

## **SHORT-TERM MATING SUCCESS OF MALE *COENAGRION PUELLA* (L.) (ZYGOPTERA: COENAGRIONIDAE)**

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Male size decreased through the breeding season. Several phenotypic characters of paired, unpaired but patrolling, and feeding males were measured and compared. There was no significant difference in mean wing loading between paired and patrolling individuals, but paired males had a lower wing loading than feeding males. No blue colour differences could be detected between paired and unpaired males. There were no differences in the mean amount of black markings between paired and unpaired males though there was significantly less variation in the index of blackness among paired than among patrolling individuals. Also there was no difference in size of the "U-shaped" mark on the second abdominal segment between paired and unpaired males. The difficulties in quantifying the proportion of non-random variation in mating success are discussed.

### **INTRODUCTION**

A study of lifetime mating success can provide a broad picture of the sources of variation in mating success, in terms of variation in survival, and variation in mating efficiency (FINCKE, 1982; BANKS & THOMPSON, 1985, 1987; KOENIG & ALBANO, 1987). However, because one wishes to limit the amount of handling of members of the study population that is desirable in such a study, few phenotypic characters (usually body weight and wing length) can be measured. In the study by BANKS & THOMPSON (1985), this caused problems in the interpretation of the data for lifetime mating success. Because the characters that could be measured were not highly correlated with mating efficiency or survival, it was not possible to assess whether most of the variation in mating success was due to phenotypic variation in mating efficiency or survival, or was merely random variation (see SUTHERLAND, 1985).

Similarly, this long-term study could not be used to measure selection on characters that could not be measured without excessive handling of the study animals. These characters include colour patterns and more complex morphological characters, such as wing loading and measures of condition.

A way to overcome these difficulties is to study short-term, or instantaneous mating success (MASON, 1964; SCHEIRING, 1977; WARD 1983; CLUTTON-BROCK, 1983), by comparing the phenotypic characters of paired and unpaired males. Paired and unpaired males can be collected from a natural population and taken to the laboratory, where a large number of characters can be measured for each individual.

The results of such a study of the characteristics of size, wing loading, condition, colour intensity and colour pattern, of paired and unpaired male *Coenagrion puella*, are presented in this paper.

## METHODS

The study was carried out in June and July 1985, at Capenhurst Ponds, Wirral, northern England (53° 18'N, 2° 54'W). At Capenhurst Ponds there are three roughly circular ponds, each with a perimeter of about 100 m, situated in an area of rough grassland. Two of the ponds are linked by an area of shallow water or marsh. *Coenagrion puella* oviposits mostly in *Potamogeton natans*, and the ponds are surrounded by *Equisetum*. Both males and females were found to feed along hedgerows and in long grass between 25 m and 150 m from the ponds.

Collections of paired and unpaired males were made on four occasions, between 1000h and 1300h GMT (Solar Noon is 1200h GMT), the period of most intense reproductive activity. On each occasion all paired males were caught before the first of the unpaired males. The females caught with paired males were retained so that the operational sex ratio was not made less male-biased by the removal of males alone, because females were also taken.

Two kinds of unpaired males were caught: males that were patrolling the pond in search of females, and males that were feeding some distance from the pond, and evidently not attempting to find mates. These two classes of unpaired males will be referred to as "patrolling males" and "feeding males", respectively. The number of males in each category caught on each collection date is shown in Table 1. All feeding males were caught on a single day, during which the weather was sufficiently warm and sunny for one to be certain that weather was not responsible for their absence from the pond. Great care was taken to ensure that these feeding males had fully developed mature coloration, and were not sexually immature.

The males were taken to the laboratory where they were stored at 10° C overnight in order for them to void the contents of their guts. Immediately after their removal to room temperature the blue colour of the abdomen and thorax was assessed using the Methuen standard colour charts (KORNERUP & WANSCHER, 1978). The males were then killed with ethyl acetate, and immediately weighed. Their wings were then cut off carefully at the proximal primary antenodal vein (HAMMOND, 1977), and dried at 60° C for at least five days. The head width and the length of each abdominal segment were then measured to the nearest 0.025

Table 1  
The number of males of each category caught on each sampling occasion during 1985

Date	Paired	Patrolling	Feeding
3 June	20	8	—
18 June	22	22	—
2 July	11	4	—
8 July	20	—	30

mm using a binocular microscope with an eye-piece graticule. The black markings on the thorax and abdomen were also measured, as indicated in Figure 1. The body was dried at 60° C for at least five days. The wings and body were dry-weighted separately on a Cahn C29 electro-balance.

## RESULTS

The size of males, measured as fresh weight, dry weight or head width, decreases through the season (Fig. 2), as was found in an earlier study (BANKS & THOMPSON, 1985). In comparing the sizes of paired and unpaired males, only males collected during the same time period have been used, to avoid the confounding effects of changes through time. Thus, paired males and patrolling males caught on the first three collecting dates have been compared, and paired males and feeding males collected on the fourth collecting date have been compared. The results of comparisons of three size variables (fresh weight, dry weight and head width) are shown in Table II. There are no significant differences in any of these variables between paired males and patrolling males, or between paired males and feeding males, except for a

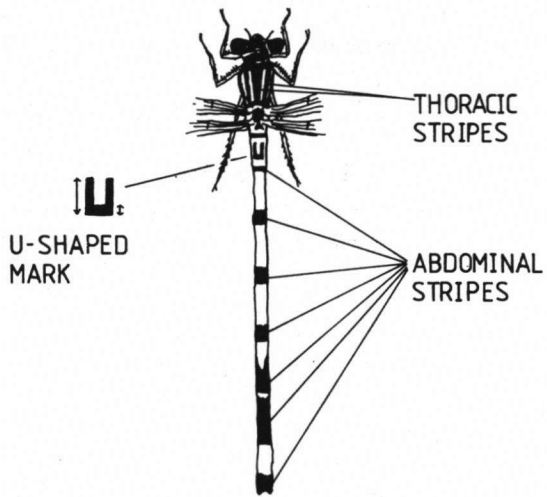


Fig. 1. The black markings on the thorax and abdomen of male *C. puella* that were measured. The two measurements that were made of the U-shaped mark on the second abdominal segment are indicated on the enlarged drawing.

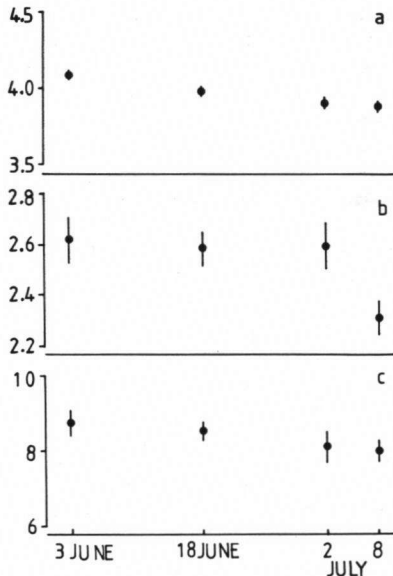


Fig. 2. The mean size (and 95% confidence intervals) of male *C. puella* on each sampling date: (a) head width,  $r_s = -0.596$ ,  $n = 137$ ,  $P < 0.001$ ; — (b) fresh weight,  $r_s = -0.387$ ,  $n = 137$ ,  $P < 0.001$ ; — (c) dry weight.

Table II  
t-test comparisons between (a) fresh weight (mg), (b) dry weight (mg),  
and (c) head width (mm), of paired and unpaired males

	Condition	Mean	SD	n	t	p
(a)	Paired	26.11	2.25	53	0.51	0.609
	Patrolling	25.86	2.25	34		
	Paired	22.23	2.65	20	2.11	0.040
	Feeding	23.72	2.31	30		
(b)	Paired	8.53	0.83	53	0.02	0.981
	Patrolling	8.53	0.67	34		
	Paired	8.11	0.96	20	0.47	0.644
	Feeding	7.99	0.75	30		
(c)	Paired	3.95	0.12	53	0.70	0.485
	Patrolling	4.01	0.10	34		
	Paired	3.92	0.10	20	1.29	0.203
	Feeding	3.89	0.09	30		

just-significant ( $P = 0.04$ ) difference in fresh weight between paired and feeding males, feeding males being heavier.

To examine the effects of the "design" of males on their ability to obtain mates a composite measure, fresh weight divided by wing dry weight, was produced. This index, the wing loading, reflects the weight supported per unit area of wing during flight (CASEY, 1976; BARTHOLOMEW & CASY, 1978). The dry weight of wings was used as a measure of wing area because of the difficulty of measuring such small areas accurately. Wing loading is positively correlated with fresh weight ( $r = 0.522$ ,  $n = 137$ ,  $p < 0.001$ ). To compare the wing loading of paired and unpaired males, only males collected during the same time period have been compared. The mean wing loadings of paired males and patrolling males are compared in Table II. There is no significant difference in mean loading between paired and patrolling males, but paired males have a significantly lower wing loading than feeding males.

Several indices of condition were produced, all designed to reflect the body mass (dry weight) of an individual, in terms of its skeletal size (head width). These indices were dry weight divided by head width, by head width squared and head

Table III  
t-test comparisons of the wing loading of paired and unpaired males

	Condition	Mean	SD	n	t	P
	Paired	43.25	4.25	53	1.55	0.124
	Patrolling	41.72	4.82	34		
	Paired	37.24	4.34	20	3.75	< 0.001
	Feeding	42.34	4.94	30		

Table IV

t-test comparisons of (a) an index of the extent of the black thoracic and abdominal markings, and (b) an index of the size of the U-shaped mark on the second abdominal segment, of paired and unpaired males

	Condition	Mean	SD	n	t	P
(a)	Paired	220.41	12.94	53	1.15	0.293
	Patrolling	224.26	18.49	34		
	Paired	224.78	10.28	20	0.87	0.386
	Feeding	221.73	13.07	30		
(b)	Paired	32.71	2.11	53	0.87	0.386
	Patrolling	33.13	2.38	34		
	Paired	32.58	3.76	20	0.09	0.932
	Feeding	32.65	2.48	30		

width cubed. Residuals from reduced major axis regressions of dry weight on head width, and of log dry weight on log head width, were also used as measures of condition. However, all of these indices proved to be correlated with either (or both) head width or dry weight, and so reflect body size as well as condition. Using any of these inadequate measures of condition to compare paired and patrolling males, and paired and feeding males, showed no significant differences (t-tests).

The colour of the blue portions of the abdomen and thorax was in all cases assessed to be either 23A7 or 23B7 in the colour charts of KORNERUP & WANSCHER (1978), or an intermediate shade. Thus, there was very little variation in the blue colour, and it was difficult to allocate males with certainty to either of the shades noted above. For this reason, no analysis of mating success in terms of the shade of the blue body colour has been made.

The effects of the total amount of black coloration on the thorax and abdomen on mating success was examined by adding together the widths of all of the thoracic and abdominal bands, together with the two measurements made on the U-shaped mark on the second abdominal segment (see Fig. 1). Surprisingly, this index of blackness is not correlated with body size, measured as head width ( $r_s=0.091$ ,  $n=137$ ,  $P=0.289$ ). Comparisons between paired males and patrolling males, and between paired males and feeding males, are shown in Table IV. There are no significant differences in the mean amount of black markings in either of these comparisons. However, there is significantly less variation in the index of blackness among paired males than among patrolling males ( $E_{34,53}=2.04$ ,  $P<0.02$ ).

The effects of the size of the U-shaped mark on the second abdominal segment on mating efficiency were examined by adding the measurements of its length and the width of the cross-piece. The resulting index is not correlated with head width

( $r_s=0.088$ ,  $n=137$ ,  $P=0.30$ ). Comparisons of the size of the U-shaped mark between paired and patrolling males, and between paired and feeding males, are shown in Table IV. There are no significant differences in either of these comparisons:

## DISCUSSION

Three classes of male have been distinguished in this study: paired males, patrolling males and feeding males. BANKS & THOMPSON (1985) suggested that the variation in daily mating rate of males might be due to either variation in the ability of males to encounter females while searching at the pond, or variation in the amount of time spent searching at the pond during the day. By dividing unpaired males into those that were present at the pond (patrolling males), and those that were not at the pond (feeding males), these two sources of variation in daily mating success can be, at least partly, distinguished. Phenotypic differences between paired males and patrolling males are likely to be due to differences in males' ability to encounter females at the pond, whereas phenotypic differences between paired and feeding males are likely to reflect variation in the amount of time males spent at the pond. This distinction is not incisive, however, since paired males may merely be the males that spent more time at the pond than patrolling males.

The effects of male body size on mating efficiency and survival were discussed by BANKS & THOMPSON (1985). Briefly, smaller males have higher daily mating rates but larger males survive longer. Because larger males emerge earlier than smaller males, the body size of males sampled on any one day is positively correlated with their age, and daily mating rate increases with age. Given these complex relationships between size, age and mating efficiency, it is difficult to predict whether differences in size between paired and unpaired males could be expected. The data presented in this chapter show no difference in body size between paired and patrolling males, but show that feeding males are heavier (fresh weight) than paired males. However, this evidence is not conclusive, because there is no significant difference in dry weight or head width between paired and feeding males. These results emphasise the importance of studies of long-term mating success, because this short-term study leads to the false conclusion that body size has little or no effect on male mating success.

BANKS & THOMPSON (1985) showed that smaller males have higher daily mating success because they have higher mating rates on days when they are present at the pond, either because they have higher encounter rates with receptive females, or because they spend more time per day at the pond. It was also suggested that smaller males might be able to spend more time per day at the breeding site because of the lower energetic costs of flight that they incur, compared with larger males. The finding that paired males have a lower fresh

weight than males that are feeding away from the pond, but are not significantly heavier than unpaired males that are present at the pond, supports this suggestion.

Further support for this suggestion comes from the examination of the wing loading of paired and unpaired males. The wing loading of paired males is significantly lower than that of feeding males, but is not different from that of patrolling males, indicating that males with high wing loadings spend less time at the pond. Wing loading in *C. puella* is positively correlated with body mass, as is the case in other insects (WEIS-FOGH, 1973, CASEY, 1976; BARTHOLOMEW & CASEY, 1978). The energetic cost of hovering flight in sphingid moths is directly proportional to wing loading (CASEY, 1976). If a similar relationship holds for *C. puella* large males, with higher wing loadings will expend more energy per unit time while searching for females, and so spend less time at the pond.

The apparent lack of variation in the blue colour of the abdomen and thorax may be in part due to the coarseness of the scale of standard colours used, and variation on a finer scale may exist. Whether damselflies are able to distinguish such fine variation in colour is not known. The blue-sensitive pigments in the eyes of some Anisoptera are sensitive to a broad range of wavelengths, rather than having a narrow peak of sensitivity (MENZEL, 1975). However, there have been no behavioural studies of the colour sensitivity of adult odonates. The lack of variation in the blue colour may be because the colour is produced by a single pigment, as is the case in some colour morphs of *Ischnura elegans* (LORD, 1961). This lack of variation may be the consequence of intense selection on colour in the past having eliminated genetic variation for colour (FALCONER, 1981).

It appears that the maintenance of the blue colour has some physiological cost, as the colour fades very rapidly after death. That all males sustain this cost suggests that the blue coloration is a component of male fitness. That only males of *C. puella*, as in other *Coenagrion* and *Enallagma* species, are bright blue, whereas females are typically more cryptic shades of green, suggests that the blue coloration may have evolved through sexual selection. However, in those coenagrionid species whose mating systems have been studied in detail (BANKS & THOMPSON, 1985; FINCKE, 1982), males engage in scramble competition for receptive females, and direct male-male interactions and female choice are unimportant. It is thus difficult to imagine how the blue coloration could be advantageous in sexual competition.

That there is less variation in the total amount of the black markings on the abdomen and thorax of paired males, compared with patrolling males, indicates that there is stabilising sexual selection for intermediate sizes of the black markings. The mechanism through which such stabilising selection might act is puzzling. Females do not appear to exercise mate choice among conspecific males; so selection on the black markings through female choice is unlikely. The

size of the black markings appears to be a poor cue for species recognition. It is also difficult to imagine a plausible mechanism by which an intermediate degree of blackness could confer an advantage on males in scramble competition for females.

The effects of the size of the U-shaped mark on the dorsum of the second abdominal segment on mating success were examined in detail because the shape of this mark is clearly different in different *Coenagrion* and *Enallagma* species. It is thus possible that females might use this mark as a cue to the species of potential mates. No effects of the size of this mark on mating success were found, though there is some variation in the size and shape of the mark. However, the variation is never such that the mark resembles that of other species.

There is further evidence that the second abdominal segment dorsal mark, or other black thoracic and abdominal markings or the blue colour are not used by females as cues for mate choice. All of these features are only present, or are most prominent, on the male's dorsal surface. However, males usually approach and grab females from above and behind, such that the female is unable to see the male's dorsal surface. In the tandem and wheel positions the female is also unable to see the male's dorsal surface. It is therefore unlikely that females use visual cues on the male's dorsal surfaces for mate choice. This contrasts with colour dimorphic damselfly species in which male colour patterns have been suggested to be important in mate choice. For example, in *Platycypha caligata* (ROBERTSON, 1982) and *Calopteryx maculata* (WAAGE, 1973), males make dispaly flights in front of the female before attempting to take her into tandem. During these displays the males' distinctive colour patterns are clearly visible to the female.

This study has been unable to demonstrate whether the variation in daily mating success found in the study of lifetime mating success (BANKS & THOMPSON, 1985) is likely to be chance variation or the result of phenotypic variation. Negative evidence, that there are no differences in the characters measured between paired and patrolling males, is inconclusive, because many other characters that were not measured, may be sources of variation in mating efficiency. Positive evidence, of phenotypic differences between paired and unpaired males, shows that some of the variation in mating efficiency is non-random. However, it is not possible to quantify the proportion of the variance in mating success that is non-random.

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