

**A LEK-LIKE SYSTEM IN *LESTES SPONSA* (HANSEMANN), WITH
SPECIAL REFERENCE TO THE DIURNAL CHANGES IN FLIGHT
ACTIVITY AND MATE-FINDING TACTICS (ZYGOPTERA: LESTIDAE)***

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Diurnal change in flight behavior was studied in Urabandai, Fukushima Pref. Japan. Marked adults were continuously followed for as long as possible throughout the day. Flight behavior was divided into cruising flight and revolving flight. The former was the flight between perching points. The latter was that in which a damselfly flew around and landed at the same perching point, and was subdivided into patrolling flights and encounter flights, which included feeding and interference. Both males and females, when sexually immature, stayed on the forest floor. The frequency of cruising flights of mature males increased toward noon and then remained at rather high levels. The frequency of revolving flights in mature males increased in the morning, attained a peak around noon, and decreased in the afternoon. However, there was no diurnal rhythm in female flight behavior in the immature or in the mature stage. A few interferences were observed between the immatures. Male-male interference on the forest floor showed a diurnal rhythm in accordance with the mating behavior of mature males. Solitary males interfered in copulation there. On the other hand, solitary males were also observed on the shoreline throughout the day, while few lone females were found. Few of them, arriving from the forest, interfered in the oviposition in tandem. A lek-like system in *L. sponsa* is discussed in view of these observations.

INTRODUCTION

After emergence, adult Zygoptera, as well as Anisoptera, take several days to mature. The habitats of damselflies at the sexually immature stage are away from water, where they emerge and/or oviposit (CORBET, 1962). The maiden flight during the teneral stages has long been known in many damselfly species (e.g.

* Comparative ecological studies on Coenagrionoidea in woodlands, 8.

GOWER & KORMONDY, 1963; LUTZ, 1968; CORBET, 1980). Although many works have been conducted on mating behavior (ALCOCK, 1982; UTZERI et al., 1983; FINCKE, 1985), no lek system in Zygoptera has been reported.

Damselflies of the genus *Lestes*, characterized by the emerald color of their bodies, have a relatively long sexually immature period (SAWCHYN & GILLOTT, 1974a, 1974b; UEDA & IWASAKI, 1982; CORDERO, 1988). In Urabandai, northern Honshu, *L. sponsa* emerges in late June and begins to oviposit in late July, suggesting that the sexually immature period lasts over a month (WATANABE et al., 1986).

WATANABE et al. (1986) pointed out that some Zygoptera (*L. sponsa*, *L. temporalis*, *Platycnemis echigoana*) tend to stay throughout their lifetime in the forest near water, where they emerge and oviposit. The first two are non-territorial and the third is a territorial damselfly. In these two *Lestes* species, the habitats of the sexually immature and mature individuals are the same. The forest floor is also known to be the site for mating, and is a site which does not hold any resource for the damselfies. CAMPANELLA & WOLF (1974) pointed out that such a mating system was a kind of lek. Although considerable evidence on the behavior and the ecology of mature *L. sponsa* is available (e.g. UEDA, 1978), little attention has been given to the diurnal change in flight activity throughout the lifespan. In this paper, the diurnal flight activity pattern at the sexually immature stage is compared with that of mature individuals. A lek-like system in *L. sponsa* relative to the mate-finding tactics is also examined.

MATERIAL AND METHODS

Field data were collected from late June to mid August (1984, 1985, 1987) in Urabandai. The study area has already been described in detail (e.g. OHSAWA & WATANABE, 1984; OHSAWA et al., 1985). Among eight study plots of forests near ponds, one main plot (K-ike) and a subsidiary one (N-ike) were chosen for observation of the flight behavior of sexually immature and mature adults of *L. sponsa*. Both were secondary forests, where the dominant species are the larch, *Larix leptolepis*, in the former, and the Japanese red pine, *Pinus densiflora*, with *Rhus trichocarpa* in the latter. The sizes of the ponds were similar (about 200 m long).

Before beginning each observation on flight behavior, we intensively patrolled the study plots for two days to mark adults. Damselflies were captured in a net, and marked individually on their hind wings with a felt pen. With a little practice, it was easy to read such marks individually during the investigation. The degree of wing wear and the color of the abdomen were recorded in order to obtain information on ageing (cf. WATANABE & ADACHI, 1987a, 1987b).

Marked adults were continuously followed for as long as possible throughout the day: from the onset of the flight activity in the morning to the time of roosting in the evening, monitoring the time spent on various flight activities. Observations were made from 6:00 to 18:00 for a total of 7 days: 3 and 4 days for immature and mature adults, respectively. The numbers observed continuously during more than 5 min were 20 and 10 in immature males and females, 90 and 36 in mature males and females, respectively.

The identities of single individuals perching, flying, fighting with conspecifics, preying upon small insects, etc., at the perching point on the forest floor were recorded by direct observations. Such

behavioral patterns were basically similar to those identified in *L. barbarus* and *L. virens* (UTZERI et al., 1987), *Calopteryx cornelia* (HIGASHI & UEDA, 1982), *P. echigoana* (OHSAWA & WATANABE, 1984) and *Hetaerina macropus* (EBERHARD, 1986). The distance and the height of each flight were also recorded. Flight behavior was divided into two types in accordance with the flight route: cruising flight and revolving flight. The former was the movement from one perch to another. The latter was the flight+landing of a damselfly returning to the same perch. Revolving flights were subdivided into patrolling flight and encounter flight. Of the flight behaviors, a flight without any reason (as seen by the observers) was regarded as a patrolling flight. Encounter flight is caused by interference from other insects coming near the perch. Since damselflies ate prey at the original perch after catching it, and since they rested at the perch after their attack on conspecific intruders, all encounter flights were included in revolving flights.

To obtain further information on the diurnal change of reproductive behaviour, the distribution in the main plot was mapped along a survey line at two-hour intervals for a whole day on the 8th and 9th August, 1987, following the recording. The survey line was divided into 35 sections which included the forest floor and the shoreline (total 823 m²; 23 sections (24.6±18.5 m²) were in the forest floor and 12 (21.4±3.7 m²) were in the shoreline (SE). They occupied 16% of the area of the main plot. All of the sections were carefully searched for perching, copulating, and ovipositing individuals. The sex, number, and age were noted. All measurements are given as mean ±SE.

RESULTS

CRUISING FLIGHT

The adults captured were classified into two broad categories: sexually immature and mature. In each sampling period, the adult population was rather

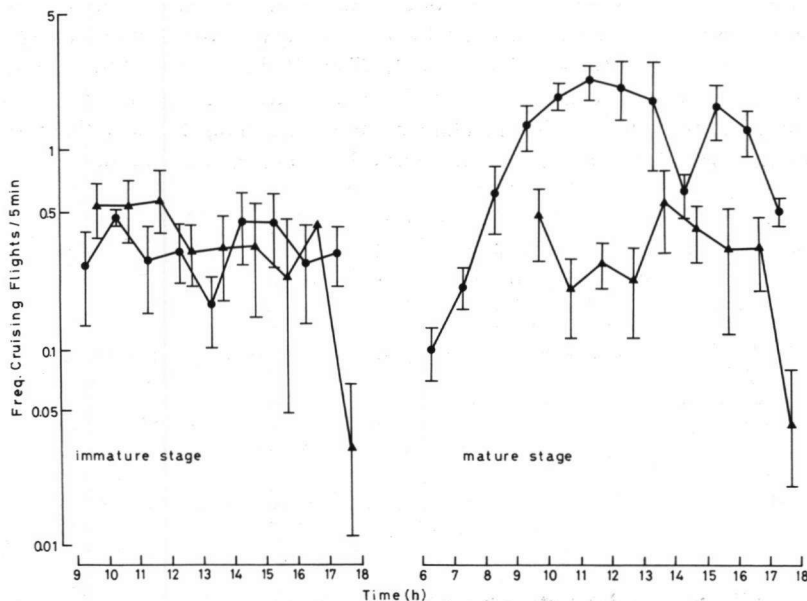


Fig. 1. Changes in the frequency of cruising flights per 5 min. for sexually immature (left) and mature (right) adults of *L. sponsa*. Circles and triangles show males and females, respectively.

homogeneous with respect to age because of the considerable synchronization of emergence. The total number of *L. sponsa* marked in the main plot, K-ike, was about 300 males and 150 females in each year.

The duration of most flights was less than 1 second, as in the case of *P. echigoana* (WATANABE et al., 1987). Cruising flight was the slowest and its duration was the longest, but did not exceed 3 seconds.

Both immature males and females tended to stay on the forest floor. They perched mainly on the stems of *Sasa paniculata*, which was dominant at K-ike. A shift of perch took place at relatively constant intervals (0.4 times per 5 min. approx.) throughout the day, except for the females in the evening (Fig. 1). There was no significant difference between the sexes in the frequency of the cruising flights per hour except at 17:00 h (F-test).

Mature females were observed after 9:00 h. The daily trend of cruising flights in mature females was similar to that of immature ones. However, with mature males the frequency of cruising flights increased in the morning after 6:00 h, remained at a higher level than that of the immature males around noon (2.5 times per 5 min. approx.), and then gradually decreased. During the early morning in particular, the frequency of the males was similar to that of the females. The daily pattern of the cruising flights in mature males seemed to be related to that of reproductive behavior.

At the immature stage, the length of cruising flights, i.e. the distance between two successive perches, was the longest in the evening in both males ($F=6.852$, $P < 0.01$) and females ($F = 6.203$, $P < 0.01$) (Tab. I). They moved further in the evening, and some left the forest floor. They may have been seeking a roosting point rather than the so-called perching point in the evening. Some of them rose from the forest floor to the tree tops, but others remained on the floor.

Table I

Changes in the length (l) of cruising flight of sexually immature and mature adults of *L. sponsa* (cm \pm SE). — [n: number of cruising flights observed]

Condition and sex	Time of day							
	06:00-09:00		09:00-12:00		12:00-15:00		15:00-18:00	
	n	l	n	l	n	l	n	l
Immature ♂	—	—	14	48 \pm 11	36	23 \pm 3	55	67 \pm 10
♀	—	—	99	33 \pm 1	68	39 \pm 4	31	57 \pm 9
Mature ♂	47	33 \pm 4	271	75 \pm 5	67	52 \pm 7	67	32 \pm 4
♀	—	—	71	35 \pm 4	70	78 \pm 8	34	83 \pm 20

A similar temporal pattern was seen in mature females ($F=5.182$, $P < 0.01$), while the length of flights in early afternoon was greater. Since some of them moved away from the forest floor in the evening, however, the aim of the cruising

flights in the evening seemed to be different from that in the daytime. On the other hand, the flight length of mature males on the forest floor increased in the morning and decreased in the evening ($F = 13.262$, $P < 0.01$). They tended to stay in the forest. The distribution of roosting points in mature adults was similar to that of the immature ones.

REVOLVING FLIGHT

After 9:00 h, the frequency of the revolving flights of immature males increased in the morning and decreased in the afternoon (Fig. 2). The maximum frequency was 1 per 5 minutes at noon. The pattern of the revolving flights of the immature females took some time to appear. The maximum number was relatively high (1.5 per 5 min.), though the frequency in each hour was not significantly different from that of the males (F-test).

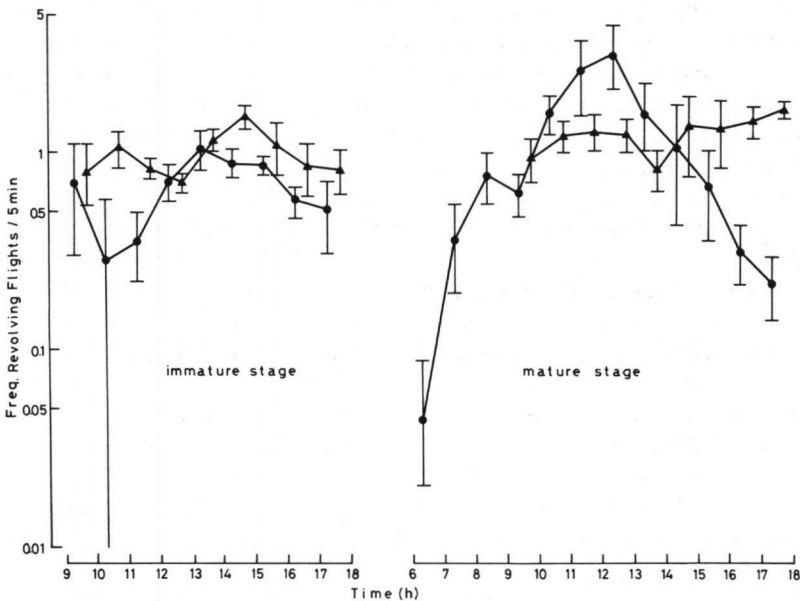


Fig. 2. Changes in the frequency of revolving flights per 5 min. for sexually immature (left) and mature (right) adults of *L. sponsa*. Circles and triangles show males and females, respectively.

The number of revolving flights in mature males attained a maximum of 3 per 5 min. at noon, and then decreased. However, mature females showed a similar tendency to that of immature ones throughout the day.

In the immature stage, some interference was observed (Fig. 3). Most of the

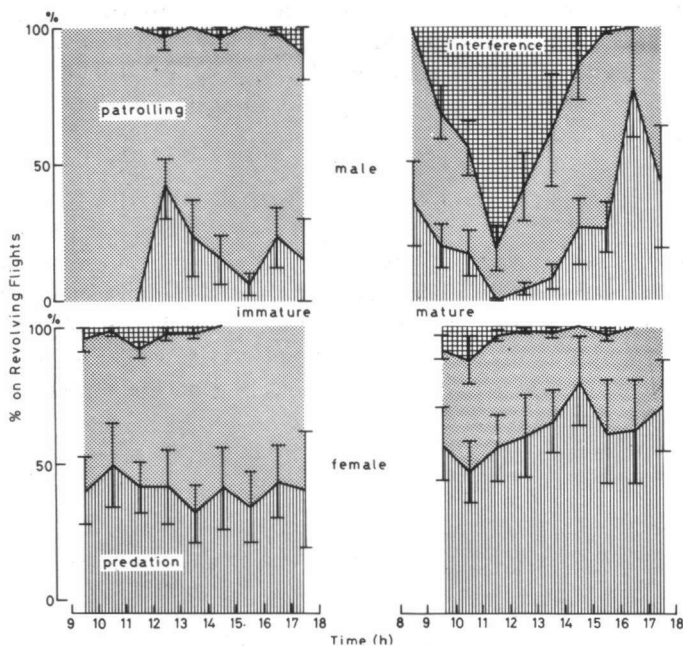


Fig. 3. Changes in the proportion of interference, patrolling and feeding (predation) flights in revolving flights for sexually immature (left) and mature (right) adults of *L. sponsa*. Males and females are shown in top and bottom, respectively.

interference was seen when another male invaded the perching male's space, which was bordered by patrolling flights. The intruder was driven away. Consequently, his cruising flight route was disturbed and, in some cases, the duration and the length of the cruising flight were increased.

The immature perching males attacked females as well as males. However, no perching female dashed members of the same sex. Females dashed exclusively against male intruders in the morning, whose flight trajectories were close to the perching point.

Among mature individuals, there was a diurnal fluctuation in male-male interaction with a peak at noon. It affected about 80% of the number of revolving flights. Only a few male-female interactions occurred. Whenever a female in cruising flight entered a male's space made by patrolling flights, the male dashed against her, and flew with her into nearby bushes. They then immediately adopted the tandem position and rapidly flew to the shoreline to oviposit. Copulations were usually observed in the forest. Therefore, mating was mainly observed around noon. Oviposition along the shoreline then followed.

On the other hand, mature perching females mainly made interference flights

Table II
Changes in the length (l) of patrolling, interference and feeding flights in the revolving flights for sexually immature adults of *L. sponsa* (cm \pm SE) — [n: number of flights observed]

Flight	Condition and sex	Time of day							
		06:00-09:00		09:00-12:00		12:00-15:00		15:00-18:00	
		n	l	n	l	n	l	n	l
Patrolling	immature ♂	—	—	28	12 \pm 1	136	15 \pm 1	95	16 \pm 1
		—	—	82	11 \pm 1	127	9 \pm 1	77	13 \pm 1
	immature ♀	—	—	109	46 \pm 6	139	40 \pm 4	8	10 \pm 2
		—	—	139	17 \pm 1	50	18 \pm 2	17	8 \pm 1
Interference	mature ♂	0	—	117	85 \pm 7	92	49 \pm 4	0	—
	mature ♀	—	—	—	—	—	—	—	—
Feeding	immature ♂	—	—	0	—	19	14 \pm 2	21	14 \pm 2
		—	—	91	16 \pm 1	94	15 \pm 1	74	20 \pm 2
	immature ♀	—	—	—	—	—	—	—	—
		—	—	—	—	—	—	—	—
Feeding	mature ♂	20	27 \pm 6	48	28 \pm 7	27	16 \pm 3	44	13 \pm 2
		—	—	156	16 \pm 1	129	15 \pm 2	143	11 \pm 0

against males. Such activity was higher in the morning than in the afternoon.

Feeding flights (predation in Fig. 3) by immature males were observed only in the afternoon, while those of immature females occurred throughout the day. When males had matured, however, the proportion of feeding flights during their revolving flights decreased around noon. The diurnal rhythm of mature females

was roughly similar to that of the immature ones, though the proportion of feeding flights at the mature stage was larger than that of the immature females.

Although the diurnal change in the length of the interference flight at the immature stages was not analyzed due to shortage of data, males and females gradually increased the length of patrolling and feeding flights towards evening, but it remained under 20 cm (Tab. II).

In mature males, longer patrolling flights (more than 40 cm) were observed around noon than in the mornings and evenings ($F = 3.741, 0.05 > P > 0.01$). The lengths of patrolling flights in the early morning and the evening were

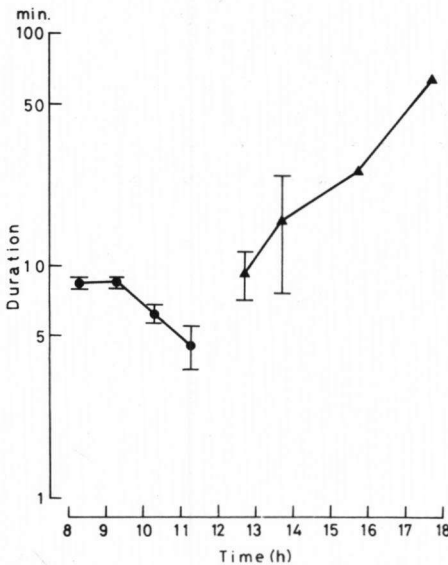


Fig. 4. Change in the duration of the copulation (circle) and one oviposition bout (triangle).

similar to those in immature individuals. The length of feeding flights was longer in the morning than in the afternoon ($F = 2.399, 0.1 > P > 0.05$), and also similar to those in immature insects. The reduction of the flight length in the afternoon coincided with the decline of sexual activity.

In mature females, on the other hand, the lengths of patrolling and feeding flights were not so different from those in the immature individuals. Therefore, females did not change their diurnal activity as they matured, except for the appearance of behavior.

When they were in tandem, sperm transfer was observed, lasting about 10 s. They then copulated.

Copulations in the morning were restricted to the forest floor. The duration of copulation was about 9 min. at 8:00 and 9:00, and decreased with time (Fig. 4). The tandem pairs were disturbed by solitary males, as the cruising flight activities increased.

CHANGES IN DENSITY IN THE FOREST FLOOR AND SHORELINE

The 8th and 9th August were sunny days. All of the *L. sponsa* adults seen were mature.

The number of females perched on the forest floor of the main plot, K-ike, was consistently less than half of that of males (Tab. III). The male densities decreased towards noon. The females disappeared at noon, suggesting that most of them flew to water. The densities of both sexes were restored by the evening. The distribution of the males on the forest floor was somewhat clumped, as suggested by the \bar{m} - \bar{m} method (IWA0, 1968). The \bar{m} - \bar{m} relation indicates the distribution pattern of the damselflies: that is, if \bar{m}/\bar{m} is near unity, it may be random, if \bar{m}/\bar{m} is larger than unity, it is clumped, and, if \bar{m}/\bar{m} is smaller than unity, it is regular. The damselflies seemed to prefer sunflecks rather than shaded areas.

Table III

Mean number (\bar{m}) and the mean crowding (\bar{m}) of solitary males, lone females and tandems in a section of both forest floor (23 sections) and shoreline (12 sections) (\pm SE)

Date & time	Forest floor						Shoreline						
	Male		Female		Tandem		Male		Female		Tandem		
	m	$\frac{\bar{m}}{m}$	m	$\frac{\bar{m}}{m}$	m	$\frac{\bar{m}}{m}$	m	$\frac{\bar{m}}{m}$	m	$\frac{\bar{m}}{m}$	m	$\frac{\bar{m}}{m}$	
8.VIII	0600	0.6±0.3	0.88	0.3±0.2	0.00	0	—	0.8±0.8	2.67	0.5±0.3	0.00	0	—
	0900	0.4±0.2	3.41	0.1±0.1	0.00	0	—	1.5±0.4	0.96	0	—	0	—
	1100	1.0±0.3	2.19	0.0±0.0	0.00	0.1±0.1	0.00	1.4±0.5	1.74	0	—	0.3±0.1	0.00
	1300	0.4±0.1	0.00	0	—	0	—	2.3±0.7	1.68	0.1±0.1	0.00	1.8±0.7	1.88
	1500	0.3±0.1	0.00	0.2±0.1	1.84	0	—	3.2±0.8	1.35	0.2±0.1	0.00	1.9±1.1	4.26
	1700	0.7±0.2	0.90	0.3±0.1	0.72	0	—	3.1±0.5	0.96	0.1±0.1	0.00	0.5±0.4	6.67
	1900	0.1±0.1	0.00	0	—	0	—	1.8±0.5	0.65	0	—	0	—
9.VIII	0600	0.7±0.3	0.56	0.4±0.2	0.00	0	—	6.3±1.2	0.95	0	—	0	—
	0900	2.3±0.4	1.24	0.2±0.1	0.00	0	—	2.8±0.6	1.23	0	—	0	—
	1100	1.6±0.3	1.24	0.1±0.1	0.00	0	—	3.1±0.7	1.19	0	—	0.2±0.2	6.00
	1300	0.7±0.2	1.02	0	—	0.0±0.0	0.00	2.8±0.7	1.26	0	—	1.8±1.0	3.76
	1500	1.4±0.3	1.14	0.1±0.1	0.00	0	—	3.3±0.8	1.36	0.1±0.1	0.00	1.5±1.2	7.85
	1700	1.0±0.2	1.04	0.2±0.1	1.84	0	—	2.5±0.4	0.91	0	—	0.9±0.8	8.93

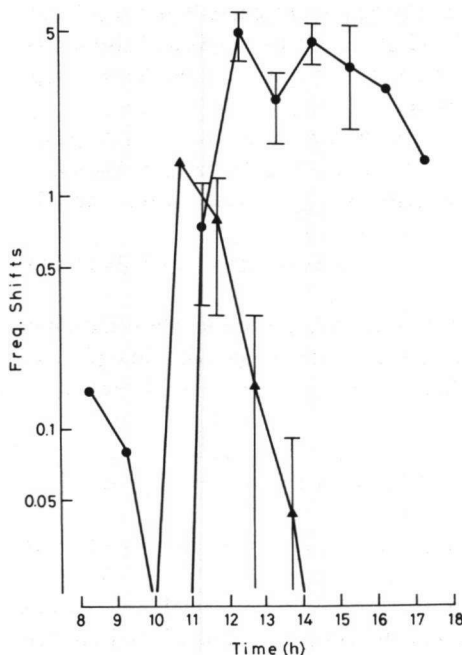


Fig. 5. Changes in the frequency of shift per 5 min. per tandem for oviposition point (circle) and the number of interferences per tandem by other tandems (triangle).

Tandems arrived on the emergent plants along the shoreline from the forest. The density of tandem pairs increased toward noon, and then gradually decreased. Most tandems found were ovipositing or resting on the emergent vegetation. Few solitary males along the shoreline disturbed the oviposition behavior of tandems, in spite of frequent nearmisses. Tandem pairs seemed to prefer a particular point to oviposit. Consequently, they competed with each other for the same oviposition plants around noon (Fig. 5). The duration of each oviposition bout was short at noon (Fig. 4).

A few solitary males moved into the forest from the shoreline around noon, while few solitary males emigrated from the forest floor. Therefore, the decline in the number of males in the forest around noon was caused by the departure of tandems to the shore.

While only a few females were observed, the solitary male density in the shoreline remained relatively higher than that on the forest floor during the day (Tab. III). They wandered in or along the emergent vegetation, and intermittently perched on the stems of emergent plants, mainly *Phragmites communis*. Consequently, their distribution was less clumped throughout the day. Although it is likely that they searched for mates, they never showed encounter flights. Male-male interference was not observed. Most of them tended to stay there, while a few of them entered the forest.

DISCUSSION

EFFECTS OF FLIGHT BEHAVIOR ON MATE-FINDING TACTICS

Throughout their lifetime, *L. sponsa* females did not change the diurnal rhythm of their cruising and revolving flights, though their physiology changed dramatically, particularly in egg production (WATANABE & ADACHI, 1987a).

They seemed exclusively to try to catch prey throughout the whole day at both the immature and the mature stages, but the success of predation was not accurately measured.

Amongst the revolving flights, the so-called patrolling flights were observed in each sex and at each stage. CORBET (1980) described territories as including a settling base from which the occupant surveys the territory, makes sallies towards intruders, and embarks on intermittent patrolling flights. However, we did not determine what targets were patrolled by the non-territorial *L. sponsa*. During patrolling flights lasting for a few seconds, they did not encounter conspecifics and/or small insect prey.

Females at both stages patrolled, despite the fact that they seemed not to want to encounter their mates. The patrolling flight seemed to be a scouting movement to establish the perching point. They encountered no conspecifics, but the space they flew around in seemed to be the hunting space. It is probable that mature males used patrolling flights to search for females. The relation between patrolling and cruising flights in mature males in a lek-like system will be discussed elsewhere.

A LEK-LIKE SYSTEM IN *L. SPONSA*

The typical mating system of territorial Zygoptera is known as resource defense (e.g. JOHNSON, 1964). ALCOCK (1982) described the mating behavior in *Hetaerina vulnerata*, where the territorial males defend stretches of streams. Males of many species defend oviposition sites and thereby gain access to respective females that come to the area to lay their eggs (e.g. CORBET, 1980). The territory of *P. echigoana* is a special case, in which males defend forest sunflecks, preferentially visited by females (WATANABE & OHSAWA, 1984; WATANABE et al., 1987). CAMPANELLA & WOLF (1974) showed a similar mating system to be a temporal lek in *Plathemis lydia*, since territorial males always encounter females in their territories and then copulate. However, males of many Zygoptera do not have territories. UEDA (1976, 1985) reported that *Cercion calamorum* males aggregate in the reproductive areas of shallow ponds where they try to catch their mates. Oviposition in tandem has been observed in many non-territorial damselflies (e.g. GOWER & KORMONDY, 1963; SAWCHYN & GILLOTT, 1975), though females of *Mortonagrion selenion* oviposit alone (MIZUTA, 1974).

In *L. sponsa*, both males and females aggregated on the secondary forest floor throughout their lifetime except during oviposition in tandem. They fed, came into conflict, copulated, and roosted in the forest. The occurrence of male and female together on the same forest floor raises the possibility of some inhibition of unfavorable mating behavior at certain times. Few abnormal couplings, such as mature males with immature females, were observed, because of their relatively

synchronized emergence. Imprudent male attacks were overcome through a diurnal rhythm for reproductive behavior. Since the time of maximum frequency of cruising flights of mature males coincided with the time of the onset of cruising flights of mature females, it is suggested that females have a diurnal physiological rhythm for the acceptance of males.

The difference between behavioral activities in immature and mature individuals has been noted in many Zygoptera (e.g. LUTZ, 1968; UEDA, 1978; CORBET, 1980). Changes in the diurnal rhythm were observed in *L. sponsa* males. They become more aggressive with ageing when they can acquire their mates only through competition with the rivals. The highest amount of interference by mature males in the forest floor was observed around noon, before reproductive activities took place. Feeding time of mature males was restricted to the morning and the evening.

In non-territorial Zygoptera, the aggregation of solitary males at available oviposition sites has been explained as a mate-finding tactics (e.g. BANKS & THOMPSON, 1985). The operational sex ratio at the oviposition site is biased in many damselfly species (e.g. UEDA, 1987). Males of those which search for females arriving at the oviposition site interfere with each other (e.g. FINCKE, 1982). However, solitary males of *L. barbarus* and *L. virens*, closely related species to *L. sponsa*, do not interrupt oviposition in tandem (UTZERI et al., 1987). Tandem oviposition appears undisturbed by any mechanism such as underwater oviposition in *Enallagma hageni* (FINCKE, 1986).

In *L. sponsa*, there was a great excess of solitary males at the oviposition site on the shoreline. Few of them mated, because most females arrived in tandem from the forest and then oviposited. Moreover, tandem pairs were seldom disturbed by solitary males staying at the oviposition site. Such non-interference by solitary males at the oviposition site favors the males aggregating in the forest, where they have the chance to encounter their mates. Encounter flight may lead to the rather constant male density in the forest. Consequently, male density in the forest was low, while male density in the oviposition site increased. Since all of the immature males were found in the forest rather than at the oviposition site, the low density in the forest might be due to the interference flights of mature males. WOLF & WALTZ (1984) concluded that territorial males stabilized defense costs across a variety of intruder pressures by maintaining dominions.

Since the forest floor was consistently used for encounters between mates, mature adults of *L. sponsa* were in reality forming a lek similar to those of the swallowtail butterfly, *Papilio zelicaon* (SHIELDS, 1967) and *P. polyxenes* (LEDERHOUSE, 1982). Although WATANABE et al. (1987) suggested a lek-like system in *P. echigoana*, no report has been published proposing a lek or an arena in Odonata except for *Plathemis lydia* (CAMPANELLA & WOLF, 1974). However, such an odonate lek is not a true lek as known in the fruit fly (e.g. SPIETH, 1968), defined as being removed from the nesting and feeding areas

(e.g. WILSON, 1975).

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