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MORPHOLOGICAL VARIATIONS IN RELATION TO MATURATION IN *PANTALA FLAVESCENS* (FABRICIUS) IN CENTRAL JAPAN (ANISOPTERA: LIBELLULIDAE)

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P. flavescens was investigated in open fields in a deciduous forest in an inland part of the Kanto region for 3 months from late June 2003. The sp. was estimated to be bivoltine from summer to late autumn. The size of the adults was unchanged throughout the season. The sex ratio of the population skewed towards ♀. Maturity degree (MD), shown as the value of body weight divided by the cube of wing length, shifted upwards until the second half of August, after which it decreased sharply. Similarly the wing loading (WL) (calculated by dividing body weight by wing area) increased until the second half of August, and decreased from September, and in early October it was not significantly different between ♂♂ and ♀♀. As the relationship of body temperature to ambient temperature showed no difference between mature and immature individuals, or between sexes, with both correlation coefficients and regression coefficients being large for a flyer type sp., they seemed to be easily affected by the ambient temperature.

INTRODUCTION

Pantala flavescens is the most common dragonfly on the earth and is famous for its migratory behaviour. In Japan it appears in mass swarms in the hot season of Bon Festival in summer, and is called *bon-tombo* or *shoryo tombo*. This dragonfly flies over the ocean from the South, and its migration has been observed from a weather ship (ASAHINA & TSURUOKA, 1967; HASHIMOTO & ASAHINA, 1969). ISHIDA (1989) observed the species flying from over the ocean at Toba City in Mie Prefecture, and WAKANA (1959) described precisely his observations of large swarms in early autumn. It is said that coming over to the mainland of Japan it goes North by repeated alteration of generations and that its eggs and larvae cannot overwinter on the mainland. Hence they are extinct there as a breeding population (ISHIDA et al., 1989).

Although many reports on migration and foraging of this species have been made, the seasonal changes of the degree of maturity, wing loading, thermoregulation and seasonal changes of maturity in the species have scarcely received any attention. This study was made to clarify the morphological variations in relation to maturation of the species coming over to open fields in a forest far from the water areas.

STUDY SITES AND METHODS

Studies were made from late June to October in 2003 at Kunugiyama forest (ca 152 ha, 35°50'N, 139°28'E, 60 m a.s.l.) on the borders of three cities and a town, Tokorozawa, Sayama, Kawagoe and Miyoshi, which are located on the Musashino lowland hills in the western Saitama Prefecture. As the inland forest is located more than 1 km from the nearest water bodies, the specimens collected there might be regarded as migrants from other regions. Supplementary investigations were made in early September at the Kabazaka Pass (810 m a.s.l.) in the Okumusashi Hills, western Saitama Prefecture, and in late July at Hino (680 m a.s.l.), Nagasaka-cho, Kitakoma-gun, Yamanashi Prefecture, about 90 km West of Kunugiyama forest.

Size and body weight were measured within six hours of capture. The hindwing was used as a measure of size, using a slide caliper, and the body weight (except in the specimens from Nagasaka-cho) was measured with an electronic balance to 0.001 g.

Degree of maturity (MD) was calculated by dividing the body weight by the cube of the hindwing length, and this also gives the specific gravity of a specimen. The volume of an adult is unchanged throughout its life and, as it matures, its weight increases. Accordingly, the weight divided by the volume, i.e. the specific gravity, may be regarded as degree of maturity. This value was used effectively for *Sympetrum frequens* by ISHIZAWA (2004, 2005).

Wing loading (WL) was calculated as follows: from the captured individuals a male and a female, of body weights 340 mg and 431 mg, respectively were selected as standards. Their wings were photocopied. Using an image size of 200%, the wing shapes of the photocopies were cut out and weighed. The ratio of the weight of each of these shapes to the weight of a 100 cm^2 cut out was calculated. This gave a value of 16.3 cm^2 for the male and 18.8 cm^2 for the female, and these were regarded as the standard wing areas (STWA). Wing areas of other specimens were calculated as follows: STWA (cm^2) × the square (cm^2) of each hindwing length ÷ the square (cm^2) of the standard hindwing length. Then each WL was calculated by dividing the body weight (mg) by this value (cm^2).

The above data on WL were compared with those of *Orthetrum albistylum speciosum*, collected at Omori pond at Iruma City, Saitama Prefecture in 2000 and 2001, and were almost the same size as *P. flavescens*.

As an index of maturity I examined how far the abdominal segments were pruinescent from the 3rd segment backwards, and defined the number of the last pruinescent segment as the degree of pruinescense (PD). In cases where half of the last segment was pruinescent, the immediately anterior segment number + 0.5 was used as the PD.

Body temperatures (Tb) of the individuals were measured by the same method applied for measuring the body temperatures of *S. frequens* (ISHIZAWA, 1998a); Tb were measured to 0.1°C with a Hoskins F-V-K-002 thermocouple (diameter 0.05 mm) set in a hypodermic needle (external diameter 0.3 mm), which was insulated with paper covering, and connected to a John-Fluke 55 double-channeled digital thermometer. The measurements were made within about 10 seconds after netting the dragonflies, by inserting the probe through the mesh of the net to the center of the thorax, 1 mm up

the mesothoracic spiracle. Ambient temperatures at a height of 1 m in the sun (Ta) were measured with an Omron HC-100 thermistor soon after the measurements of Tb.
To investigate the difference of thermoregulation among individuals in relation to MD, I divided the dragonflies into two groups (regardless of the season) in each sex by using the standards of MD 4.8 in the male and MD 5.4 in the female. Those less than the standards were called immature; those above them were called mature.

Data of coefficients of other Odonata in Figure 4 were obtained from *Anax junius* from MAY (1976), *A. parthenope julius* (Ishizawa, unpublished), *A. guttatus* (ISHIZAWA, 1998b), *Anotogaster sieboldii* (ISHIZAWA, 2003), patrolling *Cordulia aenea amurensis* (Ishizawa, unpublished), *Mnais costalis* of orange wing type (ISHIZAWA, 2000), *Orthetrum j. japonicum* (Ishizawa, unpublished), *O. albistylum speciosum* (Ishizawa, unpublished) and both sexes of *S. frequens* during the reproductive period. (ISHIZAWA, 1998a). The sex or maturity of *A. junius* was unknown. Data on all other species except *S. frequens* were from mature males.

Data of the size, body weight, MD and WL were tested using a t-test; sex ratios were tested using the chi-square test. Tb and Ta among groups of the sexes or immature and mature groups were tested using the ANOVA-test and t-test. Correlation coefficients of each group were compared using the z-test.

RESULTS

The first record in the forest was on 26th June 2003, when six individuals were sighted flying around over an open field; the last record was on 20th October.

Figure 1 shows the change of the sex ratio of captured specimens. Throughout the investigation period the sex ratio was significantly skewed towards the females (67.3%, $P < 0.05$) except that of the specimens captured in late July at Nagasaka-cho, which were skewed towards the males (73.3%, $P < 0.05$, $n = 11$).

Hindwing length was ca 40 mm and not noticeably different between sexes throughout the season; 40.2±1.2 mm, n = 53 in the male and 40.6±1.5 mm, n = 109 in the female, respectively ($P > 0.05$; Tab. I). Comparing the early season (before September) and the late season (from September onwards), the difference in length was not significant ($P = 0.46$); in the males it was 40.4±1.1 mm (n = 26) in the early season and 39.9±1.2 mm (n = 27) in the late season ($P > 0.05$), although males do

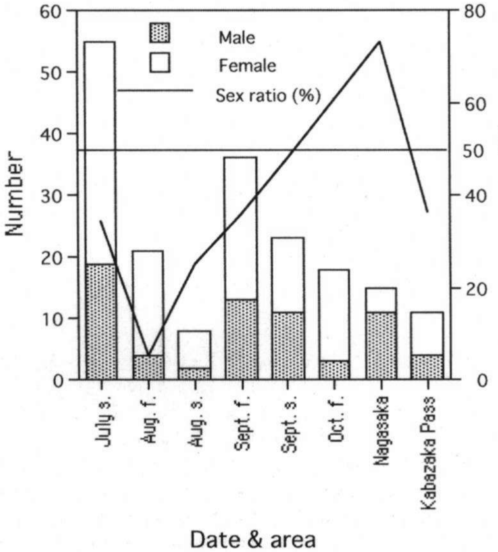

Fig. 1. Sex ratios of *Pantala flavescens* captured at surveyed areas.

have a propensity to become smaller. In the females the size was 40.6±1.2mm (n = 60) in the early season and 40.7±1.8 mm (n = 49) in the late season and the difference was not significant, although the s.d. tended to increase in the latter.

Body weight of the males increased from the second half of July (332.6±51.1 mg, n = 19), and after reaching a peak (401.0±18.0 mg, n = 2) in the second half of August, it reached its lowest level in October (Tab. I). In late September one rather heavy individual (398 mg) was captured, though most of those recorded in the late season were light (ca 200 mg). In early September one immature individual of 159 mg in weight was captured. The difference in weight between both seasons was significant ($P < 0.001$).

In the females, body weight was sustained at a level of ca 400 mg until the second half of August, when it reached a peak of 446.8±53.8 mg (n = 6). It then decreased rapidly by 100 mg, reaching its lowest level of ca 200 mg in October. The difference in the body weight between the seasons was significant as in the males ($P < 0.001$). The heaviest female specimen (537 mg) was captured on July 16 and one captured on September 28 weighed 533 mg. The second was the only one that exceeded 500 mg in the late season. The body weights of both sexes in the second half of October (228.0±37.5 mg, n = 3 in the male and 246.7±37.0 mg, n = 15 in the female) were similar to those from the Kabazaka Pass captured in early September.

Table I

Morphometric data of *Pantala flavescens* captured at Kunugiyama forest and Kabazaka Pass – [Hindwing: mm, Body weight: mg, Wing loading (WL): mg/(cm – cm). -- Abbreviations: s: second, f: first half, MD: maturity (the division of the body weight by the cube of the hind wing length), PD: pruinescens (the last pruinescent segment number, and in case of half of the last segment was pruinescent, the immediately anterior segment No.+0.5 was defined as PD). First line of values males, second females. Mean values with standard deviation]

	July s.	Aug. f.	Aug. s.	Sept. f.	Sept. s.	Oct. f.	Kabazaka Pass
Number	19	4	2	13	11	3	4
	36	17	6	23	12	15	7
Hindwing	40.4±1.1	40.5±1.0	39.4±0.8	39.9±0.8	40.4±1.1	38.3±1.6	40.2±0.6
	40.5±1.1	40.6±1.3	40.8±1.1	40.8±1.1	40.2±3.1	40.9±1.2	40.9±1.0
Body weight	332.6±51.1	358.8±20.5	401.0±18.0	263.8±51.5	321.8±45.6	228.0±37.5	230.8±57.5
	395.0±84.5	437.2±47.5	446.8±53.8	323.7±75.4	339.9±110.7	246.7±37.0	262.4±33.7
MD	5.0±0.7	5.4±0.2	6.6±0.7	4.2±0.9	4.9±1.0	4.1±1.0	3.6±0.8
	6.0±1.2	6.5±0.4	6.6±0.8	4.8±1.1	5.2±1.5	3.6±0.5	3.8±0.5
WL	19.8±2.7	21.3±0.8	25.4±2.1	16.2±3.3	19.4±3.3	15.3±3.1	13.9±3.4
	23.0±4.7	25.0±1.8	25.6±3.0	18.5±4.3	19.6±5.7	14.0±1.8	14.9±2.0
(range)	(25.9-12.0)	(22.3-20.5)	(27.5-23.3)	(20.9-9.4)	(27.4-15.4)	(18.9-11.4)	(18.7-9.4)
	(29.4-13.7)	(28.7-21.6)	(30.5-21.0)	(25.8-10.7)	(28.0-9.1)	(17.3-11.3)	(17.2-10.9)
PD	5.1±1.3	5.3±0.7	5.8±0.4	5.8±0.5	-	-	-
	(n=19)	(n=16)	(n=6)	(n=13)			

As the hindwing length was unchanged throughout the season and the body weight differed before and after the beginning of September, MD synchronized naturally with the variations in the body weight. The mean MD was 4.8±1.0 (range 2.4-7.4) in the males and 5.4±1.4 (range 2.4-8.0) in the females, respectively. The MD of both sexes increased until the second half of August, but decreased significantly from September onwards, although a small peak appeared in the second half of September (Tab. I, ♂: P = 0.00753 ♀: P = 2.664E-10). The range of MD was 2.4-7.4 in the males and 2.4-8.0 in the females, respectively. Regarding the individuals of which MD exceeded the mean value as sexually mature adults, the share rate of these in the early season and in the late season was 80.8%: 14.8% in the males and 82.8%: 28.6% in the females, respectively.

Only one male with a red abdominal dorsum was captured during the season, and it had a MD of 7.3. One female with a mature ovary (found by dissection) had a MD of 4.7, all others with a mature ovary falling in the range 5.4-7.4. Probably the individual with a MD of 4.7 might have previously oviposited.

The average wing loading (WL) of the males was 18.8±3.6 mg/cm^2, (range of 9.4 -27.5 mg/cm^2, n = 53), and that of the females was 20.8±5.5mg/cm^2, (range 9.1-30.5 mg/cm^{2,} n = 107) for all the seasons. The difference of WL between the

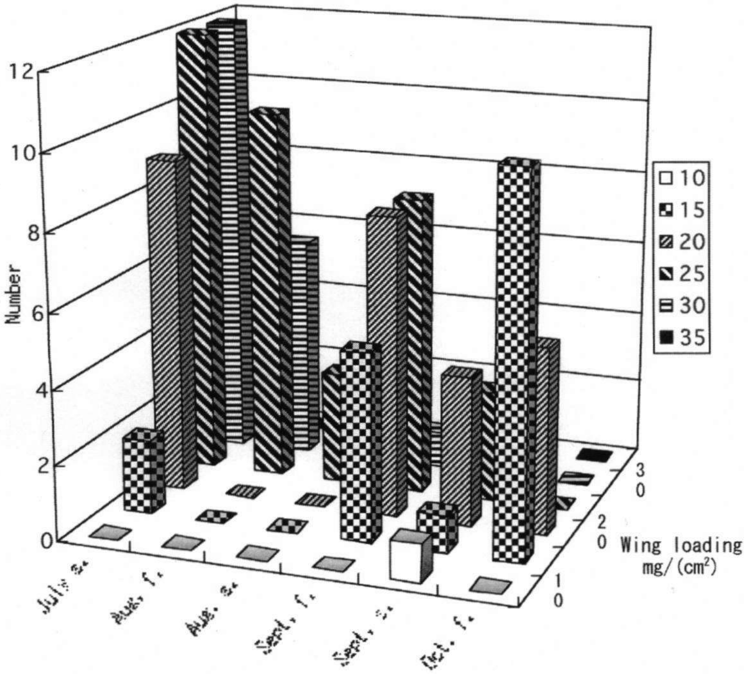

Fig. 2 3D graph of wing loadings by period in *Pantala flavescens* females captured at Kunugiyama forest from the second half of July to the first half of October in 2003.

sexes was significant ($p < 0.01$). The average WL of the males was 20.4±2.9; mg/cm^2 ($n = 26$) in the early season, and 17.4±3.6; mg/cm^2 ($n = 27$), in the late season, a significant difference ($P < 0.001$). The difference of WL between the seasons was also significant in the females (23.6±4.3; mg/cm^2, $n = 58$, in the early season and 17.4±4.7; mg/cm^2, $n = 49$, in the late season) ($P < 0.001$). In the second half of July more than two thirds of females exceeded a WL of 20 mg/cm^2 and WL was sustained until the second half of August.

Figure 2 shows a 3D histogram of the WL of the females captured at Kunigiyama forest. It indicates that mature individuals with high WL exceeded immature ones in the early season, and as the season advanced, immature individuals outnumbered the mature ones.

As females mature, most of them pruinosed on the ventral side of their abdomens from the 3rd segment backwards. The degree of pruinescens (PD) rose from 5.1±1.3 in the second half of July, to reach a peak of 5.8±0.4 in the second half of August. It remained at this level (5.8±0.5) into the first half of September, but thereafter no pruinescent individual was captured. However, there were examples where an individual of 533 mg in weight was not pruinescent, whereas one of only 330 mg in weight was pruinescent, (PD 5.5). There was no significant correlation between PD and body weight ($r = 0.140$, $P > 0.3$) or between PD and MD ($r = 0.094$, $P > 0.5$).

Figures 3A and 3B show the relationships of body temperature (Tb) to the ambient temperature (Ta) in each sex of mature and immature individuals. The correlation coefficient and the regression coefficient of immature males were 0.906

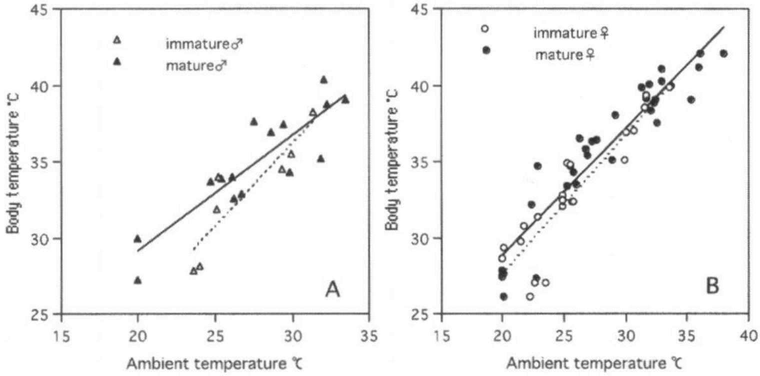

Fig. 3. The correlation between body temperature and ambient temperature in the male (A) and in the female (B), respectively. A solid and open triangle show an immature male and a mature male, respectively, and a solid and open circle show an immature female and mature female, respectively. All of the data were collected at Kunugiyama forest from July to October 2003. Equations are: immature male, $Tb = 1.085*Ta + 3.676$, $r = 0.906$ ($n = 7$); mature male, $Tb = 0.757*Ta + 14.021$, $r = 0.885$ ($n = 15$); immature female, $Tb = 0.906*Ta + 9.608$, $r = 0.906$ ($n = 21$); mature female, $Tb = 0.827*Ta + 12.420$, $r = 0.938$ ($n = 32$).

and 1.085, respectively, and in mature males: 0.885, 0.757, respectively, in immature females: 0.906, 0.906 and in mature females: 0.938, 0.827, respectively. There was no significant difference of both coefficients between the sexes or between immature and mature individuals of both sexes ($P > 0.05$, two-side, Z-test).

The mean Tb was 32.9±3.5°C in immature males and 34.9±3.4 °C in mature males; 32.8±3.9 °C in immature females and 36.2±4.5 °C in mature females (Tab. II). The Tb among these groups was significantly different ($p = 0.042$, d.f. = 3, F = 2.874, ANOVA-test) but only the Tb of mature females differed significantly from others ($P < 0.05$, t-test).

DISCUSSION

Pantala flavescens flies over to the Japanese mainland in spring, and the first record is earlier (in early and mid April) at the coastal areas of the Pacific Ocean such as southern Kyushu, Shikoku, and the Kanto region and westward than at other areas (Musashino Satoyama Research Group et al., 2004). The mean first record for 23 years between 1973 and 1995 at Amakusa, Kumamoto Prefecture was May 17th, and the earliest date was April 20th (TANAKA & HIGASHI, 2003).

The last record was October 25th at Chichibu City (ARAI, 1995). The records from various areas are mostly early and mid October; earlier in Hokkaido and the Tohoku region, the Northeast of Japan, and later at the coastal areas of the Pacific Ocean of the Tokai region and westward. The latest record, November 23rd, was reported by FUKUI (2005). The record from Kunugiyama seems to be moderate.

It deserves special mention that the sex ratio skewed towards females except for the specimens from Nagasaka. Even in the specimens collected randomly for DNA sequence from various areas in Asia it skewed towards females, 57.0%, n = 241 and 43.0%, n = 182 in the male ($p < 0.01$, chi-square test) (HAYASHI & ARAI, 2004). However, according to KUWADA (1972) the sex ratio skewed towards males (60%). Ambient temperature, time zone, period or locality may influence the sex ratio.

TANAKA & HIGASHI (2003) noted that *P. flavescens* exhibited two popu-

Table II

Thermal statistics of *Pantala flavescens* at Kunugiyama forest (°C±s.d.)

	Male		Female	
	Immature	Mature	Immature	Mature
Number	7	15	21	34
Body temperature	(32.9±3.5)	(34.9±3.4)	(32.8±3.9)	(36.2±4.5)
Ambient temperature	(26.9±2.9)	(27.6±4.0)	(25.6±4.0)	(28.9±5.2)

lation peaks in Kumamoto Prefecture, at the end of June and at the end of August, and ARAI (1995) suspected that this species might have two generations at Chichibu City after coming over there. Judging from the two population peaks at Kunugiyama, one between July and August and the other from September onward, I agree with ARAI (1995) on the assumption that *P. flavescens* may be bivoltine at settlements on the mainland of Japan (except the northern districts) after coming from overseas.

The fact that adult size remained fairly constant throughout the season and that two population peaks were observed at Kunugiyama (though size did decrease a little in the late season) may suggest no difference of larval duration between each generation. The indoor larval duration of *P. flavescens* was extremely short, 34-55 days, and outdoors at a pond outside its southern range in Australia it was 51 days (HAWKING & INGRAM, 1994), so that the larval duration of each generation may be roughly estimated at two months (TANAKA & HIGASHI, 2003). This is different from some zygopteran species such as *Ischnura asiatica* (ISHIDA et al., 1989) and *Aciagrion migratum* (UDONO et al., 1997), where larval duration and adult size are different between 1st voltine and 2nd voltine, and the adults occurring late in the season are smaller. The uniformity in the size of *P. flavescens* may be due to the short larval duration between voltines.

P. flavescens is said to start its migration in the immature stage (CORBET, 1984, 1999). According to ASAHINA & TSURUOKA (1967) all individuals collected on a weather ship at the Tango weather observation spot on the Pacific Ocean in August were mature; three males were reddened on their abdominal dorsum and the ovaries of females were mature. I do not know the maturity of adults coming over to the mainland in spring. However, as the above fact shows, many of the migrating individuals in summer may be mature. This agrees with the shifts of body weight and MD of the individuals of Kunugiyama forest. The mature individuals at Kunugiyama in the early season might represent a mixture of the mature descendants of the first comers to the mainland in spring and the mature migrant adults from southern overseas.

In autumn MD decreased sharply. As only a few mature individuals were observed in this season and individuals of seemingly soon after emergence were included in the groups at Kunugiyama, most of the individuals might have been the second generation that resulted from the mature adults of the early season. As the shifts of MD and PD show, it is assumed that the maturity of the second generation may not advance. MD of individuals of which abdomens were pruinescent exceeded 4.6 and there was not such a high correlation between MD and PD. Therefore, PD cannot be a decisive index of maturation.

WL of even mature females was significantly lower than that of mature females of *S. frequens* (28.6±2.0 mg/cm^2, n = 41), which is a migratory species like *P. flavescens* ($P < 0.05$) (Ishizawa, unpublished). In the males *P. flavescens*, the mean WL for the season was significantly lower than that of the males of *Orthetrum* *albistylum speciosum* of the same size, and also it was the same when compared with that of *O. cancellatum* males from Europe (26.4±2.54 mg/cm^2) (GRABOW & RUPPELL, 1995). Since most of migrating females captured on the ocean were mature (ASAHINA & TSURUOKA, 1967; HASHIMOTO & ASAHINA, 1969), in *P. flavescens*, the low WL may be advantageous for its migratory dispersal.

From September onward individuals of WL lower than 20 mg/cm^2 were most frequent, and in October most individuals of both sexes weighed ca 15 mg/cm^2. The WL is as low as those of some Zygoptera (RÜPPELL & HILFERT, 1993). ARAI (2003) noted that although many *P. flavescens* swarms were sighted, their oviposition was seen rarely in summer. *P. flavescens* is a tropical species, hence lowering of Ta may suppress maturation and increase of body weight, or WL may be suppressed. This is different from the case of *S. frequens*, in which body weight increases in early and mid September as Ta falls (ISHIZAWA, 2004, 2005).

According to MAY (1981), wingbeat frequency of *P. flavescens* was 22.9 Hz (25°C), the lowest among species of approximately the same WL of 20 mg/cm^2. The required power for fluttering flight is proportional to the product of the 5th power of wing length (*l*) and the cube of wingbeat frequency (*f*), while the available power is proportional to the product of the body mass (*m*) and the wingbeat frequency (f) (AZUMA, 1987). Ignoring coefficients of both equations: $l^5 \times f^3 = m \times f$ $l^5 \times f^2 = m$.

In *P. flavescens* the wing length was unchanged as the season advanced. However, body weight, as defined by WL, decreased. Hence, the wingbeat frequency may decrease in the autumn. As Tb

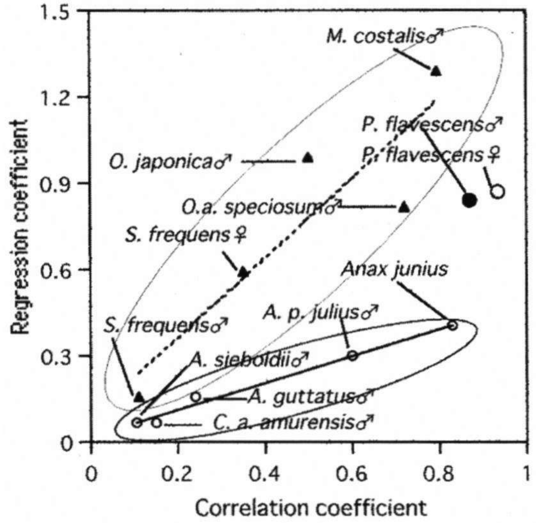

Fig. 4. Relation of regression coefficient (REG) to correlation coefficient (COR) in the percher-type species and in the flyer-type species. Data of coefficients of other Odonata: *Anax junius* (MAY, 1976), *A. parthenope julius* (Ishizawa, unpubl.), *A. guttatus* (ISHIZAWA, 1998b), *Anotogaster sieboldii* (ISHIZAWA, 2003), patrolling *Cordulia aenea amurensis* (Ishizawa, unpubl.), *Mnais costalis* of orange wing type (ISHIZAWA, 2000), *Orthetrum j. japonicum* (Ishizawa, unpubl.), *O. albistylum speciosum* (Ishizawa, unpubl.) and both sexes of *Sympetrum frequens* at reproductive period (ISHIZAWA, 1998a). The sex or maturity of *A. junius* were unknown. Other data except for *S. frequens* were from mature males. Least squares linear regressions are: the percher type: a dotted line, REG = 1.457*COR-0.099, r = 0.766, p = 0.131; the flyer type: a solid line, REG = 0.354*COR + 0.046, r = 0.907, p = 0.034.

and the wingbeat frequency are positively correlated, decrease of wingbeat frequency brings lowering of metabolic heat production (MAY, 1981), so that Tb is naturally lowered.

P. flavescens flies with less fluttering on the wind and lower WL is advantageous for its flight. The latter may be disadvantageous for thermoregulation and temperature dependency inevitably becomes large for the dragonfly. Actually, between both sexes or between mature individuals and immature individuals there was no significant difference of the regression coefficients of Tb to Ta. They appeared to be affected by Ta and this was shown in the large regression coefficients. This species belongs to the flyer type (CORBET, 1962) like Aeshnidae and Corduliidae. Regression coefficients of the flyer type dragonflies tend to be lower than those of the percher type (Fig. 4). The former are mostly endothermic whereas the second are, in general, ectothermic (MAY, 1976, 1987). However, those of *P. flavescens* approximate those of the percher type.

P. flavescens is liable to swarm even in hot daytime in mid summer. ARAI (1995) reported that some of those swarming were seen flying with their abdomens bent downward. This was often observed when Ta exceeded 30 °C and they flew against the wind with this posture. Therefore, it is assumed that they thermoregulate their Tb by exposing their abdomens to the wind. CORBET (1999) described that this is a radiator effect. In this case low WL might be profitable for them, only flying driftingly in the wind with less fluttering. The high dependency on temperature may suppress maturation of the species in the cool autumn.

Thus, the swarm migration such as observed by WAKANA (1959) may probably be a behaviour for adaptation to suitable ambient temperatures.

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