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THE EFFECT OF SEX AND AGE ON SURVIVORSHIP OF ADULT DAMSELFLIES IN THE LABORATORY (ZYGOPTERA: COENAGRIONIDAE)

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Longevity in the laboratory was measured for 1071 individuals of *Ischnura graellsii*, 75 of *I. pumilio*, 127 of *Coenagrion scitulum* and 41 of *Enallagma cyathigerum*. Individuals were maintained in 5 insectaries (50x50x50 cm) with numerous perching substrates, and adults of *Drosophila* were added as food. Results indicate that males do not live as long as females, in all spp., although the difference was not significant for *C. scitulum*. Most *I. graellsii* adults were obtained from the offspring of 33 laboratory crosses. In this sp. a 2-way ANOVA indicated significant effects of both family and sex on longevity, and family-sex interaction occurred in the F_1. It is suggested that this sex difference in longevity is mainly due to the contrasting behaviour of the 2 sexes: males spent much time in prolonged flights looking for females, and great harassment occurred between them. This activity is likely to reduce the longevity. The longevity of 3 ♀ phenotypes of *I. graellsii* was similar. Although in all spp. mortality was rather age-independent, a maximum was recorded in the age-class of 4-5 days. This could be due to the failure of some individuals to capture the *Drosophila*, and could explain the low recapture rate of teneral individuals in the field. Marking had no effect on mortality. This suggests that the low recapture rate, observed in many field studies the day after marking, is probably due to greater dispersal rather than to mortality. The sequence of emergence of both sexes was random in all spp., and so was the sequence of female phenotypes in *I. graellsii* families. Mortality and deformation during emergence affected ca 11-13% of adults. The importance of insectaries for the study of adult damselflies is discussed.

INTRODUCTION

Studies on demography in adult coenagrionids have become common in the last few years (CORBET, 1952; PARR, 1965; BICK & BICK, 1968; PARR, 1973a, 1973b; VAN NOORDWIJK, 1978; GARRISON & HAFERNIK, 1981;

ROBINSON, 1983; ROBINSON et al, 1983; CORDERO, 1987; DAY, 1987; HAMILTON & MONTGOMERIE, 1989). These are based on marking and recapturing individuals in natural populations. Usually the field data indicate that females live less long than males (e.g. CORBET, 1952; PARR, 1965; BICK & BICK, 1968; VAN NOORDWIJK, 1978; GARRISON & HAFERNIK, 1981; FINCKE, 1982; CORDERO, 1987). Nevertheless, it is commonly assumed that both sexes actually have a similar longevity, and it is their unequal distribution in the field (as a by-product of the aggressive and territorial behaviour of males and greater dispersal of females) that explains the seeming difference (GARRISON & HAFERNIK, 1981; ROBINSON & FRYE, 1986; HINNEKINT, 1987).

To test this hypothesis, HINNEKINT (1987) maintained 91 individuals of *Ischnura elegans* (Vander L.) in the laboratory, using live *Drosophila* as food. He cut the wings at the nodus and maintained the insects in plastic boxes, presenting food by forceps. The results showed that in the laboratory the longevity in both sexes was similar. To my knowledge, no other study on a captive damselfly population has been published.

I maintained a laboratory population of *Ischnura graellsii* (Ramb.) during two years (CORDERO, 1990a). In addition to the parental generation, three generations were reared and more than 2,400 adults obtained. The aim of this paper is to present data on longevity under laboratory conditions of some of these individuals and to investigate whether there are sex or phenotype-related (in females) differences in survivorship. Unlike HINNEKINT (1987) I used winged specimens, maintained in insectaries, to produce more natural conditions. Additional data on longevity under laboratory conditions are presented for *Coenagrion scitulum* (Ramb.), *Ischnura pumilio* (Charp.) and *Enallagma cyathigerum* (Charp.).

METHODS

To maintain adult damselflies in the laboratory, I used five insectaries of 50x50x50 (or 70) cm, covered with aluminium foil, which reflects sufficient light and impedes escape responses (JOHNSON, 1965). Numerous wood twigs were placed inside the insectaries to provide perches, and several culture bottles of *Drosophila* were added to supply food. Insectaries were placed in a chamber maintained at 21-23° C, 60-80% humidity and a photoperiod of 15L:9D hours. Illumination was provided by 19 fluorescent lamps of 58 W, placed 1 m above the insectaries and which produced about 1000 lux in the centre of the insectaries.

A hundred *I. graellsii* individuals were collected from 5 different natural populations in Galicia (NW Spain) during August-September 1987 (parental generation). This generation was maintained in the same insectaries but at room temperature and received natural indirect light (photoperiod of August-September). Most data are from adults obtained from the offspring of 33 females mated in the laboratory (F_1, F_2 and F_3 generations of CORDERO, 1990a). During F_1 and F_3, insectaries were examined daily, searching for dead specimens. In F_2, this was made only during a short period. Males and females were maintained separately in order to obtain virgin specimens for genetic and behavioural experiments (CORDERO, 1990a, 1990b).

Adults of *I. pumilio* were obtained from the offspring of 5 field-collected females, and 3 F_1 crosses. Larvae were reared as in *I. graellsii* (CORDERO, 1990a). Adults of *C. scitulum* and *E. cyathigerum*

were obtained from penultimate and last instar larvae collected in two ponds near Santiago (Galicia, Spain), and reared to emergence in the laboratory.

After emergence, adults were measured (total body length, to the nearest 0.1 mm), individually marked and introduced in one of the insectaries. An attempt was made to maintain the food supply (adult *Drosophila*) as abundant as possible. The damaged individuals (either as a result of marking, or by mortality and deformation during emergence) and individuals dead as result of cannibalism (which happened occasionally) were not included in the life table analyses.

RESULTS

Table I shows mean longevity under laboratory conditions for all species. Comparing longevity between sexes, it has been found that males lived shorter than females in all species other than *C. scitulum*. This difference could be due to several, mutually not excluding factors: (1) sex-related genetic factors; (2) effect of the insectaries (different availability of food), since the sexes were maintained in separate insectaries; (3) in *I. graellsii* the difference between the sexes could be an artifact, due to differences among families and the unequal distribution of data for males and females in different families.

Table I

Longevity (days from emergence to death) of damselflies in the laboratory. – [Sx = standard deviation; – N = sample size; – p = significance level from a Mann-Whitney U test comparing longevity between sexes]

Species & group	Sex	Mean	Sx	N	p
I. graellsii					
Parental	♂	13.3	9.3	27	0.290
	♀	17.0	12.7	55	
F_1	♂	8.0	6.3	211	<0.0001
	♀	11.2	7.1	238	
F_2	♂	10.1	7.2	20	0.180
	♀	13.4	6.5	57	
F_3	♂	7.1	6.1	225	0.013
	♀	8.7	6.5	238	
Total	♂	7.9	6.6	483	<0.0001
	♀	11.0	7.9	588	
I. pumilio	♂	10.7	7.1	48	0.012
	♀	16.3	10.1	27	
C. scitulum	♂	6.5	6.1	59	0.249
	♀	6.8	6.4	68	
E. cyathigerum	♂	11.3	5.0	23	0.026
	♀	16.1	7.7	18	

The available data do not allow a clear discrimination between the hypotheses (1) and (2). Unfortunately, both sexes could not be maintained in the same insectary, because I needed to obtain virgin specimens for genetical experiments and, secondly, because males produced great harassment of females when placed in the same insectary, even when males and females of different species were placed together. In *I. graellsii*, a two-way ANOVA was carried out to compare longevity between sexes and families in F_1 and F_3 generations. The results are presented in Table II. In both generations, the family and sex had a significant effect on longevity, and there was interaction between both effects in the F_1 generation. A similar analysis was made for *I. pumilio*. In this case, only 3 families were available and the results indicate significant differences between these (F-ratio: 6.71, df: 2, $p = 0.02$), but not between the sexes (F: 0.35, df: 1, $p = 0.56$), and no significant interaction was found (F: 1.71, df: 2, $p = 0.19$). The effect of families is not relevant in *C. scitulum* and *E. cyathigerum*, because these adults were unrelated.

Table II

Two-way ANOVA to compare the effect of family and sex on longevity in adult *I. graellsii*. Data were log-transformed before analysis. Only families with at least 10 data per group are included

Generation	Source of variation	Sum of squares	d.f.	F-ratio	Sig. level
F_1	Main effects	28.214	10	5.256	0.0000
	Family	13.880	9	2.873	0.0027
	Sex	13.141	1	24.480	0.0000
	Family-sex interaction	15.435	9	3.195	0.0010
	Residual	210.959	393		
	Total	254.608	412		
F_3	Main effects	32.528	11	5.121	0.0000
	Family	27.667	10	4.791	0.0000
	Sex	4.165	1	7.231	0.0075
	Family-sex interaction	4.291	10	0.743	0.6838
	Residual	254.672	441		
	Total	291.491	462		

In the F_1 generation of *I. graellsii* (the only one for which sufficient data are available) insectaries had a significant effect on female longevity (insectaries 1, 2 and 3; Kruskal-Wallis test = 16.710, $p = 0.0002$), but not on that in males (insectaries 3, 4 and 5, Kruskal-Wallis test = 3.548, $p = 0.170$). This effect could

be produced by unequal distribution of families in the insectaries. Unfortunately, due to the small sample size, a Three-Way ANOVA was not possible. Insectary number 3 was used in different moments for males and females. Taking into account data on longevity from individuals maintained in this insectary, no difference was found between the sexes (Kruskal-Wallis test = 1.238, p = 0.266, N = 14 males and 30 females).

Another factor to take into account is the possible effect of body size on longevity. In all species there are significant differences between the sexes in body size: males are smaller than females in *I. graellsii* and *I. pumilio*, but are greater in *C. scitulum* and *E. cyathigerum*. If longevity and body size were significantly correlated, then one sex would live less due to the size difference. Nevertheless, no significant relationship between size and longevity was found in males of any species (Tab. III), and in females this relationship seems inconsistent.

Table III

The relationship between body length and longevity in adult damselflies in the laboratory – [r= Spearman rank correlation coefficient; – N= sample size; – p= significance level]

Species	Group	Males			Females		
		r	(N)	p	r	(N)	p
I. graellsii	Parental	-0.388	(13)	0.18	-0.353	(35)	0.04
	F_1	-0.074	(207)	0.29	-0.005	(231)	0.94
	F_2	-0.203	(29)	0.38	-0.282	(56)	0.04
	F_3	0.008	(224)	0.90	0.114	(237)	0.08
I. pumilio		-0.087	(48)	0.55	0.454	(24)	0.03
C. scitulum		0.031	(59)	0.81	0.023	(68)	0.85
E. cyathigerum		0.015	(22)	0.94	0.115	(18)	0.63

I. graellsii has three female phenotypes of coloration: androchromotypics (A, coloured as males) and two gynochromotypics (forms *infuscans* [I] and *aurantiaca* [O]) (CORDERO, 1990a). Significant differences were found in longevity among them in F_1 (Kruskal-Wallis test = 28.4, $P < 0.001$), F_2 (K-W = 11.3, p = 0.010) and F_3 (K-W = 9.4, p = 0.025) generations (not enough data are available for the parental generation). Females were assigned to insectaries independently of phenotype, trying to maintain similar densities. But taking into account the existence of significant differences among families, the appropriate test is to compare female phenotypes within families (a two-way ANOVA is not possible due to the presence of 1, 2 or 3 phenotypes per family). Results of these comparisons (Mann-Whitney test) showed no significant differences in any of the 10 F_1

Table IV

Average lifespan [mean ± SE(N)] in days of andro- and gynochromotypic females of *Ischnura graellsii* in the laboratory. Family codes are the same as in CORDERO (1990a). Mann-Whitney U test

Family	Androchromotypics	*infuscans*	*aurantiaca*	Test	p
L	–	20.5 ± 4.4(4)	10.0 ± 6.0(2)	-1.157	0.247
M	–	16.2 ± 3.1(6)	9.1 ± 1.1(12)	-1.842	0.065
H	9.8 ± 1.4(15)	10.8 ± 2.1(11)	–	0.468	0.639
N	10.3 ± 2.1(4)	11.0 ± 8.5(3)	–	-0.360	0.719
P	–	8.3 ± 2.8(6)	11.7 ± 1.8(11)	1.160	0.246
R	7.9 ± 1.1(20)	7.0 ± 3.5(4)	–	-0.351	0.726
S	12.4 ± 1.6(23)	16.5 ± 3.2(11)	–	1.070	0.285
T	10.9 ± 0.9(19)	10.8 ± 3.5(4)	–	0.000	1
U	10.8 ± 2.3(9)	–	11.9 ± 1.8(9)	0.356	0.722
X	7.6 ± 1.4(13)	8.2 ± 1.7(18)	–	-0.407	0.684
P12	10.1 ± 1.6(17)	–	8.9 ± 1.5(15)	-0.459	0.646
H16	10.7 ± 2.1(15)	20.0 ± 4.0(2)	–	1.351	0.177
U11	–	7.2 ± 2.0(9)	9.3 ± 1.5(12)	0.394	0.694
P11	–	13.9 ± 2.3(7)	11.8 ± 1.4(15)	-0.389	0.697
S31	10.9 ± 4.5(7)	–	11.1 ± 2.5(10)	0.591	0.555
H15	5.0 ± 1.5(8)	5.0 ± 1.8(6)	–	-0.340	0.734

or 6 F_3 families that produced two phenotypes (Tab. IV).

Figure 1 shows the survivorship curves in the laboratory for all species. In general, the slope was greater in males of all species. Two interesting facts are shown in Figure 1: (1) in *I. graellsii* the parental generation had a different slope; and (2) although mortality is rather age-independent, there were two moments of greater mortality: at 4-5 days of age and, particularly in *I. graellsii* females, at 12-14 days. This is more evident if the percentage of dead individuals is plotted versus age (Fig. 2). First mortality (4-5 days) was surprisingly high in *C. scitulum* (see Fig. 2b).

Taking into account the great number of individuals that emerged in the laboratory, it is interesting to test if the sequence is random with respect to sex and female phenotype (in *I. graellsii*), or alternatively, one sex or female form emerges before (or more grouped) than other. A runs test for randomness in dichotomized data was made (SOKAL & RHOLF, 1981). Results are presented in Table V for *I. graellsii* families and Table VI for other cases. Examining the tables, we can conclude that the sequence is random, both by sexes and by female phenotypes.

A second interesting aspect of emergence is the existence of mortality and damage during this process. This mortality may be great in natural populations (5-11% in *Anax imperator*, CORBET 1957; 28% in *Pyrrhosoma nymphula*, GRIBBIN & THOMPSON, 1990). In some cases in the laboratory, individuals were unable to complete metamorphosis with part of the larval exuviae (usually

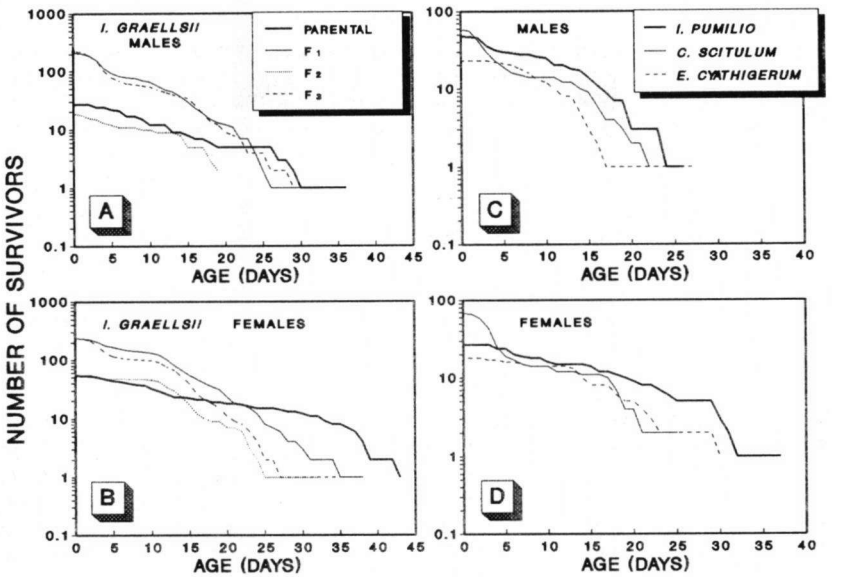

Fig. 1. Survivorship curves of adult damselflies in the laboratory: (A)-(B) parental and F generations of *I. graellsii*; – (C) males and – (D) females of *I. pumilio*, *C. scitulum* and *E. cyathigerum*.

one wing or the head, remained inside the exuviae). Data are presented in Table VII. Taking into account groups with greater sample size, this kind of mortality oscillated about 5-6% in the different species. Deformation during emergence affected another 6-7% of individuals. In *I. graellsii* these figures were similar in all generations, but some families showed surprisingly high rates of deformation and mortality (in one family 21% of females were unable to emerge, and another 11% were deformed during the metamorphosis).

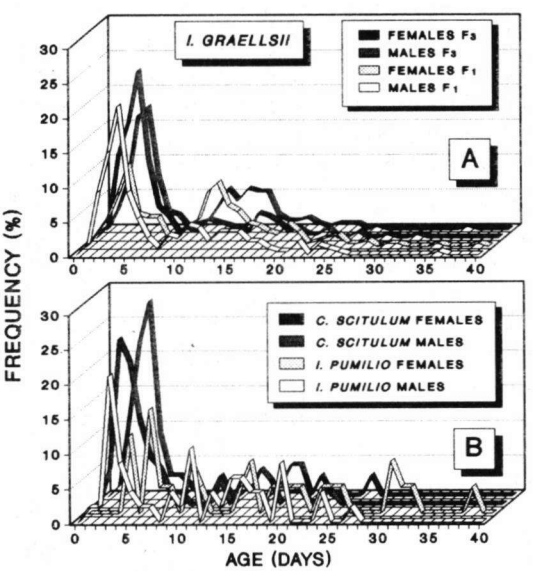

Fig. 2. Percentage of dead adult damselflies plotted versus age. Note the maximum at 4-5 days in all species and at 12-14 days in female *I. graellsii*.

Table V

Results of runs tests for randomness for the emergence sequence of both sexes (test 1) and female phenotypes (test 2, only in families that produced two female phenotypes) in laboratory-reared families of *I. graellsii*. – [Family codes are the same as in CORDERO (1990a); – letters in test 2 indicate female phenotypes (A = androchromotypics, I = *infuscans*, O = *aurantiaca*]

	Test 1			Test 2		
Family	Runs	Expected	p	Runs	Expected	p
B	17	16.4	0.957			
C	28	34.9	0.113			
L	30	29.1	0.907	19	16.9	0.573 IO
M	38	44.0	0.235	16	22.3	0.068 IO
H	56	54.9	0.911	32	28.9	0.474 AI
J	24	23.3	0.952			
K	27	24.3	0.515			
N	10	10.9	0.853	32	28.9	0.474 AI
P	45	51.5	0.227	22	23.6	0.737 IO
R	49	48.0	0.917	10	9.9	0.725 AI
S	46	53.1	0.191	21	22.4	0.755 AI
T	46	46.0	0.919	20	18.5	0.686 AI
U	48	51.0	0.618	30	26.5	0.394 AO
X	52	50.0	0.761	23	24.7	0.726 AI
S1	19	24.9	0.048			
M2	34	41.7	0.100	27	25.8	0.849 IO
S3	34	32.2	0.690	23	24.7	0.675 IO
U1	29	28.4	0.960	36	35.5	0.999 AO
C2	45	49.2	0.428			
P1	25	30.2	0.141	26	31.9	0.167 AO
N1	30	35.0	0.212			
H1	41	45.6	0.345			
P12	29	31.8	0.549	23	21.0	0.619 AO
C21	43	48.7	0.286			
H16	24	24.8	0.922	8	7.8	0.829 AI
U11	20	17.4	0.429	12	13.9	0.566 IO
P11	29	30.5	0.794	15	15.4	0.969 IO
H11	24	27.1	0.463			
S31	27	28.3	0.819	12	12.0	1.000 AO
P15	19	18.9	0.874			
H15	25	23.8	0.822	12	10.0	0.466 AI
U13	28	24.3	0.342			
H13	16	18.5	0.486			

DISCUSSION

Results of this study indicate that, in all species studied, males live less long than females in the laboratory, with significant differences in 3 out of 4 species.

Table VI

Results of runs tests for randomness for the emergence sequence of both sexes in the laboratory. Data for *I. graellsii* are from larvae collected at the same pond as *C. scitulum* larvae

Species	Runs	Expected	p
I. graellsii	141	150.7	0.285
I. pumilio			
Family 1	10	16.5	0.017
Family 2	13	11.8	0.467
Family 3	8	12.5	0.074
C. scitulum	111	105.5	0.486
E. cyathigerum	25	24.7	0.959

Table VII

Mortality and deformation during emergence of adult damselflies in the laboratory. – [N = sample size]

Species & group	Sex	Mortality (%)	Deformation (%)	N
I. graellsii				
Field collected larvae	♂	4.9	7.3	165
	♀	1.5	6.6	137
F_1	♂	3.3	2.1	517
	♀	1.5	1.8	547
F_2	♂	0.5	2.0	198
	♀	3.1	3.1	516
F_3	♂	0.7	2.5	281
	♀	2.6	1.3	309
I. pumilio	♂	1.9	7.6	53
	♀	0.0	5.9	34
C. scitulum	♂	5.8	2.9	103
	♀	7.6	2.8	106
E. cyathigerum	♂	3.5	0.0	29
	♀	0.0	0.0	20

Taking into account that experiments were made during 4 years, it is unlikely that this difference was completely due to an effect of the insectaries. First because food availability could not be always smaller in the insectaries of males, and secondly because many individuals were changed from one insectary to another, in attempts to maintain similar densities. In *I. graellsii*, some of the differences were due to an effect of the family (Tab. II). This significant effect of family on longevity could be produced by genetic differences between them. On the other hand differences in sexual behaviour between sexes could explain why males lived for less time. Males were continuously trying to find females, and harassment between them was common. This did not occur in females. Therefore, males could be expending more energy, and this could reduce longevity. This result is striking because in the field males seem to live longer than females, as was reported for *I. graellsii* in my first field experiment (CORDERO, 1987). Two populations of *I. graellsii* have been studied subsequently (Cordero, unpublished) and in both cases, perhaps due to greater sampling intensity, no difference was found in longevity between sexes. In agreement with this, HAFERNIK & GARRISON (1986) found the same survival rate for males and females of *Ischnura gemina* (Kennedy) in a low-density population, where they were able

to mark almost all individuals. Similar male and female longevities were also found by ROBINSON (1983), BANKS & THOMPSON (1985a) and HAMILTON & MONTGOMERIE (1989) in different coenagrionids.

The difference in slope from parental to F generations (Fig. 1A, B) in *I. graellsii* is likely to be due to the fact that temperature and photoperiod conditions were different and that parental generation was constituted by field-collected specimens of variable age (estimated from the thoracic coloration; CORDERO, 1987), rather than from laboratory-reared animals. The greater mortality at 4-5 days of age is noticeable if the percentage of dead individuals is plotted versus age (Fig. 2), and occurred in most species (the exceptions are *E. cyathigerum* and parental and F_2 generations of *I. graellsii*, where the sample size was smaller). This mortality was surprisingly high in *C. scitulum* (Fig. 2B). Conditions used in these experiments were not good for this species, because individuals did not show sexual behaviour (only one mating was obtained). This mortality before maturation is likely to be due to failure in capturing prey. Adults of *I. graellsii* can survive 3-4 days from emergence without food (pers. obs.). Any animal unable to seize the *Drosophila* would die at this age. The same mortality is present in HINNEKINT's (1987) results for *I. elegans*, although those animals were fed by hand. This may explain why most young and teneral specimens marked in the field are never recaptured (PARR & PARR, 1972; PARR, 1973b; CORBET, 1980; FINCKE, 1982; ROBINSON, 1983). A second greater mortality is evident in *I. graellsii* females at 12-14 days of age (Fig. 2A), and may be due to the physiological effects of egg maturation, particularly if, as in this case, most females were not allowed to oviposit. Again, a similar greater mortality is evident in HINNEKINT's (1987) data for female *I. elegans*.

Another interesting fact shown in Figure 1 is that mortality from day 0 (emergence and marking) to 1 was very low. In many field studies the proportion of recaptures after marking is significantly smaller than subsequent proportions of recaptures (PARR, 1973b; CORDERO, 1987; HAMILTON & MONTGOMERIE, 1989), and this is explained either as greater mortality, or dispersal due to marking. Results of this laboratory study indicate that this fact is likely to be due to migration out of the sampling area, rather than to increased mortality.

The fact that males and females, and the different female phenotypes, emerged in random sequence (Tabs V, VI) indicates that sex and female form have no effect on the competitive ability of larvae, at least under the laboratory conditions. In *Lestes viridis*, males and females emerged at the same time in a natural population (CORDERO, 1988), but in *Coenagrion puella*, females emerged before males (BANKS & THOMPSON, 1985b).

As this paper shows, adult damselflies are suitable for culturing in the laboratory. Some individuals live in these conditions much longer than in the field. Maximum longevity for *I. graellsii* in the field is one month (CORDERO, 1987), but one female lived 44 days in the laboratory. Similar and surprisingly long

lifespan was observed for a female *I. pumilio* fed by hand (57 days) and for this reason not included in the analysis. Although data for other species are scarce, lestids seem to survive well in insectaries, e.g. *L. viridis* [laboratory emerged]: 151 days (♂), 34 days (♀) (maximum longevity in the field is 77 days: CORDERO, 1988); – *L. virens*: 46 days (♂); – *L. dryas* [captured young in the field]: 28 days (♀). Therefore insectaries are useful for the study of adult damselflies.

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