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

I. Emergence and Pre-reproductive Periods¹⁾

By

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(With 8 Text-figures and 5 Tables)

The order Odonata is outstanding among insects by its behavioral differentiation in territoriality and mating, both released by optic signals and performed within relatively narrow and open areas. These peculiarities, which facilitate ethological observations and field experiments, resulted in the publication of numerous studies since Williamson (1906), for instance, St. Quentin (1934), Buchholtz (1951, 1955, 1956), Moore (1952), Jacobs (1955), Loibl (1958), Krieger and Krieger-Loibl (1958), Johnson (1962a, 1962b), Pajunen (1964, 1966) and Heymer (1973). However, the majority of these authors dealt with the forms belonging to Calopterygidae, Lestidae and Libellulidae, leaving many other important groups still poorly explored, nevertheless comparative studies of these groups are essential to trace the behavioral evolution in Odonata. Another promising aspect in field studies of Odonata is the population ecology, which was started by Corbet (1952) and followed by Pajunen (1962), Johnson (1962c) and Higashi (1969), but there are still much to be done for the development of this field.

Keeping these ideas in mind, I have engaged myself since 1970 in field observation of some corduliid species, which have so far not precisely been studied in bionomic and behavioral aspects, probably due to their inconspicuous features and scarcity in temperate zones. In this first report the life history and behavior during emergence and pre-reproductive periods of *Cordulia aenea amurensis* Selys, so far known only by fragmentary observations (Itagaki 1954, Fujisawa 1957, Iijima 1966), are described.

Area studied

The field survey was carried out during May 7~September 15, 1970, May 20~November 2, 1971 and June 3~July 31, 1972 at and around two stations, Pond A (Hôrai-

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

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numa, 530 m alt.) and Pond B (anonymous, 730 m alt.) both located at the foot of Mt. Muine (1,461 m alt.) near Sapporo (Fig. 1, A). Both A and B are calm mountainous marshy ponds surrounded with forests consisting of several kinds of deciduous broad-leaf trees and afforested pine trees, being 2.1 km distant from each other and at least 2.3 km separated from any other ponds or similar aquatic environments. Pond A, the main station, is nearly circular with the total shore contour 222 m, the maximum diameter 80 m and the depth at most 2 m, with slight in- and outflows through small streams (Fig. 1, B).

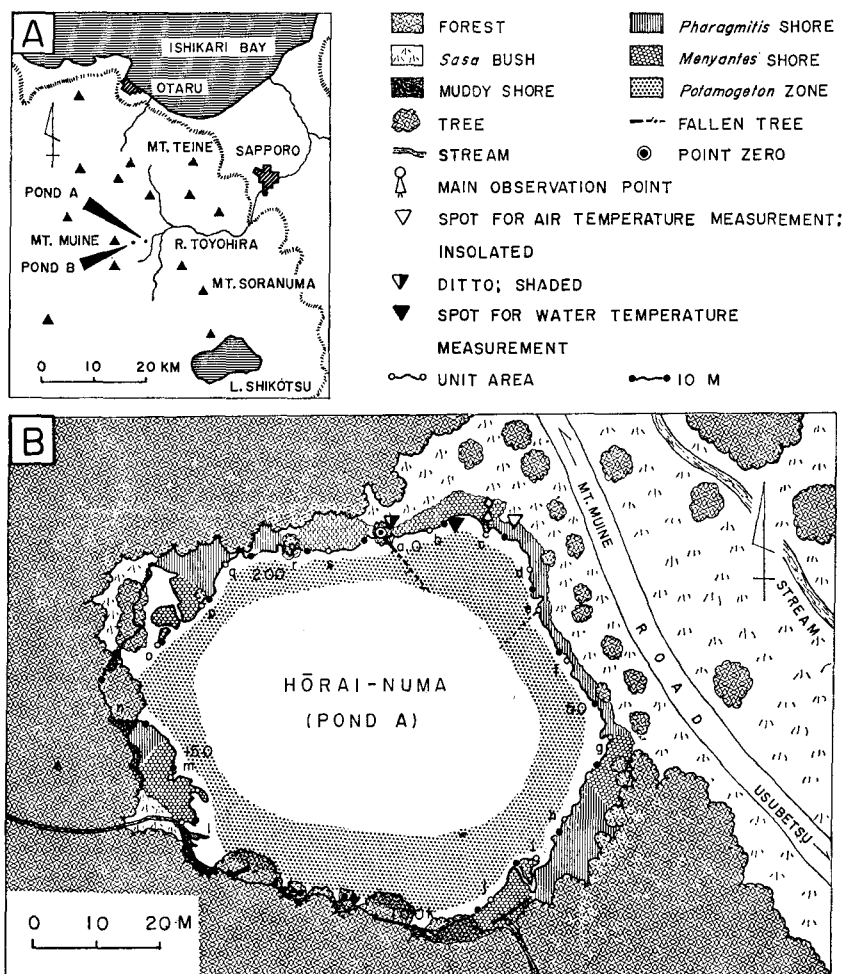


Fig. 1. Location of area studied (A) and topography of Hōrai-numa (B, Pond A). Arabic figures mean the cumulative distance (m) along the shore from Point zero. The letters a~s signify the boundaries of unit areas used to facilitate subsequent descriptions.

From the proper shore, bog mats 1~6 m wide covered mainly with *Phragmites* and *Menyanthes* extend into the water, except the shaded southern parts where these emerged plants are very sparse. The vegetation consists of emerged plants, *Phragmites communis* Trinius, *Menyanthes trifoliata* L. and *Typha latifolia* L., shore plants, *Lycopus uniflorus* Michx., *Sphagnum* sp., *Cicuta virosa* L., *Lobelia sessilifolia* Lamb., *Carex* sp., *Lastrea phelypteris* (L.) Bory and *Triadenum japonicum* (Blume) Makino and floating-leaved plants, *Potamogeton Fryeri* A. Bennett with admixture of *Nymphaea tetragona* Georgi, showing the dystrophic lake type.

The Odonata fauna of Pond A is as follows. (The species with asterisk are occasional visitors): *Agrion lanceolatum* Selys, *A. terue* Asahina*, *Sympecma paedisca* Brauer, *Lestes sponsa* Hansemann, *Mnais strigata* Selys*, *Trigomphus melampus* Selys, *Aeschna nigroflava* Martin, *Anotogaster shiiboldii* Selys*, *Epiheca bimaculata sibirica* Selys*, *Cordulia aenea amurensis* Selys, *Somatochlora uchidai* Foerster, *Orthetrum japonicum japonicum* Uhler*, *Libellula quadrimaculata asahinai* Schmidt*, *Sympetrum danae* Sulzer*, *S. frequens* Selys*, *S. baccha matutinum* Ris* and *Leucorrhinia dubia orientalis* Selys.

The general features of Pond B are similar to those of A, except for the elongated shape, about thrice in extent, steeper shores and the lack of floating-leaved plants such as *Potamogeton*.

Results and discussions

1. Habitat preference

C. a. amurensis is so far known from Eastern Siberia, Northern Manchuria, Northern Korea, Sakhalin, Hokkaidô and Honshû, while its western vicariant, *C. a. aenea* (Linné), is distributed in Europe, North Africa, Central Asia and Western Siberia.

The habitats of *C. a. amurensis* in Central Honshû are restricted to alpine high moors such as Shiga-kôgen, Kirigamine and Ozegahara, so that it was formerly regarded as a high moor inhabitant (*Tyrphobionte* by Peus 1932) (Asahina 1954). Recent records revealed the presence of this subspecies even at low moors or lowland ponds and lakes in Northern Honshû and Hokkaidô (Asahina 1957): Tonono-ike (240 m alt.), Niigata Prefecture; Lake Hakuryû (300 m alt.), Yamagata Pref.; Lake O-numa, Lake Tôro and Hôrai-numa, Hokkaidô. Thus, inhabiting both low and high moors in cool climate, *C. a. amurensis* should belong to moor inhabitants (*Tyrphophile* by Peus). On the other hand, the western subspecies, *C. a. aenea*, is one of pond inhabitants preferring also oligotrophic moors (*Tyrphoxene* by Peus) (Robert 1958, Schmidt 1967).

2. Adult life periods

The adult life of Odonata is generally divided into four successive periods: 1. Emergence, 2. Pre-reproductive, 3. Reproductive and 4. Post-reproductive period. In the present paper only the first two periods are dealt with, leaving the other two and larval stages in subsequent papers.

2.1. Emergence period

In many aquatic insects emergence is one of the critical steps in their life cycle, both physiologically and ecologically, as the turning point from aquatic to aerial life. In ecological point of view it is important to know how insects pass through such a crisis at individual and population levels.

In order to obtain the data on emergence, daily collection of exuviae was made at Pond A in late afternoon from June 3 to July 2 in 1971 almost every day, and from June 3 to June 23 in 1972 every two days. During early June, 1971, daily collection was performed several times per day at every one hour, while once per day on other days. At daily collection, all the shore was surveyed with a stick about 1 m long to examine herbs, the leaves of which harbored many exuviae. The sex of exuviae collected was sorted by the rudimentary structure of male accessory genitalia at the second and third abdominal segments (Fig. 2). The observation of emergence habit was made during daily collection.

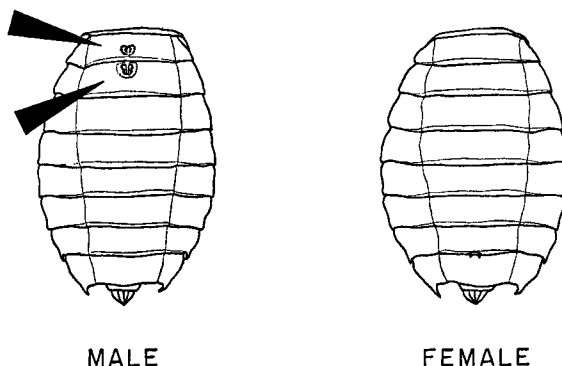


Fig. 2. Sexual difference found on abdominal venter in final instar larva.

2.1.1. Emergence habit: Unless it rains, larvae ready to emerge leave the water in the morning and crawl about on the shore until they find out suitable emergence supports. The horizontal distance of emergence supports from the nearest water edge is relatively short, ranging mostly (96%) within ± 50 cm from the water edge (average 10 cm) with an exceptional case reaching 220 cm at Pond A (Fig. 3, A). In Shiga-kôgen, the distance was 141.7 cm in average with the maximum 645 cm, probably affected by the scarcity of suitable emergence supports near the water edge (Fujisawa 1957). This assumption is supported by the present result where herbaceous plants suitable for emergence support are abundant along the water edge as in Pond A. This tendency is applicable to the western subspecies which uses mainly herbs on shore, e.g. *Carex* (Robert 1958), but tree trunks when no sufficient herbs grow along the shore (Kiauta 1965).

Once choosing the emergence supports, the larvae sit on them clinging with claws, taking the position $90 \sim 150^\circ$ to the horizontal plane directing the heads

inclined upward (Fig. 3, X). As emergence supports, following cases were observed (Pond A, 1971): *Pharagmitis* (73) stalks (55), leaves, underside (15), sets of stalk and leaf (3); *Menyanthes* (64) leaves, underside (57), ditto, upperside (3), rolled leaves (3), floral axis (1); other herbs (9); a twig of a shrub (1); and head of a stump (1). As shown in Fig. 3, the emergence height ranges mostly (99%) 5 ~ 50 cm (20 cm in average) above the water level with a single exception at 130 cm on a shrub twig. This largely depends on the growth of plants adopted; the height

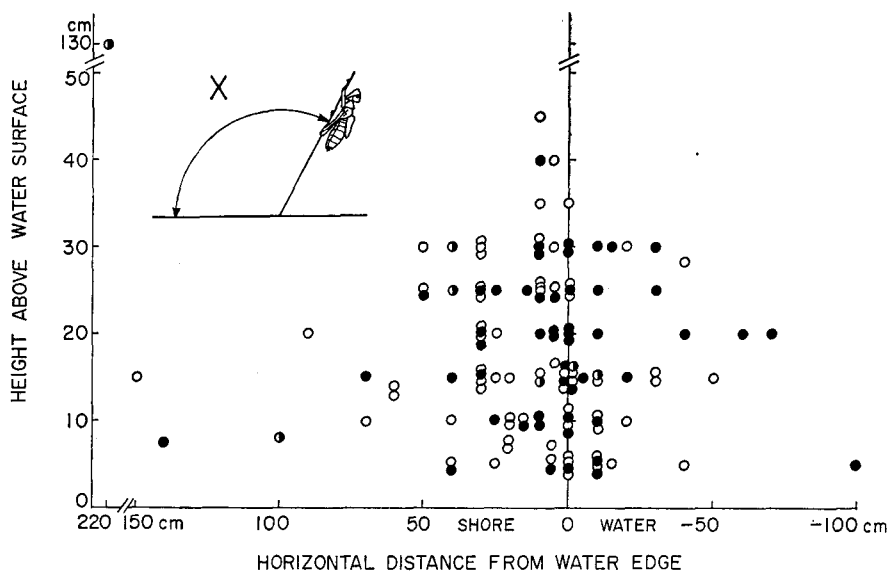


Fig. 3. Distribution of emergence positions of 125 exuviae recorded. Solid circles, on *Menyanthes*. Empty circles, on *Pharagmitis*. Half solid circles, on other plants. X Prevailing posture showing the angle to horizontal plane.

of which is 30 ~ 50 cm (*Pharagmitis*) and 20 ~ 30 cm (*Menyanthes*) during emergence period. Even after sitting on the emergence supports, larvae occasionally return to the water if it begins to rain. However, once the ecdysis is begun, they never return to the water even if disturbed by rain or the observer.

Although no complete observation of the emergence process was made, the influence of climatic conditions on the time spent for emergence was detected. As in the data presented in Table 1, the average duration between the recess (Eda 1959) and maiden flight is ca. 160 min. under cloudy weather, prolonged by rainy weather to or beyond 600 min., while reduced to ca. 100 min. by fine weather. It is suggested that either high humidity or possibly low temperature retards the emergence. The marked delay mentioned above may be explained by the inhibition of flight due to the rain, since the observed teneral adults seemed ready to

Table 1. Duration between recess stage and maiden flight under different weather conditions

Date (1971)	Weather	Time of recess	Air temperature at recess (°C)	Time of maiden flight	Air temperature at maiden flight (°C)	Duration between recess and maiden flight (min.)
June 8	rainy	8:53	12.8	18:30+	10.8	623+
June 11	cloudy, after rain	12:00	15.8	13:48+	16.9	108+
"	"	11:50	15.8	14:25+	16.9	155+
"	"	12:45	15.8	14:35+	16.9	110+
"	"	11:28	15.6	14:22-	16.9	174-
"	"	11:36	15.8	15:04-	17.5	208-
June 12	fine	6:49	14.6	8:32-	15.1	103-
"	"	7:25	14.6	9:21-	14.5	116-
"	"	9:49	13.9	11:40-	14.9	111-
June 14	cloudy	7:57	16.2	9:34+	17.5	97+

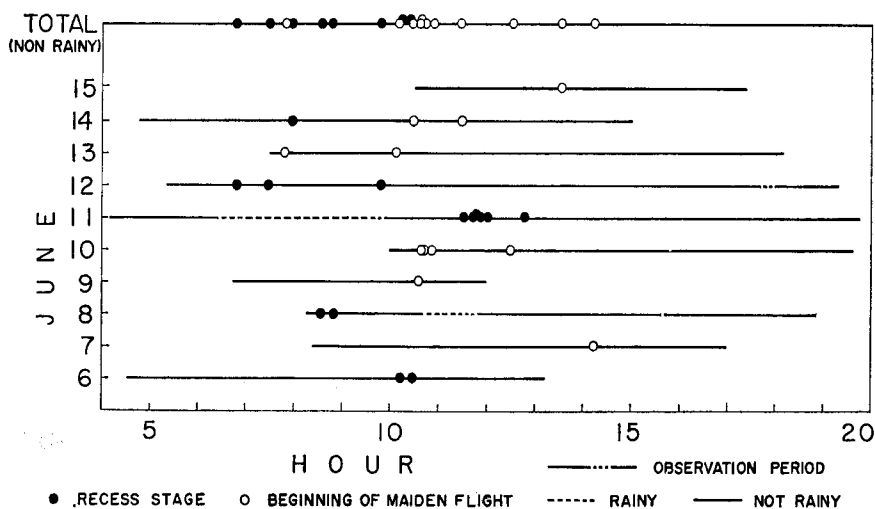


Fig. 4. Daily rhythm of emergence with influence of rain. Pond A, 1971.

fly, judging from the appearance. Including the duration of sitting (or posture, Eda 1959) (ca. 30 min.), the total duration of emergence process from sitting to maiden flight is about 3~5 hrs. (ca. 2 hrs. indoors, Fujisawa 1957).

Unless affected by rain, the emergence is apparently limited at definite hours in daytime, the recess mostly 7:00~11:00, and the maiden flight 10:00~14:00 (Fig. 4). On June 11, 1971 after the rain continued from 6:20 to 9:50 many larvae began to emerge from 10:30 to 12:00. The earliest records of landing and maiden

Table 2. Seasonal rhythm of emergence at Pond A

Year	Date of the earliest emergence	Date of emergence peak	Date of the last emergence	EM ₅₀ (See text)	Length of emergence period
1970 total	June 5	June 8	—	—	—
1971 ♂	—	June 10	June 27	9	25
" ♀	—	June 11	July 1	"	29
" total	June 3	June 10	"	"	"
1972 ♂	June 5	June 9	June 23	7	19
" ♀	"	"	June 19	"	15
" total	"	"	June 23	"	19

flight were at 4:52 and 7:43 respectively under fine weather. After completing emergence, teneral adults make a brief wing vibration and soon fly up, leaving the pond with a stolid posture slightly drooping their tails. By this maiden flight they rise up as high as 30 m, keeping the angle of 30~50° to the ground, and depart as long as 100 m from the pond without perching on trees surrounding the pond in all eight cases observed in 1971. But in 1972, in one case a teneral adult perched on a branch of such a tree. They seem to rest on branches of forest trees after a long maiden flight (Iijima 1966). The other corduliid species in Pond A, *Somatochlora uchidai*, perched on a tree along the pond after maiden flight in all three cases observed, suggesting a possible species specificity.

The emergence process of *C. a. amurensis* from sitting to the hardening of the body has already been reported by Fujisawa (1957). Its general sequence is the same to that of the other subspecies (Robert 1958) and of other corduliid species such as *Tetragoneuria* (Kormondy 1959) and *Epitheca* (Sonehara 1967), all belonging to the 'hanging type' by Eda (1963, 1964).

2.1.2. Seasonal rhythm of emergence: The emergence in Pond A began on June 3~5 and continued till the end of June (Table 2, 5). The date of EM₅₀, the time by which the half of annual emergence is reached (Taketo 1960a), is the 7~9th day after the first emergence confirmed (Fig. 5), which indicates that *C. aenea* is a *spring species* (Corbet 1962) showing *mass emergence*, as such synchronization is known in the western subspecies, *C. a. aenea*, too (Wesenberg-Lund 1913, Münchberg 1932). What mechanisms do regulate this synchronized emergence, notwithstanding the period of oviposition spread for seven weeks (Ubukata, unpubl.)? According to Portmann (1921), the final instar larvae of the western subspecies pass the second larval winter and mature rapidly in the subsequent spring. If the final instar larvae enter into a diapause in summer, they may exhibit a synchronized emergence in the following spring when the water temperature rises, as was demonstrated by Corbet (1955, 1956, 1957) in *Anax imperator* Leach. In this connection it is interesting that some individuals emerge far later in June 1971,

which makes us recollect a similar tendency in *A. imperator*. But it requires further studies to certify the mechanisms regulating the synchronization in *C. aenea*.

As shown in Fig. 5, there is no sexual difference in emergence rhythm: EM₅₀ is the same in both sexes. The emergence time in other localities are recorded: The peak is in mid and late June respectively at lower and higher altitudes in Shiga-kôgen (Fujisawa 1957), from early to late May in Lake Hakuryû, Yamagata Prefecture (Itagaki 1956). A correlation is detected between emergence time and thermal condition, when the mean air temperature in May is compared among these districts, i.e. 10.3°C (Shiga-kôgen, lower altitude, 1955), 14°C (Lake Hakuryû, 1921~1950) and 10.6°C (1970), 12.1°C (1971), 12.2°C (1972) (Usubetsu, 390 m alt., 1 km apart from Pond A).

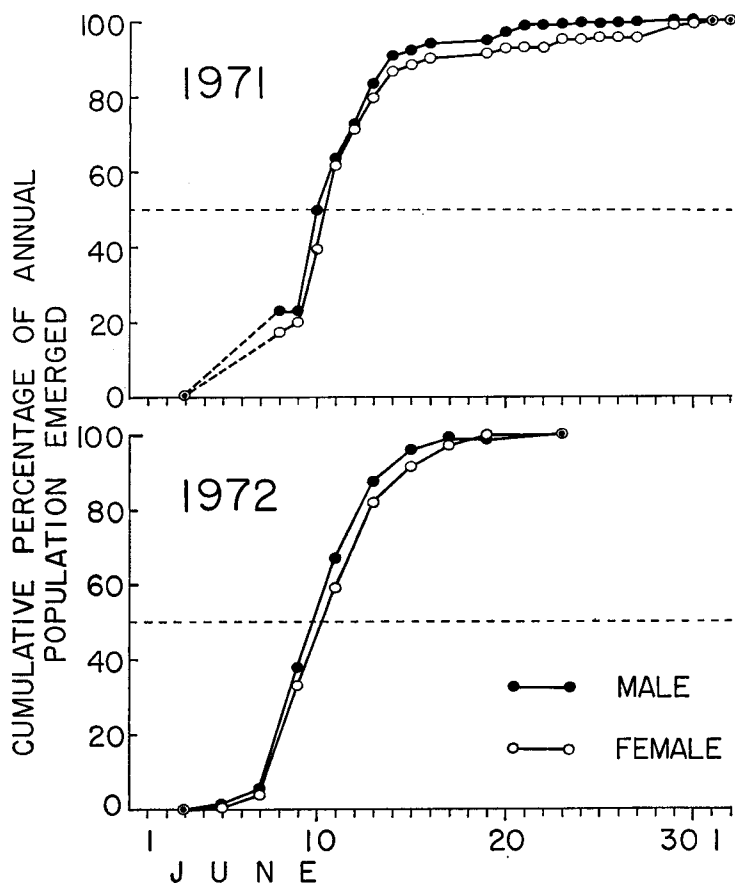


Fig. 5. Emergence curve drawn from the data of daily collection of exuviae.

2.1.3. *Size of emerging population and sex ratio:* The number of total exuviae collected in Pond A by daily collection was 255 in 1971 and 225 in 1972. Of course these figures do not show the actual number of all emerged individuals, since a considerable number of exuviae must have remained in hidden places. In order to know the efficiency of daily collection, a more precise survey was executed as mentioned below from June 26 to July 1, 1971, when the emergence time was nearly passed.

Except the southern shore which lacks bog mat and is seldom used for emergence, the shores are divided into two types, which are respectively called on the basis of predominant plants, *Phragmitis*- and *Menyanthes*-shores. Six parts (I~IV, 4.5~11.5 m along the water edge) with typical vegetation types were selected at random and examined more carefully to collect exuviae overlooked during the preceding daily collections (Table 3). From the result obtained the average efficiency of previous daily collection was calculated as ca. 55% at *Phragmitis*-shore and ca. 74% at *Menyanthes*-shore.

Table 3. Precise collection of exuviae and the efficiency of daily collection of exuviae

Locality number (unit area, Fig. 1, B)	Vegetation type	Date (1971)	Precise collection		Number of exuviae collected daily	Total number of exuviae	Collecting efficiency (%)
			1st	2nd			
I (q~r)	<i>Phragmitis</i>	June 26	6	—	9	15	60.0
II (d~e)	"	"	1	—	1	2	50.0
III(a~b)	<i>Menyanthes</i>	"	3	—	15	18	83.3
IV(o~p)	"	July 1	7	2	17	26	65.4
V (i~j)	"	"	4	1	8	13	61.5
VI(l~m)	"	"	3	2	33	38	86.8

The size of emerging population can roughly be estimated from the number of exuviae daily collected, multiplied by the reciprocal of efficiency mentioned above. The population size is estimated to be 140 at *Phragmitis*-shore, 240 at *Menyanthes*-shore and 380 in total in 1971, and in the same way 200, 160 and 360, respectively in 1972. The sex ratio (in %, ♂ : ♀) of emerging population was 52.1 : 47.9 in 1971, without significant deviation from the ratio 1 : 1 ($\chi^2=0.363$, $P>0.5$), but in 1972, 43.0 : 57.0 significantly deviating from the harmony ($\chi^2=4.31$, $P<0.05$).

2.1.4. *Mortality during emergence:* Mortality during emergence in Odonata may be provoked by three causes: by physical factors, by overcrowding, and by predation (Corbet 1962). Among them, death by overcrowding was not observed in the present study, evidently due to the abundance of emergence supports in the area and the relatively short time spent for emergence.

Ten cases of death, failure in emergence (2), predation by birds (7), and by ants (1) were confirmed by checking the position of emergence and the loss of corresponding individuals or injury of them during hourly survey in emergence season in 1971 (Table 4). These figures respectively correspond to, 0.8, 2.6, 0.4% of total

individuals collected or confirmed throughout the emergence period (255 exuviae and 10 dead individuals). In mortality records hitherto studied, *C. a. amurensis* fails less frequently in emergence than aeschnid species, i.e. *Anax imperator* (5.5~10.8%, Corbet 1957), *Aeschna juncea* (Linné) (9~22%, Kurata 1966) and *Ae. subarctica* Walker (5%, Schmidt 1964). Perhaps this low failure in *C. a. amurensis* is partly due to the emergence site preference and diurnal emergence which may be favorable in avoiding the influence of adverse conditions such as wind, cold or rain.

Table 4. Mortality during emergence period at Pond A, 1971

Cause of death	Number of cases	Percentage (%)
Failure in emergence	2	0.8
Predation by birds	7	2.6
Ditto by ants	1	0.4
Ditto, total	8	3.0
Total death confirmed	10	3.8
Total exuviae collected	255	96.2
Total emergence	265	100.0

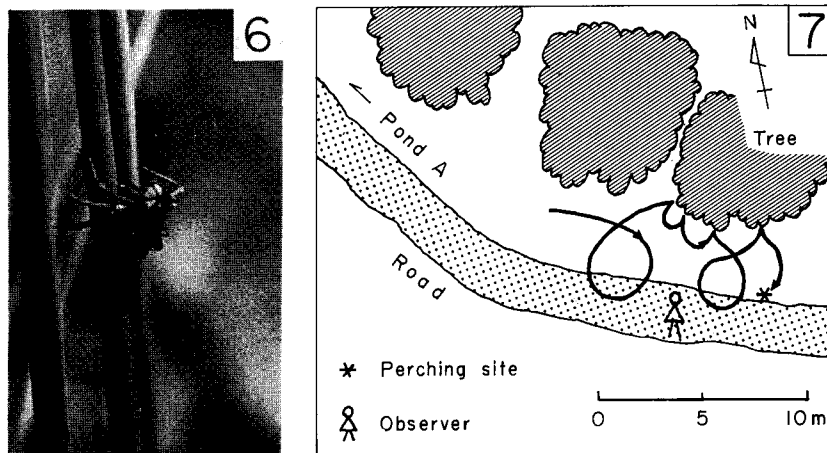


Fig. 6 (left). An emerging larva being molested by *Myrmica ruginodis*, Pond A, (12:20, June 15, 1971).

Fig. 7 (right). A flight course of a male adult making feeding flight.

The frequency of predation is evidently underestimated in the present study, since it comprises only cases confirmed by direct evidence, i.e. the loss of emerging individuals recorded; earnest prowling of jays, *Garrulus glandarius pallidifrons* Kuroda, along the shore with many emerging dragonflies was

observed throughout June, but they seldom left halfeaten corduliids. As another possible predatory vertebrate in this period, the eastern grey wagtail, *Motacilla cinerea* Leach was sometimes observed at the emergence site in Pond A in 1971.

Ants must be another serious predator for emerging dragonflies by their restless mass foraging. Around Pond A the ant population was always dense, ensuing considerable foraging activity. But the death of corduliids by ants was observed only once during daily collection of exuviae in 1971: A larva sitting on a *Phragmites* stalk 40 cm above the ground was being infested by a crowd of *Myrmica ruginodis* Nylander at 12:00, June 15, 1971 (Fig. 6). The attack especially on the thorax by as many as 17 ants continued over 13:35, so that the larva could not start the ecdysis and was destined to death. The species making diurnal emergence, such as *C. aenea*, are evidently more susceptible to the danger of predation by both birds and ants than the species with nocturnal emergence such as *Anax*. Consequently it is assumed that the mortality during emergence is mainly governed by predation, especially of birds, in this subspecies.

2.2. Pre-reproductive period

All so far studied Odonata species possess pre-reproductive or maturation period between emergence and reproductive periods, which continues for several days. During this period teneral adults spend their daily lives mainly by seeking food away from the breeding sites.

2.2.1. Feeding flight: After the emergence adult individuals leave the pond by maiden flight and never appear to the pond area until the beginning of reproductive period. During this maturation period, they dispersedly live within the forest area. Their feeding flights are, therefore, occasionally observed over the forest roads often fairly (800 m) distant from the pond at daytime in more or less fine weather. One case precisely observed is cited:

June 15, 1972, 15:25~15:30, fine with gentle breeze: A male was flying with infrequent hovering 3 m over an insolated road 400 m distant from Pond A in a peculiar way as if he was pecking at branches of a broad-leaf tree, which might be the exploration of food (Fig. 7). After such meandering flight at varying heights 0.3~5 m, he perched on a leaf of a herb at roadside with wings opened, then repeated rhythmic movements of the abdomen. About 2 min. later he flew away the perching site perhaps caused by an approach of an ant, and made a similar flight for one minute till perching on a herb ca. 30 cm apart from the first perching site. He rested there for about 1 min. till the departure.

Such feeding flights were intermittently observed in seven cases, all characterized by high and variable flight courses, infrequent hovering and occasional perching. Adult Diptera and Lepidoptera which were already abundant in the forest in early June seem to be the main food of *C. a. amurensis*.

2.2.2. *Dispersal during pre-reproductive period*: A marking experiment was executed with newly emerged individuals at Pond A in order to know the length of pre-reproductive period and the degree of dispersal during the period. First, 22 males and 23 females were marked from June 6 to 14 in 1971 with white or yellow lacquer on wings after they were sufficiently hardened. All marked individuals were able to fly up and distinguished individually with a binocular telescope ($\times 7$)

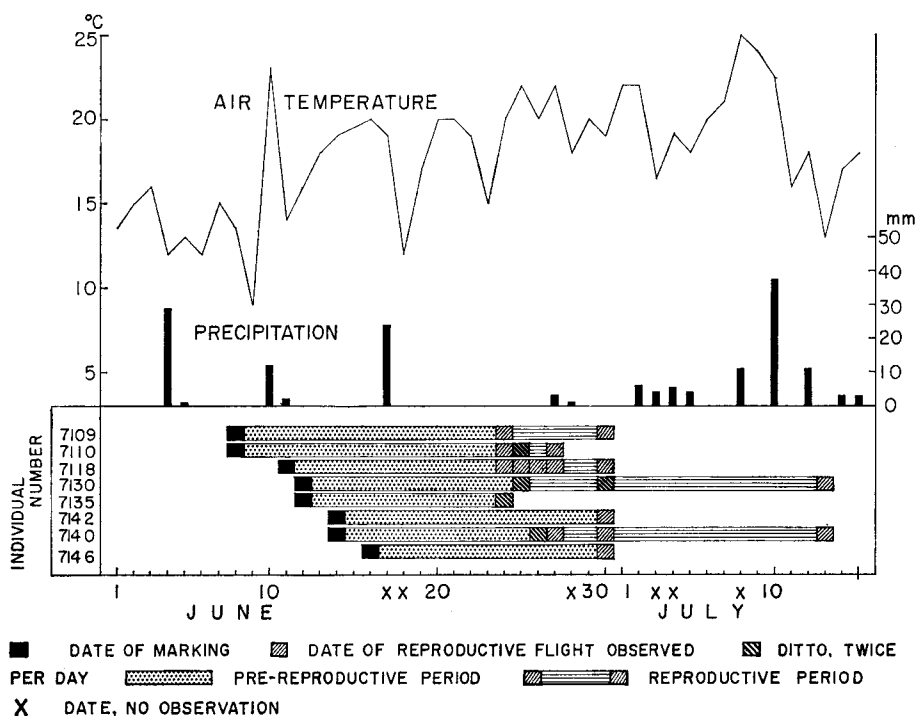


Fig. 8. Rediscovery of males marked at emergence after entering reproductive period, 1971. Weather conditions were cited from record at Usubetsu Pluviometric Station (390 m alt.) 1 km apart from Pond A.

even in flight. Among them only eight males (36.4%) were rediscovered at Pond A throughout subsequent observations on mature adult behavior described in a subsequent paper. The low rediscovery ratio of females does not necessarily represent the low frequency of their returning, since females are so furtive and transient at breeding site that they are easily overlooked by the observer. On the other hand, once returning to the breeding site, males frequently appear at the same pond and easily detected by their conspicuous behavior during the subsequent

period (Fig. 8). The majority of the other 14 males (63.6% of the marked males) may disperse to other habitats during this period, though some must have died.

Secondly, 18 males and 31 females were marked in the same manner at Pond A from June 11 to 17 in 1972, in order to study the dispersal to Pond B. But no individuals were rediscovered at Pond B in the observation made on June 26, July 6, 14 and 31. Unfortunately no simultaneous observation was made at Pond A. The time spent for the observation and the number of marked individuals were obviously too small to deny the dispersal from A to B. Moreover, Pond B is much larger than A, making rediscovery more difficult. Pajunen (1962) concluded on *Leucorrhinia dubia* (Van der Linden) that a considerable proportion of emerging individuals leave the emergence area during the pre-reproductive period. Presumably this tendency does also occur in *C. a. amurensis*, judging from the result obtained in 1971.

2.2.3. Length of pre-reproductive period: The length of pre-reproductive period can be estimated in two different ways: 1. Indirectly from the interval between emergence period and the start of reproductive period. 2. Directly by watching individuals marked at emergence as mentioned above.

Applying the first method, the interval between the first date of emergence and the date of the earliest arrival of a mature male to the pond was nine days in 1971, while the interval between the date of the seasonal peak of emergence and

Table 5. Results of daily collection of exuviae and daily counting of mature adults (part)

Year		Sex	June																							
			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24		
1970	Observation of emergence	♂, ♀	-	-	+	+	-	卅	-	-	0	-	0	+	-	0	0	+	0	0	0	-	-	0		
	Number of mature adults at the pond (noon)	♂	-	-	0	0	-	0	-	-	+	-	+	+	-	+	15	+	0	0	4	-	-	9		
		♀	-	-	0	0	-	0	-	-	0	-	0	0	-	0	+	+	0	0	0	-	-	+		
1971	Number of exuviae collected	♂	0	-	0	1	0	14	1	34	18	12	14	10	2	2	-	-	1	3	2	0	1	0		
		♀	0	-	0	0	0	11	3	23	26	12	8	8	2	2	-	-	2	1	1	2	0	1		
		?	2	-	1	13	2	6	0	4	1	0	1	1	0	1	-	-	0	0	0	0	0	0		
1972	Number of exuviae collected	♂	0	-	0	0	0	0	0	0	0	+	1	0	1	3	-	-	+	3	3	0	1	17		
		♀	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	+	0	+	+	0	0		
		?	0	-	1	-	4	-	31	-	28	-	20	-	8	-	3	-	0	-	-	-	1	-		

+: observed. ##: frequently observed. -: no observation, collection or counting.

the date of the first attainment to steady high density of male at the pond (>10 , explained in a subsequent paper) was 14 days in 1971 and nine days in 1970 (Table 5). On the other hand, females lagged behind males by six and seven days respectively in 1970 and 1971 in date of the earliest arrival at the breeding site.

By means of the second method, a more precise one, among 22 males marked in 1971 at emergence two individuals arrived first at the pond on the 12th day after emergence, two on the 13th day, one on the 14th day and three on the 16th day (Fig. 8). In the case of the last three individuals (individual number: 7109, 7110, 7142) the prolongation of pre-reproductive period seemed to be caused by some external factors, that is, rainy or cool weather on the 14 and 15th day. Consequently the length of pre-reproductive period is estimated as 9~14 days in males in 1971, while nine days in 1970. Perhaps this difference is in part due to the adverse climatic conditions in 1971; there was only one rainy day (0 mm ppt.) during the first ten days after emergence peak in 1970, while in 1971 three rainy days (12.0, 2.5, 23.2 mm ppt.) during the first ten days and, in addition, the rainy (0 mm ppt.) or cool weather on the 12 and 13th day after emergence peak inhibited the flight activity to the breeding site. According to Pajunen (1962), pre-reproductive period of *L. dubia* is delayed by cool weather. On the basis of the data presented, it is guessed that the pre-reproductive period in *C. a. amurensis* lasts ca. 10 days in males and ca. 16 days in females under favorable weather but prolonged by cool weather.

Concluding remarks

Thanks to the works of Robert (1958), Taketo (1959, 1960b), Heymer (1964) and Sonehara (1967), the life histories of 11 among 15 Palaearctic corduliid species have been hitherto studied. In the Nearctic region, three species of *Tetragoneuria* (Kormondy 1959) and 16 species of *Somatochlora* (Walker 1925) were studied. The life history of *C. a. amurensis* is compared here with the western subspecies, *C. a. aenea*, with another congeneric species, *C. shurtleffi* Scudder and with other corduliid genera, concerning emergence and pre-reproductive periods as well as habitat preference dealt with in the present paper.

The characters common to *C. a. amurensis* and *C. a. aenea* are, daily rhythm of emergence (Wesenberg-Lund 1913, Robert 1958), tendency to emergence synchronization (Wesenberg-Lund, Münchberg 1932), earlier seasonal emergence in warmer climate (Robert), feeding behavior (Wesenberg-Lund) and the length of pre-reproductive period (Robert), while differences are earlier emergence in *C. a. aenea* (from the end of April to late May; Wesenberg-Lund, Robert) and habitat preference: *C. a. amurensis* shows a stronger attachment to high moor than *C. a. aenea*.

Although little is known about the life history of another Nearctic *Cordulia* species, *C. shurtleffi*, it occasionally shows swarming, unknown in *C. aenea*, during feeding flight (Kormondy 1959). The genus *Somatochlora*, phylogenically allied to *Cordulia*, involves a good many species within the Circumboreal region (Walker

1925), so that the members have colonized into various habitats, namely, alpine ponds *S. alpestris* (Selys) (Aguesse 1968), high moors *S. arctica* (Zetterstedt) (Kiauta 1968), lakes *S. cingulata* (Selys) (Walker 1925) and small streams of low mountainous and hilly areas (*S. clavata*, Taketo 1960b). Among *Somatochlora* some differences from *C. aenea* are exhibited by certain species; later emergence season and less pronounced synchronization in emergence period (*summer species*, Corbet 1962) (*S. clavata*) and longer pre-reproductive period (three or four weeks) (*S. uchidai*, Ubukata unpubl., *S. viridiaenea atrovirens*, Taketo 1959). *Tetragoneuria* and *Epitheca* are similar to *C. aenea* in seasonal type (spring species) and daily rhythm of emergence except for oviposition sites. *Oxygastra* resembles *C. aenea* in flight season but differs by its preference for streams. *Procordulia*, a predominantly tropical genus, shows the emergence throughout the year without definite seasonal trend (Lieftinck 1933) clearly differing from the northern corduliids. Unfortunately preliminary comparison presented above on corduliid genera concerning earlier adult stages are still incomplete, due to the lack of sufficient information on the life histories of many other corduliid species, especially in *Somatochlora*.

At the familial level, the Holarctic Corduliidae may be characterized from other families in the following points: 1. Hanging type emergence made in daytime. 2. Emergence showing generally spring species type.

Nextly, the environmental characters of moor as the habitat preferred by *C. a. amurensis* are briefly discussed. The climate of boreal moor is severe by low temperature, which offers a brief period for the growth of aquatic insects including dragonflies and low productivity of small aquatic animals, sole food of odonate larvae. Under such conditions, it must be advantageous that *C. a. amurensis* emerges explosively in spring and requires not too long pre-reproductive period, which allows the oviposition in early summer and relatively long growth period before winter.

According to Kurata (1966), *Aeschna juncea* often suffers fatal damage by nocturnal emergence due to the cold and rainy weather at highlands. In this connection it may be favorable for *C. aenea* to emerge in the daytime when weather conditions are milder, while a tropical corduliid species, *Hemicordulia asiatica* Selys, exhibits nocturnal emergence (Fraser 1924).

Within the distribution range of *C. a. amurensis*, the following birds dwell at least in summer in or around marshlands and feed on many insects there (Voous 1960): *Ardea cinerea* Linne, *Botaurus stellaris* (L.), *Gallinula chloropus* (L.), *Vanellus vanellus* (L.), *Limosa limosa* (L.), *Motacilla flava* L., *Garrulus glandarius* (L.) and *Grus japonensis* (P.L.S. Müller). Among them, the Japanese crane, *G. japonensis*, makes a large territory on marshland and feed on a good deal of emerging dragonflies (Masatomi and Kitagawa unpubl.). Corbet (1957) pointed out that if a territory occupied by a pair of birds involves the emergence site of Odonata, the mass emergence may decrease the mortality by offering individuals much more than the quantity eaten by birds per day. If this hypothesis is valid, the mass emergence of *C. aenea* may reduce its mortality within a large territory of birds such as cranes. Further the mass emergence may also be favorable for sexual synchronization at

the breeding sites.

Finally, the following items observed in *C. a. amurensis* are of general odonatological interest: 1. The position of emergence is largely affected by the coverage or the degree of growth of plants used as emergence supports. 2. EM_{50} , an index of synchronization of emergence, can be affected by the number of exuviae collected or by the existence of exceptionally early emerged individuals. For example EM_{50} of *Pyrrhosoma nymphula* (Sulzer) was the 8th day by 147 exuviae in 1967, while the 16th day by 802 exuviae in 1968 (calculated from Lawton 1971). Therefore more reliable statistical treatment should be applied to have a better index of synchronization. 3. In temperate zones warmer climate seems to make emergence season earlier. 4. Attack by ants ought to be added to the list of selection pressures at emergence period, as is prominently known in *Ae. juncea* (Kiauta 1971). 5. Slower maturation in female may be a general feature in Odonata, as already known in *Anax imperator* (Corbet 1957) and *Leucorrhinia dubia* (Pajunen 1962). 6. Pre-reproductive period is prolonged by rainy or cool weather as in *L. dubia* (Pajunen 1962).

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Summary

The life history and behavior of *Cordulia aenea amurensis* Selys were studied at the foot of Mt. Muine, near Sapporo in 1970~1972.

1. The emergence period was from early to late June, with a conspicuous synchronization ($EM_{50}=7\sim 9$ th day) around June 9. Most emergence (96%) took place at the distance ± 50 cm from the water edge, and the height 5~35 cm above the water level.

2. The emergence occurred mostly between 7:00~11:00. Even after sitting, larvae returned into the water when it began to rain. Duration of emergence was ca. 3 hrs. and prolonged by rainy or cool weather.

3. Emergence of 380 (1971) and 360 (1972) individuals at Pond A was estimated by collecting exuviae. The sex ratio at emergence was approximately 1:1 in 1971, but females slightly exceeded males in 1972.

4. Mortality during emergence period in 1971 was as follows; failure in emergence (0.8%), predation by birds, mainly *Garrulus glandarius pallidifrons* (2.6% or more) and predation by ants, *Myrmica ruginodis* (0.4%).

5. Feeding flight in pre-reproductive period is characterized by high and variable flight courses, infrequent hovering and occasional perching, in contrast to reproductive flight.

6. About 36% of the males marked at emergence period were rediscovered at the original pond during the subsequent reproductive period, while no females were rediscovered presumably due to their cryptic feature in reproductive behavior and a low density due to short stay at the breeding site. The length of pre-reproductive period was estimated to be ca. 10 days (♂) and ca. 16 days (♀), though prolonged by cool weather.

References

Papers asterisked are those not directly accessible.

- Aguesse, P. 1968. Faune de l'Europe et du Bassin Méditerranéen. 4. Les Odonates. 262 pp. Masson, Paris.
- Asahina, S. 1954. Odonate fauna of the Ozegahara Moor. Ozegahara Sôgô Gakujutsu Chôsadan Kenkyû Hôkoku: 758-768. (In Japanese).
- 1957. An annotated list of Japanese Odonata with brief descriptions of their larvae. Shinkonchû 13: 51-57. (In Japanese).
- Buchholtz, C. 1951. Untersuchungen an der Libellen-Gattung *Calopteryx*-Leach unter besonderer Berücksichtigung ethologischer Fragen. Z. Tierpsychol. 8: 273-293.
- 1955. Eine vergleichende Ethologie der orientalischen Calopterygiden (Odonata) als Beitrag zu ihrer systematischen Deutung. *Ibid.* 12: 364-386.
- 1956. Eine Analyse des Paarungsverhaltens und der dabei wirkenden Auslöser bei den Libellen *Platycnemis pennipes* Pall. und *Pl. dealbata* Klug. *Ibid.* 13: 14-25.
- Corbet, P. S. 1952. An adult population study of *Pyrrhosoma nymphula* (Sulzer): (Odonata: Coenagrionidae). J. Anim. Ecol. 21: 206-222.
- 1955. A critical response to changing length of day in an insect. Nature, Lond. 175: 338-339.
- 1956. Environmental factors influencing the induction and termination of diapause in the Emperor Dragonfly, *Anax imperator* Leach (Odonata: Aeschnidae). J. exp. Biol. 33: 1-14.
- 1957. The life-history of the Emperor Dragonfly, *Anax imperator* Leach (Odonata: Aeschnidae). J. Anim. Ecol. 26: 1-69.
- 1962. A biology of dragonflies. 247 pp. Witherby, London.
- Eda, S. 1959. Observations on the emergence of *Tanypteryx pryeri* Selys. Tombo 2: 18-24. (In Japanese with English summary).
- 1963. Emergence of *Epiophlebia superstes* Selys. *Ibid.* 6: 2-7. (In Japanese with English summary).
- 1964. Emergence and oviposition of Odonata. Insect Journal, Tokyo. 1: 91-103. (In Japanese).
- Fraser, F. C. 1924. A survey of the odonate (dragonfly) fauna of Western India with special remarks on the genera *Macromia* and *Idionyx* and descriptions of thirty new species. Rec. Indian Mus. 26: 423-522.
- Fujisawa, S. 1957. Odonata of Shiga-Kogen. 160 pp. Shimosuina Kyôikukai, Iiyama. (In Japanese).

- Heymer, A. 1964. Ein Beitrag zur Kenntnis der Libelle *Oxygastra curtisi* (Dale 1834). Beitr. Entomol. **14**: 31-44.
- *——— 1973. Verhaltensstudien an Prachtlibellen. 100 pp. Paul Parrey, Berlin.
- Higashi, K. 1969. Territoriality and dispersal in the population of dragonfly, *Crocothemis servilia* Drury (Odonata: Anisoptera). Mem. Fac. Sci. Kyushu Univ. Ser. E. **5**: 95-113.
- Iijima, K. 1966. Odonata of Eastern Hokkaido. Bull. Kushiro Munc. Museum **177**: 43-46. (In Japanese).
- Itagaki, T. 1956. Collection record of *Leucorrhinia dubia orientalis* and *Cordulia aenea amurensis*. Shinkonchû **9**: 47. (In Japanese).
- Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology **36**: 566-586.
- Johnson, C. 1962a. Reproductive isolation in damselflies and dragonflies (Order Odonata). Texas Jour. Sc. **25**: 297-304.
- 1962b. A study of territoriality and breeding behavior in *Pachydiplax longipennis* Burmeister (Odonata: Libellulidae). Southwestern Naturalist **7**: 191-197.
- 1962c. A description of territorial behavior and a quantitative study of its function in males of *Hetaerina americana* (Fabricius) (Odonata: Agrilidae). Can. Entom. **94**: 178-192.
- Kiauta, B. 1965. Notes sur le dépouillement de *Cordulia aenea* (L.) (Odonata: Corduliidae). Ent. Berichten **25**: 111-113.
- 1968. Additions to the list of Odonata of the Dutch Wadden Islands, with an account of water quality data of larval habitats, and a review of the dragonfly fauna of the Dutch and German Northsea Islands. Biologisch Jaarboek 'Dodonaea' **36**: 88-114.
- 1971. Predation by ants, *Formica fusca* L. and *F. rufa polycetena* Bondr. on the emerging dragonfly, *Aeschna juncea* (L.) and its teratological consequences. Tombo **14**: 2-5.
- Kormondy, E. J. 1959. The systematics of *Tetragoneuria*, based on ecological, life history, and morphological evidence (Odonata: Corduliidae). Misc. Publ. Mus. Zool. Univ. Mich. **107**: 1-79.
- Krieger, F. and E. Krieger-Loibl 1958. Beiträge zum Verhalten von *Ischnura elegans* und *Ischnura pumilio* (Odonata). Z. Tierpsychol. **15**: 82-93.
- Kurata, M. 1966. The life history of *Aeschna juncea* Linné (Odonata: Aeschnidae) in Japan (Prediction). J. Semin. Sci. Edu., Bran. Matsumoto, Fac. Edu. Shinshiu Univ. **8**: 166-182. (In Japanese).
- Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrosoma nymphula* (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. **40**: 385-423.
- Lieftinck, M. A. 1933. The life-history of *Procordulia artemis* Lieft. (Odon., Cordul.), with comparative notes on the biology of *P. sumbawana* (Förster). Int. Rev. Hydrobiol. **28**: 399-435.
- Loibl, E. 1958. Zur Ethologie und Biologie der deutschen Lestiden (Odonata). Z. Tierpsychol. **15**: 54-81.
- Moore, N. W. 1952. On the so-called "territories" of dragonflies (Odonata-Anisoptera). Behaviour **4**: 85-100.
- Münchberg, P. 1932. Beiträge zur Kenntnis der Biologie der Libellenunterfamilie der Cordulinae Selys. Int. Rev. d. ges. Hydrobiol. u. Hydrogr. **27**: 269-297.
- Pajunen, V. I. 1962. Studies on the population ecology of *Leucorrhinia dubia* v. d. Lind. (Odon., Libellulidae). Ann. Zool. Soc. 'Vanamo' **24**: 1-79.

- . 1964. Mechanism of sex recognition in *Leucorrhinia dubia* v. d. Lind., with notes on the reproductive isolation between *L. dubia* and *L. rubicunda* L. (Odon., Libellulidae). *Ann. Zool. Fenn.* **1**: 55-71.
- . 1966. The influence of population density on the territorial behaviour of *Leucorrhinia rubicunda* L. (Odon., Libellulidae). *Ibid.* **3**: 40-52.
- * Peus, F. 1932. Die Tierwelt der Moore. 277 pp. (Handb. Moorkunde 3), Berlin.
- Portmann, A. 1921. Die Odonaten der Umgebung von Basel. Inaugural-dissertation. 101 pp. Lörrach.
- Robert, P. A. 1958. Les libellules (Odonates). 364pp. Delachaux et Nistlé S.A., Neuchâtel.
- St. Quentin, D. 1934. Beobachtungen und Versuche an Libellen in ihren Jagdrevieren. *Konowia* **13**: 275-282.
- Schmidt, E. 1964. Biologisch-ökologische Untersuchungen an Hochmoorlibellen (Odonata). *Z. Wiss. Zool.* **169**: 313-386.
- . 1967. Zur Odonatenfauna des Hinterzartener Moores und anderer mooriger Gewässer des Südschwarzwaldes. *Dt. Ent. Z.* **14**: 371-386.
- Sonehara, I. 1967. On the life history of *Epithea bimaculata sibirica* and *E. marginata*. *Tombo* **10**: 2-24. (In Japanese with English summary).
- Taketo, A. 1959. On the habitat and behaviour of *Somatochlora viridiaenea atrovirens*. *Ibid.* **2**: 3-6. (In Japanese with English summary).
- . 1960a. Studies on the life-history of *Tanypteryx pryeri* Selys (Odonata, Petaluridae). I. Observations of adult dragonflies. *Kontyû* **28**: 97-109. (In Japanese with English summary).
- . 1960b. Ecology of *Somatochlora clavata*. *Tombo* **3**: 8-15. (In Japanese with English summary).
- Vouss, K. H. 1960. Atlas of European birds. 284 pp. Nelson, Amsterdam Elsevier.
- Walker, M. 1925. The North American Dragonflies of the genus *Somatochlora*. 202 pp. Univ. Toronto, Studies, Biological Series.
- Wesenberg-Lund, C. 1913. Odonaten-Studien. *Int. Rev. Hydrobiol.* **6**: 155-228: 373-422.
- Williamson, E. B. 1906. Copulation of Odonata. *Ent. News* **17**: 143-148.
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