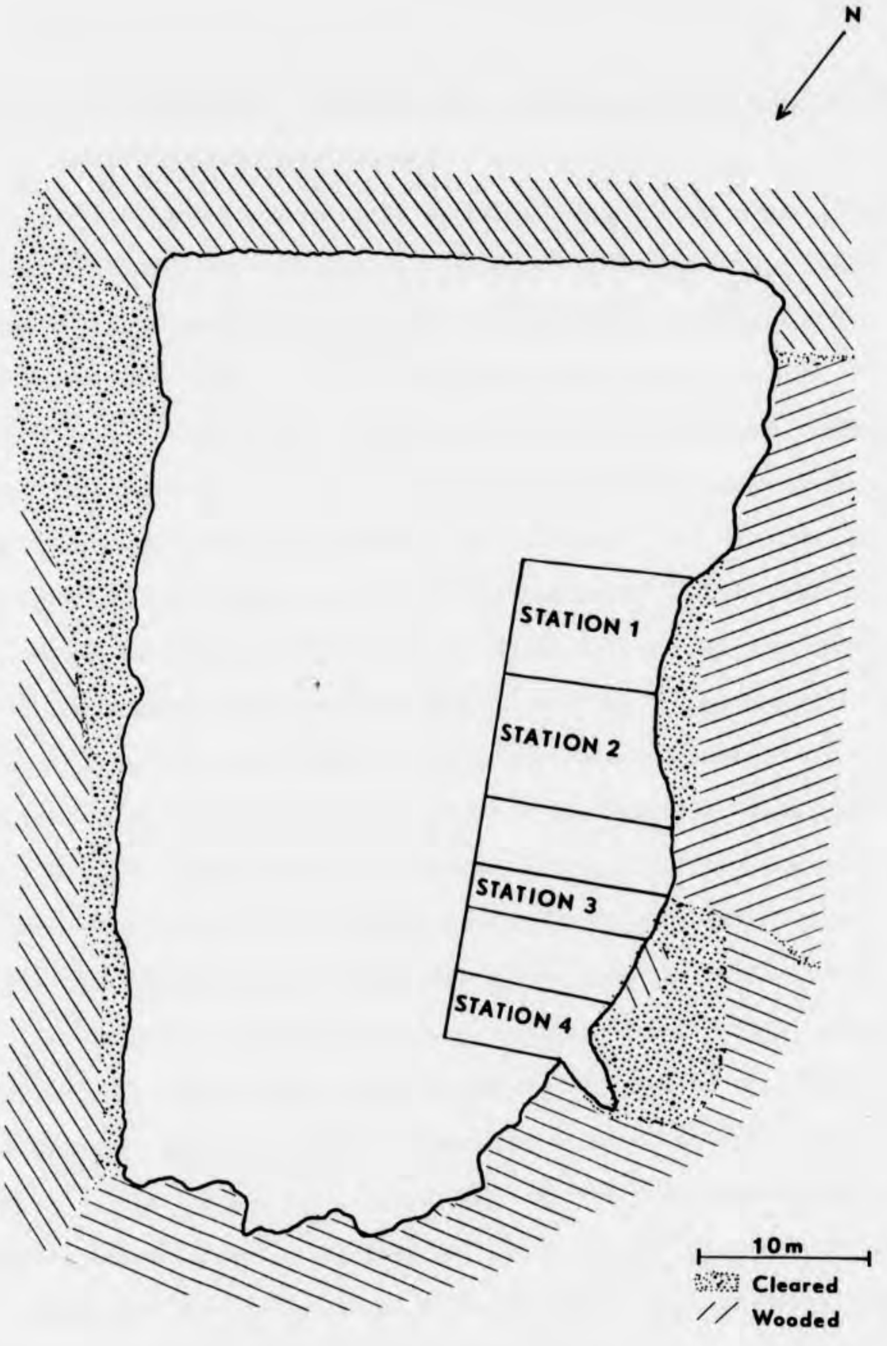

Figure 1. A diagram of the pond with the study area indicated.

Also, from late September to mid-November, Stations 1 and 2 were abandoned due to insufficient data being taken.

Observations were made on 50 different days from 8 August 1975 until 17 November 1975. To correct for local mean times, I followed the same procedure as Lutz and Pittman (1970) which is as follows: "All observations were recorded as specific clock times which were then converted to exact local mean times corrected for latitude and longitude. Further corrections were made to arrive at sundial time or apparent solar times (AST) where midnight is 0000 hr and the exact solar noon is 1200 hrs." Corrections made to local mean time during the study period varied from +5 min 40 sec to -16 min 24 sec with a median of -7 min 11 sec. (Northcutt 1975). All times in this study reflect this median correction of -7 min and are presented as hours AST. Observations under variable weather conditions ranged from 2 to 14 hrs per diem, and included times from 0453 to 1933 hrs AST. Most observations were made visually; however, the use of a pair of binoculars (7 x 35) was needed for distant observations. A portable tape recorder was occasionally used during the study period.

Temperatures recorded with a Celsius thermometer varied insignificantly between each station after readings were taken in the shade approximately 4 m from the pond. Temperatures from a Celsius thermometer placed in an open area under a stake compared with those temperatures of a thermometer placed under the shade of a tree varied insignificantly.

As in the study of Lutz and Pittman (1970) light intensity readings (in foot-candles) were taken using a Weston light meter. The meter was held horizontally over the water's edge with the receptor surface pointing towards the sky. Only the visible wavelengths of electromagnetic radiation were recorded at a specific unshaded area at Station 4 due to the diurnal variability of light intensities at the other stations.

Cloud cover was estimated on a zero-to-ten scale in which 0 was clear and 10 was completely overcast. This parameter was taken at the same time as temperature and light intensity data were recorded.

These observations were grouped into August, September, and total study period data. Numbers of individuals were based on the percentage of the populations flying, perching, or involved in reproductive activity (mating or ovipositing) for any given hour during the day. Light intensities were grouped according to the corresponding time of day so that early morning, mid-day, and late afternoon light intensities could be determined. Early morning between 0600 and 1000 hrs and late afternoon between 1500 and 2000 hrs had a maximum range of 4×10^3 ft-c. A composite of light intensities between 1000 and 1400 hrs above a minimum of 4×10^3 ft-c was designated as mid-day. Only on extremely cloudy days and during periods of thunderstorms did this maximum and minimum range of 4×10^3 ft-c deviate from its expected time during the day. In Figures 15-20, the composite data involving the temporal and light intensity ranges of activity are represented by a mid point between each interval. This mid point represents all odonate activity that was observed at any given time during that temporal or light intensity interval. The absolute temporal, thermal, and light intensity ranges are referred to in Figures 3-5.

RESULTS

Total Flight and Reproductive Period

Flight and reproductive activity for the 15 observed species ended at different times during the study period. The base lines in Figure 2 indicate the total observed flight and reproductive activity including mating and ovipositing from 7 August 1975 to 17 November 1975. Dotted lines indicate that flight activity probably occurred before the actual period of observation.

The species fell into three groups according to the last day they were observed during the study period. The first group, consisting of mostly anisopterans, was last observed no later than October 7. *Lestes vigilax* was the sole zygopteran in this group. The zygopterans were dominant in the second group and were last observed no later than October 30. In the third group *Anax junius* and *Sympetrum vicinum* were the only two species observed in November. It is interesting to note that *Sympetrum vicinum* was first observed when most of the other anisopterans had disappeared and probably represents the only true autumn species.

The species were grouped into two categories based on the percentage of time spent in observed reproductive activity in relation to the total number of days observed for each species. The days between the range of reproductive activity for each species in which no observations were made were still included since both mating and ovipositing undoubtedly occurred during this time. For example, reproductive activity for *Enallagma signatum* was observed only after 1100 hrs. If observations were

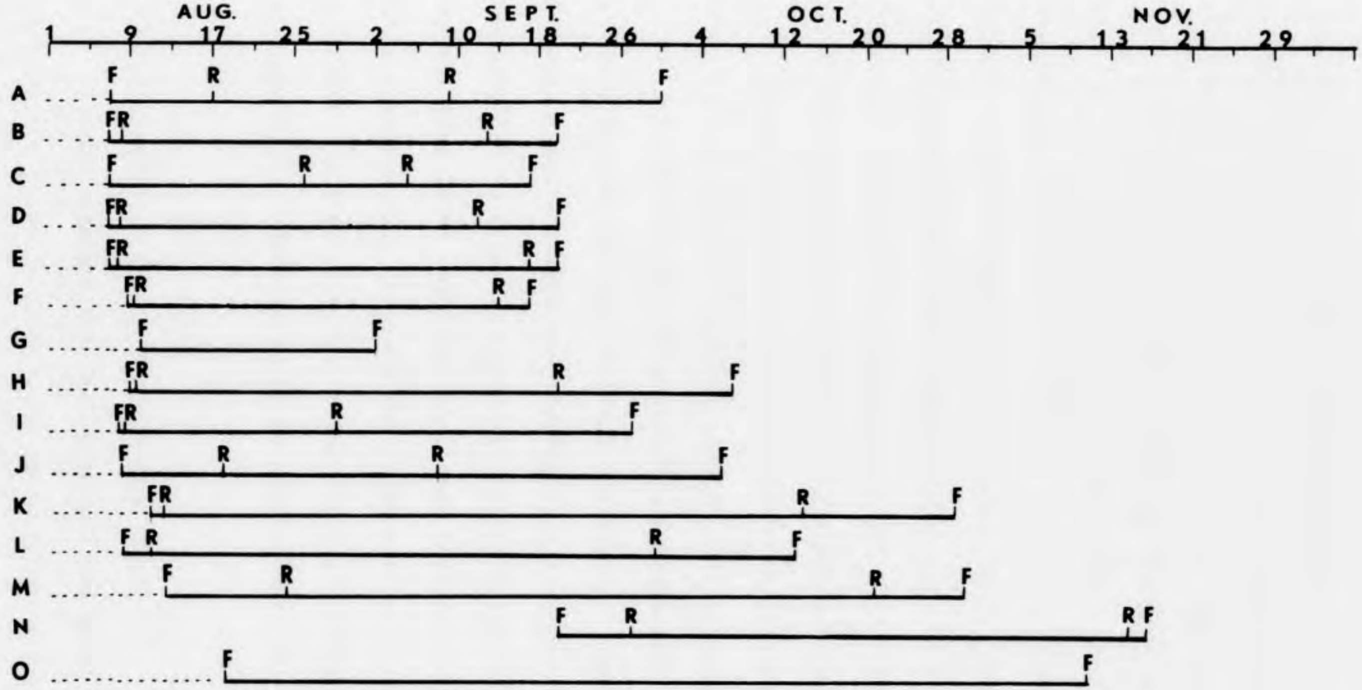

Figure 2. Flight (F) and reproductive (R) ranges of the component species in a community of adult Odonata during the study period. A = *Libellula incesta*, B = *Libellula luctuosa*, C = *Pachydiplax longipennis*, D = *Perithemis tenera*, E = *Lepthemis simplicicollis*, F = *Tramea lacerata*, G = *Plathemis lydia*, H = *Celithemis eponina*, I = *Lestes vigilax*, J = *Argia violacea*, K = *Enallagma signatum*, L = *Ischnura sp.*, M = *Enallagma civile*, N = *Sympetrum vicinum*, O = *Anax junius*.

made only during the early to mid-morning hours, reproductive activity for this species would not be observed for that particular day even though it probably occurred in the middle to late afternoon.

The species that were relatively abundant spent much of the time each day either mating or ovipositing. Those involved in reproductive activity for more than 50% of their total active period included Libellula incesta, Libellula luctuosa, Perithemis tenera, Lepthemis (=Erythemis) simplicicollis, Sympetrum vicinum, Celithemis eponina, Tramea lacerata, Enallagma civile, and Enallagma signatum. The remaining species including Argia violacea, Lestes vigilax, and Pachydiplax longipennis spent less than 50% of their active period in reproductive activity. No reproductive activity was observed for Anax junius and Playthemis lydia.

Most of the species observed had begun their period of reproductive activity by the time the earliest observations were made for this study. For most species flight and reproductive activity were first observed on the same day as shown in Figure 2. Reproductive activity was observed several days later than initial flight activity for species that were first observed much later in the study period (i.e. Sympetrum vicinum) or had fewer numbers. For all of the observed species except Sympetrum vicinum, daily flight activity terminated much later than reproductive activity.

Daily Reproductive Activity and Flight Times

The 15 observed species initiated and terminated flying and reproductive activity at or near the water at different times during the day. The base lines of Figure 3 indicate the absolute daily flight extremes as measured from the time of the earliest to last individual

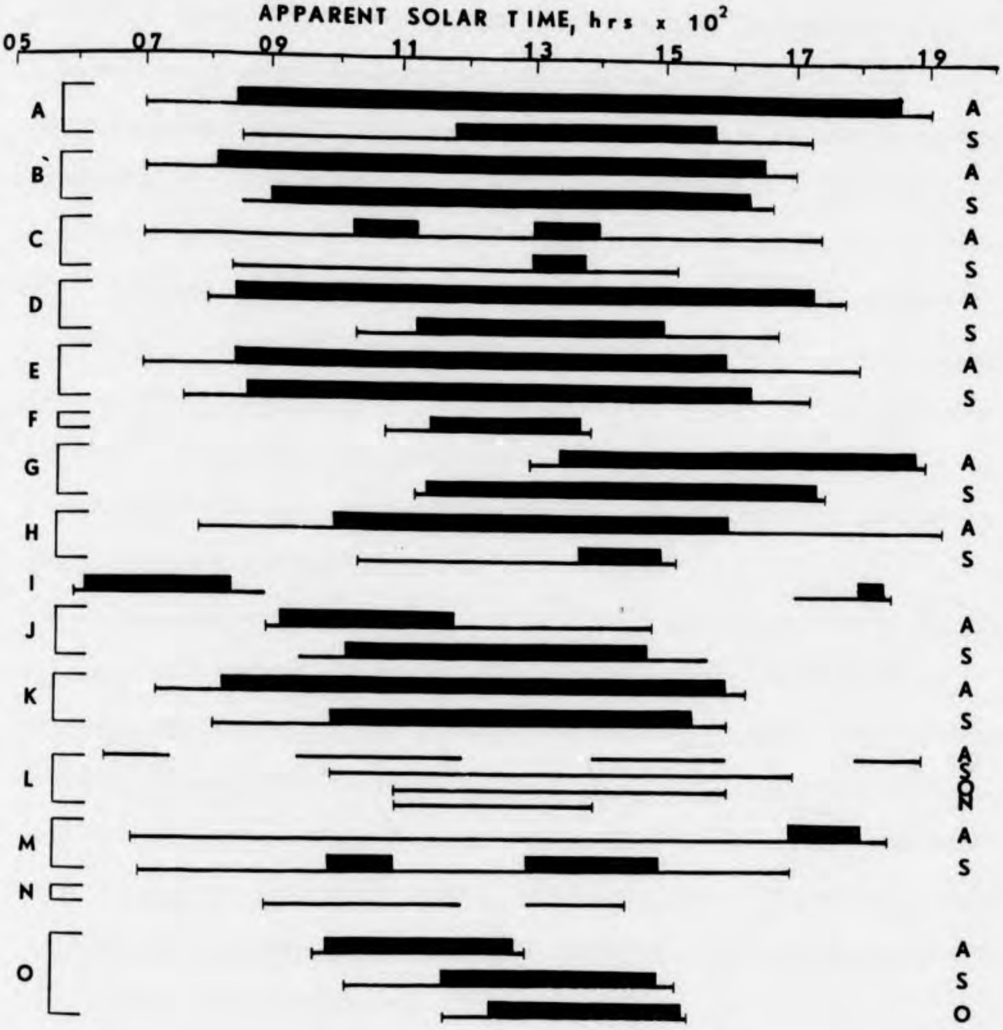

Figure 3. Temporal ranges for flight activity (lower line) and reproductive activity (upper line) for fifteen species of Odonata. A = Libellula incesta, B = Libellula luctuosa, C = Pachydiplax longipennis, D = Perithemis tenera, E = Lepthemis simplicicollis, F = Sympetrum vicinum, G = Enallagma signatum, H = Argia violacea, I = Lestes vigilax, J = Celithemis eponina, K = Tramea lacerata, L = Anax junius, M = Ischnura sp., N = Plathemis lydia, O = Enallagma civile.

observed flying. The upper bar line above the base line represents reproductive activity including both mating and ovipositing. For most species flying behavior and reproductive activity were grouped according to the August and September data, but for several species this was extended into October and November when data were available.

The species fell into three groups according to their initial daily flight time. An early-morning group was composed of Lestes vigilax, Ischnura sp., and Anax junius. Those flying initially between 0700 and 1100 hrs, the late-morning group, included all the remaining species except one. Enallagma signatum was the sole species in the afternoon group; it never appeared before 1115 hrs.

The species were grouped into four categories according to their terminal flight time. In August adults leaving before 1500 hrs were Enallagma civile, Celithemis eponina, and Plathemis lydia. Those leaving between 1500 and 1700 hrs included L. luctuosa and T. lacerata. The early-evening group (those leaving between 1700 and 1800 hrs) consisted of P. tenera, P. longipennis, and L. simplicicollis. In August L. incesta, Ischnura sp., A. junius, L. vigilax, E. signatum, Argia violacea were the late evening group flying even after sunset.

Beginning and ending flight times for each species varied between the August and September periods. Individuals of each species except one were observed flying earlier in August than September; the exception was E. signatum. Terminal flight times for all species observed in August were much later than those observed in September. The daily range of flight activity for most species in September compared to August appeared to be compressed at both early and late time extremes probably as a result of day lengths continuing to decrease throughout the study period.

Reproductive activity was closely associated with male patrolling and varied widely between species. Species in which data were adequate for reproductive activity included L. incesta, L. luctuosa, P. tenera, S. vicinum, E. signatum, A. violacea, C. eponina, and T. lacerata. Patrolling was defined as the typical flying behavior of an individual of that species (Lutz and Pittman 1970). For instance short-term flights over water within a given area were typical for most of the perchers. Species with long-term patrol flights such as C. eponina were seldom observed perching.

For nearly all observations, males appeared first at the water. Several times, however, a female of L. luctuosa was observed ovipositing eggs before any males of this species were observed. Usually females came to the pond between 0.25 - 3 hrs later than males and were immediately taken into tandem, copulated with, and allowed to oviposit; then the females left. Females of L. simplicicollis and P. longipennis were located at the pond near the water's edge but at times apparently unnoticed by males patrolling or perched.

Maximum reproductive behavior usually occurred at a time near the mid-point of the patrolling period which for many species was from mid-day to late afternoon. For example, L. incesta and luctuosa had maximum reproductive activity during the middle to late afternoon and three-quarters of the way through their patrolling period. Initial reproductive activity in September for most species was observed later in the day than during August. In September initial reproductivity activity for E. signatum was approximately 2.0 hrs earlier than observed in August.

Flying Behavior, Reproductive Activity, and Ambient Temperature

Figure 4 relates adult flying behavior and reproductive activity to ambient temperatures. At mid-day on clear days, temperatures at the pond averaged less than 1°C lower than those reported in the official local Climatological Data (1975) from the nearby airport. In this Figure the short vertical lines at the left end of a base line indicate the observed lower thermal limits for flying. Upper thermal limits for flying were not observed since flight activity was observed at the highest thermal readings recorded.

For all species for which data were available, a minimum thermal threshold for flight activity varied widely between August and September. The minimum thermal limits for flight activity in August were always higher than those in September. For instance, E. signatum initiated flight activity at a temperature of 9°C lower in September than that in August. For all species during September the minimum thermal thresholds for flight activity ranged between 1° and 9°C lower than those observed in August. Lepthemis simplicicollis, E. signatum, Ischnura sp., and A. junius initiated flying between 13° and 16°C, inclusive; all others were observed flying between 17° and 26°C. The lowest temperature on clear days during the active flight period for most species was recorded at 0740 hrs (10°C) compared to 17°C at mid-day.

Reproductive activity generally was observed at much higher temperatures than those for initial flight activity. This was particularly true for mating activity, but several times individual females were observed ovipositing near the lower limits of flight activity for that species. Females may have a higher thermal threshold for flight activity

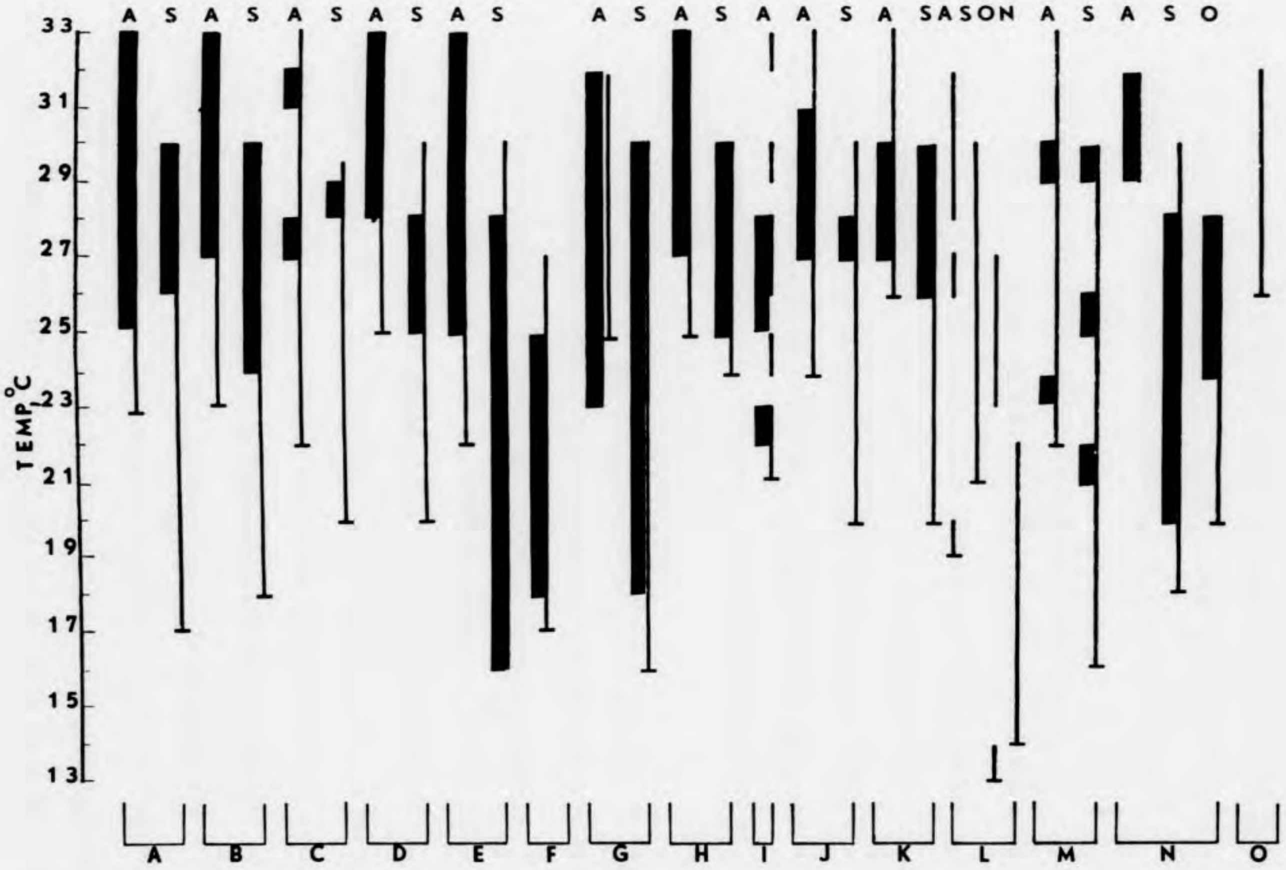

Figure 4. Thermal ranges for flight (lower line) and reproductive (upper line) activity for each species of Odonata. A = Libellula incesta, B = Libellula luctuosa, C = Pachydiplax longipennis, D = Perithemis tenera, E = Lepthemis simplicicollis, F = Sympetrum vicinum, G = Enallagma signatum, H = Argia violacea, I = Lestes vigilax, J = Tramea lacerata, K = Celithemis eponina, L = Anax junius, M = Ischnura sp., N = Enallagma civile, O = Plathemis lydia.

than males since mating and ovipositing were always observed above the minimum thermal threshold for flight activity. Also, maximum reproductive activity for most species was observed at higher temperatures. Only males were observed flying at the lower thermal limits of flight activity. Females of _L_. _simplicicollis_, however, were observed mating and ovipositing near the lower thermal threshold for flight activity.

Flight, Resproductive Activity, and Light Intensity

Figure 5 compares adult flight and reproductive activity to recorded light intensities. The left-hand margin of the Figure represents the lowest morning light intensity at which the first individual of a species flew at the water; the right-hand extremes indicate the lowest afternoon intensity at which the last individual was seen flying. The highest intensities were recorded between 1000 and 1400 hrs and appear in the middle of this illustration.

In six species (_L_. _luctuosa_, _L_. _simplicicollis_, _A_. _junius_, _Ischnura sp_., _E_. _civile_, _P_. _lydia_) flight began and ceased at essentially the same light intensity. For four other species (_P_. _longipennis_, _T_. _lacerata_, _S_. _vicinum_, _C_. _eponina_), however, flight ceased at a much higher light intensity than that when it began. The reverse relationship was shown by _L_. _incesta_, _P_. _tenera_, _E_. _signatum_, and _A_. _violacea_ which stopped flying at much lower light intensities than those at which they began. For each species flight activity as a function of light intensity varied between August and September. In September for nine species for which data were adequate, flight activity began and ceased at a higher light intensity than in August. In September, _C_. _eponina_ and _T_. _lacerata_ were first observed flying at much higher light intensities than in August, but

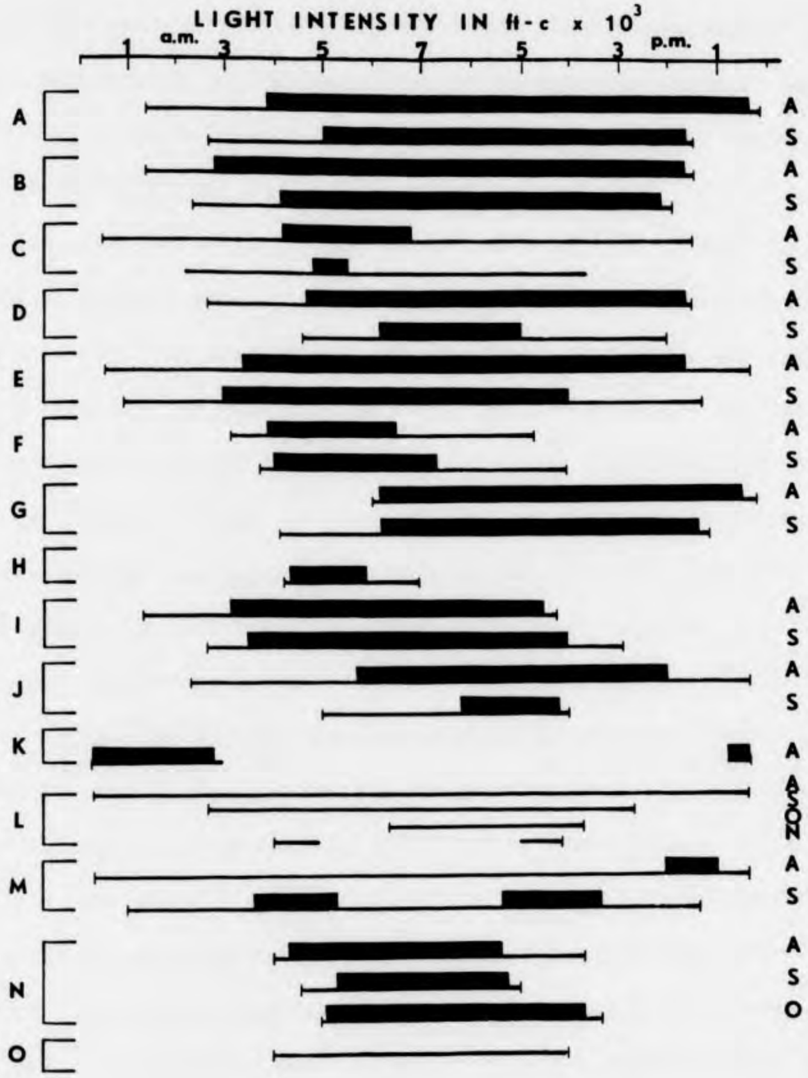

Figure 5. Flight (lower line) and reproductive (upper line) activity in a community of Odonata in relation to light intensity. A = Libellula incesta, B = Libellula luctuosa, C = Pachydiplax longipennis, D = Perithemis tenera, E = Lepthemis simplicicollis, F = Celithemis eponina, G = Enallagma signatum, H = Sympetrum vicinum, I = Tramea lacerata, J = Argia violacea, K = Lestes vigilax, L = Anax junius, M = Ischnura sp., N = Enallagma civile, O = Plathemis lydia.

ceased flight activity at considerably lower light intensities. The reverse relationship of this was shown by E. signatum which in September began flying at much lower light intensities than those in August, but ceased flying at higher light intensities.

Reproductive activity (bar above the base line in Fig. 5) in relation to light intensity began at much higher light intensities than flight activity. In most of the observed species, flight and reproductive activity ceased at essentially the same light intensity. The reversal of this was observed for C. eponina and S. vicinum, in which light intensities for initial flight and reproductive activity were approximately the same. Lestes vigilax was observed mating, ovipositing, and flying in tandem during its entire flight period which only extended into the early-morning and late-evening light intensities. This species was never observed during the higher light intensities at mid-day. Although reproductive for L. vigilax was not frequently observed, it probably was maximum during the early morning light intensities (Lutz and Pittman 1970).

For most species maximal flight and reproductive activities were observed at or near the highest light intensity during the mid- to late afternoon. Celithemis eponina was the only species in which maximum reproductive activity was observed at the highest mid-day light intensities ($6.0 - 7.0 \times 10^3$ ft-c).

Interspecific and Intraspecific Non-Mating Interactions

Table I summarizes interspecific and intraspecific interactions (except reproductive activities that led to mating) in the 10 most common species. These data represent actual numbers of interactions recorded during the entire study period. The species frequencies were based on

Table I. Intra- and Inter-Specific Interactions by the Most Active Adults. The first number in each set indicates numbers of contacts; the second represents numbers of threats. The figures in parentheses after each species listed in the vertical column are relative frequencies of individuals within the community.

Species	*Libellula incesta*	*Libellula luctuosa*	*Perithemis tenera*	*Lepthemis simplicicollis*	*Tramea lacerata*	*Celithemis eponina*	*Pachidiplax longipennis*	*Sympetrum vicinum*	*Anax junius*	*Enallagma signatum*
Libellula incesta (13.7)	61/129	26/48	0/1	6/29	2/14	1/2	16/88		0/6	
Libellula luctuosa (8.8)		80/67		0/11	0/16	3/7	1/6		0/3	
Perithemis tenera (7.9)			0/11	0/4		0/2	0/5			
Lepthemis simplicicollis (14.4)				117/137	2/4		7/39		0/1	
Tramea lacerata (3.2)					10/8		0/2		0/1	
Celithemis eponina (3.5)						26/32				
Pachidiplax longipennis (10.4)							20/142			
Sympetrum vicinum (0.5)								1/6		
Anax junius (1.2)									4/4	
Enallagma signatum (36.5)										5/31

6,797 individual observations made from 7 August to 30 September. These relative frequencies are slightly deflated for most species since 2,478 individual observations were recorded for the most abundant species, *E. signatum*. The first number in each set represents all actual contacts between males or between non-mating males and females. The second number represents interactions involving no contact and were considered threat interactions where one individual challenged another or hovered near it in a threatening manner; this method was initially used by Lutz and Pittman (1970). Most contacts and all observed threat interactions were between males.

The most abundant species, *E. signatum*, had no observed interspecific contacts or threats. Intraspecific threats (31) were 6.2 times more frequent than contacts (5). Intraspecific contacts for this species were only observed between males competing for the same female. Intraspecific interactions among the second most abundant species, *L. simplicicollis*, had almost as many contacts(117) as threats (137). Interspecific threats for *L. simplicicollis* were many times more common than interspecific contacts. One *Lepthemis simplicicollis* was observed feeding on a male *Argia violacea*, but this was not counted as an interspecific interaction. *Libellula incesta*, the third most common species, was much more aggressive than *L. simplicicollis* with the second highest number of intraspecific (61 contacts, 129 threats) interactions. Individuals of *L. incesta* physically dominated the entire community even though *L. simplicicollis* appeared to be more numerous at Stations 3 and 4. *Pachydiplax longipennis*, the fourth most abundant species with its familiar threat display, had 7.1 times more intraspecific threats (142) than contacts (20). There were almost as many contacts (16) between L. incesta and P. longipennis as intraspecific contacts (20) for the latter. Interestingly enough, there were more intraspecific contacts than threats for individuals of L. luctuosa (80 contacts, 67 threats) and T. lacerata (10 contacts, 8 threats). On one occasion two males of A. junius were patrolling in the same area (in cove, Station 4) which resulted in four intraspecific contacts and threats. Sympetrum vicinum, the late September species, had six times more intraspecific threats (6) than contacts (1), but no interspecific interactions were observed.

For any given species considerably more intraspecific interactions were observed compared to interspecific ones. There were also many more threats than contacts for most species. The greatest number of intraspecific interactions was observed for the most abundant species. Numerous interspecific interactions (both contact and threat) occurred between the following pairs of species: L. incesta and L. luctuosa, P. longipennis and L. incesta, L. simplicicollis and P. longipennis, L. incesta and L. simplicicollis

Observations For a Single Day

Figures 6-14 represent numbers of individuals for nine species observed on three different days between 8 August and September 30. The same day in August was chosen for all the species except S. vicinum and E. signatum in which data were optimum for two different days in September. Thus, each species was observed during its entire active period for a single day. These days were selected so that the whole range of flight, perching, and reproductive activity for each species could be observed under optimal conditions. Environmental conditions for the August

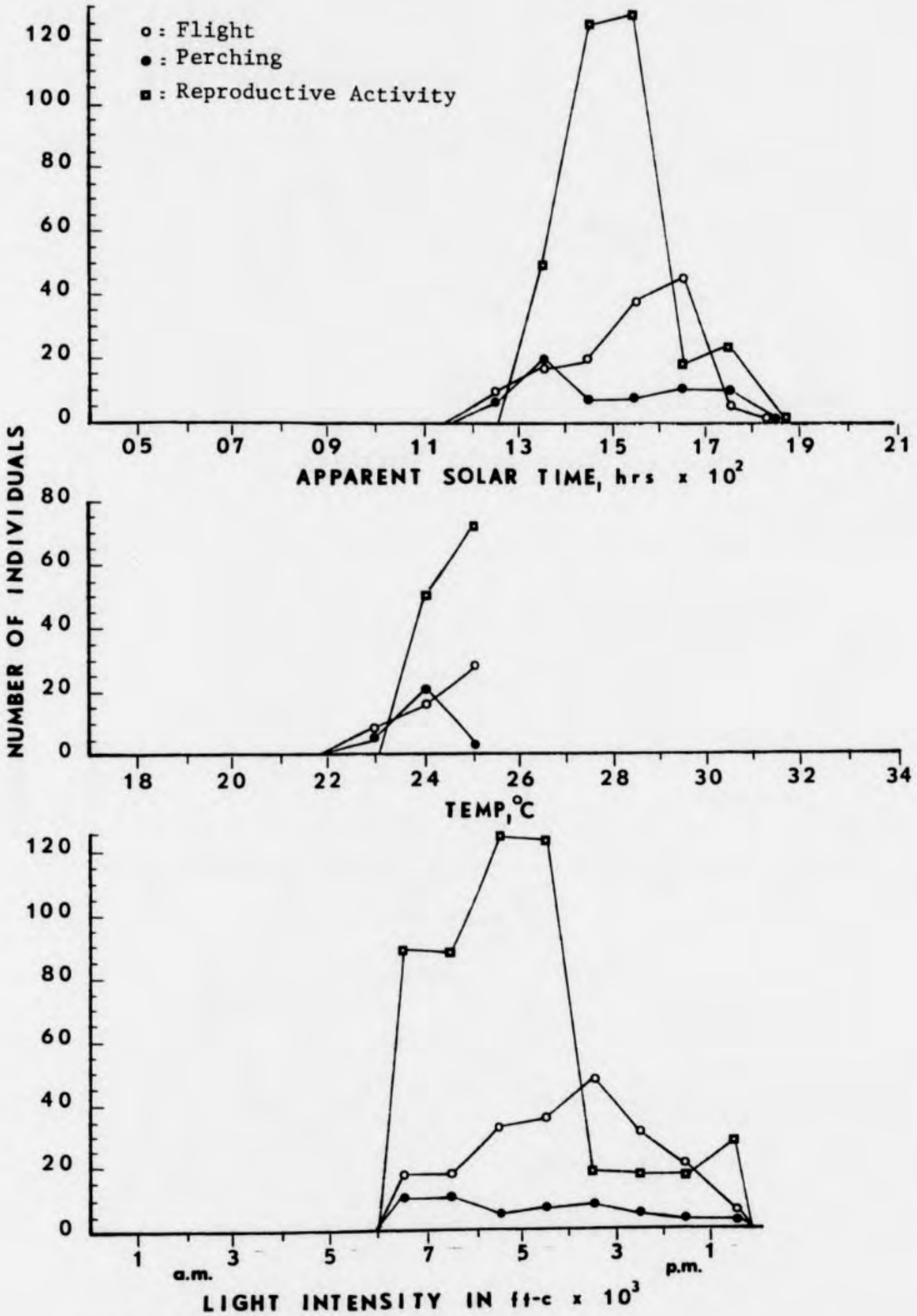

Figure 6. <u>Enallagma signatum</u>

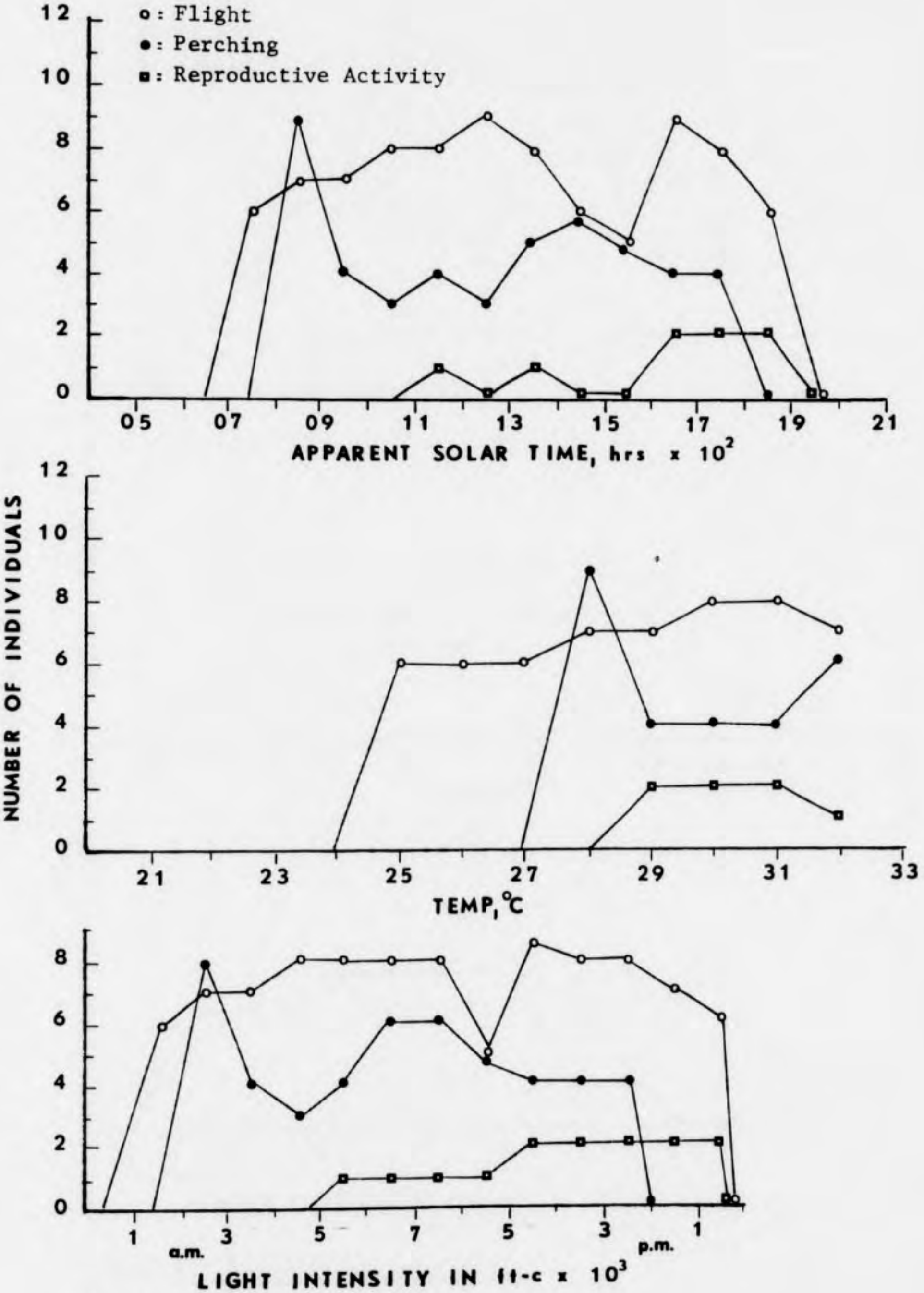

Figure 7. <u>Libellula</u> <u>incesta</u>

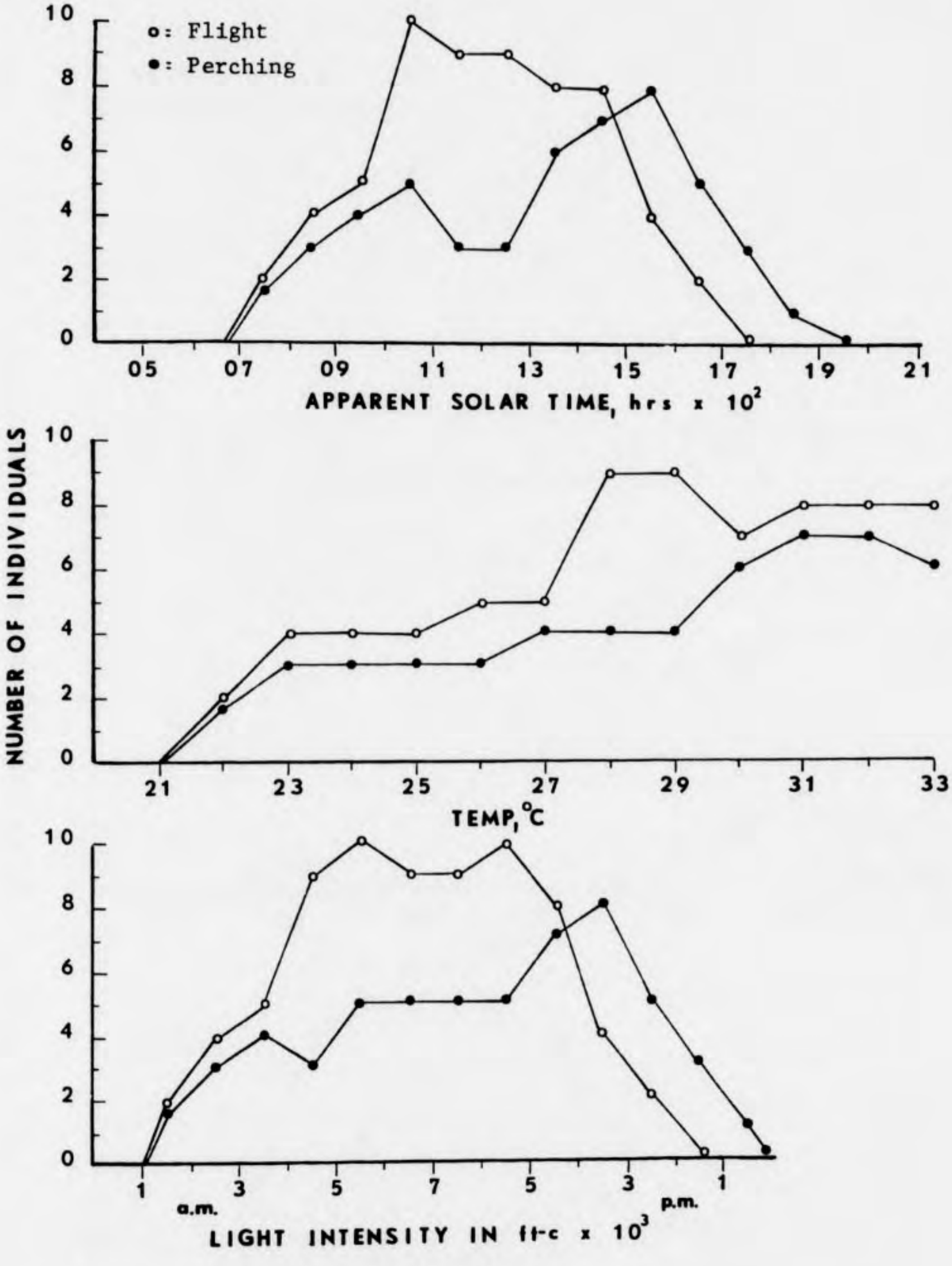

Figure 8. Pachydiplax longipennis

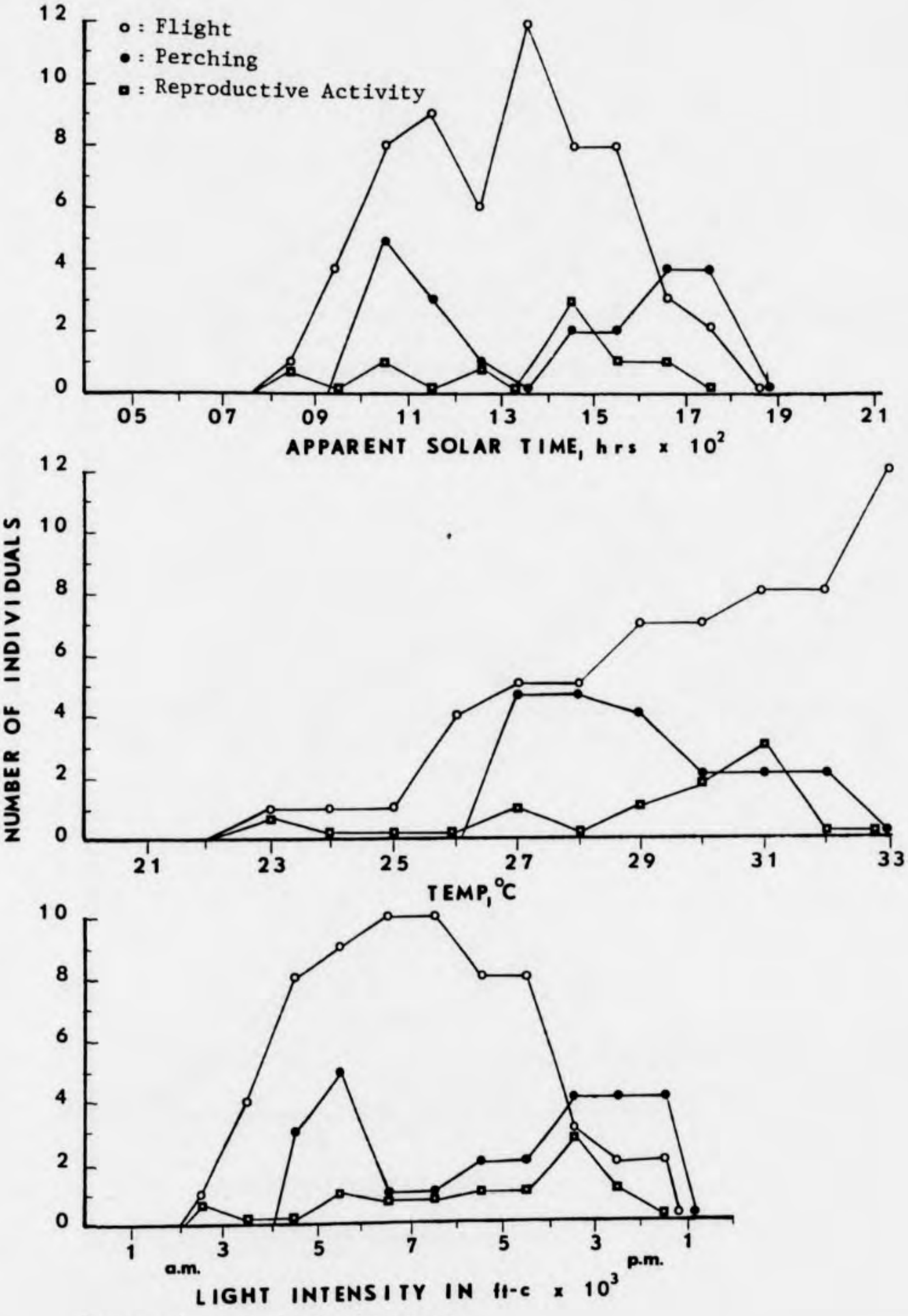

Figure 9. Libellula luctuosa

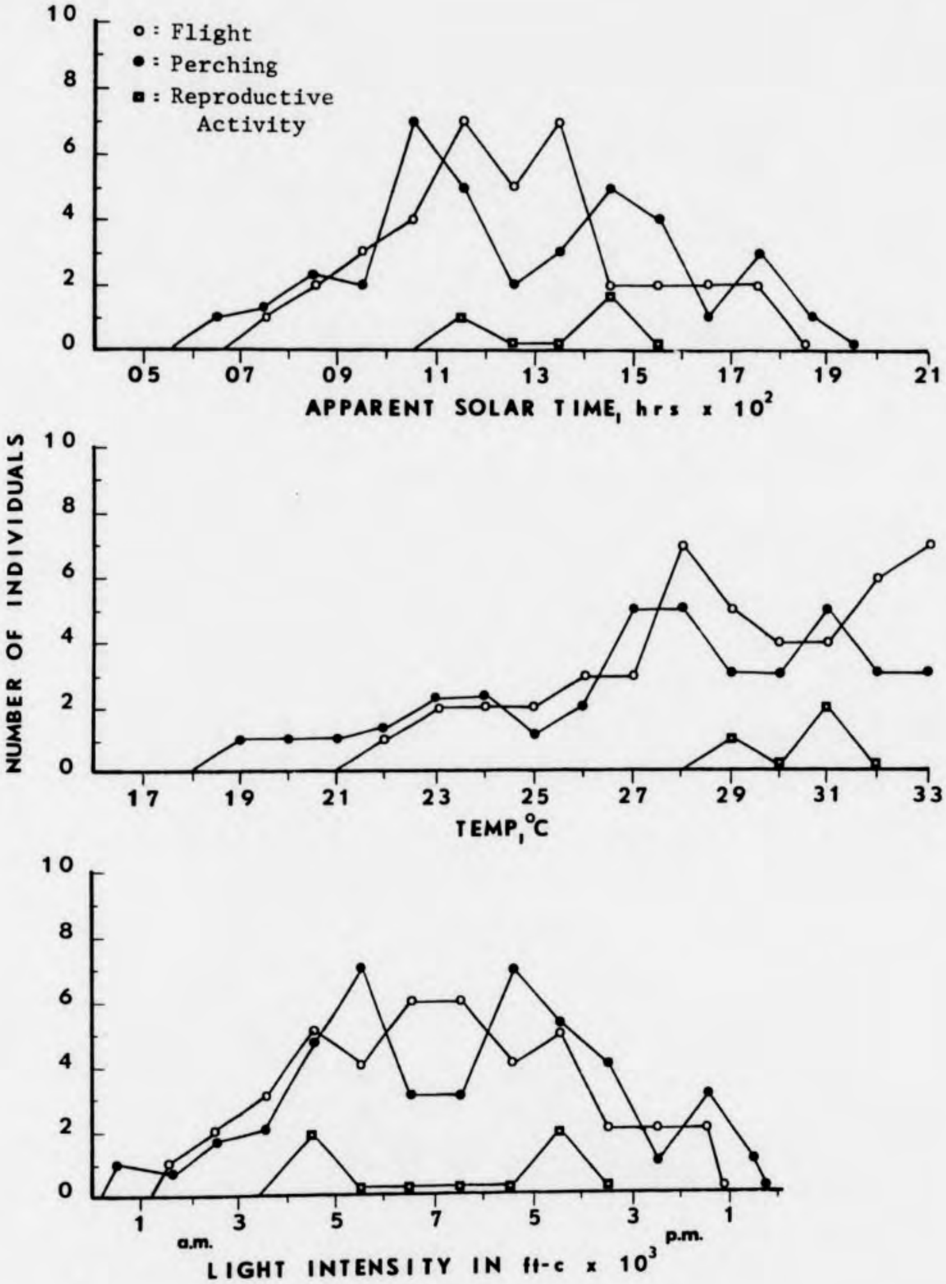

Figure 10. <u>Lepthemis simplicicollis</u>

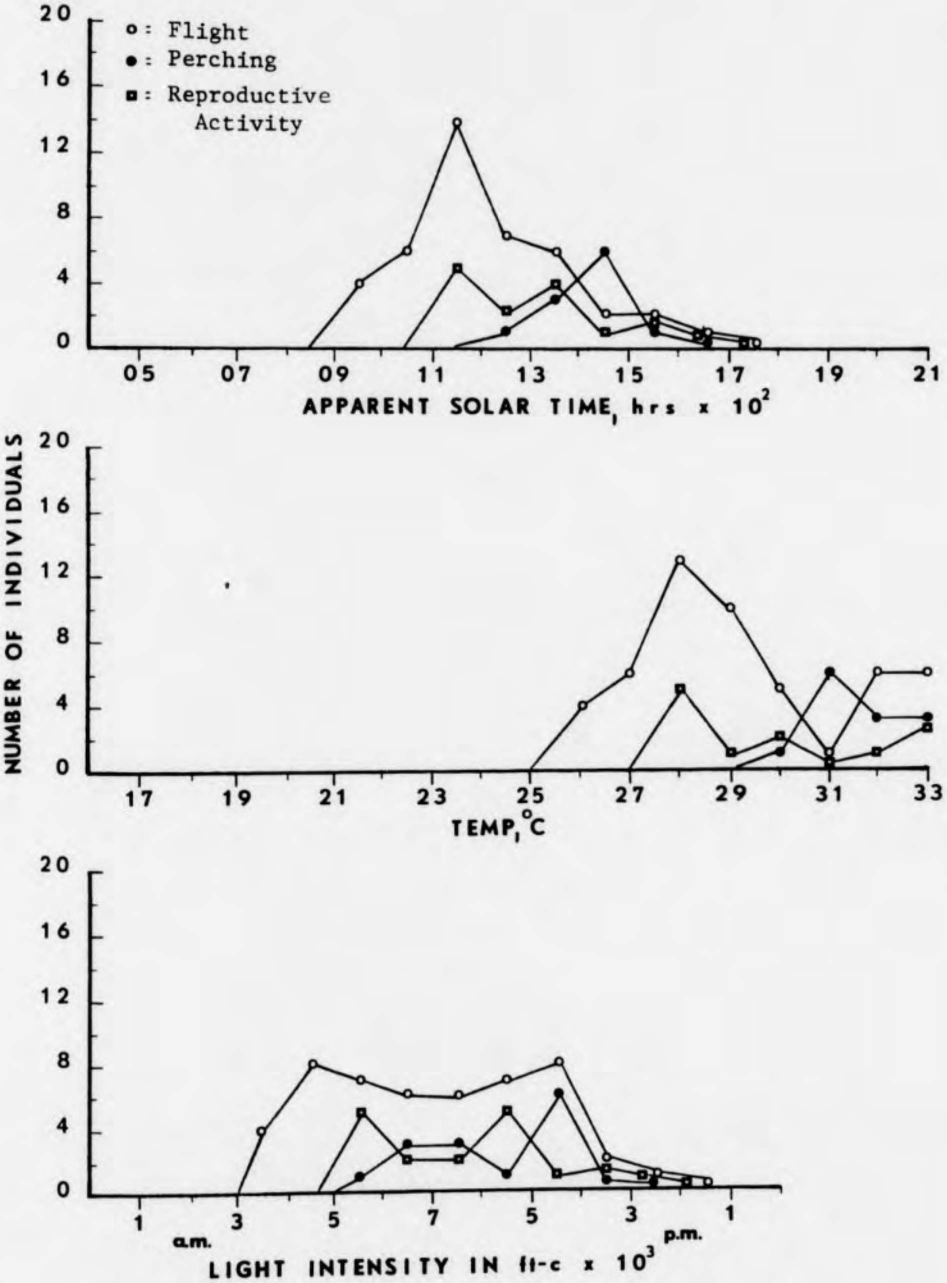

Figure 11. Perithemis tenera

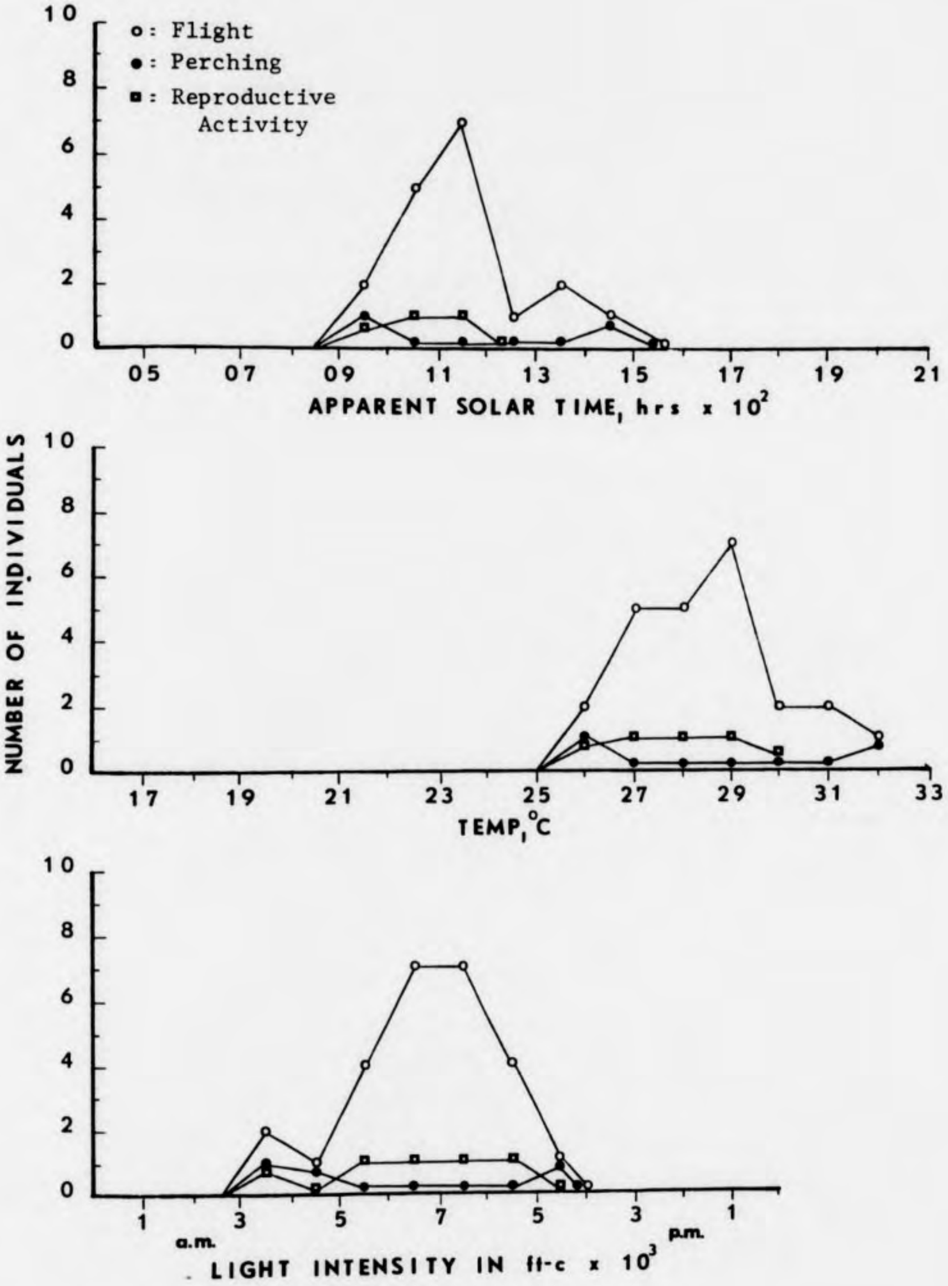

Figure 12. Celithemis eponina

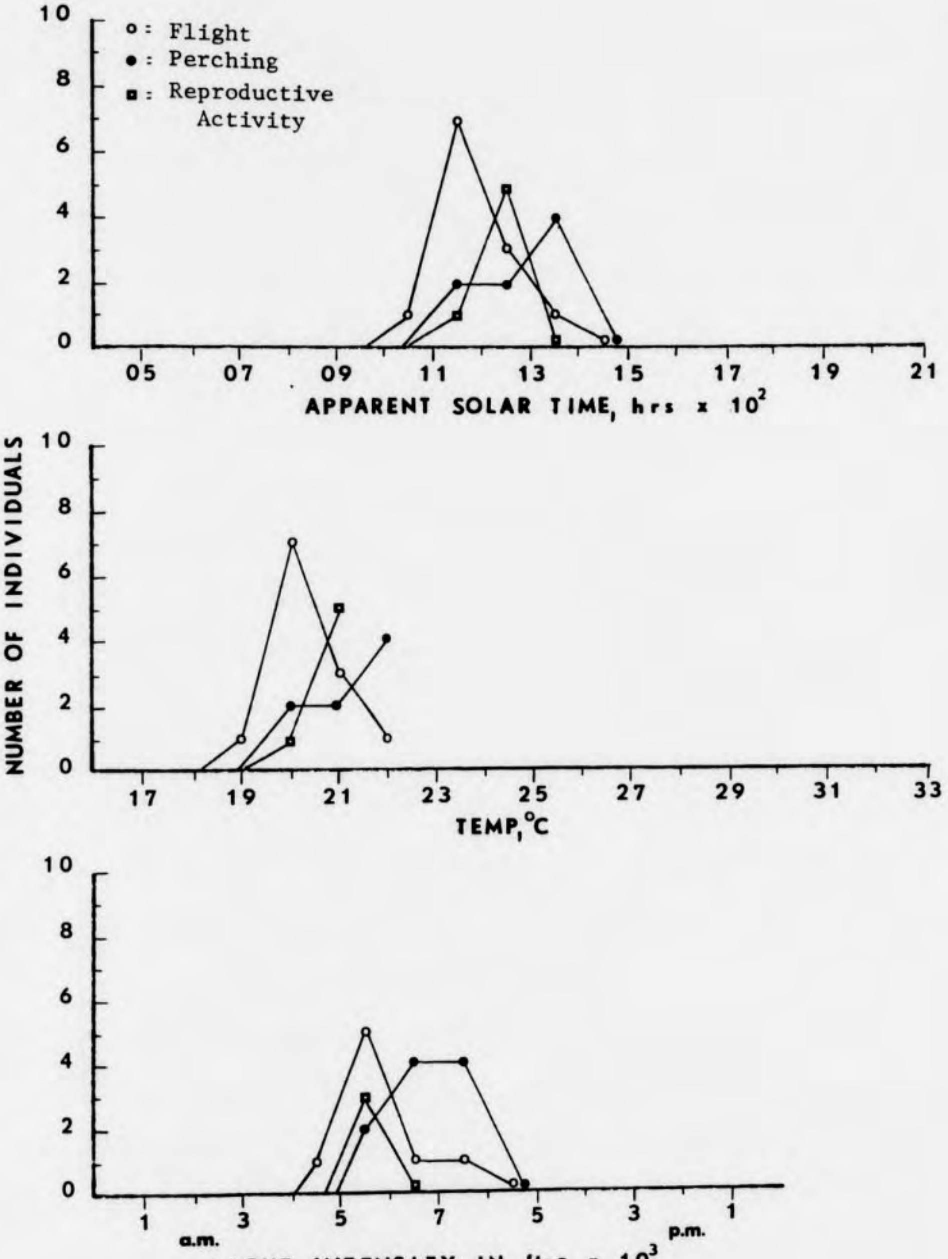

Figure 13. *Sympetrum vicinum*

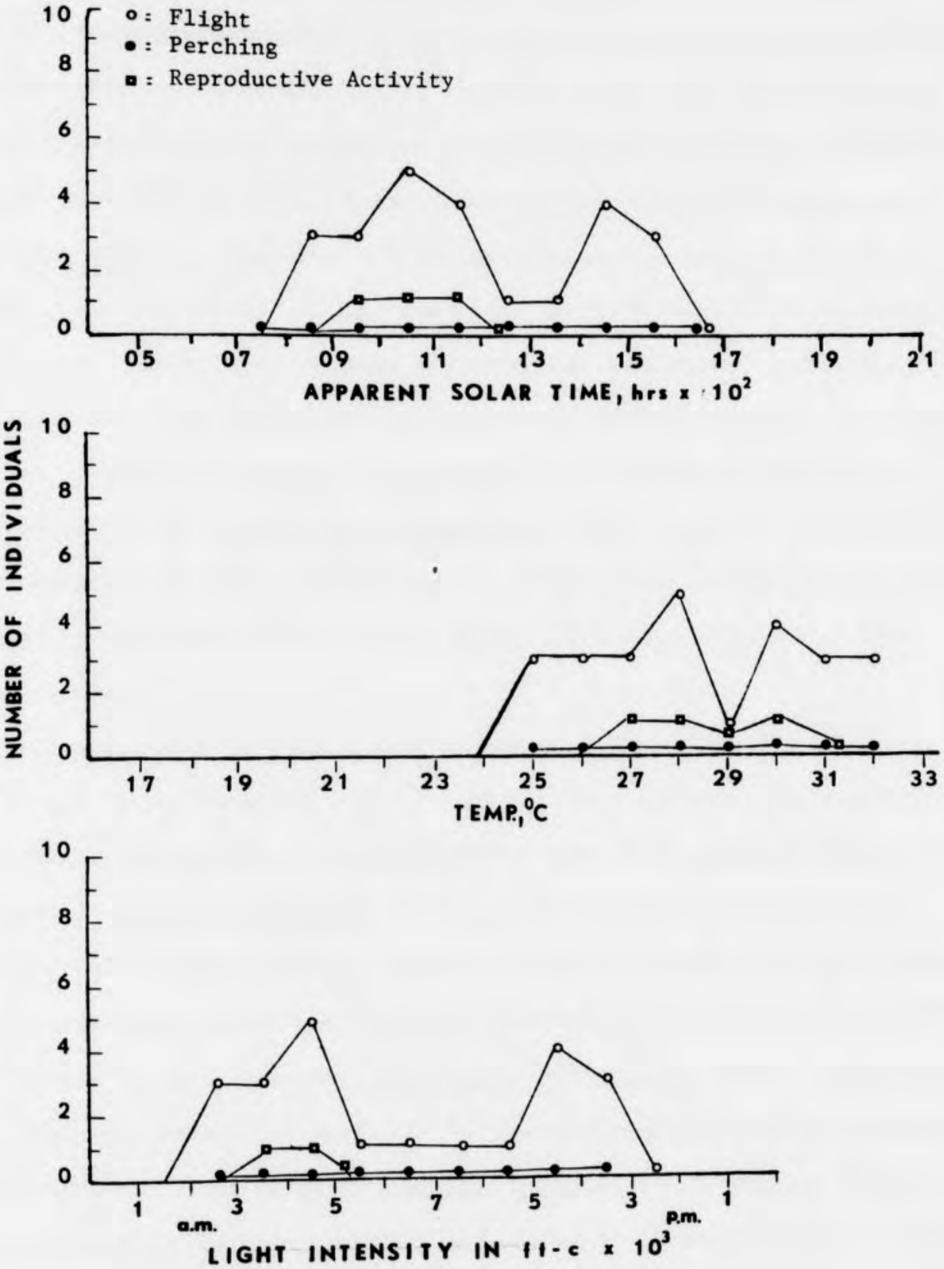

Figure 14. Tramea lacerata

observations consisted of the full range of light intensities (sunrise to sunset), temperatures from 19° to 33°C, and 15% cloud cover for most of the day. The two different days in September (i.e., one day's observation for each species for *S. vicinum* and *E. signatum*) were clear with moderate temperatures (19° to 25°C) and reflected the full range of activity for these two species. Composite information for several days of behavioral activity was considered but later abandoned since numbers of individuals at the pond changed with variable environmental conditions. Also, population numbers in the latter part of August were decreasing rapidly for most species. There was, however, in September, an increase in numbers of individuals for *S. vicinum* and *E. signatum*. These numbers of individuals and behavioral activity for each species at different temperatures, light intensity, and time of day were also typical for other days during the study period.

Synchronized behavioral activity among individuals of a species was virtually not observed. Peak flight activity for most species was observed at mid-day with the corresponding high temperature and light intensity. *Enallagma signatum*, however, did not reach maximum flight activity until late afternoon. Maximum perching activity for most species was observed when flight activity was beginning to increase in the morning or decrease in the afternoon. *Lepthemis simplicicollis* and *P. longipennis* were typical perchers and gradually increased this activity as the thermal level reached a limit of 33°C. *Libellula luctuosa* and *P. tenera*, moderate fliers, decreased perching activity and increased flying behavior at the maximum thermal threshold for that day. Maximum perching activity for *S. vicinum* and *E. signatum* was only observed at the highest recorded temperature and light intensity. Celithemis eponina and T. lacerata spent nearly all of their time at water flying so that perching was seldom observed.

Reproductive activity (between late-morning and afternoon) was optimal for all observed species. Tramea lacerata and C. eponina were observed mating and ovipositing between late-morning and mid-day. Perithemis tenera and S. vicinum reached maximum reproductive activity at mid-day. Only one female of L. luctuosa was observed ovipositing during the mid-morning hours. For the remainder of these species, peak reproductive activity was observed during mid- to late afternoon. No reproductive activity was observed for P. longipennis during this particular day of observation.

Reproductive activity for each species was observed at the highest recorded temperatures for those days in August and September. A female of L. luctuosa, however, was observed ovipositing at a temperature of 23°C.

Maximal reproductive behavior, occurred at the middle to high light intensities during the warmest part of the day. Celithemis eponina, for example, exhibited maximum reproductive and flight activity at the highest range of light intensities recorded during that day. For the other observed odonate species there was a slight reduction in reproductive activity at the highest mid-day light intensities. In Figure 11, Perithemis tenera showed a major reduction in reproductive behavior accompanied by both a slight decrease in flight activity and increase in perching at the highest recorded range of light intensities. This pattern of reproductive behavior, perching, and flight activity was typical for other days during the study which exhibited these same climatic conditions.

Numbers of individuals for these particular days in August and September represent the highest numbers recorded during the study period. For any given hour during the active period for this day in August, *P. tenera* was the most abundant species (19). The second most abundant species was *L. incesta* with 16 observed individuals between 0800 and 0900 hrs. *Tramea lacerata* was the least abundant of these particular species with a maximum of six individuals observed between 1000 and 1100 hrs.

For a single day in September, *E. signatum* had more individuals than the rest of the species during any time in the study period. Reproductive behavior for *E. signatum* was dominant over all other activities with 64 mating or ovipositing pairs between 1600 and 1700 hrs. Numbers of individuals observed flying and perched for that hour were 38 and 7, respectively.

Ecological Factors Influencing Adult Behavior For Two Representatives Within the Odonata Community

In Figures 15-20 two of the most common odonate species are represented and grouped into August, September, and total study period data. This comprehensive record of adult behavior was based on the relative observed frequency of individuals within the Odonata community during flight, perching, or reproductive activity for any given hour during the day. The zygopteran, *Enallagma signatum*, and the anisopteran, *Libellula incesta*, were selected as representatives from the odonate community for their large numbers, habitat preferences, and differing behavioral and adaptive responses to variable environmental factors.

LIBELLULA INCESTA

Flight, perching, and reproductive activity for L. incesta were observed under variable light intensities, temperatures, and times of day between 8 August 1975 and 30 September 1975. Sexual dimorphic coloration was not pronounced in this species with females being distinguished by a much duller grayish-brown thorax and abdomen. Clear-winged males were typically much darker (i.e., navy-blue) than females and were always seen flying much earlier in the day. Flight activity commenced each day from roosting sites behind Stations 3 and 4. Perch sites at Stations 2 and 4 were occupied first by males; these stations were much nearer the roosting area than Station 1. Perching at Station 3 was avoided by all individuals until this area was directly illuminated with solar radiation. Perching time decreased with increasing population density until flight activity appeared to be continuous during mid-day. Thus, the time at water, with the exception of mating, inter- and intraspecific interactions, or short patrol flights, was spent perching on tall grasses, small bushes, or overhanging tree limbs.

Flight Activity. In Figure 15 flight activity for L. incesta varied during different times of the day. Earliest recorded flights toward the water followed by patrolling was observed at 0700 hrs and ended at 1900 hrs (see Fig. 3). Between 62 and 80% of the observed population flew intermittently from 0700 hrs until 1800 hrs with maximum flight activity occurring between 1200 and 1300 hrs. Ninety-two percent of the observed population between the hours of 1800 and 1900 was observed flying until all activity ceased at 1900 hrs.

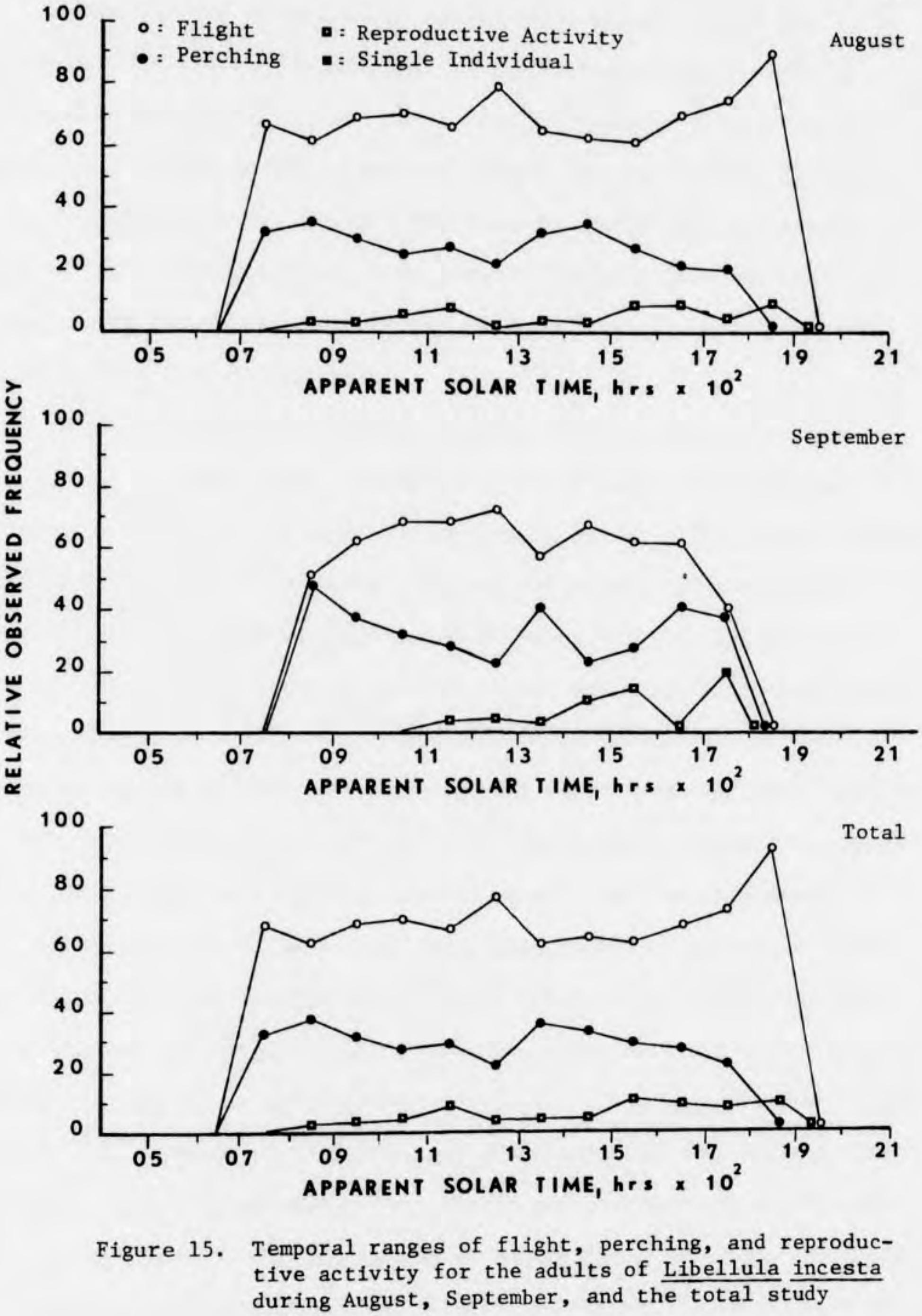

Figure 15. Temporal ranges of flight, perching, and reproductive activity for the adults of Libellula incesta during August, September, and the total study period.

Beginning and ending flight times varied between August and September. The earliest flight time during September was observed at 0830 hrs, approximately 1.5 hrs later than the earliest flight time in August. All flight activity, however, ceased 1.75 hrs earlier (1715 hrs) during September than in August. There was no significant difference in maximum flight activity (i.e., 1200-1300 hrs) between 0800 and 1900 hrs during either August or September except for a slightly lower percentage flying at this time in September.

Flight activity in Libellula incesta, shown in Figure 16, varied with changes in temperature. Flight activity in only a few observed individuals was initiated at a minimum temperature at 17°C. Flight activity at 17°C was generally short, sluggish, irregular, and atypical of normal flight at higher temperatures which was usually strong with less frequent intervals involved in perching. The threshold for normal flight activity was at 20°C with the highest percentage (i.e., 76%) of the population flying at 25°C. No less than 50% of the observed population was observed flying between 20° and 33°C. The maximum temperature threshold at which flight activity was prohibited could not be determined, but Lutz and Pittman (1970) have shown that activity for L. incesta increased with temperatures up to 39°C when a marked decrease in activity occurred.

Minimal and optimal temperatures for flight activity varied significantly between August and September (Fig. 16). In August, initial flight activity was observed at 23°C which was 6°C higher than that recorded in September. Only one individual was seen flying in September at 17°C and two at 18°C. Maximal flight activity in August was observed at 25°C, and there were no less than 57% of the observed population flying between 23

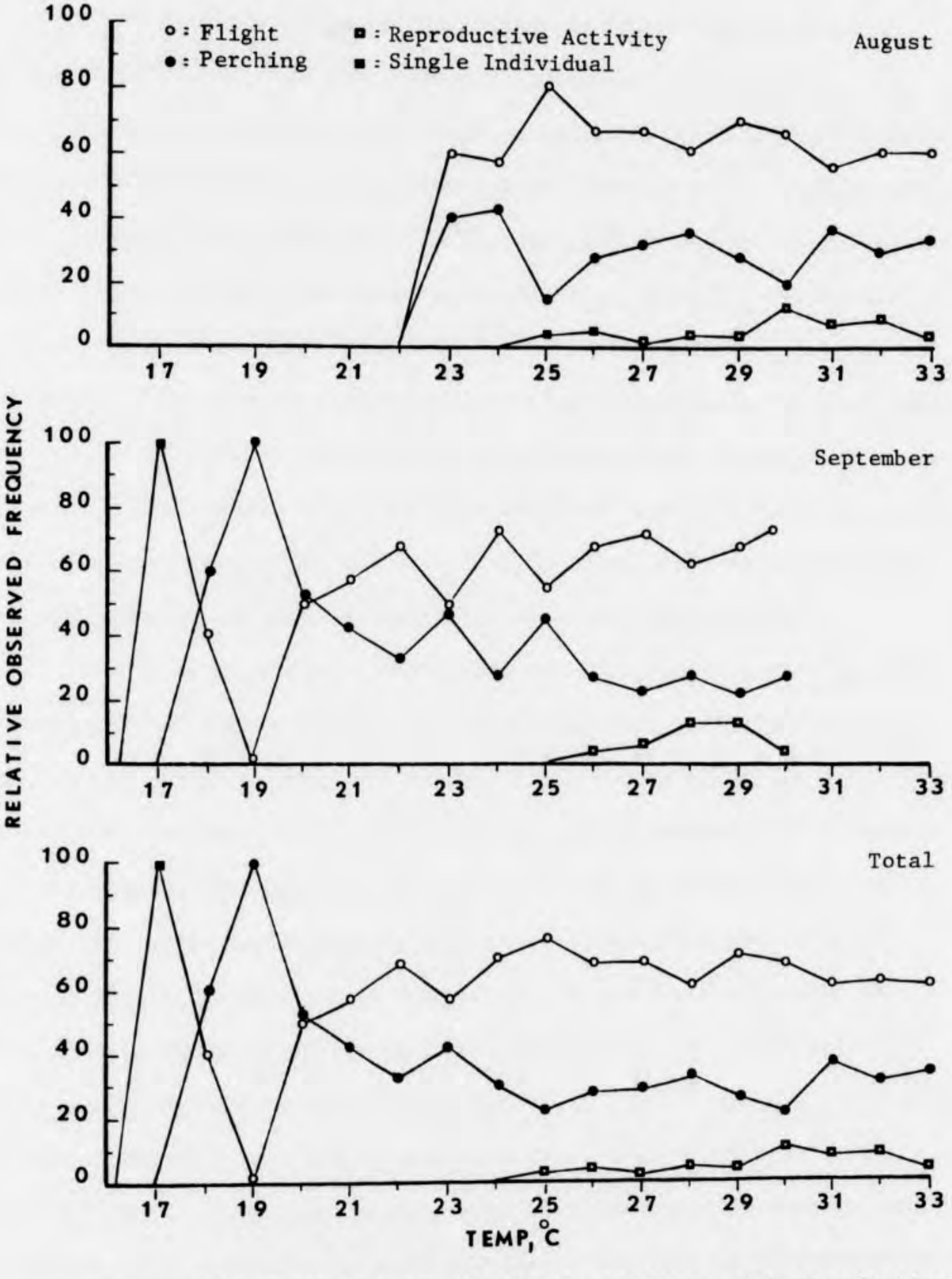

Figure 16. Thermal range of flight, perching, and reproductive activity for the adults of Libellula incesta during August, September, and the total study period.

and 33°C. In September, the optimal flight activity commenced and terminated 3°C lower than that recorded in August.

There were two clear, cold days in September in which temperatures between 9° and 17°C were recorded during the normal active flight period for L. incesta. No flight activity was observed during this below-normal thermal range even on these clear and cold days. Flight activity was delayed 4 to 6 hours later than normal until temperatures reached a minimum of 17°C. Normal numbers of individuals were never observed after this brief cold weather even though temperatures later returned to normal. Even with a few numbers observed after this cold weather, flight activity continued sporadically for at least 15 consecutive days later when temperatures were above this unusually low recorded temperature.

Flight activity varied during the day between early morning, mid-day, and late afternoon light intensities (Fig. 17). Flight activity began in the early morning at a minimal light intensity of 1.4×10^3 ft-c and ended as low as 0.12×10^3 ft-c in the late afternoon. It is important to note that L. incesta was observed flying at much higher light intensities in the early morning than those intensities when flight ceased in the late afternoon. Most of the population flew during the early morning and late afternoon light intensities. For example, 100% of the early morning population flew between 1.0×10^3 and 2.0×10^3 ft-c and 94% of the late afternoon population flew between 1.0×10^3 and 0.12×10^3 ft-c. Libellula incesta generally increased in numbers with increasing light intensities until mid-day. There was no evidence of a synchronized attendance at the pond for any time of day, light intensity, or temperature. Flights toward perch sites located away from the water

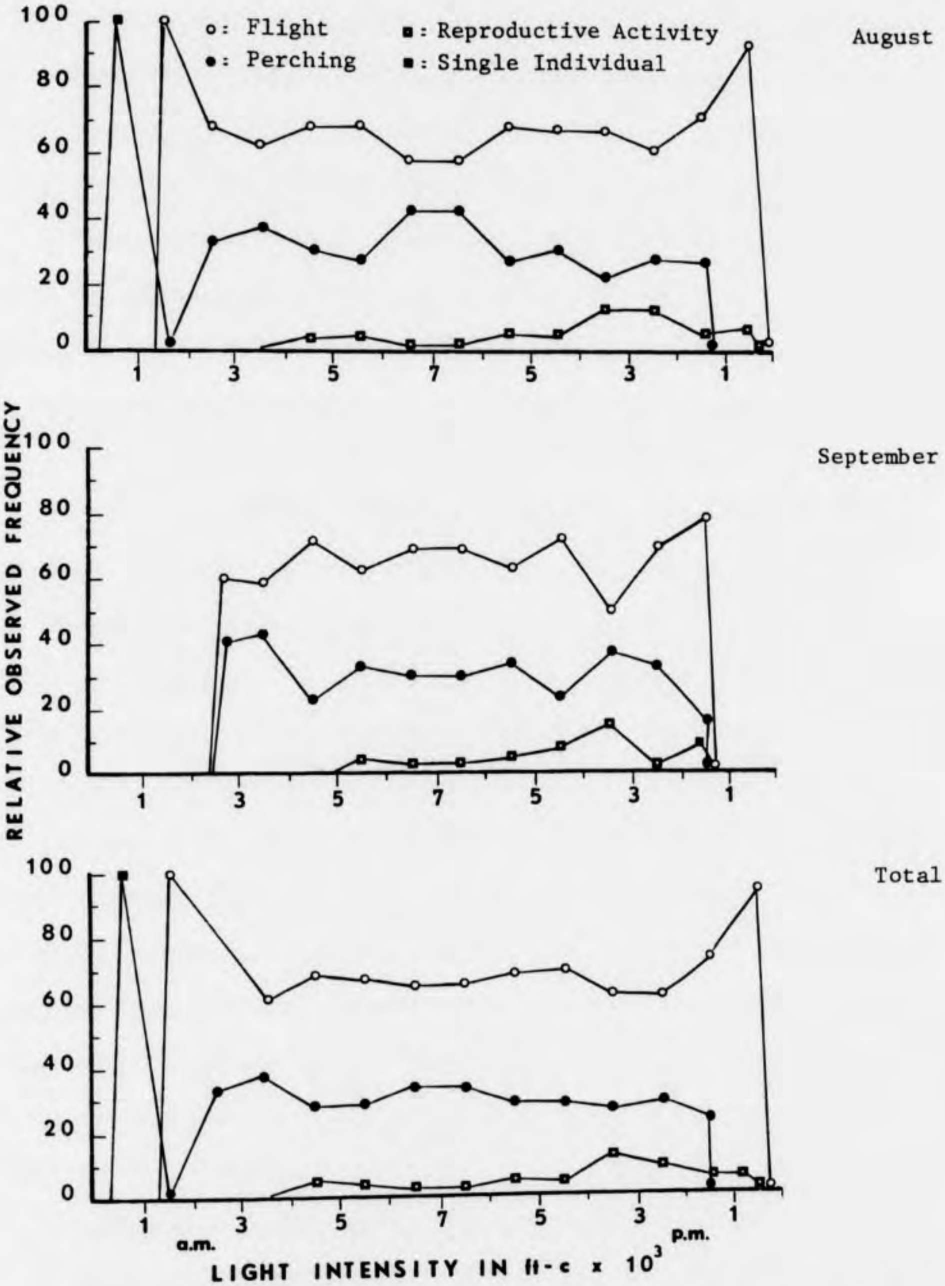

Figure 17. Flight, perching, and reproductive activity for adults of Libellula incesta in relation to light intensity.

in the late afternoon were believed to contribute to the high percentage of the population flying at that time. Flights toward the water and fewer numbers in the early morning hours were also responsible for the high percentage of the observed population flying at that time.

There was a considerable difference in flight activity in relation to light intensity between August and September. The earliest recorded flight in August showed a much earlier arrival at the pond at a lower light intensity than in September. The earliest flight activity in August was observed at a minimal light intensity of 1.4×10^3 ft-c compared with 2.6×10^3 ft-c in September. In August (i.e., composite data for different days in August) the earliest morning light intensity at which flight began was 12 times greater than the lowest light intensity at which flight ceased in the late afternoon. In September, flight commenced at an early morning light intensity approximately twice as high as the lowest light intensity at which flight ceased in the late afternoon.

Perching. In between short-term flights *L. incesta* spent most of its time perching. Based on the total observed population at any one time, this appeared to vary inversely with flight activity. *Libellula incesta* was observed perching as early as 0725 hrs approximately 25 minutes later than the first patrol flight, and ended as late as 1801 hrs which was 59 min earlier than the last observed flight. In September, perching and flight activity began and ended during the same hours with equal percentages of the total observed population. Initial perching activity in September was observed approximately one hour later than that in August, but ended 38 min earlier at 1722 hrs. Increased perching in September is believed to be the result of fewer individuals and less inter- and intraspecific interactions. Thus, less competition for perch and oviposition sites reduced flight activity and increased normal perching time.

Perching in relationship to the thermal range of activity during the total study period generally showed the same inverse relationship with flight activity. Perching was more frequent at the lower temperatures, but fluctuated greatly between 20° and 33°C. Only a few individuals were observed at the lowest recorded temperature of 18°C at which perching was observed. This might account for the high percentage of the population that was observed perching at this temperature. Normal perching and flight activity probably did not occur until 20°C which represents the minimal temperature at which normal numbers were observed. Only six individuals during the total study period were observed perching below this temperature.

Temperature at which perching was observed varied between August and September. In August, perching commenced at a temperature 5°C higher (i.e., 23°C) than in September. Perching in September for _L_. _incesta_ generally decreased as temperatures increased, but this was difficult to determine for August. In August, perching fluctuated widely within the 23° to 33°C range, but warmer temperatures and greater population density may have contributed to the appearance of more flight activity and less perching than was expected.

September observations showed a greater percentage of the population perching at lower temperatures than those in August. A maximum of 42% of the August population at 24°C was observed perching in comparison with 100% of the September population that was perched at 18°C. A minimum of 22% of the September population was perched at 28°C, but minimal perching values in August were difficult to determine.

Perching in relation to light intensity varied during the total study period (Fig. 17). Perching was first observed in the early morning at 0.50×10^3 ft-c and ended at a minimum of 1.4×10^3 ft-c in the late afternoon. Since only one individual was observed in the early morning at 0.5×10^3 ft-c, it is believed that an intensity between 1.0×10^3 and 3×10^3 ft-c represents the minimal earliest light intensity at which perching occurs. A maximum of 36% of the population was perched at the early morning light intensities and decreased slightly to between 24 and 34% of the population during the remaining active part of the day. Perching increased slightly at the highest mid-day light intensity, but was less than the early morning perching activity.

Comparison of perching activity between August and September showed slight differences in early morning, mid-day, and late afternoon light intensities. Perching activity in August began earlier in the morning than in September, but ended in the late afternoon at approximately the same light intensity as observed in September for the same time. The incidence of perching at mid-day in August during maximal light intensities and temperatures was greater than in September for same time period. There was observed a greater increase in early morning and late afternoon perching activity in September at lower temperatures and population density than those in August.

Reproductive Activity. Earliest and latest observed reproductive activity varied widely between August and September. In August, the earliest mating followed by immediate ovipositing, was observed at

0855 hrs. The latest mating was observed at 1605 hrs, approximately 2.5 hrs earlier than the last observed ovipositing. Earliest reproductive activity in September was observed three hours later at 1155 hrs and ended with the last ovipositing at 1550 hrs. No mating was observed later than 1441 hrs.

In relation to perching and flight activity, reproductive behavior was never greater than 20% of the observed population for any given time of day, light intensity, or temperature. Maximal reproductive activity generally occurred in the middle to late afternoon between 1500 and 1900 hrs at an optimal temperature of 30°C. In September, only one L. incesta was observed ovipositing between 1700 and 1800 hrs, but the population had fewer absolute numbers resulting in the percentage of the reproductive activity becoming slightly inflated.

The thermal range for reproductive activity began at a much higher temperature than that observed for perching or flight activity. Reproductive activity generally increased with rising temperatures up to 30°C. Females were not observed below 25°C, but male patrol flight began at much lower temperatures. In September, no females were seen below 26°C. In August, there were only a few days during the study period that temperatures above 30°C were recorded so that optimal reproductive activity appeared to be at lower temperatures than normally expected.

Reproductive activity during August and September showed increases in mating and ovipositing during the late afternoon. Only a few individuals in August were observed mating and ovipositing in the early morning at a minimal light intensity of 3.8×10^3 ft-c. In September, the earliest reproductive activity occurred at mid-day at a minimal light intensity of 5 X 10^3 ft-c and continued until late afternoon to a minimum of 1.4 X 10^3 ft-c. Reproductive activity in August appeared to be completely inhibited at the highest light intensities between 6 X 10^3 and 7 X 10^3 ft-c, but reached a maximum between 4 X 10^3 and 2 X 10^3 ft-c in the late afternoon. Thus, reproductive activity in August began earlier in the day at a lower light intensity than was observed in September for the same time.

ENALLAGMA SIGNATUM

The reproductive activity of the zygopteran *E. signatum* was significantly more frequent than perching or flight activity. Mating was only observed while *E. signatum* was perching in contrast to ovipositing which was interpreted as a combination of perching and flight activity. Thus, reproductive activity in this study was defined as any mating or ovipositing pair engaged in either perching of flight activity. Perching and flight activity in Figure 18 refer to only single males or females within the study area. Observations were based on August and September data even though animals were present during October 1975.

Flight Activity. *E. signatum* flew at different times of the day between August and September. The earliest flight time during August was observed at 1300 hrs, approximately 1.8 hrs later than the earliest flight time in September. In August, flight activity ceased 1.43 hrs (at 1858 hrs) later than September. Optimal flight activity in August may have begun an hour later than observed at 1300 hrs since only two individuals were observed at that time. There was no significant difference in maximal flight activity between the hours of 1400 and 1800 for August or September. Flight activity during both these months gradually increased

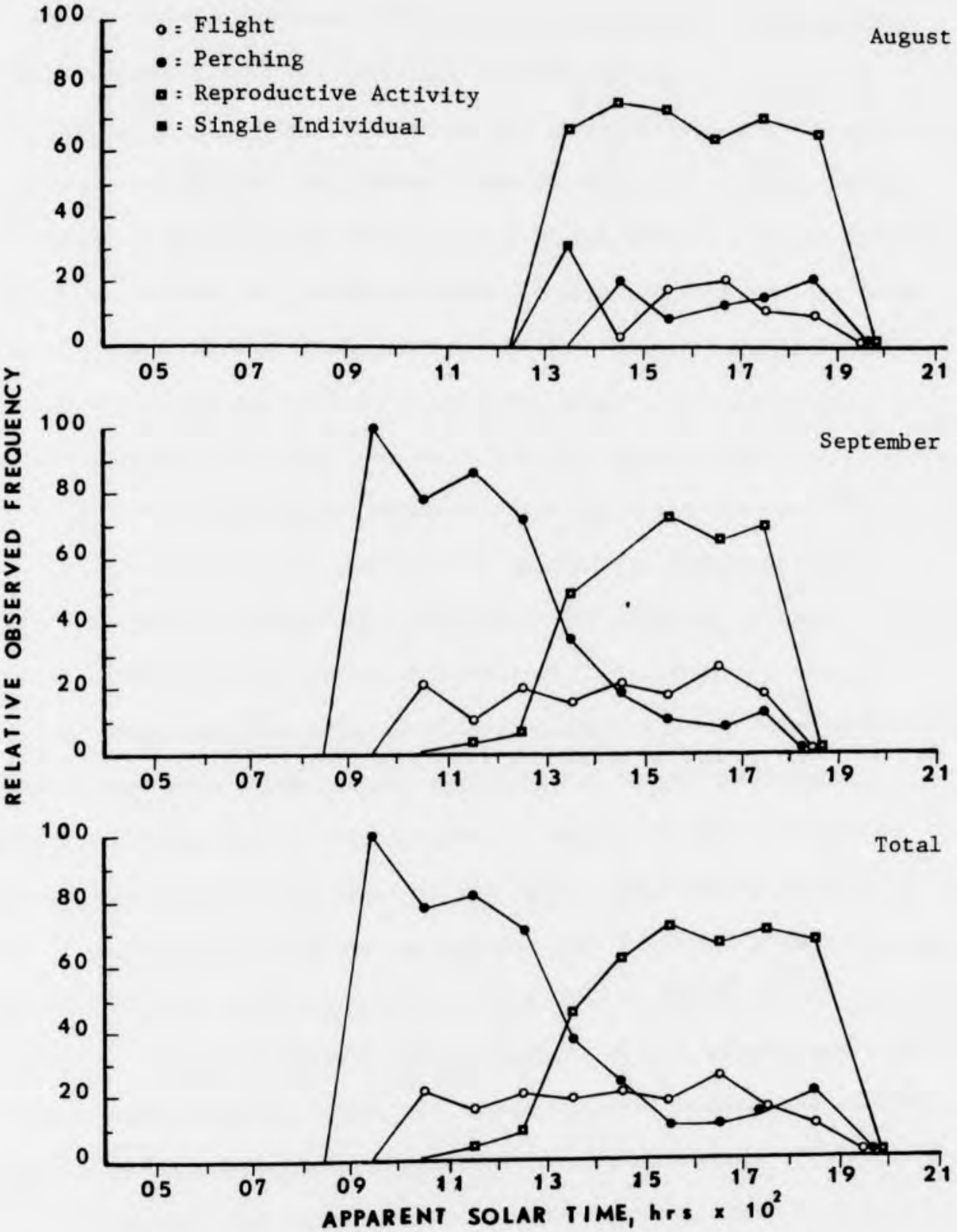

Figure 18. Temporal ranges of flight, perching, and reproductive activity for the adults of Enallagma signatum during August, September, and the total study period.

to a maximum between 1600 and 1700 hrs. A decrease in flight activity was observed after 1700 hrs until all activity ceased.

Enallagma signatum, compared to the anisopterans, was a weak flier, but expressed a similar territorial behavior and patrol flight. Males defended small areas around perch sites from intruders by threat displays (i.e., wing warning) or frontal attacks. Aggressive behavior was never observed while male and female were in tandem. Patrol flights involved hovering motionless over the water or short flights from perch sites. This hovering behavior above the water may have been a post-reproductive patrol since mating was never observed while males were in this formation.

Flight activity for single males and females varied with temperature as shown in Figure 19. Maximal flight activity in August was observed at the minimal thermal threshold of 25°C. Post-reproductive patrol was observed frequently at this temperature in the late afternoon. In September, the minimal thermal threshold for flight activity was observed 9°C lower (16°C) than in August. Maximal flight activity in September was generally observed at the higher temperatures between 20° - 30°C. A maximum of 31% of the non-reproductive September population was observed flying at 29°C compared to 67% at 25°C in August. There was no reduction in flight activity or of individuals at any temperature during the normal active period. Even the lowest recorded temperature of 16°C during the normal active period appeared to have no effect.

Flight activity in relation to light intensity, shown in Figure 20, varied between August and September. The earliest diurnal appearance of E. signatum in August was later during the day at a higher light intensity than for that seen in September. The earliest non-reproductive

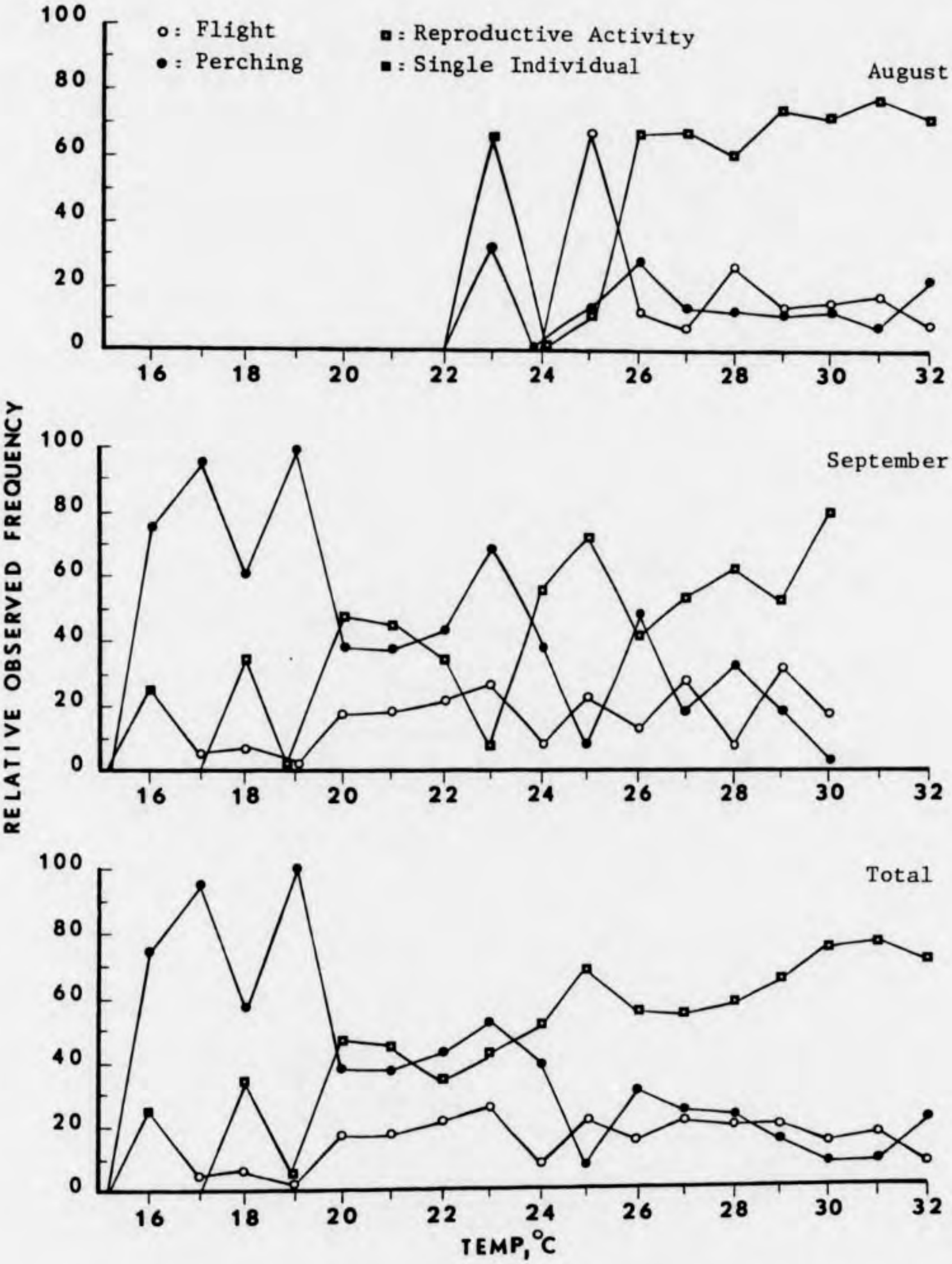

Figure 19. Thermal range of flight, perching, and reproductive activity for the adults of Enallagma signatum during August, September, and the total study period.

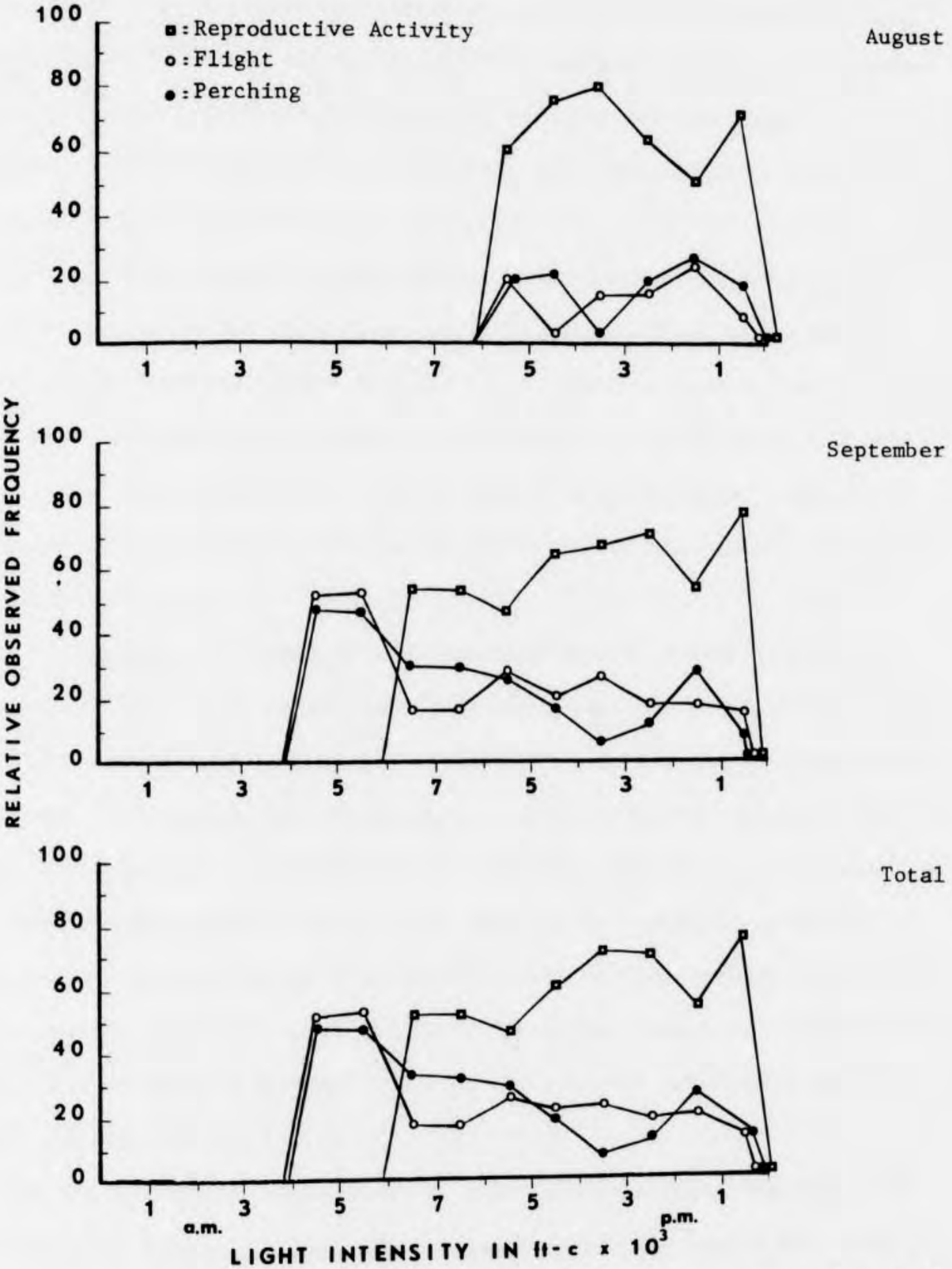

Figure 20. Flight, perching, and reproductive activity for adults of Enallagma signatum in relation to light intensity and relative observed numbers of individuals.

flight activity in August and September was observed at a minimal light intensity of 6.0 X 10^3 and 4.2 X 10^3 ft-c, respectively. In September, initial flight activity was observed at an early mid-day light intensity and was 7.5 times greater than the lowest light intensity at which flying ceased in the late afternoon.

Non-reproductive flight activity never totaled more than 28% of the population at any light intensity. In August, there was a gradual increase in flight activity from the lowest mid-day light intensities to the lowest afternoon light intensities between 1.0 X 10^3 and 2.0 X 10^3 ft-c. The percentage of the population flying in September fluctuated between light intensities with minimal activity at the highest range of light intensities.

Perching. Non-reproductive perching varied between August and September (Fig. 18). In September, perching was observed 1.9 hrs (i.e., at 0920 hrs) earlier than flight activity, but terminated at approximately the same time in the late afternoon. Perching in August commenced 1.0 hrs (i.e., at 1400 hrs) later than flight activity, but ended at the same hour in the late afternoon. Frequency of perching in September gradually decreased with time of day. Between 9 - 100% of the perching population was observed from 0920 until 1732 hrs. In August, perching increased from a minimum of 8% to a maximum of 22% of the observed population between 1500 and 1900 hrs.

The effects of temperature in relation to perching activity were difficult to determine (Fig. 19). Since temperatures during the study period were inconsistent with particular times of day or light intensities, only the effects of maximal and minimal temperatures on perching behavior could be determined. Temperatures in August between 22° and 34°C did not appear to have any effect on the percentages of the perching population. Fluctuation in percentages between temperatures was due to either small numbers or observations taken at the same temperature for different times of the day. In September, the minimal thermal threshold at which perching was observed was 16°C. If temperatures had been recorded lower than this during the normal active period, I believe that the existing minimal thermal threshold may have been lower. In September, there was no significant increase or decrease in numbers of individuals at the reported minimal thermal threshold.

Perching varied with light intensity (Fig. 20). In August, perching was first observed during mid-day at 6.2×10^3 ft-c and ended at a minimum of 0.12×10^3 ft-c in the late afternoon. Perching in September compared with that in August was observed earlier in the mid-day and late afternoon at a minimum of 4.2×10^3 and 0.56×10^3 ft-c, respectively. No activity was observed at the early morning light intensities. In September, a maximum of 58% of the population was observed at the lower mid-day light intensities. The percentage of the September perching population continued to decrease to a minimum of 6.0% between 3.0×10^3 and 4.0×10^3 ft-c but increased again at the lower afternoon light intensities. Perching in August based on population percentages was consistent with September. Initial perching activity in August, however, was observed at much higher light intensities than for that in September.

Reproductive Activity. Enallagma signatum spent most of its time at the water either mating or ovipositing. In August, mating and ovipositing were first observed at 1300 and 1330 hrs, respectively and continued until after sunset. Mating in September was observed 1.7 hrs (i.e., at 1120 hrs) earlier than in August, but ceased 1.4 hrs earlier in the later afternoon. It is important to note that even though _E. signatum_ arrived at and departed from the pond earlier in September the maximum reproductive time spent at the pond during both months was approximately the same. For example, in August, _E. signatum_ spent a maximum of 6.0 hrs in reproductive activity compared to 6.2 hrs during September.

Maximal reproductive activity varied slightly between August and September. A maximum of 74% and 73% of the population during August and September, respectively, was observed between 1500 and 1600 hrs. In August, reproductive activity was never less than 62% of the population during the normal period of activity compared to only 4.0% in September. In September, there was a gradual increase in reproductive activity from mid-day to late afternoon.

Reproductive activity fluctuated widely between temperatures. The higher percentage of the population mating or ovipositing in September (i.e., 80% at 30°C) and August (i.e., 77% at 31°C) was generally observed at the higher temperatures. In August, maximal reproduction was observed between 27 and 33°C. Only one reproductive pair was observed ovipositing in the late afternoon at 23°C. In September, the minimal thermal threshold for reproductive activity was observed at 18°C, approximately 2°C higher than initial perching or flight activity.

Reproductive activity in relation to light intensity was only observed from mid-day to late afternoon. No reproductive activity was observed at the early morning light intensities. In September, reproductive activity was observed earlier during mid-day than August, but at approximately the same light intensities. For example, in September between 1100 and 1200 hrs mating was observed at 6.0 X 10^3 ft-c. In August, mating and ovipositing were observed at the same light intensity, but at a different time of day (i.e., 1300 - 1400 hrs). Later reproductive activity during the day in August and September ceased at 0.12 X 10^3 ft-c and 0.56 X 10^3 ft-c, respectively. In September, this minimal light intensity for reproductive activity was approximately five times greater than for that observed in August.

DISCUSSION

Environmental Factors

To understand clearly the separate and combined roles of temperature, light intensity, and time of day on adult odonate behavior, it was necessary to make observations during days in which two of the three environmental factors did not appear to have any controlling effect on their daily activities. These days were characterized as clear and cold (minimum - below 20°C), clear and hot (maximum - above 33°C), overcast (100% cloud cover) with normal temperatures (22° - 33°C), and normal weather (20-60% cloud cover, 22° - 33°C) typical of the season (i.e., late summer). Upper thermal limits (clear and hot) were never recorded during the study period.

In my study the lower thermal limits (20° - 26°C) recorded in August were almost identical with those of Lutz and Pittman (1970). In September, the minimal thermal range for normal flight activity (16° - 24°C) was considerably lower than that observed in August. On two very cold and clear days in September initial flight activity was delayed four or five hours until air temperatures reached a minimal thermal threshold for most species. Prior to normal flight activity most species were observed either making short flights (ca. 0.5 m) or adjustments in body orientation so that their dorsal thoracic muscles were exposed to direct solar radiation. Mittelstaedt (in Pringle, 1957) has shown experimentally that the body orientation of dragonflies is controlled by movements of the head as a response to a light stimulus. This response has been referred to as the dorsal light reaction.

The avoidance of shaded perch sites during the early morning hours was apparent for all observed odonates. Short flights toward shaded perch sites at Station 3 were never observed during the early morning. Later on during the mid-morning hours when Stations 1, 2, and 4 were sufficiently illuminated, an occasional odonate would fly towards Station 3, perch there for only a brief moment, and then fly on. Corbet (1962) states that daily temperature fluctuations are probably the most important factors determining the pattern of adult activity. He further concludes that the characteristic diurnal rhythms of flight, feeding, and reproduction all appear to be under strong exogenous control by temperature (Corbet 1962). Moore (1953), however, reported that shade temperatures are largely unimportant since dragonflies perch and fly in the sun whenever possible. I would modify Moore's conclusions based on observations in which many odonates were seen perching in the shade of Stations 1 and 2 during mid- to late afternoon. This difference is probably due to the latitudinal differences between his study area (Great Britian) and mine (North Carolina). Many species engaged in normal flight activity and those characterized as "perchers" flew in and out of shaded areas particularly during warm to hot weather. I arbitrarily define "perchers" as species whose members spent a majority of their time at the pond perching and whose flights were of short duration. "Flyers", on the other hand, were seldom seen perching and spent most of their time in active flights. On several occasions during August, the earliest morning flight activity for _P_. _longipennis_, _L_. _incesta_, and _L_. _luctuosa_ was observed following a warm night. Areas of shaded water (early morning and late afternoon) adjacent to the shoreline did not appear to affect flight activity. The immediate flight response by P. longipennis, L. incesta, and L. luctuosa following a warm night is believed to be regulated by the dorsal light reaction referred to by Middlestat, but only when ambient temperatures were above their minimum thermal thresholds for flight activity.

My observations substantiate the importance of temperature as the main controlling factor for flight activity. Clear, cold days in September delayed flight activity until the minimal threshold for flight activity had been reached. Cold, sunless days appeared to inhibit flight activity altogether when ambient temperatures were below 16°C. Warm, overcast days reduced flight considerably, but most species still remained at the water. For many of the "perchers" an immediate and elevated flight response was observed on these days when the sun appeared intermittently between the heavy cloud layers. Moore (1953) also observed that on cold cloudy days odonates were not found at water and that if the sun was followed by clouds and cold, adults could frequently be seen flying back to the roosting area much earlier than they would have if the day had been warm and clear.

Prior to thunderstorms on warm days, flight activity for most species was reduced considerably which further supports the hypothesis (Lutz and Pittman 1970) that sudden drops in light intensity may inhibit or reduce flight activity. Temperatures always decreased during such periods of low light intensity, but never below the minimal thermal limits for flight activity for most species. However, immediately before a thunderstorm (overcast and warm), Libellula incesta increased flight and reproductive activity to a maximum recorded for any hour during that day until it began to rain. For L. incesta, the reproductive drive, which also appeared to be the focal point for adult activity in all odonates, may have been stronger than the "instinct of survival" on that particular day.

Thermoregulation for species which are termed "fliers" or "perchers" was reviewed by Corbet (1962). In this community study, quantitative data have been presented for the first time which includes perching activity based on the percentage of the population for any given temperature, time of day, and light intensity. Corbet states that fliers are usually more active at lower air temperatures than are perchers. Fliers by remaining on the wing for much of day tend to maintain their body temperature at a higher level than perchers which can regulate their body temperature by developing various postures in relation to the angle of the sun (May, 1976). It would therefore seem important than that fliers either reduce their temperature by seeking a cool place or by flying at a cool time of day. Most of the species observed in this odonate community were perchers except for A. junius, T. lacerata, and possibly C. eponina. Anax junius was observed flying at every temperature recorded between 12° - 33°C, and was last to leave the study area. Sympetrum vicinum, a typical percher, did not appear at the pond until 20 September and was observed flying normally at the cooler temperatures through most of November. Tramea lacerata flew continuously for six or seven hours during the day at the highest temperatures recorded (33°C). Lutz and Pittman (1970) have shown that at temperatures of 36° - 38°C flight activity was either terminated or significantly reduced. Avoidance of higher temperatures by the "fliers" was not observed even though many more perchers flew at the higher thermal conditions.

In my study attendance at the water for most species occurred later in the day with decreasing daylength. Departure from the water, however, was a reversal of this in which most species left the pond earlier as the days became shorter and temperatures cooler. For eight species (five libellulids) attendance at water ranged between 0.5 - 3.2 hrs later in the morning during September than in August. Departure from the water ranged between 0.25 - 3.0 hrs earlier in the afternoon during September than August. In September, this decrease in daily flight activity was attributed to the cooler temperatures in the early morning and late afternoon in response to shorter periods of direct solar radiation. Time of day and light intensity have also been shown here to be important in affecting flight activity (Lutz and Pittman 1970). Maximal flight activity at mid-day has been reported by many workers (Moore 1953, Jacobs 1955, Bick and Bick 1961, 1963, Bick and Sulzback 1966, Green 1974). Lutz and Pittman (1970) first reported the diurnal cycle of attendance at the pond for a community of adult odonates as a function of daily solar time. This was supported by a recent study (Green 1974) for seven species of odonates in which those arriving early stayed late, and those arriving late left early. Green (1974) attributed this phenomenon to a minimal temperature required for each species until territorial activity begins.

Quantitative data for the first time clearly showed the separate and combined roles of temperature, light intensity and time of day on the adult behavioral patterns for _Enallagma signatum_. Lutz and Pittman (1970) considered the adult activity of _E. signatum_ whose thermal threshold for flight was 24°C, yet who were never observed before 1430 hrs. Individuals of this species were clearly not responding to temperature, but rather to time of day (or perhaps decreasing light intensity). My observations were taken in approximately the same locality as Lutz and Pittman (1970) and show that time of day was the main controlling factor of adult behavior. The August data in respect to the thermal threshold for flight activity were only 1°C (25°C) higher than reported by Lutz and Pittman (1970) for June and July 1968. In this study flight activity was observed 1.5 hrs (1300 hrs) earlier in August than reported by Lutz and Pittman for June and July 1968. Temperature could not have been the controlling factor for adult activity since in September the thermal threshold for flight activity of this species was 9°C (16°C) lower than recorded in August. Flight activity also commenced 1.75 hrs (1115 hrs) earlier in September than August. The most important evidence in support of the time of day theory was the fact that the total period of daily activity for _E. signatum_ during August (6.0 hrs) and September (6.3 hrs) was approximately the same. Lutz and Pittman (1970) suggested that possibly decreasing light intensity may have contributed to this adult behavior since observations were made only from the maximum to minimum light intensities. In September, _E. signatum_ initiated flight activity at light intensities typical of late-morning, but below the maximum recorded for that day. In summary, I conclude that adult behavioral activity of _E. signatum_ was being controlled by time of day as evidenced by a closely synchronized attendance at water and wide thermal tolerance range. This factor may also insure the population of maximum reproductive activity during the highest daily temperatures. Temperature, however, can overide time of day and inhibit or delay flight activity if it is below the thermal limits for flight behavior. Light intensity did not appear to have any effect on the adult activities of E. signatum. Some adults were even observed perched on or flying short distances over aquatic vegetation (algal mats) during a light rain.

The effects of time of day, ambient temperature, and light intensity on flying and reproductive activity could also be separated for other adult odonates in the community. Quantitative data on two clear, cold days in September clearly demonstrated that flight activity for all the observed species in this community was inhibited below their thermal threshold. Flight activity for L. incesta, L. luctuosa, and T. lacerata was delayed six hours until the ambient temperature rose to 17°C. Lepthemis simplicicollis for the same day was delayed four hrs, E. civile three hrs, and Ishnura sp. two hrs. Perithemis tenera, A. violacea, L. vigilax and A. junius were never observed at water on these two days, and E. signatum was not inhibited at all (1115 hrs - 16°C). It was obvious, therefore, that without the ability to initiate flight activity, no other adult behavior (i.e., mating, ovipositing, feeding, etc.) could be performed. Thus, time of day as a function of the diurnal cycle of attendance at water, and light intensity appeared to have no significance during cold weather. If, however, adult odonates were exposed to a typical warm, clear day, then the diurnal cycle of attendance becomes an important characteristic of adult odonate community behavior.

Each odonate species in the community not only has a minimal thermal flight threshold, but probably an optimum one also. For most species observed this could explain the differences in the thermal thresholds and attendance at water between August and September. Several observations suggested that most early to mid-morning species were ready to initiate flight activity immediately following a warm night. Flight activity for many of the libellulids and zygopterans commenced as soon as they were exposed to direct solar radiation. Further studies on Odonata should attempt to determine quantitatively the effects of pre-dawn ambient temperatures on the regulation of flight activity and nocturnal habits. I suggest this could be done by placing "stadium lights" strategically around a small pond with regulatory controls on light intensity and wave lengths of electromagnetic radiation. Green (1974) observed seven species (20 individuals) at mid-day at a small pool with an area of only 3.25 m^2. A pool of this size with an abundance of species would be ideal for such an experiment.

The controlling effects of light intensity on adult odonate behavior in relation to temperature and time of day were most pronounced prior to a thunderstorm on warm days. It is the sudden and rapid increase or decrease in light intensity that temporarily terminates flight activity for most of the observed species. At first signs of a thunderstorm on warm days, many anisopterans (L. incesta, P. longipennis, L. luctuosa, L. simplicicollis) were perched at water, but some had disappeared from the pond altogether (P. tenera, C. eponina, and T. lacerata). The zygopterans that were observed prior to thunderstorms did not appear to be affected by rapid decreases in light intensity. Immediately before the rain began to fall (0.2 X 10^3 ft-c) most individuals and species had disappeared from the pond. Pachidiplax longipennis (male), for example, was observed in a wooded area behind Station 2 approximately 7 m from its original perch site. At Station 3, six L. incesta atypically were observed flying over water (1545 hrs) at a light intensity of 0.42 X 10^3 ft-c at 29°C. The temperature and light intensity had dropped 4°C and 5.38 X 10^3 ft-c, respectively, since the previous hours. Other data support the fact that L. incesta was observed flying at much lower light intensities (0.12 X 10^3 ft-c) in the evening than when it started in the early morning (1.4 X 10^3 ft-c).

The most misleading response to light intensity was observed on the cold and partially cloudy days. On 15 September, for example, no odonates were observed between 0715 and 1055 hrs at temperatures ranging from 11° - 18°C. Cloud cover for the same period was variable (10 - 80%), but averaged approximately 60% most of the period. At exactly 1105 hrs (18.5°C, 7 X 10^3 ft-c, and 30% cloud cover) males of L. simplicicollis, L. incesta and luctuosa, and P. longipennis flew from the roosting area to perch sites at Stations 3 and 4. No flight activity was observed over the water, and all but L. incesta and L. simplicicollis flew back to the roosting area when the sun went behind the clouds. Direct solar radiation (i.e., stimulation of the dorsal light reaction) and not simply light intensity appeared to be the prerequisite for flight activity. On cold days the normal ambient temperature was probably too low to maintain the higher internal body temperature necessary for extended periods of flight. Light intensity on cold days in the form of direct solar radiation determines adult activity which can appear to be erratic when the sun shines intermittently through the clouds.

The relationship of time of day with reproductive activity showed a tendency of females for most species to appear at water later in the day than males. Corbet cited examples of Aeshna viridis (Rantalinen and Kanervo 1928, in Corbet 1962) in which males were active some four hours before females arrived and Platycnemis pennipes (Buchholz 1956, in Corbet 1962) in which the males arrive 10 - 60 min before the females. A similar time lag of 10 - 60 min in P. tenera was reported by Jacobs (1955). In five species reported by Lutz and Pittman (1970) only the sexes of C. fasciata appeared at water at the same time. In my study, Celithemis fasciata was never observed but within the same genus the sexes of C. eponina arrived at the pond at the same time. Sometimes C. eponina and P. tenera females arrived 30 min later than males. In this study females of L. incesta (1.3 hrs), L. luctuosa (1.0 hrs), L. simplicicollis (2.8 hrs), E. signatum (1.2 hrs), S. vicinum (0.8 hrs) and T. lacerata (0.9 hrs) arrived at the pond later than their respective males.

The arrival times of females mentioned above (i.e., in parentheses) came from August data except for S. vicinum which was not observed until September. Numbers of individuals for many species in September may have been too low to give a reliable estimate of arrival times for both sexes. Enallagma signatum, which was numerous in September, showed females arriving approximately 2.0 hrs later than males compared to 1.2 hrs in August.

In Figure 4 the relationship of temperature to reproductive activity is shown. For the first time quantitative data for a community of Odonata show the possibility that in some species the two sexes have different temperature thresholds for flight activity. Reproductive activity for nearly all females usually was observed as soon as they flew over water. Pittman (1971, unpublished) stated that it was difficult to determine if this response was temperature-dependent because in 30 min there was little change in ambient temperature. Although the data were inconclusive, it was not unusual to find rapid increases in temperature from 0600 to 0900 hrs. In fact a 2°C increase in temperature during a 30 min period between these hours was quite common. There was no way of knowing precisely whether females simply spent more time feeding away from water than males or if warmer temperatures stimulated the female flight or reproductive drive. Females of *L. simplicicollis* and *P. tenera* were the only observed anisopterans that were not immediately seized by conspecific males when they arrived at water. *Lepthemis simplicicollis* females were often observed occupying the same perch sites as conspecific males but were never seen flying over water without a male in pursuit. The earliest arrival time at the pond for both *L. simplicicollis* and *P. longipennis* still corresponded to the initial observed reproductive activity. Therefore it seems logical that if differences in conspecific male-female thermal thresholds for adult behavior actually exist, then it should be demonstrated first in females that occupy the same microhabitat as their male counterparts. In both these species there were temperature and time lags between conspecific males and females. Thus, reproductive activity was delayed until females arrived at the water at the higher temperature and later times during the day. Females and reproductive activities of *P. longipennis* were observed so infrequently that immature males may have been mistaken for females. Only males of this species were captured and identified. During the total study period, *L. simplicicollis*, *S. vicinum*, and *E. signatum* were the only species in which females were observed flying below 23°C. More information concerning female activity away from water will be needed in future studies to determine to what extent temperature effects the male-female reproductive drive.

Interactions

The work of Campanella (1972, in Green 1974) indicates that some libellulids are not strictly territorial in the usual sense, but assemble in "temporal leks" at traditional mating sites and establish a dominance hierarchy among the males. In my study the most dominant species was *L. incesta* having the second highest number of interactions (61 contacts, 129 threats). Territoriality in this species was difficult to interpret because areas of defense were never localized and often conspecific males were observed in close proximity without apparent conflict. Movement over water within the visual radius of perching males nearly always stimulated aggressive behavior in males. The work of Mayer (1975, in Moore 1951a) suggests that male dragonflies can distinguish between males and females and between their own species and others, and have accurate habitat selection mechanisms. Moore concludes that abnormal behavior such as homosexual and aggressive attacks, interspecific mating and fighting, and poor habitat selection (i.e., only for males) are directly dependent on density. Pajunen (1962a), with the aid of cinephotography, concluded that most male encounters were of an indifferent nature with definite aggressive or sexual reactions being a clear minority. Also signals involving flight approach, orientation, and movement of the abdomen were distinctly different between sexual and aggressive behavior (Pajunen 1962a). Sexual dimorphic coloration for *L. incesta* was not distinct and may in part explain the inability of this species to recognize its own sex. *Pachydiplax longipennis*, on the other hand had well defined territories and sexually dimorphic coloration. Johnson (1964) reported that sex recognition seems to stimulate increased territorialism in which certain behavioral characteristics (sexually dimorphic coloration and flight styles) appear to be the sign stimuli that reinforce this purpose. Odonates that do not recognize sexes very well usually do not have well defined territories. In this community study, I have attempted to divide the most common species into three categories based on the accepted definitions of 1) territoriality (i.e., defense of an area), 2) "temporal leks" (i.e., dominance hierarchy), and 3) passive occupancy (i.e., no defense of an area). Species included in the category of territoriality were S. vicinum, A. junius, P. longipennis, and P. tenera. The dominance hierarchy group consisted of L. incesta and luctuosa, L. simplicicollis, T. lacerata and C. eponina. Lestes vigilax, Ischnura sp. and E. signatum showed passive occupancy.

Interactions between males at water may be described as contacts (physical fighting) or threats. Lutz and Pittman (1970) reported considerably more intraspecific than interspecific interactions between males, and many more threats than contacts. In this study I reported more contacts than Lutz and Pittman (1970). Interestingly enough, there were more intraspecific contacts than threats for individuals of L. luctuosa (80 contacts, 67 threats) and T. lacerata (10 contacts, 4 threats). Misinterpretation of threat behavior could vary widely between different observers, but vagueness in defining physical contact is doubtful. Most of the physical contacts between males were observed at the highest population densities near mid-day. Population densities in certain species (L. simplicicollis, P. tenera, E. signatum) compared to the available habitat were so high at times that perch sites extended to floating debris, algal mats, and sometimes the observer (i.e., white notebook attracted many species). Thus, it appeared that the dispersal rate or regulation of numbers in the study area was controlled by the population density.

Atypical behavior such as homosexual or aggressive contacts may be a response to environmental stress conditions. Environmental stress in this instance would be considered any factor that would influence adults to respond abnormally to suboptimal stimuli. Light intensity, temperature, wind, inclement weather, predation, and population density may all be factors controlling normal odonate behavior. Changes in the diurnal rhythm of many species in this community study were directly affected by inclement weather (cold and overcast). Corbet *et al.* (1960) describe a change in the diurnal rhythm of a male *L. quadrimaculata* as a response to inclement weather. Cold weather even on a sunny day prevented dragonflies from their normal flight over water. Thus, they correlated abnormal behavior with the unusually bad weather typical in Britain. Corbet *et al.* state, "that the bad weather by preventing sexual activity causes an increase in the tendency to act sexually, and so males react to stimuli which are suboptimal." This is interpreted to mean that environmental stress influences the sexual behavior in overcoming aggression where homosexuality, for example, is expressed rather than normal conspecific heterosexuality. Moore (1957) hypothesized similarly to Corbet that the cold climate prevents the normal sexual activity of males, and thus induces them to react sexually to the suboptimal stimuli presented by other males. Pajunen (1962b) also suggested a strong relationship between temperature and sexual behavior by concluding that anisopteran species of colder climates were behaviorally different than others found in warmer climates.

Colder climate anisopteran males, for example, displayed only sexual attacks, and warmer climate species were typically aggressive in behavior (Pajunen 1962b). The influence of climatic conditions and population density on contact and threat behavior for most adult odonates in this community study were not determined although several trends were noted. Observations for a single day with the greatest amount of odonate activity showed an increased number of total contacts between adult males in September (34 contacts) than for that in August (11 contacts). Threat behavior was much more prevalent during the warmer August study period when relative numbers of individuals in the community were high. Preliminary interpretation of these data suggests that 1) threat behavior is typical of normal interactions between most adult male odonates and is directly influenced by population density and optimum climatic conditions (i.e., warm and clear), and 2) contact behavior is atypical of normal interactions between most male odonates and is directly influenced by adverse climatic conditions and/or declining population density. More quantitative data will be needed in future studies to determine exactly how normal odonate behavior is altered or influenced by suboptimal stimuli.

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