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Observations on the Behavior of Some Odonata in the Bonin Islands, with Considerations on the Evolution of Reproductive Behavior in Libellulidae¹⁾

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(With 28 Text-figures and 4 Tables)

Since the studies by Buchholtz (1951, '55, '56) and Jacobs (1955) the descriptions and analyses of the reproductive behavior of Odonata have been performed with various species, and some interpretations of behavioral evolution were presented by Johnson (1964) and Heymer (1973). But the species so far observed still do not cover all principal supraspecific taxa of the order. The accumulation of further information on other yet unexplored species is required to interpret the behavioral evolution upon the sound basis. Concerning the Japanese Odonata, Ishida (1969) reviewed bionomic and ethologic information so far obtained. But his review involves no reference to the species inhabiting the Bonin Islands, nevertheless five endemic forms are recorded there. The present paper deals with some casual observations made by S.F.S. and M.J.T., who visited the Islands in April, 1973 to collect other materials. H.U. participated in bibliographical survey, preparation of results as well as their interpretations. Further studies are now in progress by M.I., being resident in the Islands. Some observations made by him during May~October, 1973, were incorporated in the paper. Due to circumstantial limitations the observations were mainly casual, and some derived conclusions would require further qualification. Nevertheless, we believe that something was added to our knowledge on the comparative ethology of Odonata.

The Bonin Islands (Ogasawara Shotô) are typical oceanic islands in the Western Pacific, located approximately 27°N and 142°E, and being about 1,000 km remote from the Mainland of Japan. The Islands consist of 97 islands and islets, forming three major groups, Mukojimas (Parry), Chichijimas (Beechey) and Hahajimas (Bailey). Two largest islands, Chichijima and Hahajima, are about 25 sq. km. and the highest altitude is respec-

1) Studies on the biology of Japanese Corduliidae. III. (by H. Ubukata).

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tively 323 and 462 m. The islands had originally been covered with luxuriant evergreen forests with a high endemism, but the invasion of secondary vegetations is now drastic in many islands.

The climate is subtropical and oceanic with poor seasonal differentiation, as is reflected on an obscure phenologic sequence in odonate reproductive activities. The mean annual air temperature is 22.6°C and the mean monthly temperature exceeds 18°C except for January and February (17~18°C). Further accounts on geology, topography, climate and vegetations are found in Gressitt (1954), Tuyama and Asai (ed., 1970) and the report by Ministry of Education and Agency for Cultural Affairs, Japan (1970). Concerning the life of Odonata in the Islands, the poverty of stable freshwater habitats as common to many oceanic islands must be emphasized as a severe limiting factor.

Species observed or collected

The species observed by S.F.S. and M.J.T. during April 6~21, 1973, are listed below, together with the name of the island (H. Hahajima; C. Chichijima; O. Otôtojima; Mi. Minamishima). The asterisked records are those observed by M.I. in June, 1973, and Gothic letters show the new records. The endemic forms were not collected as they are under legal protection, except for several specimens captured carelessly before identification.

<i>Rhinocypha ogasawarensis</i> Oguma	<i>Hemicordulia ogasawarensis</i> Oguma
H, C, C*.	H, C, O, C*
<i>Lestes boninensis</i> (Asahina)	<i>Boninthemis insularis</i> (Oguma)
C*.	C*, H*, O*.
<i>Ischnura (Boninagrion) ezoin</i> (Asahina)	<i>Diplacodes bipunctatus</i> (Brauer)
H (1 ♀ IV 11), C (1 ♀ IV 8).	C (1 ♀ IV 17, 1 ♂ IV 19), Mi, C*.
<i>Ischnura senegalensis</i> (Rambur)	<i>Pantala flavescens</i> (Fabricius)
H, C (1 ♂ IV 7, 1 heterochromatic ♀ IV 19), O, Mi (1 ♂ 1 heterochr. ♀ IV 21). The females of this species are dimorphic (Asahina 1956), but no homoeochromatic female was collected.	C, O, C*.
<i>Anax parthenope julius</i> Brauer	<i>Tramea virginea</i> (Rambur)
H, C, Mi, C*.	C*.
	<i>T. transmarina euryale</i> Selys
	C*.
	<i>Macrodiplax cora</i> (Brauer)
	Mi (2 ♂ IV 21), C*.

The odonate fauna of the Bonin Islands was revised by Asahina (1952), Lieftinck (1962) and later listed by Nakane (1970) and Asahina (1970). Table 1 compiles the distribution records so far known. All forms are recorded from Chichijima. Their presence is plausible also as to Hahajima. The distribution in other small islands is still poorly studied. The poor species number (12 forms) and high endemism (5 forms) characterize the odonate fauna of the Islands as in many other insects (155 out of 560±recorded insect species or 27% are endemic, cf. Hasumi 1970).

The relative abundance in terms of individual number could approximately be arranged in the following descending order (Endemic forms asterisked): *Ischnura senegalensis* > *Diplacodes*, *Hemicordulia*,* *Pantala*, *Tramea transmarina* > *Anax* >

Table 1. Distribution records of Odonata species in each island. Island: C (Chichijima), Ai (Anijima), O (Otôtojima), Mi (Minamishima), H (Hahajima), Mu (Mukôjima), Ae (Anejima), M (Mukojima). Authority: N (Nakane 1970), A (Asahina 1970), X (present survey). * Endemic form.

Species	Island	C-Group				H-Group			M-Group
		C	Ai	O	Mi	H	Ae	Mu	M
* <i>Rhinocypha ogasawarensis</i>		N, X	N			N, X	N		
* <i>Lestes boninensis</i>		N, X							
* <i>Ischnura ezoin</i>		N, X	N			N, X		N	
<i>I. senegalensis</i>		N, X	N	X	N, X	X		N	
<i>Anax p. julius</i>		N, X		N	X	X			
* <i>Hemicordulia ogasawarensis</i>		N, X		X		N, X	N?		
* <i>Boninthemis insularis</i>		N, X		X		N, X	N	N	
<i>Diplacodes bipunctatus</i>		N, X	N		X	N	N	N	N
<i>Pantala flavescens</i>		N, X		X		N			
<i>Tramea virginea</i>		N, X							
<i>T. t. euryale</i>		N, X				N			
<i>Macrodiplax cora</i>		A, X			X				

*Rhinocypha**, *I. ezoin**, *Boninthemis**, *Lestes**, *T. virginea*. Except for *Hemicordulia*, the population size of endemic forms seems very small and their protection is urgently needed. When the extreme poverty of stable freshwater habitats characteristic of the Islands is reflected, their extinction is not unlikely, unless some counter-measures are executed, for instance, the maintenance of stable freshwater habitats, limitation of excessive forest cutting and careless land use to avoid flooding and water pollution. Obviously these should be taken not for Odonata alone, but as a part of an integral protection of ecosystems.

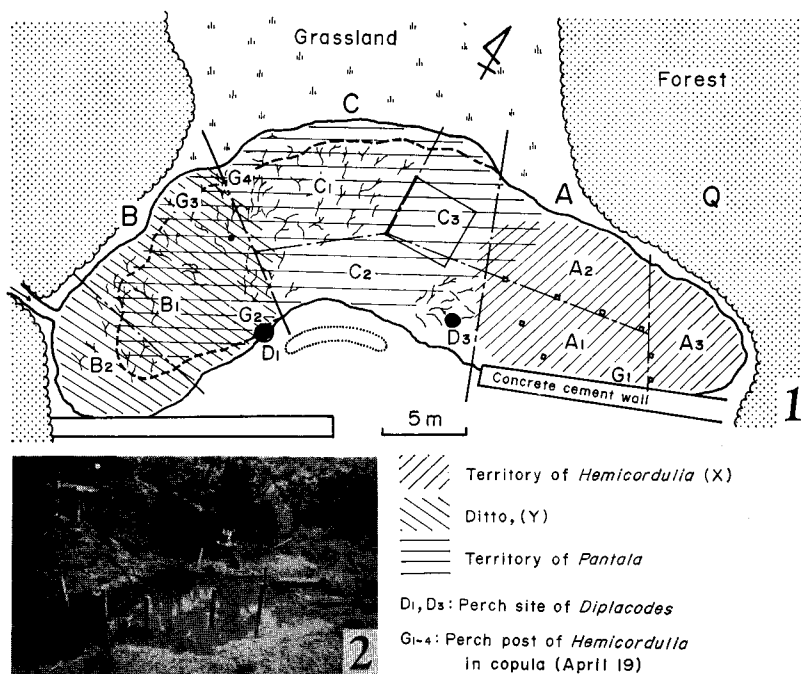
Results and discussions

The field studies were undertaken at various points of Chichijima, Hahajima, Otôtojima and Minamishima, but precise observations were mainly performed at the following two areas, both in Chichijima:

1. *Komagari Dam*: An artificial pond made by a dam for drinking water, about 70 m wide and more than 100 m long with the size 6,000 m², surrounded by secondary forests (Fig. 9). Completed in May, 1971 and numerous trees still projecting from the water surface of the peripheral zones.

2. *Pond W*: A small ruined water reservoir at the foot of Mt. Yoakeyama, crescent shaped, about 40 m long and 10 m wide (Figs. 1, 2). The southern shore was partly bordered by a half-ruined concrete cement wall of about 4 m high and sparsely surrounded by trees. The northern shore faced at its middle section a grassland of ca. 100 m deep and surrounded with trees at the sides. The pond received the water input at the western corner, but only intermittently so that the water was stagnant and rather polluted. Daily change of the water level was relatively conspicuous as shown by the difference between April 9 and 19 (Fig. 1). In early to mid June, the surface extent doubled by

continuous rains, but thereafter recovered the previous state. To facilitate observations, the pond was divided into three sections, from east to west, A, C, B, with further subdivisions. Observations were mainly made from the middle of the southern shore (Dotted contour in Fig. 1).



Figs. 1, 2. General view of Pond W (Chichijima). Fig. 1. A, B, C: Sections explained in text. Dotted: Observation points, Solid and broken contours: Water level on April 9 and 19. Fig. 2. Photo taken from Q, in Fig. 1.

1. Behavior of each species with special reference to reproductive behavior

In this section behavior observations and related comments on nine forms are successively given, in each of them, in the order of pre-mating (territorial), mating, and oviposition behavior, followed by some notes on other aspects as far as observed. The efforts were mainly concentrated upon the territorial behavior of *Hemicordulia*. Most observations were made without individual marking. The bibliographical survey is incomplete as to widespread forms such as *Ischnura*, *Diplacodes* and *Pantala*. The usage of several terms are defined here:

Fixed area: An area kept by a male for a definite time span, but without invasion of other males. Consequently the defense by the occupant is not confirmed.

Territory: Ditto, but the defense by the occupant confirmed.

Communal flight area: Communal occupation of an area by two males or more, with mutual chasing but without division of the area in territories.

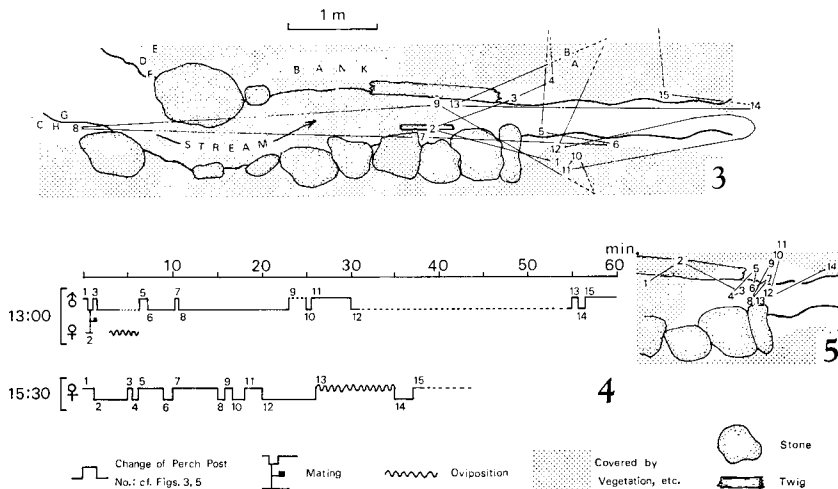
Residence (Residentiality): Stay within a fixed area, a territory or a communal flight area for a definite time span.

Rhinocypha ogasawarensis Oguma

This endemic species exhibits a conspicuous sexual dimorphism, with the abdomen bright red in males while much darker in females. Brief observations of three males at and near Kitamura, Hahajima, suggested their residentiality. This assumption was strengthened by a continuous observation of a male on April 15 at the bank of a small stream, one of a few stable streams within the Islands.

The observation was made at the point about 150 m upstream of Kitamura harbor, where the stream was about 1 m wide and 30 cm in the maximum depth. The water was not polluted, with the current relatively rapid. The observation site was under a sparse forest and moderately insolated. The bank was densely covered with undergrowth, leaving a narrow exposed belt along the stream margin. At the upper part of the site, the stream was completely covered by the enormous root system of a fallen fig tree.

A male stayed during 13:00~13:30 in the area, with translocations given by numerals 1~12 in Figs. 3, 4. Thereafter, a male, possibly the same individual, appeared three times during 13:55~15:07 (Figs. 3, 4, 13~15 and A~B), and on the next day 7:30~9:40 (Fig. 3, C~H, intermittently observed). The points



Figs. 3~5. Spatial and temporal records of observations on *Rhinocypha ogasawarensis*. (Kitamura, April 15). Fig. 3. Translocation of male during observations. Numerals and alphabets show perch posts (cf. Text). Fig. 4. Temporal sequence of male (above) and female (below) behavior. Broken lines (individuals out of sight), other symbols of Legend. Fig. 5. Translocation of female at oviposition site.

selected for perching were leaves, twigs and rocks, all oriented more or less horizontally. No particular perching posts were preferred. At perching the wings were folded. The flight course was not straight as in *Agrion*, involving frequent turns of directions. The observation given above suggests the residence of a male in a fixed area for a certain time. The presence of territorial behavior was not confirmed as no alien male invaded in the area. Ishida and Hamada (1973) suggested a similar residentiality in *R. uenoi* Asahina inhabiting the Yaeyama Islands.

Mating and oviposition were confirmed on April 15 during and after the observation cited above. At ca. 13:02 a female entered into the area, taking a linear flight course about 30 cm above the stream. The male at point 1 (Fig. 3) took wing and chased her, who alighted on a rotten twig floating on the stream

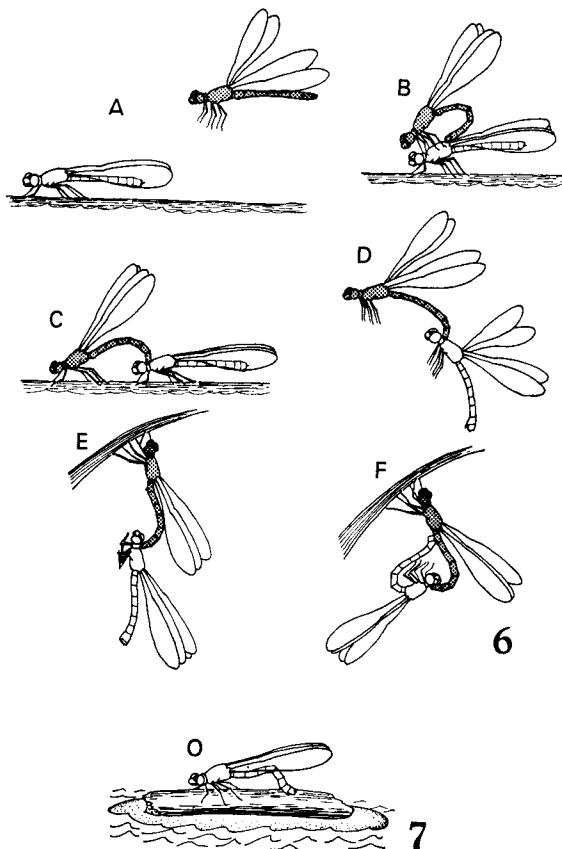


Fig. 6 (A~F). Mating process of *R. ogasawarensis* (Male, shaded). Fig. 7 (O). Oviposition posture of *R. ogasawarensis* (cf. Text).

(Fig. 3, point 2). The subsequent behavior is given in Fig. 6.

The male alighted on the thorax of the female (B). Tandem formation took place (C) and the male perched on the underside of a leaf, about 80 cm apart from point 2 and 1 m high above the stream surface (Fig. 3 point 3 and Fig. 6E). The copula followed immediately (Fig. 6F), and continued for ca. 1.5 min., during which the male performed pumping three times. It was not ascertained whether the male pressed or not the female's head to his accessory genitalia before the copula, as is recorded in *Hetaerina* and *Calopteryx*. But this must have been very brief even if practiced.

After the separation, the male remained within the area as already described (Figs. 3, 4, points 4~). The female left the area but 2 min. after, a female, possibly the same individual, visited the area. She alighted on the twig where she was caught by the male, and took the oviposition posture by immersing the abdominal tip. In this time the male was indifferent. The posture continued for 3 min. followed by the departure. Nine min. after, the female visited the same twig, took the oviposition posture for 1 min. and left the area. In both instances, the actual oviposition seemed unrealized, probably due to the smooth surface of the twig without cracks. At 15:30, a female, possibly the same individual, arrived at the area. After changing the places (cf. Figs. 4, 5), she alighted twice on a piece of rotten wood with numerous cracks, lying on the surface of a rock projecting above the stream level but receiving constant spraying. After alighting on the wooden piece, she slowly walked forward and pressed her abdominal tip repeatedly on the surface of the piece (Fig. 7). The abdomen was only gently curved, not taking an omega shape.

Beside these observations the flights of two teneral males were noted. Both were still not well pigmented, and left the stream by a weak flight made about 4 m high.

The behavior of the species of Libellagidae, to which *Rhinocypha* belongs, has so far virtually been ignored except fragmentary notes by Fraser (1934), etc. Therefore, the results obtained are tentatively compared with two well studied zygopteran genera, *Hetaerina* (Hetaerinae, 2 spp.) and *Calopteryx* (Calopterygidae, 5 spp.). The items of information given in Table 2 are by no means equivalent. While the behavior of two cited genera was clarified through numerous and precise observations, only a single and casual observation is available for *Rhinocypha*. Nevertheless, the table seems to suggest the relatively unspecialized habits of this genus, especially in the absence of the following characteristics: Courtship display, tandem formation in the air, oviposition in tandem or guarded by male and completely submerged oviposition. These characteristics would be, after further confirmation, incorporated in the interpretation of the phylogeny of these groups.

Ischnura senegalensis (Rambur)

This is the commonest species in the Islands, found at diverse environments. Males perch on twigs or stalks at shores or those projecting from the water surface, taking the posture common to other agrionid species (Fig. 8). They either stay at a definite point for a while or wander to other places. No positive evidence

Table 2. Comparison of mating and oviposition behavior in three calopterygoid genera.
 (* — in all species observed, U: Unspecialized S: Specialized)

Genus	<i>Rhinocypha</i>	<i>Hetaerina</i> (Johnson 1961, Bick and Sulzbach 1966)	<i>Calopteryx</i> (Buchholz 1951, '55, Johnson 1962, Heymer 1973)
1) Approach of ♀ to ♂	Flying in fixed area, — perching, without conspicuous behavior U	Flying in territory, — hovering at definite point *S	Flying in territory, — perching on exposed site *U
2) Approach of ♂ to ♀	Quickly flying to ♀	Ditto *	Hovering with rapid wing beats in front of ♀
3) Courtship display	Absent U	Absent *U	Present *S
4) ♀ body part first alighted on by ♂	Thorax	Thorax *	Wing tip, or thorax in <i>maculata</i>
5) Place of tandem formation	Resting on horizontal place U	In the air *S	Resting on leaf, etc. *U
6) Precopula tandem flight	Present before perching for copula	Present but short before perching for copula *	Absent, or very short if present (<i>splenedens</i>)
7) Rubbing ♀ head by ♂ accessory genitalia	Not precisely observed but very short if present	Present (Johnson), absent (Bick <i>et al.</i>)	Mainly present, absent in <i>maculata</i>
8) Copulation site	On the underside of leaf	On leaf, etc. *	On leaf, etc. *
9) Duration of copula	90 sec.	2.0~6.0 min. *	85~90 sec. (5 min. in <i>maculata</i>)
10) Post-copula tandem	Absent U	2~6 min. (resting) *S	Absent *U
11) Arrival at oviposition site	Solitarily U	By tandem *S	Solitarily *U
12) ♂ guarding at oviposition	Absent U	Present (max. 40 min.) *S	Present S
13) Complete submergence at oviposition	Absent U	Present *S	Present S, but not in <i>xanthostoma</i>

to keep a fixed area was obtained. There may be no territorial behavior because males were indifferent to other ones passing by at distances 5~10 cm. The copula was observed on April 21 in Minamishima, but no detailed record was taken. The oviposition observed at Pond W (April 9 and 19) were made in all cases by a solitary female into twigs or stalks floating on the water surface. At oviposition,

each lasting 15~45 sec., the abdomen was bent in an omega shape. Thereafter, the female walked for a short distance and made the second laying. Through these repeated acts, the guarding by male was never observed.

Interestingly some species of *Ischnura* and *Agriocnemis* make solitary oviposition, presenting exceptions in Agrionidae, in which tandem oviposition is a rule. In the mainland of Japan, too, only solitary oviposition has been recorded for *I. senegalensis* (Ishida 1969). Schiementz (1953) suggested the differentiation of local populations into solitary and tandem oviposition groups in *I. elegans* (Van der Linden). How females avoid the sexual approach of males at solitary oviposition not guarded by male partners is open to the question. At least two devices have been recorded at such situation: Temporal segregation of mating and oviposition within a day (*I. elegans*, Krieger and Krieger-Loibl 1958) and presence of female threat display as found in *I. verticalis* (Say) (Jurzitza 1970) and *I. pumilo* (Charp.) (Bick 1966). Further critical observations with *I. senegalensis* on these and other possible devices are required.

A concentration of exuviae were found in a concrete cement tank (1.5×1.0 m sq.×0.5 m high) abandoned along the road at the northernmost area of Chichijima (April 20). Numerous larvae of mosquitoes and chironomids were found within the tank and the exuviae were attached on a branch projecting above the water surface, 19 ones at 5~15 cm high, 4 at 20 cm and 7 at 25~30 cm, some ones forming a multilayered cluster. Indubitably the ability to live in such narrow waterbody may partly explain the abundance of this species in the Islands. The emergence was observed at Pond W during 11:00~17:00 (April 9 and 19) with no concentration on particular hours. The maiden flight was first vertical. At 3~5 m above the water surface, the newborn adults changed the direction to the forest.

Anax parthenope julius Brauer

On April 19, the cruising of two to three males were observed at the center of Komagari dam (Fig. 9). Each male cruised at heights of 50~80 cm above the water, making a circle of about 40~50 m in diameter. The flight continued up to 10 min., virtually without hovering. At encounter they chased for each other momentarily. Similar mutual chasing was observed between this species and *Pantala flavescens*, which cruised similarly with a smaller circling. The same behavior pattern — cruising and mutual chasing — was confirmed at the pond (40~50 m in diameter) in Minamishima (April 21).

From the observation made at a pond (90×40 m sq.) in Tokyo, Miyakawa (1967) reported the possession of territory by a male of this species, who expelled intruding males by violent clashes. The division of a pond by two males, each occupying his own territory, was also recorded in the same pond. Such territoriality was not confirmed in the cases described above, where the pond formed a communal flight area. The discrepancy may depend on physiological conditions of the participants, local populations or topographical conditions, which will be

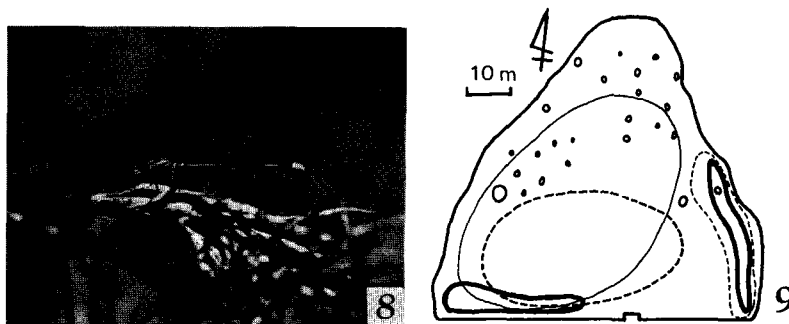


Fig. 8. Perching posture of *Ischnura senegalensis* (male). Fig. 9. Cruising area of three dragonfly species at Komagari dam (April 19). Thick line, *Hemicordulia ogasawarensis* (Thin broken, Boundary of territory). Thin line, *Anax parthenope julius*. Thick broken, *Pantala flavescens*. Dotts, Trees projecting from the water surface.

solved by comparative observations.

The oviposition by a solitary female was observed on April 10 at Pond W. Perching on a twig projecting above the water, she bent the abdomen and oviposited in the submerged part of the twig. During the oviposition lasting one min. the wings were kept open and motionless. Although this species is famous by its tandem oviposition, the solitary oviposition is also recorded by Aino (1936), etc. Numerous full grown larvae were collected from the pond in Minamishima. The pond was brackish ($\sigma_{15}=1.0038$), indicating the resistance of this species to a moderately brackish water.

Hemicordulia ogasawarensis Oguma

This species is relatively common among the endemic forms. Several aspects of its life are separately described and discussed.

Territorial behavior: Males are definitely territorial and each stays within a relatively narrow area. For instance, at Komagari dam with an ample space (ca. 70 m wide), a male kept the elongate territory, 10~20 m long and 2~3 m wide for 40 min. along a shore (Fig. 10) by repeated goes and returns at a height about 40 cm above the water (Fig. 11). The flight pattern is characterized by the absence of perching and frequent performance of hovering, which lasts up to five sec. virtually without changing location. The incessant flight activity in a narrow area with frequent hovering is common to many other cordulid species, for instance, *Cordulia aenea amurensis* Selys, *Somatochlora viridiaenea viridiaenea* (Uhler) (Ubukata unpubl.), etc., suggesting the effective use of landmarks within the area. The intruding male is nearly always chased and expelled by the occupant of the area. The chasing is mostly unilateral. The occupant approaches with a speedy flight to the intruder, who mostly leaves away the area with a U-turn. But the behavior pattern alters

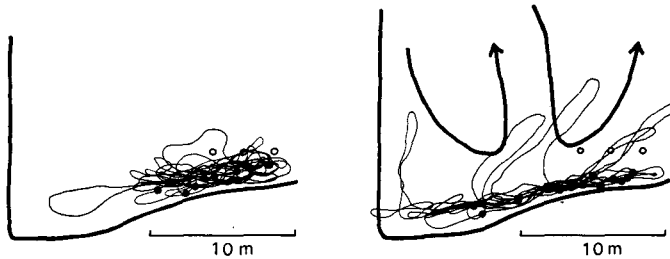
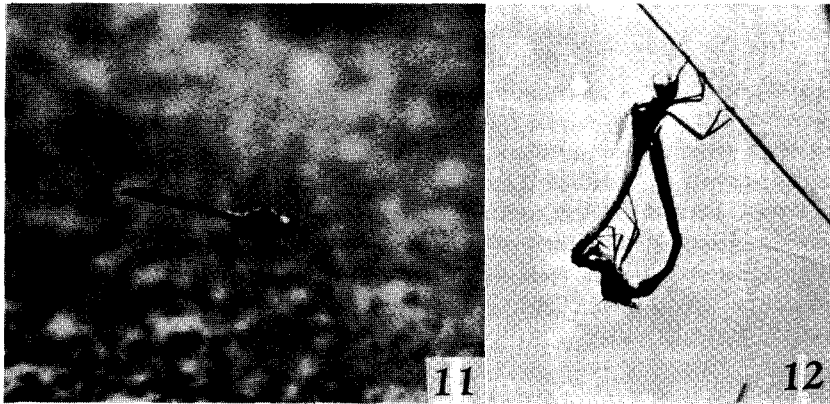


Fig. 10. Trace of flight courses of *H. ogasawarenis* (male) in Komagari dam (April 19). Left, 10:55~11:10, Right, 10:30~10:45, with responses to invasions by another male (thick line).



Figs. 11, 12. *H. ogasawarenis*. Fig. 11. Hovering posture of male at territory. Fig. 12. Copula hanging down from a twig.

when the defensive motivation of two males is in equilibrium as is the case in the occupants of two adjacent territories (cf. below), taking the following sequence: 1) Mutual approach, 2) Mutual ascending by facing with the venter for each other, 3) Mutual grappling sometimes followed by falling down of a male on the water surface or 3') Biting by a male of the abdomen of the opponent. But the combat usually stops by the separation after step 2, rarely reaching step 3. Miyakawa *et al.* (1972) regarded the pattern similar to step 2 in *Somatochlora v. viridiaenea* as a threat display. But further observations by M.I. on *H. ogasawarenis* suggest a mere mutual avoidance of collision than a specialized display.

Further description is given based upon continuous observations made at Pond W (April 9 and 19, Figs. 1, 13, 14). Three sections of the pond, A, B, C, were about equal in size but different in the surrounding vegetation and abundance

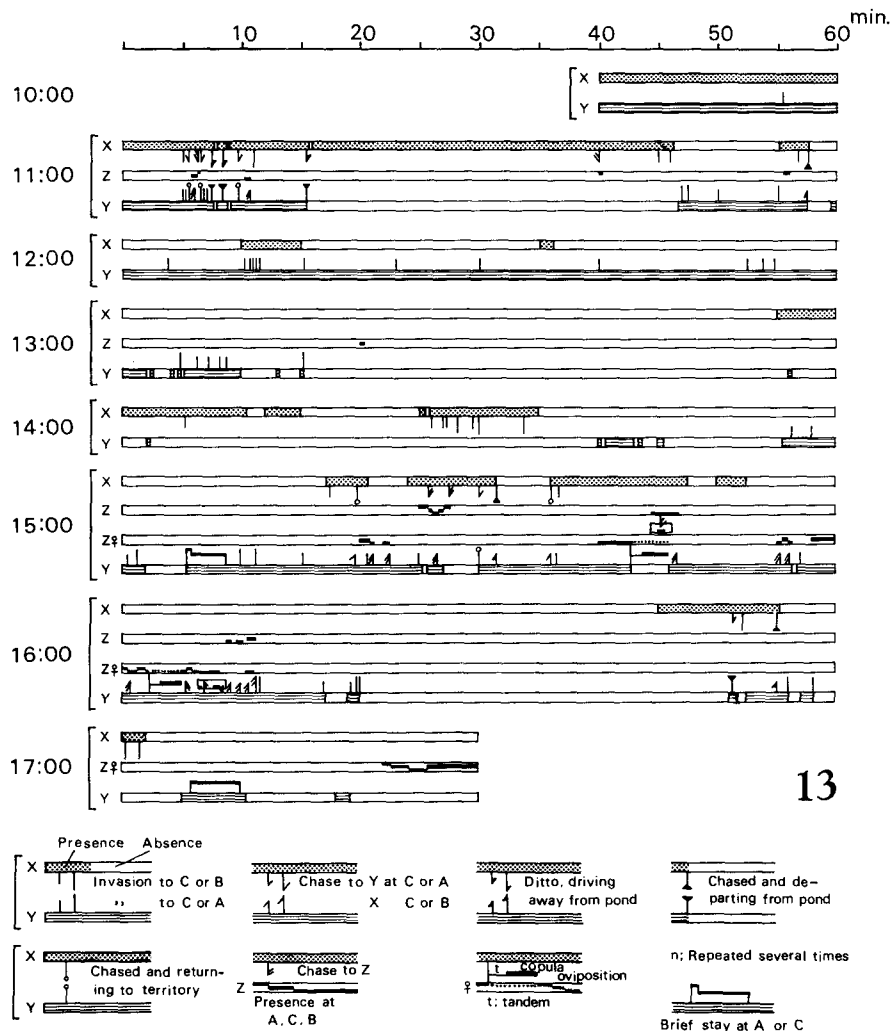


Fig. 13. Continuous observations of *H. ogasawarensis* at Pond W (April 9). Explanations in Fig. 14.

of emerged plants and wooden posts projecting above the surface. In this small pond the limitation of territory along the shore as in Komagari dam was not seen. When only one male occurred at W, he stayed usually at one half of the pond (Fig. 15) with occasional entries into the other half, mostly followed by immediate returns.

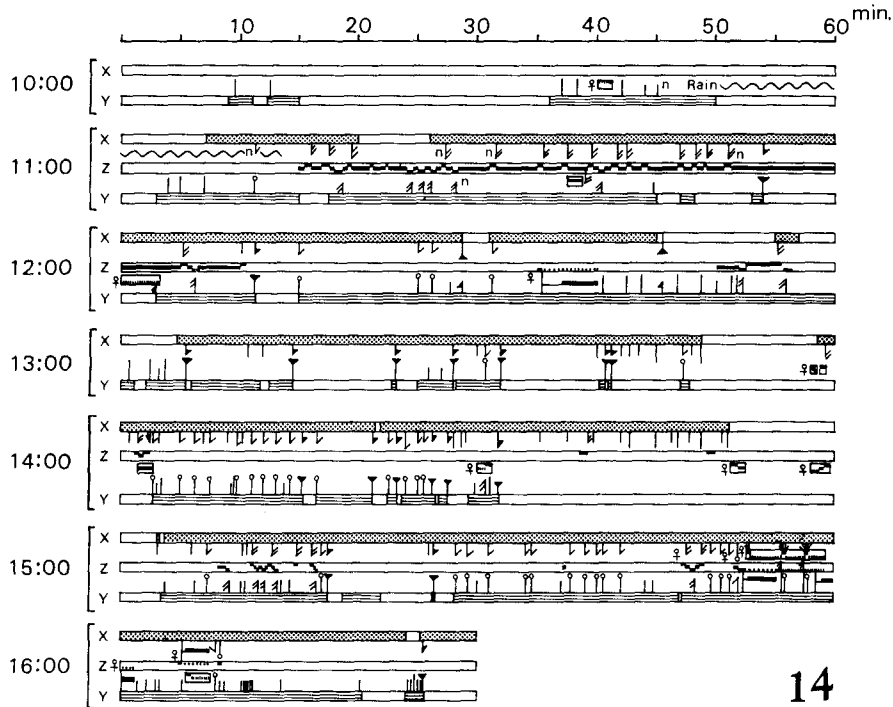
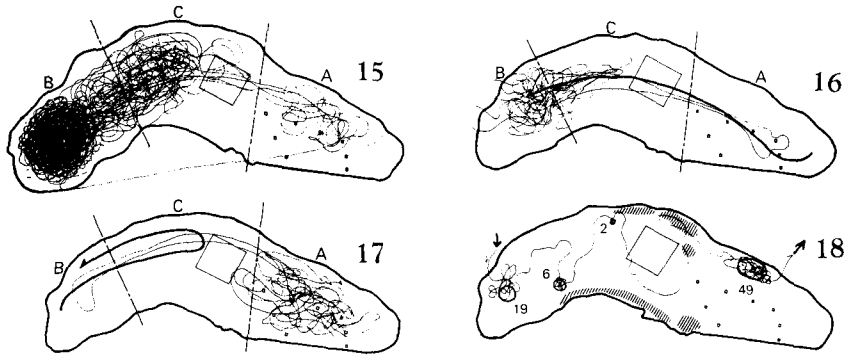


Fig. 14. Continuous observations of *H. ogasawarenensis* at Pond W (April 19). A, B, C correspond to the sections given in Fig. 1. X and Y, occupant males of A and B respectively. Z, non-occupant male visitors, mainly staying at C. Some females (shown by ♀) are also included in Z. Other symbols in Fig. 13.

The frequency of such visits in *all males*¹⁾ occupying A was 6.3 times per hour with both B and C, while in all males occupying B was 16.0 with C and 15.1 with A. The mean stay at C was 5.8 min. in B males while A males did not stay there. Thus, ignoring possible individual differences, the flight was more dispersed at B than at A. The duration of stay at W fluctuated 1~81 min. (mean 13.8), which was not affected by the interference by other individuals. When no other males stayed at W, the frequency of entires was B (18 cases) > A (8) > C (3). At the presence of a male at A, visits were B (17) > C (4), and of a male at B, A (12) > C (8), showing frequent departures and arrivals at B than at A and the attractiveness of C much lower than B and A.

1) It is probable that same males frequently visited the same section and stayed there. But individual recognition marks were not applied to, so that all males successively visited and left the respective section were regarded as different individuals, unless the interval between removal and the next visit was one min. or shorter.

When two males occurred at W, two territories were formed at A and B. The owners of A and B are henceforth called X and Y (cf. the foot-note in page 734). Among 10 invasions by Y into A occupied by X, six cases were unnoticed by X as Y soon returned before perceived by X, and four cases were expelled by X. (Figs. 13, 14). One invasion by X into B was expelled by Y (Fig. 14, 15:52). Therefore, the effect of prior residence was distinct between X/A and Y/B. On the other hand, the result was erratic at C. The win by the preoccupants was 18 out of 19 cases by X and 3/(5+n) by Y. Citing particular records, Y reached C at 11:03 (April 19) before X but expelled by the latter, similarly Y by X at 13:02, 16:24 (April 19), etc. Thus, C functioned more as a buffer zone than an area allowing the establishment of a stable territory. This topographical differentiation is also suggested by the result given later.



Figs. 15~18. Flight course of *H. ogasawarensis* at Pond W. Fig. 15. Male Y (Occupant of B) at the absence of other individual (April 9, 15:05~:12). Fig. 16. Ditto, at the presence of male X at A, with one invasion of Y in A with return chased by X (thick line) (April 19). Fig. 17. Male X (Occupant of A) at the presence of male Y at B, with one invasion in B followed by chasing by Y (April 19). Fig. 18. Oviposition flight by a solitary female (April 19, 14:58~15:00). Thick rings: Oviposition points (Number of dippings given by numerals). Hatched: Oviposition points by another solitary female (July 2).

The frequency of invasions per hour into the adjacent territories (A↔B) was compared before, during and after the presence of both X/A and Y/B:

		Before	During Coexistence of X and Y	After
Invader	X	6.3	0.7	2.8
	Y	15.1	2.3	3.7

Beside the obvious decrease of frequency during the coexistence, the invasions were less frequent after than before the coexistence, implying the presence of an

aftereffect to avoid the invasion.

Nextly the coexistence of three males at W is dealt with. When a third male, Z, entered in the pond at the situation X/A+Y/B, he was chased by both X and Y (Figs. 13, 14), and was forced to cruise mainly at C. Rarely the stay of Z prolonged, for instance, during 11:15~12:10, April 19 (Fig. 14), who stayed at C for 55 min. and expelled a fourth male. But even such unstable territory was only exceptional, and most Z left the pond 1~2 min. after entry. Therefore, the extent of the pond observed in April was insufficient to realize three stable territories. During June, the water surface increased by lasting rains and the highest instantaneous density attained 8 males (June 30), though dropped to 4 after several minutes. These observations clearly demonstrate the significance of male territorial behavior in this species, acting to limit the population density at reproductive site.

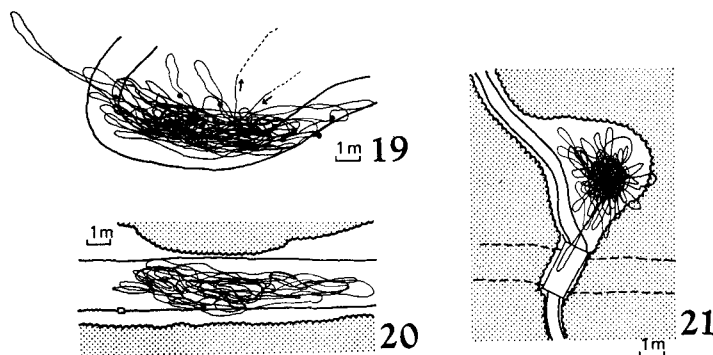
Mating: When a territorial male perceived a female entering the pond, he immediately approaches her and clasps her dorsum. Males seem to discriminate females or pairs in copula even though the last ones are not in flight. Because once a male discovered a copulating pair hanging from a branch and circled around it without further approach. Females usually escape from approaching males. Among 11 approaches, males clasped the females only five times. After clasping, the tandem is formed in the air. It flies about 40~100 cm high for 20~70 sec., though longer flight is suggested as referred to later. Then the pair hangs down from the underside of leaves or branches about 30~60 cm high at shores (Fig. 1, G₁₋₄ and Fig. 12). The copula continues for 1~3 min. After the separation, the female either starts ovipositions (9 cases) or leaves the pond. The male mostly (13/14) remains there, continuing territorial cruising. Frequently (5/9 cases), the male hovered 30~50 cm over the ovipositing female and chased away other male intruders. This guarding territory was much narrower than ordinary pre-mating territory, about 1.5 m in diameter. The additional copula between guarding male and laying female was twice observed (One additional copula in one case, two in the other).

This guarding behavior is, even though not obligatory, recorded in several genera of Calopterygidae, Libellulidae and Gomphidae (*Ictinus clavatus* (Fabricius), Eda 1956), but so far not in Corduliidae. Taketo (1961) interpreted the guarding in Libellulidae as an inhibited sexual approach: The male approaches the female for mating. But her oviposition posture inhibits the clasping and releases the hovering flight. On the other hand, Pajunen (1962a) and Arai (1972) presented another explanation: The male approaches the female, driven by sexual motivation. But the threshold to release clasping is raised by the previous copula. Thus, the defensive motivation compensately increases and releases the guarding. In the present cases, the duration of copula, C, and of guarding, G, in successive copulae were C₁(165 sec.), G₁(35), C₂(15), G₂(105), C₃(10) in one case and C₁(300), G₁(60), C₂(240) in another, both showing a gradual shortening of copula, probably by an accelerated decrease of motivation. But the presence of successive copulae indicates that guarding males are continuously under sexual motivation, the threshold of which raises by copula but gradually lowers in due time. Further observations and experiments are required to explain the

causal mechanism underlying the guarding, including crucial tests for interpretations cited above.

Oviposition behavior: As described above, oviposition is made either solitarily or guarded by male, exhibiting the following behavior pattern: The female flies about 10 cm above the surface, distinctly lower than in the male. At laying sites, she further descends to 6~8 cm. Hovering at this height, she repeatedly descends to 3~4 cm, bends the abdomen and beats the water by its tip. Fig. 18 shows the record of oviposition sequence (April 19, 14:58-15:00) of a female at Pond W, when no male stayed at the pond. During this sequence she beat the water 76 times. Incorporation of the observation on June 2 in the figure indicates the preference for the water surface along shores with emerged plants.

Extra-aquatic fixed area of males: Beside the territories at Pond W and Komagari dam, the occupation of a fixed area by males out of aquatic environment was observed in several places in the Islands. Among 15 individuals observed in April out of aquatic environment, nine passed the place by linear flight while six, all males, stayed at such fixed areas. The areas preferred were invariably the places well insulated along roads, at forest margins, at small clearings within forests. This habit, also briefly touched by Hasumi (1970), appears rather uncommon in Odonata so that some representative cases are cited below:



Figs. 19~21. Extra-aquatic fixed areas by male *H. ogasawarensis*. Cases 1~3 (cf. in text). Black points in Fig. 19, lasting hovering.

Case 1 (Fig. 19): Hahajima, near pass Kuwanoki, at a curve of mountain path embracing a dry valley. April 11; 11:30~45: A male cruising within an area of 15 m long and 3 m wide at heights 50~80 cm, taking a more or less definite course (a five min. trace in Fig. 19), with frequent hovering as in aquatic territories. Chase of a lycaenid butterfly, *Celastrina ogasawarensis* Pryer, capture of a small fly and chase of another conspecific male intruder were observed each once. 11:45: Driven away by *O* (the observer, S.F.S.). No return for ten min. until *O* left the place. 13:00: *O* returned to the area. One male, possibly the same individual, cruising similarly, twice expelling *Diplacodes*

intruders, once leaving the area with immediate return. Remaining until removal of *O* at 14:03. Same cruising observed at 14:30 and April 13, 11:30.

Case 2: Hahajima, southern district, along a road partly fringed with trees. April 12, 10:05~10: Cruising of a male in an area 12 m long and 3 m wide at 80 cm high (Fig. 20). 10:20: Driven away by *O*. 10:25: Arrival (or return?) of a male, cruising with a more erratic manner in an area 15~20 m long and 4 m wide, slightly south of the previous area. 10:30: The area dwindled and moved northward, approximately converging the previous area.

Case 3 (Fig. 21): Hahajima, southern district, at a narrow open space, 4 m in diameter, in forest. April 12, 10:45: Cruising of a male at 80 cm high. Reflecting the narrow space, mostly spent by hovering within the extent 1 m in diameter. 10:00: Chased by *O*. 11:03: Return, continuing hovering until removal of *O* at 11:10. 15:40: A male at the same site with same flight manner. 16:20: Absent.

Case 4: Chichijima, northern district, at a widened part of road. April 22, 14:00: A male flying with an erratic manner at 30~150 cm high, with few hoverings. 14:06: Leaving the area for chase of a small fly, followed by immediate return. 14:10: Sudden ascending to 300 cm — capture of an insect — return. Active chase of small flying insects several times observed. 14:20: Expelling an intruding *Diplacodes*. 16:52: Still flying. April 25, 13:45: Absent. April 26, 15:15: Present.

While the male behavior in Cases 1~3 and other two cases observed by S.F.S. in April does not much differ from that in aquatic territories, Case 4 is somewhat different by erratic and relatively high and variable flight with little hovering and sensitivity to passing insects, resembling the feeding flight during teneral stage in *Cordulia aenea amurensis* (Ubukata 1973). Presumably Case 4 represents the feeding flight of a teneral male. Although not precisely observed, similar flights were frequently seen in June~July by M.I. at the grassland north of Pond W. These males did not visit the pond, flying with occasional hovering around the boundary between openland and forest at 50~100 cm high. A brief simultaneous comparison of flight pattern between one of such male and X/A in the pond was undertaken. Within 10 min., the former made horizontal darting (more than 1 m, regarded as prey chasing) eight times and actual capture thrice, while the latter made no such attempts.

In the pioneer work on the odonate territory, St. Quentin (1934) suggested the presence of feeding territory. This opinion was rejected by Jacobs (1955), Moore (1957), etc. At the present, it is generally accepted that the main function of odonate territory is reproductive. Although this seems valid in most territorial species, the observations mentioned above suggest that the possession of a fixed area for food intake is circumstantially not impossible in some species.

On the other hand, Cases 1~3 imply the presence of extra-aquatic reproductive territory. Unfortunately, no entry of female in such fixed area was confirmed, but the entry of tandem pairs into Pond W followed by oviposition was occasionally noted in June~July. This suggests the possible mating out of aquatic territories. Such extra-aquatic mating was confirmed in a corduliid species, *Somatochlora v. viridiaenea* (Miyakawa et al. 1972) and in *Anax parthenope julius* (Eda 1966). In the former species, Ubukata (unpubl.) observed male territorial flights

in the daytime not only above the water surface but also over roads and openland at 30~50 cm high, nevertheless in the evening both sexes gregariously fly at 3~10 m high for food intake. These fragmentary items of information indicate the occurrence of two different types of extra-aquatic fixed area or territory, one for feeding and the other for reproductive function.

Comparing our observations with those on other corduliid species, the behavior pattern is quite similar except for the presence of male guarding at oviposition in *H. ogasawarensis*. In both *Cordulia a. amurensis* and *Somatochlora uchidai* Foerster, the pair formed at male aquatic territory goes to the forest nearby, where it dissolves and the female visits the oviposition site solitarily (Ubukata unpubl.). This habit excludes the possibility of male guarding and virtually no such behavior has been confirmed. The lasting copula of odonate species at oviposition site generally evokes the disturbance by other males. In *Cordulia* and *Somatochlora*, this interference is avoided by the departure of the pair from the site. The resulting increasing of interference at oviposition is partly avoided by the selection of sites with dense emerged vegetation. In *H. ogasawarensis* the interference in the copula is seemingly avoided by its brief duration and also by the possible inhibition emitted from the mating posture. The latter possibility is suggested by the behavior of a male invaded into territory B at Pond W., where male Y was at copula. The first male circled around the pair without further approach and finally driven away by Y after finishing the copula.

Boninthemis insularis (Oguma)

This endemic species forming a monobasic genus is not abundant in the Islands. On June 3, 1973, M.I. observed the presence of a male, a tandem pair and a male of *H. ogasawarensis* at a puddle of ca. 50 cm in diameter within a dry valley, Chichijima. The tandem was soon expelled by the solitary male, who coexisted with *H. ogasawarensis*, both circling over the puddle, until the departure of the latter. Ten min. later, a male of *H. ogasawarensis* entered in the area but after clash with *B. insularis* was expelled by the latter.

As shown by this case, males of this species stay at fixed areas, generally perching on the insolated shores, and drive away the conspecific males and other species. The mating was observed on July 4, 1973, 8:30 at Pond W. The pair hung down from a herb stalk in copula for 1 min. 20 sec. Thereafter, the female took rest for a while on a leaf. When the female flew into the center of the pond, the male followed her. But he soon returned to the shore and the female left the pond. This brief record suggests the solitary oviposition but does not exclude the possibility of male guarding as in *Libellula* and *Orthetrum*. Although both observations were made at stagnant water bodies, this species usually prefers the lotic environments for the formation of territories and for oviposition.

On October 3, 1973 (14:50~15:50), the feeding activity of a male was observed

at sedge field along a small stream emptying Pond W. The male perched on the top of a branch of a dead tree, 1.5 m high. From this post he frequently, 28 times during 1 hr, departed for the search of the prey and returned there after a flight of 20~200 cm, with intervals lasting 10 sec.~8.5 min. Only one of these flights was rewarded by the capture of a minute insect.

Diplacodes bipunctatus (Brauer)

This pacificopolitan species is abundant in the Islands and the behavior was intermittently observed at various places. A continuous record of some males taken on April 9 at Pond W, together with that of *H. ogasawarensis* is given in Fig. 22 (Three males, $D_1 \sim D_3$, individually recognized). The male perches on a horizontal substrate about 0~30 cm high at shores or those on or projecting above the water, such as horizontal branches, floating stalks, etc. (Figs. 23, 24). Occasionally he takes a flight for 1~2 min., circling the extent of 50~100 cm in diameter around the perching post at intervals of 1~30 min. (D_1 9.5 min., D_3 20 min. in average). The flight either appears spontaneously or is released by the passing through of other individuals, both con- and heterospecific ones. The resulting chase is responded by a counter-attack in case of *H. ogasawarensis* or *Pantala flavescens* but not in conspecific males, though the clash is frequent. The higher frequency of chasing by D_1 than by D_3 is circumstantial, that is, the perching post of D_1 faced a free water surface with frequent traffic of other individuals (Fig. 1). This mutual chasing brings the spacing of males along the shore.

Perceiving a female, the male approaches from a distance of up to 5 m, and chases her. Occasionally the female hovers about 20 cm in front of the perching male. The copula is performed in the air and lasts for 2~3 sec. Usually the tandem oviposition follows the copula but once (June 29) a pair hung down from a plant at the shore. The oviposition behavior is similar to that of *Sympetrum*. The longest tandem flight lasted 10 min., during which the female beat the water surface 50 times. Oviposition by female alone was observed rarely. After the separation the female leaves the pond. The male remains in the area and occasionally makes a second copula within a short time (D_1 , Fig. 22). A tandem pair was marked on June 26 and the female oviposited at the same site the next day, forming tandem with another male. From marking experiment, it was confirmed that one male mated three times during four days, and a female four times during five days, in both cases changing the partners.

In *Orthetrum albistylum speciosum* (Uhler), Itô (1960) suggested a "polygamy-oligandry system" from the presence of some males remaining lifelong unmated for the failure of possessing territories. In *Diplacodes*, however, males lifelong failing to occupy the territories seem not too many. The result of a marking experiment, made at Pond W in June~July, 1973 (Table 3), shows frequent daily change of daytime perching places between pond and grassland nearby. All marked males, including MB 7 with a strong

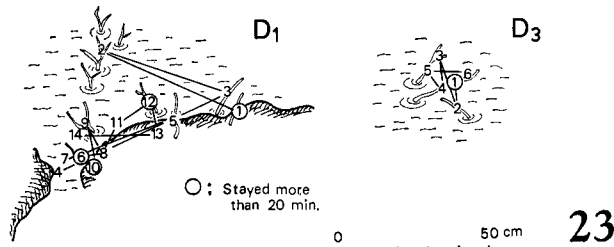
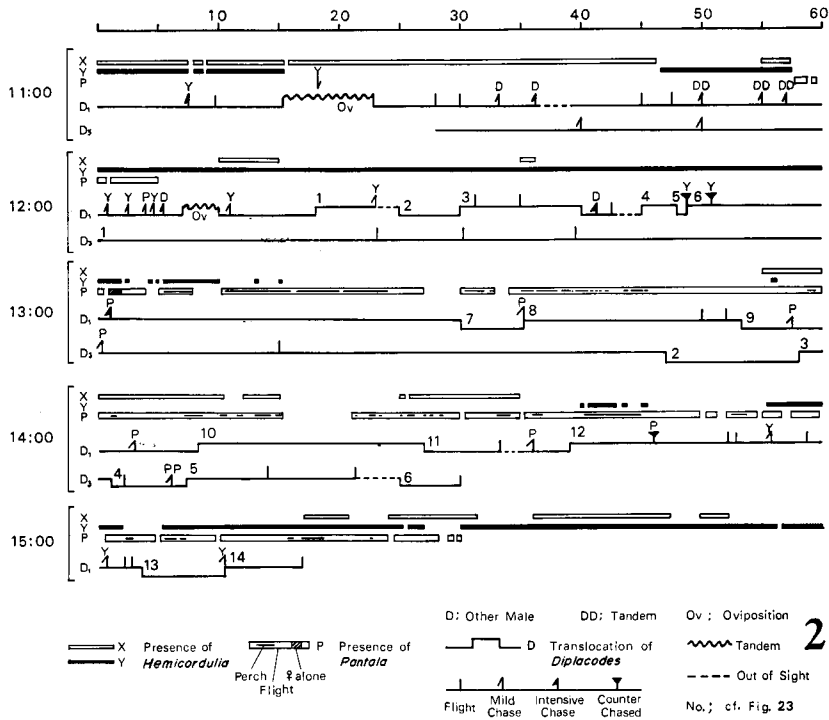


Fig. 22. Continuous observations of two males (D₁, D₃) of *Diplacodes bipunctatus* at Pond W (April 9) including interference with *H. ogasawarensis* and *Pantala flavescens* (Compare Figs. 13 and 26). Fig. 23. Translocation during the observation in Fig. 22.

attachment to grassland, possessed at least once the aquatic territories. This implies the scarcity of males failed to have territories in this species, at least in the population observed, suggesting a promiscuous relation.

Table 3. Daily change of daytime perching place in marked individuals of *Diplacodes bipunctatus*. M, Marked at Pond W. P, presence at Pond W. G, ditto, at glass-land. Gothic letters, performance of copula.

Recognition mark	Date	June					July						
		26	27	28	29	30	1	2	3	4	5	6	7
MB1			M										
MB2			M										
MB3		M	G	G	P	P		P					
MB4♀		M	P		P	P							
MB6			M	P	P	G		P					
MB7			M	G	G	G		G		G			P
MB8			M	P	G					P			
MB9			M							P			G
MB10			M										
MB11			M	P	G								
MB12			M		P	G				P			P
MB13			M	P	P	P		P					
MB14			M							G			G
MB15				M	G	P		G		P			G
MB16				M	G	G				P			
MB17				M	P	P							
MB18				M									
MB19					M	P		P		P		G	
MB26					M							P	
MB29					M	P		G					
NB31											M	P	
MB32											M		P
MB33											M	G	P
MB34											M	P	P

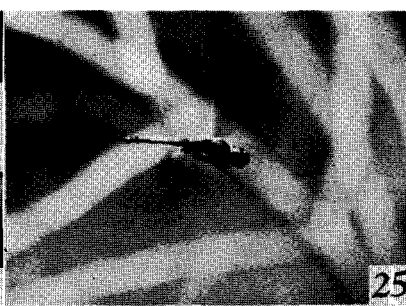
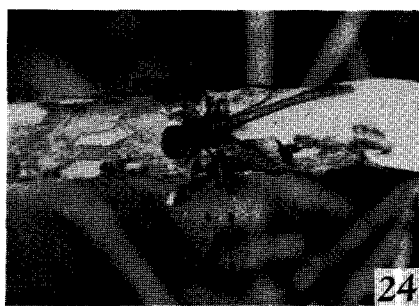


Fig. 24. Perching posture of *Diplacodes bipunctatus*. Fig. 25. Male flight posture of *Tramea transmarina euryale*.

Pantala flavescens (Fabricius)

This circumtropic species is famous by its transoceanic invasion into temperate regions. On April 9, 1973 (11:00~16:00), the male behavior was traced at Pond W together with *H. ogasawarensis* and *D. bipunctatus* (Fig. 26). Arriving at the pond, the male stays from several to thirty minutes, cruising over the entire surface of the pond at heights 1~1.5 m, occasionally to 2 m, with the speed far higher and the admixture of hovering much scarcer than in *H. ogasawarensis*. Further, in contrast to the latter species, the perching is frequent, preferring the top of an emerged plant about 60~100 cm high. The duration of unit perching is 1~5 min., and the proportion of the time spent by cruising and perching is approximately 2:1.

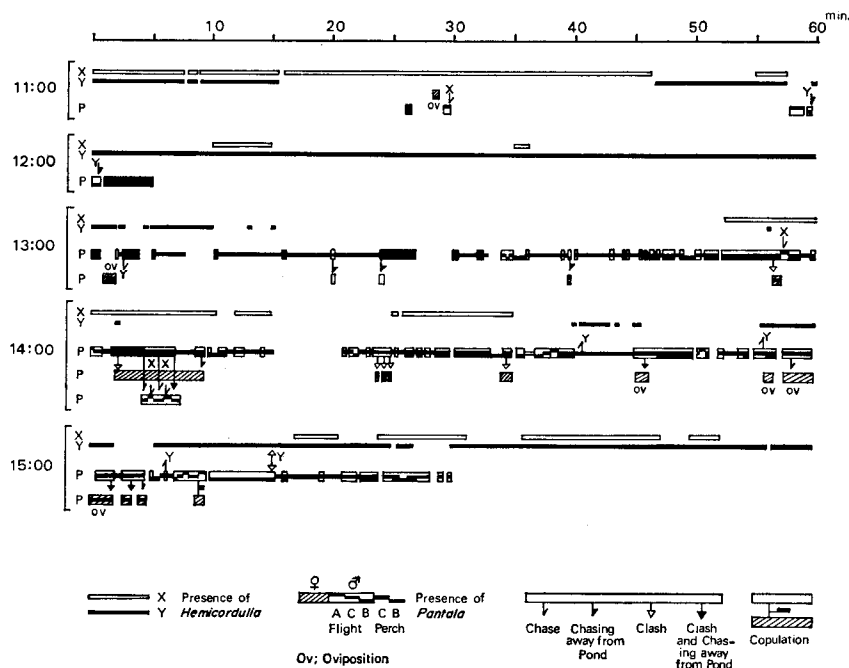


Fig. 26. Continuous observation of *Pantala flavescens* (P) at Pond W (April 9) including interference with *H. ogasawarensis* (X, Y. Compare with Fig. 13).

On April 19 the cruising of two males was observed at Komagari dam. The behavior was similar to that of *Anax p. julius* simultaneously observed, that is, forming a communal flight area without segregated in territories, though mutual chasing was frequent (Fig. 9). At Pond W the male occupants always expelled the conspecific males. At frequent entries, the coexistence of two males with mutual chasing was observed for a short time. In such instance, however, the division of the pond by two males appeared only briefly, usually soon replaced by the cruis-

ing over the pond. Probably the flight pattern of this species, characterized by high speed and few hoverings, is less apt to keep narrow territories as possessed by *H. ogasawarensis*.

Mating and oviposition were observed at Pond W. The record taken on June 28, 1973 is cited:

10:26: Entry of a female in the pond, followed by oviposition. The occupant male chased her and mated in the air. The copula position continued for 1 min., then replaced by tandem flight. 10:30: The female began to oviposit. Cruising 20~30 cm over the water, she occasionally lowered to the surface, and beat the water 4~5 times (maximum 13) by bending the abdomen. This sequence was repeated approximately for every 1 m. During this laying flight the male accompanied with the female, cruising at 1 m high.

The post-mating tandem flight is relatively long, in the longest case lasting 10 min. (April). On April 19, the entry of tandem pairs in Pond W was observed three times, all chased and expelled by the solitary male occupant. Two pairs left the pond and the other one dissolved and the female began to lay eggs.

From these observations the mating-oviposition pattern of this species is summarized as aerial mating — search of oviposition site by tandem flight — separation — oviposition occasionally accompanied with male. The guarding by male is possible but no invasion of alien males was observed at oviposition accompanied with male partner. However, the oviposition pattern of this species could be variable, because Rokuyama (1961) and Svihla (1961) respectively confirmed its tandem and *Tramea* type oviposition. The approach of males to females does not particularly differs from that to males. The successful mating is not frequent, being one out of seven approaches on April 9 and 2/4 on April 19.

Tramea transmarina euryale Selys

The observations of this Oriental species were made in June~July, 1973, at Pond W. The male cruises at 1~2 m high the area of ca. 20 m in diameter, and perches on the wooden post or stalk projecting from the water surface (Fig. 25). The territorial behavior is relatively clear. In late June, the extent of Pond W doubled by incessant rains and three stable territories were disturbed by invasion of many males. Once, five males coexisted during a short time and the territorial ownership became indistinct by frequent interference. The fighting within the territory resulted in the expulsion of intruders in eight cases while that of owners in two cases, showing the occupant right fairly though not absolutely effective.

Finding the female entering in the territory, the male soon chases her and makes copula, which is completed in the air, measured as 2 min. in one case, followed by tandem flight. In one instance, however, the pair rested on the vegetation for 12 min. After mating, the pair goes to the oviposition site, which is the water surface along shores with sparse emerged plants. The pair expels the solitary males cruising there before oviposition, which shows the cohesion of, and

aggression by tandem being much stronger than in *Pantala*. At oviposition, the female momentarily separates from the male, descends to the water surface. After beating 1~5 times the water with the abdomen, she ascends and again forms the copula position with the male having hovered at 10 cm high. This sequence (Fig. 27), separation — oviposition — recombination, lasts 6~67 sec., mostly 20~30 sec., and repeated many times, though occasionally interrupted by perching in tandem. The duration of oviposition by a pair was measured: 2.5 min. (10 dippings), 3 (6), 4 (7) and 5 (10).

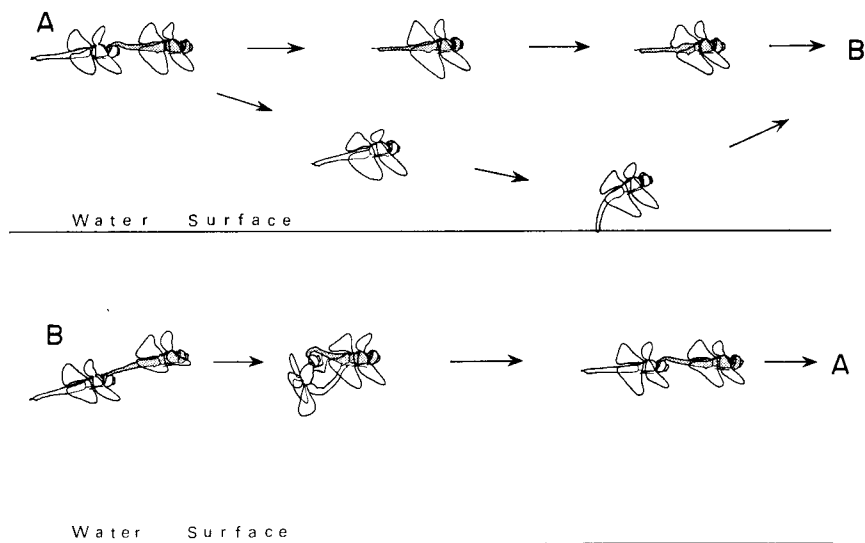


Fig. 27. Peculiar oviposition process in *Tramea transmarina euryale*, repeating cycle AB. Male, shaded.

At separation the female is often disturbed by other conspecific males or by *Diplacodes*. Occasionally the accompanied male was also expelled and the remained female either left the site or continued the oviposition solitarily. Once an alien male disturbed a tandem and after its separation mated with the female. Further, the entry of a solitary female in Pond W followed by solitary oviposition was once observed. The peculiar oviposition pattern described above is so far known only in *Tramea onusta* Hagen (Needham and Heywood 1929), *T. virginia* (Rambur) (Okamoto 1954, Ishida 1958) and *Pantala flavescens* (Svihla 1961).

Macrodiplax cora (Brauer)

This halophilous pantropic species was first recorded by Asahina (1970, cf. also Hasumi 1970). Dr. S. Asahina, who identified our specimens, suspects the

permanent residence of this migratory species in the Bonin Islands.

Many males were found at the brackish pond in the center of Minamishima (cf. *Anax p. julius*) on April 21. The males cruised the water surface with a high speed. The flight pattern resembles that of *Pantala*, characterized by few hoverings, occasional perching on plant stalks projecting 60~80 cm above the surface, and the prevalence of cruising against perching. Possessing the pond as a communal flight area, no territorial behavior was observed but the encounter with other males or the males of *Anax* resulted in chasing for each other. On July 4, 10:12, the flight of a pair in copula was noticed at Pond W but no further observation was undertaken.

2. Interspecific interference

In the preceding section, several instances of interference between different species were briefly referred to. This aspect was not specially observed but some findings are summarized here. In April and June~July, the following combinations were recorded in Pond W (Relatively frequent cases asterisked):

Chasing/chased between males: *Diplacodes/Hemicordulia*,* *Pantala/Anax*, *Diplacodes/Boninthemis*, *Boninthemis/Hemicordulia*, *Hemicordulia/Tramea*, *Tramea/Boninthemis*, *Tramea/Pantala*, *Hemicordulia/Pantala*, *Pantala/Hemicordulia*.

Interference with oviposition Male/female: *Diplacodes/Tramea*,* *Diplacodes/Hemicordulia*,* *Hemicordulia/Tramea*, *Pantala/Tramea*, *Tramea/Pantala*, *Pantala/Hemicordulia*, *Hemicordulia/Pantala*.

The interference between anisopteran and zygopteran species, or that within the former group, were not observed. As to the latter group, all species frequently visiting the pond interfered and were interfered with one another. The frequent interference by *Diplacodes* without being interfered is apparently caused by its specific trait already described: Spending most time by perching with little cruising. The interference between *Hemicordulia* and *Pantala* observed on April 9 is cited in Fig. 26. *Pantala* chases *Hemicordulia* but not so frequently as in intraspecific encounter. Within the limit of observations, no definite interspecific rank order (Hediger 1940) was confirmed.

The interference with mating has not been observed, certainly due to the absence of prolonged aerial copula in the species observed. A single exception was the failed mating of a pretandem pair of *Boninthemis* clashed by a *Diplacodes* male. The interference with oviposition, all practiced by males, was rather frequent as given above, mainly by *Diplacodes*. In *Hemicordulia*, however, the oviposition was disturbed only in case of solitary females, not of those guarded by male partners. In *Tramea*, too, tandem pairs were less susceptible while solitary females or those separated from the partners at oviposition were often disturbed, suggesting the significance of these habits. On the other hand, the frequent interference by *Diplacodes* with other species is remarkable, possibly due to its weak ability of species discrimination or strong innate darting tendency. It would be worth to

explore, how this trait affects the reproductive efficiency of its own and of other species.

3. Rediscovery of marked individuals

In June~July, 1973, some individuals of four species were marked at Pond W and their rediscovery was checked on June 26~July 7. Although the experiment is still of preliminary nature, the result is briefly presented here.

At marking the individuals were captured by a net, marked on wings with "magic ink" (a water insoluble quick-drying paint), and liberated immediately. All marked individuals kept the normal flying ability at liberation. The rediscovery was attempted at the pond and surrounding moist grassland for 1~1.5 hrs per day during 8:00~12:00.

The number of marked (M) and rediscovered (R) individuals were as follows:

Pantala: M. 3 ♂♂ (V 25~26), R. absent.

Tramea: M. 14 ♂♂, 6 ♀♀ (VI 27~VII 6), R. 6 ♂♂ (42.9%), no ♀. Among the rediscovered ones, MH7 visited the pond on five successive days. Other five males were each rediscovered once, 1~3 days after being marked.

Hemicordulia: M. 43 ♂♂, 3 ♀♀ (VI 26~VII 4), R. 2 ♂♂ (4.7%), 1 ♀. All once, 1~9 days after marked.

Diplacodes: M. 25 ♂♂, 2 ♀♀ (VI 26~VII 4), R. 21 ♂♂ (84.0%), 1 ♀ (Table 3). All rediscovered males visited the pond on successive days. The number was small on VII 1 and 6, for cloudy weather. The longest attachment to the pond was recorded in MB 19 (June 29~July 19; 23 days).

Comparing the ratio of rediscovery of males among the species, a remarkable difference is found between *Diplacodes* and *Hemicordulia*, which is explained by the different habits described in the previous sections. The fact that most daytime is spent by perching in *Diplacodes* shows its sedentary nature with a stronger attachment to a narrow habitat, which must increase the chance of rediscovery. On the other hand, *Hemicordulia*, certainly possessing a wider roaming area with its rather wide cruising territory, cannot maintain a high density in a small pond, resulting in the frequent replacement of individuals. This may give the decreased chance of rediscovery. *Tramea* may occupy the position intermediate between *Diplacodes* and *Hemicordulia*, and *Pantala* the type with a more wide-roaming tendency. But further studies are required for the relation between ratio of rediscovery and life modes.

Concluding remarks

Among nine forms observed in the Bonin Islands, the tendency of mutual exclusion among males was confirmed in all anisopteran species, though its expression was not linked with fixed territories in *Anax*, *Macrodiplox* and partly *Pantala*. In contrast to birds, in which the territory is usually kept by the owner for a considerable time, the odonate territory is rather ephemeral with frequent replacement of the owners (Moore 1957). Nevertheless, in the sense that a definite area is

defended by a male for a definite time against the conspecific males, it fulfils the conditions proposed by Noble (1939) for the definition of territory. The functions of odonate territories have variously been discussed (St. Quentin 1934, Jacobs 1955, Moore 1957, Johnson 1964). Its primary function is probably to guarantee the mating and in some groups, e.g. *Hemicordulia*, *Orthetrum*, etc. to exclude the disturbance to oviposition by other males. The secondary function would be the dispersal of males, etc. Further the possible feeding territory was suggested in *Hemicordulia ogasawarensis*, being rather exceptional in Odonata.

The territories (*s. lat.*) of the anisopteran species observed in the present study are divided into several types according to the flight pattern of the owner males (Uncertain cases or those from literature in parentheses):

	Real territory	Mutual chasing not linked with definite area
I. Perching type	<i>Diplacodes</i> , (<i>Boninthemis</i>)	—
II ₁ . Cruising type with occasional perching	<i>Pantala</i> , <i>Tramea</i>	<i>Pantala</i> , <i>Macrodiplax</i>
II ₂ . Cruising type with little perching	(<i>Anax</i>)	<i>Anax</i>
III. Hovering type	<i>Hemicordulia</i>	—

Various other species so far studied more or less exhibit one of these types, which are to some degree fixed within particular supraspecific taxa. These types are regarded as the manifestation of the coaction between the parallel evolution of flight ability among different phyletic lines as a general trend in Odonata and its secondary modifications due to niche diversification, which would not exclude the possible reduction of the trend mentioned above. However, the facts that *Pantala* behaved differently according to the situations and a similar difference was suggested in *Anax* give a warning to a premature conclusion upon the territorial types without comparing the behavior under diverse situations. The same could be applied to the mating and oviposition types, the variability of which was suggested in some species, *Anax*, *Pantala*, *Hemicordulia*, and *Tramea* in the present study. The local variation of reproductive behavior is recorded in *Ischnura elegans* (Schiemenz, op. cit.), *Platynemis* (Heymer 1967), *Calopteryx* (Heymer 1973), *Hetaerina* (Bick and Sulbach 1966). As mentioned in the section dealing with *Anax*, local populations, topography of the area observed, density, age and other physiological conditions must be kept in mind in future studies on the reproductive behavior of Odonata.

Evolution of reproductive behavior in Libellulidae

In the present survey our efforts were concentrated on the reproductive behavior of *Hemicordulia ogasawarensis*. But casual observations on some Libellulid species revealed various types of reproductive behavior as already reported by many authors. The family Libellulidae is certainly one of the most successful

groups in the recent Odonata and involves the largest number of species so far studied ethologically. The tentative to compare the differentiation of reproductive behavior in the family has been undertaken by some authors. But in these studies either the species referred to were scarce in number (Aguesse 1959, Schmidt 1965) or the analysis was still of preliminary nature (Eda 1960, 1964). Using this occasion, various behavioral types in the family are compared and possible evolutionary trends are suggested, mainly based upon the observations made in Japan, though some important contributions on exotic species are incorporated. The aim of this attempt, mainly undertaken by H.U., is, first of all, to stimulate further studies with various species, which would support or reject the assertions held below.

The previous information on the reproductive behavior in Libellulidae is presented in Table 4, with behavior formulae.¹⁾ The symbols used are explained as follows ("?" indicates the absence of information):

Territorial type (There is no libellulid species in which the absence of territorial behavior was positively confirmed): R. Perching, R_c: Perching with occasional cruising; C_r. Cruising with occasional perching; C. Cruising virtually without perching.

Copulation type (All started, as a rule, in the air): P. Completed after perching; P_f. Ditto, but occasionally completed in the air; F_p. Completed in the air, but occasionally after perching; F. Completed in the air.

Arrival at oviposition site of female: V. Solitarily; V_w. Ditto, occasionally in tandem; W_v. In tandem, occasionally solitarily; W. In tandem; X. In copula.

Oviposition type: S. Solitary; G. Guarded by male; T. Tandem; T'. *Tramea* type, with alternate insertion of tandem flight. . . Some transitional types are expressed as S_g, T_{sg}, etc.

The table shows a correlation between behavioral types and tribal system mainly established by morphology. Concerning territorial types, perching type (R, R_c) prevails in most tribes. Cruising type (C, C_r), as is widespread in Corduliidae, Macromiidae, etc., appears only in Trameini. Moreover, the exclusive aerial copula (F) is prevailing in this tribe, though Trithemini adopts an interesting combination of perching territory and aerial copula. Probably the aerial copula developed in parallel with the change from perching to cruising territory type, which would be a manifestation of increasing flight ability evolved in some tribes independently²⁾. Another feature probably linked with this trend is the shorten-

1) All libellulid species practice the exophytic and aerial oviposition with beating. But this feature, oviposition habit, must be adopted as an important item when the reproductive behavior of all odonate groups is compared.

2) But the problem is not so simple as supposed. It is generally accepted that Libellulidae evolved from a corduliid like ancestor. Considering the amazing flight ability in many recent corduliid species, the prevalence of perching territory in Libellulidae can be explained by one of the following alternatives: 1. Libellulidae evolved from a corduliid like ancestor still without high cruising ability. 2. Perching tendency in Libellulidae is a behavioral atavism. At the present, it is still not decided which of these alternatives is more likely. Anyhow, the C type in *Tramea* is regarded as a revival of once reduced flight ability, if the second alternative is valid.

Table 4. Mating and oviposition types in libellulid species, classification system follows Tillyard (1917) (cf. Asanina 1961). 1) Asterisked: Species precisely studied. 2) First W, later V. ?: Unknown.

Tribe	Species ¹⁾	Locality	Behavior formula	Author
Libellulini				
	<i>Boninthemis insularis</i> (Oguma)	Bonin Ids.	RPV _w S(?)	Sakagami <i>et al.</i>
	<i>Lyriothemis pachygastra</i> (Selys)	Japan	??S	Ishida '69
	<i>Orthetrum albistylum speciosum</i> (Uhler)*	Japan	RPV _G _s	Itô '60
	<i>O. cancellatum</i> (Linné)	France	RPW _v G ²⁾	Aguesse '59
	<i>O. triangulare melania</i> (Selys)*	Japan	RPX _v G _s	Taketo '61, Arai '72
	<i>Libellula quadrimaculata asahinai</i> Schmidt	Japan	R _c PV _S _g	Miyakawa <i>et al.</i> '72, Ishida '69
Brachydiplacini				
	<i>Nannophya pygmaea</i> Rambur*	Japan	RPV _S _g	Yamamoto '66, '68, Eda '66
Sympettrini				
	<i>Sympetrum eroticum eroticum</i> (Selys)	Japan	?PWT	Kani '52
	<i>S. vicinum</i> Hagen	USA	?PW _v T _s _g	Needham and Heywood '29
	<i>S. parvulum</i> (Barteneff)	W. Virginia	?PW _v G	Jurzitza '71
	<i>S. danae</i> (Sulzer)	Japan	?PW _v T _s	Rokuyama '63, Ishida '69
	<i>S. illotum</i> Hagen	Japan	RPW _v T _s	Sonehara '65
		USA	??V _w S _t	Needham and Heywood '29
	<i>Acisoma panorpoides panorpoides</i> Rambur	Japan	?P?S	Ishida '69
	<i>Diplacodes bipunctatus</i> (Brauer)*	Bonin Ids.	RFW _v T _s	Sakagami <i>et al.</i>
	<i>Crocothemis servilia</i> (Drury)	Japan	R _c ?VS	Higashi '69, Ishida '69
	<i>C. erythraea</i> (Brullé)*	France	R _c F _p V _G _s	Aguesse '59
	<i>Deselia phaon</i> (Selys)	Japan	R _c ??S	Ishida '69
Leucorrhiniini				
	<i>Leucorrhinia dubia</i> (Van der Linden)*	Finland	R _c PV _G _s	Pajunen '62b
	<i>L. d. orientalis</i> (Selys)	Japan	R _c PVS	Fujisawa '57
	<i>L. intermedia ijimai</i> Asahina	Japan	R _c PVS	Ishida '59
Trithemini				
	<i>Pseudothemis zonata</i> (Burmeister)*	Japan	R _c FV _G _s	Miyakawa '67, Ishida '69
	<i>Trithemis aurora</i> (Burmeister)	Japan	RFVS	Naraoka '72
Trameini				
	<i>Pantala flavescens</i> (Fabricius)*	Burma	C _r FW _v S _t '	Svihla '61
		Japan	C _r FW _v S _t	Rokuyama '61
		Bonin Ids.	C _r FW _v S	Sakagami <i>et al.</i>
	<i>Zyxomma petiolatum</i> Rambur	Ryukyu	C _r F'S	Ishida '69
	<i>Tholymis tillarga</i> (Fabricius)	Ryukyu	?F'S	Ishida '69
	<i>Rhyothemis fuliginosa</i> Selys	Japan	?F'S	Ishida '69
	<i>Tramea transmarina euryale</i> Selys*	Bonin Ids.	C _r F _p W _v T _s '	Sakagami <i>et al.</i>
	<i>T. t. yayeyamana</i> Asahina	Ryukyu	??T _s '	Ishida '69
	<i>T. virginia</i> (Rambur)*	Japan	C _r FW _v T _s '	Okamoto '54

ing of time spent by copula, but the available records are still insufficient to make a closer comparison.

Because the territorial type is not mentioned in many species cited in Table 4, further discussions are confined to three other features. From the table, the following basic reproductive types are obtained, with various intermediated ones in each of three features.

O. PVS	II. PVG	III ₁ . FVG
I. PWT	III. FVS	III ₂ . FWT
		III ₃ . FWT'

Among these types, PVS is inferred as the most ancestral, because it represents the lowest step of both aerial life and sexual behavior, it prevails in most non-libellulid anisopteran groups so far observed, and also it is the type adopted by *Epiophlebia superstes* (Selys) (Anisozygoptera, Asahina 1938, Kobayashi 1956). Type PVS is confirmed in Leucorrhiniini but its presence in Libellulini, Brachydiplacini and Sympetrini is likely. The hypothetical courses through which other six types evolved from PVS are presented in Fig. 28. First, three differentiations appeared, I. tandem oviposition (PWT), II. Oviposition guarded by male (PVG), and III. aerial copulation (FVS). Type II further produced II' and III ramified into three types, male guarding (III₁), tandem oviposition (III₂) and *Tramea* type (III₃). Various transitional steps between these basic types, given in Table 4, do not necessarily mean the unilateral evolution. The secondary return to the earlier steps is not excluded. Next, these evolutionary trends are traced for each tribe.

Libellulini, *Brachydiplacini*, *Leucorrhiniini*: Relatively simple, exhibiting only courses O→II or O→II→II'.

Sympetrini: Apparently most diversified in Odonata as to reproductive behavior. Type III (PWT) characterizes the genus *Sympetrum*. FW_vT_s represented by *Diplacodes* could be a derivation from either PW_vT_s or FVS. At the present, there is no crucial evidence favoring either of these alternatives. But we adopt, for the time being, the second one by the following reasons: 1) Type P_fWT* assumed as a probable link between PWT and FW_vT_s is hitherto unrecorded. 2) Another instance of change P→F is suggested in another genus in the tribe, *Crocothemis* (FVG_s). 3) Possibility FVS→FW_vT_s is also realized in *Trameini*.

Trithemini: III→III₁ in the tribe presumably took the course FVS→FVG_s, than PVG_s→FVG_s, because, 1) Type P_fVG_s* is hitherto unrecorded. 2) Cases suggesting S→G are more frequent than those of P→F, supporting the appearance of the former easier than of the latter.

Trameini: Two independent trends, III (FVS)→III₂ (FW_vT_s) and III→III₃ (FWT') are assumed. Type T' is very peculiar and seemingly characteristic of *Tramea*. Svihla (1961) observed a similar behavior in *Pantala flavescens* as an exceptional instance. This species seems rather plastic in reproductive behavior, for Rokuyama (1961) observed tandem oviposition in early morning, replaced later by solitary oviposition. Therefore, the behavior formula of *Pantala* is expressed

Finally, a few words are given as to the factors contributing the evolution of reproductive behavior postulated above. Certainly several factors must have acted jointly for the realization of various behavioral types. As one of such probable factors, the importance of interference by males upon oviposition is pointed out, which has so far repeatedly been recorded and some instances were described in the present paper, too.

There are known several devices to avoid such interference: Segregation of diurnal activities, that is, oviposition made in the late evening after cessation of male activity (*Aeschna juncea* (Linné), Bartenev 1932; *Ischnura elegans*, Krieger and Krieger-Loibl 1958), seasonal segregation (*Aeschna nigroflava* Martin. Females appearing with a seasonal delay, Ubukata 1974), topographical segregation (*Cordulia a. amurensis*. Oviposition usually made at sites with dense emerged vegetation, Ubukata unpubl.), possession of threat display intimidating approaching males (*Ischnura* spp., op. cit.), submerged oviposition (*Calopteryx*, *Hetaerina* spp., op. cit.), etc.

While these cases represent the avoidance of male interference by solitary females, another course was chosen by a number of other groups, where the cooperation by the male partner played an important role, through either guarding or tandem oviposition. The efficiency of male guarding was confirmed by Jacobs (1955) and Arai (1972), and that of tandem oviposition is inferred from the rarity of triple connection (tandem by 1♀2♂♂) and separation caused by other solitary males. These two devices appeared independently in some groups, e.g. Tandem oviposition: Agrionidae, Platycnemididae, Lestidae, Aeschnidae (*Anax parthenope*), Corduliidae (*Somatochlora viridiaenea atrovirens* Selys, Taketo 1959), Epallagidae (*Bayadera brevicauda ishigakiana* Asahina, Ishida and Hamada 1973), Libellulidae, and Guarding: Calopterygidae, Hetaerinae, Gomphidae (*Ictinus clavatus* (Fabricius), Eda 1956), Corduliidae (*Hemicordulia ogasawarensis*), Libellulidae.

The evolution of such male protective behavior must be an outcome of interactions of various factors, both extrinsic and intrinsic. The interference by other males is indubitably an important extrinsic factor, which depends on the male density per habitat and average intensity of male sexual activity. As intrinsic factors a fine aerodynamic technique involving adjustment against the movements of female partner may be a prerequisite for tandem oviposition, and an established territoriality as well as maintenance of sexual motivation after copula (cf. *Hemicordulia*) for guarding. The clarification of the relative role of these factors must be regarded as an important part of the comprehensive bionomics of Odonata and its evolution.

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Summary

1) The reproductive behavior of nine forms of Odonata inhabiting the Bonin Islands was described, together with some additional chorologic data.

2) Territorial behavior was confirmed in *Hemicordulia ogasawarensis* Oguma, (Hovering type), *Pantala flavescens* (Fabricius) and *Tramea transmarina euryale* Selys (Cruising type), *Diplacodes bipunctatus* (Brauer) and *Boninthemis insularis* (Oguma) (Perching type). But *P. flavescens* did not show the attachment to territories in the area with ampler space. *Anax parthenope julius* Brauer behaved similarly, nevertheless its territoriality was recorded elsewhere.

3) The territorial behavior is very clear in *H. ogasawarensis*, and the defense against intruders is strong at the central part of the territory, while weaker at the periphery. Further, extra-aquatic territories were observed, some of which seemed to relate with mating but some others to feeding.

4) Mating and oviposition types of observed species were as follows: 1) Perching-Solitary. *Rhinocypha ogasawarensis* Oguma, *Ischnura senegalensis* Rambur, *A. parthenope julius*, *B. insularis* (?); 2) Perching-Guarded. *H. ogasawarensis* (New record to Corduliidae), 3) Aerial-Solitary. *P. flavescens*; 4) Aerial-Tandem. *D. bipunctatus*; 5) Aerial—Alternation of tandem and solitary. *T. t. euryale*. No courtship display was confirmed in the species observed.

Based upon these observations and those by other authors, the evolutionary course of mating-oviposition behavior in Libellulidae was tentatively presented.

5) Interspecific interference was observed among all anisopteran species, involving both mutual chasing between males and male interference to oviposition. No interspecific rank order was confirmed.

6) The rediscovery of some marked individuals was attempted. A conspicuous contrast was found between *H. ogasawarensis* and *D. bipunctatus*. The ratio of rediscovery was very high in the latter, certainly caused by its sedentary habit. The result also suggested a promiscuous relation in *D. bipunctatus*.

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- 1) Single asterisked: Papers written in Japanese.
 - 2) Double asterisked: Ditto, with English summary.
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