FECUNDITY AND OVIPOSITION PATTERN IN THE DAMSELFLY
COPERA ANNULATA (SELYS)
(ZYGOPTERA: PLATYCNEMIDIDAE)*

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In order to determine the fecundity and the number of eggs deposited, females were captured in field, dissected and classified into 7 age classes. The period of maiden flight (4 age classes) was estimated in a laboratory-reared population as 19 days. Change in the bursa copulatrix volume of mature females suggests sperm displacement. The mature egg size decreases with female age. Egg maturation appears to occur mainly in the pre-mature period. Not counting the immature eggs, the numbers of mature and submature eggs (fecundity) were estimated to be 300 and 150, resp. However, the difference in the mature egg number between females at the beginning and at the end of the mature period was about 250, which may be the actual life span reproductive performance. This is about half the estimate obtained by dissection.

INTRODUCTION

Copera annulata inhabits woodlands by water, and shows no territorial behaviour. MIZUTA (1974) stated that it lives in ponds or slowly flowing streams shaded by trees: the males search for females in the periphery of the forests. The imagos are found from mid-May to mid-September in central Japan. Except for tentative life history studies and occasional observations (e.g. ISHIDA, 1976), little is known about this damselfly.

This paper is concerned with fecundity and its ecological consequences; fecundity and oviposition pattern are important parameters in the interpretation of population dynamics of the damselfly. Populations of the damselfly seem to fluctuate, in general, with less variation from generation to generation

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(OHSAWA & WATANABE, 1986). In order to analyze such population dyna-
mics, studies not only on dispersals and movements of adults but also on
ovipositions and survivorships of immature stages are important. However, there
have been no reports on the fecundity of damselfly species in which oviposition is
in tandem, because it may be difficult to obtain eggs from females under labo-
ratory conditions. We estimated the fecundity of feral adults of the damselfly by
dissection.

MATERIAL AND METHODS

Material originates from Mie and Shizuoka Prefectures, both in the warm-temperate zone of
Japan, where the populations were entirely univoltine. Females were collected during feeding,
roosting, tandem flight and ovipositing, from May to September in 1985. They were immediately
put into 50% ethyl alcohol, and the condition and length of their hind wings and abdomen were
recorded. Since the colour of the abdomen and the degree of worn wing condition may indicate the
attainment of physiological female sexual maturity (e.g. McVEY, 1985; ROBERTSON, 1985), they
were classified into seven age classes, viz.: T: newly emerged; — I: immature with yellow abdomen;
— II: older immature with yellow-orange abdomen; — P: premature with yellow-green abdomen; —
M: mature with green abdomen and wings with no visible damage; — MM: older mature with soiled
tip of the abdomen and tattered wings; and — MMM: the oldest category with soiled abdomen and
very tattered wings.

All dissected individuals were examined for the number of eggs remaining in the ovaries. The
height, the width and the length of the bursa copulatrix were measured for calculation of its volume
as a spheroid.

Eggs in the ovaries were classified into three categories: mature, submature and immature eggs.
Mature eggs were large, coloured yellow-orange, and seemed large enough to be ready for oviposi-
tion. The volume of the mature egg was also calculated as an oval, though it had a process of about
0.17 mm. The submature eggs were smaller and coloured lighter than the mature ones. Immature
eggs, which include oocytes, contain no yolk and are white.

The numbers of mature and submature eggs were counted directly. Since immature eggs were not
separated from each other under a microscope, we were not able to evaluate the number. Instead, we
assessed the abundance of immature eggs in the ovaries by four degrees: r, +, ++ and +++.
These are rare, a few, common and abundant, respectively.

Besides the dissection of wild-caught adults, last instar larvae were collected near the study sites in
order to clarify the duration of each adult stage in the laboratory. The larvae were reared individu-
ally. When the adults emerged, they were each put into a cage (30 cm × 40 cm × 45 cm), in which they
were fed mosquitoes.

All means are reported with their standard errors.

RESULTS

DURATION OF EACH AGE CLASS IN LAB-REARED POPULATION

Fifty-eight males and 58 females were reared in the laboratory from larvae.
There were no differences in size (length of hind wing) between wild-caught and
laboratory-reared females (F = 0.175, n.s.).

A shown in Figure 1, the duration of the age T was 1 day in both sexes. Then,
males spent ca 7 days at age I, and ca 5 days at age II, while females spent ca 6 days

and 7 days at ages I and II, respectively. However, these values were not significantly different between sexes in each age (U-test, n.s.) or among the ages in both sexes (F = 3.022 in males, F = 0.611 in females). Therefore, it is likely that the duration of each immature age might be about 6 days in each sex, though we only examined one female during ages P and M. If so, the period of maiden flight in this species was estimated as 19 days. Since the adults were sacrificed before age MM, we could not evaluate the duration of MM or MMM.

VOLUME OF THE BURSA COPULATRIX IN FIELD-CAPTURED FEMALES

Ninety-six females were collected in the field and dissected. The length of the abdomen was 37.89 ± 0.17 mm (max. 41.5 mm and min 32.0 mm) and that of the hind wing was 24.43 ± 0.17 mm (Max 28.0 mm and min 19.0 mm).
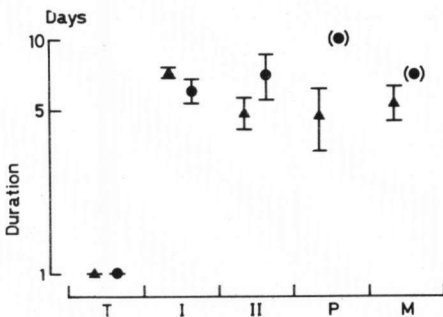

Fig. 1. Duration in each age class. A circle and a triangle represent a female and a male, respectively. Parentheses indicate one sample. See text for the ages T, I, II, P and M. Sample size was, 8, 8, 7, 4 and 3 in males, and 11, 11, 6, 1 and 1 in females of the age T, I, II, P and M, respectively.

Newly emerged females (age T) had a small fat body which filled in the cavity of the abdomen. However, the fat body increased toward the age M and then decreased. The fat body therefore seemed not to represent reserves stored from larval feeding as in lepidopteran insects (e.g. STERN & SMITH, 1960).

At age T, the bursa copulatrix was a thin flat ellipse and the volume was about 0.007 mm³ (Fig. 2). It gradually increased to about 0.01 mm³ in ages I and II, and became thicker in age P (about 0.02 mm³). However, no sperms were found in it. From age M, the bursa copulatrix became oval (Fig. 3), with a volume that was rather constant throughout the three age classes (M, MM and MMM). About 0.08 mm³ was the maximum volume of the bursa copulatrix.

THE NUMBER OF EGGS IN THE OVARIES OF FIELD CAPTURED FEMALES

As shown in Figure 4, the abundance of immature eggs decreased with age (r² = 0.29, P < 0.001). Submature eggs appeared at age II, and their number increased until age P, but decreased throughout subsequent reproductive ages. On the other hand, mature eggs were found from age P, the peak number being about 363 at age M. They decreased to 110 eggs during age MMM. Such a

difference may be accounted for by egg deposition.

Mature egg volume ($\times 10^{-3}$ mm³) of each age was 12.04 ± 0.27 (n =70), 11.35 ± 0.21 (n =100), 10.69 ± 0.16 (n =120) and 11.33 ± 0.24 (n =72) in age P, M, MM and MMM, respectively. It showed that mature egg size decreased significantly with age (t =2.845, 0.005 > P > 0.001).

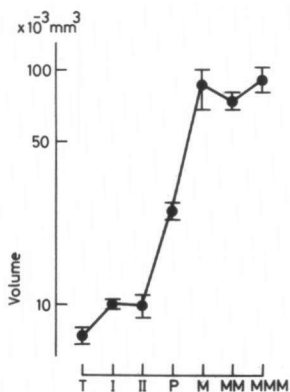Fig. 2. Change in the volume of the bursa copulatrix in relation to female age. Sample size was 12, 27, 8, 14, 11, 16 and 8 in age classes of T, I, II, P, M, MM and MMM, respectively.

If egg maturation occurred during the oviposition period, the proportion of the number of submature to mature eggs should be rather constant in any female, even though they will oviposit. In other words, when the number of submature eggs is plotted against the number of mature eggs in each age class, the regression coefficient, b, must be constant (cf. WATANABE et al., 1986). As shown in Figure 5, a significant correlation was found in age P, M, and MMM, with a probability less than 0.01. The regression coefficient in age P was the highest (4.55) but that in age M was the lowest (-0.33). Although the correlation in age MM was not clear (b =-0.14, t =0.71, n.s.), the regression coefficient again increased toward the age MMM (1.40). Since the oldest females have a few submature and some mature eggs, little egg maturation was supposed to occur in MM and MMM, and egg maturation seemed to occur mainly in the age P. Three regressions intersected each other at the point about 150 submature and 300 mature eggs, though the regression in the age MM did not.

DISCUSSION

A maiden flight period, during which the colour changes occur, has been observed in many damselfly species. For example, CORBET (1952) reported an initial maturation period of 15 days in *Pyrrhosoma nymphula*. UEDA (1978) estimated the duration of the maiden flight to be about 2 weeks in *Lestes sponsa*. The time between the onset of emergence and the onset of oviposition in *L. rectangularis*, was 21 or 24
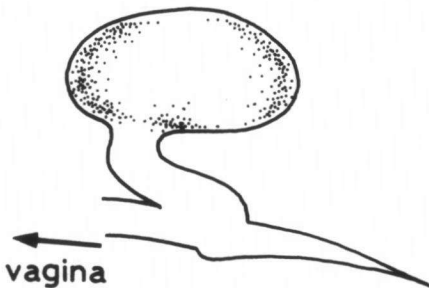

vagina

Fig. 3. Illustration of bursa copulatrix filled with sperm in a mature female.

days, and oviposition continued for 4.5 weeks following the cessation of emergence (GOWER & KORMONDY, 1963). In a laboratory-reared population of *C. annulata,* the duration of the immature stages from age T to P was estimated as about 19 days. McVEY (1985) showed that the actual age of wild imagos is difficult to determine from the colour change of the abdomen because such parameters were much dependent on rearing conditions such as temperature and solar radiation. In this study, however, we collected individuals at age T in mid-May, but at age M in early-June, suggesting a maiden flight period of about 2 or 3 weeks in a wild environment, which was similar to the value observed in the laboratory-reared population.
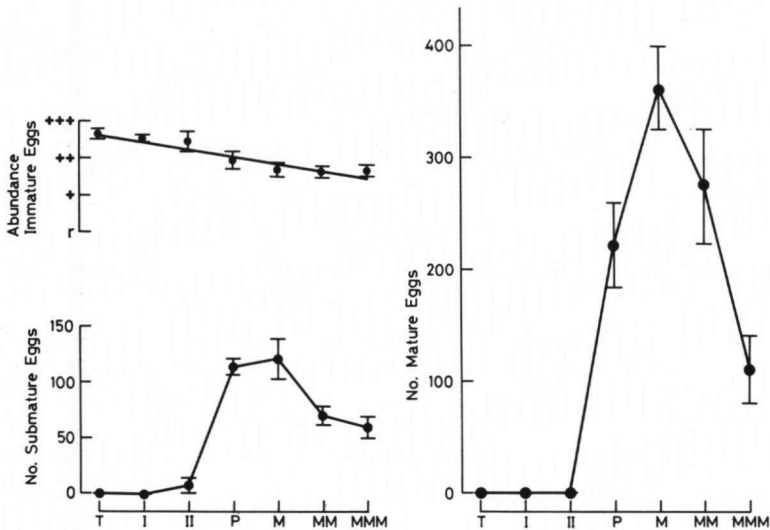

Fig. 4. Change in the abundance of immature eggs (above left) and the number of submature (below left) and mature eggs (right) in relation to female age. See Fig. 2 for sample size in each age class.

The volume of the bursa copulatrix has been measured in many damselfly species from the view point of sperm competition (e.g. WAAGE, 1979, 1982; FINCKE, 1984). In this study, the fact that the bursa copulatrix remained at a similar volume throughout the reproductive age of a female suggested that *C. annulata* males may remove the sperm of previous males and inseminate with a similar volume (cf. WAAGE, 1979).

There has been no report on the decrease in mature egg size in Odonata. However, Watanabe & Adachi (unpublished) observed a similar decreasing tendency in this and other damselflies, such as *L. sponsa, L. temporalis,* and *Platycnemis echigoana.* Although we do not know the adaptive significance of

smaller eggs deposited by older females, WIKLUND & PERSSON (1983) suggested that neither egg survival, larval survival, larval development time nor pupal weight is correlated with egg size, particularly egg weight, in the speckled wood butterfly, *Pararge aegeria*. Generally, the decrease of egg size is assumed to be due to the decrease in yolk size (e.g. KIMURA & TSUBAKI, 1985). However, KARLSSON & WIKLUND (1984) reported that there was no significant difference in hatchability, length of larval period or survival rate of larvae between larger and smaller eggs in the wall brown butterfly, *Lasiommata megera*. Therefore, damselfly females may increase their fecundity by depositing smaller eggs at an older age, at which they probably counteract their shorter life-expectancy with their low fat body.

CORBET (1962) stated that the number of eggs is difficult to determine accurately except by dissecting mature females which have not yet oviposited. It is
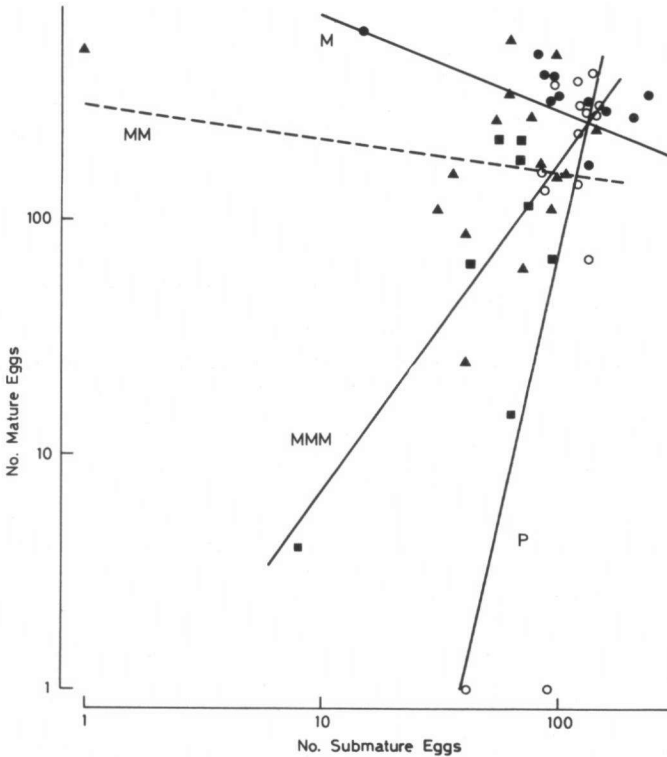

Fig. 5. Relation between the numbers of submature (s) and mature (m) eggs. — [Age P (circle): log m = 7.24 + 4.55 log s, r^2 = 0.53, 0.005 > P > 0.001, Age M (dot): log m = 3.20-0.33 log s, r^2 = 0.49, 0.025 > P > 0.01, Age MM (triangle): log m = 2.49-0.14 log s, r^2 = 0.04, n.s., and Age MMM (square): log m = -0.57+1.40 log s, r^2 = 0.58, 0.05 > P > 0.025].

still unknown, however, how quickly mature eggs are generated after oviposition. Figure 5 suggests little recovery of mature egg number during the reproductive period. A female increased her mature egg number only at age P, though she still had some immature eggs. Since a female at age P had not mated yet, such an increase in the egg number may result in high and low oviposition rates at the younger (age M) and the older (age MMM) reproductive ages, respectively. Therefore, in this species, 300 mature and 150 submature eggs is a reasonably conservative estimate of the fecundity and therefore the potential reproductive capacity, allowing the underestimate inherent in the measurement. The difference in the mature egg number between ages M and MMM of about 250 may be the fertility which is the actual reproductive performance in a female life span. This was about half the fecundity estimated on the basis of dissection.

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