

**AN EXPERIMENTAL STUDY OF SEX RECOGNITION IN *CORDULIA AENEAE AMURENSIS* SELYS (ANISOPTERA: CORDULIIDAE)\***

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The mechanism of sex recognition in adult males of *C. a. amurensis* was studied in an experiment in which the movement patterns of intact and modified test individuals were manipulated. Patrolling males usually behave agonistically (i.e. attack and retreat) against an individual which rushes at them, without perceiving sexual differences in external morphology. On the other hand, such males respond sexually to (i.e. try to copulate with) an individual which makes swinging (egg-laying) or escape movements and which has an abdomen thick at the base. Sexual differences in external morphology are perceived after an approach has been made.

INTRODUCTION

Recent studies on animal mating systems have provided much evidence for the theory that any individual behaves in a manner such that its reproductive success is maximized (cf. CAMPANELLA & WOLF, 1974; PARKER, 1978; BORGEA, 1979). According to this theory, if a species shows slight sexual dimorphism (including dichromatism), an individual better able to recognize the sex of another conspecific will have more reproductive success. It is argued, for instance, that for a male to chase another male for a long time while attempting to mate with it entails a loss of energy and time for the former male.

In the Odonata, MOORE (1952) proposed that the attacks and clashes seen among adult males result from their attempts to mate while being unable to discriminate the sex of another individual. Later, JACOBS (1955) demonstrated experimentally that males of *Perithemis tenera* can distinguish the sex of

\* Ecological studies of *Cordulia aenea amurensis* Selys, pt V.

encountered individuals and behave accordingly. As for species in which sexual color dimorphism is slight, KORMONDY (1959) supported Moore's view for the corduliid *Epiheca cynosura*, whereas PAJUNEN (1964) showed that sexual difference in the relative thickness of the base of the abdomen and in flight style act as releasers for sexual responses in males of *Leucorrhinia dubia*. Pajunen could not, however, show experimentally what the sexual difference in the flight style is, because he used the "fishing-line technique" for every experiment, and this did not allow him to control the movements of the test individuals.

In order to investigate more precisely the role of flight style in sex recognition of dragonflies, the present author made an experimental study with the corduliid, *Cordulia aenea amurensis*, the ecology of which has been intensively studied (UBUKATA, 1973, 1975, 1980, 1981). The present paper is the fifth report derived from this work. The behavior patterns of adults were described in detail by UBUKATA (1975).

## STUDY SITE, MATERIAL AND METHODS

### STUDY SITE

The field observations were made during 1970-1976 at a dystrophic pond (Hōrai-numa) in Usubetsu near Sapporo, Hokkaido, Japan. The habitat, its odonate fauna and the climatic conditions were described by UBUKATA (1973, 1974, 1980, resp.). The experiment using models was made during July 9-28, 1973, at point "e", as marked in UBUKATA, 1973, fig. 1; 1975, fig. 1.

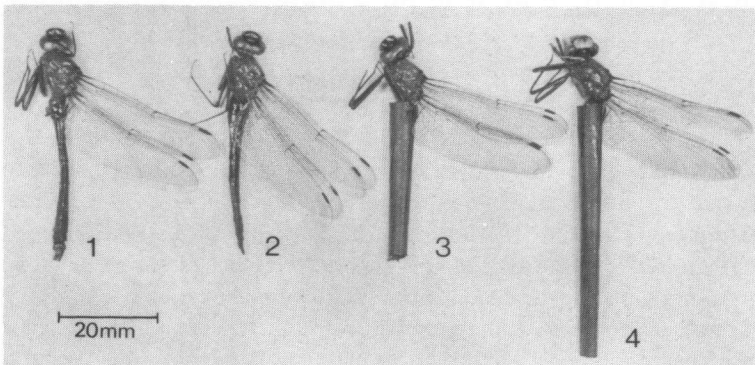


Fig. 1. Test individuals of *Cordulia aenea amurensis* used in the experiment: (1) Male; — (2) Female; — (3) Male with abdomen encased in a short paper tube; — (4) Male with abdomen encased in a long paper tube.

### MATERIAL

The external morphology of *C. a. amurensis* is characterized by the following features. Average measurements (♀ values parenthesized): body length 47.1 mm (45.2 mm); abdomen length 33.8 mm

(32.6 mm); abdomen thickness, see Table 1; hind wing length 30.0 mm (29.6 mm). — Coloration: head, eye and thorax metallic green; abdomen dark metallic green to lusterless black posteriorly; the third abdominal segment with pale spot (slightly larger in female); wings hyaline, amber yellow at basal 2 mm.

Thus, the most remarkable sexual difference is seen in the thickness at the basal part (around the third segment) of the abdomen: that of the female is thicker than that of the male (Fig. 1). In addition to these morphological differences, there is a sexual difference in the flight posture: males usually raise their abdomens ca. 20° upward, whereas those of females are kept horizontal (UBUKATA, 1975).

## METHODS

**Hypothesis** — Males flying at the pond seem to discriminate the sexes of other conspecifics first by the difference in flight style (henceforth called "movement pattern") and then more precisely by the relative thickness at the basal part of the abdomen. The movement pattern of females differs from that of males in the vertical swinging motion they adopt to lay eggs, in their inclination to escaping from males and in their generally low flight height (cf. UBUKATA, 1975).

**Experiment.** — This was conducted as follows: four types of test individuals (TIs) with four different patterns of movements were held out at two different heights (10 and 30 cm) in front of patrolling males near the shore (Fig. 2); then the responses of the patrolling males were recorded. For use as TIs, some conspecific adults were collected at the pond prior to the experiment. Some individuals were left intact, and some males were encased in paper tubes of two sizes, painted black with quick-drying ink and placed over the abdomen to change its thickness and/or length (Fig. 1, Tab. 1). Such modified TIs are henceforth called "short-tubed TI" and "long-tubed TI", respectively.

So that their movements could be controlled, the TIs (alive or not) with wings kept open (ca. 160°-180°) were each attached to the tip of a flexible stick (ca. 1.2 m long) made of two thick iron wires (4 mm Ø) twisted together (Fig. 2). A thin iron wire (1.5 mm Ø, 10 cm or 30 cm long), connected to the stick, was thrust into the body (pterothorax and abdomen) of the TI at the venter of the mesothorax; this secured it to the stick. The wings of the TI were occasionally vibrated by TI. The abdomen of each male TI was raised ca. 20° as in a normal patroller, whereas those of female and modified TIs were kept horizontal. As a control experiment, a test without any TI, i.e. that with iron wire only, was executed in the manner described below.

The experimenter set up each TI before the entry of each patrolling male up to 4 m from the experimental site and made four patterns of movements for each TI: i.e., rushing at the patroller,

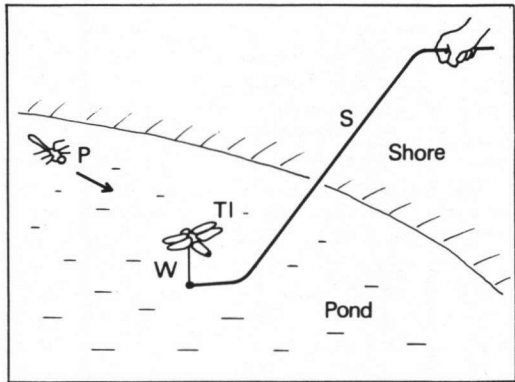


Fig. 2. Instrument used to control the movement of a TI: S: stick; — W: iron wire; — TI: test individual; — P: patrolling male.

Table I  
Abdominal sizes (mm) of test individuals used in the experiment

Test individual	Length (abd. app. incl.)	Thickness in dorsoventral dimension		
		at 3 mm from anterior end	at 6 mm from anterior end	at 6 mm from posterior end
Female <sup>1</sup>	32.6 ± 1.5	4.8 ± 0.2	3.8 ± 0.6	2.4 ± 0.7
Male <sup>2</sup>	33.8 ± 0.1	4.0 ± 0.1	2.7 ± 0.1	2.7 ± 0.2
Ditto, with short tube <sup>3</sup>	32.8 ± 0.0	5.4 ± 0.2	5.2 ± 0.1	4.2 ± 0.1
Ditto, with long tube <sup>4</sup>	52.1	5.4	5.3	4.0

Number of individuals measured: <sup>1</sup>=3; — <sup>2</sup>=3; — <sup>3</sup>=2; — <sup>4</sup>=1

escaping from it, vertical swinging (amplitude 1-3 cm, frequency 2-3 Hz) at the same horizontal position, and remaining motionless. The maximum velocity in each test of rushing and escaping was 2-5 m/sec; this being approximately the velocity of the sexual chase under natural conditions. The motion of "vertical swinging", however, contained slightly horizontal components in the test conducted at 10 cm height. The horizontal oscillation was no longer negligible in the test at 30 cm height, since its amplitude reached 2-3 cm. In every case, the face of the TI was directed to the patroller, except in the escaping movement. The test of vertical swinging was begun before the patroller approached to within 2 m of the TI. When the patroller came to within 40 cm of the TI, the test was regarded as complete. The escaping movement of the TI was begun at this moment. When another patroller approached a patroller during a test, the test was stopped so as to exclude any effect he might have had. Cases in which the patroller approached the experimenter during a test were also excluded from the data for analyses. Each kind of test was carried out 30 times, as far as possible avoiding immediate repetition of the same test for the same patroller, so that the patroller could not be influenced by the memory of the TI's movement.

The responses of the tested males (patrollers) were recorded according to the following classification (modified from MOORE, 1952): (1) nil, i.e. no detectable change of flight direction and velocity in spite of passing within 40 cm of the TI; (2) approach, i.e. change of the flight route toward the TI and coupled with acceleration; (3) retreat, i.e. turning aside or back; (4) clash; (5) hovering, i.e. staying within 30 cm of the TI by hovering or circling; (6) *pretandem*, i.e. seizing the body of the TI from above with the legs; and (7) *tandem*. Inevitably, no copula position was adopted because the TIs were fixed by the iron wire. Among the type listed above, (3) and (4) are treated as agonistic behavior, and (6) and (7) as sexual behavior.

## RESULTS

The frequency of each response by patrollers to each test individual is shown in Table II. Statistical comparisons are made among each type of test, the Chi-squared test and Fisher's direct probability method being adopted when the lowest frequency is higher than five, and lower than or equal to five, respectively, in a 2x2 contingency table. In the following descriptions, the words "increase" and "more frequent" are used when the difference is statistically significant ( $p < 0.05$ ) unless otherwise noted. The letter T and following numerals in parentheses refer to the consecutive numbers of the tests shown in order in Table II.

Table II

Observed number of responses by patrolling males for each test

Test No.	Sex of TI	Movement of TI	Height (cm)	Responses of patrolling males						
				<i>Nil</i>	<i>Ap</i>	<i>Ho</i>	<i>Pr</i>	<i>Ta</i>	<i>Cl</i>	<i>Rt</i>
T1	♂	Ml	30	16	9	4	—	—	—	1
T2	♂	Ml	10	23	4	3	—	—	—	—
T3	♂	Ru	30	6	9	—	1	—	2	12
T4	♂	Ru	10	9	9	—	1	—	7	4
T5	♂	Es	30	12	17	—	—	1	—	—
T6	♂	Es	10	3	25	—	2	—	—	—
T7	♂	Sw	30	6	14	9	—	—	1	—
T8	♂	Sw	10	13	11	5	1	—	—	—
T9	♀	Ml	30	24	4	2	—	—	—	—
T10	♀	Ml	10	27	3	—	—	—	—	—
T11	♀	Ru	10	7	9	—	—	—	6	8
T12	♀	Es	10	11	19	—	—	—	—	—
T13	♀	Sw	30	5	15	7	1	—	2	—
T14	♀	Sw	10	8	6	7	8	1	—	—
T15	ST	Ml	10	28	2	—	—	—	—	—
T16	ST	Sw	10	4	7	9	7	—	3	—
T17	ST	Es	10	9	20	1	—	—	—	—
T18	LT	Sw	10	14	9	6	1	—	—	—
T19	Wl	Sw	30	28	2	—	—	—	—	—

Each type of test was carried out 30 times. — Abbreviations: TI: Test individual; — ST: male TI with short tube; — LT: ditto, with long tube; — Wl: no TI, wire only; — Ml: motionless; — Ru: rushing; — Es: escaping; — Sw: swinging; — *Nil*: no response; — *Ap*: approach; — *Ho*: hovering; — *Pr*: pretandem; — *Ta*: tandem; — *Cl*: clash; — *Rt*: retreat

Existence of TI. — The total frequency of positive responses (those other than nil) was not significantly increased by the existence of the motionless TI irrespective of sex and the modification by paper tubes (T2, T15, T9, T10) except for male TI at 30 cm height (T1), comparing with the test (T19) in which swinging motion was made at 30 cm height without any TI.

Existence of any motion. — The total response was increased by any motion of TI (T3, T7 vs. T1; T4, T6, T8 vs. T2; T11, T14, T12 vs. T10; T13 vs. T9; T16, T17 vs. T15), except for the male TI with escaping movement at 30 cm height in which the increase was not statistically significant (T5 vs. T1). The change in each response due to the existence of motion is described in the following sections.

Difference in the movement pattern. — The *rushing* of male TI caused an increase over any other motion in retreat response at 30 cm height (T3 vs. T1, T5, T7), or in clash response at 10 cm height (T4 vs. T2, T6, T16). Rushing of female TI at 10 cm height increased the retreat response (T3 vs. T1, T5, T7) and

probably ( $p < 0.06$ ) clash response (T11 vs. T10, T14).

The *swinging* motion of female and short tubed TI both at 10 cm height caused an increase in sexual responses over any other motion of the same TI (T14 vs. T10, T11; T16 vs. T15, T17). Such an increase by other TIs with swinging motion (i.e. T8, T13, T18) was not statistically significant. Hovering sometimes ensued from the test with swinging motion.

The approaching response which includes subsequent chasing was significantly more frequent in male and short-tubed TIs both with *escaping* motion (T6, T17, T12) than in any other motion of the same TIs at the same heights, except for swinging male TI at 30 cm height (T7). Escaping of female and short-tubed TIs did not cause any sexual response (T12, T17).

Difference in the height of the TI. — The sexual responses were increased by lowering the height of female TI with swinging motion from 30 cm to 10 cm (T14 vs. T13). This difference may be in part due to the disparity in the amplitude of the horizontal component of the swinging. The total response increased due to the lowering of height in male TI with escaping movement (T5 vs. T6). Retreat response was more frequent at 30 cm height than at 10 cm height in rushing motion of male TI, though the difference was not statistically significant.

Difference in external morphology. — There was no significant difference between male and female TIs in the frequency of the total, agonistic and sexual responses with motionless, escaping and rushing movements (T1 vs. T9; T2 vs. T10; T4 vs. T16). But the swinging motion at 10 cm height caused different responses between both sexes: the female TI elicited more frequent sexual behavior from the patrollers than the male TI (T18 vs. T14), while such a difference was not obvious at 30 cm height (T7 vs. T13).

With reference to the *modified TIs* vs. intact ones, the short-tubed TI induced more frequent sexual responses than the male TI in the tests of swinging at 10 cm height (T16 vs. T8). On the other hand, the sexual responses to the long-tubed TI were as few as those to the male TI in the tests of swinging at 10 cm height (T18 vs. T8). The short-tubed TI brought about no significant difference in each response from other TIs in the tests with motionless or escaping movement at 10 cm height (T15 vs. T2, T10; T17 vs. T6, T12).

The long tubed TI induced fewer total and sexual responses than the short-tubed TI in the test with swinging motion at 10 cm height (T18 vs. T16).

## DISCUSSION

### RECONSTRUCTION OF THE RELEASING MECHANISM

It was often observed in the experiment that patrolling males of *C. a. amurensis* respond differently to each TI and to each movement pattern. The frequencies of sexual and agonistic responses, however, are lower in the experiment than under

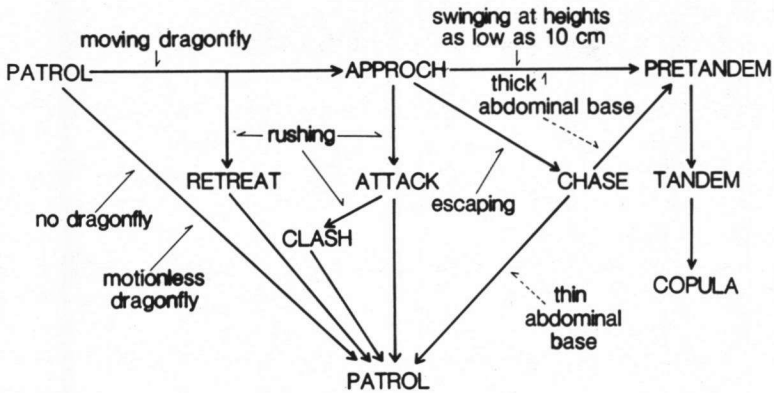


Fig. 3. Sequence of each behavioral element in males, and the inferred releasing mechanisms. Capitals: behavioral elements; — Small cast: releasers; — Thick arrow: temporal sequence; — Thin arrow: verified by experiment; — Dotted arrow: inferred from observations.

natural conditions, because the tested patrollers often stopped the response at the stage of approach and hovering, probably due to the somewhat unnatural movements of the TIs and to the existence of the iron wire. The releasers which induce a given response can be inferred from the differences in frequencies of responses shown in Table II. The releasing mechanisms for male behavior are reconstructed as follows from the results of the experiment, making reference also to the observations under natural conditions (Fig. 3).

Patrolling males seldom approach either an object whose body has a shape and size unlike that of conspecifics or a dragonfly without any motion. In other words, neither sexual nor agonistic behavior is usually released in such cases. The virtual inability of a male to detect a motionless female was illustrated by the following observation: a female chased by a male suddenly settled and hung on the underside of a leaf of *Phragmites* and remained motionless there, whereupon the male could not get near the female even though he hovered ca 50 cm from her (July 9, 1973; at 17.28).

If a dragonfly of about the same size rushes at a patroller, the latter turns (i.e., retreat response) or dashes at the former ("attack"; cf. UBUKATA, 1975), sometimes resulting in a physical clash. That is to say the former is recognized as a male by the latter. The sexual differences in the external morphology of the former are not perceived by the latter when rushing. The discrimination of sex by only the movement pattern is sufficient for males in such a case, because females never rush at males.

If a conspecific or similar dragonfly goes away from a patroller, the latter chases the former. Under natural conditions, females often escape from approaching males, but copulation usually ensues in such cases unless the females

fly into the shore vegetation (UBUKATA, 1975). Therefore, the sex of the escaping dragonflies seem to be recognized by the pursuing males under natural conditions on the basis of external morphology and posture, though the frequency of sexual attempts was very low in the experiment. This low frequency in the experiment might be due to the unnatural flight paths of the TIs: the TIs were controlled by hand, so that their flight paths were curved upwards and towards the shore, whereas free females fly away over the water surface, maintaining about the same height.

If a conspecific or a similar object makes swinging movements at heights as low as 10 cm above the water surface in the manner of egg-laying movement, patrolling males approach it. Then if the former has an abdomen which is thick at the base, the approaching males try to mate. On the other hand, any dragonfly with an abdomen thin at the base does not elicit sexual responses from approaching males, even if the former makes swinging movements. The thickness at the base of the abdomen is effective in releasing a male's attempt to mate if the abdomen is of normal length; that is to say, relative thickness rather than absolute thickness is important in this connection. In the experiment, the abdomens of the male TIs were raised, whereas those of the female and the tubed TIs were kept horizontal. However, the angle of the abdomen seems not to be important for sex recognition: females elicit the sexual behavior of males under natural conditions, even though the abdomens of the females are not kept horizontal during oviposition.

In conclusion, males recognize the sex of conspecifics first, though not perfectly, by the movement pattern peculiar to each sex, and then do so more precisely by the thickness at the base of abdomen. The characteristic movement patterns for each sex are as follows: male — rushing; female — escaping and vertical swinging.

#### SEX RECOGNITION BY FEMALES

No experiment on sex recognition by females was undertaken in the present study. But the following observations suggest that females also recognize the sex of conspecifics by their movement: any female ovipositing often escapes from (cf. UBUKATA, 1975) or quite exceptionally "threatens" approaching males before being seized by the latter, whereas she continues to lay eggs if another female approaches. Such threat behavior was observed only in one case during the present study: a female which was ovipositing near the shore was chased by an approaching male; then the former turned and hovered facing the latter. After a repetition of male chase and female threat, the female entered the shore vegetation, thus escaping from the male (July 28, 1973, at 13.41). An instance in which two females laid eggs while close to each other was observed on June 25, 1971 (at 4.37): A female was ovipositing above the *Potamogeton*-zone (cf.



UBUKATA, 1973); another female slowly approached laying eggs up to one meter from the former. But they continued to oviposit, apparently being indifferent to each other.

#### SPECIES RECOGNITION

Species recognition is an indispensable mechanism for sexual isolation among closely related species and must be built up by natural selection (e.g. DOBZHANSKY, 1970). During the field survey at the pond, sexual behavior by the males of *C. a. amurensis* towards other anisopterans, especially *Trigomphus melampus*, was occasionally observed, though it never resulted in tandem formation (UBUKATA, 1975). Therefore, visual species recognition is incomplete in *C. a. amurensis*, though, such interspecific interactions are much less frequent than intraspecific ones. Where visual recognition of species during sexual behavior is inadequate as in this case, the morphological incompatibility between male anal appendages and the surface of female head or thorax may act as an efficient isolating mechanism (cf. CORBET, 1962). Nevertheless, heterospecific tandem is widespread among Odonata (BICK & BICK, 1981). Recently, TENNESSEN (1975) and ROBERTSON & PATERSON (1982) have revealed that a tactile recognition of conspecific male by female in tandem is likely to be effective at least in some coenagrionids. Under this mechanism, if a female in tandem refuses to copulate, the male will be aware of that she is either a heterospecific or an unwilling conspecific one.

#### CONCLUDING REMARKS

Experimental studies on the ethology of Odonata have been made by various authors (e.g. for Zygoptera: BUCHHOLTZ, 1951, 1955, 1956; LOIBL, 1958; KRIEGER & KRIEGER-LOIBL, 1958; BICK & BICK, 1965; HEYMER, 1973; TENNESSEN, 1975; WAAGE, 1975; MIZUTA, 1977; for Anisoptera: MOORE, 1952; TAKETQ, 1960; JOHNSON, 1962; PAJUNEN, 1964; KAISER, 1974; PARR & PARR, 1974). In the zygopterans studied, external morphology, especially coloration of the wing or thorax are generally most important for visual recognition of sex by males.

In the anisopterans, the coloration on the thorax or on the abdomen is also important for sex recognition in the sexually dichromatic libellulid species, *Nesciothemis nigeriensis* (PARR & PARR, 1974) and *Pachydiplax longipennis* (JOHNSON, 1962). However, most anisopterans, including the majority of corduliid species, have less conspicuous sexual dichromatism, suggesting the importance of flight style and body shape in sex recognition rather than coloration. Nevertheless, no study of Anisoptera in which the movement of test individuals has been manipulated by the experimenter has so far appeared.

Because the fishing-line technique by which the normal movement of the tied dragonflies might be disturbed was used in the study by MOORE (1952), he could not discover the ability of sex recognition in some species studied (cf. TAKETO, 1960). This is because, using the fishing-line technique, it is possible that the tied male dragonflies are trying to escape and thus making movements unlike those of normal males. Although PAJUNEN (1964) was aware of the importance of flight style in sex recognition and of the defect of the fishing-line technique, he did not conduct any experiment using an improved method.

In the present study, movements of test individuals were manipulated so as to stimulate four categories of movement: motionless, rushing, escaping and swinging. Accordingly, the present study has confirmed the role of movement in addition to external morphology in sex recognition, even though the velocity, swinging frequency, etc. of test individuals were not kept precisely constant because of the difficulty of simulating this manually. Thus, adults of *C. a. amurensis* can discriminate the sexes of encountered conspecifics and behave differently according to the sex of the individual encountered, so that males compete for the acquisition of territories by showing agonistic behavior towards other males and by chasing females in order to mate with them (UBUKATA, 1975), whereas females escape from or exceptionally show threat behavior towards males when laying eggs and are indifferent to other females.

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