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ADULT ECOLOGY OF *CERIAGRION MELANURUM* SELYS AND *C. NIPPONICUM* ASAHINA (ZYGOPTERA: COENAGRIONIDAE). 2. MOVEMENTS AND DISTRIBUTION

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The individual distribution is less aggregated in *C. melanurum*; the mate locating tactics of the male are of the "searching" type, while in *C. nipponicum* the tactics are of the "sit-and-wait" type, and the individual distribution is more aggregated. In *C. nipponicum*, the male groups hold their position near the waterside and the female groups gather outside the male groups, thus increasing the probability for the two sexes to encounter each other. *C. melanurum* travels further in its day-to-day movements, but there is a strong tendency for both species to stay at or return to their original sites.

INTRODUCTION

The mode of mate-locating of *Ceriagrion melanurum* Selys is different from that of *C. nipponicum* Asahina, the former being of the "searching" type and the latter of the "sit-and-wait" type. The female of *C. melanurum* and both sexes of *C. nipponicum* spend more than 98% of time in perching during a day when they are not engaged in reproductive activities. The male of *C. melanurum*, however, actively makes searching flights for females throughout a limited period of a day and mates only during this period whereas the male of *C. nipponicum* mates over a longer period of a day (MIZUTA, 1988).

These two types of mate-locating tactics are assumed to be related to the spatial distribution of individuals. For example, it is not unlikely that the perching site of the male of *C. nipponicum* has been selected in such a direction that the male has a better chance to encounter the female at the site. I therefore investigated whether the mate-locating modes in *C. melanurum* and *C. nipponicum* reflect the day-to-day movements and distribution of individuals.

METHODS

The research was carried out at a part of a pond surrounding Iwanohimenomikoto Mausoleum, Nara (N 34° 41.9′, E 135° 48.2′, about 80 m above sea level). *Nuphar japonicum* is growing over the whole area of the 50 cm deep pond. There are *Brasenia schreberi* and *Phragmites communis* also growing in some parts of the pond. *C. nipponicum* occurred in this place alone while *C. melanurum* occurred in the neighbouring places as well. On banks surrounding the pond where these damselflies are living, evergreen trees such as *Pinus thunbergii, P. densiflora, Cryptomeria japonica, Cinnamomum camphora, Ilex rotunda* and *Quercus* spp. are planted. The underbush is composed mainly of *Zoysia japonica* or *Arundinaria* sp., and partly of *Miscanthus sinensis* and other grasses (Fig. 1).

Newly caught individuals were numbered on a wing with a black, oily felt-tipped pen to be identified, when they were sighted later again, by visual observation alone, not necessitating re-capture. The site where they were sighted was plotted on a map. This research was conducted on mature adults.

The research was conducted, in principle, between 10:00 and 13:00 h every day from July 28 to August 11, 1981 excluding August 8 and 9, and from August 4 to 13, 1982. Fine weather prevailed during the research periods both years.

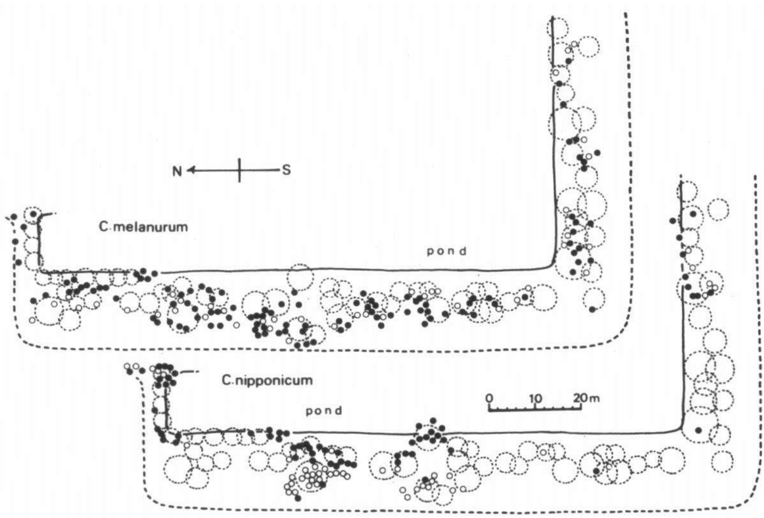

Fig. 1. Map showing the distribution of individuals sighted during 9:00-10:00 h, July 28, 1981. Solid and open circles show male and female individuals respectively.

RESULTS

The population size of mature adults was estimated according to the method of MANLY & PARR (1968). It remained almost unchanged throughout the respective research periods. The approximate figures estimated for 1981 were as follows: 370 males and 160 females of *C. melanurum*; 150 males and 110 females of *C. nipponicum*. For 1982 they were 290 males and 140 females of *C. melanurum*, and 300 males and 170 females of *C. nipponicum*. The daily survival rate was estimated for both species as approximately 0.9.

MOVEMENTS OF INDIVIDUALS

When marked and released individuals were sighted again on other days, straight-line distances from their original locations were measured in terms of the distance moved per day. Table I and Figure 2 present these data for 1981

Table I

Day-to-day moved distances, measured as straight-line distances from the original site

Day	No. of samples observed	$\bar{x} \pm$ SD (meters)	Range (meters)	No. of samples observed	$\bar{x} \pm$ SD (meters)	Range (meters)
	Males of *C. melanurum*			Females of *C. melanurum*		
1	390	11.1±12.5	0.4- 96.4	28	9.1± 9.5	1.2-33.8
2	274	15.2±17.4	0.6-132.2	17	8.0± 5.5	2.0-21.2
3	217	15.4±16.5	0.6-130.4	20	10.0± 8.3	0.8-31.0
4	198	18.0±17.2	0.4- 85.2	13	12.7± 9.7	2.4-30.6
5	176	21.1±19.8	0.8- 93.8	9	14.8±20.9	2.2-69.0
6	142	22.8±21.7	1.4-107.6	10	11.6± 8.8	3.8-28.0
7	99	25.1±25.4	1.0-122.8	6	19.3±17.0	2.0-49.8
8	81	24.3±24.3	2.0-135.0	1	31.4	
9	60	22.7±22.5	2.0- 95.2	3	11.1±13.9	1.0-27.0
10	33	18.2±11.5	1.4- 40.8	4	35.6±27.9	13.6-75.4
11	25	25.8±25.2	1.8- 87.6	-		
12	25	23.0±23.2	0.8- 91.8	1	11.2	
13	11	25.2±21.7	4.0- 76.6	1	5.6	
	Males of *C. nipponicum*			Females of *C. nipponicum*		
1	469	6.1± 7.6	0.4-68.2	125	4.9± 6.3	0.4-45.8
2	337	7.8±10.1	0.4-86.8	88	7.5±11.2	0.6-52.4
3	265	9.1±11.1	0.6-89.0	85	9.7±13.1	0.4-86.4
4	252	8.9±11.2	0.4-96.4	65	10.9±12.9	0.6-56.6
5	181	10.6±13.7	0.4-82.0	44	12.9±15.8	1.0-72.4
6	134	10.9±13.6	0.4-73.4	37	10.9±11.0	0.8-39.2
7	102	11.7±14.2	0.2-90.8	28	14.6±13.0	0.4-46.0
8	80	10.9±11.5	0.6-57.6	27	16.4±19.1	0.6-54.6
9	54	9.1± 8.4	0.4-42.6	13	29.1±16.4	7.4-52.8
10	25	11.3±13.6	1.2-65.4	8	22.8±12.1	10.6-46.8
11	13	13.1±11.5	2.0-43.6	4	20.0±21.2	8.2-51.6
12	13	10.6±13.1	0.8-47.2	2	8.2, 20.0	
13	19	12.4±11.2	1.2-33.0	4	15.9± 8.6	7.2-24.8
14	9	17.3±19.9	0.6-62.4	2	9.2, 22.8	

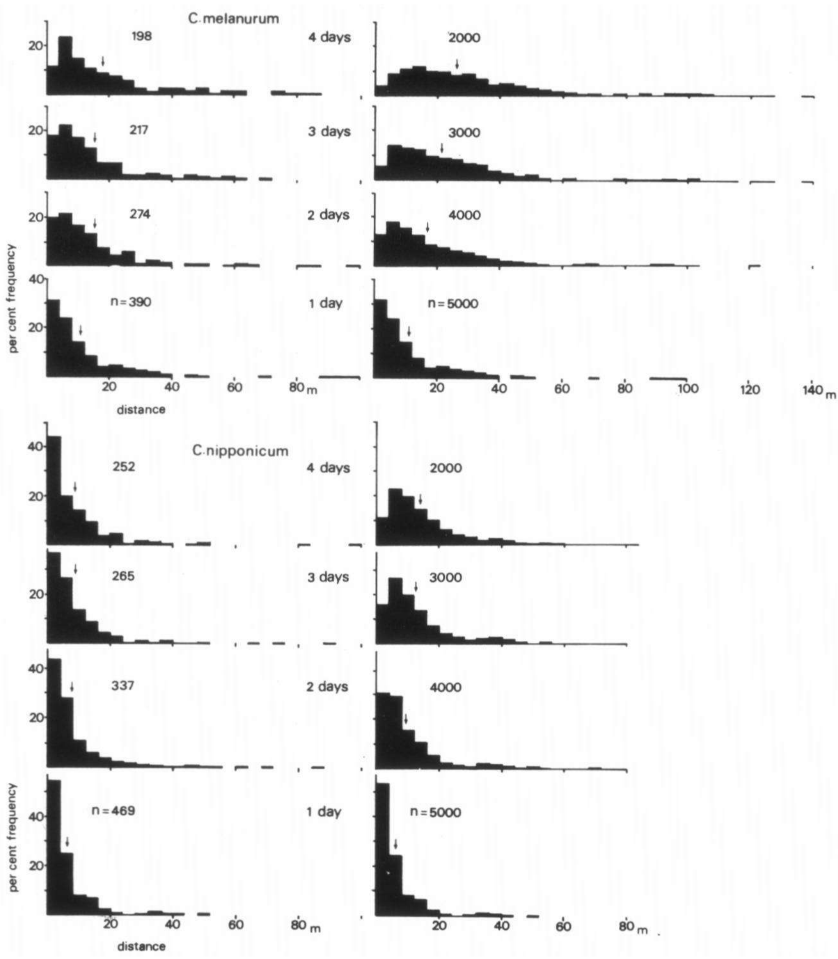

Fig. 2. Frequency distribution of distances moved in the male. A result of random flights obtained by a computer simulation (which was conducted assuming the individuals moved in all directions at random on the basis of the frequency distribution of distances moved for one day) is shown on the right side of the figure. Mean values are arrowed.

together with 1982. As seen from Table I, there was no marked male/female difference for both species in the distance moved per day during the first 5 days or so. When investigating further details of males (for which more measurements had been made than for females), even after 12 days, more than 90 percent of the individuals stayed within 40 m in *C. melanurum* and 20 m in *C. nipponicum* of their original locations.

The frequency distribution was calculated from the measurements of distances moved between consecutive days, i.e. distances moved for one day, which had been obtained for males of the two species. On the basis of this, a computer simulation was conducted on the daily movements of individuals, assuming they moved in all directions at random. Figure 2 shows the frequency distribution of the distances from original locations obtained over 4 days. It is quite clear from the figure that both *C. melanurum* and *C. nipponicum* are more or less resident in nature staying mainly at their original living sites and returning if they move away from there. In both sexes of both species cases were often observed in which an individual, after having moved over 10 m away to the waterside, was found to have returned to the neighbourhood of its original site the following day.

In *C. nipponicum,* most individuals, both males and females, shifted their perches to the waterside gradually from the morning, some male individuals perching on emergent plants on the surface of water. Late in the afternoon, on the other hand, they moved in the opposite direction. The distance moved was mostly within 1-3 m when oviposition had not taken place.

DISTRIBUTION OF INDIVIDUALS

Figure 1 shows a case (one day, 9:00 - 10:00 h July 28, 1981) in which individuals were sighted at the place of research. The following analysis was conducted on individuals actually sighted.

The data for all days were processed to give a frequency distribution of the number of individuals sighted in a certain quadrate (4 m x 4 m), from which the mean crowding (LLOYD, 1967)* was calculated. The relation between the mean crowding and each mean value is illustrated in Figure 3. Since the habitat partly underwent land modification in 1982 and became narrower, Figure 3 illustrates the results for each year separately. According to IWAO (1968), there is a linear relationship between the mean (m) and mean crowding ($\overset{*}{m}$), giving a random (Poisson) distribution if the gradient of the regression line equals 1, and aggregated distribution if the gradient is greater than 1.

All of the linear regressions in Figure 3 were found to be statistically significant ($p < 0.01$ in all cases). The values of the gradient were as follows: 1.89 ($r = 0.85$) and 1.39 ($r = 0.80$) in the male of *C. melanurum* in 1981 and 1982, respectively; 1.85 ($r = 0.87$) and 1.56 ($r = 0.91$) in the female of *C. melanurum* in 1981 and 1982, respectively; 5.22 ($r = 0.85$) and 3.44 ($r = 0.90$) in the male of *C. nipponicum* in 1981 and 1982, respectively; 9.05 ($r = 0.88$) and 7.87 ($r = 0.92$) in the female of *C. nipponicum* in 1981 and 1982, respectively. All these results indicated an aggregated distribution and it was far more aggregated in *C. nipponicum* than in *C. melanurum* (Fig. 3).

* LLOYD (1967): mean crowding ($\overset{*}{m}$): $\overset{*}{m} = m + \frac{\sigma^2}{m} - 1$, where m is the mean of the number of individuals per quadrate and σ is the standard deviation.

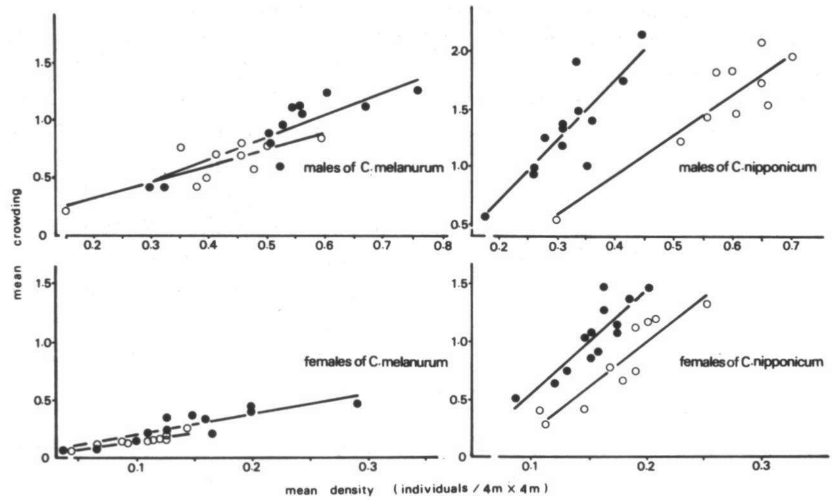

Fig. 3. Relation between mean crowding and mean density of individuals sighted. Solid and open circles are for 1981 and 1982, respectively.

As shown in these results, both sexes of *C. nipponicum* had an aggregated distribution. Groups of males stayed close to those of females, i.e. males formed their groups near the waterside and females crowded about surrounding them (Fig. 1).

The oviposition sites of *C. nipponicum* were usually located at the waterside in front of the sites where males crowded and so the oviposition site of this species was more localized than that of *C. melanurum*.

DISCUSSION

There is a pronounced tendency for mature adults of both *C. melanurum* and *C. nipponicum* to remain at or return to places where they had originally been staying, not moving a long way off. The female-searching flight by males of *C. melanurum* lasts longer than other types of flight (MIZUTA, 1988). They make about two hundred searching flights within a day on the average, the total flight distance amounting to about 900 m; nevertheless, they make relatively few day-to-day movements from one site to another (Tab. I and Fig. 2). Thus, the two species are considered to be strongly resident in nature. PARR (1973, 1976) and PARR & PARR (1979) have observed the movements of adults of *Ischnura elegans, Enallagma cyathigerum* and *Ceriagrion tenellum*. In sectors averaging 100 m long, 71.1% of *I. elegans* males were always recaptured in the same sector in which they had been marked (PARR, 1973). In sectors averaging 44 m long, about 47% of *I. elegans* males always remained in the same sector, but only 22.6% of *E. cyathigerum* males did so (PARR, 1973, 1976). In *C. tenellum* 81.4% of males stayed in the same sector (average length: 83 m) (PARR & PARR, 1979). PARR & PARR (1979) have concluded that *C. tenellum* seems to be the most static of the three species. GARRISON (1978) has worked with *Enallagma cyathigerum* and *Argia vivida* in California for ten consecutive days. The farthest distance moved was 288 m for a male *E. cyathigerum* and 200 m for a male *A. vivida*, and 27% of *E. cyathigerum* males moved more than 100 m (GARRISON, 1978). MESKIN (1986) has observed the territorial behaviour of *Pseudagrion hageni tropicanum*. At the waterside males of this species occupy small areas (about 1 m from one side to the other) throughout the day, driving other conspecific males. The male returns to the same territory on successive days. MESKIN (1986) has reported that some males occupied the same territory for up to 39 days.

The distribution of individuals of *C. nipponicum* is strongly aggregated. On the other hand, in *C. melanurum* which has less aggregated distribution and the male of which makes female-searching flights, the day-to-day distances moved from one site to another are greater than in *C. nipponicum* (Tab. I).

How to find a mating partner and copulate with it has much in common with how to get food resources. In general, this is reduced to a problem of optimal searching (PARKER, 1978). PIANKA (1986) has classified the foraging modes in desert lizards into two types: "sit-and-wait" type and "widely foraging" type, and has discussed the relation between these types and the characteristics of their prey. He argues that it is necessary in order for the foraging tactics of "sit-and--wait" type to pay off that prey moves and it is distributed densely. Basically, the distribution of prey seems to be of importance. When these foraging tactics are compared to the mate-locating tactics in damselflies investigated in this study, the "widely foraging" type will correspond to the "searching" type in the male of *C. melanurum* and the "sit-and-wait" type will correspond to the "sit-and-wait" type in the male of *C. nipponicum*.

Individuals of both sexes in both species mate only once a day, but they can mate every day (K. Mizuta, unpublished). In *C. melanurum*, where receptive females are distributed relatively sparsely, males make searching flights actively and, once they find females, mate on the spot. In *C. nipponicum*, on the other hand, female individuals make their relative distribution density higher by gathering together while male individuals make their mating probability higher by gathering in the vicinity of the female groups. Also the female of this species does not fly very often (MIZUTA, 1988). So it is necessary for the male waiting for females to make investigatory flights and identify female individuals in order not to miss the chance to mate. Consequently, the frequency of investigatory flights among male individuals is increased but this interaction among males does not go so far as to bring about fighting. The male individuals become distributed about

50 cm away from each other as a result of the interaction among themselves. This type of behaviour has been observed in *Enallagma cyathigerum* and *Ceriagrion tenellum* as well (PARR, 1976; PARR & PARR, 1979).

There is a spectrum of types of territoriality. Males of *C. nipponicum* defend the perch site only for a short time. It is rather considered that the "perch defence" mechanism has evolved to a certain extent so as to reduce the loss caused by fighting. Therefore, the male distribution in *C. nipponicum* is considered to be a spaced-out aggregation.

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