



カラカネトンボにおける精子移送と交尾行動

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Intra-male Sperm Translocation and Copulatory Behavior in the Dragonfly, *Cordulia aenea amurensis* Selys (Odonata; Corduliidae)¹⁾²⁾

Hidenori UBUKATA

Department of Science Education, Kushiro College, Hokkaido University of Education,
Kushiro 085

生方秀紀：カラカネトンボにおける精子移送と交尾行動

北海道教育大学釧路分校理科教育研究室

Abstract

The entire process of the mating of the dragonfly *Cordulia aenea amurensis* Selys was observed at a pond (Horai-numa) near Sapporo, Hokkaido, in 1976. Some additional observations were also made in 1975 and 1983. Intra-male sperm translocation does not occur when males are in tandem with females but is executed when they are taking part in nonsexual activities (e.g. patrolling). The behavior of both sexes while they are copulating is described in detail. The duration of copulation takes from 37 to 62 min., during which a characteristic rhythmical movement of the anterior segments of the male abdomen is observed. The ultimate factors in the behavioral traits that occur during mating, such as the undulation of the male abdomen, a long copulation time and departure from the pond while copulating are discussed from the view point of reproductive success, especially of sperm competition.

Introduction

The genus *Cordulia* is composed of two species, Palaearctic *C. aenea* (L.) and Nearctic *C. shurtleffi* Scudder. The former involves two subspecies, *C. a. aenea* and *C. a. amurensis* Selys.

1) Ecological studies of *Cordulia aenea amurensis* Selys, VI.

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The behavior of these species and subspecies has recently been reported in detail by Robert (1958; for *C. a. aenea*), Ubukata (1975; for *C. a. amurensis*) and Hilton (1983a; for *C. shurtleffi*). None of these studies, however, was able to describe the entire process of copulation, because mated pairs leave the breeding site (pond) and fly away as soon as they form copula (wheel position).

As the behavior of both sexes during copulation needs to be closely observed in order to clarify the reproductive strategy of each sex (cf. Parker, 1970 ; Waage, 1979 ; Miller, 1983), I adopted the so-called 'fishing-line technique' (Moore, 1952) to prevent the flying away of the mated pairs. By means of this technique, the copulation of *C. a. amurensis* was closely observed from the formation of the tandem to the final separation of the pair. In addition to the results of the above observation, this paper reports a reconfirmation of the time of intra-male sperm translocation (sensu Bick, 1972) in this subspecies, i.e. the sperm transference in a male from the genital pore on the ninth abdominal segment to the accessory genitalia on the second and third abdominal segments. I do so now because I reported in a previous paper (Ubukata, 1975) a motion that I regarded as intra-male translocation during patrol flight without showing whether sperm was really transferred or not.

This report is a part of a comprehensive study of the ecology and behavior of this subspecies (Ubukata, 1973, 1975, 1980, 1981, 1983 and in press).

Study area and method

The observations were made at a pond (Horai-numa ; Fig. 1) in Usubetsu near Sapporo, Hokkaido. The location and the features of the pond have been reported in detail by Ubukata (1973 and in press). Observations using the fishing-line technique were made three times (July 7, 9 and 13) in 1976. On each day a female was collected from an 'emergence trap' set up to collect emerging individuals, into which she flew probably to lay eggs but from which she was unable to escape. A black cotton thread (ca. 3-4m long) was then tied to her pterothorax at a position between the fore and hind wings. The motion of wings and legs was not disturbed by the thread. I held the pterothorax of the insect between fingers and the opposite end of the thread with the other hand, then released her when a patrolling male was approaching the area in front of me. She flew less smoothly than intact females and sometimes dropped into the water, probably due to the weight of the thread. When the flight ability of a tied dragonfly appeared to be reduced, I placed her on a plant leaf for an interval and repeated the presentation of her to patrolling males until copulation occurred.

As well as making these observations, I observed mating between intact individuals on July 2, 1983, to reconfirm that the intra-male sperm translocation does not occur when both sexes are in tandem. In order to know whether patrolling males contain sperm in their sperm storage organs on the third abdominal segment or not, I captured a male at point e (Fig. 1 ; cf. also Fig. 1 of Ubukata, 1973 and 1975) of the pond while he was patrolling along the shore and dissected him in a laboratory (Zoological Institute, Hokkaido University) on the same day.

The sperm storage organ (seminal vesicle) at the base of the penis was then excised and observed under a microscope.

Results

The behavioral sequence of both sexes before copula formation has already been reported in detail (Ubukata, 1975). I therefore concentrate now on describing the behavior of both sexes *after* copula formation.

Observation on July 7, 1976

A female was collected at 15.40 hours and looked active, judging from wing and abdominal

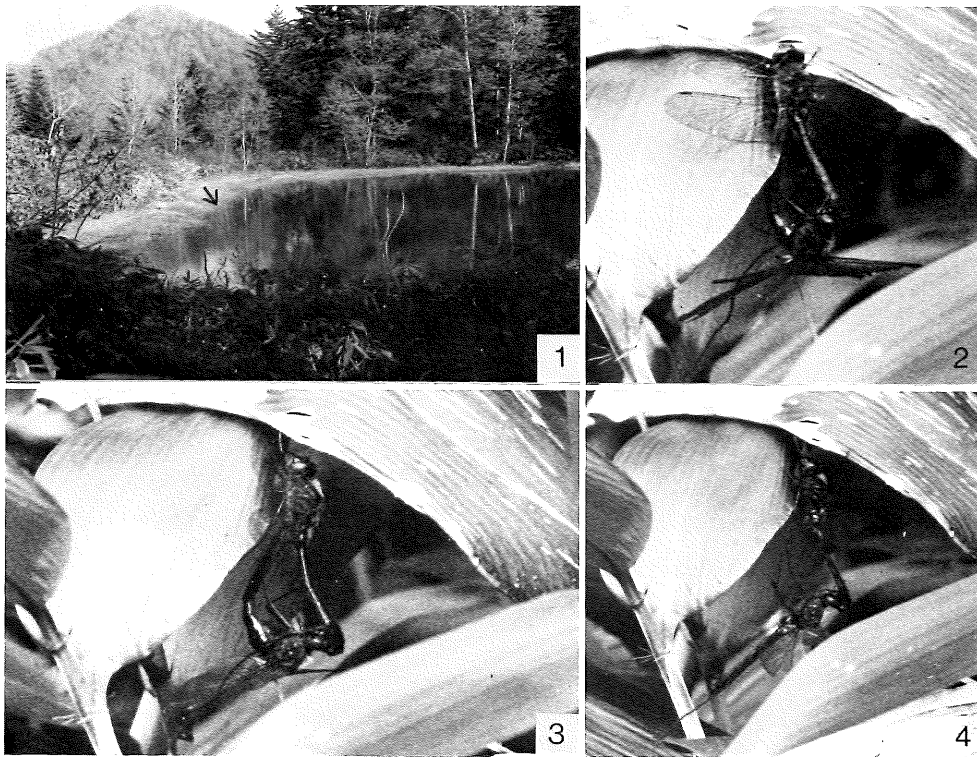


Fig. 1. Study site (Horai-numa), showing a northeastern sector (NE ; cf. Ubukata, 1975) and the northern half of a southeastern sector (SE) of the pond. Floating leaves of *Potamogeton Fryeri* A. Bennett were not yet put forth. Arrow indicates the location (point e) at which tethered females were released.

Fig. 2—4. Postures of a mating pair of *C. a. amurensis* (July 13, 1976 ; Horai-numa). 2. Posture of the pair alighting on a leaf of *Sasa* soon after the copula formation. 3. The pair before beginning copulatory movements. 4. The pair in post-copulatory tandem.

movements. After being tethered, she was released at point b of the shore (cf. Fig. 1 of Ubukata, 1973, 1975). A male approached her and formed the tandem position, although she flew more or less upwards. The pair further formed copula while flying as if they were drawing a circle around my hand that held the end of the thread. I then pulled them to change the flight direction toward the shore. As the result, they perched on a leaf of a *Sasa* sp. standing by the shore. They soon attempted to fly away, but, impeded by the thread, fell into the bush of *Sasa*. Pulled by me, they flew and perched again, maintaining copula, on a leaf of *Sasa* 30 cm distant from the first perch site (16.43 hours). At 16.47 the male began a rhythmical movement of the anterior segments of his abdomen in the dorsoventral direction (undulating movements; cf. Waage, 1979), while his head, wings and legs remained immobile. The female held the abdomen of the male with her legs but did not show any other motion. The wings of both were held open (ca. 180°; cf. Fig. 2). At 17.09 he vibrated his wings when a calypterate insect (Diptera) walked around his legs. At 17.10 he moved his mouth parts and a fore leg, after which the dipteran left there. At 17.11 and 17.17 the leaf was slightly swung by wind, but the insects did not fly up. At 17.26 the male walked sideways and sat on the opposite side of the leaf. At 17.43 he fluttered his fore wings momentarily when a tipulid flew near them. At 17.44 he again walked sideways. The tipulid insect flew away. At 17.45 copulation terminated, but the pair stayed there in tandem. She still held his abdomen by her legs and stretched her abdomen horizontally. At 17.46 she kicked against his legs with her hind legs. Nearly simultaneously, he kicked her in the similar manner. At 17.48 he vibrated both his wings twice for 0.5 sec. At 17.50 he fluttered his hind wings. At 17.51 he vibrated his wings for 5 sec., repeating this action several times. At 17.53 she fluttered her wings for a moment. At this point he stopped the wing vibration but quickly resumed it. Soon afterwards she moved her legs. At 17.54 he bent his abdomen ventrally. Her abdomen was also curved by this act. About 30 sec. later, he loosened his caudal appendages and the tandem position then terminated. At this moment, she remained on the leaf, hanging down on it with her legs, and he raised his body posteriorly by ca. 40° with stretched abdomen. At 17.55 he flew off after vibrating his wings continuously. At 18.00 I untied the thread, marked her wings and placed her on a *Sasa* leaf. She then vibrated her wings, and I ended the observation.

Observation on July 9, 1976

A tethered female was released several times at point e (Fig. 1) of the shore. Finally, a male seized her and entered into copula formation (17.53 hours). They fell but perched on a leaf of *Sasa* because their flight out of the pond area was disturbed by the thread. At 17.54 she vibrated her fore wings. They then tried to fly away three times, but at last hung down on a stem of *Sasa*, held by the male's legs. At 17.57 both were immobile, the wings open (male, ca. 180°; female, ca. 150°). She held his abdomen by her fore and hind legs; her mid legs were folded. At 17.58 the second and third abdominal segments of the male were pushed out ventrally for a moment. This undulating movement was repeated very slowly. At 17.59 undulation was made again. At 18.01 undulation occurred three times at intervals of 7-8 sec. She rubbed his abdomen three times with her hind legs. His abdomen was undulated twice.

At 18.03 undulation was repeated nine times. At 18.04 the undulation became more rhythmic, being repeated at intervals of 4 sec. His right fore leg moved. Her left hind leg moved. At 18.05 undulation was repeated at intervals of 2 sec. At 18.07 undulation became weaker. About 30 sec. later, obvious undulation was resumed and repeated at intervals of 3-4 sec. At 18.08 she moved her hind legs five times. The undulation of the male abdomen was continued at intervals of 2 sec. At 18.15 the rate of undulation decreased (interval, 6 sec.). At 18.17 undulation ceased. Both sexes were immobile. At 18.19 his abdomen moved once. At 18.24 his legs moved slightly. At 18.26 he flapped his fore wings once ($180^\circ - 120^\circ - 180^\circ$). Her hind legs moved at intervals of 5 sec. and were detached from his abdomen. Her fore legs still held his abdomen. At 18.30 his abdomen moved weakly. His left fore leg moved. At 18.31 her mid and hind legs moved several times. At 18.32 she held his abdomen with her legs. At 18.33 he vibrated his wings for a moment. Her hind leg moved seven times. At 18.36 his abdomen moved once. At 18.37 his abdomen moved slightly. At 18.38 copula ended but they remained in tandem. She moved all her legs. About 30 sec. later, he began wing vibration. She moved her mid and hind legs. At 18.40 she became motionless. His wings continued to vibrate. At 18.41 she fluttered her wings and moved her legs. He flapped his wings twice. The movement of her legs ceased. About 30 sec. later, he released her, terminating the tandem position; he then rubbed his head by a fore leg for 2 sec., flew up and left. At 18.42 she remained motionless on the *Sasa* leaf. I untied the thread, marked her wings and replaced her on the same leaf. Several minutes later, she began to vibrate her wings, and I ended the observation.

Observation on July 13, 1976

An active female was collected, tethered and repeatedly released at point e. A male took up the copula position with her and perched on a leaf of *Sasa*. They shifted their perch post 3-4 times (Fig. 2). Finally they hung from a leaf of *Sasa* (Fig. 3). She held his abdomen with her right three legs and left fore leg and kept her wings open (ca. 180°). At 14.23 he began an undulating motion of his abdomen. Because of this motion, the second abdominal segment of the male was jerked ventrally, so that the abdominal end of the female moved toward the anterior end of the male by 1 mm. He moved his abdomen with a higher amplitude and a higher rate than the male observed on July 9. At 14.29 undulation continued at a rate of 28 times per 30 sec. At 14.41 undulation ceased. At 14.43 he flapped his wings three times. At 14.50 he rubbed his head with his right fore leg, during which the top of his head was continuously turned toward the right. At 14.52 the abdominal undulation of the male resumed at a rate of six times per min. At 14.56 he vibrated his wings for ca. 5 sec. and copula ended. They remained in tandem in the same place (Fig. 4). He continued wing vibration until he terminated the tandem position 15 sec. later. Immediately he flew up and left. She remained. I untied the thread, marked her and replaced her on a leaf. Soon she flew away.

Observation on July 2, 1983.

On this day, I began observation of intact individuals at the pond from 07.44 hours. At 08.28 hours, a male seized a female 2 m offshore near point e and formed the tandem position with

her, after which they flew approximately 2 m parallel with the shore. Soon they formed copula flying obliquely upwards approximately 4 m; they then left the pond. I paid close attention to the movement of the male's abdomen while they were in tandem, but he never showed any obvious bending motion of his abdomen so that the venter of the ninth abdominal segment never touched the second and third abdominal venters.

Dissection of seminal vesicle

A patrolling male who was captured at 15.04 hours on June 20, 1975, and was dissected at 19.20 hours, carried many spermatazoa in the seminal vesicle (the basal part of the penis) of the accessory genitalia.

Discussion

Heymer (1973) tentatively generalized from both his own observations of several species of *Calopteryx*, *Oxygastra* and *Orthetrum* and those reported by other workers that intra-male sperm translocation always occurs after both sexes take up the tandem position in the Odonata. In *C. a. amurensis*, however, the sperm translocation has not been observed when both sexes are in tandem and the sperm storage organ of the accessory genitalia of a patrolling male has been found to contain sperm already. Moreover, Ubukata (1975) has observed that the sperm translocation was made during patrolling at the pond, although this behavior was very rarely witnessed. Heymer's generalization must therefore be rejected.

Pajunen (1963) and Kiauta (1964) have also denied the occurrence of sperm translocation when individuals of *Leucorrhinia* are in tandem, and they observed sperm in the sperm storage organ of every male collected while it was patrolling or in tandem or copula. Further, Pajunen (op. cit.) confirmed that the sperm content varied considerably depending on the time spent in copulation and that it did not differ between males captured in nonsexual activity and those captured in tandem. This suggests that spermatazoa contained in the sperm storage organs of patrolling males are not the remnants left after the injection (into female genitalia) of those transferred before last copulation but are transferred when the males are in nonsexual activities, at least in the case of *Leucorrhinia dubia* (v. d. Lind.) and *L. rubicunda* (L.). Pajunen (op. cit.) did not observe sperm translocation at the breeding site (pond, etc.), so that he assumed that it occurs before arrival at the water, while Kormondy (1959) observed it at breeding sites (lake) prior to tandem formation in *Tetragoneuria* (= *Epitheca*) *cynosura* (Say) as well as in *C. a. amurensis*.

The present observations are probably the first confirmation of the entire mating process of the genus *Cordulia*. Although the time from tandem formation to the perching in copula on leaves was not measured absolutely, it did not exceed a couple of minutes. But as untied pairs always fly far away from the pond, the time when the insects are intact may exceed several minutes. Combining the results obtained from the three pairs, a characteristic movement of the anterior segments of the male abdomen (undulation) began 4 min. after the establishment

of copula and lasted for 18–19 min. The rate of the undulation was 1–0.12 per second. After this undulatory phase, a relatively immobile period ('post-undulatory phase') continued for 15–21 min. with intermittent, slight undulation. Females seemed to be passive throughout the copulation. In total, the copula position was held for 37–62 min. For *C. a. aenea*, Münchberg (1932) reported 10–15 min. as the duration of copulation. Even if certain climatic conditions, especially ambient temperature, are likely to influence the duration of copulation, such a large difference may be based on a geographical variation with genetic bases. Post-copulatory tandem lasted for 15 sec. – 9 min. The males flew away in all cases 1–30 sec. after the separation of tandem, while females remained alone for at least 5 min. and eventually left. Oviposition was not taken up immediately after the copulation as far as the tethered females were concerned.

The above observations on behavior during copulation were made upon tethered insects. However, this method does not seem to have deeply influenced the behavior of the mated pairs, because the thread disturbed the motion of no part of the body of either sex once they had rested on leaves. Moreover, the motion during copula was mainly exhibited by the male, who had not been tethered. Waage (1979) also adopted this method for *Calopteryx maculata* Beauvois, from which he drew an important conclusion, as shown below. By dissecting the spermathecae and bursae copulatrices of females of *C. maculata* and measuring the sperm content, Waage (op. cit.) clarified that the spermatazoa contained in these organs are almost entirely removed by the last mated males during the undulatory phase of copulation and that the sperm transfer to females follows this phase. A remarkable undulating motion during the copulation of *C. a. amurensis* also seems to be related with the displacement of sperm. More precise observations and experiments are needed, however, to validate this assumption.

The duration of copulation in Odonata varies widely from species to species (3 sec. – 340 min. ; Corbet, 1962). The copulation of *C. a. amurensis* belongs to the group of those with longer duration. Miller (1983) revealed that wandering (non-territorial) males of *Orthetrum chrysostigma* (Burm.) hold females in the copula position 17 times longer than territorial males. He then conjectured that the wanderers derive a greater benefit by a more complete removal of other males' sperm from the female organs and that the territorial males copulate more frequently and spend more time in defence of a territory. Moreover, Uéda (1979) revealed that wanderers of *Sympetrum parvulum* Bartenev lessen the duration of copula and show guarding behavior when the density of territories is low, while territorial males copulate for a brief period at any density and guard their mates.

In spite of the fact that the males of *C. a. amurensis* show territorial behavior (localization and spacing by defence behavior) when the male density at the pond is high (Ubukata, 1975), this subspecies does not adopt the strategy of short copulation and immediate reoccupation of the same territory to copulate with more females. For the adoption of this strategy the followings may be prerequisite : (1) high probability of female arrival at territories, and (2) high probability of access of the males to the females. Item (2) is well maintained whenever the male is an occupant of a territory (e. g. Jacobs, 1955), so that the high defendability of the territory which can be judged from the duration of occupation must accelerate the adoption of this strategy.

Guarding by wanderers of *S. parvulum* may be made possible by the increase of defendability by the low density (Ueda, op. cit.). The rate of female arrival is likely to be high at a territory in which the substrata for oviposition are concentrated. In such cases, many mature males must compete for the acquisition of such territories, resulting often in a rigid, or long lasting territoriality (Johnson, 1964). Thus, the territorial males of a species which occupies territories for longer periods at oviposition sites with a concentration of substrata may often adopt this strategy. On the other hand, the males of a species which have short lasting territories with frequent take-over of the sites by intruders and where oviposition substrata are not strongly concentrated may not adopt this strategy but may copulate for longer duration as do the wanderers of *O. chrysostigma* who often leave the breeding site in copula. Leaving a thorough survey of literature on this matter aside, I list below some examples among Anisoptera supporting the above hypothesis. The males of the following species occupy short lasting territories (<40 min.), copulate for periods longer than 30 min. and do not return to the territories immediately after copulation: *C. a. amurensis* (Ubukata, 1975 and the present study) and *Somatochlora viridiaenea viridiaenea* Uhler (Ubukata, 1979). On the other hand, the males of the following species have long lasting territories (occupancy >1 hour), copulate for periods shorter than 5 min. and remain in the same territories after copulation: *Plathemis lydia* (Drury) (Jacobs, 1955; Campanella and Wolf, 1974), *Nannophya pygmaea* Rambur (Mizuta and Tani, 1970; Nakamuta et al., 1983) and *Libellula julia* Uhler (Hilton, 1983b).

Being exceptional among the Corduliidae, males of *Hemicordulia ogasawarensis* Oguma adopt the strategy of short copulation (1-3 min.) and guard the oviposition of mates in their own territories, during which they sometimes engage in additional copulation (Sakagami et al., 1974). The territorial occupancy of this species is longer (average, 13.8 min.; maximum, 81 min.; Sakagami et al., op. cit.) than that of *C. a. amurensis* (average, 7 min.; maximum, 40 min.; Ubukata, 1975). The observed territories of *H. ogasawarensis* covered most of the oviposition sites of a pond (Pond W; Sakagami et al., op. cit.). The defendability of territories (judged from the duration of occupation and the ratio of chasing to being chased) in *H. ogasawarensis* seems to be higher than in *C. a. amurensis* (Sakagami et al., op. cit.; Ubukata, op. cit. and unpublished). All these differences also support the above hypothesis. Moreover, in *C. a. amurensis*, the effect of prior residence is probably obtained by a newcomer within a couple of minutes when an area is unoccupied by others (Ubukata, unpublished). This trait may often disturb the reoccupation of the same territory after copulation.

Nevertheless, the strategy of short copulation and immediate patrolling may not always be related to the defendability and the quality of territories. I have noted above a general tendency in the correlation between the adoption of each strategy and territoriality. Without being related to territoriality, items (1) and (2) listed above may be attained by some species. The duration of copulation, however, may not always be related to the acquisition of new mates by immediate patrolling, since males of *E. cynosura* copulate for periods shorter than 5 min. without immediate patrolling (Kormondy, 1959) and males of *Aeschna cyanea* Müll. restart patrolling immediately after long lasting copulation (Kaiser, 1974). But the reasons for these combinations of behavior are open to future studies.

Pairs of *C. a. amurensis* in copula leave the pond without exception. The following can be enumerated as the ultimate factors in this departing behavior. (1) This behavior must prevent them from being interfered with by other males. This item seems to be applied to this subspecies, because pairs flying above the pond in copula or tandem are subject to the interference by other males, sometimes resulting in the separation of the pair or the formation of a triple connection (Ubukata, 1975). On the other hand, territorial males of *H. ogasawarensis* and *S. parvulum* copulating at the shore are not disturbed by other males (Sakagami et al., op. cit. ; Uéda, 1979). (2) Copulation at distant places from the pond must prevent the mated females from revisiting the pond immediately, for this may often result in remating with other males. But this still remains a speculation, so that comparative and experimental studies need to be made in the future. And (3), the risk of predation may be mitigated by leaving the pond. Yet even if the predation pressure is higher at the shore than in the forest, the distance for which the copulating pairs travel is too long (more than 50 m ; Ubukata, op. cit.). The avoidance of predation is therefore unlikely to be a major reason for the leaving of the pond.

Females collected when they visited the pond, yet who had not mated on those occasions, held sperm in their spermathecae and bursae copulatricae (Ubukata, in press ; cf. also Hilton, 1983a). And oviposition (made always solitarily) is observed at as early as 04.30 hours. Females are therefore considered to revisit the pond on subsequent days after copulation to lay eggs. They oviposit often at hidden places, such as dense emergent vegetation (Ubukata, 1975 and in press), so that additional mating can be, even if incompletely, avoided. This may be one of the reasons why males of this subspecies do not guard the mated females.

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