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**Life History and Behavior of a Corduliid Dragonfly,
Cordulia aenea amurensis Selys.**

**II. Reproductive Period with Special Reference
to Territoriality¹⁾**

By

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(With 17 Text-figures and 4 Tables)

Since St. Quentin (1934) the territoriality of Odonata has been studied in many species and its functions were discussed from various aspects (Moore 1952, 1957, Jacobs 1955, Johnson 1964, Pajunen 1966, Higashi 1969). For a more thorough understanding, however, it is required that structures and functions of the territoriality are analyzed quantitatively and properly placed within its life history. From this point of view, the life history and behavior of a territorial corduliid species, *Cordulia aenea amurensis* Selys, have been studied since 1970 in Hokkaido. The present paper is the second report dealing with reproductive period, following the previous paper on emergence and pre-reproductive periods (Ubukata 1973).

Area studied and methods

The field survey was carried out mainly at and around a dystrophic pond, Hôrai-numa (Pond A), near Sapporo during the flight season in 1970~1974. The biotopic feature and the phenology and faunal makeup of Odonata there have already been reported (Ubukata 1973, 1974). To facilitate later descriptions, the pond surface is divided into five sectors, i.e. NE (shore length=55 m), SE (42 m), SS (43 m), SW (40 m) and NW (42 m) and the central part (CP) (Fig. 1).

The behavior observation was made from the shore sometimes with aid of a binocular telescope ($\times 7$) and 8 mm ciné-camera. An individual marking was executed for the purposes of obtaining population parameters and tracing flight behavior. A total of 356 individuals of both sexes were marked on wings with lacquer paint or quick-drying ink and released immediately. All such individuals could fly without appreciable damage. The mark was so bright that most individuals, even in flight, were discriminated even from distance up to 10 m. The number of active male individuals at the pond for each moment (=NAI) was counted in two ways: 1. counting from a fixed point (c, Fig. 1) with the telescope within 1~3 min. (standing census). 2. counting by walking around the pond within 10~30 min. (circling census). There were only negligible difference in the efficiency between the both methods.

1) Studies on the biology of Japanese Corduliidae. IV.

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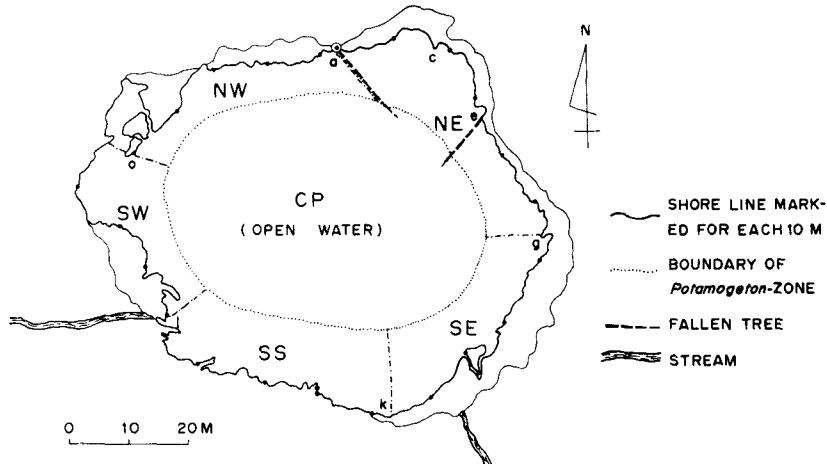


Fig. 1. Topography of the studied pond, Hôrai-numa (Pond A). *Potamogeton*-zone was divided into five sectors, NE, SE, SS, SW and NW. Cf. Ubukata (1973), Fig. 1.

Results and discussions

The results are divided into four parts, phenology, daily activity, behavior pattern and territoriality. Some related discussions are given in each section.

1. Phenology

1.1. Seasonal trend of flight activity at the pond

This section deals with the phenology of adult stage in 1971. The adult population of Hôrai-numa emerged from June 3 to July 1 with a considerable synchronization around June 10 ($EM_{10}^{90}=7$) (Ubukata 1973, 1974). They started the visit to the pond or other reproduction sites about 10~16 days after emergence, during which they spent the period for feeding in woodlands (Ubukata 1973). The earliest visit of male to the pond was observed on June 12 (Table 1). Thereafter the number of mature males at the pond (NAI) at 13:00 gradually increased until reaching the high level (NAI>10) on June 24 (Fig. 2). NAI exceeding the value of 26 was never observed throughout the reproductive period owing to the density regulating mechanism by male territorial behavior (cf. 4.3.). Therefore the seasonal peak of the male reproductive activity was not detected from change of the value of NAI. Nevertheless, it is obvious that the population size of mature individuals around the pond was in its maximum in late June~early July by which most individuals of the population should accomplish the maturation and start the visit to the pond. NAI dropped in mid July due to adverse weather conditions, rose again in late July and early August, owing to the recovery of the weather. Thereafter NAI decreased in mid August probably due to the gradual deaths of

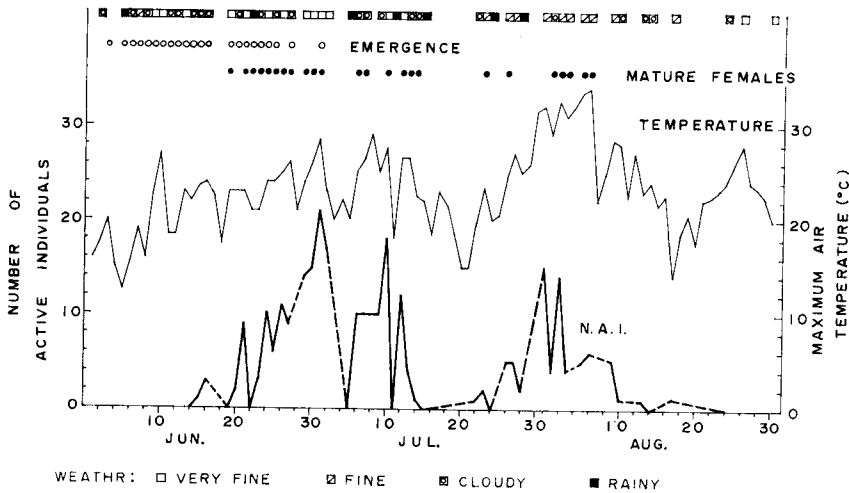


Fig. 2. Seasonal change of activity of *C. aenea* adults at the pond in 1971, together with weather record at each census occasion. Maximum air temperature was cited from record at Usubetsu Pluviometric Station, 1 km apart from the pond. NAI means the number of active individuals (mature males) at the pond censused at about 13:00. The air temperature at Hôrai-numa (13:00) is 4.8°C lower than at Usubetsu (maximum).

Table 1. Adult phenology of *C. aenea* at Hôrai-numa

Year	Sex	Emergence		Reproductive period		Maximum longevity (days)	Pre-reproductive period (days)
		first	last	first visit	last visit		
1970	♂	Jun. 5	Jun. 18	Jun. 11	Aug. 11	54	6
	♀	Jun. 5	Jun. 18	Jun. 17	Aug. 7	50	12
1971	♂	Jun. 3	Jun. 27	Jun. 12	Aug. 17	51	9
	♀	Jun. 3	Jul. 1	Jun. 19	Aug. 6	36	16
1973	♂	Jun. 3	Jun. 25	Jun. 12	Aug. 2	38	9
	♀	Jun. 3	Jun. 25	Jun. 13	Aug. 2	38	10
1974	♂	Jun. 7	Jul. 4	Jun. 17	Aug. 3	30	10
	♀	Jun. 7	Jul. 2	Jun. 27	Aug. 3	32	20

old individuals. The last male was observed at the pond on August 17.

Females were observed from June 19 to August 6. In order to obtain the knowledge of the seasonal change of the female activity, the mean number of copula per hour during clear weather was calculated for every decade of month (Table 2). The table shows that the female activity reached high level in late June and maintained similar level till mid July. Thereafter the value decreased toward the cessation of the female activity in early August. Generally the reproductive period continues from mid June to early (♀) or mid (♂) August in every year.

Table 2. Seasonal change of the frequency of copula per hour in 1971

Month	June		July			August
	mid	late	early	mid	late	early
The number of copula per hour	0.07	2.01	1.81	2.12	0.71	0.00
The number of copula	1	63	13	19	3	0
Total length of observation (min.)	824	1,882	432	539	252	362

1.2. Adult longevity and sex ratio

For closer understanding of the phenology, some results on population parameters are presented below, leaving detailed accounts and discussions elsewhere.

1.2.1. Maximum longevity: In sufficiently isolated population the maximum adult longevity can be estimated from the interval between the dates of the last emergence and of the last visit of mature individual at the pond as long as the length of post-reproductive period can be ignored (Moore 1951). The studied area and population seem to satisfy more or less above conditions. As shown in table 1, the maximum longevity of this population is estimated to be 51~54 days including pre-reproductive period. The figures of female, taking 36~50, are shorter than those of male in part due to the difficulty in censusing than in male.

More reliable estimation of longevity was made by marking and rediscovery in 1970 and 1971. Among 85 (1970) and 44 (1971) marked males respectively 58 (68.2%) and 22 (50.0%) individuals were rediscovered during observation at the pond throughout the flight season. The longest interval between the dates of marking and last rediscovery was 35 days (July 3~August 7, 1970) or 20 days (July 12~August 1, 1971). The smaller value of 1971 was probably due to the relative paucity of the number of marked individuals and the time spent for observation in late July and early August. Adding the mean length of pre-reproductive period (10 days) to the above figures, the maximum adult longevity confirmed by marking was 45 days (1970). As for the maximum adult longevity, little difference between the values obtained by two methods favors the Moore's method.

1.2.2. Mean longevity in reproductive period: A first approximation of the mean longevity is obtained from the mean interval between marking and last rediscovery dates. The value was 10.3 days among 42 males marked at mature stage in June, 1970. In the case of 1971, in which marking study was less sufficient, it was 5.7 days among 27 males marked in June.

1.2.3. Sex ratio: Real sex ratio during reproductive period is difficult to be

obtained because of the sexual differences in behavior and collecting efficiency. In this section only superficial sex ratio at the pond is calculated. There exists extreme difference in the abundance between sexes at the pond. Among 937 individuals recorded in the circling census throughout the reproductive period in 1971, the number of females was only 9 being 1.4% of the total, whereas the real ratio does not significantly deviate from 1:1 in emergence period (Ubukata 1973). The principal cause of the relative scarcity of females at the reproduction site is evidently due to the time interval spent by them at the site far shorter than in males by two ways: the lower frequency of visit to the site than in males and the short stay for each visit at the pond (1.3 min. in average of 23 cases).

2. Daily activity

In order to know the daily change of activity, the all day observation was executed at the pond on several days, together with an hourly standing census of NAI. The results of four days are presented in Fig. 3.

2.1. Daily fluctuation of the number of mature males

On a clear and warm day in late June, the first male arrives at the pond much before the sun begins to shine on the pond site but on the tree tops in the forest (e.g. at 4:38 a.m., June 25, 1971). NAI reaches the high level (>10) by 6:00 when the pond receives bright morning sun beam. Fluctuating between 10 and 25 till 17:00, NAI drops toward the dusk and the flight of male terminates at about 19:00. The general trend is the same on days of July. As mentioned before, NAI seldom exceeds the value of 26 due to the territoriality so that the pattern of daily fluctuation of NAI forms a typical plateau shape though the members are changing frequently. The daily fluctuation of the female activity was not traced quantitatively, but the following tendencies, in common with male, are suggested from Fig. 3; 1. wide temporal range of flight activity. 2. the pattern without distinct peak.

2.2. Climatic factors affecting flight activity

Some climatic factors are discussed here concerning their influence on the flight activity (NAI of male).

Air temperature: As shown in Fig. 4, the lower limit of air temperature at which the flight is suppressed is 5.8°C (under fine weather) and 10.4°C (under cloudy weather). The upper limit of air temperature for the flight was not detected since the air temperature did not exceed 28.8°C (August 2, 1971), at which NAI was 14, during reproductive period. If an extreme warmth, e.g. 35°C , assailed the pond area, the activity might be suppressed. Anyway, the thermal range permitting the flight is fairly wide in this species. Further, it is noted that no correlation of NAI with temperature exists between these extremity.

Illumination: Unfortunately the intensity of illumination was not measured

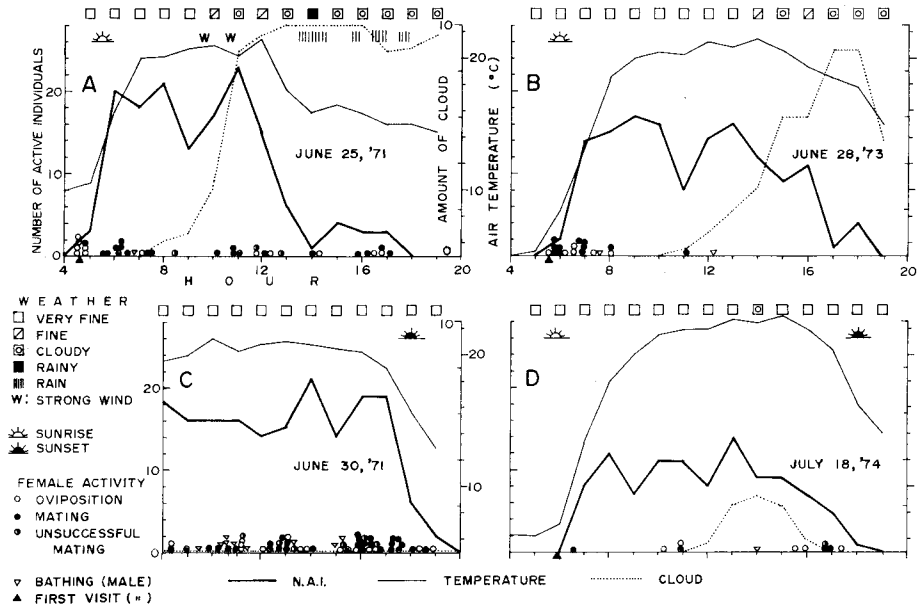


Fig. 3. Daily change of activity of mature adults with weather conditions.

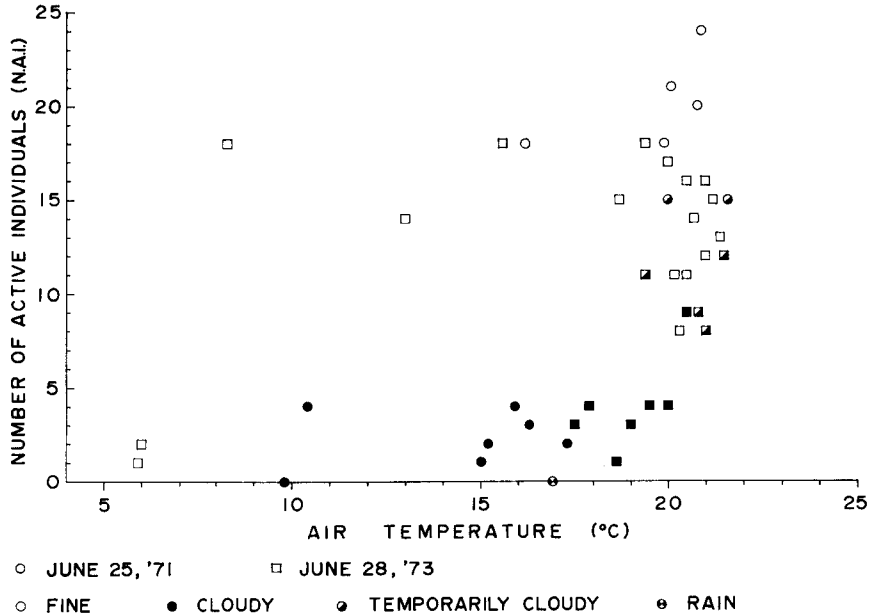


Fig. 4. Correlation of the number of mature males at the pond to air temperature. Air temperature was measured at shaded part of the shore (near point a, Fig. 1).

in the present study, making quantitative analysis impossible concerning its effect. But the relation between NAI and relative intensity of illumination is referred to. Even at optimal air temperature, NAI drops by reduced illumination. For instance, on June 28, 1973 (Fig. 4), within the range of air temperature 20~22°C, NAI was 8~17 under fine weather but it lowered down to 4~9 when the sun beam was intercepted by thick cumulous clouds.

Rain: Rain has also a strong effect on the activity: NAI was zero at 13:00 on June 22, July 5, 11, 15 and 24, 1971, under the rain even though the temperature was high enough to permit flight (15~16°C) (Fig. 2). However, when the air temperature is tolerable, a slight rain does effect less seriously. For instance, some males continued their flight even in the weak rain on July 28, 1971 (Fig. 2).

Wind: The influence of wind on the activity is slight. For instance, on June 25, 1971, there blew strong wind (force of wind 4~5) repeatedly, but NAI did not lower much (Fig. 3A). Of course, much stronger wind should disturb the flight.

3. Behavior pattern

To facilitate subsequent references and comparisons, the patterns of behavior confirmed during the observation at Pond A and B (cf. Ubukata op. cit.) are described below.

3.1. Male behavior

After maturation males make short visit to the pond up to thrice a day. Throughout the period of 1~40 min. of the stay at the pond, they continue *patrol flight*, by which they encounter other males and seek mates.

Patrol flight: This behavior represents the majority of the male activity at the pond. The characteristics of patrol flight are as follows: The flight height is low and stable (20~30 cm above water level) (Fig. 5). The speed is rather high. The flight course is more or less straight, restricted over the water surface and

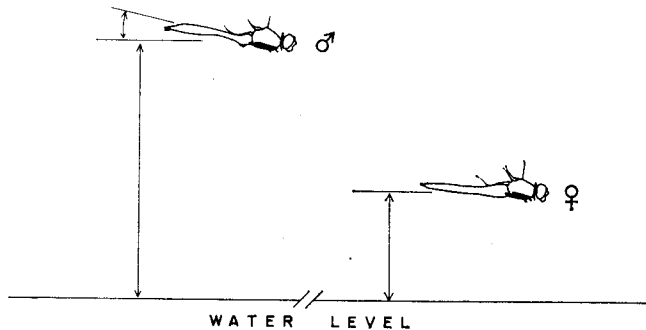
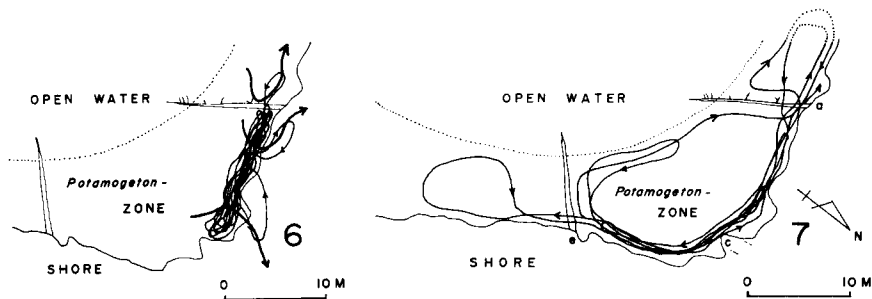


Fig. 5. Flight posture of mature individual at the pond. ♂: Patrol flight. ♀: Pre-mating flight.



Figs. 6, 7. Traces of patrol flight of male. Fig. 6 (left). Territorial flight. Thick line: flight course of intruder chased by the territory occupant. Fig. 7 (right). Nonlocalized patrol flight.

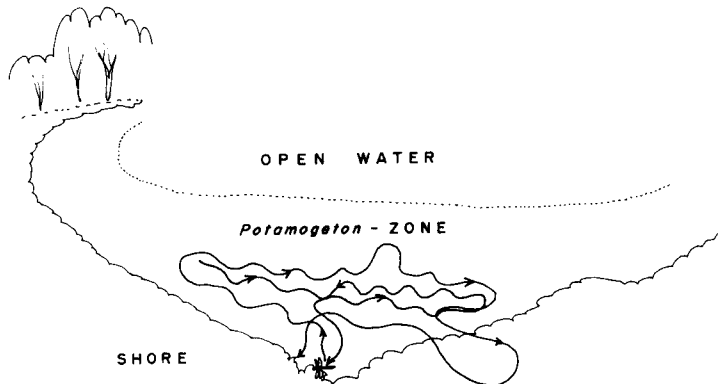


Fig. 8. Unstable type of patrol flight by a young male.

usually parallel to the shore line 0.4~1 m distant from it, with occasional cruising over *Potamogeton*-zone (Figs. 6, 7). Hovering (each ca. 1 sec.) is interposed repeatedly at the interval of 1~2 m. During this flight the wings continue beating, the abdomen raised ca. 20° upward and the legs are folded tightly to the thorax.

Beside the above normal patrol flight, there observed the other type of patrol flight, *unstable patrol flight*, at the pond (Fig. 8). The latter differs from the former in the following points: variable height (0.5~2 m), somewhat lower speed, infrequent hovering, flight range covering the shore, winding flight course, occasional insertion of resting or feeding. In 1971 the occurrence of this unstable type was restricted to June 12~13, the first and second days of the reproductive period of the population. By this seasonal limitation and similarity to the feeding flight during pre-reproductive period (Ubukata 1973), this type is regarded as the behavior performed by individuals being in the transitional stage from pre-reproductive to reproductive period.

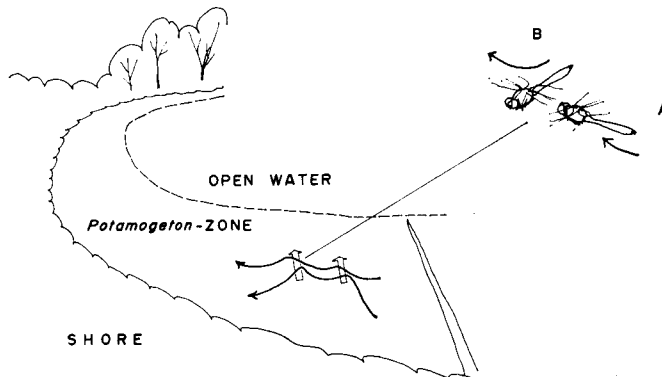


Fig. 9. Posture and flight course of attack.

Attack: The response of the patrolling male to other males is attack in most cases. On perceiving another male in the range of 2~3 m, the male dashes swiftly upon him, without particular display posture as in *Plathemis lydia* (Drury) (Jacobs 1955) (Fig. 9). The attacker tries to push up the thorax of the opponent from below with his head, but at the same time the latter usually jumps up avoiding violent clash. In spite of this jerky motion the height of the both does not exceed 1 m, as they return immediately to the original height after each attack. In many cases, by the repetition of the attack for 2~3 times the attacked male flies away from the place. Besides, *counter attack* is sometimes exhibited. The repetition of attacks is sometimes persistent, causing the retreat of the attacked male for a long distance, for example, 20 m along the shore (13:17, July 23, 1971). Such attack is often released also by the flight of other anisopteran male visitors to the pond, i.e., *Trigomphus melampus* Selys, *Libellula quadrimaculata asahinai* Schmidt, *Leucorrhinia dubia orientalis* Selys and *Aeschna nigroflava* Martin. Apart from attack, sexual contact is rarely observed between males (only 5 cases in 1971). This *homosexual contact* resembles the heterosexual one but stops nearly always at the stage of pretandem.

Feeding at the pond: In spite of a considerable amount of small dipteran insects as potential prey for the dragonflies, both males and females seldom catch them during the flight at the pond. However, feeding is observed exceptionally there. In catching the prey, the dragonfly darts upon it from the normal height of patrol flight, followed by return to the previous height, holding the victim in the mouth parts and chewing it without using the legs.

Self-cleaning during patrol flight: Males rarely join and brush their legs (tibiae and tarsi) for 2~3 sec. during patrol flight. Occurring independently of interaction with other individuals, this behavior is inferred as self-cleaning. Perhaps self-cleaning is performed more scrupulously during resting in woodland.

Sperm transfer (?): Males of North American corduliid species, *Tetragoneuria*

cynosura Say transfer sperm from the gonopophyses on the ninth abdominal segment to the seminal vesicle on the second abdominal segment prior to mating (Kormondy 1959). In *C. aenea* a behavior that seems to be identical to the sperm transfer is rarely observed during patrol flight. A typical instance is cited below.

July 27, 1974, 15:00. A male, making patrol flight along the shore, bend suddenly his abdomen ventrally. This attempt was interrupted by an approach of another male to him. After chasing away the intruder, he tried again the same behavior and touched the abdominal tip with the basal portion of abdomen for within a second. Then he continued normal patrol flight with the abdomen stretched as usual.

Resting: Mature males as well as females seldom perch at the pond, except very early or late in the reproductive period. The duration of such resting is short (1~13 min.). The posture is as follows: Sitting on leaves of *Menyanthes*, *Sasa*, etc. or hanging down from leaves of *Phragmitis*, shrubs, etc. with all six legs. The perching sites are 0~4 m distant from the water edge and 0.3~1.5 m high. Abdomen is not curved, touching the leaf surface or not, and wings fully opened.

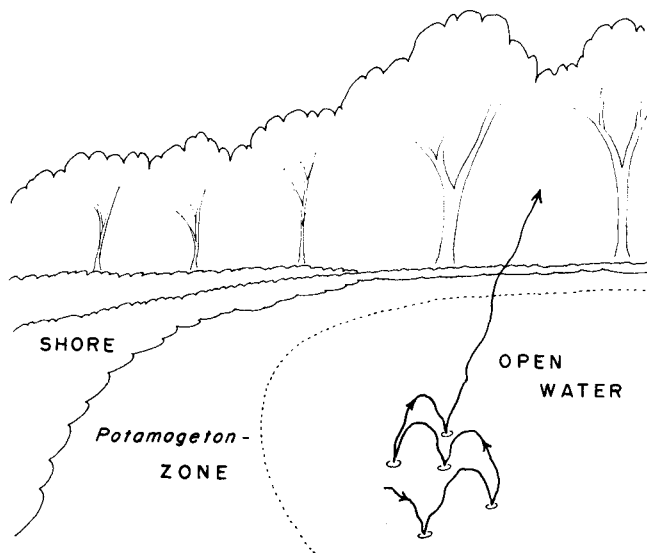


Fig. 10. Flight course of bathing.

Bathing: Bathing is the other type of flight exhibited by males at the pond. Flying about with a zigzag course over the central part of the pond, males throw themselves onto the water surface for at most 1 sec. (Fig. 10). Immersing all the body with wing opened in the water at that moment, they fly upwards to the height of 1~2 m and repeat it in the same manner for 1~8 times. After bathing most individuals leave the pond flying high up. The function of the bathing may

be one of the following items rather than food- or water-intake: body cleaning, lowering of body temperature, some cases might be a displacement activity of males defeated by other males (Taketo 1961).

3.2. Female behavior

At the pond females show simple behavior, consisting of only three patterns: pre-mating flight, oviposition and resting.

Pre-mating flight: This corresponds to the patrol flight of male, during which they meet each other and copulate. After passing through the shore vegetation at 0.5~1.5 m height, females begin the pre-mating flight 10~15 cm above the *Potamogeton*-zone, or rarely above the open water, too (Figs. 5, 11). The posture differs from that of males only in the angle of the abdomen, kept nearly horizontally

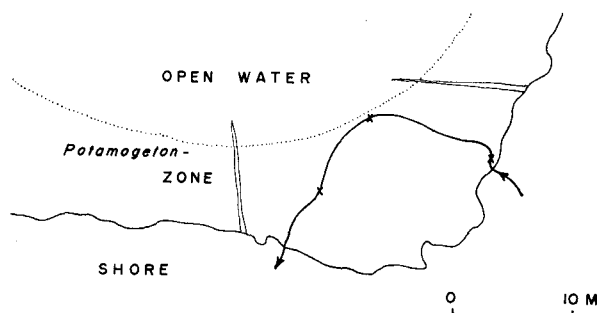


Fig. 11. Course of pre-mating flight of a female. ×: Hovering.

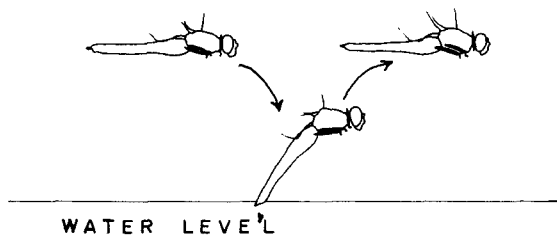


Fig. 12. Posture and movement of oviposition.

(ca. 5° upward). Flight course is gently sinuate not paralleling with the shore line as in male. The speed is somewhat lower than that in male patrol flight, and the frequency of hovering is very low (e.g. one per 10 m). Unless approached by males they leave the pond within a minute, flying close to the shore vegetation as in the visiting moment. But the majority of the females in pre-mating flight are found by males flying near-by and are brought to copula. Beside this flight females in oviposition also often enter in copula as mentioned in the next section. The encounter between females in pre-mating flight was not observed.

Oviposition: As in other corduliid species so far studied, *C. aenea* makes flying oviposition into water by solitary females. As soon as visiting the pond to lay eggs, females fly about at 7~9 cm height over the *Potamogeton*-zone or within the emerged vegetation especially of *Menyanthes*, with the same posture as in pre-mating flight. During this flight they strike the water by their abdominal tips (Fig. 12). When the tip is immersed in the water, a lump of 3~5 eggs is washed off and sink in the water. Unless disturbed, the water striking is repeated for every 0.7~1.3 sec. There are some differences in flight pattern of oviposition according to the structural difference between emerged and floating-leaved vegetations. At the *Potamogeton*-zone, females fly widely changing the direction at random, sometimes as wide as 5 m×4 m with less interposing of hovering. The points of striking are confined to the water surface close to the plant body; Open water (CP) apart from *Potamogeton*-zone is never selected for oviposition, unless fallen trees etc. are provided closely under the water surface where some eggs are laid. On the other hand, at the pond margin, smooth advance is disturbed by the dense plants. Therefore females move inch by inch repeating alternately hovering and water striking. Out of 35 cases of oviposition observed within a distance of 5 m from the observer 18 (51.4%) were made at pond margin. In the same manner in pre-mating flight, they leave the pond after oviposition lasting 5 sec.~4 min.

As already touched upon, ovipositing females are also frequently approached by males and copulate. In 1970 and 1971, 36 out of 82 females observed ovipositing at the *Potamogeton*-zone were approached by males: 24 (29.3%) copulated and 12 (14.6%) fled from the male. At the marginal area, four (7.7%) females copulated and six (11.5%) fled among 52 ovipositing females. These results suggest that the female ovipositing at *Potamogeton*-zone are found and copulate more frequently than those ovipositing at the pond margin.

Those which escape from the approaching male dash toward the shore vegetation, at which they pass through the thicket of *Phragmites* or perch on herbs, which are effective to get rid of the chasing male. As a particular case in such a situation, an *akinesis* was observed as below.

July 12, 1974, 13:28. A female, being chased, rushed into the thicket of *Phragmites*; the body inclined laterally was caught between the stalks of the *Phragmites*. All body parts were kept motionless for ca. 10 sec. Then, she walked slowly and climbed up a *Phragmites* stalk up to 20 cm, from which she flew off after brief wing vibration, and restarted oviposition at the margin 3 m distant.

Resting: See the description in male behavior.

3.3. Mating behavior

On perceiving a female, the male in patrol flight approaches her at the highest speed and form the copula position. With this position the pair fly away from the pond (Fig. 13). In approaching, the sex is discriminated by the relative

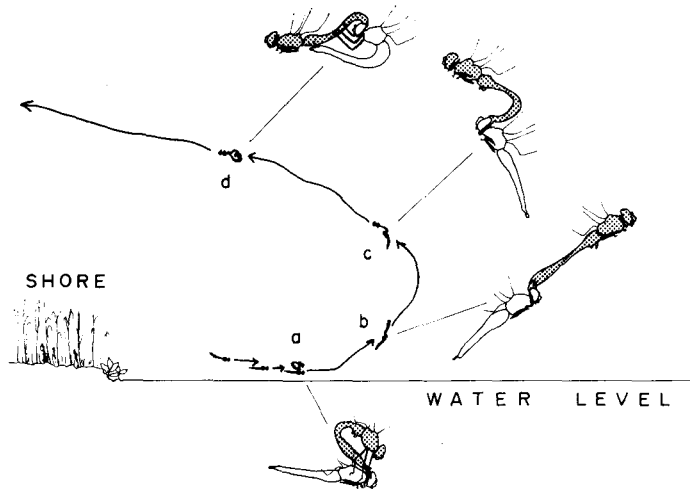


Fig. 13. Mating process at the pond. (Male, shaded). a: pretandem. b: tandem. c: ditto, trying copula position. d: copula position leaving the pond.

thickness of the basal part of abdomen and the difference in flight pattern (Ubukata, unpublished experiment). The male tries to clasp her head with his abdominal appendages bending his abdomen fully ventrally. No special courtship posture is displayed as in *Plathemis* (Jacobs 1955) or *Calopteryx* (Buchholz 1951, Heymer 1973, Waage 1973). The *pretandem* position lasts usually at most 1~2 sec. at 5~10 cm above the water surface, in which the both continue wing beating. In only four out of 121 cases of pretandem the female body fell to the pond or ground surface. As soon as taking the *tandem* position, they fly upwards with a moderate speed for 2~3 sec., until they perform the *copula* position at the height of 2~4 m. Rarely the female does not comply quickly with the male's attempt to copula. Then he continues the tandem flight wandering about over the pond for 1~2 sec. till the accomplishment of the copula position. The flight of pair in copula leaving the pond far away (more than 50 m) is less smooth than in tandem due to the discordance of wing movements between the partners. The pair must perch on a tree in the forest, during which they carry through the transfer of sperm from male to female. The duration of copulation was not measured, since the observations were concentrated in the behavior at the pond in the present study. According to Münchberg (1932), the copulation lasts 10~15 min. in *C. a. aenea* (Linné).

During the mating process there are some atypical situations as follows: When a male finds out a female making oviposition among emerged plants which prevent the male from approaching her, the male confines the patrol flight within one meter circle around her and drives off every other males approaching there. This behavior superficially resembles the guarding exhibited in some species such as *Orthetrum albistylum speciosum* (Uhler) (Itô 1960), *Calopteryx splendens* (Harris)

(Buchholtz, *op. cit.*) and *Hemicordulia ogaswarensis* Oguma (Sakagami et al. 1974), in which the previously copulated male guards the female, but differs in the following essential points: The male of *C. aenea* will try to copulate if the female flies out of the vegetation. The female has not mated with him before oviposition.

At male's approach, females sometimes try to fly away. In such cases the female scuttles with the highest speed at 20~30 cm height, and the male chases behind her. At the early phase with her speed is still low, he succeeds in mating. But thereafter, it becomes difficult, because she accelerates and moreover enter the *Phragmites*-vegetation. In female's rushing into the vegetation, the male hovers for a few seconds and restart the patrol flight. During this *sexual chase* other males patrolling nearby often join it. When the male density is high such chase often contains up to six males for a single female. These males make a procession at nearly regular interval (0.8~1.2 m) between each other. Three (12.0%) out of 25 cases of procession resulted in mating with the nearest male.

Since the copulating pair leaves the pond, disturbance on mating behavior is much rarer than in *Trigomphus melampus* in which the 17.4% of mating occasions are disturbed by other males, leading to *triple connection* (Ubukata, unpubl.). Whereas triple connection was only once observed (0.3%) during the present study, it was rarely (4 cases) observed that a male attempted to form tandem position with a copulating pair in flight.

July 1, 1971, 11:16. A group of three individuals was flying high over the pond. A male clasped the head of another male that is in tandem with a female (type A, Eda 1970):

The mating behavior of male *C. aenea* is sometimes released by females of *Trigomphus*, a contemporaneous anisopteran, which possess external feature and flight pattern similar to those of female *C. aenea*. But the attempt never results in tandem formation, probably due to the incompatibility of the abdominal appendages with the surface of the female head of *Trigomphus*, so *C. aenea* male gives up it and restart the patrol flight.

4. Territoriality

Territoriality in the definition by Noble (1939) has been confirmed in males of many Odonata species since St. Quentin (1934) and Jacobs (1955). *C. aenea* also shows a conspicuous territorial behavior during patrol flight, provided by the population density exceeding a certain level.

4.1. Confirmation of territoriality

The requirements for the confirmation of territoriality are localization and spacing by defense behavior. the localization is easily confirmed by tracing the flight course of marked males. As shown in Fig. 6, the male confines his patrol flight to an elongated circular area (12.2 m×3 m in averag) along the shore. Such

males occupy the area for 1~40 min. and drives off any conspecific males intruding the area by the attack behavior. A typical example is cited below.

June 17, 1974.

- 13:35 A male (A) was making patrol flight at sector SE (cf. Fig. 1).
 13:38 An alien male intruded the flight range of A and was driven off immediately by A.
 13:42 Another male was driven off by four attacks.
 13:46 Ditto, attack — counter attack — attack.
 13:46 Ditto, attack thrice. 13:47 Ditto, attack twice.
 13:47 Ditto, attack twice.

In the territoriality of *C. aenea*, however, the owner abandons the territory at most within 40 min. (7 min. in average of 38 cases) and leaves the pond. Such vacant territory is soon reoccupied by another male. For instance, a male (No. 7412) occupying a territory at NE (a~c) left there to go to NW and soon returned again to the previous site but was driven off by the male newly occupying there (July 13, 1974, 12:13). Repeated use of the same territory site by a particular male among successive days was not observed in the marked individuals, showing the case is unusual. The dominance in the territory is acquired by the males occupying there earlier though few exceptions were observed: The effect of prior residence is maintained until the owner leaves there.

4.2. Influence of population density on the territorial behavior

Beside the territorial flight, when the male density is low, males show another type of flight, *non-localized patrol flight*, which extends over wide area (30~60 m along the shore) without defense of area, i.e. males often pass each other after slight mutual attack. A typical case is referred below.

June 23, 1971 (cf. Fig. 7)

- 14:35 No *C. aenea* at the pond. 14:36 A male arrived and started patrol flight along the NE-shore. 14:40 He flew widely ranging over 50~60 m. 14:42 Leaving the pond.

At sector NE such flight is observed only at NAI smaller than 4: when NAI becomes larger than 4~7, the flight localizes with defense of area. The change of flight types from nonlocalized to territorial may be released by the increase of frequency of encounter per unit time interval, and *vice versa*. To confirm the correlation of the length of patrol flight range to NAI, the length of traced flight area at NE was plotted against the corresponding NAI (Fig. 14). The reduction of the flight range is apparent: 20~50 m at NAI=1~3, 13~20 m at NAI 4~9 and 7~15 m at NAI 11~22 (12.2 m in average at NAI 4~22). On the other hand, the duration of territorial flight does not show correlation with NAI (Fig. 17)

4.3. Spacing by territoriality

As mentioned above, the territory of *C. aenea* more or less shrinks by increased population density. Therefore it should be asked whether the territoriality func-

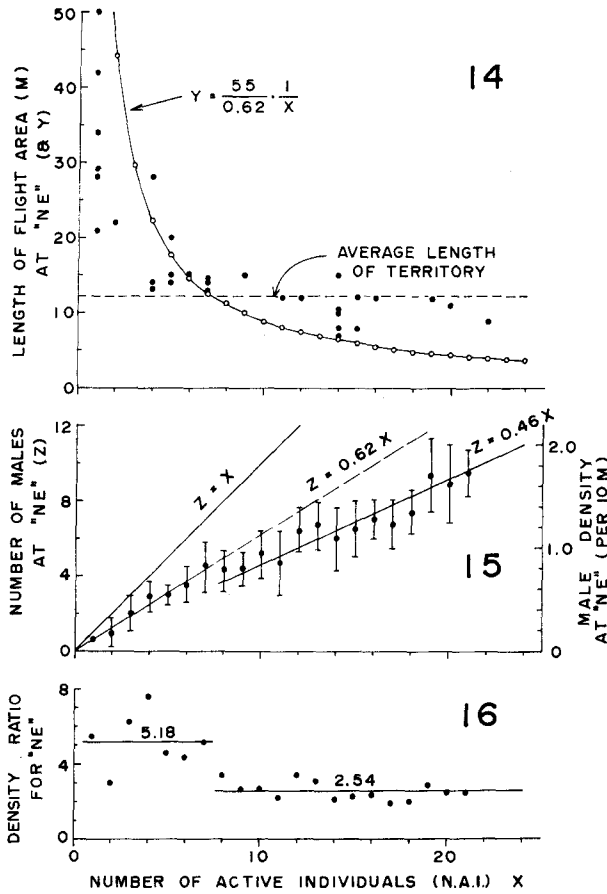


Fig. 14. Length of patrol flight area against NAI (solid circle). Shore length per male at NE according to the linear increase of NAI under ineffective spacing mechanism (rate=0.62; open circle).

Fig. 15. Correlation of male number (Z) and density at NE to NAI. Horizontal bar: standard deviation.

Fig. 16. Density ratio (density at NE/density at the other sectors) against NAI.

tions to disperse the males within the pond. If the population density at the most preferred sector is kept constant after the saturation regardless of increasing NAI, the spacing by territoriality should be completely effective. Conversely, if the density is proportional to NAI, then the density regulating function of territory should be rejected. These alternatives were tested as follows:

Among five sectors (cf. Fig. 1), there are preference order by patrolling males given by the relative preference (Table 3). When the males are few (NAI=1~7),

Table 3. Relative preference for each sector by mature individuals at NAI=1~7 when *Aeschna* males are absent (1971, '73 and '74)

Sector		NE	SE	SS	SW	NW	Total	Number of census occasions
Shore length (m)		55	42	43	40	42	222	
♂	A	165	27	18	11	35	256	70
"	" %	64.4	10.6	7.0	4.3	13.7	100.9	
♂	B	84	48	12	21	20	185	47
"	" %	45.4	25.9	6.5	11.4	10.8	100.0	
♀	"	25	4	3	7	11	50	200
"	" %	50.0	8.0	6.0	14.0	22.0	100.0	

A. Data from the standing census. B. Ditto from the circling census.

♀; Oviposition, pretandem or copula.

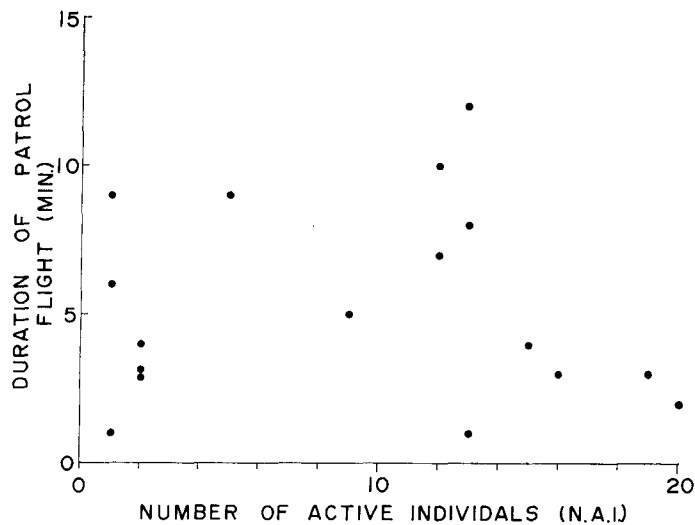


Fig. 17. Duration of patrol flight at NE against NAI. That of surplus males are excluded, 1970, '71 and '73.

they show the following preference order (from circling census), NE>SE>NW>SW>SS¹⁾. The order is the same as that of density (number of individuals/shore length). The main difference of NE from SS are the presence of abundant emerged plants and the scarcity of shades by trees. This order is nearly parallel with that of females. Therefore it may be said that the preference order of male is related with the mating expectancy. Henceforth the numerical data are dealt with

1) The ratio of CP is small (0.3%) enough to be ignored.

Table 4. Averaged number of males at each sectors for each NAI in standing census when *Aeschna* males are absent at the pond, 1971, '73, '74. Parenthesized: range

NAI	Sector	NE	SE	SS	SW	NW	CP	Number of cases
1		0.6 (0-1)	0.1 (0-1)	0.0 (0-0)	0.1 (0-1)	0.3 (0-1)	0	16
2		1.0 (0-2)	0.7 (0-2)	0.0 (0-0)	0.2 (0-1)	0.2 (0-1)	0	6
3		2.0 (0-3)	0.3 (0-1)	0.1 (0-1)	0.0 (0-0)	0.6 (0-3)	0	11
4		2.9 (1-4)	0.2 (0-2)	0.6 (0-2)	0.2 (0-1)	0.2 (0-1)	0	13
5		3.0 (2-4)	0.6 (0-3)	0.5 (0-2)	0.0 (0-0)	0.9 (0-2)	0.2 (0-1)	7
6		3.5 (2-5)	0.4 (0-1)	0.2 (0-2)	0.7 (0-2)	0.9 (0-2)	0	9
7		4.5 (3-7)	1.0 (0-2)	0.6 (0-3)	0.1 (0-1)	0.8 (0-2)	0	8
8		4.3 (2-6)	1.4 (0-3)	0.4 (0-2)	0.8 (0-4)	1.1 (0-2)	0	10
9		4.4 (3-6)	1.4 (0-4)	0.8 (0-3)	0.5 (0-2)	1.8 (1-3)	0	10
10		4.8 (2-6)	1.7 (1-3)	0.9 (0-2)	0.7 (0-3)	1.7 (1-3)	0.1 (0-1)	11
11		4.7 (2-7)	2.3 (0-5)	1.5 (0-3)	0.6 (0-2)	1.9 (0-4)	0	17
12		6.5 (4-8)	1.7 (0-3)	1.0 (0-2)	0.6 (0-2)	2.3 (1-4)	0	7
13		6.6 (5-9)	2.1 (0-4)	1.6 (1-2)	0.1 (0-1)	2.5 (2-3)	0.1 (0-1)	11
14		5.9 (3-9)	2.5 (1-4)	1.7 (0-3)	1.0 (0-3)	2.9 (1-5)	0.1 (0-1)	13
15		6.5 (3-8)	3.5 (2-6)	2.0 (1-5)	0.6 (2-3)	2.3 (1-4)	0.2 (0-1)	8
16		7.0 (6-9)	2.9 (2-4)	1.8 (0-4)	1.0 (0-4)	3.4 (2-5)	0	12
17		6.8 (5-9)	2.4 (1-4)	2.4 (0-6)	2.0 (1-4)	3.4 (2-5)	0.2 (0-1)	7
18		7.4 (6-10)	4.1 (3-6)	2.3 (1-4)	0.9 (0-3)	3.2 (1-6)	0	10
19		9.5 (6-12)	3.0 (2-4)	2.9 (2-4)	1.1 (0-3)	2.7 (1-3)	0	5
20		8.8 (5-11)	4.2 (3-7)	2.2 (1-4)	1.8 (0-4)	3.0 (1-4)	0	7
21		9.5 (8-11)	4.0 (3-6)	3.8 (3-5)	1.1 (0-3)	2.7 (1-5)	0	4
22		8.0 (8-8)	5.0 (5-5)	3.0 (3-3)	3.0 (3-3)	3.0 (3-3)	0	1
23		8.0 (8-8)	8.0 (8-8)	0.0 (0-0)	2.0 (2-2)	5.0 (5-5)	0	1
26		11.0 (11-11)	3.0 (3-3)	3.0 (3-3)	3.0 (3-3)	6.0 (6-6)	0	1
Shore length (m)		55	42	43	40	42	—	(Total) 222
Maximum number of Territory (8 m)		7	5	5	5	5	—	(Total) 27

by the average value. The occurrence of some deviations from the average is always possible, but a general tendency could be recognized by this way. The number recorded at NE-sector for each NAI was averaged from 202 cases censused in 1971, 1973 and 1974 (Table 4, Fig. 15). Against the increase of NAI, the number of males at NE does not increase with constant ratio with NAI; the ratio is higher (0.5~0.73, average 0.62) at NAI=1~7, while lower (0.40~0.54, average 0.46) at NAI=8~21. Therefore, spacing mechanism is recognized to be effective though not complete. The cause by which the ratio does not lower in accordance with the further increase of NAI is the aggregation of surplus males to the off-shore part of the NE-sector, beside the contraction of the territories. Some of such surplus males localizes their patrol flight without defending behavior. For instance, a male (No. 7104) was flying about over the inner half of NE (a~e) for several min. without leaving there. Whenever he approached the shore, he was driven off by the territory owner (June 21, 1971, 9:10).

To analyze the fact that the ratio changed at NAI=8, the expected shore length occupied by an individual under inefficient spacing mechanism (Y) at NE was calculated for each NAI. The value of Y against NAI (X) is expressed by the following formula:

$$Y = \frac{s}{r} \cdot \frac{1}{X}$$

where s is shore length of the sector, 55 m for NE, and r is the relative preference to NE under ineffective spacing mechanism (NAI<8), 0.62 for the present case. The theoretical values are plotted in Fig. 14. At NAI=8, where the relative preference is converted to 0.46, Y becomes lower than 12.2 m, coinciding with the mean size of territory. The alternation of preference at NAI=8 (or Y=12.2) would be grasped more clearly, when the density ratio (density at NE/density at the other four sectors) is plotted against NAI (Fig. 16). The ratio is 5.2 in average (3.0~7.6) at NAI=1~7, while 2.5 (1.9~3.4) at NAI=8~21.

Summarizing, this result can be explained as follows: The density at NE increase at a higher ratio (0.62) till NAI=8 when the shore length per one male at NE get smaller than the mean size of the territory. When NAI exceeds 8 all males at NE become territorial, causing more or less the displacement and spacing of newcomers. Thus, the spacing mechanism by territoriality in *C. aenea* was proved quantitatively.

The theoretical value of the upper limit of NAI for Hôrai-numa (Pond A) is calculated to be 27 by dividing the total shore contour (222 m) by the minimum length of territory (8.0 m). This value fairly agree with the observed highest value (26; cf. 2.1.), which supports the effectiveness of territoriality.

Concluding remarks

The wide range of daily activity of *C. aenea* adult was revealed in the present

study. The hour of presence at pond extends over 14 hours from sunrise to beyond sunset. Such data have hitherto seldom been reported, so that the comparison is made with other six dominant Odonata species cohabiting at Hôrai-numa. Among them, the lower limit of air temperature (measured at the pond) permitting the visit to the pond is lowest in *C. aenea* (5.8°C): That of *Lestes sponsa* Hansemann and *Sympecma paedisca* Brauer is 11~12°C, in *Sympetrum frequens* Selys, *Aeschna nigroflava* Martin, *Trigomphus melampus* and *Agrion lanceolatum* Selys 14~16°C (Ubukata, unpubl.). The suppression of activity by either of wind, dimness or rain in *C. aenea* is less intensive than in *Agrion* and *Trigomphus* surveyed on the same days. These relatively high endurance against adverse weather conditions may be adaptive to the life of *C. aenea* in their cool habitats.

The behavior of *C. aenea* was classified into several patterns which are not so much specialized among Odonata, lacking either of threat posture or courtship display. Each behavior pattern as well as daily activity of *C. a. amurensis* does not differ from those of the European subspecies, *C. a. aenea* (L.), (Robert 1958, Münchberg 1932) except for the height of patrol flight (30~50 cm in *C. a. aenea*) and the distance of the flight by just mated pairs (shorter in *C. a. aenea*). The following behavior pattern may be characteristic to *C. aenea*: Oviposition performed among emerged plants and sexual chase by many males. The former must have some role in decreasing the disturbance by sexually active males regardless of con- or heterospecific. The latter is observed in *Aeschna*, too, and may be confirmed in some other species as one form of courting.

It was confirmed that territoriality, in spite of the flexibility in territory size and frequent alternation of the occupants, causes spacing and dispersion at the habitat. Up to the present, the following items have been proposed as functions of odonate territoriality: 1. prevention of food shortage (St. Quentin 1934), 2. colonization of new breeding areas, 3. reduction of depredation, 4. prevention of interference with oviposition, 5. reduction of time spent in aggression, 6. prevention of interference with mating (Moore 1957), 7. sexual selection (Jacobs 1955). Among these items, 1, 3, 4 and 7 are denied for the function of the territory of *C. aenea* by the reasons as follows: 1. Feeding is made scarcely at the pond in spite of the relatively abundant presence of small insects (cf. 3. 1.), but in woodland. 3. Throughout the present study no mature individual has been observed to be killed by predators at the pond. 4. Oviposition is performed by females alone without guarding by territorial males. Moreover, males regardless of territorial or not, chase such females and try to copulate. Therefore territoriality of *C. aenea* brings neither increase or prevention of disturbance with oviposition. 7. Females are passive during mating, so that the individual differences of male seem not to be selected by females. Although the dispersal within the pond was proved in 4.3., the dispersal to new breeding areas (the item 2) caused by territoriality seems not usual as discussed below. In contrast with the strong tendency of avoiding the pond and the considerable exodus from the pond emerged (only 36.4% of the

males marked at emergence were returned to the pond) during pre-reproductive period, mature males show strong attachment to the pond (rediscovery ratio of males marked in June 1971=63.0%) and visit the pond almost every day. Similar tendency was reported also in *Leucorrhinia dubia* V.d. Lind. (Pajunen 1962). Consequently 5 and 6 are probably more or less effective in *C. aenea*. As already mentioned a pretandem pair separates in few cases disturbed by another male. If the territoriality were removed from *C. aenea*, the male density might pile up locally on occasions and the pretandem pair would be disturbed much more (the item 6). Reduction of aggression (5) should be always accompanied with effective territoriality. From above discussions the functions of the territoriality common among Odonata are assumed to be 1. Prevention of interference with mating, 2. uniformization of distribution of mature males within the reproduction site.

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Summary

The life history and behavior of a dragonfly, *Cordulia aenea amurensis* Selys during reproductive period were studied at a dystrophic pond, Hōrai-numa, in Usubetsu near Sapporo in 1970~1974.

1. The reproductive period was June 12~August 17 (♂) or June 19~August 6 (♀) in 1971, generally coincided with the results in 1970, '73 and '74, with the peak from late June to mid July. Studies of marking and rediscovery revealed the maximum and mean male adult longevities respectively as 45 and 10.3 days (1970). The sex ratio at the pond during reproductive period extremely biased 928 (98.6%) ♂♂ and 9 (1.4%) ♀♀ in 1971, apparently caused by the behavioral difference between sexes.

2. The pattern of diurnal flight activity at the pond is typically plateau-shaped, extending over 4:40~19:00 on clear days at the end of June. The activity is suppressed completely by cool air temperature lower than 5.8°C or ordinary rain, while only lowered by the strong reduction of illumination or slight rain. The suppression by neither high temperature (28.8°C) nor strong wind (force of wind=5) was recognized.

3. Behavior patterns exhibited at the reproduction site were classified and described: Male behavior; patrol flight, attack, feeding, self-cleaning, sperm transfer, resting and bathing. Female behavior; pre-mating flight, oviposition and resting. Mating behavior; pretandem, tandem, copula, sexual chase and triple connection.

4. Localization and spacing by the male territorial behavior were discussed in relation with population density and its heterogeneity among sectors. As the

function of territory in *C. aenea*, prevention of interference with mating was assumed.

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