EXPERIMENTS ON POPULATION DENSITY OF MALE *COENAGRION PUELLA* (L.) BY WATER (ZYGOPTERA: COENAGRIONIDAE)

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Males were subtracted from or added to existing populations of *C. puella* beside small ponds in field experiments at Woodwalton Fen, Cambridgeshire, United Kingdom (1992, 1993). When insects were subtracted the population returned to the original level within 1½ h. Addition of insects from elsewhere raised low populations to a certain level, but did not raise populations already at that level. *C. puella* do not fight, but the pursuit of one male by another can lead to the pursued one leaving the water. Whether or not this is the mechanism controlling male population density by water, clearly the behaviour of the insects is at least partly responsible. The quasi-territorial behaviour in *C. puella* operates at low as well as high population densities. It enables a higher steady population density to occur than is found in the truly territorial species so far studied. An interesting and unexplained anomaly of population density in *C. puella* is described.

INTRODUCTION

BANKS & THOMPSON (1985), who have made extensive and thorough studies on the reproduction of *C. puella* on a pond near Liverpool, call the species "a non-territorial damselfly". *C. puella* was an abundant species at the ponds studied for 27 years at Woodwalton Fen, Cambridgeshire by the present author (MOORE, 1991). During that period no fights nor overtly aggressive behaviour between males were observed. However, the highest densities of males by water did appear to range between fairly narrow limits (68 to 156 males per 100 m of water's edge). At three ponds elsewhere at Woodwalton Fen, which were surrounded by much denser marginal vegetation, the highest population density observed over 11 years ranged between 250 and 333 males per 100 m edge. Thus, while the amount of suitable habitat bordering the water's edge clearly influenced the number of males present, the rather small variation within ponds of the same type indicated that male population density was being controlled to some extent by the behaviour of the males themselves. It was suggested (MOORE, 1991) that this hypothesis could be tested by experiments in which males were added to and subtracted from known populations. This paper describes the results of preliminary experiments of this kind, which were carried out on some of the Woodwalton Fen ponds in 1992 and 1993.

METHODS

The ponds used for the experiments are circular with a circumference of ca 16 m. Each pond is surrounded by a grass strip, which is backed by some scrub. Thus each pond is surrounded by suitable habitat for *C. puella* which are not patrolling or perched by the water's edge. For further details of the ponds see MOORE (1991).

The addition and subtraction experiments were of the kind used to test the values of highest steady density of territorial dragonflies at water-filled bomb holes in Dorset (MOORE, 1964). In the subtraction experiments mature male *C. puella* were collected out from the pond whose population was being studied. They were then used in addition experiments on other ponds. In some addition experiments mature males were also collected from ditches to the east of the study area. From whatever source, the insects were put in containers or a large gauze-covered cage, transferred to the experimental pond and carefully released at the water's edge. In a very few instances a released insect was seen to fly upwards and leave the pond; no movement of insects between ponds was observed.

Before and after adding or subtracting insects, transect counts (MOORE, 1953) were made of male *C. puella* present by water. These included pairing males.

In one addition experiment (Experiment 4) the insects which had been transferred from another pond were marked with a quick drying red paint before release. This was done to check that introduced insects could remain at their new pond despite disturbance caused by capture and release.

Further observations on the behaviour of *C. puella* were made at the author's pond 22 km away at Swavesey.

RESULTS

The results of the addition and subtraction experiments are summarised in Table I. The data for experiments 4, 5, 6 and 9 are shown diagrammatically in Figures 1, 3, 2 and 4, respectively.

Counts made at pond 8 acted as a control. They confirmed observations made in the 27 year study at Woodwalton and elsewhere that peak numbers occur about noon. However the values obtained on two consecutive days (Experiments 13 and 14) show that the peak

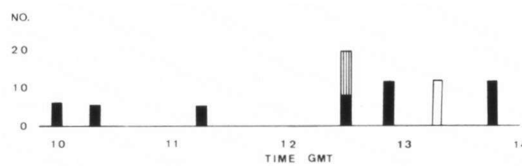

Fig. 1. Experiment 4: the effects of adding males to a low population of male *C. puella* and later subtracting males from it. Pond 12, 4-VI-1993. (Compare Fig. 3). Note: highest number recorded 1961-1988 was 19 (MOORE, 1991). – [Black: males present by water; – grey: males added; – white: males subtracted.

Table I

Numbers of male *Coenagrion puella* before and after adding to or subtracting males from the edge of ponds. – [Roman type: times (GMT); – bold type: numbers of males; – bold in brackets: numbers added or subtracted; – C: controls]

Experiment no.	Type	Pond	Date	Times, numbers of males, additions and subtractions a.m.	p.m.
1	+	12	11-VI-1992	1143 **12**	1201 **13**, 1230 **[+6]**, 1259 **[+5]**, 1317 **20**, 1337 **13**, 1413 **12**
2	+	12	12-VI-1992	1051 **13**, 1055 **[+6]**, 1125 **[+8]**	1211 **13**
3	+	12	30-VI-1992		1210 **4**, 1249 **4**, 1250 **[+8]**, 1258 **9**, 1314 **10**, 1335 **[+8]**, 1343 **13**, 1406 **[+8]**, 1414 **12**
4	+-	12	4-VI-1993	1000 **6**, 1020 **5**, 1115 **5**	1228 **8**, 1230 **[+11]**, 1252 **12**, 1317 **[-12]**, 1346 **12**
5	+	12	5-VI-1993		1237 **21**, 1246 **[+43]**, 1340 **26**, 1346 **24**, 1358 **23**, 1408 **19**
6	+	2	4-VI-1993	1025 **22**, 1116 **10**, 1124 **[+12]**, 1137 **17**	1204 **15**, 1244 **20**, 1334 **13**, 1337 **[+12]**, 1352 **24**, 1408 **21**
7	-	16	11-VI-1992	1140 **4**, 1141 **[-5]**	1225 **1**, 1226 **3**, 1302 **4**, 1402 **2**
8	-	16	4-VI-1993	1003 **8**	1225 **15**, 1226 **[-12]**, 1248 **21**, 1344 **26**
9	-	16	5-VI-1993	1133 **18**, 1135 to	1235 **[-46]**, 1236 **0**, 1247 **5**, 1318 **6**, 1331 **7**, 1354 **18**, 1411 **20**
10	-	20	11-VI-1992	1135 **4**	1255 **[-5]**, 1312 **5**, 1411 **6**
11	-	8	11-VI-1992	1146 **8**	1234 **[-5]**, 1306 **6**, 1408 **7**
12	C	8	12-VI-1992	1145 **6**	1209 **6**
13	C	8	4-VI-1993	1006 **9**	1239 **20**, 1405 **12**
14	C	8	5-VI-1993	1137 **12**	1326 **17**, 1356 **19**, 1405 **19**

period can last longer on some days than others. Observations made in the course of Experiment 6 (Fig. 2) shows that the number of males by water can fluctuate within the peak period.

When insects were added to small populations (Experiments 3 and 4; Fig. 1) there was an increase to a high level characteristic of the pond. Similarly when additions were made at low points in an unusually high peak period the result was also an increase in numbers (Experiment 6; Fig. 2). However, when insects were added to ponds which already had large populations (Experiment 1, 2 and 5; Fig. 3) there was no increase (Experiment 2), or only a small and short-lived one (Experiments 1 and 5; Fig. 3).

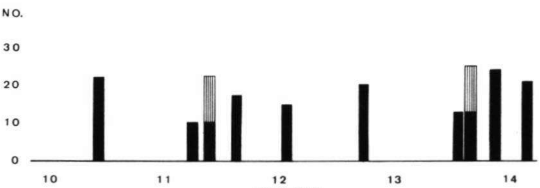

Fig. 2. Experiment 6: the effects of adding males to a high, fluctuating population of male *C. puella*. Pond 2, 4-VI-1993. Note: highest number recorded 1961-1988 was 15. The pond's water level was often low during this period and so the pond was often smaller (MOORE, 1991). – [Black: males present by water; – grey: males added]

In Experiments 7, 8, 10 and 11 all the insects originally present were removed. In Experiment 9 (Fig. 4) insects were collected out for one hour. In each experiment the population returned to approximately its original size (Experiments 7, 9, 10 and 11) or became larger (Experiment 8).

In Experiment 4 the 11 insects released at 1230 had been marked. When 12 insects were collected out at 1317 three of them were marked insects and nine were unmarked. This showed that introduced insects could remain at their new pond.

Male interactions were recorded during a 2½ hour period of observations at Swavesey on 7.VI.93. The results are recorded in Table II. At 99 meetings between males (events A-F in Tab. II) males were in close contact. At a further 16 meetings the males did not react to one another (G). On 19 occasions male *C. puella* were observed to leave the water's edge: in 12 of these the stimulus appeared to be internal (H), but in seven a male left following pursuit by another male (C).

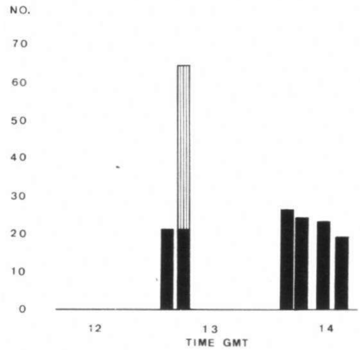

Fig. 3. Experiment 5: the effect of adding a large number of males to a high population of *C. puella*. Pond 12, 5-VI-1993. (Compare Fig. 1). Note: highest number recorded 1961-1988 was 19 (MOORE, 1991). – [Black: males present by water; – grey: males added]

CONCLUSIONS AND DISCUSSION

The subtraction experiments show that when male *C. puella* by water are taken away the number of males by water returns to its original level within 1½ hours or less. In other words, males waiting in the vicinity of the pond quickly fill the gap left by those which were taken away. The addition experiments show that a small population can be increased by adding insects to it, but above a certain level of population size additions do not change it. Together these experiments give strong support to the hypothesis that the size of the population of male *C. puella* by water is controlled by the behaviour of the insects themselves.

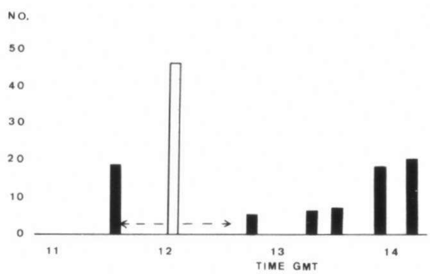

Fig. 4. Experiment 9: the effect of subtracting male *C. puella* for an hour (1135-1235 GMT). Pond 16, 5-VI-1993. Note: highest number recorded 1961-1988 was 23 (MOORE, 1991). – [Black: males present by water; – white: males subtracted during period 1135-1235 GMT]

The observations on the behaviour of *C. puella* show that much interaction between males takes place and that encounters between males can lead to a male leaving the water's edge. The types of interaction described for *C. puella* can all be observed in zygopteran species

Table II

Behavioural elements of male *Coenagrion puella* observed from a fixed point at the Swavesey pond 0801 - 1032 (GMT) on 7 June 1993

	Type of behaviour	Number of events observed	Occasions when male left pond
A	Flying at mating pair	4	0
B	Flying at pair in tow	3	0
C	Flying at flying male	39	7
D	Flying at recently perched male	9	0
E	Head-on confrontation with male	35	0
F	Investigating perched male which lifted wings	9	0
G	Meeting male but no reaction	16	0
H	Leaving water's edge without obvious external stimulus	12	12

which are clearly territorial. The difference between the behaviour of *C. puella* and that of territorial species is that the pursuit of one male by another never leads to behaviour which is obviously aggressive to the human observer. It should not be assumed that the pursuit of males is the mechanism by which male population density is controlled, although it seems most likely that it is.

In *C. puella* control of population density of males by water is achieved without wasteful expenditure of energy and without physical damage which results from fighting. The highest steady density of *C. puella* is higher than that of other zygopterans studied (MOORE, 1964, 1991): this may be a consequence of the absence of overt aggression in *C. puella*. It may help the species to survive in the very small waterbodies in which it is frequently found.

Counts of male insects by water on all 20 ponds at Woodwalton Fen on 11.VI.92 showed that the numbers at several ponds, including pond 16 (Experiment 7), pond 20 (Experiment 10) and pond 8 (Experiment 11) were low. As the weather was fine, and other ponds such as pond 12 (Experiment 1) had high numbers, the low numbers must reflect low total populations. Thus, subtraction experiments 7, 10 and 11 were done on small, suboptimal populations. Nevertheless, the experimental results were the same as those carried out on large populations at pond 16 on other occasions. This indicates that even when there are only a few male insects by water their presence can inhibit other males from going to it. In other words the be-haviour observed operates at low as well as high densities.

An interesting, and so far unexplained feature of the observations is that there appear to be two levels of highest steady density (Tab. I). The level in pond 12 was about 12 or 13 insects (75 per 100 m edge) on 11.VI.92, 12.VI.92, 30.VI.92 and 4.VI.93 (Fig. 1) but about 21 insects (131 per 100 m edge) on 5.VI.93 (Fig. 3). On pond 2, which is similar in size to pond 12, it was also about 12 on 4.VI.93 (Fig. 2). There are indications that this phenomenon occurred throughout the period of previous studies at Woodwalton (MOORE, 1991). Weather, like vegetation, can affect density of males by water. For example, a cool wind can make part of the pond's edge unsuitable for perching insects. However, weather cannot explain the different values obtained on pond 12 since both 4.VI.93 and 5.VI.93 were fine days without wind. Also, the high level in pond 12 did not coincide with the high level in pond 2. Further study is required to explain this phenomenon.

If, as is postulated here, *C. puella* does possess a form of territorial behaviour, this fact needs to be taken into account in population studies. For example, BANKS & THOMPSON (1985) show that the number of days a male spends at the breeding site is the major determinant of breeding success. Territorial behaviour, even if it is the peculiar kind found in *C. puella*, must affect the amount of time which individuals spend on the breeding site.

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