

**SEXUAL SIZE DIMORPHISM  
IN *COENAGRION PUELLA* (L.)  
(ZYGOPTERA : COENAGRIONIDAE)**

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Body size in *C. puella* has been shown to have opposing costs and benefits in terms of the animals' lifetime mating success. Large size is positively correlated with increased longevity in males and females, but negatively correlated with daily mating rate in males and clutch size in females. The optimum sizes for males and females were calculated in terms of their expected lifetime mating successes. The predicted optimum male size fell close to the mean male size observed in the field. The optimum female size was larger than that observed for females in the field. There is evidence for stabilizing selection in male damselflies and weak directional selection in females. The predicted optimum female size is larger than that for males ; this is a sufficient explanation for the sexual size dimorphism.

**INTRODUCTION**

Many studies of sexual dimorphism in size have approached the dimorphism itself as the feature of interest, rather than the nature of the different selective forces acting on size in the two sexes. Several authors have used a comparative approach, attempting to correlate the degree of sexual dimorphism with, for example, the degree of polygyny (RALLS, 1976, 1977 ; CLUTTON-BROCK *et al.*, 1977). While this approach has produced some interesting generalisations (for example, a correlation between the degree of size dimorphism and the degree of polygyny in primates (CLUTTON-BROCK *et al.*, 1977)), it cannot provide a complete understanding of the origins of sexual dimorphism, since it ignores the nature of selection on females. For sexual dimorphism to arise, the selective forces acting on the two sexes must be different, since selection on size in one sex alone will produce a correlated response in size in the other sex (LANDE, 1980). It is the difference in the selective forces acting on the two sexes that provides the full explanation of sexual dimorphism. This difference can best be investigated by studying selection on size in both sexes.

The aim of this paper is to provide such a study, on the nature of selection on body size in *Coenagrion puella* (L.), a medium-sized, sexually dimorphic, non-territorial damselfly.

## METHODS

The study was made in the summers of 1983 and 1984 at Bungalow Pond, Wirral, England. Bungalow Pond is a small, roughly circular, isolated pond with a perimeter of about 60 m.

In the first season, 1983, three observers attempted to catch every adult that emerged from the pond and which came to the pond to breed. Captured animals were lightly anaesthetized with carbon dioxide in the laboratory, and their weights and forewing lengths recorded. They were uniquely marked with a number on the left hindwing in waterproof pen (Edding 404) and a dot of Humbrol enamel paint on the dorsum of thorax. They were kept overnight at 10°C and released next morning near the edge of the pond. The marking procedure appeared to have no deleterious effects on behaviour.

Once mature individuals had begun to arrive at the pond, the identities of single males perching or patrolling in search of females, and of females alone at the pond were recorded either by direct observation or by catching them in a butterfly net. The identities of both males and females in pairs were also recorded, usually by direct observation or through binoculars rather than by capture. Pairs in which one or both of the individuals were unmarked were caught and the unmarked individual retained for measuring and marking that evening. Marked males caught in this way were retained for over an hour to simulate the period during which they would have been unable to search for another female.

In the second season, 1984, we marked a large number of mature females and allowed them to lay a variable number of clutches (females lay a clutch of eggs on average every one or two days, weather permitting). As many of the marked females as possible were re-captured just as they were in copula on a subsequent visit to the pond. They were weighed, measured and dissected; the number of mature eggs that would have been laid on that pond visit was counted.

## RESULTS

For two reasons most of our analysis of male mating success is on data on 186 individuals whose entire reproductive spans fell between 30 June and 28 July: firstly, because the weather during this period allowed reproductive activity on every day except two, while in June the weather was an additional, complicating variable, particularly as it almost certainly affects feeding as well as reproductive activity. Secondly, we are more confident that we saw the vast majority of matings that occurred in July, as the number of animals at the pond each day was lower than in June. All the animals in this 'July' data set were caught and marked as mature adults. Results presented here refer to this 'July' data set unless explicitly stated otherwise.

We are confident that we saw around 88% of pairs present at the pond and 96% of males and that there is little or no dispersal between ponds after adults have reached maturity (BANKS & THOMPSON, 1985a). In addition, we know that females lay almost all their mature eggs when they oviposit at the pond (BANKS & THOMPSON, 1987a). BANKS & THOMPSON describe emergence and longevity

(1985b), male lifetime success (1985a) and female lifetime reproductive success (1987a) in *Coenagrion puella*. In this paper we are concerned only with lifetime reproductive success in relation to body size.

### MALES

Any effects of size on mating success would be confounded with effects of the time in the reproductive season that a male was alive, as males that emerge and reach maturity later in the season are smaller than those that emerge earlier (BANKS & THOMPSON 1985a). However, partial correlations of date of reaching maturity (which is taken to be the date of first appearance at the breeding site), number of mates gained and average mating rate controlling for lifespan and either weight or forewing length are not significant. Partial correlations between date of reaching maturity and lifespan, controlling for either weight or forewing length are also not significant. Date of reaching maturity does not affect either survival or mating success. Weight, measured on the first day of reproductive activity, is positively correlated with lifespan (Kendall's tau = 0.113,  $n = 186$ ,  $P = 0.03$ ), and negatively, but not significantly correlated with average mating rate (Kendall's tau = -0.067,  $P = 0.193$ ). As mating rate is positively correlated with lifespan a more appropriate test of the effect of weight on mating rate would be a partial correlation, controlling for the effect of lifespan; this shows a significant negative relationship (partial correlation coefficient = -0.177, 183 df,  $P = 0.016$ ).

The inverse relationship between mating rate and body weight arises in part because lighter males spend a greater proportion of their lives at the breeding site, as the proportion of days on which males were present at the pond is negatively correlated with body weight (Kendall's tau = -0.115,  $n = 186$ ,  $P = 0.043$ ). Smaller males also have a higher mating rate on days when they are present at the pond, as there is a significant negative partial correlation between mating rate averaged over the days on which males were actually present at the pond, and body weight, controlling for the correlation between lifespan and body weight (partial correlation coefficient = -0.168, 183 df,  $P = 0.023$ ).

Comparing those males that failed to mate with those that mated at least once shows no difference in weight ( $t = 1.02$ , 48 df,  $P = 0.365$ ), but a significant difference in variance, there being more variance amongst unmated males ( $F_{38,148} = 1.82$ ,  $P = 0.013$ ).

The overall relationship between mating success and body size was calculated from the regressions of average mating rate with body weight, and lifespan with body weight. Since lifetime mating success is the product of mating rate and lifespan, the relationship between lifetime mating success and body weight can be calculated as the product of the two regression equations:

mating rate =  $1.499 - 0.0183 \text{ weight}$ ;  $r = 0.122$ ,  $n = 186$ ,  $P = 0.048$ .

lifespan =  $0.2059 \text{ weight} - 0.4434$ ;  $r = 0.141$ ,  $n = 186$ ,  $P = 0.028$ .

lifetime mates =  $0.2449 \text{ weight} - 0.0038 \text{ weight}^2 - 0.5099$

Estimated lifetime mating success as a function of body weight is shown in Figure 1, together with the distribution of male weights for males weighed as mature adults in both June and July. Note that because many large males were weighed at emergence early in the study, Figure 1 underestimates the number of large males.

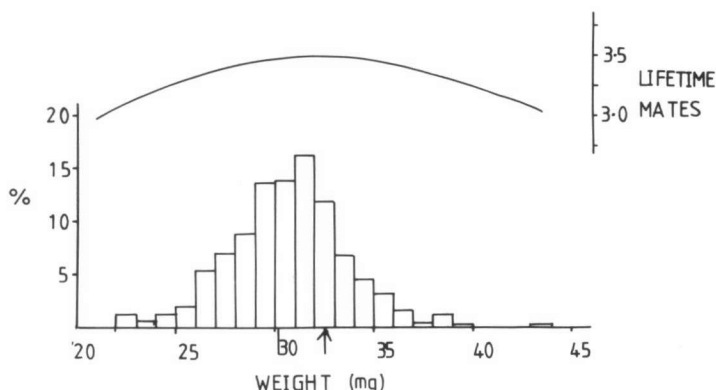


Fig. 1. Estimated lifetime mating success as a function of male weight, and the observed distribution of male weights, of all males weighed as mature adults in both June and July. The bar on the abscissa indicates the mean male weight, and the arrow indicates the calculated optimum weight.

### FEMALES

There is a negative correlation between female skeletal size (measured as head-capsule width) and clutch size for one-day clutches ( $r = -0.422$ ,  $n = 25$ ,  $P = 0.018$ ). For the smaller sample of two-day clutches there is no significant relationship ( $r = 0.167$ ,  $n = 11$ ,  $P = 0.623$ ). (A two-day clutch is a clutch laid two days after the previous clutch was laid).

The negative relationship between female skeletal size and clutch size for one-day clutches is real. It is not a spurious correlation generated by correlations between female size and inter-clutch interval, or temperature, or the date, as partial correlations controlling for the effects of these three variables show a significant negative correlation between female size and clutch size (BANKS & THOMPSON, 1987a).

There is a positive correlation between lifetime clutch production and female skeletal size ( $r = 0.219$ ,  $n = 174$ ,  $P = 0.004$ ). Larger females produce more clutches because they live longer, not because they produce clutches more rapidly (BANKS & THOMPSON, 1987a). This correlation between number of clutches and body size is not a spurious correlation caused by the correlation of body size with date of entry into the reproductive population, since the number of clutches produced is not correlated with date of entry into the population (Kendall's tau =  $-0.035$ ,  $n = 174$ ,

$P = 0.530$ ). Note that although female size was measured as weight in this study, it has been converted to head width in Fig. 2 using a relationship given by BANKS & THOMPSON (1987a). Females used to establish this relationship encompassed the full range of clutch sizes found.

The relationship between lifetime egg production and female skeletal size was found as follows. Lifetime egg production is the product of the mean number of eggs per clutch and the number of clutches produced. The regression equations for the relationships of both clutch size with body size, and clutch number with body size are known, and by multiplying the two equations together, an equation for the relationship between lifetime egg production and body size is obtained :

$$\begin{aligned} \text{eggs per clutch} &= 699.19 - 6.4851 \text{ headwidth} ; \\ r &= -0.422, n = 25, P = 0.018 \end{aligned}$$

$$\begin{aligned} \text{number of clutches} &= 0.6137 \text{ headwidth} - 45.45 ; \\ r &= 0.219, n = 174, P = 0.004 \end{aligned}$$

$$\begin{aligned} \text{lifetime egg} \\ \text{production} &= 7.23.81 \text{ headwidth} - 3.98 \text{ headwidth}^2 - 31778.6 \end{aligned}$$

Note that for simplicity, this relationship is calculated assuming that all clutches are produced after an inter-clutch interval of one day.

Lifetime egg production as a function of female skeletal size is plotted in Figure 2, together with the frequency distribution of female head widths for females first caught as mature adults in both June and July 1983. The frequency distribution of female sizes underestimates the proportion of large females, because many large females that emerged early in the season were caught and measured at emergence, so are not included in Figure 2.

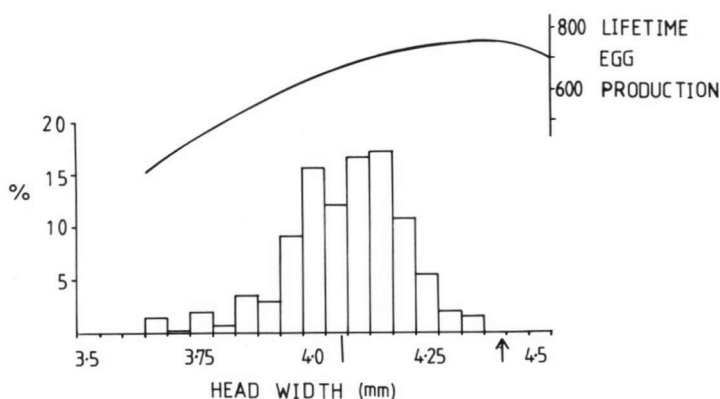


Fig. 2. Estimated lifetime egg production as a function of female head width (top), and the observed frequency distribution of female head widths in both June and July. The bar on the abscissa indicates the mean head width, and the arrow the calculated optimum head width.

## DISCUSSION

In both males and females, body size and longevity are significantly positively correlated. Positive correlations between longevity and body size have been reported in *Drosophila melanogaster* (PARTRIDGE & FARQUHAR, 1983), the moth *Tyria jacobaeae* (DEMPSTER, 1971) and other insects. In males this advantage of large size is opposed by the lower daily mating rate of large individuals. In females it is opposed by the inverse relationship between female skeletal size and clutch size for most (i.e. one-day) clutches. A possible explanation for the relationship between clutch size and mating rate with body size is in the way in which the energetic cost of flight, and other metabolic costs scale with size. The energetic cost of hovering flight scales as body mass<sup>1.167</sup>, and other metabolic costs of insects typically scale as body mass<sup>0.75</sup> (PETERS, 1983, and references therein). Thus, a female's energetic expenditure, excluding her investment in eggs, is a positive function of her size. Unless the rate of food intake is also a positive function of body size, increasing at a sufficient rate, the amount of energy remaining to be put into eggs per unit time will be a decreasing function of body size. Since egg size is independent of body size (BANKS & THOMPSON, 1987a), clutch size will be a decreasing function of body size. Because *C. puella* feeds on the wing on abundant but dispersed prey, it is likely that the feeding rate is determined by the number of encounters with prey, and is independent of body size.

Irrespective of the functional explanations of the relationships between longevity and body size, and clutch size and body size, the consequences of these relationships in terms of selection on body size can be deduced from the relationship between lifetime egg production and body size (Fig. 2). The relationship is humped, with an optimal body size with respect to lifetime egg production, but the optimal size is larger than any female actually observed. This optimum size should not be regarded as a precise estimate, since it is derived from multiplying together regression equations from two weak relationships, and also because it requires extrapolating outside the range of the data. Nevertheless, it is reasonable to suggest that it implies that there is directional selection for increasing female body size.

Why then have females not responded to this selective pressure such that female sizes are clustered around the optimal size? There are three possible reasons. First, there may be no genetic variation for larger size (BRADSHAW, 1984). Second, present female size is the result of selection in the past. It may be that the optimal size in the past was different from the present optimum, and that female size has not yet responded to the change in selection. Third, there may be another selective force acting directly or indirectly on female size. An obvious possibility is that female size is constrained by the amount of time available for development, since it is likely that it is advantageous for females to emerge early in the season in order to give their larvae an advantage over late hatching, and thus smaller, competitors (see BANKS & THOMPSON, 1987b).

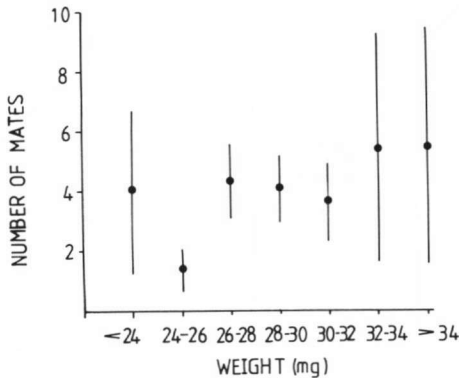


Fig. 3. The relationship between male lifetime mating success and male weight for the July data set; means and 95% confidence intervals are displayed.

This study is unusual in finding that short term mating success is inversely correlated with size, smaller males being better at obtaining matings. The most likely explanation for this relationship rests on the way that energy intake and expenditure scale with body size. The overall effect of body size on mating success is weak, the 'worst' sized males expecting only about 0.25 fewer matings than optimal size males. The weakness of this relationship is reflected when observed mating success is examined as a function of size (Fig. 3).

The observed mean body weight is slightly less than the optimum weight predicted from the relationship between lifetime mating success and body weight. However, the distribution of observed body weights is biased towards smaller individuals because many larger individuals were weighed at emergence, and so are excluded from Figure 1. Also, the estimate of the optimum is not a precise estimate, as it is derived by multiplying together regression equations from two weak relationships.

The distribution of male body weights is clustered around the size predicted to be optimal with respect to mating success, and the relationship between body weight and mating success is an adequate explanation for the typical size of male *C. puella* observed.

Few studies have found stabilising selection on size with respect to mating success. MASON (1964) and SCHEIRING (1977) found stabilising selection in the milkweed beetle *Tetraopes tetraophthalmus* in which intermediate sized males have high short term mating success. RIDLEY & THOMPSON (1979) found several advantages of large size in terms of acquiring mates in the freshwater isopod *Asellus aquaticus*, balanced by higher mortality among larger males, and WARD (1983) found similar results in the freshwater amphipod *Gammarus pulex*. FINCKE (1982) found stabilising selection on body size in the damselfly *Enallagma hageni*, though she was not able to relate either survival or mating rate to body size (but see FINCKE, 1988).

That directional selection for larger body size is reported more frequently than stabilizing selection in studies of mating success may be because all of these studies are of short term, rather than lifetime, mating success. Components of selection on size that arise from variation in survival are thus not detected.

*Coenagrion puella* is sexually dimorphic in body size ; females are bigger than males. This is the typical case in Zygoptera (HAMMOND, 1977 ; D'AGUILAR *et al.*, 1986). In insects which show sexual dimorphism in size, females are generally bigger than males, in contrast to most dimorphic mammal and bird species, in which males are usually bigger than females (RALLS, 1976 ; CLUTTON-BROCK, 1983).

The explanation for the evolution of sexual dimorphism in *C. puella* depends on the nature of selection on the size of females and males, respectively. The optimum size for females, with respect to lifetime egg production, is bigger than the optimum size for males, with respect to lifetime mating success. Thus, the different selective forces acting on the two sexes have favoured females and males of different sizes, producing the observed sexual dimorphism.

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