

## EMERGENCE, LONGEVITY AND BREEDING AREA FIDELITY IN *COENAGRION PUELLA* (L.) (ZYGOPTERA: COENAGRIONIDAE)

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Two thousand 714 newly emerged adult *C. puella* were collected over a 41 day emergence period. These animals were uniquely marked with a number on the left hindwing and a spot of paint on the thorax. Females emerged on average 1.4 days earlier than males, but had a longer immature period (16.5 days compared with 13.2 days). Males were twice as likely as females to return to the emergence site to breed. The sex ratio at emergence was not significantly different from unity. (50.96% males). The mean mature adult lifespan was 5.6 days in males and 5.4 days in females. Most individuals of both sexes breed at only one breeding site.

### INTRODUCTION

WARINGER & HUMPECH (1984) pointed out that although *Coenagrion puella* (L.) is a very common European damselfly, little is known about its life history. CORBET et al. (1960) stated that *C. puella* is a summer species and assigned it to the group that is usually univoltine. PARR (1970) described a population from northern England in which about one quarter of the population was semi-voltine. He reported that *C. puella* is normally on the wing from the second week in May to the end of the second week in August and is common in July. WARINGER & HUMPECH (1984) themselves investigated embryonic development and larval life of *C. puella* both in the laboratory and in a pond in Lower Austria.

The aim of this paper is to fill in the gaps in our knowledge of the life cycle of *C. puella* particularly with reference to early adult life. We provide data on emergence, length of immature period, longevity in general and breeding area fidelity.

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These data are discussed in relation to other zygopteran species.

The study differs from others in which a population has been followed at the breeding site for a season in that no population estimates are made using the statistical techniques of mark-release-capture methods, as is usual. Instead, each individual in the population was captured, either at emergence, or on its first appearance at the breeding site, and subsequently given an individual mark. Detailed observations of each day's breeding population enabled us to provide more precise data on the prereproductive period, longevity and fidelity to the emergence site than have been published previously.

#### STUDY SITE

The study was made in May, June and July 1983 at Bungalow Pond, Wirral, northern England, Nat. grid. ref. SJ 234857. Bungalow Pond is a small, roughly circular pond with a perimeter of about 60 m. The aquatic vegetation, in which oviposition occurs, consists of *Nuphar lutea* and *Potamogeton crispus*, virtually all of which can be reached by wading. The emergent vegetation is mostly *Glyceria* spp. with one small patch of *Iris pseudacorus*. The only other zygopteran species present in the pond was *Ischnura elegans* (Vander L.). The nearest other population of *C. puella* was at a larger pond (Top Pond) about 800 m away and separated from Bungalow Pond by a large meadow and an arable field. The *C. puella* population in Bungalow Pond was entirely univoltine.

#### METHODS

From the first day of emergence, 15 May, the emergent vegetation around the pond was searched at least twice per day. All newly emerged adults were collected and returned to the laboratory in transparent plastic pots 8 cm deep, 4 cm radius, with clip-on lids made from gauze netting, to which the animals could cling. Losses and damage were negligible. Exuviae found with an adult were destroyed; exuviae found without an adult were kept as a record of the number and sex of individuals not caught. Emerging adults were "missed" mainly on days on which large members emerged and when the temperature was so high that animals took less time to complete emergence. Few animals were lost to predators in 1983 unlike 1984 (cf. THOMPSON et al., 1985). In the laboratory the newly emerged adults were lightly anaesthetised with carbon dioxide; they were uniquely marked with a number on the left hindwing in waterproof ink (using an "Edding 404" pen) and a dot of "Humbrol" paint on the dorsum of the thorax. They were kept overnight at 10° C, and released next morning near the edge of the pond. Marking had no apparent effects on behaviour and the marked animals seemed to fly as well as unmarked animals.

From 4 June, when the first mature individuals were seen at the pond, observation during the middle of the day 10 am. — 3 pm. was concentrated on reproductive activity rather than emergence, though searches for emerging adults were carried out before and after these times.

During the main reproductive part of the day, 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 was 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. We attempted to record every patrolling male and tandem pair present at the pond throughout the entire breeding season.

In addition to those animals caught and marked at Bungalow Pond, on seven occasions through-

out the study we caught and marked teneral and adult animals at the nearby Top Pond. On these visits we also searched Top Pond for animals marked at Bungalow Pond.

## RESULTS

The first adult emerged at Bungalow Pond on May 16. The last individual was seen there on 31 July, though a few were still present at the nearby Top Pond until 7 August. Figure 1a-b shows the percentage frequency histograms for the emergence of males and females respectively. Data are presented only for those animals which were subsequently marked, since we could not be absolutely certain about the emergence dates of those animals from which we had exuviae only. The curves are similar; they are skewed to the right. The mode for both

males and females was day 12, which was 27 May, on which 19.5 and 20.3% of the adults of the respective sexes emerged. However, 36.4% of the females and only 17.5% of the males had emerged before this date. Females emerge significantly earlier than males (mean date of emergence  $13.9 \pm 0.15$  (S.E.) as opposed to  $15.3 \pm 0.13$  (S.E.) days from the onset of emergence ( $p < 0.001$ ;  $n = 2714$ )). There is evidence of a second peak around day 23, 7 June, but this was probably due to changing weather conditions around that date. Emergence was greatly affected by weather conditions. For example, the numbers of adults emerging on days 12, 13 and 14 were 537, 12 and 380 respectively (cf. Fig. 1a-b). Day 13 was memorable as a very cold rainy day. The

second peak was certainly not due to any real bimodality in the larval population which is always univoltine at the Bungalow Pond. The emergence period lasted slightly longer than the 41 days shown on Figure 1, but after this time systematic searches for emerging animals were discontinued.

The sex ratio of adults (marked animals plus exuviae) was not significantly different from unity (50.96% males;  $n = 3756$ ;  $p > 0.05$ ). The sex ratio of animals actually marked was 50.88% males ( $n = 2714$ ).

Figure 2a-b shows the percentage frequency distribution of the lengths of the immature period for females and males respectively. The mean length is  $16.5$  days  $\pm 0.34$  (S.E.;  $n = 170$ ) for females and  $13.2 \pm 0.22$  (S.E.;  $n = 302$ ) for males. The modes were 10 and 14 days respectively. Of 1381 males marked at emergence at

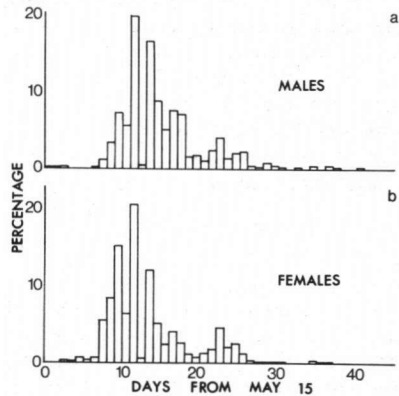


Fig. 1. Frequency histograms which show the percentage of the population of *Coenagrion puella* which emerged daily throughout the summer of 1983. Day 0 = 15 May; day 40 = 24 June (a: males; — b: females).

Bungalow Pond 23.2% returned there to breed, compared with 12.7% of females (out of 1333). Males, then, were almost twice as likely to return to their emergence site than females. This difference can be attributed to greater mortality amongst females during their longer immature period.

Figure 3a-b shows the survivorship curves for marked males and females respectively. The points plotted on the ordinates for day 0 represent the numbers of animals marked at emergence. The data have been plotted as if all the animals belonged to a single cohort that emerged on the same day. We assumed that the disappearance of a mature adult from the population represents its death rather than dispersal (see below). The mean mature lifespan for adults present in the population in July was 5.6 days  $\pm$  0.02 (S.E.) for males and 5.4 days  $\pm$  0.03 (S.E.) for females. The daily survival rate which is roughly constant and independent of age for both males and females was 0.83 for males and 0.82 for females (BANKS & THOMPSON, 1985). The longest lived male lived for 39 days, and one female lived for 46 days.

Of 568 immature and mature (mainly the latter) adults (474 male and 94 female caught and marked at Top Pond), only one (male) was later seen at Bungalow Pond. We did not mark these animals individually so have no way of knowing whether it was an immature or mature animal. Of these 568 individuals, eight (7 males and 1 female) had previously been marked at emergence at Bungalow Pond. No individual (out of a possible 1442) that had been seen as a mature adult at the Bungalow Pond was later seen at Top Pond although the prevailing wind direction was from Bungalow to Top Pond. We conclude that *C. puella* breed in one place unless weather conditions such as strong winds force them to move elsewhere.

The results described above are summarised in Table I.

## DISCUSSION

CORBET et al. (1960) classified *C. puella* as a summer species. Although emergence begins quite early in the season (May 16 in 1983), the emergence lasts

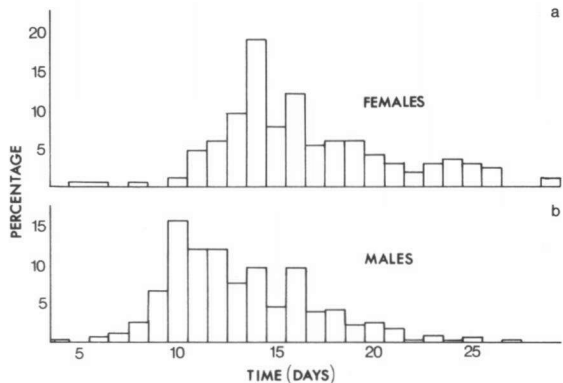


Fig. 2. Frequency histograms which show the percentage of adult *Coenagrion puella* with different lengths of the immature period. (a: females; — b: males).

Table I  
Summary of data on emergence, prereproductive period and longevity of *Coenagrion puella*

	Males	Females
Mean ( $\pm$ 1 S.E.) time of emergence (days after 15 May)	15.3 $\pm$ 0.13	13.9 $\pm$ 0.15
Sex ratio at emergence (%)	50.96 (n = 1914)	49.04 (n = 1842)
Mean ( $\pm$ 1 S.E.) length of immature period of those adults reaching maturity (days)	13.2 $\pm$ 0.22 (n = 302)	16.5 $\pm$ 0.34 (n = 170)
Adults returning to emergence site to breed (%)	23.2 (n = 302)	12.7 (n = 170)
Mean ( $\pm$ 1 S.E.) mature adult lifespan (days)	5.6 $\pm$ 0.02	5.4 $\pm$ 0.03
Daily survival rate of mature adults (proportion surviving per day)	0.83	0.82
Maximum total lifespan (days)	39	46

over six weeks and the flight period is long, typical of summer species. Over 95% of the population emerged in a 19 day period (Fig. 1), but the emergence period is such that it is not difficult to see how at similar or more northerly latitudes, some populations may contain univoltine and semi-voltine sub-populations (PARR, 1970).

Emergence occurred mainly in mid-morning, as with *Pyrrosoma nymphula* (CORBET, 1952). Like *Pyrrosoma*, *C. puella* larvae swim towards the shore a few minutes before emerging, or even crawl there on top of the leaves of *Nuphar lutea*. CORBET (1952) suggested that larvae may be able to orientate to the shore by responding to a rising temperature gradient. More larvae emerged in the middle of the pond late in the season when the flower spikes of the *Potamogeton* were above the water level, so the essential requirement is not to reach the shore, but to find something to climb up.

Females emerge significantly earlier than males, and show a wider spread of emergence times. However, an important parameter of early adult life is the time at which the adults are first present at a breeding site in breeding condition. The significantly shorter immature period of males more than compensates for their later emergence. The reproductive behaviour of *C. puella* which is essentially a scramble by males for females arriving at the breeding site, requires that males be present when females come to lay eggs. The shape of the frequency distributions of

emergence time and times to maturity of each sex in insect populations is of considerable theoretical interest at present (cf. PARKER & COURTNEY, 1983).

The sex ratio of odonates at emergence was last reviewed by LAWTON (1972). The figure of 50.96% males in the present study is the lowest percentage of males of *C. puella* reported, but the sample size is nearly twice as high in the combined total of the other three studies. In LAWTON's (1972) study, and that of PARR & PALMER (1971), the sex ratio differed significantly from equality though it did not in that of VAN NOORDWIJK (1978). As CORBET (1962) pointed out, emergence curves of males and females need not be identical, so that unless exuviae collections are made throughout the entire emergence period, a false picture of the sex ratio might be gained. Indeed, collections of *C. puella* after day 12 of emergence in the present study would have given a male-biased sex ratio.

The fact that one sex may return to breed before the other has been used by CORBET (1962, based on WALKER, 1953) to imply that the sexes may have different emergence times. However, the present study has shown that the immature period of adult Zygoptera can differ significantly between sexes, so the appearance of adults at the breeding site

cannot be used for such a measure. In any case the variation in prereproductive period is much too great for such an inference to be made. In his post-1960 review of recent advances in odonate biology, CORBET (1980) has collected data on the times to maturity of zygopteran species; *C. puella* falls well within the normal range of three weeks or less. Four other studies have shown that males return to the breeding site in a shorter time than females (PAJUNEN, 1962; SCHMIDT, 1964; UBUKATA, 1974; FINCKE, 1982) while no studies, to our knowledge,

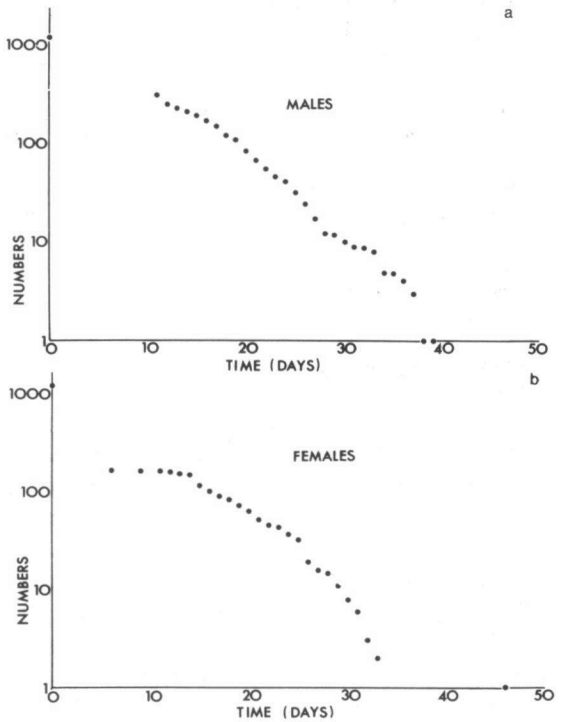


Fig. 3. The survivorship curves of *Coenagrion puella* which were marked on emergence at Bungalow Road and returned to breed there: (a) males; — b) females).

have found the opposite result.

Once they arrive at a suitable breeding site, *C. puella* tend to perform all their reproductive activity at this site, returning each suitable day (cf. WARINGER, 1982) to search for females or lay a clutch of eggs. Breeding area fidelity has been recorded before for Zygoptera. MITCHELL (1962) estimated that a population of ten to twenty thousand *Ischnura verticalis* (Say) lost less than 2% through dispersal to a pond just 100 m away during ten days of normal weather. He also showed that this figure increased tenfold following two days of stormy weather. UEDA (1976) marked mature males of *Cercion calamorum* and found that two small sub-populations living in close proximity (in a study area of 312 m<sup>2</sup>) were relatively independent. This finding is of immense importance, if universal, for those who have been using damselflies as subjects for studying lifetime reproductive success (FINCKE, 1982; BANKS & THOMPSON, 1985) and for those modellers of damselfly population dynamics. It means that dispersal during the reproductive stage can be virtually ignored.

As CORBET (1980) pointed out, most records of longevity in nature refer only to the reproductive period. *Coenagrion puella* in the present study had a mean reproductive life of 5.6 days for males and 5.4 days for females. PARR (1973, 1976) has provided estimates of the lifespan of two of the other common zygopteran species occurring in northern England. The mean mature adult lifespan for male *Enallagma cyathigerum* was 12.2 days and for *Ischnura elegans* between 3.3 and 12.4 days depending on location and estimation procedure. PARR (1973) points out some of the pitfalls of using mark-release-recapture methods to estimate lifespan and survival in zygopteran populations (cf. BEGON, 1979 for more general criticisms of these methods). The daily survival rate for *C. puella* in the present study was 0.83 for males and 0.82 for females; these figures fall well within the range of 0.72 to 0.93 given by CORBET (1980). The daily survival rate was independent of age during the reproductive period. This is an important point. Although we were not able to estimate survivorship during the immature period, by extrapolating the survivorship curve back to the ordinate, it is clear that while survival expectation may be lower in the immature period than in the reproductive period, it was not drastically lower in the present study. This contrasts with the findings of PARR (1973) working with *Ischnura elegans*. He found a low survival rate in general insects.

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