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MORPHOLOGICAL VARIABILITY, FEMALE POLYMORPHISM AND HERITABILITY OF BODY LENGTH IN *ISCHNURA GRAELLSII* (RAMBUR) (ZYGOPTERA: COENAGRIONIDAE)

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Morphological variability was studied in laboratory-reared adults. The size of the postocular spots and the antehumeral stripes was surveyed in 1064 F_1 individuals, as was the size of the black dorsal spot of the eighth abdominal segment in 994 F_1 and F_2 females. Total body length was measured in 884 ♂ and 1404 ♀ from F_1 to F_4 generations. Results indicated significant differences among families in all morphological characters, suggesting the existence of genetic variability. Most individuals had no postocular spots, and many males had incomplete antehumeral lines. Female phenotypes are described and figured, and an identification key is provided, based on these morphological characters. Heritability of body length was estimated to be about 0.5 in females and 0.4 in males. No differences in body length were observed between female phenotypes when compared within families. Some aberrant specimens are described.

INTRODUCTION

Ischnura graellsii (Rambur) is a small non-territorial damselfly, widespread in many areas of Spain (OCHARAN, 1987). This species shows striking morphological variability, and several forms have been named, although they are seasonal or individual variations (CORDERO, 1988). Furthermore, females are polymorphic in body coloration (CORDERO, 1990), and both sexes show morphological colour changes during maturation (CORDERO, 1987). All this variability may be observed in individuals from the same population.

During the last years I maintained a laboratory population of *I. graellsii*, in order to analyze the genetics of its female polymorphism (CORDERO, 1990). More than 2400 adults were obtained in two years. Female phenotypes in *I.*

graellsii are one androchromotypic (coloured as the male) and two gynochromotypics: the *aurantiaca* form (orange to brown coloured) and an unnamed brown form that for its similarity to the *infuscans* form of *I. elegans* (Vander L.), I have also previously named *infuscans* (CORDERO, 1990). The first aim of this paper is to analyze morphological variability in laboratory specimens, especially with regard to female polymorphism, and to present the first estimates of the heritability of body size in one odonate species. The second aim is to describe in detail the female phenotypes, providing a key for their identification, and to describe some aberrant specimens found among the laboratory and field specimens so far examined.

METHODS

Adults of *I. graellsii* were reared in the laboratory at 21-23°C and under a photoperiod of 15:9 hours of light:darkness, as described in CORDERO (1990). The parental generation was constituted by 100 individuals captured in five natural populations at Pontevedra (NW Spain), during August-September 1987. Some of these specimens were crossed in the laboratory to obtain F_1 adults. Crosses were repeated until F_4.

All undeformed adults were measured (total body length, to the nearest 0.1 mm) after emergence, individually marked and some maintained in insectaries. During the F_1 generation all adults were also examined and the following characters were surveyed: size of postocular spots, size of antehumeral stripes of thorax, and size of black spot on the 8th abdominal segment (in females). The latter was also scored in F_2 individuals.

Heritability of body length was estimated by analysis of single pairs (BECKER, 1975). The model is a type II ANOVA:

$$Y_{ij} = \mu + a_i + e_{ij}$$

where the length of the j-th individual of the i-th family (Y_{ij}) is expressed as the sum of the common mean (μ), the effect of the i-th family (a_i) and the uncontrolled environmental and genetic deviations attributable to individuals within single pair matings (e_{ij}). These effects are assumed random, normal, and independent with expectations equal to zero. Mean square within and between groups were obtained from an ANOVA, and the variance components, heritability (h^2), and standard error of h^2, were calculated as described in BECKER (1975). These estimates approach the genotypic heritability, which is the quotient of the total genetic variance and the total phenotypic variance, because ½ of the dominance variance and all the maternal effects variance are included in the estimate (BECKER, 1975).

In F_1 and F_3 females, variance was heterocedastic. Because no transformation yielded homocedasticity, 5 families with very unlike variances (2 F_1 and 3 F_3) were considered as outliers, and were excluded from analysis. This augments the error of the estimate, because sample size is smaller, but it homogenizes the variance, and allows analysis.

RESULTS

MORPHOLOGICAL VARIABILITY

Most adults (90% of males and 60% of females) had no postocular spots (Tab. I). Presence of postocular spots is a character used to differentiate genera in the odonatological literature (AGUESSE, 1968; ASKEW, 1988). This is not appro-

Table I

Variability in the size of postocular spots in F_1 individuals of *I. graellsii* (number of specimens) – [Codes of families are the same female codes as in CORDERO, 1990]

Family	Size of postocular spots									
	no spots		one dot		two dots		two spots		two big spots	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
B	12	5	1	0	2	2	2	7	0	0
C	37	22	0	1	0	3	0	4	0	0
L	22	11	0	1	0	3	0	14	0	2
M	40	20	0	1	5	4	0	10	0	5
H	45	43	0	3	1	1	1	9	0	0
J	16	13	0	1	0	5	2	7	0	0
K	19	27	0	0	0	0	0	0	0	0
N	8	9	0	0	2	1	0	1	0	0
P	48	18	0	1	5	2	1	7	0	18
R	33	24	2	1	0	10	5	12	0	0
S	47	57	0	2	2	0	0	0	0	0
T	43	29	0	3	0	4	0	8	0	0
U	45	24	0	0	4	7	0	6	0	13
X	29	16	3	4	4	7	9	21	0	0
Total	*444*	*318*	*6*	*18*	*23*	*49*	*20*	*106*	*0*	*38*
%	90.1	60.1	1.2	3.4	4.7	9.3	4.1	20.0	0.0	7.2

Males $\chi^2 = 99.398$, $p<0.0001$; Females $\chi^2 = 246.877$, $p<0.0001$.

Table II

Variability in the size of antehumeral stripes of thorax in F_1 males of *I. graellsii*. – [Codes of families are the same female codes as in CORDERO, 1990]

Family	Number of males		
	no stripes	interrupted	2 stripes
B	0	1	15
C	1	13	24
L	15	5	2
M	13	16	11
H	0	25	26
J	0	1	17
K	1	5	13
N	1	7	0
P	0	3	47
R	1	6	38
S	6	22	19
T	0	13	32
U	0	0	42
X	0	18	26
Total	*38 (8.6%)*	*135 (30.5%)*	*270 (60.9%)*

$\chi^2 = 271.658$, $p<0.0001$

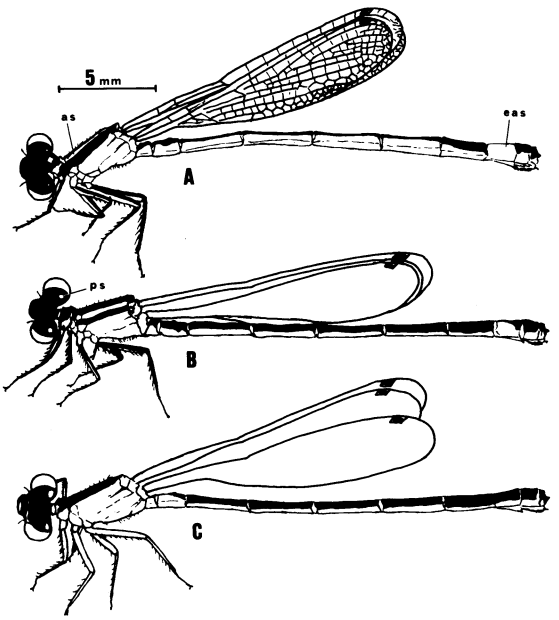

Fig. 1. Female polymorphism in *Ischnura graellsii*, typical specimens of: (A) androchromotypic; – (B) *infuscans*; – (C) *aurantiaca*. – Note the difference in width of antehumeral stripes (as), in size of postocular spots (ps) and in the black spot on the eighth abdominal segment (eas).

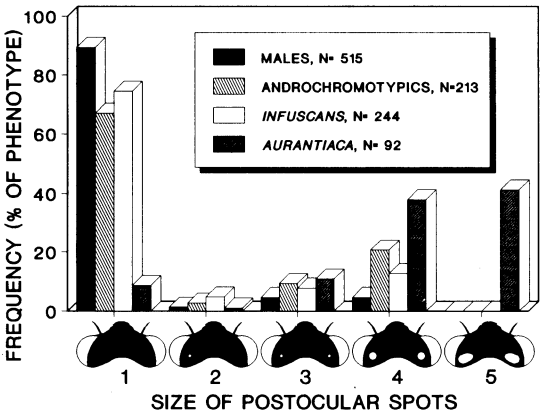

Fig. 2. Size of postocular spots in F_1 males and females of *I. graellsii* reared in the laboratory: (1) no spots; – (2) one dot; – (3) two dots; – (4) two spots; – (5) two large spots. – Note the difference between *aurantiaca* and other phenotypes.

priate for *I. graellsii*, because, contrarily to what is assumed in all identification keys, most specimens have no spots. This character shows a seasonal change in the field: spring individuals have postocular spots absent or reduced, but most summer specimens show conspicuous spots (CORDERO, 1988). When the frequency of the different size classes of the postocular spots is compared between families, significant differences are observed (Tab. I). This result suggests the existence of genetic variability for this character, because all families were reared at the same temperature and photoperiod conditions.

Similar results are obtained when the size of the blue antehumeral stripes is analyzed (Tab. II). Many males have incomplete or no stripes, and significant differences are observed between families, suggesting genetic differences. In females, lines are usually complete, but their width is related to the phenotype. Androchromotypics are the most similar to males, with narrow antehumeral lines (very broad black humeral stripes) or, very rarely, no antehumeral lines (only 2

females). The *infuscans* females have broad antehumeral stripes (similar in width to black humeral stripes). Females of the *aurantiaca* form typically have only one mid-dorsal black stripe, but some rare specimens are similar to *infuscans* females.

Figure 1 shows female phenotypes of *I. graellsii*. Besides the width of the antehumeral stripes, female phenotypes also show different-sized postocular spots (Fig. 2) and a different black pattern on the dorsum of the eighth abdominal segment (Fig. 3). Most androchromotypics and *infuscans* females have no postocular spots, as is the case in males. In clear contrast, most *aurantiaca* females have large spots (Fig. 2). With respect to the size of the black dorsal spot of the eighth abdominal segment of females, androchromotypics have no or a very small spot (CORDERO,

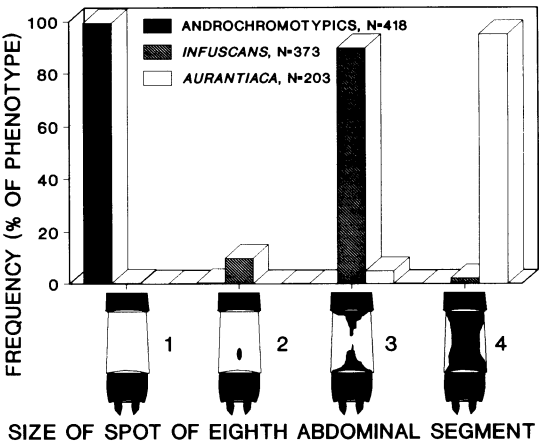

Fig. 3. Size of black dorsal spot at the eighth abdominal segment of F_1 and F_2 female *I. graellsii* reared in the laboratory: (1) no spot; – (2) one dot; – (3) one spot of variable shape and size; – (4) black dorsum. – This is the best character to differentiate between female phenotypes.

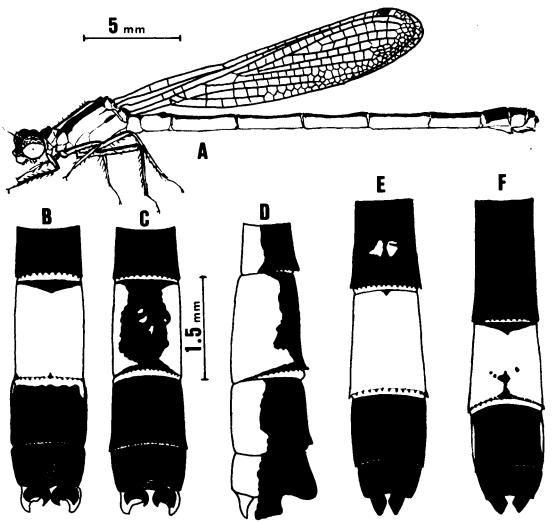

Fig. 4. Some peculiar specimens of *I. graellsii*: (A) Female with intermediate coloration between androchromotypic and *infuscans*. Note the narrow antehumeral lines (typical of androchromotypics) and the black eighth abdominal segment (typical of *infuscans*). – (B-D) Abdominal segments 7-10, in dorsal view, from a typical male (B) and a probable gynochromotypic male (C, dorsal view and D, lateral view). – (E) Abdominal segments 7-10 in dorsal view, from an androchromotypic female with two additional blue spots on the seventh abdominal segment; and – (F) same from an *infuscans* female with the black spot at the eighth segment very reduced.

1987), and both gynochromotypics have very variable spots. This character is the best to differentiate female phenotypes (Fig. 2). There were also significant differences between families, probably because the percentage of andro- and gynochromotypic females varied between families.

Among the adults obtained in the laboratory, some aberrant individuals were observed. The most interesting was one male that had a great black spot on the dorsum of the eighth abdominal segment (Fig. 4c, d), resulting in a phenotype similar to that of gynochromotypic females. To my knowledge no gynochromotypic male has ever been observed in any damselfly. Unfortunately, I do not know if this specimen was a gynochromotypic male, because it died at 2 days of age, without developing mature coloration. Some other aberrant individuals are shown in Figures 4e and f.

With regard to female polymorphism, there are two observations of field specimens that had intermediate characters between androchromotypics and *infuscans* females. One of these specimens is shown in Figure 4a. This female had the thoracic coloration of androchromotypics (blue), but olive-green coloured antehumeral stripes and a black and brown eighth abdominal segment (these are always blue in mature androchromotypics). This specimen was collected in a natural population of *I. graellsii* at Berreo (A Coruña, Spain, UTM: 29TNH4159). The other specimen was marked during a study at O Rosal (Pontevedra, Spain, UTM: 29TNG1742). This female had the dorsal part of the thorax brown (including the antehumeral stripes) and the remaining parts blue, and also a blue eighth abdominal segment. Both specimens could not be identified as *infuscans* or androchromotypics. A third strange female was also observed at O Rosal. This was an androchromotypic female, but it showed a very dark blue-violet thorax (similar to the *violacea* form of *I. elegans*), a coloration never observed before amongst more than 4000 field females so far examined.

Taking into account the morphological variability of all female phenotypes, it is possible to distinguish between them by means of the following key:

1 Thoracic coloration orange, reddish (young females), or ochre-brown (mature specimens). Thorax with only one mid-dorsal black stripe, very rarely with two additional humeral stripes. Most females with large postocular spots. Dorsum of first and majority of second abdominal segment the same colour as thorax, never black. Eighth abdominal segment usually black dorsally. Legs without black longitudinal stripes ..... ***aurantiaca***

– Thoracic coloration very variable (white, yellow, violaceous, green, blue or brown). Never only a mid-dorsal black stripe in the thorax. Postocular spots absent or small in most specimens. Dorsum of first and second abdominal segments black. Dorsum of eighth abdominal segment with or without black spot. Legs with black longitudinal stripes 2

2 Thorax whitish, yellow, yellow-green or blue. Antehumeral lines narrower than black humeral stripes. Postocular spots whitish or blue. Females with no or very small black spots on the eighth abdominal segment ..... Androchromotypics

– Thorax white-violaceous, green or brown. Antehumeral and humeral stripes of similar width. Postocular spots never blue, usually the same colour as thorax. Dorsum of eighth abdominal segment with a black spot (rarely covering all dorsum or without spot), and never blue in mature specimens ..... ***infuscans***

Table III

Mean body length (mm) ± SE (N) of adult *I. graellsii* in laboratory specimens. Codes of families are the same female codes as in CORDERO (1990). – [Test 1 = probability after a t-test with the null hypothesis that both sexes have the same mean body length (two-tailed). – Test 2 = probability after a t-test (or F when there are 3 phenotypes) with the null hypothesis of equality of body length between female phenotypes. – A = androchromotypics, I = *infuscans*, O = *aurantiaca*]

	Family	Male	A	I	O	test 1	test 2
F_1	B	29.5±0.2 (16)	27.0±0.1 (14)			<0.001	–
	1	27.6±0.5 (5)	26.9±0.0 (1)	27.2±0.9 (2)		0.518	–
	2	26.3±0.1 (7)		26.9±0.3 (2)		0.090	–
	3	26.5±0.3 (4)		26.9±0.2 (8)		0.373	–
	4	28.7±0.3 (4)	28.7±0.2 (4)	27.6±0.4 (3)		0.295	0.039
	C	29.3±0.1 (36)		29.9±0.2 (28)		0.012	–
	L	28.9±0.2 (20)		29.5±0.1 (17)	29.4±0.2 (15)	0.013	0.691
	M	28.6±0.2 (38)		29.0±03 (14)	29.7±0.2 (23)	0.002	0.069
	H	29.4±0.2 (49)	30.4±0.2 (25)	30.0±0.2 (28)		0.001	0.187
	J	28.3±0.1 (17)		29.1±0.1 (24)		0.005	–
	K	28.4±0.2 (18)		28.8±0.1 (23)		0.041	–
	N	27.9±0.2 (7)	28.7±0.4 (5)	28.0±0.6 (3)	28.8±0.8 (2)	0.136	0.637
	P	28.5±0.1 (49)		29.5±0.2 (19)	29.6±0.1 (26)	<0.001	0.660
	R	28.2±0.2 (40)	29.2±0.2 (41)	29.7±0.2 (5)		<0.001	0.295
	S	28.1±0.1 (41)	28.5±0.1 (42)	28.9±0.2 (14)		0.009	0.228
	T	28.3±0.2 (41)	28.7±0.2 (32)	29.1±0.3 (12)		0.022	0.245
	U	27.7±0.1 (44)	28.3±0.2 (24)		28.1±0.3 (25)	0.017	0.496
	X	28.4±0.1 (43)	29.1±0.4 (26)	29.3±0.2 (26)		0.002	0.711
F_2	S1	27.4±0.2 (10)	28.8±0.1 (54)			<0.001	–
	M2	27.1±0.2 (30)		28.9±0.3 (18)	28.4±0.4 (17)	<0.001	0.296
	S3	26.7±0.2 (20)		28.4±0.1 (50)	28.2±0.2 (13)	<0.001	0.361
	U1	27.5±0.3 (17)	28.1±0.2 (32)		28.1±0.2 (30)	0.038	0.947
	C2	26.4±0.2 (35)		27.7±0.1 (60)		<0.001	–
	P1	27.1±0.2 (14)	29.0±0.2 (27)		28.7±0.2 (33)	<0.001	0.338
	N1	27.4±0.2 (20)	29.1±0.2 (33)	28.9±0.2 (16)	29.2±0.3 (12)	<0.001	0.523
	H1	27.8±0.2 (29)	29.3±0.1 (63)			<0.001	–
F_3	P12	27.4±0.2 (23)	28.3±0.2 (19)		27.7±0.1 (21)	0.006	0.018
	C21	27.3±0.1 (44)		27.9±0.2 (49)		0.002	–
	H16	27.4±0.1 (20)	28.2±0.2 (20)	28.4±0.1 (2)		<0.001	0.750
	U11	28.3±0.3 (11)		27.8±0.4 (11)	28.5±0.4 (13)	0.836	0.232
	P11	28.0±0.2 (26)		27.8±0.3 (10)	27.9±0.3 (16)	0.785	0.838
	H11	28.1±0.2 (22)	29.1±0.1 (32)			<0.001	–
	S31	27.6±0.2 (35)	28.8±0.3 (10)		28.4±0.3 (11)	<0.001	0.406
	P15	28.2±0.1 (25)			29.3±0.2 (13)	<0.001	–
	H15	27.4±0.1 (28)	28.2±0.3 (7)	28.3±0.2 (9)		<0.001	0.732
	U13	27.5±0.2 (20)			28.2±0.2 (23)	0.018	–
	H13	27.9±0.2 (13)	28.3±0.2 (20)			0.139	–
F_4	U134				26.9±0.2 (35)	–	–
	P111	30.5±0.0 (1)	28.0±0.3 (11)	28.0±0.3 (26)		–	0.842
	U111	27.5±0.0 (1)	28.8±0.2 (35)		28.7±0.4 (3)	–	0.883

Table III (continued)

	Family	Male	A	I	O	test 1	test 2
F_4	P122		26.9±0.6 (9)	27.6±0.2 (21)	26.2±0.5 (6)	–	0.032
	U135		27.7±0.4 (10)	26.9±0.2 (16)	27.7±0.2 (32)	–	0.626
	P121	27.3±0.0 (1)	27.8±0.2 (46)	27.8±0.3 (38)	27.8±0.3 (18)	–	0.988

Table IV

Estimates of heritability of body length in adult *I. graellsii*

Sex	Generation	N1	N2	h^2	SEh^2
♂	F_1	13	443	0.380	0.143
	F_2	8	174	0.246	0.157
	F_3	11	267	0.168	0.102
♀	F_1	11	423	0.504	0.184
	F_2	8	457	0.401	0.185
	F_3	8	223	0.382	0.194
	F_4	6	301	0.550	0.268

N1 = number of families (females); – N2 = total number of data; – h^2 = heritability; – SEh^2 = standard error of the estimate of h^2.

BODY LENGTH

Table III shows means and standard errors for body length of all families. Note the great variability between families. In most cases, males were smaller than females, as occurs also in other coenagrionids (FINCKE, 1982; THOMPSON, 1989). Families B to 4 of Table III were reared with less food than others, because there was not enough space to rear all families. This treatment drastically reduced adult body length (compare means of these families with remaining F_1 families). This effect of food shortage of larvae on adult body length was also reported for *Pyrrhosoma nymphula* (Sulz) by HARVEY & CORBET (1985).

Taking into account that there are significant differences in body length between families (see below), the way to test the hypothesis that there are no differences in body length between female phenotypes is to compare phenotypes within families (a two-factor ANOVA is not possible because only 2 out of 3 possible phenotypes are present in most families). This analysis is conclusive: only 3 out of 24 families that produced more than 20 females, showed significant differences between phenotypes (Tab. III).

Heritability of body length was estimated to be about 0.5 in females and 0.4 in males (Tab. IV). This value indicates high genetic components, as is usual for many morphological characters (FALCONER, 1989).

DISCUSSION

Ischnura graellsii shows striking morphological variability. In a previous study I found that there is a seasonal change in the size of the postocular spots and antehumeral lines: most spring specimens had no spots and very reduced lines, but summer individuals had the black coloration very reduced, showing large spots and broad lines (CORDERO, 1988). This suggested great influence of temperature and photoperiod on the expression of these characters. Results of the present study also confirm the existence of genetic variability for all these morphological characters. Furthermore, at the end of this study it became apparent that the phenotype changes with age: individuals with very small spots or stripes, usually lost them during maturation. Adult odonates need a high thoracic temperature to be able to fly (MAY,1976). Perhaps this seasonal change allows individuals to acquire the appropriate thoracic temperature faster in spring, when air temperature will be often limiting for the activity of adults. In agreement with this, it is known that body coloration has a thermoregulatory function in some insects (FUZEAU-BRAESCH, 1985). Experiments are needed to test this hypothesis.

The existence of great morphological variability is not a special characteristic of *I. graellsii*. JOHNSON (1969) found great variability in wing venation patterns in other *Ischnura* species, and males of *I. elegans* and *I. pumilio* (Charp.) show great variability in the coloration of the tip of the abdomen (AGUESSE, 1968). Furthermore, there are many intraspecific forms in the *I. elegans* complex (AGUESSE, 1968; ASKEW, 1988).

This study presents a detailed description of the female phenotypes of *I. graellsii*. The key will allow the identification of all phenotypes in a rapid field inspection. It would be interesting to estimate phenotype frequencies in natural populations of *I. graellsii*, because it seems very likely that androchromotypics are more common in high density populations (CORDERO, 1992). Table III indicates that there are no differences in body length between female phenotypes, when compared within families. Therefore, the genes that control the polymorphism have no pleiotropic effects on body size, nor are they linked to genes that affect body size. CORDERO (1990) showed that this female polymorphism is due to three alleles of one autosomic locus, with sex-restricted expression. Androchromotypic and *infuscans* females have similar young phases (whitish to violaceous; CORDERO, 1987; 1990). The existence of two females with some characteristics of both phenotypes could be due to a mutant allele with intermediate effects. Its frequency is so low (2 females amongst more than 4000 field specimens; none in more than 1000 laboratory-reared females) that these specimens cannot be considered as another female form.

Estimates of the heritability of body length are based on two important assumptions: (1) that the variance between the plastic boxes where families were separately reared was not significant (there was homogeneity in treatment between

families), and (2) that families are constituted by the offspring of one single pair from a random-mating population. We can test the first assumption using data from the F_4 generation, because different clutches of the same female were reared apart. This analysis indicates that only in 1 out of 8 families was this variance significant (I consider 8 families rather than 6, because 2 females produced enough offspring from two different males). If the same happened in the remaining generations, we can use this model with confidence. The second assumption implies that this analysis is only adequate for the F_1 generation, because individuals were progressively more related in subsequent generations. We expect that genetic variance would become progressively smaller, as would heritability (FALCONER, 1989; p. 267). This diminution of heritability is observed in Table IV for both males and females, excepting the F_4 generation in females. In fact, some of the males were used in 2-3 matings to obtain an F_1 (this was convenient for the genetic analysis of female polymorphism; CORDERO, 1990). Therefore genetic variance is underestimated (differences among families are smaller than expected for unrelated specimens). On the other hand, the estimates of heritability contain ½ of the dominance variance and all the maternal effects variance (BECKER, 1975). As a conservative estimate we can use 0.5 in females and 0.4 in males, the values found in F_1. These results are interesting because recently it has been shown that body size has significant effects on reproductive success of male and female coenagrionids (FINCKE, 1988; THOMPSON, 1989). The existence of additive genetic variance for body size is a prerequisite for a response to selection on this character.

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