

**ENERGY EXPENDITURE IN PATROLLING MALES
OF *CORDULIA AENEA AMURENSIS* SELYS
(ANISOPTERA: CORDULIIDAE)**

N. ISHIZAWA

1644-15 Yamaguchi, Tokorozawa, Saitama, 359-1145, Japan
sieba4318@rivo.mediatti.net

Received June 16, 2006 / Revised and Accepted February 9, 2007

The ♂♂ hover frequently during patrolling flight, and fiercely chase rival ♂♂. Their patrolling flight was videotaped and analyzed. The average net-patrol flight speed (except hovering) was 161.6 ± 30.6 cm/s faster in the morning and the evening than during the day. Also, hovering frequency was more frequent and the duration of hovering bouts was longer in the morning and the evening than during the day, and was synchronized with patrolling flight speed. However, chasing flight was not related to patrolling or hovering and the duration of chasing bout was about 4-5 seconds with an average flight speed of 274.6 ± 64.7 cm/s. The body temperatures of patrolling flight and chasing flight were significantly different; the former, $39.8 \pm 1.4^\circ\text{C}$, the latter was $40.4 \pm 1.0^\circ\text{C}$. The time budget of patrolling males based upon video pictures was calculated and the relative energy expenditure of patrolling ♂♂ was estimated by standardizing the average net-patrolling flight speed as 1. Energy expenditure of the ♂♂ was greater in the morning and the evening than during the day. It is assumed that energy expenditure was affected by ambient temperatures, with ♂♂ changing the flight speed and duration of hovering. The ♂♂ are inferior in their sex recognition and it is assumed that their frequent hovering with concurrent large energy expenditure is to enable ♂♂ to distinguish ♀♀.

INTRODUCTION

According to a recent DNA analysis (JÖDICKE et al., 2004), *Cordulia aenea amurensis* Selys was considered as a species rather than a subspecies. However, since these authors noted that more sampling is required I shall consider *Cordulia aenea amurensis* as a subspecies in the far East of the range of *C. aenea*.

This dragonfly, of which the body length is less than 5 cm, is rather small for a 'flier type' (CORBET, 1962), and its hindwing is about 30 mm, which is shorter than that of *Sympetrum frequens*. There have been few reports made except for

those of UBUKATA (1975, 1983, 1984a, 1984b, 1986, 1987). According to him, the mature males patrol with frequent hovering parallel to the shoreline of the oviposition site of a pond. The flight style of the flier type dragonflies is said to be energetically more expensive than that of the percher type (CORBET, 1999; MAY, 1977, 1979, 1984), and the former are mostly large in size. However, *C. a. amurensis* is extremely small for a 'flier type'; therefore it may be disadvantageous for the dragonfly to patrol with frequent hovering, which is more expensive than ordinary forward flight (AZUMA & WATANABE, 1988).

This study deals with the energy budgets of ordinary forward flight, hovering and chasing of patrolling *C. a. amurensis* males based upon videotape data.

STUDY SITE, MATERIAL AND METHODS

STUDY SITE – Quantitative data were collected at Mizubasho Pond, a reservoir at Tokiwano, Hirosaki city, Aomori prefecture (Fig. 1). It has an area of 1 ha and is located at 410 m a. s. l., 40°37'N, 140°16'E. Investigations were conducted for twelve days on 6-9th of June 2004 and on 15-22nd of June 2005. Throughout the study period sympatric odonates were sighted at the pond; *Epi eca bimaculata sibirica |* (Selys), which is larger than *C. a. amurensis*, small sized *Trigomphus melampus* (Selys), *Orthetrum albistylum speciosum* (Uhler), *Libellula quadrimaculata asahinai* Schmidt and *Coenagrion lanceolatum* (Selys), as well as *C. a. amurensis*.

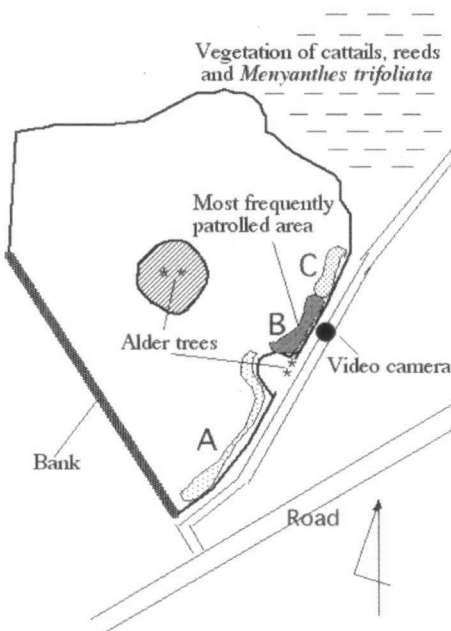


Fig. 1. Study site at the E bank of Mizubasho Pond. Patrolling site was composed of three areas; A was temporally patrolled, B was most frequently patrolled, and C was subordinately patrolled.

SIZE AND WINGLOADING – I marked 121 males on their wings with a silver felt-pen (Mitsubishi PX-21 Paint Marker) for the purpose of discrimination of individuals and took caliper measurements of the length of the thorax, abdomen and hindwing; also the height of the cross-section of the 3rd and 5th abdominal segments. They were then released. The same measurements were also made on males of sympatric *E. bimaculata sibirica* and *T. melampus*. The body weight of six males of *C. a. amurensis* was measured with an electronic balance to 0.001 mg within ten hours of collection.

Wingloading (WL) of the males was calculated using the same method as applied to *Pantala flavescens* (ISHIZAWA, 2007). Thus the forewings and hindwings were photocopied at 200%, and the same shapes as those photocopies were clipped out for weighing. Wing areas were calculated in proportion of the weights of the clipped areas to the weight of the fixed area (100 cm²) of a sheet of photocopy paper. WL was calculated by dividing the body weight by the wing area.

WINGBEAT FREQUENCY – I painted right hindwing tips with a silver felt-pen and

measured wingbeat frequency of the dragonflies, which were put horizontally on the ground, from the start of warm-up to taking off with a non-contact tachometer, CUSTUM, RM-2000 (measuring range: 30.0-30000 rpm, sampling time: 1.0-2.0 s).

VIDEOTAPING OF PATROLLING MALES – Patrolling flight of males along the shore was videotaped with a Panasonic NV-MX2000 3CCD digital camcorder at 60 fields/s (one frame is composed of two fields) at point B (Fig. 1), where females visited frequently, for five minutes on the hour from 7:00 to 18:00 except 9:00 on 20 June 2005. I counted population density (PD) at the site.

DEFINITION OF PATROLLING – *C. a. amurensis* males patrol with interposed frequent hovering. Patrolling flight of an interval of hovering is distinguished from patrolling flight with interposed hovering. The former is defined as net-patrol or net patrolling flight (NPT), and the latter as patrol or patrolling flight (PT).

FLIGHT VELOCITY, HOVERING DURATION AND CHASING DURATION – Flight speed of net-patrolling (NPV) males was calculated as follows: the distance of shift between 6-10th field from the start of forward flight of dragonflies in the pictures on the TV display (Fig. 2) ÷ the real length of dragonflies in the pictures × the average body length (4.86 cm) ÷ field number × 60. Duration of a hovering bout (DHV) was measured with a stopwatch on the slow motion video five times and the results were divided by 5.

Chasing flight speed (CHV) was calculated in the same way as for NPV at any point between several fields of the video pictures. Hovering frequency (HVF) and chase frequency (CHF) per minute during patrolling flight and the duration of chase bouts (CHD) were measured with a stopwatch during the observation period separately from the video monitoring. Duration of stay bout of the males at the patrolling site was measured with a stopwatch for the marked individuals.

The time budget for one second of chasing (CH), hovering (HV) and net-patrolling (NPT) was calculated as follows: the residual of (300 sec-CHF×CHD: gross chasing duration) was divided proportionally to gross hovering duration (HVF×HVD and gross net-patrolling duration (PTD) of the video monitored duration, then each result was divided by 300 (Tab. II).

RELATIVE ENERGY EXPENDITURE – I took the average NPV (161.6 cm/s) as 1 for the flight speed at which the duration of stay bout of patrolling males is maximal. The relative energy expenditure (REE) of patrolling dragonflies was estimated by the relative flight speed being substituted for x in the equation ($y = -0.095x^3 + 7.716x^2 - 14.773x + 14.883$), which was obtained from the figure of the curve of the necessary power presented by AZUMA (1986) (Fig. 3). The necessary power is the sum of induced, profile and parasite powers (AZUMA, 1986; NORBERG et al., 1993). The energy budget of each item per second was the time budget of each item × the result of the above estimation (Tab. III).

BODY TEMPERATURE – Body temperature (Tb) of dragonflies was measured by thrusting a Hoskins F-V-K-002 thermocouple (diameter, 0.05 mm) set in a hypodermic needle (external diameter 0.3 mm) and connected to a digital thermometer, John-Fluke, into the mezothorax just above the trachea within ten seconds after capture (see ISHIZAWA, 1998). Ambient temperature (Ta) at a height of one meter above the ground was measured with a digital thermistor thermometer soon after the measurement of Tb.

INCLINATION OF BODY AXIS DURING HOVERING – Inclination of body axis of dragonflies to the horizontal line in the pictures on the TV display was measured with a protractor. Vibration of the body axis over a few degrees during the inclination was observed and the angle was also measured on the TV display.

RESPONSE TO DUMMIES – Response to dummies (Fig. 4) was tested on males by changing the rotation speed (Hz), stopping rotation and attaching a black paper tube of 10 cm in length (5 mm in diameter).

STATISTICAL ANALYSES – Analysis of variance (ANOVA) was used to compare means of body sizes among sympatric dragonflies, and data between sexes or species were tested using a t-test. Least squares linear regression analyses were applied to the thermoregulatory data and quadratic or hyperbolic regression analyses applied to data relevant to CHD and HVF and CHF.

RESULTS

SIZE, WINGLOADING, WINGBEAT FREQUENCY AND REVISITING RATE

Table I shows the sizes of *C. a. amurensis*, *E. bimaculata sibirica* and *T. melampus*, and WL of *C. a. amurensis* males. Body size of *C. a. amurensis* was 48.6 ± 1.2 mm ($n = 17$) in the male and 46.3 ± 0.5 mm ($n = 2$) in the female and the size difference between sexes was significant ($p < 0.01$). Abdominal length was 34.3 ± 1.0 mm ($n = 8$) in the male, 34.6 ± 1.7 mm ($n = 4$) in the female; length of hindwing was 30.6 ± 0.8 mm ($n = 121$) in the male, and 30.3 ± 1.3 mm ($n = 4$) in the female but neither of these were significant between sexes (t-test, probability was $p < 0.7$ for abdominal length and $P < 0.8$ for hindwing length). However, the thoracic length was significantly different between sexes ($p = 2.26E-13$, t-test): 8.4 ± 0.3 mm ($n = 9$) in the male and 7.9 ± 0.4 mm ($n = 4$) in the female.

The body length of sympatric *E. bimaculata sibirica* males was 60.7 ± 2.0 mm ($n = 3$), abdominal length 42.4 ± 1.3 mm ($n = 5$), thoracic length 10.0 ± 0.3 mm ($n = 5$) and hindwing length 36.2 ± 1.4 mm ($n = 5$). In *T. melampus* the corresponding measurements were 43.4 ± 0.9 mm ($n = 10$); 32.8 ± 0.9 mm ($n = 10$); 7.0 ± 0.3 mm ($n = 10$); 25.1 ± 0.8 mm ($n = 11$). The length of each measurement was significantly different between the males of the three species (ANOVA-test, $p < 0.0001$).

The height of the abdominal segment of male *C. a. amurensis* was 2.9 ± 0.1 mm ($n = 10$) in the 3rd segment and 1.7 ± 0.1 mm ($n = 11$) in the 5th segment. In the female the heights were 4.6 ± 0.1 mm ($n = 2$), 2.4 ± 0.0 mm ($n = 2$), respectively. The corresponding measurements in *E. bimaculata sibirica* were 2.9 ± 0.2 mm ($n =$

Table I

Body size, wing area, weight and wing loading of sympatric *Cordulia aenea amurensis*, *Epithea bimaculata sibirica* and *Trigomphus melampus* at Mizubasho Pond at Tokiwano, Hirosaki, Aomori prefecture

Species	<i>Cordulia aenea amurensis</i>		<i>Epithea bimaculata sibirica</i>	<i>Trigomphus melampus</i>
	male	female	male	male
Body (mm)	48.6 ± 1.2 (17)	46.3 ± 0.5 (2)	60.7 ± 2.0 (3)	43.4 ± 0.9 (10)
Thorax (mm)	8.4 ± 0.3 (9)	7.9 ± 0.4 (4)	10.0 ± 0.3 (5)	7.0 ± 0.3 (10)
Abdomen (mm)	34.3 ± 1.0 (8)	34.6 ± 1.7 (4)	42.4 ± 1.3 (5)	32.8 ± 0.9 (10)
Height of 3rd segment (mm)	2.9 ± 0.1 (10)	4.6 ± 0.1 (2)	2.9 ± 0.2 (4)	2.3 ± 0.1 (10)
Height of 5th segment (mm)	1.7 ± 0.1 (11)	2.4 ± 0.0 (2)	2.2 ± 0.1 (4)	1.4 ± 0.1 (10)
Hindwing (mm)	30.6 ± 0.8 (121)	30.3 ± 1.3 (4)	36.2 ± 1.4 (5)	25.1 ± 0.8 (11)
Wing area (cm ²)	9.2 ± 0.4 (6)	-	-	-
Weight (mg)	293.7 ± 9.2 (6)	-	-	-
Wing loading (mg/cm ²)	31.9 ± 1.9 (6)	-	-	-
Wing-beat frequency (Hz)	30.0 ± 6.2 (25)	28.4 ± 4.6 (2)	-	-

4), 2.2 ± 0.1 mm ($n = 4$) and in *T. melampus* they were 2.3 ± 0.1 mm ($n = 10$), 1.4 ± 0.1 mm ($n = 10$). The height of both segments was significantly different among the three species (ANOVA-test, $p < 0.001$) except that there was no significant difference in the height of the 3rd segment between males of *C. a. amurensis* and *E. bimaculata sibirica*.

The wing area of *C. a. amurensis* males was 9.2 ± 0.4 cm² ($n = 6$), the body weight was 293.7 ± 9.2 mg ($n = 6$) and the wingloading was 31.9 ± 1.0 mg/cm² ($n = 6$). As it took about ten hours for me to measure the specimens at home after capturing them early in the morning at the observation site, the body weight might have decreased by 10%, and the real WL might have been ca. 35 mg/cm².

Wingbeat frequency during warming-up was 30.0 ± 6.2 Hz (range: 18.3–42.5 Hz, $n = 12$) in the male and 28.4 ± 4.6 Hz (range, 25.2–31.7 Hz, $n = 2$) in the female. The wingbeat frequency was rather higher in the male than in the female, however there was no significant difference between the sexes ($p < 0.4$, t-test). The average wingbeat frequency at take off in the male was 27.2 Hz.

The revisiting rate of 121 marked males was 59.5% ($n = 72$), and the revisiting frequency was 155; the average revisiting time was 22 and the revisit rate of marked individuals that revisited more than twice a day was 30.5% (22/72). Nine individuals revisited more than three times a day and the maximum frequency observed was five times a day. Among the marked individuals, there were those of which Tbs were measured; hence, there was a possibility of an impediment to patrol flight due to punctures of the thermo-couple probe. However, the revisiting rate was not significantly different between the measured group and non measured group (measured group, 66.7%, 38/57; non measured group, 51.6%, 33/64, $P > 0.05$, chi-square test). Also, there was no significant difference between duration of stay bouts in the two groups, 15.8 ± 7.9 min ($n = 16$) in the measured group and 16.7 ± 6.4 min ($n = 23$) in the none measured group; $P < 0.8$, t-test).

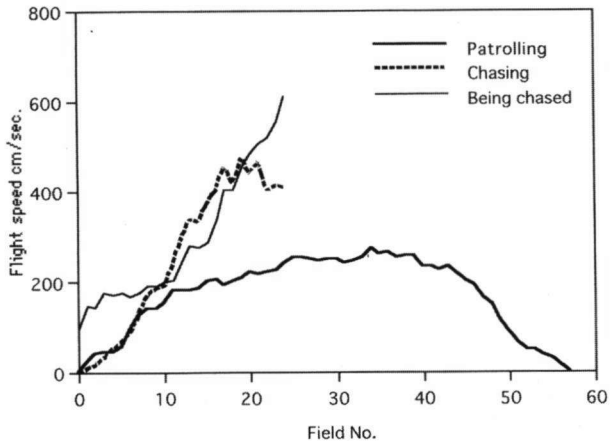


Fig. 2. Changes of flight speed in net-patrolling (NPT) and chasing *Cordulia aenea amurensis* males. Flight speed was analyzed based on video-taping at Mizubasho Pond on 6 June 2006. Patrolling: 7:00:38 a.m., field No. 1-57; – chasing and being chased: 8:06 a.m., field No. 1-25.

PATROL, HOVERING AND CHASE

The shore line on the east side of the pond was short, ca 45 m, and the maximum population density (PD) was three during observation by video-monitoring (maximum density was five for other hours). Patrolling flight was concentrated at B area (Fig. 1), of which distance was ca 13 m. Males patrolled along the shore at a height of 20-30 cm, and repeated round-trip flight with frequent hovering within the patrolling area. When males encountered rival males on the border of the area, after stopping face to face for a moment, they used to violently chase the rivals.

In one case, one male of *C. a. amurensis* appeared at the ovipositing site before sunrise at 4:30 a.m. (Ta, 15.8°C) on 22 June 2006. Another male appeared even at the low Ta of 12.7°C at 5:42 a.m. on 9 June 2004. Sunrise is late at the pond because it is obstructed by the ridge of Mt. Iwaki-san, and it is ca. 5:00 a.m. when the sun shines on the pond. Males usually appeared later than this time, i.e. at ca 5:40 a.m. Males were sighted patrolling in slight rain. However, when it had rained on the previous day and Ta was low, in the next morning males did not appear until 9:00.

The latest time of disappearance was 18:37 p.m. (Ta, 19.5°C) on 19 June 2005, and even when Ta was high males sometimes disappeared. Also, even it was early for their disappearance but Ta was around 16°C at 17:00 p.m., they disappeared.

Table II

Statistical data on patrolling *Cordulia aenea amurensis* males by the time. Data were obtained at Mizubasho Pond at Tokiwano, Hirosaki, Aomori prefecture by video-taping for five minutes/hour from 7:00-18:00 (except 9:00) on 20 June 2006. [Ta=ambient temperature; CHF=chase frequency; CHD=duration of chase bout (sec), calculated by the equation of $CHD = -0.049x^2 + 2.066x - 16.943$; $x = Ta$, $r = 0.605$, $p < 0.05$, $n = 11$; CHV=chase flight speed (cm/s); HVF=hovering frequency; HVD= duration of a hovering bout (s); PTF= frequency of patrol; PTD=gross duration of net-patrol in monitoring (s), NPV=net-patrol flight speed (cm/s); PD=population density at the observation site; AVG=average; s.d.=standard deviation; $AVG \pm s.d.$; *=total]

Hour	Ta	CHF	CHD	CHV	HVF	HVD	PTF	PTD*	NPV	PD
7:00	21.7	7	4.8	247.4	45	1.2±0.7	25	31.2	168.8±32.0	3
8:00	21.3	10	4.8	254.0±48.1	30	1.1±0.5	24	54.6	162.1±21.8	2
10:00	23.6	11	4.5	233.4±45.8	33	0.8±0.5	27	61.4	146.7±21.6	3
11:00	23.8	3	4.5	258.9±49.0	46	1.0±0.5	30	40.6	136.0±16.1	3
12:00	24.2	8	4.4	277.0±66.8	55	0.7±0.3	37	46.4	152.5±27.0	2
13:00	23.4	10	4.6	272.2±67.4	31	0.9±0.6	16	56.6	145.9±34.1	2
14:00	23.3	17	4.6	266.9±81.0	55	0.9±0.6	38	32.9	160.8±28.0	3
15:00	22.5	3	4.7	240.7±20.9	34	1.0±0.8	28	44.0	167.6±30.8	1
16:00	22.6	8	4.7	314.5±43.6	39	1.2±0.9	30	27.2	178.1±29.2	2
17:00	21.3	20	4.8	316.3±64.4	51	1.0±0.5	41	23.3	183.7±28.6	2
18:00	21.1	0	-	-	13	1.1±0.6	8	57.6	184.4±12.3	1
AVG	22.7±1.1	97*	4.7	274.6±64.7	432*	1.0±0.6	304*	475.8*	161.6±30.6	24*

Figure 2 and Table II show the results of the analysis of videotaping patrolling flight of *C. a. amurensis* males. As far as the figure of analyzed flight speed of the video is concerned, NPV and CHV seem irregular, even if analysis errors are permitted. Particularly in chasing flight, chasing males seemed to change their own flight speed by corresponding to that of rivals.

Figure 5 shows the relation of NPV to T_a . The average NPV was 161.6 ± 30.6 cm/s ($n = 245$, range: 81.0-265.7 cm/s), and the flight speed was faster in the morning and the evening at low T_a than in the daytime with high T_a . In a multiple correlation coefficient of NPV on T_a and PD, NPV showed higher correlation on T_a than on PD (T_a , $p = 0.0122$, PD, $p = 0.301$, $F = 0.00902$)

The average HVD was 1.0 ± 0.6 s (range: 0.2-4.0 s, $n = 364$), and showed high

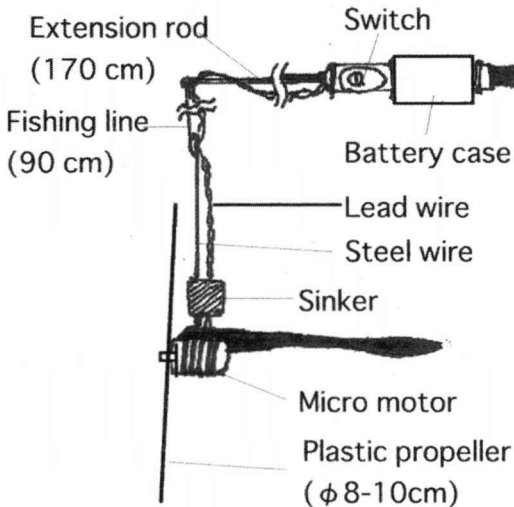


Fig. 4. Dummy used for the test of response of patrolling males.

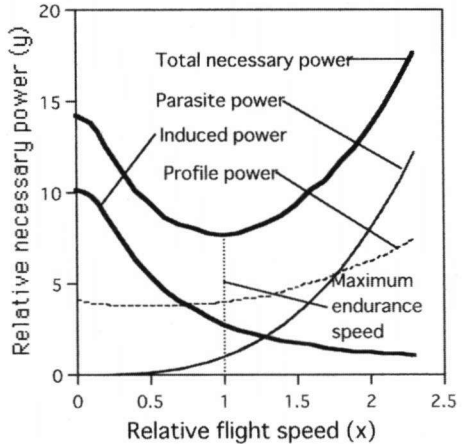


Fig. 3. Curves of the power required for the flight of fluttering creatures. (Modified from AZUMA, 1986). The equations are as follows: induced power (a): $y = -1.095x^3 + 6.524x^2 - 13.468x + 10.791$ $r = 0.998$; - parasite power (b): $y = 1.000x^3$; - profile power (c): $y = 1.192x^2 - 1.305x + 4.092$ $r = 0.999$; - necessary power (a+b+c) $y = -0.095x^3 + 7.716x^2 - 14.773x + 14.883$.

correlation with T_a ($p < 0.02$), but low to PD ($P > 0.5$) (Fig. 6). Also, the hovering frequency per minute showed significant correlation with T_a (23.5 ± 4.8 /min; $n = 35$, $r = 0.459$, $p < 0.01$). The average patrolling flight speed, including hovering (PTV), was estimated by the time budgets of hovering and patrol (Tab. III); $(NPV \times (PT \div (HV + PT)))$; it was 85.7 cm/s (range: 60.2-148.0 cm/s).

Chasing flight speed (CHV) was 274.6 ± 64.7 cm/s (range: 162.0-500 cm/s, $n = 86$), and the fastest CHV exceeded more than 3 times as NPV

Table III

Time budgets and relative energy expenditure (REE) per second of patrolling *Cordulia aenea amurensis* males. [CH=chase; HV=hovering; NPT=net patrol; time budget was estimated as follows; CH=CHF×CHD÷300; HV=(300-CH)×(HVF×HV)÷(PTD+HV×HVF)÷300; NPT=(300-(CH+HV))÷300; relative flight speed=CHV÷161.6 or NPV÷161.6; REE was estimated by the each time budget×each value per second calculated by the equation shown in Fig. 3; $y=-0.095x^3+7.716x^2-14.773x+14.883$, x =relative flight speed]

Hour	Time budget (s)			Relative flight speed		Relative energy expenditure (s)			Total
	CH	HV	NPT	CHV	NPV	CH	HV	NPT	
7:00	0.11	0.57	0.32	1.53	1.04	1.1	8.5	2.5	12.1
8:00	0.16	0.32	0.52	1.57	1.00	1.7	4.8	4.0	10.4
10:00	0.17	0.25	0.58	1.44	0.91	1.6	3.7	4.5	9.8
11:00	0.04	0.50	0.46	1.60	0.84	0.5	7.4	3.6	11.5
12:00	0.12	0.39	0.50	1.71	0.94	1.4	5.8	3.8	11.0
13:00	0.15	0.27	0.57	1.68	0.90	1.7	4.1	4.5	10.3
14:00	0.26	0.45	0.29	1.65	1.00	2.9	6.7	2.3	11.8
15:00	0.05	0.43	0.53	1.49	1.04	0.5	6.4	4.1	10.9
16:00	0.13	0.56	0.31	1.95	1.10	1.8	8.4	2.5	12.7
17:00	0.32	0.46	0.22	1.96	1.14	4.8	6.9	1.7	13.4
18:00	0.0	0.20	0.80	-	1.14	0.0	2.9	6.4	9.3
AVG	0.14	0.41	0.46	1.70	1.00	1.7	6.0	3.6	11.3
(%)	13.7	40.6	45.7			15.0	53.1	31.9	100.0

(Fig. 2). However, CHV showed no correlation to Ta and PD ($r = 0.323$, $p < 0.5$; Fig. 5). The average duration of a chasing bout (CHD) was 4.1 ± 2.8 s (range: 0.9–17.0 s, $n = 180$), and it was significantly correlated with Ta ($r = 0.605$, $p < 0.05$, $n = 11$). CHD was short at low Ta and high Ta. However, at Ta of ca 20°C it tended to be extended (Fig. 7). Chasing frequency (CHF) was 1.9 ± 2.0 /min, range: 0–8, $n = 34$, and it increased as Ta rose, showing significant correlation with Ta ($r = 0.555$, $P < 0.01$).

Figure 8 shows the relationship of CHF to HVF. The same individual cannot simultaneously chase and hover and, therefore, the relationship between the two is a trade off and they differed significantly ($r = 0.721$, $p < 0.0001$).

The average duration of stay of males at the site was 16.0 ± 7.0 min (range: 1.3–30.4 min, $n = 41$), and this showed a low correlation to Ta ($r = 0.256$, $P < 0.1$). There were cases when females appeared early in the morning and late in the evening, but there was no regularity in their appearance. The earliest observation of oviposition was at 4:30 a.m. at Ta 15.2°C on 22 June 2005 and the latest was 18:11 p.m. at Ta 16.5°C on 18 June 2005. The lowest Ta during oviposition was 14.2°C (05:28 a.m. on 16 June 2005). The average duration of stay of females at the oviposition site was 36.5 ± 16.5 s (range: 18–49.6s, $n = 3$) and the duration measured from halfway through oviposition in five females exceeded one minute and in one female of them exceeded two minutes.

RELATIVE ENERGY EXPENDITURE

Table III shows time budgets per second of net-patrolling flight, hovering and chasing flight and energy budgets of the same items that were calculated by the relative flight speed. Each time budget per second was 0.46 s (45.7%) for NPT, 0.40 s (40.6%) for HV and 0.14 s (13.7%) for CH. The time budget was balanced between HV and NPT, being rather larger in the latter than in the former. CH decreased at times of wind (11:00 and 15:00) or at low PD (18:00). When rival males did not exist at the shore (e.g. 18:00), hovering interval and patrol distance were extended.

Relative energy budgets per second were 3.6 (31.9%) for NPT, 6.0 (53.1%) for HV and 1.7 (15.0%) for CH, with hovering energy clearly the largest. Each elasticity of energy budget to the change of 1% of each time budget was 0.7 for NPT, 1.3 for HV and 1.1 for CH. Elasticity was the largest in HV, and the second was CH and NPT was the smallest among them. This suggests that hovering is largest in energy expenditure.

The correlation of gross REE of duration of stay bout with HVD, CHV, NPV, Ta and PD was significant ($r = 0.932$, $F = 0.029$), and the most effective factor was HVD (regression coefficient = 2203.955, $P = 0.349$), followed by PD (543.609, $P = 0.218$), Ta (339.554, $p = 0.457$), NPV (68.095, $p = 0.043$), with CHV the least effective (10.432, $p = 0.022$), REE differed significantly among hours (chi-square test, $p < 0.001$).

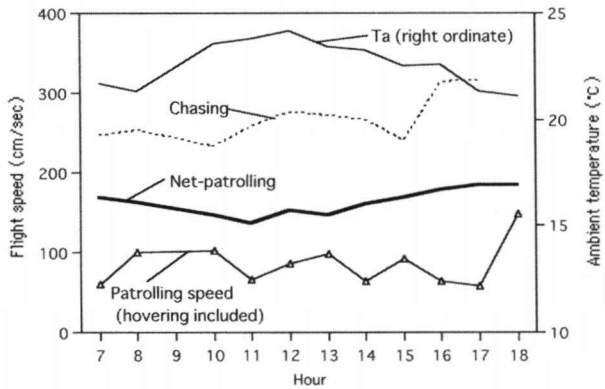


Fig. 5. Changes of flight speed in NPT males and ambient temperature. The equation of least squares linear regression of the flight speed in NPT males on to ambient temperature and population density was $y = -10.008x_1 - 5.122x_2 + 399.968$ $r = 0.831$, $p_1 = 0.012$, $p_2 = 0.301$, $F = 0.009$.

BODY TEMPERATURE

Table IV and Figure 10 show the data for Tb of *C. a. amurensis* and Ta. The average Tb of patrolling males was $39.8 \pm 1.4^\circ\text{C}$ (range: $37.2\text{--}42.2^\circ\text{C}$, $n = 39$) and that of chasing males was $40.4 \pm 1.0^\circ\text{C}$ (range: $38.8\text{--}42.6^\circ\text{C}$, $n = 39$), with the difference of between the two groups significant ($p < 0.05$, $t = 2.231$). Also comparing Tbs among both groups and the females ($41.8 \pm 1.0^\circ\text{C}$, range: $40.9\text{--}42.7^\circ\text{C}$, $n = 4$), Tb

of females was significantly different from those of male groups ($p < 0.01$, ANOVA-test). T_a of each group measured soon after T_b was measured was not significantly different among the groups ($p < 0.7$, range: 14.1–28.5°C, ANOVA-test). I had a chance to measure T_b of a chasing male soon after it bathed in the water at 12:22 p.m. on 17 June 2005, and its T_b was 39.5°C (T_a 21.3°C). The T_b of the male might well have exceeded 40°C just before bathing in the water.

Most of females were captured during oviposition, so that the T_b of females tended to be high. Even in the evening at low T_a , one female was sighted bathing in the water on the way back to her roosting site after oviposition. Probably it might have been due to high T_b by the large energy expenditure of hovering and ejection of eggs (ISHIZAWA, 1998).

I could not collect quantitative data on T_b of hovering, because HVD was short, ca 1 s. However, I was able to measure one male that hovered for 10 s. Its T_b was 42.2°C (T_a 21.1°C). There was only one case when the T_b of a patrolling flight exceeded 42°C at a lower T_a than this. Accordingly, it was assumed that hovering produced large metabolic heat.

The correlation coefficient and regression coefficient of T_b to T_a were 0.1450 and 0.068 in the patrolling flight, respectively and 0.669, 0.242 in the chasing flight, respectively; each coefficient was clearly larger in the latter than in the former in both types of flight.

HOVERING

Figure 11 shows the hovering posture of a *C. a. amurensis* male. The dragonfly males usually hover toward the shore of the pond or in the forward direction. During hovering males often incline their body axis forward at an angle of $19.7 \pm 3.1^\circ$ (range: 12–23°, $n = 20$). Moreover, vibration of the abdomen (perhaps body axis) at a few degrees (ca 3–5°) was observed when their body axis was inclined. When the wind blew, males hovered against the wind. However, when

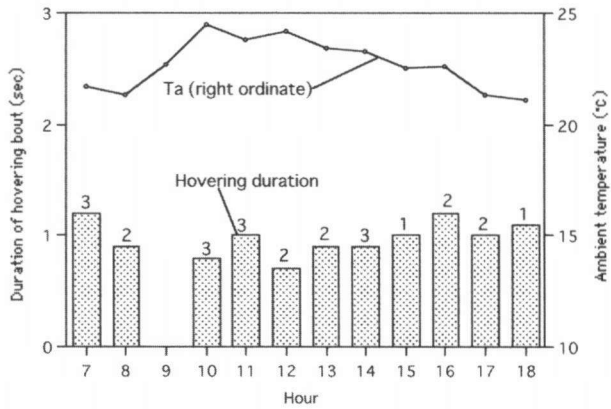


Fig. 6. Changes of duration of a hovering bout (HVD) and ambient temperature. The equation of least squares linear regression of HVD in patrolling males on to ambient temperature and population density was $y = -0.127x_1 + 0.044x_2 + 3.777$ $r = 0.726$, $p_1 = 0.019$, $p_2 = 0.521$, $F = 0.050$.

the wind blew towards the shore from the center of the pond, males could not hover towards the shore, and they hovered toward the center of the pond, presumably to prevent stalling, and HVD tended to be extended a little longer (see data of 11:00 in Tab. II). In this case, air-speed increases so that energy expenditure is saved by the wind. Particularly sympatric *Epitheca bimaculata sibirica* males avoided stalling in the tailwind by hovering during patrolling towards the shore, and disappeared often. Accordingly, interference to *C. a. amurensis* males by the dragonflies decreased, so the energy expenditure for chasing flight to *Epitheca bimaculata sibirica* males seemed to decrease.

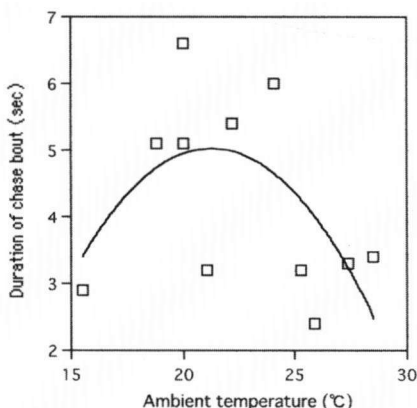


Fig. 7. Relationship of duration of a chase bout (CHD) to ambient temperature. Solid line is the quadratic regression, CHD, $y = -0.049x^2 + 2.066x - 16.943$, $r = 0.605$, $p < 0.05$, $n = 11$.

RESPONSE TO DUMMIES AND OTHER SPECIES BY MALES

Table V shows the response frequency (RF) (RF for each 30 times of test) of *C. a. amurensis* males to a stationary or rotating dummy. As the heads or abdomens of the males were often cut by rotating propellers, each test was restricted to 30 times.

When the dummy was stationary no males responded to it, regardless of the presence of the long tube. In the dummy with an 8 cm propeller, the difference of RF to the presence or absence of the long tube was not significant (attached, RF 20 at 50.8 Hz; not attached, 25/51.7 Hz). Also, RF differed little over a range of rotation speed between 21.5 Hz and 40 Hz.

When a live male was hung from a fishing rod no male responded even when it was swung up and down like an ovipositing female, unless it fluttered. When

the dummy was rotated RF tended to increase with the rotation frequency ($r = 0.954$, $p < 0.0001$, $F = 5.0322E-05$).

In encounters *C. a. amurensis* males often chased sympatric males of *E. bimaculata sibirica* and *T. melampus* and dogfights were seen

Table IV
Body temperatures of both sexes of *Cordulia aenea amurensis* by the phase. Data were obtained at Mizubasho Pond at Tokiwano, Hirosaki, Aomori prefecture 15-22 June 2005

Sex Phase	Male		Female
	Patrolling	Chasing	Ovipositing
N	39	39	4
Tb (AVG±s.d.)	39.8±1.4	40.4±1.0	41.8±1.0
Range of Tb	37.2-42.2	38.8-42.6	40.9±42.7
Ta (AVG±s.d.)	21.5±3.1	22.0±2.7	22.3±0.9

between the *C. a. amurensis* and *E. bimaculata sibirica* males like an intraspecific conflict, but CHD was shorter than for intraspecific fights. Interspecific conflict with *T. melampus* was observed on six occasions over three days, and *C. a. amurensis* males pursued both males and females of *T. melampus*, and often tried to copulate with them. When this occurred, 'pairs' often fell into the water.

FORAGING

Foraging in *C. a. amurensis* at the patrolling site was rarely sighted, as UBUKATA (1975) indicated, in spite of abundant midges at the site. However, foraging was observed early in the morning at 4:40 a.m. (T_a , 14.9°C) on 22 June 2005 before sunrise and at low PD of 2.

DISCUSSION

Foraging was rarely sighted at the patrolling site, as UBUKATA (1975) noted, hence patrolling can be regarded as mate searching. He also noted that patrol flight speed (PTV) was fast, however, the estimated PTV was slow, ca 0.5 m/sec (UBUKATA, 1987). The PTV of my data was 85.7 cm/s, 1.7 times that recorded by Ubukata. Net patrol flight speed (NPV) differed in the morning and the evening compared to the daytime, and exhibited higher correlation with T_a than PD at

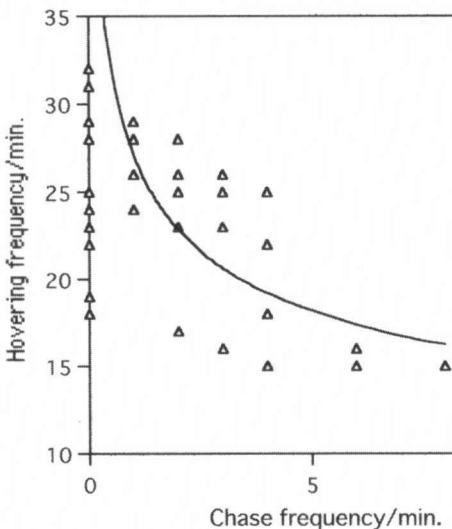


Fig. 8. Relationship of hovering frequency (HF) to chase frequency (CHF) per minute in males. Dashed line is the hyperbolic regression, $y=27.188x^{-0.249}$, $r=0.721$ $p<0.0001$, $n=35$.

the patrolling site. MAY (1995) indicated that patrol flight speed was influenced by T_a , and *Anax junius* controlled metabolic heat production by adjusting flight speed and wing-beat frequency according to T_a , and that heat production was inversely proportional to T_a . Also, KAISER (1976) noted that the flight style of *Aeshna cyanea* was influenced by T_a . In *C. a. amurensis*, males seemed to maintain T_b at low T_a by active metabolic heat production with speeding up by seemingly high wingbeat frequency. However, high-speed flight at low T_a robs the body surface of T_b and this may be compensated by hovering. HVD and HVF seemed to increase as T_a declined. The hovering interval seems to be influenced by PD at the patrolling site, and when

rival males decreased at low Ta (shown at 14:00-15:00 in Fig. 6, Tab. II), hovering interval and patrolling distance were extended, with HVF being increased.

As Ta declined CHV increased and CHD showed a high correlation with Ta. However, time budget (13.7%) and energy expenditure (15.0%) for CH were not so large. The largest was for hovering, which had a share of more than 50% (53.1%) of the energy requirement. Comparing energy expenditure per unit time among items of patrol flight, HV of *C. a. amurensis* males was 1.9 times that of NPT. In *Anax parthenope julius* (AZUMA & WATANABE, 1988) HV was 2.3 times that of NPT (NPV, 170 cm/s), and this species does not hover more frequently than *C. a. amurensis*. As this species hovers more frequently than other flier type dragonflies, the energy expenditure naturally becomes large.

Then, why does this small flier type dragonfly conduct hovering when the energy expenditure is so great? MILLER (1982) noted that periodic stationary hovering allows visual fixation to occur, improving discrimination and a better chance of seeing ovipositing females in the shaded regions. As CORBET (1999) noted that the visual field of dragonflies is almost 360° and has wide visual range, *C. a. amurensis* males may easily find ovipositing females. But as a matter of fact, they often could not find females ahead downward of them. Such a case was often seen also in *Anotogaster sieboldii* males, that could not recognize females ovipositing behind a fallen tree when they flew over the tree (Ishizawa, pers. observ.). Consequently, males *C. a. amurensis* and *A. sieboldii* seemingly have narrow visual fields, particularly of ahead downward. I consider that dragonflies have outstanding kinetic vision but not good resolving power.

In hovering *C. a. amurensis*, males incline their body axis at ca. 20° perpendicular to the horizon. CORBET (1999) argued that such body axis inclination is a display to females and a function of embellishment of the patrol flight. However, I suppose that this widens visual field of ahead downward.

Also, the forward inclination of body axis enables the instantaneously forward

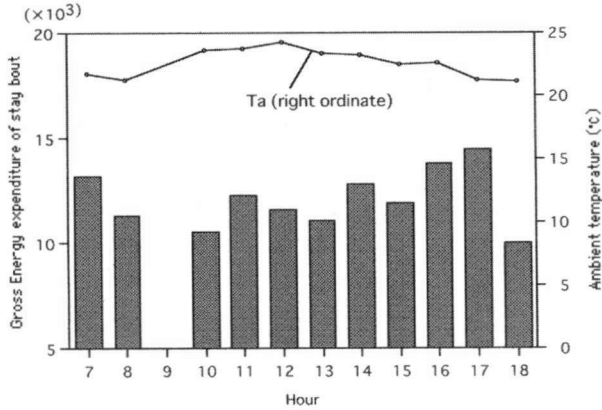


Fig. 9. Changes of gross relative energy expenditure (GRE) for the stay bout of males. The multiple regression coefficient of GRE on HV (x_1), CHV (x_2), NPV (x_3), Ta (x_4) and PD (x_5) was significant ($p < 0.05$); $-y = 2203.955x_1 + 10.432x_2 + 68.095x_3 + 339.554x_4 + 543.609x_5 - 12559.861$, $r = 0.932$; $-p_1 = 0.349$, $p_2 = 0.022$, $p_3 = 0.0432$, $p_4 = 0.457$, $p_5 = 0.218$, $F = 0.029$.

flight of the males. A helicopter inclines its body forward when it starts forward flight from hovering, therefore, the forward inclination of body axis has two merits: widening of the visual field and instantaneous forward flight. The reason for the vibrations of 3-5° is not yet clear.

Hovering was correlated with Ta and, as mentioned above, when rival males did not occur at the site, males conducted long intervals of hovering and long distant patrol flight, and this brought skew of energy expenditure to patrol flight. This suggests that hovering may be a behaviour of consciousness of rival males. UBUKATA (1975) noted the non-localized patrol flight, which seems to be a 'long distance type' different from the normal type. As energy expenditure of net-patrol flight (NPT) is half that of hovering, the duration of stay of patrolling males may be extended. However, NPV is influenced by Ta and even if HF decreases, HVD is extended, so that the duration of stay may not be extended so long.

Also it may be assumed that HV decreases encounters of males with rival males but it has a higher energy expenditure per unit time than CH. However, parasite power works at CH, and this is proportional to the cube of CHV. Hence, as the CHV increases, energy expenditure increases geometrically. When the average CHD at 22.7°C is 4.7 s, the energy expenditure corresponds to 3.8 times that of HV. Converting this into the time of usual patrolling flight, this corresponds to 5.1 s of patrolling flight; 2.8 s for NPT and 2.3 s of HV, rather extending 0.4 s (8.5% of CHD) of the duration of stay. If CH continues for two seconds at the 5 m/s of CHV, the energy expenditure would be 5.4 times that of HV for one second, and corresponds to 7.3 s of PT.

There is a problem as to whether a *C. a. amurensis* male can discriminate the sexes of the intraspecies or not. MOORE (1952) stated that the territories of dragon-

Table V

Response frequency to the dummy of various rotation velocities of the propellers of different sizes. Each experiment was tested 30 times. The paper tube, which was 10 cm in length and 0.5 cm in diameter and was painted black, was set behind the motor of the dummy in the case of "attached"

Size (cm)	Rotation velocity (Hz)	Paper tube	Response frequency
8	50.8	attached	20
8	51.7	not attached	25
8	30.8	not attached	14
10	40.0	not attached	20
10	21.5	not attached	18
8	0	attached	0
8	0	not attached	0
10	0	attached	0
10	0	not attached	0

* The response frequencies among the phases of rotating and stationary were significant (Chi-square test, $p < 0.001$).

flies differ from those of birds, and the behaviour with respect to rival males is the same as that of males to females, and that clashes between males do not seem to be due to aggressive behaviour. *C. a. amurensis* males were often observed chasing the larger *E. bimaculata sibirica*, and the small *T. melampus*, and attempting to copulate with the latter. UBUKATA (1975) described the frequent attempts at interspecific copulation, and (UBUKATA, 1983) noted that the fat and long abdomen and the up-and-down movements of ovipositing females could be cues for recognition of females by the males. Nevertheless, my experiment on *C. a. amurensis* males indicates that such an external morphology or a movement could not be the significant cues. UBUKATA (1983) noted that a male could not detect a motionless female.

(A shortcoming of his experiment is the circumstance that he did not use dead specimens). Wing fluttering is the crucial releaser of female recognition in this species and also in *A. sieboldii* (ISHIZAWA, 2005; ISHIZAWA & ARAI, 2003). The fat abdomen or the swinging similar to the oviposition behaviour had no significance. Recognition of females by males only occurs when the former flutter. The response by *C. a. amurensis* males to the propeller rotation of the dummy suggests that males could not distinguish between dummy males and females, and that the chasing flight did not mean exclusive attack to rival males. Some dragonflies, such as male *Leucorrhinia dubia*, have the ability of sexual recognition and attack rival males (PAJUNEN, 1964), while in *C. a. amurensis* such recognition behaviour has been misidentified as attack.

Thus, chasing rival males can be regarded as a waste of energy, and patrolling interspersed with hovering is most profitable for distinguishing females. Hovering is a function of extension of the duration of stay by avoiding waste of energy. Hence, it can be said that *C. a. amurensis* males maximize duration of stay at the patrolling site by controlling NPV, HVD and HVF according to T_a and by extending patrol distance at low PD.

UBUKATA (1986) discussed the mate searching strategy of *C. a. amurensis* males and the profit or loss of returning to the border of the territory by using

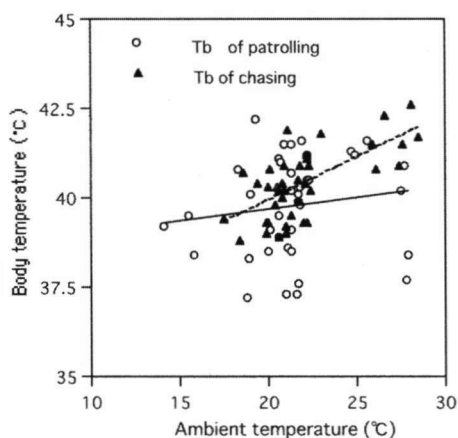


Fig. 10. Relationship of T_b to T_a in chasing and patrolling males. The thin line indicates the linear regression of T_b to T_a in chasing flight; the heavy line patrolling flight. Chasing $T_b = 0.242T_a + 35.076$, $r = 0.6689$, $p < 0.001$, $F = 3.2427E-06$, $n = 39$; patrolling $T_b = 0.068T_a + 38.326$, $r = 0.150$, $P < 0.5$, $F = 0.363$, $n = 39$. The difference of average T_b between chasing males and patrolling males were significant (t-test $p < 0.05$, $t = 2.231$, $df = 68$).

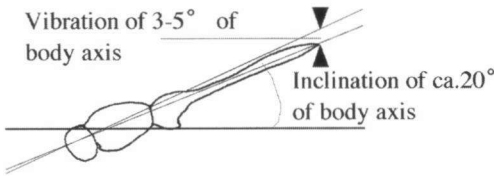


Fig. 11. Inclination of body axis in a hovering male. Average slope of degree was $19.7 \pm 3.1^\circ$ ($n=20$).

the inequality of $D > (\sqrt{2}-1) CV$ or $D < (\sqrt{2}-1) CV$ (where the visual range of the male = D , the flight speed of the male = V and the duration of oviposition bout by the female = C). He determined the former as Type I, which might gain a profit of maximal mate searching success

by the patrol of round trip, while his Type II might do so by the patrol of straight flight and considered *C. a. amurensis* was the latter type. But *C. a. amurensis* adopts actually a round trip flight and it should be regarded as Ubukata's Type I. In my opinion, the returning on the border of the territory or flying over the border by extending patrol distance are all profitable because the returning to the border decreases encounters with rival males and avoids the waste of energy expenditure; consequently, the duration of stay is extended. Flying over the border extends the duration of stay by saving energy expenditure due to decreasing of HVF. As long as the male ability to recognize the sexes is weak, the visual range of the male is not significant for the condition of mate searching; even if it were allowed, it would be useless because an exhausted male cannot seize a female when she comes within his visual range. Thus, the prolonged stay of the male at the oviposition site by minimizing energy expenditure is the optimum for mate searching, and most of the dragonflies (both fliers and perchers) may adopt this strategy. In percher males, perching and waiting for females at an optimal post is the most advantageous way of maximization the duration of stay. Also, in several *Sympetrum* species and in *P. flavescens*, both sexes act always together, and this may be the most praiseworthy strategy for mate searching.

ACKNOWLEDGEMENTS

I wish to acknowledge the kindness of Mr H. NARAOKA, who provided information on the locality and helped at the observation site. Thanks are also due to Dr A. AZUMA for access to his publications and to Dr Y. TSUBAKI for his useful advice on thermoregulation.

REFERENCES

- AZUMA, A., 1986. *Those magnificent motions of creatures*. Kyoritsu Shuppan, Tokyo.
 AZUMA, A. & T. WATANABE, 1988. Flight performance of a dragonfly. *J. exp. Biol.* 137: 221-252.
 CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
 CORBET, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Cornell Univ. Press, New York.
 ISHIZAWA, N., 1998. Thermoregulation in *Sympetrum frequens* (Selys), with notes on other Sym-

- petrum species (Anisoptera: Libellulidae). *Odonatologica* 27(3): 317-334.
- ISHIZAWA, N. & Y. ARAI, 2003. The response to rotating objects by *Anotogaster sieboldii* (Selys) males (Anisoptera: Cordulegastridae). *Odonatologica* 32(1): 19-28.
- ISHIZAWA, N., 2005. The response to rotating objects by *Anotogaster sieboldii* (Selys) males, pt 2 (Anisoptera: Cordulegastridae). *Odonatologica* 34(3): 211-218.
- JÖDICKE, R., P. LANGHOFF & B. MISOF, 2004. The species group taxa in the Holarctic genus *Cordulia*: a study in nomenclature and genetic differentiation (Odonata: Corduliidae). *Int. J. Odonatol.* 7(1): 37-52.
- KAISER, H., 1976. Quantitative description and simulation of stochastic behaviour in dragonflies (*Aeschna cyanea*, Odonata). *Acta biotheor.* 25: 163-210.
- MAY, M.L., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus *Micrathyria*. *Ecology* 58: 787-798.
- MAY, M.L., 1979. Energy metabolism of dragonflies (Odonata: Anisoptera) at rest and during endothermic warm-up. *J. exp. Biol.* 83: 79-94.
- MAY, M.L., 1984. Energetics of adult Anisoptera, with special reference to feeding and reproductive behavior. *Adv. Odonatol.* 2: 95-115.
- MAY, M.L., 1995. Dependence of flight behavior and heat production on air temperature in the green darner dragonfly *Anax junius* (Odonata: Aeshnidae). *J. exp. Biol.* 198: 2385-2392.
- MILLER, P.L., 1982. Temporal partitioning and other aspects of reproductive behaviour in two African libellulid dragonflies. *Ent. mon. Mag.* 118: 177-188.
- MOORE, N.W., 1952. On the so-called "territories" of dragonflies (Odonata-Anisoptera). *Behaviour* 4: 85-100.
- NORBERG, U.M., T.H. KUNZ, J.H. STEFFENSEN, Y. WINTER & O. von HELVERSEN, 1993. The cost of hovering and forward flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory. *J. exp. Biol.* 182(1): 207-227.
- PAJUNEN, V.I., 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). *Annls zool. fenn.* 1: 55-71.
- UBUKATA, H., 1975. Life history and behavior of a corduliid dragonfly, *Cordulia aenea amurensis* Selys. 2. Reproductive period with special reference to territoriality. *J. Fac. Sci. Hokkaido Univ.* (VI) 19(4): 812-833.
- UBUKATA, H., 1983. An experimental study of sex recognition in *Cordulia aenea amurensis* Selys (Anisoptera: Corduliidae). *Odonatologica* 12(1): 71-81.
- UBUKATA, H., 1984a. Oviposition site selection and avoidance of additional mating by females of the dragonfly, *Cordulia aenea amurensis* Selys (Corduliidae). *Res. Popul. Ecol.* 26: 285-301.
- UBUKATA, H., 1984b. Intra-male sperm translocation and copulatory behavior in the dragonfly, *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *J. Hokkaido Univ. Educ.* (IIB) 35: 43-52.
- UBUKATA, H., 1986. A model of mate searching and territorial behaviour for "Flier" type dragonflies. *J. Ethol.* 4: 105-112.
- UBUKATA, H., 1987. Selection of mode in territorial behaviour according to the population density of males. In: K. Higashi, H. Ubukata & Y. Tsubaki, [Eds], *Dragonfly mating systems*, pp. 63-106. Tokai Univ. Press, Tokyo.