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ADULT ECOLOGY OF *CERIAGRION MELANURUM* SELYS AND *C. NIPPONICUM* ASAHINA (ZYGOPTERA: COENAGRIONIDAE) 1. DIURNAL VARIATIONS IN REPRODUCTIVE BEHAVIOUR

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The male mate-locating tactics are of the "searching" type in *C. melanurum*, and of the "sit-and-wait" type in *C. nipponicum*. The male of *C. melanurum* actively makes searching flights for females during a limited period within a day and mates only during this period, while the male of *C. nipponicum* mates during a longer period within a day. When it becomes cloudy, the reproductive activities of the male of *C. melanurum* sharply go down, whereas the reproductive activities of *C. nipponicum* are not affected so much as those of *C. melanurum*.

INTRODUCTION

Ceriagrion melanurum Selys and *C. nipponicum* Asahina are damselflies living in old ponds and swamps or marshes abounding with emergent plants. The adult weight of *C. nipponicum* is about one half of that of *C. melanurum*, but both abdomen and wing lengths of the two species are almost the same, being about 30 mm and 20 mm, respectively (ISHIDA, 1969).

AOYAGI (1973) studied the adult behaviour and postures of *C. melanurum*. According to his report, the mode of mate-locating of this species is searching for females by males. On the other hand, it is reported that mature males of *C. nipponicum* adopt territories by perching on emergent plants (MIYAZAKI & MURAKI 1984). Thus, though *C. melanurum* and *C. nipponicum* belong to the same genus and are of similar size, the mate-locating mode of the male seems to differ in each species. The mode in *C. melanurum* would be regarded as the "searching" type and that in *C. nipponicum* as the "sit-and-wait" type.

Detailed studies have not been published on the adult activities of either species. Concentrating on the mate-locating tactics of both species, I have observed and described the time budgets and diurnal activities in mature adults.

METHODS

The research was conducted from the end of July till the middle of August, 1965, at Midorogaike, Kyoto (N 35° 3.3', E 135° 46.3', about 80 m above sea level), and from the end of July till the middle of August, 1969, at Iwanohimenomikoto Mausoleum, Nara (N 34° 41.9', E 135° 48.2', about 80 m above sea level). During the research periods, the sun rose and set at about 5:00 — 5:15 h and 18.45-19.00 h JST, respectively. Both species occur in the two places.

The research was conducted on mature individuals under field conditions using three methods as follows: (1) Hourly fluctuations of the time budgets of activities: The flights and their durations were observed over 5 min. or sometimes longer, per individual. Feeding and copulating individuals were excluded from the observation. Time measurements of flights were made to the unit of 0.1 s by a stopwatch. I traced the flight route on a map (the scale of which is 1:50) and measured its length, and then calculated the average speed of flight dividing the length of the flight route by the flight duration. Light intensities were measured by a Toshiba Photocell Illuminometer SPI-5; — (2) Counts of ovipositing individuals: The ovipositing tandem pairs flying over a certain area (about 3 m x 5 m) in the pond of Iwanohimenomikoto Mausoleum were counted every hour. The study was carried out on August 12, 13 and 15, 1969; — (3) Tandem response by males to tethered females: In order to study the presence and intensity of sexual drives of males, tandem response was observed by presenting a tethered female 20-50 cm in front of a male to be tested.

The above observations were made mainly on fine days.

RESULTS

The activities could roughly be grouped as follows: (a) Perching; — (b) Simple flight: a short and brief flight for unknown reason (Tab. I). A return to

Table I
Duration of flight of each type

Species & type of flight	No. of samples observed	$\bar{x} \pm SD$ (sec)	Range (sec)
C. melanurum			
Simple flight ♂	234	2.1± 1.1	0.5- 7
Simple flight ♀	90	2.4± 1.5	0.5-10
Feeding flight ♂	110	3.3± 2.0	0.5-11
Feeding flight ♀	92	3.1± 1.8	0.5- 8
Searching flight ♂	1085	22.0±13.9	1-90
C. nipponicum			
Simple flight ♂	297	1.8± 1.0	0.5- 8
Simple flight ♀	227	1.5± 0.8	0.5- 6
Feeding flight ♂	83	3.1± 1.8	0.5-10
Feeding flight ♀	171	3.1± 2.1	0.5-12
Investigatory flight ♂	184	4.5± 2.8	0.5-17

the original perch after such a flight was often observed. This corresponds to the "normal flight" as described by AOYAGI (1973); — (c) Feeding flight: a dashing flight to catch small insects flying near the perch (Tab. I). This activity could be observed during other types of flights as well, when a dashing flight was often made to perching insects or, in some cases, to mud spots on a leaf. The catch rate (the ratio of the number of successful catches to that of feeding flights) in *C. melanurum* was investigated. The result was 0.11 (=7/64) in the male and 0.12 (= 13/112) in the female; — (d) Escape flight: When a large anisopteran, or an insect net, were close to an individual, it made a hasty and linear escape flight. When these appeared suddenly, the damselfly sometimes dropped down folding

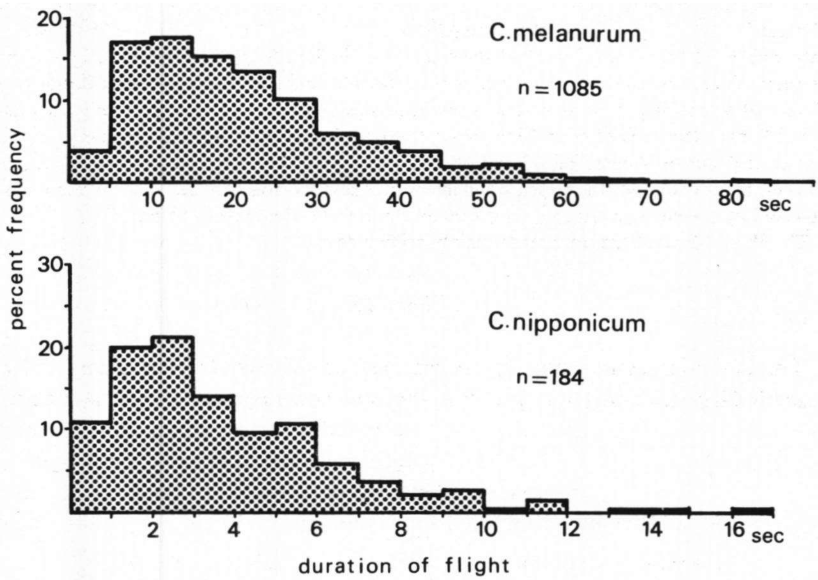

Fig. 1. Frequency distribution of durations of searching flight in the male of *C. melanurum* (top) and investigatory flight in the male of *C. nipponicum* (bottom).

the wings instantly. This type of response was not observed during the study of time budgets of activities; — (e) Searching flight: a flight made by males of *C. melanurum* apparently searching for females. The males made a zig-zag flight at the height of about 50 cm, shaking their bodies up and down among or 10-20 cm above the surrounding bushes. They mainly flew forwards but sometimes hovered. When a female was found, they dashed towards it. The duration of flight was long compared with other types of flights (Tab. I, Fig. 1). The flight speed measured in flights lasting over 5 seconds was 20.5 ± 5.0 cm/s ($\bar{x}$ ± SD, n=45). MIZUTA (1974) termed this type of flight "sexual flight"; — (f) Investigatory flight: a type of flight made by males of *C. nipponicum.* The males of this species, when finding damselflies passing about 50 cm from their perch sites, made this flight and approached them at a distance of 5-10 cm and then hovered for a short time (Tab. I, Fig. 1). The investigatory flights observed are broken down as shown in Table II. This type of flight could be considered to be sexual, since when the males have approached the flying insects and found them to be females, they try to form a tandem. In many cases, however, interactions occurred involving more than three male individuals, in which males approached each other at a distance of about 5-10 cm and hovered almost "face to face". As a result of these interferences among males, their perches are defended in some cases but, in other cases, taken over by other males. The male of *C. nipponicum* shifts from one perch to another within a day, defending each in turn. Consequently, the males get spaced out at least about 50 cm away from other individuals.

Table II
Objects for which the male *C. nipponicum* made investigatory flights

Objects	Frequency observed
C. nipponicum, ♂	152
C. nipponicum ♀	12 (8)*
C. melanurum, ♂	17
C. melanurum, ♀	5
C. nipponicum, tandem	1
C. melanurum, tandem	3
Copera annulata, ♂	2

* Successful tandems

The time between finding and gripping a female in tandem, i.e. after starting the investigatory flight in the case of *C. nipponicum*, differs between *C. melanurum* and *C. nipponicum.* An experiment in which a tethered fluttering female was presented at a distance of 50 cm showed that the above mentioned time was 0.85 ± 0.49 s ($\bar{x} \pm$ SD, n=23) and 2.52 ± 1.51 s ($\bar{x} \pm$ SD, n=35) in *C. melanurum* and *C. nipponicum*, respectively, when the male succeeded in forming a tandem. The male of *C. melanurum* grasped the female instantly whereas the male of *C. nipponicum* did so after hovering for a short time about 10 cm diagonally above her.

Copulation in both species is of the long duration type as defined by CORBET (1962). In case of *C. melanurum,* the duration of the wheel position was 37.2 ± 12.7 min ($\bar{x} \pm$ SD, n=6, range: 18-53 min). Only two measurements were made for *C. nipponicum* (32 min and 48 min).

Oviposition is conducted in a male-upright tandem position. The site used for oviposition is communal and several pairs in tandem were often observed ovipositing as close as about 10 cm away from each other. The time during which a tandem pair stayed at the oviposition site was found to be about 2 hours (range: 0.5-4 hr, n=35 in *C. melanurum* and n=15 in *C. nipponicum*).

The male and female individuals in both species copulated and oviposited, in general, only once a day. Moreover in both species some individuals, both male and female, copulated and oviposited every day for several consecutive days (Mizuta, unpublished).

TIME OF DAY AND TIME BUDGETS

Table III shows hourly fluctuations of the ratio of time consumed for each type of flight. Apart from the male of *C. melanurum*, these damselflies act as "perchers" (CORBET, 1962). The female of *C.melanurum* and both sexes of *C. nipponicum*, when they were not engaged in any reproductive activities, i.e. copulation and oviposition, spent more than 98 percent of time throughout the day in perching (Tab. III). The average number of flights made during a period of 5 minutes was less than two for any type of flight.

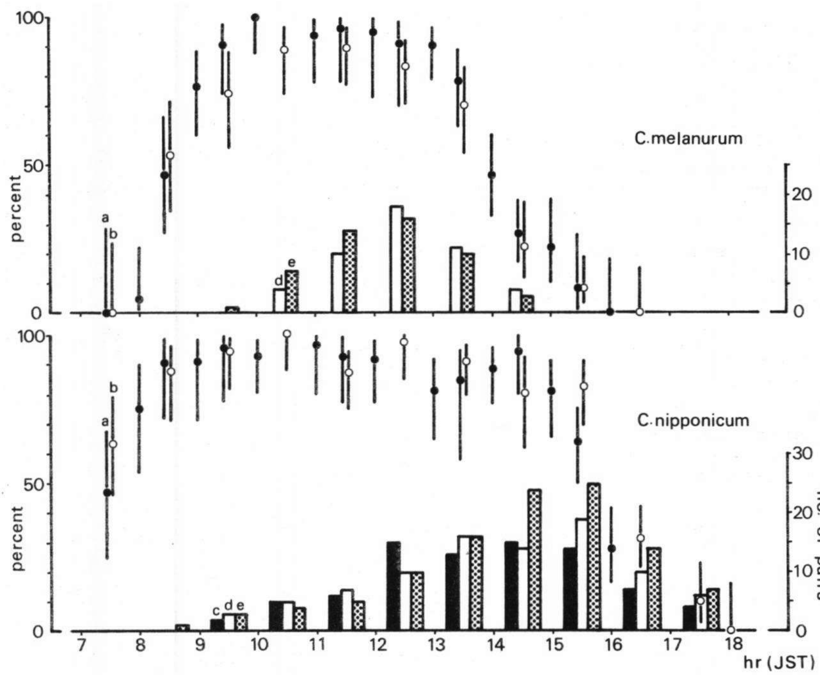

Fig. 2. Hourly fluctuations in the tandem response of males and number of ovipositing pairs at a certain area of the pond. Top: *C. melanurum*, bottom: *C. nipponicum*. The small letters indicate the day when the observation was carried out: (a) 10, (b) 11, (c) 12, (d) 13, (e) 15 of August, 1969. The number of pairs of *C. melanurum* was not counted on August 12, 1969. Vertical lines indicate 95% confidence limits.

However, the male of *C. melanurum* was observed to make searching flights between 9:00 and 12:30 h. In particular, between 10:00 and 12:00 h it spent, on the average, more than 30 percent of time in making searching flights (Tab. III).

Table III
Hourly fluctuations in the percent of time spent in each behaviour

Time	No. of Individuals observed	Total duration observed (min)	Simple flight	Feeding flight	Searching flight (*C. melanurum* ♂) or Investigatory flight (*C. nipponicum*, ♂)	Perching
C. melanurum, ♂						
6	4	20	0.2	—	—	99.8
7	7	35	0.2	—	—	99.8
8	10	50	0.5	0.1	—	99.4
9	23	115	0.8	0.1	4.8	94.3
10	37	185	0.3	—	33.1	66.6
11	29	220	0.3	0.0	42.7	57.8
12	36	230	0.3	0.2	32.3	67.2
13	43	215	0.9	0.5	6.7	91.9
14	32	160	0.9	1.0	0.0	98.1
15	19	95	1.1	0.6	—	98.3
16	9	45	1.3	0.6	—	98.1
17	10	50	0.6	1.2	—	98.2
18	9	45	0.5	0.5	—	99.0
C. melanurum, ♀						
6	3	15	0.2	—		99.8
7	3	15	0.4	—		99.6
8	9	45	0.5	0.6		98.9
9	7	35	1.5	0.7		97.8
10	9	45	0.2	0.8		99.0
11	7	35	0.6	0.0		99.4
12	4	20	0.8	0.8		98.4
13	9	45	0.6	0.2		99.2
14	9	45	0.3	0.4		99.3
15	7	35	0.2	0.9		98.9
16	9	45	0.5	0.4		99.1
17	8	40	0.7	1.4		97.9
18	10	50	1.5	0.6		97.9
C. nipponicum, ♂						
6	31	155	0.3	0.0	0.0	99.7
7	24	120	0.6	0.2	0.2	99.8
8	25	125	0.6	0.3	0.7	98.4
9	20	100	0.4	0.1	0.8	98.7
10	26	130	0.3	0.3	1.0	98.4
11	52	260	0.4	0.2	0.8	98.6
12	35	175	0.4	0.3	0.8	98.5
13	54	270	0.5	0.2	0.9	98.4
14	52	260	0.3	0.2	1.0	98.5
15	34	170	0.4	0.3	0.7	98.6
16	39	195	0.4	0.2	0.3	99.1
17	27	135	0.3	0.1	0.1	99.5
18	28	140	0.4	0.0	0.0	99.6
C. nipponicum, ♀						
6	5	25	0.3	—		99.7
7	7	35	0.7	0.2		99.1
8	8	40	0.8	0.2		99.0
9	9	45	0.7	0.4		98.9
10	26	130	0.6	0.7		98.7
11	32	160	0.6	0.6		98.8
12	26	130	0.8	0.8		98.4
13	25	125	0.5	0.8		98.7
14	30	150	0.5	0.7		98.8
15	27	135	0.6	0.8		98.6
16	30	150	0.9	0.9		98.2
17	30	150	0.6	1.0		98.4
18	9	45	0.4	—		99.6

When expressed in terms of the number of flights per 5 min., this corresponds to 4-6 flights.

The tandem response of the male of *C. melanurum* to a tethered female reached its peak at about 10:00 h and the peak lasted for about 3 hours (Fig. 2). The peak duration of tandem response coincided with that of searching flight, but almost half of the males reacted by making tandem responses even at 8:30 and 14:00 h (Fig. 2).

In the male of *C. nipponicum*, the number of investigatory flights increased between 8:00 and 15:00 h compared with that before and after this period (Tab. III). Even then the average number was less than one per 5 min. The number depended on the density of the damselflies passing by.

About half of the male individuals of *C. nipponicum* responded to the tethered female by making tandem responses even at 7:30 and 15:30 h. The peak of the tandem response lasted from 8:30 till 15:00 h (Fig. 2).

The hourly fluctuation in the number of tandem pairs at oviposition sites is shown in Figure 2. Ovipositing pairs of *C. nipponicum* could be observed over nearly twice as long a period within a day as those of *C. melanurum*. As stated above, this result does not contradict that obtained for the sexual flights and tandem responses in the male individuals of each species in consideration of the time required for copulation and oviposition.

EFFECT OF LIGHT INTENSITY

During a season when mature adults of both species are active, it is usual for the temperature to rise to 25° C after 8:00 h and for the maximum daytime temperature between 13:00 and 14:00 h to exceed 30° C when it is sunny. The light intensity between 9:00 and 15:00 h rises to 40,000 lx or more.

When it was cloudy, only a small number of individuals making searching flights was observed, suggesting a marked effect of light intensity on the sexual activities of the male of *C. melanurum*. In fact, even on sunny days, individuals which had been making searching flights would stop flying or make flights only occasionally when it suddenly became cloudy.

The number of searching flights per 5 min. made by the male of *C. melanurum* was counted when the weather had suddenly turned cloudy remaining so for longer than 5 min. between 10:00 and 12:00 h (the peak period for searching flights by *C. melanurum*). During the observation the temperature did not change or dropped only by less than 1° C. The data obtained at 60,000-74,000 lx and 82,000-86,000 lx, as presented in Figure 3, correspond to those that could be obtained under sunny weather conditions. The frequency distribution of the number of searching flights per 5 min. significantly differed between each of the following three pairs of adjoining light intensity steps in the Figure: 10,000-13,000 lx and 17,000-18,000 lx; 17.000-18,000 lx and 26,000-28,000 lx; 26,000-28,000 lx and 32,000-40,000 lx (Mann-Whitney's U-test, $p < 0.01$ in all cases). It can be seen from Figure 3 that the number of searching flights sharply decreased when the light intensity dropped below 20,000-25,000 lx. However, when a tethered female was displayed to perching males at 7,000-10,000 lx, twelve among 15 individuals tested reacted by making tandem responses. This reaction ratio is not significantly different from that obtained under sunny weather conditions. Therefore, male individuals do not seem to lose all of their sexual drive when it becomes cloudy.

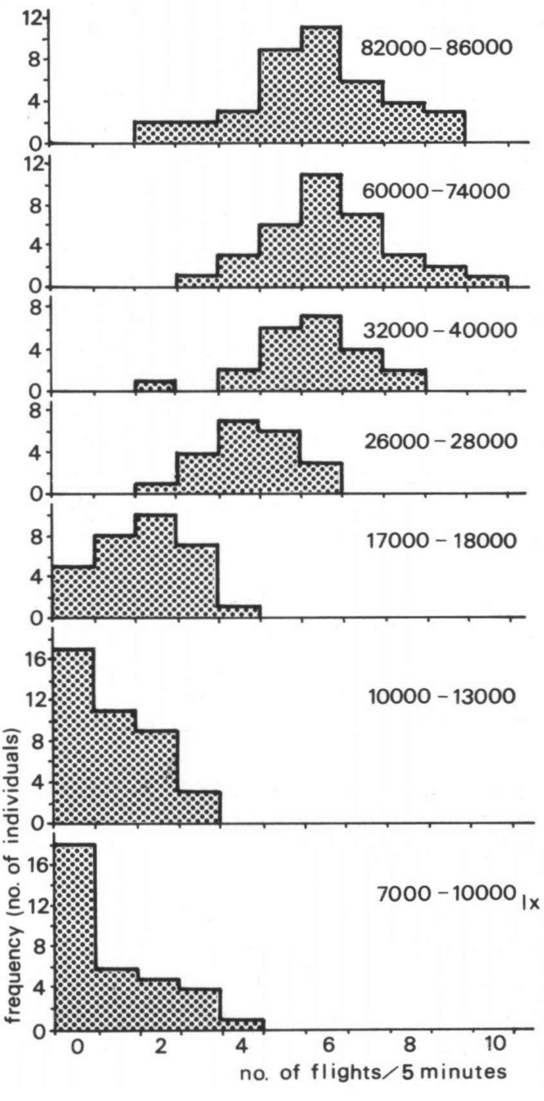

Fig. 3. Frequency distribution of the number of searching flights per 5 min at different levels of light intensity in the male of *C. melanurum*.

The effect of light intensity on the sexual activities in *C. nipponicum* did not seem to be so strong as in *C. melanurum*. The number of ovipositing pairs in *C. nipponicum* did not decrease so sharply as in *C. melanurum* when it became cloudy, although detailed counting was not conducted. Ovipositing pairs of *C. melanurum* were hardly found on cloudy days, even when a considerable number of pairs of *C. nipponicum* were observed ovipositing at the waterside. Since on rainy days, however, ovipositing pairs could not be observed in both species, their sexual impetus seems to be completely inhibited when it rains.

DISCUSSION

SCOTT (1974) has investigated the mate-locating modes of butterflies and classified them into two types as follows: (1) Perching: a male takes its perch and waits for females passing by; (2) Patrolling: a male flies almost continuously in search for females. These mate-locating modes correspond to the tactics shown by the males of *C. nipponicum* and *C. melanurum*, respectively. According to SCOTT (1974), most of the butterflies whose mate-locating tactics are of the patrolling type mate at any time throughout the day whereas about half of the species of the perching type mate only during a limited period within a day. In the present study, just the opposite observation has been obtained with *C. melanurum* and *C. nipponicum*.

The mate-locating tactics of the male of *C. nipponicum* are classified into the "sit-and-wait" type. The males identify approaching females by making investigatory flights and may then mate with them. The sexual drive of the males is maintained at high levels from 8:00 to 15:30 h (Fig. 2), and they are capable of mating at any time within that period. Mating is observed at any time over a relatively long period between 10:30 and 16:30 h in *Ceriagrion tenellum* as well, whose mate-locating tactics are considered to belong also to the "sit-and-wait" type (PARR & PARR, 1979). On the other hand, in *C.melanurum* the mate-locating tactics of the male are of the "searching" type, and actual matings by the majority of males occur between 10:00-12:30 h when the male makes frequent searching flights though the sexual drive is present between 9:00 and 13:00 h (Fig. 2). FINCKE (1985) has found that males of *Enallagma hageni* have two alternative tactics for finding mates: (1) they search the banks of the pond for unmated females, or (2) wait at oviposition sites for females that resurface prematurely from underwater oviposition. The searching tactics were generally used earlier in the day than the waiting tactics. But FINCKE (1985) has concluded that the use of the two tactics was not strictly time-dependent.

Of the other Odonata which I have investigated, almost all male individuals reacted to tethered females by making tandem responses over a period of 9 hours (8:00-17:00 h) in both *Orthetrum albistylum speciosum* and *O. triangulare melania* (MIZUTA, 1982), and *Mnais p. pruinosa* did so for 8 hours (9:00-17:00 h) (Mizuta, unpublished). These species are of the "territorial" type or, at least, of the "sit-and-wait" type, while *Mortonagrion selenion* which is of the "searching" type was found to react by making tandem responses during the particular period between 5:00 and 8:00 h and it made searching flights only during this period (MIZUTA, 1974). Accordingly, the above described case is in agreement with that of *C. melanurum* and *C. nipponicum*.

Since the females of both *C. melanurum* and *C. nipponicum* do not make flights very frequently (Tab.III), the "searching" type of mate-locating tactics as done by *C. melanurum* males is considered to be more effective in terms of locating females. Instead, in the case of *C. nipponicum*, which is of the "sit-and-wait" type, male individuals spend more time within a day in mating activities than in *C. melanurum*. Moreover, they are less influenced by unfavourable weather than the males of *C. melanurum*. Such behaviours can be understood to be adaptive. However, not only the period within a day when mating is done, but also the site where mating is carried out and/or the distribution and movements of individuals are considered to be important as a system for finding a mating partner.

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