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SEXUAL MATURATION, BODY COLOUR CHANGES AND INCREASE OF BODY WEIGHT IN A SUMMER DIAPAUSE POPULATION OF THE DAMSELFLY *LESTES SPONSA* (HANSEMANN) (ZYGOPTERA: LESTIDAE)

T. UÉDA

Laboratory of Natural Science, Ishikawa Agricultural College, 1-308 Suematsu, Nonoichi-machi, Ishikawa Prefecture 921, Japan

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Due to a reproductive diapause, *L. sponsa* has a postponed prereproductive period in the southern half of Japan. In 1987, in Kanazawa City, the prereproductive period lasted 70-90 days: emergence commenced from late May, but reproductive behaviour did not begin until late August. During the summer the oocyte development was suppressed and ripe ova did not appear until mid-August. The colour maturation of the female body, however, proceeded without delay, independently of sexual maturation. The colour maturation and spermatogenesis in males also proceeded without delay and almost all males were fully mature in both features by early July. Body weight, exclusive of lipids, also rapidly more than doubled during the colour maturation period in both sexes. Thus, freshly emerged individuals required a post-teneral development not only of the gonads, but also of such basic body structures as e.g. the muscles, the cuticle, etc.

INTRODUCTION

The length of the prereproductive period between emergence and the beginning of reproductive activities is three weeks or less in most Zygoptera and two weeks or less in most Anisoptera (CORBET, 1980). In *Lestes sponsa,* at northern latitudes above 40° N, the length is about 20 days, which is within the range for Zygoptera. In the southern half of Japan, however, it is progressively prolonged southward up to more than 100 days. This prolongation of the prereproductive period is caused not simply by the earlier starting of emergence, but also by the later beginning of reproductive activities toward the South (UÉDA, 1978). That is, it is due to the occurrence of reproductive diapause, associated with the hot

summer (i.e. summer diapause: MASAKI, 1980) in the southern half of Japan.

A considerable number of biological, especially physiological, studies on adult reproductive diapause have been made in insects (reviewed by NORRIS, 1964; MASAKI, 1980; PENER & ORSHAN, 1983; TAUBER et al., 1983). In odonates, however, there is little information on this subject. Although it is known that several tropical species, which breed in temporary pools, aestivate during the long dry season as adults (GAMBLES, 1960; CORBET, 1962; KUMAR, 1972), no one has yet studied this systematically. In temperate regions there are few reports on the species showing summer diapause. No intensive inquiry has yet been undertaken save for the ecological study on *Lestes temporalis* by UÉDA & IWASAKI (1984).

During the dragonfly prereproductive period, morphological and/or physiological changes occur sequentially in the body (CORBET, 1980). Among these, those in body colour conditioned by age are well known in many species (e.g. PARR, 1973; McVEY, 1985; UÉDA, 1987). Although it has been a general view that colour change may indicate the attainment of sexual maturity (CORBET, 1962), there are only a few studies that have examined gonad development in relation to changes in body colour (PAJUNEN, 1962; JOHNSON, 1973). The growth of cuticular layers during the prereproductive period was also reported by VERON (1973), but the post-teneral increment of body weight has not yet received attention.

In this paper I describe the body colour change, the process of sexual maturation and the body weight increase during the prereproductive period in a summer diapause population of *Lestes sponsa*. I will also discuss the changing pattern of such features in relation to the occurrence of reproductive diapause.

METHODS

Specimens of *L. sponsa* were regularly collected from July to September in 1986 and from late May to September in 1987 at an abandoned paddy field and its surroundings (alt. 300 m approx.) in the suburbs of Kanazawa City (36° 30′ N; 136° 40′ E).

The specimens, wrapped in paper triangles, were brought to the laboratory in a cooling box. In the laboratory, the length of the right hind wing and the abdomen, and the fresh weight of each specimen were measured, and its colour phase was recorded (cf. Tab. I).

The specimens were dissected on the day of collection, if possible. If not, they were kept alive in a refrigerator (3° C approx.) and dissected within a few days.

The volume of the seminal vesicle (= primary reservoir) was examined. As the seminal vesicle is assumed to be composed of a pair of ellipsoids (Fig. 1), the length (L) and width (W) of each half of the seminal vesicle, which was soaked in 0.9% NaCl solution, were measured with an ocular micrometer to calculate its volume (V) according to the formula $V = \pi LW^2/6$, and then the calculated volumes of the two were added up.

Next, the seminal vesicle was cut off from the specimen and was placed on a glass slide. It was crushed with a coverslip to check for the presence of sperm under a microscope (x 150).

All dissected females were examined for the presence of mature eggs and of sperm in their bursa

copulatrix. When a dissected female had no mature eggs, the length of the largest terminal follicle was measured (only in 1987). This procedure, however, is not always reliable since there is a thick layer of fatty tissue in the interovariole space.

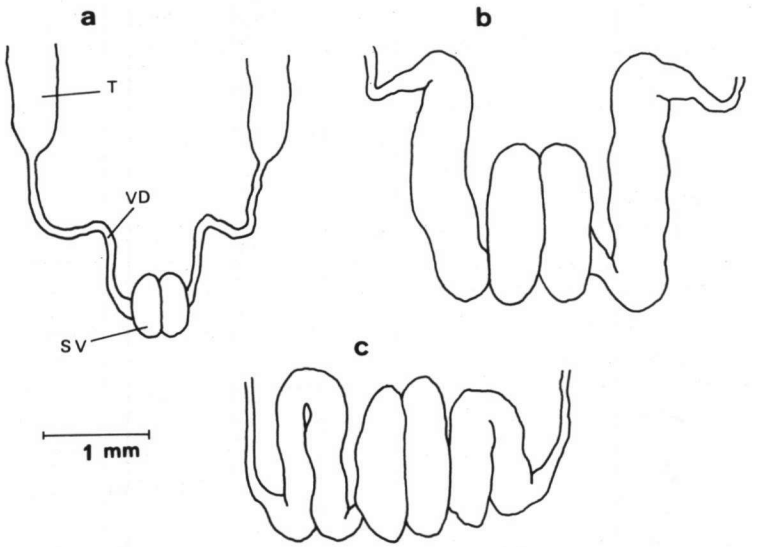

Fig. 1. Internal reproductive organs of male *Lestes sponsa:* (a) of an individual in colour phase M_4; — (b-c) of two fully colour-mature individuals, collected in August. — [T = testis; — VD = vas deferens; — SV = seminal vesicle].

Finally, in all specimens, save for the dissected females, dry weights and lipid-free dry weights were determined. First, the insects were dried in an oven at 70-80° C for more than 3 days and stored in a desiccator. After measuring the dry weights, the specimens were individually soaked for 3 or more days in glass tubes containing 20 ml of ethyl ether. The ether was renewed twice, consequently, all the specimens remained soaked in ethyl ether for a total of 9 or more days. Then they were dried again and their lipid-free dry weights were measured. The lipid weight was taken as the difference between the dry weight and the lipid-free dry weight.

PHENOLOGY

The emergence of *L. sponsa* at the study site began in mid-June in 1986, and in late May in 1987. The reproductive season commenced in late August in both years (cf. Tab. III). Thus the greatest length of the prereproductive period was about 70 to 90 days. The flying season lasted approximately until the end of October.

COLOUR MATURATION

During the prereproductive period, melanism in the lateral metathoracic yellow area and the progressive deposition of pruinescence on several parts of the body occurred in all males and in some females. Table I shows the male colour phases, which, with age, progressively changed from T to M_6, though I could not clarify the age in days corresponding strictly to each colour phase.

Table I
Colour phases in male *Lestes sponsa*

Colour phase	Description
T	Metathorax laterally slightly brownish yellow; — app. sup. yellow
M_0	Metathorax laterally yellow; — app. sup. become black or brownish black
M_1	Thin and unclear black stripe appears along metapleural suture
M_2	Deposition of pruinescence commences on occiput, on dorsal surface of prothorax and on abd. segm. 9, but remains poorly visible; — black stripe along 2nd lateral suture becomes wider and clearer than in M_0
M_3	Deposition of pruinescence progressed and clear on ventral surface of meso- and metathorax, on coxae, on lateral surface of metathorax, and on abd. segm. 8-10; — the lateral metathoracic pruinescence appears only on the black stripe, which becomes wider, replacing almost half of the yellow area
M_4	Same as M_3, but pruinescence clear on thoracic dorsum and on abd. segm. 1 & 2
M_5	Metathoracic black stripe replaces most of the yellow areas; — lateral thoracic pruinescence spread out to the remaining parts of the yellow area beyond the black stripe
M_6	Pruinescence spread out to the metallic green area of metathoracic epimeron; — metathoracic black stripe with pruinescence completely replacing the yellow area

Phase T may include, in addition to freshly emerged insects, perhaps also older individuals, within a few days after emergence. M_0 was distinguished from T by the pigmentation of the superior appendages (or the outer valve in females), which changed to black or brownish black. Laterally on the thorax, the blackening in the yellow area begins to appear as a stripe along the metapleural suture at the M_1 stage. The black stripe gradually widens and replaces the yellow area up to M_6 though in the present population, not always completely so. Pruinescence begins to appear in M_2 individuals, whose age may have been 7 to 10 days after emergence. Then it progresses and spreads out over several regions. After males have reached phase M_6, the pruinescence does not

appear on any other part of the body, although it thickens where present, and the colour gradually changes from bluish white to white. M_6 is therefore the final phase in terms of the developmental degree of pruinescence.

Our post-teneral females were dimorphic in metathoracic colour pattern, independently of age: (1) in the andromorphic type the change of colour was almost identical to that in males, (2) in the non-melanotic type the blackening did not occur on the metathorax, though slight pruinescence occurred mainly in the

Table II
Seasonal changes in the percentage of individuals in various colour phases (1987)

♂	Season		Colour phase T	M_0+M_1	M_2-M_5	M_6	Sample size
	May	late	100	0	0	0	7
	June	early	50.0	34.6	15.4	0	26
		mid	20.8	37.5	37.5	4.2	24
		late	2.6	23.1	61.1	12.8	39
	July	early	0	20.0	33.3	46.7	15
		mid	0	0	0	100	7
		late	0	0	0	100	12
	Aug.	early	0	12.5	0	87.5	8
		mid	0	0	0	100	22
		late	0	0	0	100	18

♀	Season		Colour phase T	M_0+M_1	M_2-M_4	M_5+M_6	MP	Sample size
	May	late	100	0	0	0	0	8
	June	early	89.5	10.5	0	0	0	19
		mid	69.2	30.8	0	0	0	13
		late	20.0	0	33.3	6.7	40.0	15
	July	early	7.1	0	0	57.2	35.7	14
		mid	0	0	20.0.	20.0	60.0	5
		late	0	0	0	60.0	40.0	5
	Aug.		0	0	0	30.0	70.0	10

ventral part of the thorax. The ratio of the two types (September 1985) was nearly 1:1 (66 andromorph, 64 non-melanotic). No pruinescence was observed on the abdominal segments 8-10 of either type of female.

The andromorphic females could be categorized in the same way as the males. The aging of the non-melanotic females could be ascertained only by the presence of pruinescence (phase MP) and could not be divided further. Consequently only three phases could be discerned, viz. T, M_0 and MP.

At the study site, reproductive behaviour was shown by the males in phase M_6

or by the females in M_5 and M_6. The colour of some females did not advance beyond phase M_5. Hereafter I will treat the males in M_6 and the females in M_5 and M_6 as mature individuals in terms of colouration (mature-coloured individuals). The first males in phase M_6 and the first female in phase M_5 were collected (1987) in mid-June and late June, respectively (Tab. II). This does not indicate faster colour maturation in males than in females as the number of samples of the andromorphic type of female taken on each collecting day was small. Most individuals of both sexes had already completed colour maturation by mid-July (Tab. II).

The time lag between the first emergence, which was late May in 1987, and the earliest appearance of mature-coloured individuals suggests that the damselfly requires about 20 days for colour maturation after emergence. It is noteworthy that this is almost the same as the prereproductive period for populations at northern localities (see above).

The colour of the male compound eyes also successively changes from brown to light blue and then to indigo blue. In our population such colour changes occurred only in M_6 males. Almost all males collected after late August had indigo blue eyes and mating behaviour was likely to be shown only by those males. The colour of female compound eyes, however, did not change into blue except in a few cases.

Body metallic green also changed to copper in some older individuals of both sexes, but this does not seem to be the general rule.

SEXUAL MATURATION

The presence of sperm in the seminal vesicle was confirmed for some males in phase M_0. The proportion of males with sperm rapidly increased in the subsequent phases. From M_4 onwards all males had sperm.

Seminal vesicles, containing no or only small quantities of sperm, were

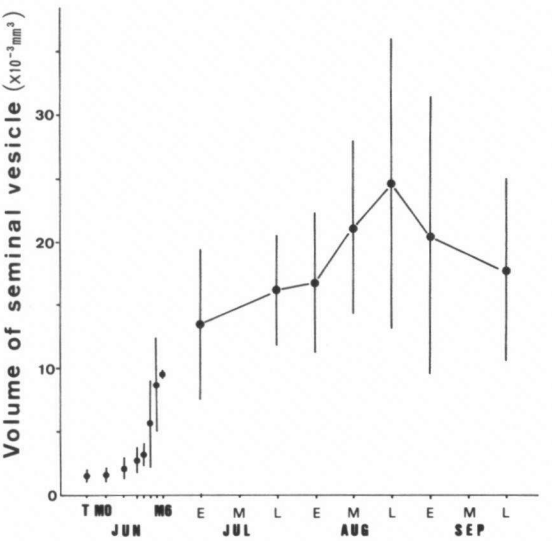

Fig. 2. Age-dependent changes in volume of seminal vesicle of male *Lestes sponsa* in Kanazawa, 1987. Mean values plotted against colour phase in June, and against collection date after July. — [Vertical lines indicate standard deviation].

small and transparent, whereas those containing much sperm were large and greyish white. Thus, the volume of a seminal vesicle appears to indicate the amount of sperm in it. As is shown in Figure 2, the volume of the seminal

Table III

The presence or absence of ripe eggs in the ovary and of sperm in the bursa copulatrix of females in the diapause population of *Lestes sponsa* in Kanazawa

1986				1987			
Date	Age[1]	Presence of sperm	Presence of ripe eggs	Date	Age	Presence of sperm	Presence of ripe eggs
				16 June	T	—	—
					M_0	—	—
					M_0	—	— (0.06)[2]
				26 June	M_4	—	—
					M_5	—	—
				30 June	M_4	—	—
				08 July	M_5	—	— (0.28)
					M_6	—	— (0.32)
					M_6	—	— (0.27)
19 July	M_0	—	—	14 July	M_3	—	— (0.42)
	M_1	—	—		MP	—	— (0.20)
	M_4	—	—		MP	—	— (0.35)
	MP	—	—				
30 July	T	—	—	28 July	MP	—	— (0.50)
	M_0	—	—		M_6	—	— (0.55)
	M_5	—	—				
	MP						
04 Aug.	M_5	—	—	05 Aug.	MP	—	— (0.36)
	M_6	—	—		MP	—	— (0.36)
	MP	—	— (0.30)				
12 Aug.	M_5	—	— (0.78)	13 Aug.	MP	—	+
	MP	—	+				
	MP	—	+				
14 Aug.	M_6	—	+				
	MP	—	+				
25 Aug.	M_5	—	+	28 Aug.	M_6	+	+
	M_6	+	+		MP	+	+
	MP	—	+		MP	—	+
					MP	—	+
03 Sep.	M_6	+	+	02 Sep.	MP	+	+
	M_6	+	+				
	MP	+	+				
10 Sep.	M_6	+	+				
	MP	—	+				

[1] Age is given in terms of colour phase (cf. Tab. I)

[2] Length of the largest terminal follicle (mm). Ripe ova are 1.40 mm.

vesicle increases slowly at first and then more rapidly, with a sevenfold enlargement on average during colour maturation (0.016 mm^3 in phase T as to 0.11 mm^3 in M_6, at the end of June). After the males reached colour maturity, the volume increased further, though more slowly, until mid-August, just before the breeding season started. After July, the vas deferens of most mature males was also enlarged (Fig. 1) and it stored a great quantity of sperm. Assuming that the volumes of the seminal vesicle and vas deferens show the relative quantities of sperm in them, this evidence indicates continuous production of sperm during summer.

Most of the spermatozoa pushed out of the seminal vesicle swam about actively. It was often observed that many aggregated to form spermatodesms, some of which were perfectly circular in shape like a flower, while others resembled a powder-puff, similar to those of *Davidius nanus* described by ASAHINA (1954).

Each ovary consists of a great number of panoistic ovarioles. Mature eggs were observed in all specimens collected after mid-August (Tab. III). Seasonal change in the length of the largest terminal follicle suggests that the maturation of oocytes might occur rapidly around mid-August (Tab. III). This is also supported by the rapid increase of lipid-free dry weight of the female abdomen which occurs at the same time (cf. Fig. 4).

Among the female specimens collected in July, I frequently observed ovarioles whose terminal ends had no oocytes. Their shape was similar to the elongated follicular relics described by JOHNSON (1973). This suggests that follicle resorption (cf. JOHNSON, 1973) might have occurred in females in July.

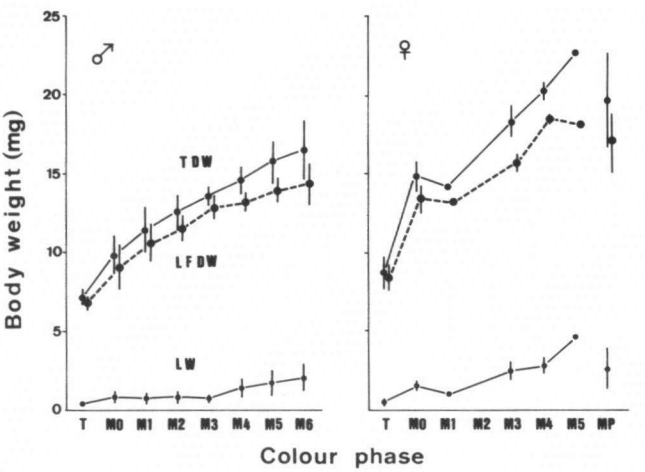

Fig. 3. Body weight increase during colour maturation. Body weight is shown by total dry weight (TDF), lipid-free dry weight (LFDW) and lipid weight (LW). — [Vertical lines indicate standard deviation].

BODY WEIGHT INCREASE

The body weight of both sexes also increased during colour maturation as shown in Figure 3. The total dry weight (TDW) increased more than twice from teneral individuals to just colour-mature ones. This increase was almost entirely due to the increase of the lipid-free dry weight (LFDW). LFDW is the weight of substances poorly soluble in ethyl ether, and may mainly consist of various kinds

Table IV
Seasonal changes of body weight[1] in colour-mature males (1987)

Season		Dry weight	Lipid free dry weight	Lipids weight	Lipids content (%)	No. of samples[2]
June	late	16.5±1.89	14.4±1.15	2.1±0.86	12.7	5
July	early	17.3±0.74	14.9±0.47	2.4±0.69	13.9	5
	mid	19.2±1.62	15.4±1.30	3.8±0.97	19.8	4
	late	17.5±1.59	14.4±1.05	3.1±0.96	17.7	10
Aug.	early	18.0±1.98	13.3±1.63	4.3±1.06	23.9	2
	mid	19.4±1.54	15.1±0.96	4.3±0.95	22.2	15
	late	19.8±2.31	15.7±1.29	4.0±1.40	20.2	11
Sep.	early	20.4±1.48	15.9±1.02	4.5±1.29	22.1	11
	mid	—	—	—	—	—
	late	17.4±0.67	15.7±0.67	1.8±0.91	10.3	7

[1] Mean ±standard deviation (mg)
[2] The samples are restricted to males with hind wing lengths 20.5-21.5 mm.

Table V
Seasonal changes of body weight[1] in colour-mature females (1987)

Season		Dry weight	Lipids free dry weight	Lipids weight	Lipids content (%)	No. of samples[2]
July	early	23.7±2.71	18.6±1.50	5.0±1.60	21.1	9
	mid	23.9	19.4	4.5	18.8	1
	late	21.7±1.99	17.7±1.68	4.0±0.98	18.4	4
Aug.	early	19.8±4.88	14.3±1.77	5.5±3.11	27.8	2
	mid	24.8	18.2	6.6	26.6	1
	late	30.0±5.07	25.2±4.05	4.8±1.07	16.0	4
Sep.	early	30.3	23.3	7.0	23.1	1
	mid	—	—	—	—	—
	late	25.9	23.6	2.3	8.9	1

[1] Mean ±standard deviation (mg)
[2] The samples are restricted to females with hind wing lengths 22.0-23.5 mm.

of protein, making the basic body structure. The increase of lipid weight during colour maturation was only slight.

After the individuals had reached colour maturity, LFDW hardly increased, though TDW increased slightly owing to the successive accumulation of lipids until the breeding season started (Tab. IV).

Tables IV and V show that TDW was likely to increase again in August in females, but not in males. This is due to the increase of the LFDW of the female abdomen, as clearly shown in Figure 4. The other parts of the female body kept a constant weight. The sudden increase of the LFDW of the female abdomen must be caused by rapid synthesis of egg yolk since it coincides with the first appearance of mature eggs in the abdomen, in mid-August (Tab. III).

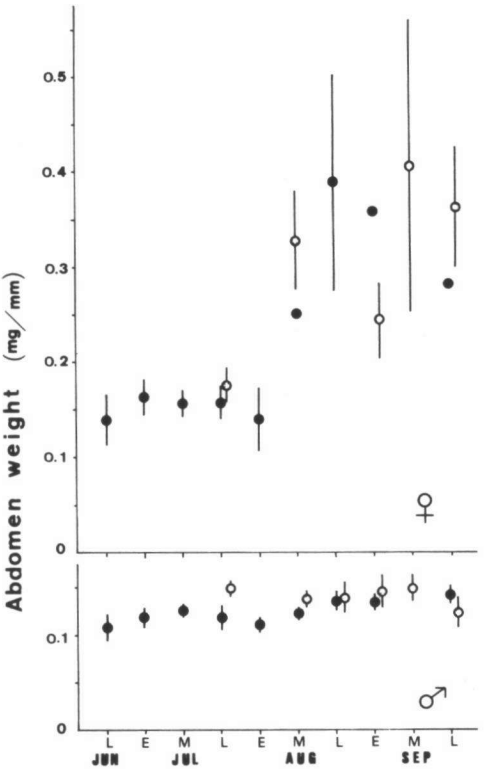

Fig. 4. Seasonal changes in lipid-free dry weight of abdomen (LFDWA) for colour-mature individuals (O: 1986, • :1987). The value presented is the weight (mg) divided by the abdominal length (mm). — [Vertical lines indicate standard deviation].

DISCUSSION

In *Lestes sponsa*, the length of the prereproductive period, which lasts for 20 days in most areas of the distribution range, is progressively prolonged southward, below about 40° N in Japan. This prolongation is caused by the occurrence of reproductive diapause, associated with the hot summer; ultimately it is a seasonal adaptation, enabling the overwintering at the egg stage (UÉDA, 1978). In the Kanazawa population studied, the prereproductive period lasts about 70-90 days at the most, and the reproductive season begins in late August. The development of oocytes is suppressed during the summer and ripe ova do not appear until close before the beginning of reproductive activities in mid-August.

In contrast to the slow development of oocytes, spermatogenesis proceeds very

rapidly starting about a week after emergence at the earliest, in colour phase M_0. Such an early beginning of spermatogenesis even in the larval stage, has already been reported for several non-diapause species of Odonata (for a review see PAJUNEN, 1962). The beginning of spermatogenesis, however, does not always indicate the attainment of sexual maturity in males. The volume of the seminal vesicle, which should indicate the volume of sperm stored in it, increases with colour maturation, and the average volume in males that have just attained colour-maturity (i.e. those in phase M_6, collected in late June) was about equal to or bigger than the average in sexually active males in a non-diapause population, breeding at a higher altitude (about 700 m) near Kanazawa (Uéda, in preparation). This suggests that the males are fully developed sexually by the completion of colour maturation at the latest. Colour maturation of the body is likely to be completed in about 20 days in both sexes. This is important, since the time for colour maturation corresponds to that of the prereproductive period for non-diapause populations of *L. sponsa* in the northern localities (cf. UÉDA, 1978). This fact suggests that in the present population colour maturation, and therefore also sexual maturation in males, occur without a delay, unlike the development of oocytes.

Thus, most males were sexually mature at the latest by the beginning of July (1987). The volume of the seminal vesicle and vas deferens increased further throughout the summer until late August or early September, when the sperm began to be spent in copulations. This suggests that spermatogenesis continued during the summer, unlike oogenesis. Thus, in the population studied, there is a difference in sexual maturity of males and females during the summer.

Among other orders of insects, it is well known that males vary considerably in the degree to which spermatogenesis is suppressed during diapause (reviews by NORRIS, 1964; PENER & ORSHAN, 1983; TAUBER et al., 1983). In some species, no reproductive diapause occurs in males and they can copulate before or during diapause. In our population of *L. sponsa,* no reproductive behaviour was evidenced before late August, when the females reached sexual maturity. In most species, as in *L. sponsa,* the female is refractory until her diapause ends. According to PENNER & ORSHAN (1983), in most insects males also have a true reproductive diapause, although in some, there is a pseudodiapause. The males in pseudodiapause are sexually inactive towards diapausing females but not towards receptive females. The males seem to need only the presence of receptive females to become sexually active. In *L. sponsa,* it is unknown whether the male is in true diapause or in pseudodiapause. I could not find any indication in the gonads showing the presence of true reproductive diapause. However, as has already been mentioned, if the colour change of the compound eyes is associated with mating behaviour, the males are likely to be in true reproductive diapause. In non-diapause populations colour changes of the compound eyes occur with the colour maturation of the body (Uéda, in preparation). A similar colour change of

the compound eyes of post-diapause males was observed in a tropical species, *Lestes virgatus,* by GAMBLES (1960).

Anyway, the mechanism which controls the development of the male gonad is dissociated from that which determines readiness to copulate (NORRIS, 1964). ASHIDA & MATSUDA (1983) indeed showed that in some species of univoltine leaf beetles male mating behaviour appears to be exhibited when the corpus allatum is activated, regardless of spermatogenesis.

It has been a general view that the colour change of the body in Odonata indicates the attainment of sexual maturity. However, as already mentioned, the colour maturation of the body except the compound eyes was likely to be completed in about 20 days, which in the earliest individuals was 1-2 months before the reproductive season began or before most individuals reached sexual maturity, at least in the females. Thus the present study clearly demonstrates that colour maturation occurs independently of sexual maturation in the females. Therefore the general view is not applicable, at least so to females in the diapause population of *L. sponsa.*

In the Kanazawa population, even females with mature colour, which were collected before mid-August, had no mature eggs. On the other hand, WATANABE & ADACHI (1987) have reported that mature eggs are (always?) found even in the last age-class of immature *L. sponsa* in the warm-temperate zone of Japan. Their data, however, are not comparable to the present data because they did not present any description of the age classes used by them.

After emergence, body weight increased with colour maturation. This increase, though partially due to the increase in lipid content as referred to by WATANABE & ADACHI (1987), was mainly due to the increase of substances poorly soluble in ethyl ether. In general, newly emerged odonates, including *L. sponsa,* are still incompletely pigmented and the cuticle may be so soft and thin that they can only fly weakly. The growth of endocuticular layers in post-teneral individuals with age was confirmed in several species of damselflies by VERON (1973). The flight muscles of some insects are not fully developed at emergence and they increase in size subsequently (JOHNSON, 1969). Thus, the newly emerged individuals of *L. sponsa,* like those of some other insects, require further development to build up their basic body structure. The increase of LFDW must be due to such post-teneral development.

The LFDW rapidly increased during colour maturation and reached a maximum by the time the colour had matured. This means that the colour-mature individuals also had a fully developed body and that the development of the body structure also occurred without delay in the present population.

Thus the present study revealed that in *L. sponsa* (and perhaps also in some other odonates), newly emerged individuals require post-teneral development not only of the gonads but also of the basic body structures. Probably, in non-diapause populations, such development of the gonads and the body structures

may be completed with colour maturation. In such cases, the so-called "maturation period" can be used as a synonym for "prereproductive period", otherwise the two terms should be distinguished from each other.

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