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ECOLOGICAL AND BEHAVIORAL ISOLATION AMONG *MORTONAGRION SELENION* RIS, *CERIAGRION MELANURUM* SELYS, AND *COPERA ANNULATA* (SELYS) (ZYGOPTERA: *COENAGRIONIDAE, PLATYCNEMIDIDAE*)

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The mechanisms by which the very small *M. selenion* avoids predation by *C. melanurum* and *C. annulata* are analyzed. These are: (1) difference in perching site; – (2) *C. selenion*'s remaining perched immobile for long periods; – (3) difference in place of maximal activity; – (4) non-overlapping periods of maximal activity; – (5) simple escape.

INTRODUCTION

Dragonflies are generalized and obligate carnivores, yet predation by other odonate species appears to be less important than by the same species (CORBET, 1962). There are reports of one zygopteran preying upon another (e.g. BICK & BICK, 1961, 1968; BICK & SULZBACH, 1966; CORBET, 1962; HOBBY, 1933, 1936), but these often involve capture of tenerals by matures of the same species, or capture of few individuals. No one has considered interspecific predation among mature Zygoptera an important factor in reducing population size. It would be significant to learn how the small and apparently vulnerable Zygoptera avoid being preyed upon by the larger zygopterans with which they are closely associated. The present research considers temporal, spatial, and behavioral mechanisms in an attempt to explain how the very small *Mortonagrion selenion* Ris (a member of a subfamily which FRASER, 1957 states contains the smallest members of the entire Order) avoids predation by the larger *Ceriagrion melanurum* Selys and *Copera annulata* (Selys).

THE HABITAT AND THE SPECIES

The study area was eight small, shallow (0-40 cm) ponds, four of which were used for raising carp, on the campus of Hiroshima Agricultural College. Only one had extensive open water; in the others vegetation was abundant with *Isachne globosa* the dominant species.

The study was from 12-25 July, 1973. On 12 July, sunrise was at 05.07 hours (JST), sunset at 19.25; on 25 July, sunrise was at 05.15, sunset at 19.18. Fine to fairly fine weather prevailed throughout. Average minimum temperature was 23°C at about 05.00, average maximum 33°C at 14.00-15.00.

Zygopterans present in small numbers in a restricted area were: *Cercion sieboldii* (Selys), *C. calamorum* Ris, *Ischnura asiatica* Brauer; while *selenion, melanurum*, and *annulata* were abundant. The anisopterans: *Orthetrum triangulare melania* Selys, *O. albistylum speciosum* Uhler, *Crocothemis servilia* Drury engaged in territorial behavior at the ponds every morning, but, flying at greater heights, scarcely ever encountered the zygopterans.

M. selenion, the smallest (TL. 25 mm, HW. 15 mm, Abd. 21 mm) of the three species studied, lives among emergent plants scarcely ever flying over open water. On 18 July, density, including immatures and matures of both sexes, was $4.7 \pm 2.6/m^2$ and the total population was estimated at 500-1000. Adults were present from 1 May to mid August with a peak from the middle of to the end of June. Females oviposit unaccompanied near the water surface.

Adults of *melanurum* (TL. 38 mm, HW. 20 mm, Abd. 30 mm) were present from the end of May to 1 September, and were most abundant from the middle of to the end of July. They rest on grasses a short distance from water. Oviposition is in tandem with the male in the upright position.

C. annulata (TL. 40 mm, HW. 25 mm, Abd. 35 mm) lives in ponds or slowly flowing streams shaded by trees. The diffuse emergence extends from 1 May to the end of September with a peak from 1 June to mid August. Oviposition is as in *melanurum*.

At seven areas, both *selenion* and *melanurum* were present; at four *melanurum* occurred alone, but *selenion* never occurred without *melanurum*.

METHODS

All work was with mature individuals under field conditions. Three categories of information were obtained:

(1) Responses to anaesthetized models. A freshly anaesthetized individual was fixed from the abdomen by a thin wire set on top of a small rod. Such a model was presented 10-20 cm in front of the individual to be tested and the response recorded. By this method, experiments were performed to test: (a) reactions of males and females of the same or of other species (Tab. I), (b) hourly fluctuation

in the male's tandem response (Fig. 1).

(2) Counts of males in sexual flight and of pairs (Fig. 2) were determined by slowly walking a fixed course at each hour on July 12, 16, 18, 25.

(3) Hourly activity of *selenion* (Tab. II, Fig. 3). Each behavior and its duration was recorded for a 5-min interval during each hour of the day. This interval was sufficient to score behavior because of the usual brevity of each event. A tape recorder was sometimes used to record more than two individuals simultaneously. Feeding and copulating individuals were excluded. There was no difficulty in placing all activity (or lack of it) in the following categories: (1) perching, (2) simple flight – a short, quick flight for unknown reason followed by a return to the same perch, (3) feeding flight – a dashing flight to a small insect or even to mud spots usually with a shift of perch site, (4) sexual flight – when searching for females, males flew among plants in a distinctive zigzag pattern 10-40 cm above the surface.

RESULTS

(1a) Responses to anaesthetized models (Tab. I). Three results were of primary importance: (a) capturing and biting responses did not differ significantly between 10.30 and 15.30; (b) both *melanurum* males and *annulata* males showed medium to strong biting reactions to *selenion* males and females; (c) *selenion* males often showed escape reactions to *melanurum* and *annulata* females, and even to a female of the same species.

(1b) Hourly fluctuations in the tandem response (Fig. 1). The time of tandem response was much briefer in *selenion* than in the other two. It commenced 15 min before sunrise, was at a maximum from 05.00 to 07.00 and never occurred after 09.00. Tandem response in *melanurum* was at a maximum near noon and then decreased rapidly although it lasted until 16.00. These in *annulata* reached a maximum at 10.00 and thereafter decreased with a few still occurring at 17.00.

(2) Hourly fluctuations in pairing and in male sexual flight (Fig. 2). The unique sexual flight of males searching for females could be distinguished readily from all other flights. Males of *selenion* began sexual flight 10-15 min before sunrise when light intensity was only 20-50 lux and they were active for about four hours thereafter. Pairing, at a maximum from 06.00 to 07.00, coincided with male sexual flight and with the tandem response reactions given above. There are apparently no records of sexual activity so early in the morning for any other zygopteran. Sexual flight in *melanurum* was from 09.00 to 14.00, tandem oviposition from 10.00 to 14.00. In contrast, sexual flight and pairing in *annulata* continued for many hours; the 08.00 peak for pairing was earlier than in *melanurum*, later than in *selenion*. Time in copulation was: *melanurum* – 1-3 min, *annulata* – about 0.5 hr, *selenion* – 0.5-1.5 hr.

(3) Hourly activity of *selenion* (Tab. II, Fig. 3). This species is an outstanding

Table I

Response (%) of three zygopteran species, *Mortonagrion selenion, Ceriagrion melanurum*, and *Copera annulata*, to anaesthetized male and female models of these species

Response of	to anaesthetized	Time of trial	No. of trials	Tandem	Approach flight from behind	Orientation	Capturing & biting	Dashing flight	Escape flight	No response
melanurum ♂	*selenion* ♂	10.30	27	–	–	7.4	37.0	18.5	–	37.0
melanurum ♂	*selenion* ♂	15.30	40	–	–	–	47.5	15.0	–	37.5
melanurum ♂	*melanurum* ♀	10.30	26	80.8	7.7	3.8	–	–	–	7.7
melanurum ♂	*melanurum* ♀	15.30	38	10.5	10.5	15.8	2.6	–	15.8	44.7
melanurum ♂	*annulata* ♀	10.30	42	2.4	4.8	28.6	4.8	–	9.5	50.0
annulata ♂	*selenion* ♂	10.30	40	–	–	5.0	20.0	7.5	–	67.5
annulata ♂	*selenion* ♂	15.30	43	–	–	–	20.9	4.7	4.7	69.8
annulata ♂	*melanurum* ♀	10.30	36	–	–	16.7	–	–	11.1	72.2
annulata ♂	*annulata* ♀	10.30	31	80.6	9.7	9.7	–	–	–	–
annulata ♂	*annulata* ♀	15.30	80	31.3	6.3	13.8	–	–	11.3	37.5
selenion ♂	*selenion* ♀	10.30	21	–	23.8	23.8	–	–	–	52.4
selenion ♂	*selenion* ♀	15.30	24	–	12.5	16.7	–	–	8.3	62.5
selenion ♂	*melanurum* ♀	10.30	25	–	8.0	8.0	–	–	56.0	28.0
selenion ♂	*annulata* ♀	10.30	28	–	–	14.3	–	–	35.7	50.0
melanurum ♂	*selenion* ♀	15.30	56	–	–	–	60.7	23.2	–	16.1
annulata ♂	*selenion* ♀	15.30	47	–	–	–	14.9	12.8	6.4	66.0
selenion ♂	*selenion* ♂	15.30	22	–	4.5	13.6	4.5	–	9.1	68.2

percher and, except for the early morning male sexual flights, spends approximately 90% of its time during every hour of the day perched – usually on vertical stems of *I. globosa* and *Eleocharis* spp. Perch heights, always lower than those of *melanurum* and *annulata*, varied with time and sex. Between 09.00 and 15.00 the average was 9 cm (♂), 5 cm (♀), from 17.00 to 19.00 it was 13 cm (♂), 11 cm (♀), and during the night both sexes perched at 10-30 cm. At mid day most males perched on the shaded part of the stem and oriented to avoid the direct sun rays.

Simple flight for both males and females never occupied more than 1% of the 5 min interval at any hour. With regard to feeding, it is interesting to note that the daily average capture rate was only 2.8% (♂), 2.7% (♀), and that it took 0.5-1 hr to chew and ingest a large chironomid. Although posture and duration was the same for males and females during both simple and feeding flights, frequency was slightly lower in males, especially near noon.

The unique sexual flights of males, occurring only from 05.00 to 08.00, were at a maximum at 06.00 when they consumed 31% of the time and occurred at a

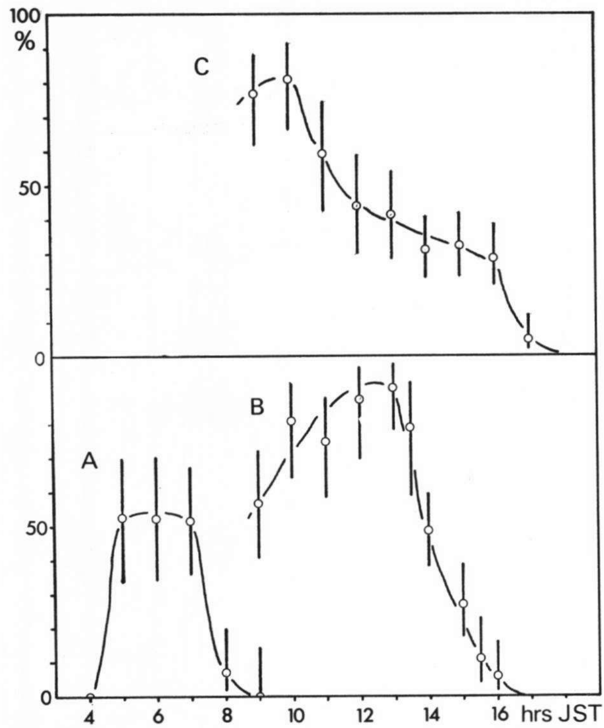

Fig. 1. Hourly fluctuations in the tandem response of males of *selenion* (A), *melanurum* (B), *annulata* (C) to conspecific anaesthetized females expressed as percent of the individuals showing such a response. Vertical lines show 90% confidence limits.

rate of approximately four per 5 min interval. These times of male sexual flight coincide with the foregoing results for anaesthetized females and for daily counting.

Oviposition was between 09.00 and 17.00, and the greatest proportion of time spent in oviposition flight was at 11.00. A change in oviposition site by the unaccompanied female was rare, occupied an extremely small proportion of time, and such oviposition flights lasted only 1-3 sec.

DISCUSSION

I have shown (unpublished) that the upper threshold of size and form eliciting biting in *melanurum* is as large as its own species and that this nearly equals the critical size eliciting escape response. Clearly, *selenion* satisfies conditions which will elicit biting in *melanurum*, and this was demonstrated by a high biting response even at 10.30 when the intensity of the sexual drive in

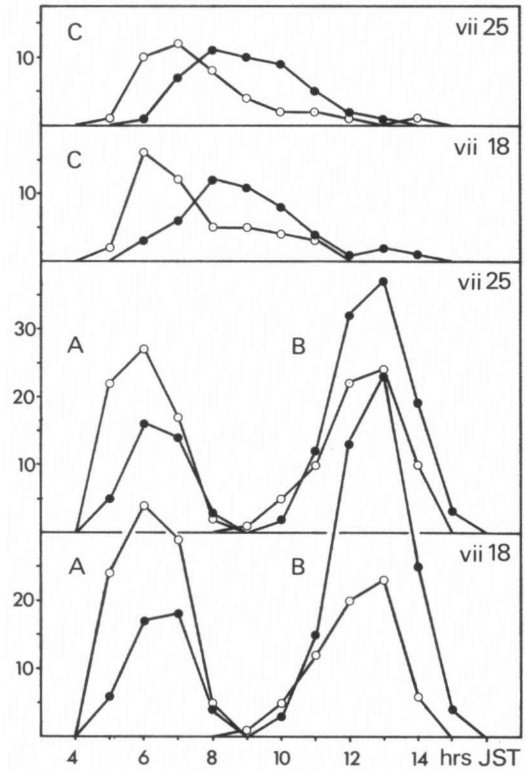

Fig. 2. Hourly fluctuations in number of males in sexual flight (open circles) and pairs (solid circles) based on hourly counts on two days. (A) *selenion*, (B) *melanurum*, (C) *annulata*.

melanurum was high. Despite the possibility that *selenion* might be heavily attacked by *melanurum*, I saw such predation only twice. This study shows that the following mechanisms shield *selenion* from predation by other zygopterans:
(1) The only possible zygopteran predators of *selenion* were *melanurum* and *annulata*, and, since *selenion* never left the aquatic habitat, contact could only be at water. Because *annulata* perched in tree-shaded areas where *selenion* was scarce and flew over open water where *selenion* never occurred, there was hardly a chance for *selenion-annulata* contact. Encounters between *melanurum* and *selenion* were more likely, but the former oviposited in deeper water.
(2) In unpublished results, I showed that *melanurum* is more sensitive to mobile objects than to immobile ones. Except for sexual flight, *selenion* remains perched for 90% of the time and apparently avoids *melanurum* predation by simply remaining perched for such long periods.
(3) All *selenion* activity is very close to water, that of *annulata* and *melanurum*

Table II

Hourly fluctuation in the per cent of time spent in each behavior by *selenion*, based on a 5 min observation period for each hour

Time	No. of ♂♂ observed	♂ Sexual flight	♂ Feeding flight	♂ Simple flight	♂ Perching	No. of ♀♀ observed	♀ Feeding flight	♀ Simple flight	♀ Oviposition	♀ Oviposition flight	♀ Perching
5	20	26.6	–	–	73.4	–	–	–	–	–	–
6	26	31.5	–	0.2	68.3	–	–	–	–	–	–
7	20	19.9	0.5	0.1	79.5	–	–	–	–	–	–
8	24	2.9	0.8	0.2	96.1	9	1.3	0.0	–	–	98.7
9	25	–	2.7	0.2	97.1	21	1.8	0.2	0.2	–	97.8
10	30	–	2.7	0.2	97.1	23	3.6	0.5	2.8	0.1	93.0
11	35	–	2.6	0.3	97.2	17	3.7	0.6	14.5	0.3	81.0
12	39	–	0.7	0.2	99.1	28	4.2	0.5	7.4	0.1	87.8
13	35	–	0.6	0.2	99.3	19	2.7	0.3	5.3	0.0	91.6
14	31	–	0.3	0.1	99.6	31	2.2	0.7	4.1	0.1	92.9
15	41	–	0.8	0.1	99.1	35	2.8	0.5	4.1	0.1	92.4
16	42	–	1.5	0.1	98.4	31	3.1	0.3	2.2	0.0	94.4
17	52	–	1.2	0.2	98.6	45	4.1	0.4	0.8	0.0	94.6
18	46	–	2.1	0.2	97.7	28	3.4	0.2	–	–	96.4
19	23	–	0.8	0.2	99.0	29	0.4	0.3	–	–	99.4

at greater heights.

(4) In contrast with other zygopterans (BICK & BICK, 1963; LUTZ & PITTMAN, 1970), *selenion* is most active and very likely most vulnerable to predation during male sexual flight and pairing. The extraordinary early morning reproductive activity of *selenion* in no way overlaps that of *melanurum* and thus rules out *melanurum* as an effective predator of *selenion* at these morning hours. Time of sexual activity in *selenion* and *annulata* did overlap, but habitat differences rule out an effective predatory role for *annulata*.

(5) The final mechanism is simple escape. The escape reaction of *selenion* males when presented with *melanurum* and *annulata* female models suggests that, in the rare event these species would approach *selenion*, the latter would avoid predation by simple escape flight.

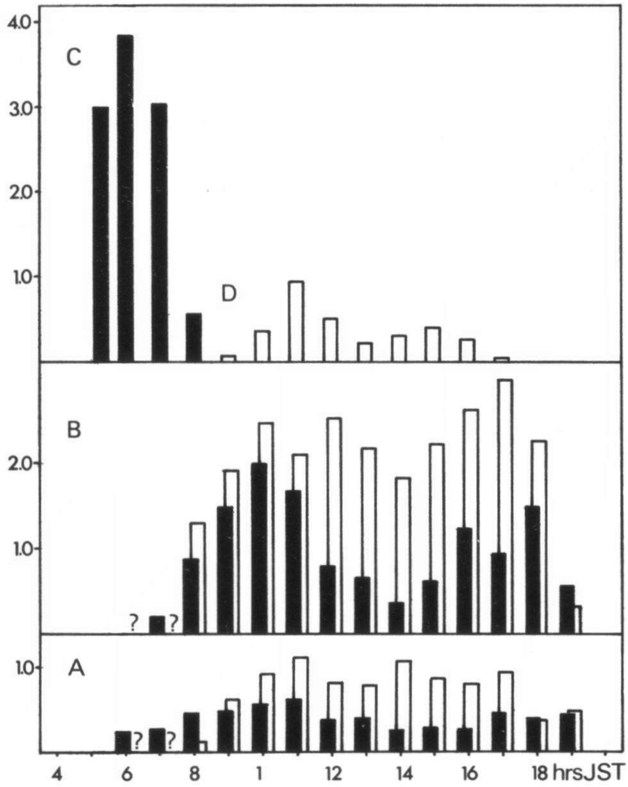

Fig. 3. Hourly fluctuations in average number of activities per 5 min interval in *selenion*. (A) simple flight, (B) feeding flight, (C) sexual flight, (D) oviposition flight. Solid columns indicate males, open ones females.

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