

FECUNDITY OF *ISCHNURA GRAELLSII* (RAMBUR) IN THE LABORATORY (ZYGOPTERA: COENAGRIONIDAE)

A. CORDERO

Area de Ecología, Facultade de Bioloxía, Universidade de Santiago, ES-15071 Santiago,
Galicia, Spain

Received May 2, 1990 / Accepted July 24, 1990

Lifetime fecundity was studied in 50 females. In *I. graellsii*, fecundity is a positive function of reproductive lifespan (number of days after first oviposition) and body length. First clutch size is positively related to female body length; the age has no effect. The subsequent egg clutches are positively related to the inter-clutch interval (days from last oviposition) and body length, and negatively to female age. Maximum egg production is obtained with clutches every day. Consequently, females would maximize their lifetime egg production by minimizing their inter-clutch intervals rather than by maximizing the size of each clutch. Since the fecundity is positively related to female size, and larval density is negatively related to adult size, there may be a density dependent regulatory process of the population size.

INTRODUCTION

Female fecundity is potentially a very important factor in the regulation of insect populations (PRICE, 1975). In most arthropods it is considered axiomatic that increased weight or size results in increased fecundity, but LEATHER (1988) has pointed out that female longevity could be more important for regulating fecundity in natural populations than any relationship between size and fecundity.

Until now, factors affecting fecundity have been studied in detail only in *Coenagrion puella* (BANKS & THOMPSON, 1987a). The results of this study show that larger females produce more eggs because they live longer, but the size of one-day clutches is negatively correlated to female body size. This inverse relationship could be due to the way in which the energetic cost of flight scales with size (BANKS & THOMPSON, 1987a). For example, WICKMAN & KARLSSON (1989) showed that in some butterflies, larger individuals have a proportionately smaller wing area than would have been expected from

geometric similarity, and probably they would be forced to expend more energy in flight.

CROWLEY et al. (1987) have produced a model of the dynamics and regulation of a generalized damselfly population, and have indicated the lack of studies on the relationship between size and fecundity in Odonata. This study and BANKS & THOMPSON (1987a) have indicated the possible existence of a density-dependent regulatory process of the population, acting through the reduction in adult female size (and therefore fecundity) caused by high larval population density.

In this paper I present the results of a laboratory study on the lifetime fecundity in *Ichnura graellsii* (Rambur). The use of insectaries allows the study of animals during their whole life, eliminating mortality caused by predation and thus providing the potential fecundity. A second advantage is that in the laboratory, unlike in the field, it is possible to know the reproductive history of every individual. This study, therefore, complements the work of BANKS & THOMPSON (1987a) on a natural population.

METHODS

Fifty females obtained from laboratory-reared larvae were maintained in insectaries of 50x50x50 cm, placed in a chamber maintained at 21-23°C, 60-80% humidity and 15:9 hours of light:darkness (detailed methods are in CORDERO, 1990a, 1990b). All individuals were marked and measured from head to the tip of abdomen (to the nearest 0.1 mm) in the first hours after emergence.

In a first series, I measured the fecundity of 31 females obtained from the F₂ generation reared in the study of female polymorphism of this species (CORDERO, 1990b). This series includes 25 females previously used in the study of the relationship between copula duration and fecundity (CORDERO, 1990a). In the second series I measured fecundity of 19 females from the F₄ generation.

After 1 or 2 copulations insects were allowed to oviposit every 2-3 days in the first series and every day in the second series. They were placed for at least 2 hours in individual oviposition chambers with damp filter paper as an oviposition substrate. Eggs were maintained in the same conditions as adults, and after larval eclosion eggs were fixed in 70% ethanol and counted under a binocular microscope. Five females produced first clutches that were less than 5% of the size of second clutches. These were considered as outliers, therefore, eggs of first clutches were added to second clutches which were considered as the first.

Data on number of copulations, age, longevity, mature lifespan, interval between clutches, and order of the clutch (x) were transformed as $\sqrt{x + 1/2}$ before being entered into the correlation analysis (STEEL & TORRIE, 1985). Equations are presented for transformed variables. Values are given as means \pm 1 SE.

RESULTS

The 50 females laid a mean of 1019 ± 78.4 eggs over their lifetime. Both series were homogeneous in fecundity (Mann-Whitney $U = 0.18$, $p = 0.857$) and longevity ($U = 0.53$, $p = 0.596$), although mean body size of females of the first

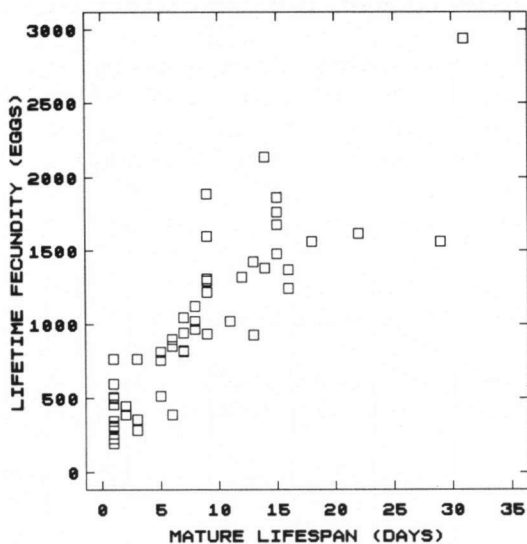


Fig. 1. The relationship between fecundity and mature lifespan in 50 females of *I. graellsii*.

clutches (zero in 9 females that only produced one clutch). The only correlated variables were mature lifespan (L) and body length (B), both variables accounting for 83% of variance. The predictive equation is:

$$\text{Lifetime fecundity (eggs)} = 471.365 L + 123.635 B - 3869.890 \quad [1]$$

$$r = 0.909, N = 50, p < 0.0001$$

An equation was obtained for the number of eggs of the first clutch of the female, using body size and age as predictor variables (one female that laid very few eggs in her three first ovipositions was excluded). Surprisingly only body length (B) was correlated. Figure 2 shows the relationship between both variables. The equation is:

$$\text{First clutch (eggs)} = 78.594 B - 1917.659 \quad [2]$$

$$r = 0.595, N = 49, p < 0.0001$$

The equation for clutch size for subsequent clutches of each female was obtained using body length (B), inter-clutch interval (days, I), age and order of the clutch (O). Age did not enter in the model, because order was more correlated:

$$\text{Clutch size (eggs)} = 132.529 I + 17.897 B - 49.903 O - 433.529 \quad [3]$$

$$r = 0.599, N = 220, p < 0.0001$$

As expected, clutch size depends on the inter-clutch interval (Fig. 3). For 1-day clutches, the effect of female body length on clutch size was not significant ($r = 0.02$, $N = 93$, $p = 0.841$, Fig. 4A), but for 2-day clutches, body size was positively correlated with clutch size ($r = -0.33$, $N = 102$, $p = 0.0006$, Fig. 4B). The effect of female age was negative on 1-day clutches ($r = -0.37$, $N = 93$, $p = 0.0002$, Fig. 5) and 2-day clutches ($r = 0.33$, $N = 102$, $P = 0.0007$, Fig. 5). For longer inter-clutch inter-

series (29.4 ± 0.2 mm, $N = 31$) was greater than that of the second series (28.0 ± 0.2 mm, $N = 19$; $t = 4.71$, $p < 0.0001$).

The lifetime fecundity clearly depends on the duration of the mature lifespan (the number of days lived after first oviposition, Fig. 1). Using a stepwise multiple regression procedure, I obtained a predictive equation for the lifetime fecundity (F to enter in the model = 4). I used as predictive variables longevity, mature lifespan, number of matings, body length, number of clutches, and mean interval between

vals the small sample size impedes the analysis. The partial correlation coefficient between body length and clutch size, controlling for the effect of age, was also not significant for 1-day clutches ($r = -0.05$, $p > 0.5$) and significant for 2-day clutches ($r = 0.35$, $p < 0.001$).

Lifetime fecundity of the three female coloration phenotypes of this species (CORDERO, 1990b) was similar (Kruskal-Wallis ANOVA = 4.19, $p = 0.123$), as was body length ($F = 0.43$, $p = 0.650$), but not longevity (Kruskal-Wallis ANOVA = 19.61, $p < 0.0001$). An a posteriori test (SIEGEL & CASTELLAN, 1988) showed that the only difference was that longevity of *aurantiaca* females (15 ± 0.9 days, $N = 20$) was less than that of both androchromotypic (21.7 ± 1.3 , $N = 17$) and *infuscans* (25.7 ± 2.1 , $N = 13$) females. This was due to differences among families and not to an effect of the phenotype (Cordero, unpublished data).

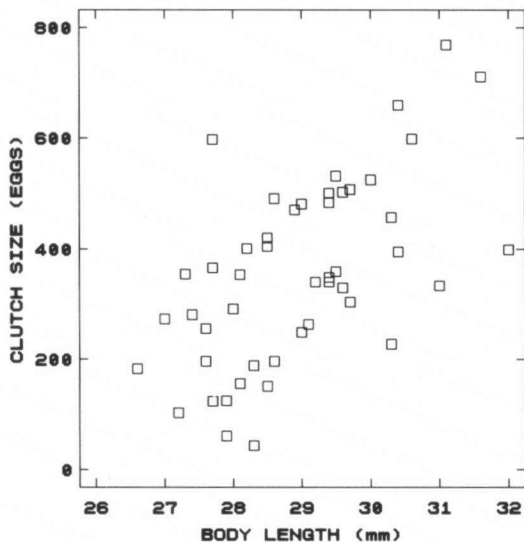


Fig. 2. The effect of female body length on the number of eggs of the first clutch ($N = 49$ females).

DISCUSSION

CORDERO (1990a) showed that copula duration is not correlated with female fecundity in *I. graellsii*. The present study indicates that mature lifespan and body length are the most important factors affecting lifetime fecundity in this species. Because mean mature lifespan is about 5–6 days in different natural populations (Cordero, 1987, unpublished data), most females will not realise their potential fecundity (one female was able to lay 2937 eggs in 32 days of mature lifespan). This occurs in many insect species (LEATHER, 1988).

In *C. puella*, for 1-day clutches there is a negative relationship between female body size and clutch size, but larger females lay more eggs because they live longer (BANKS & THOMPSON, 1987a). In our study, female size had no effect on 1-day clutches, but its effect was positive on 2-day clutches, first clutch and lifetime fecundity. There was no relationship between female size and longevity (series 1, $r = -0.28$, $p = 0.126$; series 2, $r = -0.30$, $p = 0.208$). If the energetic cost of

flight is greater in large females, then the amount of energy available for egg production may be a decreasing function of body size (BANKS & THOMPSON, 1987a). If larger females mature eggs more slowly, for 1-day clutches the effect of female body length on clutch size would not be important. Unfortunately, data on the size of 1-day clutches for the largest females (31-32 mm) are not available (Fig. 4A). For 2-day clutches the positive relationship may be produced because larger females have more room for eggs inside, as indicated by the relationship between the size of the first clutch and body length (Fig. 2). In 7 butterfly species and one fly, WICKMAN & KARLSSON (1989) have shown that abdomen size shows a positive allometric increase with body size, despite the increased cost of flight suggested by the scaling of wing area and muscle mass to body size. Therefore, an increase in fecundity with body size is not self-evident (LEATHER, 1988; VICKMAN & KARLSSON, 1989), since abdomen size could be more important.

A surprising result of this study is that age had no effect on the size of the first clutch (partial correlation coefficient between clutch size and age, controlling for the effects of body size, $r = 0.14$, $p > 0.3$). The age of females at first oviposition was 10.8 ± 0.4 days ($N = 49$, range 7-22 days). This indicates that egg maturation is very fast after emergence, and that first clutch size depends only on the space to store eggs. Aging reduces egg production (Fig. 5) as in other species of damselflies (WATANABE & ADACHI, 1987a, 1987b).

Figure 3 indicates that a 2-day clutch is smaller than two 1-day clutches, as occurs also with other inter-clutch intervals. Therefore, as in *C. puella* (BANKS & THOMPSON, 1987a) females maximize their lifetime egg production by minimizing the interval between clutches, rather than by maximizing clutch size.

Several studies have indicated that high larval densities (or the diminution of available food per individual) reduce adult body size in damselflies (PICKUP &

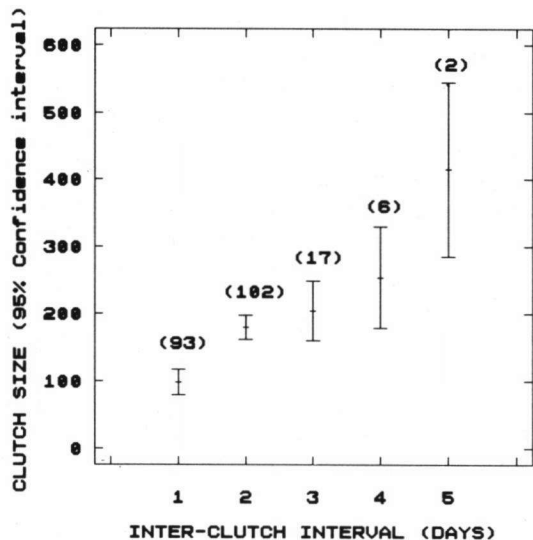


Fig. 3. The effect of inter-clutch interval on clutch size (first clutch is not included). Numbers are sample size.

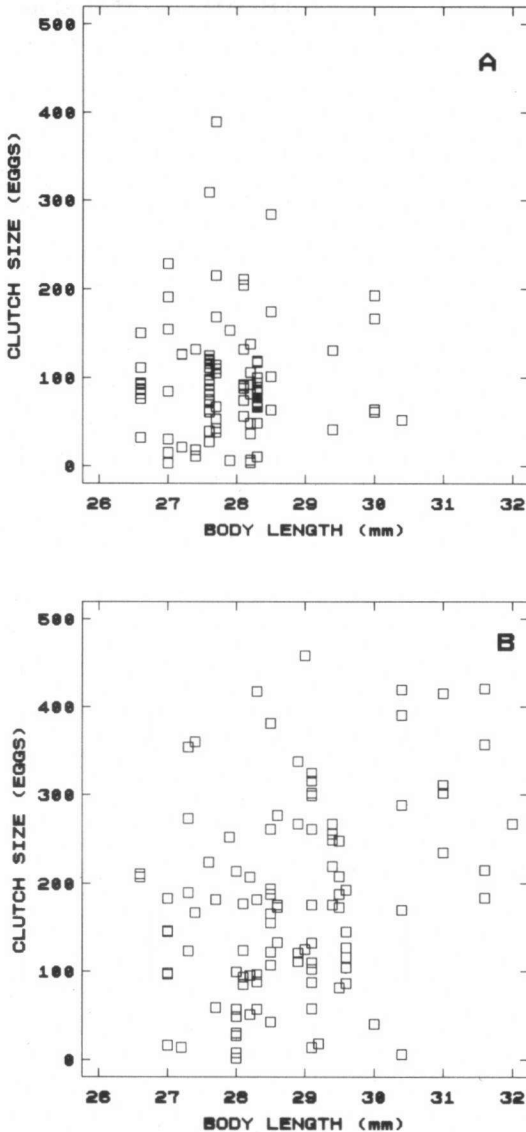


Fig. 4. The effect of female body length on the size of 1-day clutches (A) and 2-day clutches (B).

study females of both series laid similar numbers of eggs (although they differed in size) probably because they lived the same time.

In this study temperature was maintained constant at 21-23°C. BANKS &

THOMPSON, 1984; HARVEY & CORBET, 1985; BANKS & THOMPSON, 1987b). This occurs also in *I. graellsii* (Cordero, unpublished data). Therefore, it is possible that this mechanism could act as a regulatory process of the population size as BANKS & THOMPSON (1987a) and CROWLEY et al. (1987) suggested: when larval density increases, adult size will be reduced, resulting in reduced fecundity and then lower larval density. Nevertheless, taking into account the fact that the proportion of larvae that die during aquatic life is very high (99.8% of the eggs laid in *Cordulia aenea amuriensis*, UBUKATA, 1981; 97-99.6% of the maximum larval density in 14 dragonfly species, WISSINGER, 1988) it is difficult to know the importance of this mechanism in natural populations. Furthermore, very few adults (if any) will live long enough in the field to make evident a size effect on fecundity (LEATHER, 1988). For example, in this

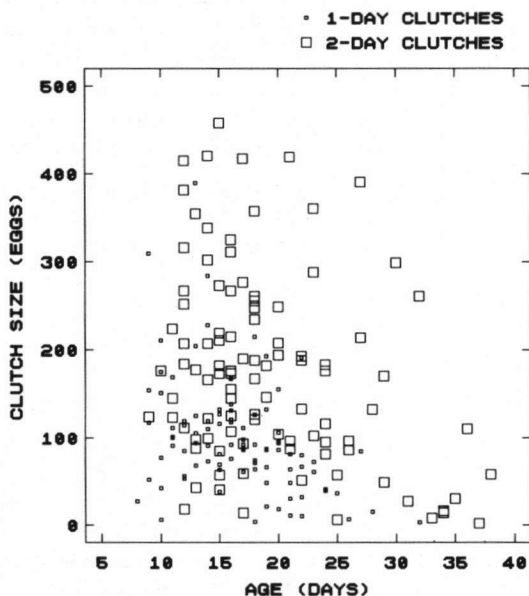


Fig. 5. The effect of female age on the size of 1 and 2-day clutches.

THOMPSON (1987a) indicate that bad weather reduces lifetime egg production of *C. puella* in two ways: by reducing clutch size and by increasing the inter-clutch interval. Therefore, it would be interesting to study how temperature affects fecundity in *I. graellsii*, because this species has two-generations per year (CORDERO, 1988). Low temperature would reduce egg production of the spring generation, and therefore a cyclic process could be produced, even in populations stable from year to year. Nevertheless, body size is greater in the spring generation than in the summer one (CORDERO, 1988), which has the opposite effect on egg production.

ACKNOWLEDGEMENT

This study was supported by a fellowship from the Spanish Ministry of Education and Science (Plan de Formación del Personal Investigador).

REFERENCES

- BANKS, M.J. & D.J. THOMPSON, 1987a. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *J. Anim. Ecol.* 56: 815-832.
- BANKS, M.J. & D.J. THOMPSON, 1987b. Regulation of damselfly populations: the effect of larval density on larval survival, development rate and size in the field. *Freshw. Biol.* 17(2): 357-365.
- CORDERO, A., 1987. Estructura de población en *Ischnura graellsii* Rambur, 1842 (Zygop. Coenagrionidae). *Biol. Asoc. esp. Ent.* 11: 269-286.
- CORDERO, A., 1988. Ciclomorfosis y fenología en *Ischnura graellsii* Rambur, 1842 (Odonata: Coenagrionidae). *Actas 3 Congr. ibér. Ent.* 419-430.

- CORDERO, A., 1990a. The adaptive significance of the prolonged copulations of the damselfly, *Ischnura graellsii* (Odonata: Coenagrionidae). *Anim. Behav.* 40(1): 43-48.
- CORDERO, A., 1990b. The inheritance of female polymorphism in the damselfly *Ischnura graellsii* (Rambur) (Odonata: Coenagrionidae). *Heredity* 64(3): 341-346.
- CROWLEY, P.H., R.M. NISBET, W.S.C. GURNEY & J.H. LAWTON, 1987. Population regulation in animals with complex life-histories: formulation and analysis of a damselfly model. *Adv. ecol. Res.* 17: 1-59.
- HARVEY, I.F. & P.S. CORBET, 1985. Territorial behaviour of larvae enhances mating success of male dragonflies. *Anim. Behav.* 33: 561-565.
- LEATHER, S.R., 1988. Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos* 51: 386-389.
- PICKUP, J. & D.J. THOMPSON, 1984. The effects of prey density and temperature on the development of larvae of the damselfly *Lestes sponsa* (Hans.) (Zygoptera: Lestidae). *Adv. Odonatol.* 2: 169-176.
- PRICE, P.W., 1975. *Insect ecology*. Wiley, New York.
- SIEGEL, S. & N.J. CASTELLAN, 1988. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- STEEL, R.G.D. & J.H. TORRIE, 1985. *Bioestadística: principios y procedimientos*. McGraw-Hill, Bogotá.
- UBUKATA, H., 1981. Survivorship curve and annual fluctuation in the size of emerging population of *Cordulia aenea amuriensis* Selys (Odonata: Corduliidae). *Jap. J. Ecol.* 31: 335-346.
- WATANABE, M. & Y. ADACHI, 1987a. Fecundity and oviposition pattern of the damselfly *Copera annulata* (Selys) (Zygoptera: Platycnemididae). *Odonatologica* 16: 85-92.
- WATANABE, M. & Y. ADACHI, 1987b. Number and size of eggs in three Emerald damselflies, *Lestes sponsa*, *L. temporalis* and *L. japonicus* (Odonata: Lestidae). *Zool. Sci.* 4: 575-578.
- WICKMAN, P.-O. & B. KARLSSON, 1989. Abdomen size and the reproductive effort of insects. *Oikos* 56: 209-214.
- WISSINGER, S.A., 1988. Spatial distribution, life history and estimates of survivorship in a fourteen-species assemblage of larval dragonflies (Odonata: Anisoptera). *Freshw. Biol.* 20: 329-340.