

SHORT COMMUNICATIONS

**REPRODUCTIVE ALLOCATION IN DIFFERENT-SIZED  
ADULTS *ISCHNURA GRAELLSII* (RAMBUR)  
(ZYGOPTERA: COENAGRIONIDAE)**

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The scaling of body proportions in *I. graellsii* is analyzed as body mass in dried specimens and linear dimensions are measured from photographic slides. Results indicate that abdomen mass shows positive allometry with body mass in both sexes, and thorax mass also does so in males. Wing area increases with body mass as expected from geometric similarity, but head width shows negative allometry with body length in both sexes. All traits excepting wing area are sexually dimorphic, but no difference was found in body proportions between female phenotypes of this species. Results indicate that larger individuals allocate more energy to reproduction. This is discussed in relation to the constraints imposed by the energetics of flight in larger individuals.

INTRODUCTION

The study of the influence of body size on form and function, has become a prominent focus in ecology and evolution (LABARBERA, 1989). Body size is a trait closely related to many morphological and ecological traits, although the functional relationship between body size and the correlated trait is unknown in most cases (FAIRBAIRN, 1992). Therefore allometry is a basic topic in ecology (REISS, 1989).

Female fecundity is positively related to body size in many insects (and other animals), although it should be related mainly to abdomen size (WICKMANN & KARLSSON, 1989). Recent studies that have analyzed the relationship between reproductive effort and body size in some Lepidoptera, Odonata, Coleoptera and Diptera (WICKMANN & KARLSSON, 1989; MARDEN, 1989; BERRIGAN, 1991a), suggest that the scaling of reproductive effort is constrained by locomotor performance in flying insects.

WICKMANN & KARLSSON (1989) showed that the abdomen makes up a greater proportion of the body mass of heavier individuals than of light ones in seven species of Lepidoptera and one of Diptera. This result indicates greater reproductive allocation in larger individuals than in smaller ones of the same species.

In this paper I present a study of scaling of body proportions in the damselfly *Ischnura graellsii*. This species is a small, non-territorial damselfly, common in many areas of Spain and Northern Africa (ASKEW, 1988). The first aim of this study is to investigate the relationship between abdomen and body mass in this damselfly, because in contrast with some Lepidoptera, adult Odonata feed throughout their lives, preying upon small flying insects. Therefore reproductive allocation might be less dependent on weight at eclosion. *I. graellsii* shows female-limited colour polymorphism (CORDERO, 1990). Females may be blue when mature (the androchromotypic form) or brown (the gynochromotypic *infuscans* and *aurantiaca* forms). These morphs show different reproductive behaviour (CORDERO, 1989), and in one natural population blue females were larger than brown females (CORDERO, 1992). In a laboratory study, I have found that female fecundity is positively related to female body size in this species (CORDERO, 1991). The second aim of this study is to look for possible differences between female morphs in body proportions, that could be important in the maintenance of this polymorphism. If one female form has a heavier abdomen for the same body size, then the number of eggs that these females can lay may be difficult to estimate from measurements of body size alone.

## METHODS

Individuals included in this study were mature adults captured at an artificial pond near O Rosal (Pontevedra, NW Spain) in August and September 1990. I captured 27 males and 51 females; (14 androchromotypics, 24 *infuscans* and 13 *aurantiaca*) trying to cover all the size variation found in the population. This was made to achieve greater precision in estimating the slope of body size relationships. The range in total body length was 23.5-30.6 mm in males, 25.9-30.7 in androchromotypics, 24.3-32.2 in *infuscans* and 25.4-30.6 in *aurantiaca* females. These specimens were dried at 50°C to constant weight. I measured total, thoracic (without legs and wings) and abdominal weight using an electrobalance (Mettler AJ100) to the nearest 0.1 mg. Wing area (left hind wing) was measured with an image analysis system.

Linear dimensions were estimated from a set of photographic slides, taken from 162 males and 110 females at the above mentioned population in August-September 1990. To take the picture, the insect was placed in a transparent plastic envelope in lateral view and photographed over a paper with a scale drawn on it, at 0.5x magnification. This was done as quickly as possible, and usually required only 1-2 minutes from capture to release. I measured total body length, thorax length, abdomen length, wing length and head width of photographed individuals, with a digital caliper to the nearest 0.01 mm on 3x projections of the slides. The correlation between estimates of body length obtained with this method and measurements made on the live animal was 0.97 for males (N=160,  $P < 0.0001$ ) and 0.96 for females (N=106,  $P < 0.0001$ ). This is therefore a good method for estimating body measurements in this damselfly. Total body length was measured from labium to

the tip of the abdomen, including cerci. Thorax length was defined as the distance from the tubercle in the prothorax to the basal insertion of the abdomen. Abdomen length was the distance between the basal insertion of the abdomen and the tip of the cerci. Wing length was measured from the base to the tip of the posterior wing. Finally, head width was taken as the maximum width of the head in dorsal view.

To analyze how the size ( $y$ ) of an organ scales to body size ( $x$ ), I fitted the allometric equation  $\log_{10}y = a + \log_{10}x$  by the technique of principal axis (LABARBERA, 1989). When both variables have the same dimensions, the expected slope is  $b=1$  for isometry,  $b<1$  for negative allometry and  $b>1$  for positive allometry. When the two variables have different dimensions, the expected slope for isometry is the ratio of dimensions: wing area is expected to have the slope  $2/3$  with body mass under isometry (the relationship of area to volume, LABARBERA, 1989). Both the equation and the significance value (two-tailed) were calculated as described in SOKAL & ROHLF (1981).

## RESULTS

Results of the allometric analysis of body proportions are summarized in Table I. Abdomen mass shows positive allometry with body mass in males and females (Fig. 1a), and thorax mass in males (Fig. 1b). Nevertheless, abdomen length is isometric with body length in both sexes.

Thorax length is proportionally greater in larger individuals of both sexes. Wing area increases with body mass as expected from geometric similarity ( $b=2/3$ ), and wing length is also isometric for males but not for females (Tab. I).

Table I

Results of the allometric analysis of body proportions in *Ischnura graellsii* - [ $H_0: b=1$ , excepting wing area, where  $H_0: b=2/3$ ]

Organ	Sex	N	b	p	a	Differences between <sup>1</sup>	
						Sexes	Phenotypes
Thorax mass	males	27	1.18	<0.05	-1.43	<0.001	0.527
	females	51	1.00	ns	-0.92		
Thorax length	males	156	1.40	<0.001	-3.31	<0.001	0.516
	females	108	1.49	<0.001	-3.62		
Abdomen mass	males	27	1.24	<0.05	-2.34	<0.001	0.704
	females	51	1.64	<0.001	-3.82		
Abdomen length	males	161	1.00	ns	-0.27	<0.001	0.478
	females	108	0.98	ns	-0.18		
Wing area	males	27	0.53	ns	1.26	0.109	0.764
	females	51	0.57	ns	1.12		
Wing length	males	162	1.06	ns	-0.87	<0.001	0.480
	females	110	1.16	<0.05	-1.11		
Head width	males	161	0.70	<0.001	-1.07	<0.001	0.468
	females	110	0.70	<0.001	-1.06		

<sup>1</sup> Probability after an ANCOVA comparing sexes or female phenotypes, with body mass (or body length) as covariate.

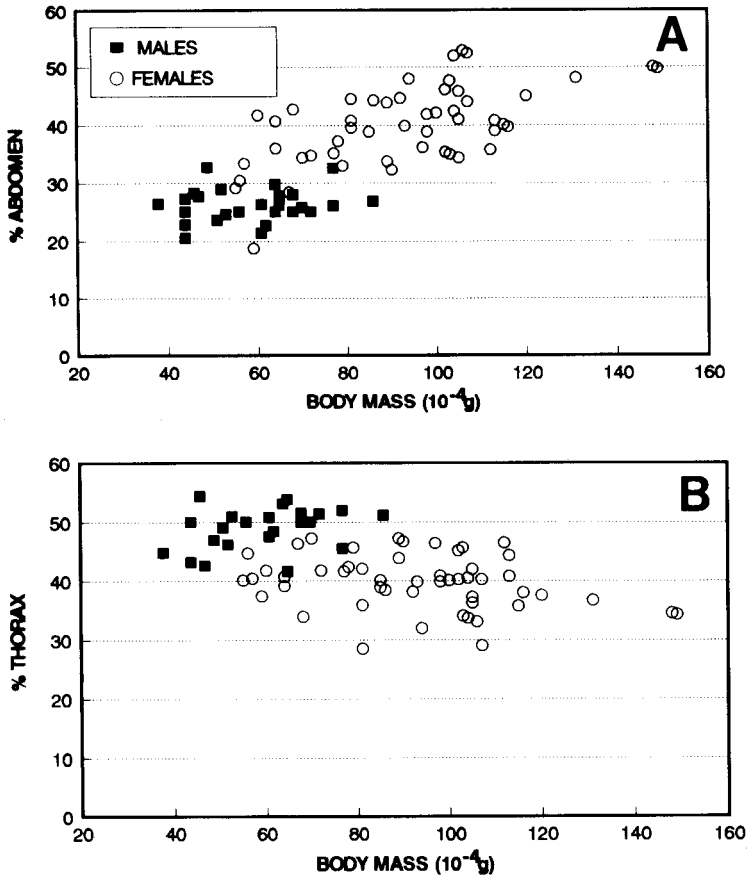


Fig. 1. The relationship between body size and the percentage of body mass allocated to the abdomen (A) and the thorax (B) in male and female *I. graellsii*.

An interesting result is that head width shows negative allometry with body length in both sexes: smaller damselflies have a proportionally wider head than expected from geometric similarity. Unfortunately, head weight was not measured.

An ANCOVA controlling for body mass (or body length) was made to compare the size of these organs between sexes and between female phenotypes (Tab. I). This analysis indicates that except for wing area all traits are sexually dimorphic: the abdomen makes up a greater part of body mass in females than in males (Fig. 1a) and the opposite is true for the thorax (Fig. 1b). On the other hand, no difference was found between female phenotypes in any of these body dimensions (Tab. I).

## DISCUSSION

WICKMANN & KARLSSON (1989) showed that in seven species of Papilionoidea and one of Diptera abdomen size shows a positive allometric increase with body size. This pattern is repeated in males and females of *I. graellsii* (Tab. I): the abdomen makes up a greater part of body mass in heavier individuals (Fig. 1). Female fecundity is positively related to body size in *I. graellsii* (CORDERO, 1991), but probably it correlates better with the mass of the abdomen. If so, there is a change in the amount of energy allocated to reproduction in individuals of different size. A possible explanation of this fact could be based on the energetics of flight: because wing area is isometric with body size (Tab. I), heavier individuals are probably spending more energy in flight. A proportionally heavier abdomen could compensate this size-related cost allowing a greater reproductive output in larger individuals. A second explanation is that individuals that exceed a certain size might have excess resources that they can shunt into gametes (Dr M.L. May, pers. comm., 1992). The increased abdomen size of larger males could be related to increased ejaculate production. BERRIGAN & LOCKE (1991) demonstrated that sperm number scales to body size with an exponent of 0.67 in the fly *Neobellieria bullata*. This is the slope expected if the number of sperm produced by a male were proportional to the surface area of the testicular epithelium, and if there was an isometric relationship between body weight and the area of the epithelium of the testes. In male *I. graellsii* ejaculate size is positively related to male size (CORDERO & MILLER, 1992), but the scaling of both variables was not examined. The existence of a positive correlation between male body size and sperm number suggests, as BERRIGAN & LOCKE (1991) noted, that sperm production is costly, contrary to what is generally assumed. This possibility needs confirmation with more experimental work.

Head width shows negative allometry with body length in both sexes (Tab. I). In some studies of adult odonates, head width is used as an estimator of body size (e.g. HARVEY & CORBET, 1985). These results suggest caution when using head width as a measure of size, because the differences between individuals may be smaller than the actual difference in body size.

This study shows that there is sexual dimorphism in body shape (Tab. I). The fact that abdomen mass is greater in females than in males for the same body size is due to the mass of eggs. ANHOLT et al (1991) showed that female odonates are usually significantly heavier than males when mature, although both sexes emerge with similar weight. This additional mass could have heavy effects on female flight performance. In the fly *Neobellieria bullata*, females suffer a 40% reduction in the net lift production during egg development, due to the increase in abdomen mass (BERRIGAN, 1991b). This fact could explain why males and females differ in the relationship between muscle (thorax) mass and body size (BERRIGAN, 1991b). In *I. graellsii*, males and females did not differ

in wing area (Tab. I), as was also the case in *N. bullata* (BERRIGAN, 1991b). The head is sexually dimorphic, being wider in females than in males for the same body size. Given that both sexes seek prey visually, the meaning of this dimorphism is unclear.

Finally, the comparison between female phenotypes of *I. graellsii* indicates that there are no morphological differences (Tab. I) between them. Androchromotomics (male-like coloured females) were significantly larger than gynochromotomics in one high density population, but the maintenance of this polymorphism seems related to density-dependent mating success of the different female forms (CORDERO, 1992) and not to female morphology.

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