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# REPRODUCTIVE BEHAVIOUR AND LIFE SPAN OF ADULT *CALOPTERYX ATRATA* SELYS AND *C. VIRGO JAPONICA* SELYS (ODONATA : ZYGOPTERA)

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*Calopteryx atrata* has weak sexual dichromism of the wings, and females lack pseudopterostigmata whereas *C. cornelia* and *C. virgo japonica* have stronger sexual dichromism, with pseudopterostigmata present in the female. The mating sequence of *atrata* is described and compared with that of the other two, based on a review of 6 species hitherto studied by several authors. Life span estimates for *C. atrata* and *C. virgo japonica* are presented. Their survival curves are somewhat different from each other.

## INTRODUCTION

The genus *Calopteryx* has been intensively studied from the ecological and ethological view points in Europe and America (BUCHHOLTZ, 1951, 1955; ROBERT, 1959; ZAHNER, 1960; JOHNSON, 1962; PAJUNEN, 1966; KLÖTZLI, 1971; HEYMER, 1973; WAAGE, 1972, 1973, 1979 and others). For the Japanese *Calopteryx*, however, only two species have been studied: *C. cornelia* (YAMAMOTO, 1955; ASAHINA & EDA, 1960; OSADA, 1961; SUZUKI & TAMAISHI, 1981; HIGASHI, 1973; SATO, 1982) and *C. virgo japonica* (AIDA, 1974). No paper has appeared for *C. atrata*.

During the summers of 1980 and 1981, I carried out an investigation on natural populations of adult *Calopteryx atrata* and *C. virgo japonica*, inhabiting the same section of Koma river, Hidaka, Saitama Prefecture, Japan.

This paper deals with reproductive behaviour and life span of adult *C. atrata* and *C. virgo japonica*, with comparative notes on the mating behaviour of *C. cornelia*, and gives a review through the genus.

## STUDY AREA AND METHOD

Investigations were made along a 50 m section of the Koma river. The river at this section is 30 to 40 m wide and water flows above the stony river bed. In the permanent water region along the shore, *Elodea nuttali* and *Potamogeton crispus* grow, and on the bank, *Phragmites japonica.* The shore vegetation is composed of grasses, bamboos, shrubs and trees. This section of the river is inhabited by several species of Odonata. For the genus *Calopteryx,* this area is used for breeding by *C. cornelia* from the last week of May to the first week of June, by *C. virgo japonica* from then to mid-July and by *C. atrata* from then to early October. Interspecifical competition for the breeding sites was observed only for a very short period in mid-July between males of *C. atrata* and *C. virgo japonica. C. cornelia* was present throughout the summer, but was scarce except in very early summer.

Individuals were marked on the ventral side of both hind wings with an oil colour paint. Marked individuals usually behaved normally within several minutes of being released, and the mark was easily recognized even in flight from a distance of more than 10m by using binoculars. For recording data, a portable tape recorder and a 35 mm reflex camera with 105 mm lens were used. Observations were made for 1 to 2 hrs a day, every day whenever possible, or at intervals of 2 or 3 days.

## OBSERVATIONS

### REPRODUCTIVE BEHAVIOUR

The sequence of reproductive behaviour of territory forming males hitherto known in the genus *Calopteryx* can be summarized as follows:

(A) Pair-forming display – in which the male displays his wings and often his abdomen to an approaching female at the oviposition site

(B) Courtship flight – facing the perched female, with the same mode of flight as in the pair-forming display

(C) Mounting the folded wings of the perching female usually after refusal display of the female

(D) Grasping the female with his abdominal appendages on the same perch to form the tandem

(E) Sperm translocation to his accessory copulatory organ on the perch
(F) Copulation on the perch
(G) Postcopulatory display of wings and abdomen to female at the oviposition site
(H) Postcopulatory guard for oviposition of the mated female.

In non-territorial males, processes A, G and H are lacking.

*Calopteryx atrata*

The sequence of mating behaviours of this species is illustrated in Figure 1.

When the female approaches, the male begins the pair-forming display with rapid wing beating, facing her, hovering above the aquatic vegetation which serves as the oviposition site (A). *C. atrata* males do not curl their abdomens dorsally, as happens in most of the other *Calopteryx* species. The venter of the tip of the abdomen in *C. atrata* is whitish pruinescent, but is much duller than that of *C. virgo japonica.* When the approaching female perches on the vegetation, the male performs the courtship flight hovering in front of her (B), and attempts mounting by landing on the base of her folded wings (C). In *C. atrata* females the pseudopterostigma is lacking. This position of mounting differs from that in *C. cornelia* and *C. virgo japonica* and also other *Calopteryx* species reported by several authors. In the latter group of species, the male mounts on or near the pterostigma at the top of the folded wings of the female and then walks down the front edge of the wings to grasp the female's prothorax and form the tandem. When grasping, the male holds the middle and hind femora and rear edge of the folded wings of the female with his tarsal claws, and pushes her head forwards with his mouthparts (D). After the tandem is formed, the male moves onto the perch and translocates sperm from the genital pore on the 9th abdominal segment to the sperm vesicle of his accessory copulatory organ on the 2nd abdominal segment (E). The female then bends her abdomen forwards, and copulation takes place (F). Its mean duration was 77 sec (range 31-157 sec, N = 50). Immediately after copulation, the male returns to the perch near the water surface, while the female remains resting there for some minutes. When the mated female flies down to the water surface, the male guides her to the oviposition site. Occasionally he alights on the site displaying the venter of his abdominal tip, like the perching display of other species (G). During her oviposition, he chases approaching males (H). The female prefers *Elodea, Po-*

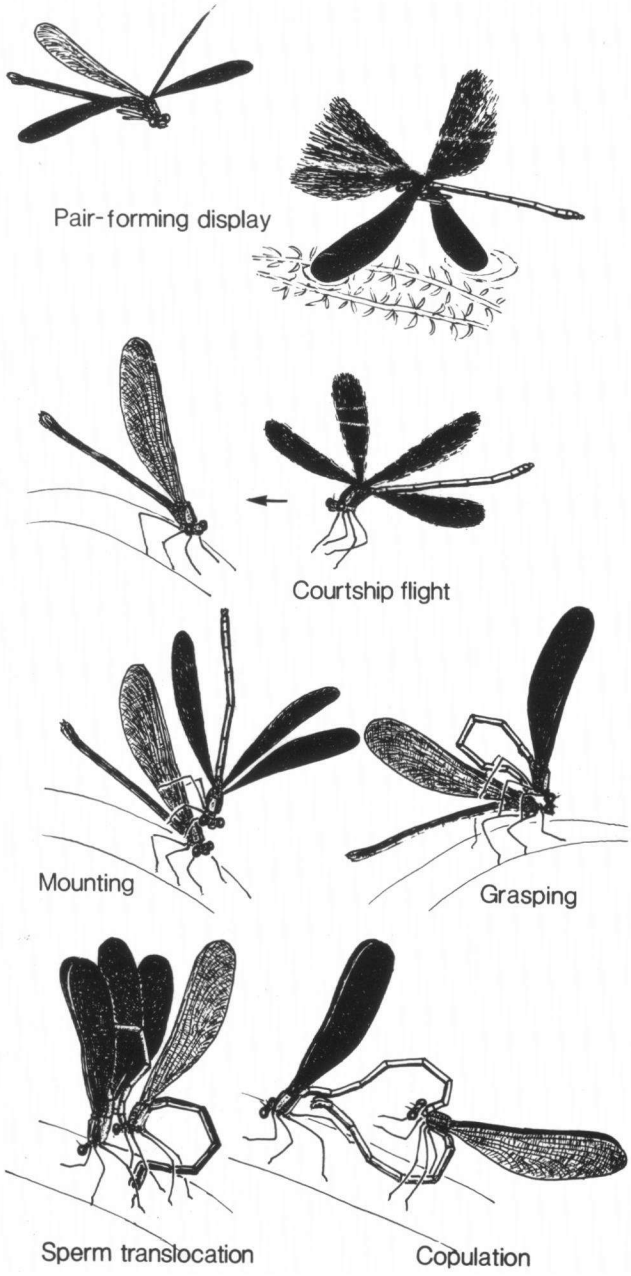



**Fig. 1. Mating sequence of *Calopteryx atrata* Selys. For further explanation see text.**

*tamogeton* and *Phragmites* as oviposition sites. Oviposition is of the surface type only.

*C. virgo japonica*

As a large part of the sequence of mating behaviour of the species is similar to that of *C. atrata*, only some points of difference are described here.

The *C. virgo japonica* males perform the pair-forming display differently. He perches on emergent aquatic plants or floats on the water surface, adopting a posture with wings nearly closed or pointing postero-lateralwards at a small angle and with the abdomen tip strongly curled dorsally (A). The venter of the 10th abdominal segment and of the inferior appendage have a brilliant white colour.

Another difference is found in the mounting of the female (C). After courtship flight, the male mounts on or near the tip of the folded wings of the female and at the level of the pterostigma. Mean duration of copulation was 104 sec (range 56-183 sec, N = 19). Like *C. atrata*, females prefer *Elodea, Potamogeton* and *Phragmites* for oviposition sites, but they adopt both surface and subsurface oviposition. The latter type of oviposition was often observed in a rapidly flowing area. Duration of subsurface oviposition ranged from 26-123 min (N = 10).

*C. cornelia*

Mating behaviour of *C. cornelia* closely resembles that of *C. virgo japonica*. The pair-forming display of the male (A) is exclusively of the floating type and is quite similar to that of *C. virgo japonica* in posture. After courtship flight (B), the male mounts on the tip of the folded wings of the female and walks slowly along the front edge of the wings (C). These processes, B and C, closely resemble those in *C. virgo japonica* but motion of *C. cornelia* appeared slower than *C. virgo japonica*. In *C. cornelia* females, the pterostigma is present. After the sperm translocation, copulation occurs and its mean duration was 254 sec (range 230-278 sec, N = 2). The females oviposit into dead or hard plants, rather than soft aquatic plants, and they adopt both surface and subsurface oviposition. Thus the oviposition site of this species is somewhat different from *C. atrata* and *C. virgo japonica*.

### LIFE SPAN OF IMAGINAL STAGE IN *C. ATRATA* AND *C. VIRGO JAPONICA*

Duration of the teneral period of both these species was estimated from the length of time between the beginning of emergence and beginning of activity on the water area. In addition, 11 males and 4 females of *C. virgo japonica* were marked just after emergence and 5 of the males were seen again after their teneral period. Six of the males returned to the water between 9 and 17 days after marking and one returned at 7 days but was still teneral. Both these estimates suggest that the teneral period is about 11 days. Data from the marked males suggest that several more days are needed to reach the age of reproduction. This additional delay until the commencement of reproductive activity may be due to difficulty in obtaining territories during the breeding season, except at its beginning.

Adult life span was estimated from the time between marking and last resighting within the study area.

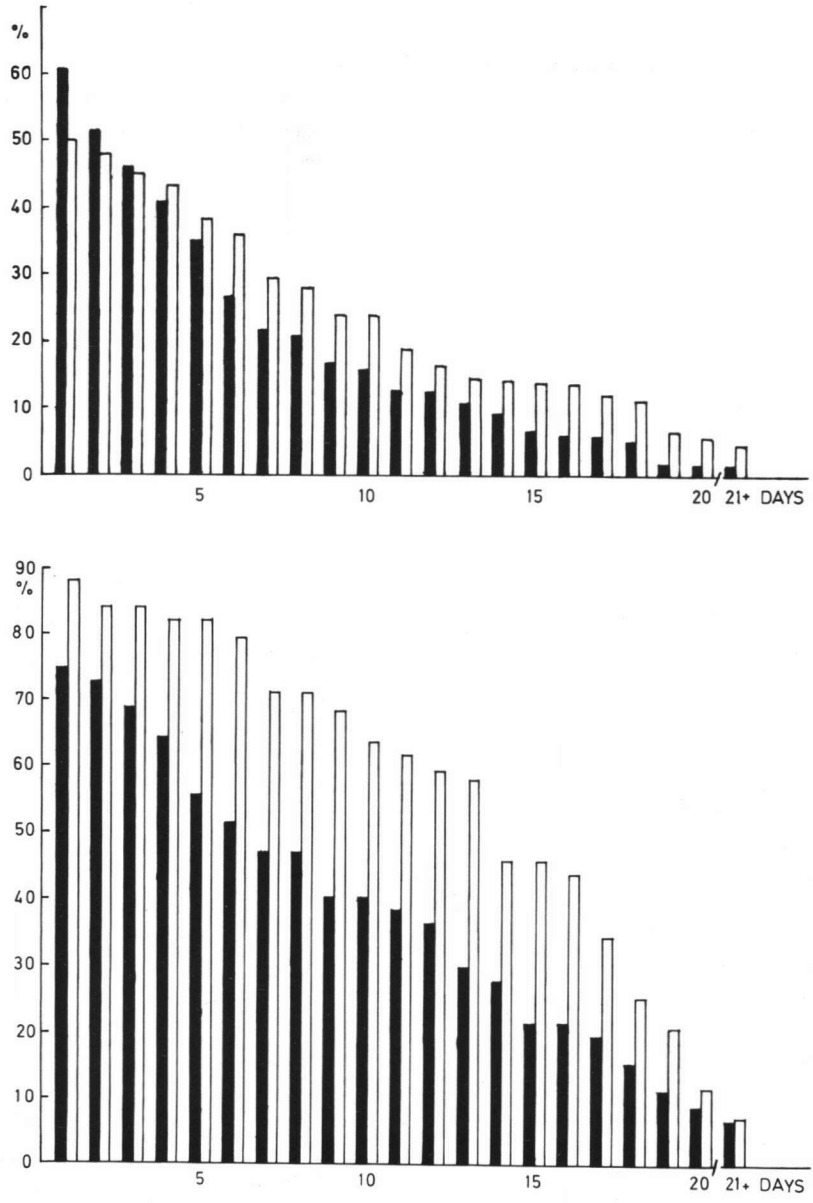
Between 14 August and 12 October 1980, 120 males and 124 females of *C. atrata* were marked and 73 males and 61 females were resighted. Mean life span was 6.88 days (S.E. = 0.69, Max. = 28) for males and 10.33 days (S.E. = 0.93, Max. = 34) for females. Seasonal difference between August and September was not significant. The survivorship curve for *C. atrata* is shown in Figure 2. Between 10 June and 16 July 1981, 47 males and 44 females of *C. virgo japonica* were marked and 35 males and 39 females were resighted. Mean life span was 8.77 days (S.E. = 1.25, Max. = 26) for males and 12.09 days (S.E. = 1.10, Max. = 32) for females. The survivorship curve for *C. virgo japonica* is shown in Figure 3.

## DISCUSSION

### COMPARATIVE NOTES ON THE REPRODUCTIVE BEHAVIOUR IN THE GENUS *CALOPTERYX*

My observations on the reproductive behaviour of *C. cornelia* and *C. virgo japonica* are identical with those of previous workers (YAMAMOTO, 1955; ASAHINA & EDA, 1960; OSADA, 1961; HIGASHI, 1973; AIDA, 1974; SATO, 1982). *C. virgo japonica* behaves similarly to European *C. virgo* (ZAHNER, 1960; PAJUNEN, 1966; HEYMER, 1973), but further observations by myself showed that the latter species behaved more slowly in mounting and grasping than the former (Miyakawa, unpublished data at Bergerac, France, 1981).

Pair-forming display of *Calopteryx* males can be divided into 5




Figs 2-3. Histograms of survival rates during post-maturation period based on number of days from marking to last resighting, expressed as the percentages surviving out of total number (N) of individuals marked. Black, male; White, female: (2) *Calopteryx atrata* male N =120. max. 28 days; female N = 124. max. 34 days; – (3) *C. virgo japonica*, male N = 47, max. 26 days; female N = 44, max. 32 days.

Table I

Pair-forming display of *Calopteryx* males

| Display type | Species | Locality | References |
|---|---|---|---|
| Hovering above the oviposition site; spread wings, without abdominal display | *aequabilis* | USA | Waage, 1973 |
| | *atrata* | Japan | present study |
| Gliding on the water surface; spread wings, abdomen display | *haemorrhoidalis* | Europe | Heymer, 1973 |
| | *splendens* | Europe<br>Asia min. | Buchholtz, 1951, 1955; Robert, 1959; Zahner, 1960; Heymer, 1973 |
| Floating on the water surface; folded wings, abdomen display | *cornelia* | Japan | Asahina & Eda, 1960; Higashi, 1973; Sato, 1979, 1982; |
| | *virgo* | Europe | present study, Zahner, 1960; |
| | *v.japonica* | Japan | Pajunen, 1966; Aida, 1974; |
| | *dimidiata* | USA | present study Waage (pers. comm.) |
| Perching on the oviposition site; nearly folded wings, abdomen display | *virgo* | Europe | Heymer, 1973; Miyakawa, (unpublished) |
| | *v. japonica* | Japan | Aida, 1974; present study |
| | *cornelia* | Japan | Miyakawa (unpublished) |
| Perching on the oviposition site; spread wings, abdomen display | *maculata* | USA | Waage, 1973 |

Table II

Duration of copulation (sec) in *Calopteryx*

| Species | Locality | Mean | Range | References |
|---|---|---|---|---|
| *atrata* | Japan | 77 | 31-157 | present study |
| *cornelia* | Japan | 254 | 230-278 | present study |
| *dimidiata* | USA | 144 | 77-228 | Waage (p. comm.) |
| *maculata* | Northern USA | 101 | 30-300 | Waage, 1973 |
| *maculata* | Southern USA | 300 | little variation | Johnson, 1962 |
| *splendens* | Europe | 90 | 50-150 | Buchholtz, 1951 |
| *splendens* | Asia Minor | 55 | – | Buchholtz, 1955 |
| *splendens* | Europe | – | 120-180 | Robert, 1959 |
| *virgo* | Europe | – | 120-300 | Robert, 1959 |
| *v. japonica* | Japan | – | 50-100 | Aida, 1974 |
| *v. japonica* | Japan | 104 | 56-183 | present study |

types, according to presence or absence of movement with flight and of abdomen display. In this behaviour, *C. atrata* is similar to *C. aequabilis*, while *C. virgo japonica* is close to *C. virgo*, *C. cornelia* and somewhat to *C. maculata* (Tab. I). These facts suggest a possible phylogenetic affinity. Duration of copulation in *Calopteryx* varies even in the same species (Tab. II). Subsurface oviposition is adopted

Table III

Types of oviposition in *Calopteryx*

| Type of oviposition | Species | Locality | References |
|---|---|---|---|
| Surface only | *atrata* | Japan | present study |
| | *haemorrhoidalis* | Europe | Heymer, 1973 |
| | *maculata* | USA | Johnson, 1962; Waage, 1973 |
| Surface and subsurface | *aequabilis* | USA | Johnson, 1962 (Kormondy) |
| | *cornelia* | Japan | Yamamoto, 1955, Asahina & Eda, 1960; Higashi, 1973; present study |
| | *splendens* | Europe | Buchholtz, 1951; Robert, 1959; Heymer, 1973 |
| | *virgo* | Europe | Robert, 1959; Pajunen, 1966; Heymer, 1973; |
| | *v. japonica* | Japan | Aida, 1974; present study |
| Subsurface only | most *aequabilis* | USA | Waage, (pers. comm.) (obs. in sympatry with *maculata)* |
| | *dimidiata* | N.E. USA | Waage, (pers. comm.) |

Table IV

Duration of subsurface oviposition (min) in the genus *Calopteryx*

| Species | Locality | Duration | References |
|---|---|---|---|
| *cornelia* | Japan | – to 18 | Yamamoto, 1955 |
| *cornelia* | Japan | – to 40 | Osada, 1961 |
| *cornelia* | Japan | – to 45 | Higashi, 1973 |
| *splendens* | Europe | – to 30 | Buchholtz, 1951 |
| *splendens* | Europe | – 15 to 20 + | Robert, 1959 |
| *splendens* | Europe | 25+ | Heymer, 1973 |
| *virgo* | Europe | –10 to 15+ | Robert, 1959 |
| *v. japonica* | Japan | 26 to 123 | present study |
| *H. americana* | USA | – to 52 | Bick & Sulzbach, 1966 |

by several *Calopteryx* species, and its maximum duration was found to exceed 2 hrs (Tabs III and IV).

## COMPARATIVE NOTES AND CONSIDERATIONS ON IMAGINAL LIFE SPAN IN *CALOPTERYX*

Maturation period and longevity estimates for different *Calopteryx* species are shown in Table V. These estimates reveal a uniform pattern of teneral periods and longevity, except for BUCHHOLTZ's (1951) and KLÖTZLI's estimates of the teneral period in

Table V

Life span estimates for different species of *Calopteryx* (in days)

| Species | Sex | Teneral | Adult Mean | Adult Max. | N | Locality | References |
|---|---|---|---|---|---|---|---|
| *atrata* | ♂ | 11 | 6-7 | 28 | 73 | Japan | present study |
| *atrata* | ♀ | 11 | 10-11 | 34 | 61 | Japan | present study |
| *cornelia* | ♂ | ten.+ adult | 16-17 | 52 | 62 | Japan | Suzuki et al., 1981 |
| *cornelia* | ♀ | ten.+ adult | 14-15 | 40 | 45 | Japan | Suzuki et al., 1981 |
| *haemorrhoidalis* | ♂ | 10 | 7-9 | 29 | 88 | Europe | Heymer, 1973 |
| *maculata* | ♂ | 11 | 5-8 | 37 | 235 | USA | Waage, 1972 |
| *maculata* | ♀ | 11 | 7-10 | 37 | 143 | USA | Waage, 1972 |
| *maculata* | ♂+♀ | 11 | 4-6* | 37 | 378 | USA | Waage, 1972 |
| *splendens* | ♂+♀ | 1-4 | 12** | | 10 | Europe | Buchholtz, 1951 |
| *virgo* | ♂ | 1-3 | 10-12 | 41 | 114 | Europe | Klötzli, 1971 |
| *virgo japonica* | ♂ | 11 | 8-10 | 26 | 35 | Japan | present study |
| *virgo japonica* | ♀ | 11 | 11-13 | 32 | 39 | Japan | present study |

* Median value analysed with U-statistic

** Data on 8 ♂ + 2 ♀ marked just after emergence

*C. splendens* and *C. virgo*.

Comparing the survivorship curves of the postmaturation period for *C. atrata* and *C. virgo japonica* (Figs 2 and 3), some specific and sexual differences are found. That for *C. atrata* is concave and is comparable to an exponential function curve, whereas that for *C. virgo japonica* is approximately linear in the male and convex in the female. When the survivorship curve is concave, the ecological life span is considerably shorter than the physiological life span. If it is convex, then both are close. The ecological life span is affected by predation and accidental death. *C. atrata* has a longer breeding season, higher population density and shorter individual life span than *C. virgo japonica*. Longevity differences between the sexes may be caused by territoriality which results in emigration by surplus males. On the other hand, an upstream migration was occasionally observed in both sexes. ZAHNER (1960) and WAAGE (1972) reported similar migration in other *Calopteryx*. This may also affect estimates of life span, unless the study area is large enough. Waage attempted to examine the influence of movement on longevity estimates.

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