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THE DEVELOPMENT OF DRAGONFLY COMMUNITIES AND THE CONSEQUENCES OF TERRITORIAL BEHAVIOUR: A 27 YEAR STUDY ON SMALL PONDS AT WOODWALTON FEN, CAMBRIDGESHIRE, UNITED KINGDOM

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20 small ponds were constructed at the Woodwalton Fen National Nature Reserve in 1961 and 3 elsewhere in the reserve in 1974 and 1977. The Twenty Ponds were allowed to develop naturally except for scrub control on their perimeters. In the other (Heathfield) ponds emergent plants were planted immediately after their construction. The ponds were visited near noon on fine days as often as possible and the numbers of adult and teneral dragonflies were recorded. Of the 20 spp. breeding within 6200 m of the Twenty Ponds, 6 bred in all the ponds, 4 bred irregularly, 3 rarely, 5 visited the ponds but did not breed and two were never seen on the ponds. The dragonfly community of the Twenty Ponds went through a short pioneer stage in which *Ischnura elegans* and *Sympetrum striolatum* were virtually the only visitors and breeders, then a developmental stage of 11 yrs in which 6 other spp. colonised the ponds and in which *Pyrrhosoma nymphula* and *Brachytron pratense* appeared and disappeared, and finally a climax stage, which has lasted 15 yrs, in which 5 spp. breed regularly, 1 frequently and 2 occasionally. In the 3 Heathfield ponds the pioneer stage was eliminated by planting emergent plants following construction, but in 2 of the ponds a fourth senescent stage followed the climax owing to colonisation by reeds *(Phragmites australis)*. All 23 ponds varied considerably in their simple aquatic vegetation but their odon. faunas were very similar. No one plant sp. was necessary for larval development and most spp. bred successfully when waterweed was totally absent. The partial dependence of the odon. fauna on surrounding populations was evident, notably after the exceptional drought of 1976. Records made throughout the 27 yr period showed that the value of highest steady density for each sp. was remarkably similar for all 20 ponds. The highest steady densities of the spp. of the Twenty Ponds were also very similar to those at the Heathfield ponds and at ponds at Arne in Dorset in the 1950s. The behavioural basis of highest steady density and its ecological consequences are discussed. The implications for conservation strategy of this study on suboptimal populations are outlined.

INTRODUCTION

Very few long-term studies have been made on dragonfly populations. Notable exceptions are those of DUMONT (1971) on the dragonfly communities of a variety of ponds in East Flanders, Belgium, of MACAN (1974) on larvae of *Pyrrhosoma nymphula* (Sulz.) and *Enallagma cyathigerum* (Charp.) at a pond in Cumbria, England, of RUDOLPH (1978, 1979) on dragonfly communities of small ponds near Münster, Germany, of CLAUSNITZER (1983) on the succession of dragonfly species at a pond in Lower Saxony, Germany, which was successively used for fish culture, feeding herons and storks, and for the conservation of anurans and aquatic insects, of DE RICQLÉS (1988) on changes in the status of dragonflies in the Dordogne, France and of CLAESSENS (1989) on changes in odonate communities in relation to developments in a large peat bog area in the southern Netherlands over a period of twenty-five years. Long-term phenomena require long-term studies. Unfortunately long-term research is very difficult to achieve because research sites are often vulnerable to extraneous development, and Ph D students and other workers can rarely devote more than a few years to a project. In the present study security of tenure of the research site was assured because it was situated in a National Nature Reserve. Continuity was made possible because the author lived in its vicinity throughout the period of observation. Inevitably this study has many imperfections due to the demands and priorities of other work, but long-term studies are so rare that it seems worth recording fully.

Ideally, a study of changes in dragonfly numbers should include daily counts of adult insects and daily collections of exuviae. Obviously this sort of work cannot be carried out year after year by one person. Therefore, if long-term work is to be done at all, routine observations have to be made quickly and easily and with longer and often irregular time intervals. Such work is not a substitute for the ideal, but it can provide useful data. Previous observations (MOORE, 1953) showed that transects, in which imaginal dragonflies on the edges of water bodies were counted, took little time to make, yet revealed significant information for the study of odonate behaviour and ecology. In this study counts of adult and teneral dragonflies were used to compare dragonfly populations of 23 small ponds at Woodwalton Fen from year to year. Twenty of the ponds were constructed for the purpose of studying the indirect effects of aquatic herbicides and four were eventually used for this purpose (NEWBOLD, 1976; COOKE et al., 1980); they were made as similar as possible. The other three ponds were dug elsewhere on Woodwalton Fen to determine the feasibility of reintroducing acid water dragonflies to the area (MOORE, 1986).

The aim of this paper is to describe qualitatively and quantitatively the colonisation of the new ponds and the development of their dragonfly communities in relation to surrounding communities and to seral changes in the vegetation of the ponds. The significance of rare events (which are generally missed in short-term studies) is assessed.

The counts of territorial males are used to compare values of highest steady density in Cambridgeshire with those obtained in a very different habitat elsewhere in England (MOORE, 1964). Quantitative data on male densities, together with incidental observations on behaviour, which were made when carrying out the transects, are used to discuss the biological basis of highest steady density. Finally the practical implications of the whole study for conservation are outlined.

DESCRIPTION OF SITE AND METHODS

Woodwalton Fen consists of open water, ditches, marsh, meadows and carr woodland. Its dragonflies were the subject of a special survey by the late A.E. GARDNER (1960) in 1958 and extensive observations were made from 1961 onwards by the author and latterly by the present Warden, Mr Ron Harold.

The Twenty Ponds (see Fig. 1) were constructed in silty soils in a field which had been cultivated during the Second World War and had subsequently reverted to grassland and then became invaded by Hawthorn *(Crataegus monogyna)* scrub. The field was bordered by parallel ditches on its western side. In the winter of 1978-9 ditches and banks were constructed on the remaining sides so that the grassland between the ponds could be used by cattle when lower areas of the fen were flooded. Each pond was wired to keep the cattle out. Scrub, which developed within the wire fences was controlled by cutting when it threatened to impede observations.

The mean circumference of the ponds was 16 m (SD ± 0.51). The spoil from the excavations was used to make banks round each pond in order to isolate them from each other at times of flooding. There was no connection between the ponds, which were about 20 m apart and approximately 2 m deep when completely full.

The water table of the area, and hence the water level of the ponds, underwent irregular annual fluctuations. Measurements (to the nearest 15 cm) were made of the width of the exposed shore of each pond rather than the depth. Since the ponds were steep-sided moderate changes in the water level did not have major effects on the water edge circumference of the ponds.

The three Heathfield ponds were constructed in an area of acid peatland 500 m to the east of the Twenty Ponds (Fig. 1). Pond A of 28 m circumference was dug in 1974 and ponds B and C of 24 m circumference were dug in 1977. In all three Heathfield ponds emergent plants (mainly *Carex*, but also some *Juncus* and *Cladium*) were planted round the edge following construction.

At all ponds records were kept of aquatic plants. Counts varied in accuracy; whenever possible emergent plants, such as *Typha*, were counted individually, and submerged plants such as *Chara* and floating plants such as *Lemna* were assessed as the percentage of the pond which they covered. Incidental notes were kept on mammals, birds, reptiles, amphibia, fish and some invertebrates.

Meteorological records were kept from 1966 onwards at Monks Wood Experimental Station, which is 4.5 km from Woodwalton Fen. For the earlier years, records of sunshine were supplemented by records from the Boxworth Experimental Husbandry Farm which is 24 km from Woodwalton (Fig. 1).

If counts of territorial males of British species are to be comparable they must be made within two hours of noon on days when the sun is shining most of the time and there is no strong wind (MOORE, 1953). Accordingly, nearly all visits to Woodwalton were made under those conditions. 345 visits were made and they covered 155 of the 162 months of flying seasons during the 27 year period.

On each visit all dragonflies observed at each pond were recorded. It is difficult to check the accuracy of counts because the observer, while slowly walking round the pond on the first count, can cause individuals to leave, or can initiate territorial encounters which can also cause individual insects to leave. However, counts of Anisoptera at such small ponds can be taken to be virtually 100% accurate. The danger of missing individual Zygoptera or counting them twice occurs mainly when population densities are very high. It is safe to assume that the accuracy of counts of Zygoptera exceeded 80% on nearly all occasions.

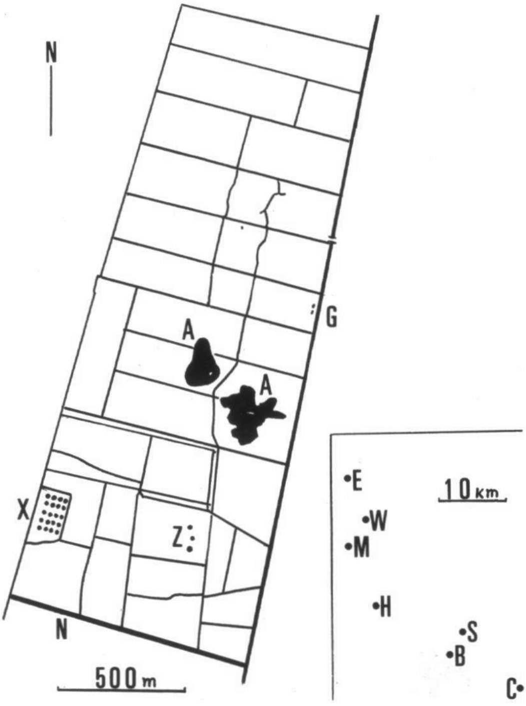

Fig. 1. Woodwalton Fen National Nature Reserve, the study area within the complex of ditches and meres, 1987. — X: The Twenty Ponds (numbered from left to right and from top to bottom: 1, 2, 3, 4; 5, 6, 7, 8; . . . 17, 18, 19, 20). — Z: The Heathfield Ponds (from top to bottom: C, B, A). — A: Meres; — G: Great Raveley Drain; — N: New Drain. — Inset: B: Boxworth; — C: Cambridge; — E: Holme Fen; — H: Huntingdon; — M: Monks Wood; — S: Swavesey; — W: Woodwalton Fen.

Methodical searching for exuviae is a time-taking process and — except for Aeshnid species —could not be attempted within the constraints of this study. However a useful index of successful breeding can be obtained by counting insects at the early teneral stage at the water's edge. This method is valid because, once they have emerged, teneral insects of the species studied always avoid water, therefore the chance that a teneral insect found by the edge of one pond has flown from another pond is negligible. On numerous occasions observations of teneral insects were supported by finding exuviae incidentally.

In this study gross population changes are indicated by comparing the maximal numbers of insects (both adult males and tenerals/exuviae) observed each year. Since the number of visits varied from year to year so did the accuracy of counts of maxima. Therefore an assessment of accuracy is given for each value in the tables.

Studies on a pond at Swavesey (see below), which could be visited daily, suggest that maximal values of males may be missed unless records are made at least once a fortnight during that part of the year when the species can peak in that area (N.W. Moore, unpublished). Accordingly the potential peak period for each species was determined by plotting the peak data for all those years in which at least five visits were made in the season of the species concerned, and which included the rise and fall of the adult population. A similar method was used for teneral insects. For tenerals, especially spring species with a synchronized emergence, ponds should be visited at least weekly. This was rarely possible in this study, hence values for teneral insects are less reliable than those for adult males.

Categories of accuracy were allotted as follows:

- Category 1 (most accurate). — Gaps between visits within the potential peak period were less than two weeks; or, where a two week gap occurred, observations showed that it occurred after the population had begun to decline. Values in this category are shown underlined in the tables.
- Category 2. — Gaps between visits within the potential peak period were more than 2 weeks, but less than 3 weeks. Values in this category are shown in plain fount.
- Category 3 (least accurate). — Gaps between visits within the potential peak period were more than 3 weeks. Values in this category are shown in brackets.

This system enables all records to be used but indicates those which may be less than the true maximal value. Inspection of the tables suggests that many visits made in a season when the number of visits was inadequate did actually occur in the peak period for that year. In other instances the record obtained merely provides a minimal value which may have been exceeded.

In this paper some reference is also made to a larger pond (90 m in circumference) which was dug in clay in a field in 1983 at the author's home in Swavesey, Cambridgeshire (see Fig. 1) and is designed as a dragonfly habitat. It is being studied more intensively.

RESULTS

CHANGES IN THE POND ENVIRONMENT 1962-1988

The Twenty Ponds at Woodwalton were dug in similar soils on flat grassland, therefore physical changes observed during the period of observation affected all the ponds more or less uniformly.

Most of the early summers, which had more sunshine than the average, occurred in the period 1962 to 1976. This pattern did not extend to late summers, although the three seasons with most sun in late summer did occur in the 1962-76 period. The individual months showing the largest amount of sunshine for the 27 year period were randomly distributed. It can be concluded that the 1962-76 period was likely to be more favourable to spring species than the 1977-88 one.

While the amount of sunshine in any one year is likely to affect adult populations, the amount and distribution of rain determines water level and hence the size, temperature and chemistry of the larval habitat. For most years the pattern was similar: winter rains caused the ponds to fill and all ponds were still fairly full when the season started in May. Water levels then declined and were at their lowest in October. As regards individual water levels, there was more variation between ponds at the end of each season than at the beginning.

There were striking exceptions to this general pattern. Heavy summer rainfall in 1968 caused the highest water levels that year to occur in August, and the lowest occurred in June. In the dry years of 1966, 1976 and 1986 the lowest levels were recorded in August. In the phenomenally dry summer of 1976 18 out of the 20 ponds completely dried out for the only time during the period of observations. The effects of this rare event are described.

Data on the aquatic plants of the Twenty Ponds are summarised in Table I. They show that the ponds differed in their species composition. However, all

Table I

Aquatic plants in the Twenty Ponds — [X: species present for more than 50% of years of observation; — x: species present for less than 50% of years of observation; — *: sprayed with diquat in 1972, + sprayed with dichlobenil in 1972]

Pond	Emergent species					Floating species			Submerged species		
	Typha	*Alisma*	*Lythrum*	*Juncus*	*Sparganium*	*Polygonum*	*Potamogeton*	*Lemna*	*Algae*	*Chara*	*Fontinalis*
1	X	x			x	x		x	x	x	
2	X	X							X	X	
3	X	X		X					X	x	
4	X	x				X	x		X	X	
5*	X	X	x			X		x	X	x	x
6+	X	X	X			X	X		X	x	x
7+	X	x	X			X			X	X	
8	x	X	x			X			X	X	
9	X	X	x			x	x		X	X	x
10	x		X			x		X	X		x
11	X		X	x		X		x	x		
12	x		X	x		X	x		X	X	
13*	X	x	X	x		X	x		X	X	x
14	x	X	X	X		x		x	X	x	
15	x	X	X			X			X	x	x
16	X	X	X			X			x	x	
17	x		x			X			X	X	x
18	X		X			X	x		X	x	x
19	X	X	X	x		x			X	x	x
20	x	X	X			x			x	x	x
Total no. of ponds species present	20	15	16	6	1	18	6	5	20	18	10
Season species first observed	1	3	8	14	23	4	5	8	1	3	11

ponds, other than pond 17, contained emergent, floating and submerged species most years. Pond 17 supported *Typha* in 1962 and 1979 and *Lythrum* in 1988, otherwise it had no emergent plants other than the flowering heads of *Polygonum amphibium,* which was present most years. In six other ponds (8, 10, 12, 14, 15 and 20) *Typha* failed to maintain itself but these ponds all contained other emergent species.

Colonisation of the ponds by plants was a gradual process. However, there were three distinct phases in the development of the community:

(1) Phase with no macrophytes and little or no submerged vegetation (first half of 1962)

(2) Phase with *Typha* in practically all ponds, and submerged plants in some but not all ponds (second half of 1962-1963)

(3) Phase with varying but generally increasing numbers of emergent, floating and submerged plants (1964-1988)

Emergent plants *(Carex, Juncus* and *Cladium)* were deliberately planted round the edges of the three Heathfield ponds following construction. *Sphagnum magellanicum* was introduced into ponds B and C in 1980. *Utricularia vulgaris* and *Phragmites australis* colonised pond A within one year. *P. australis* similarly invaded ponds B and C, and by 1988 covered most of the surface of these ponds.

Scrub (mainly *Crataegus monogyna* and *Salix* spp.) invaded the edges of most ponds to some extent; in some cases it overhung the water and thus shaded some areas. It was partially controlled until 1987 when it was allowed to develop freely on ponds 1, 3, 6 and 14.

There were no signs of exceptional, spasmodic attack by animals on aquatic or bank vegetation. The gastropod mollusc *Radix peregra* was first seen in the ponds in 1966 but never became abundant. Water voles *(Arvicola amphibius)* were rarely seen. Rabbits *(Oryctolagus cuniculus)* exerted variable but generally slight pressure on the grassy rims of the ponds.

The ponds were quickly colonised by other aquatic insects in 1962, e.g. Coleoptera (*Gyrinus* spp.) and Hemiptera (*Notonecta*, corixids, and *Gerris*). Diptera, Lepidoptera and other insects were common round the edges of the ponds and appeared to increase as they became more sheltered by scrub. Food for both larval and imaginal dragonflies appeared to be abundant.

Only ponds 14 and 17 ever contained fish (Ten-spined Stickleback *Pungitius pungitius*). They were first seen in 1968 and none was observed after 1972, so predation of dragonfly larvae by fish must have been negligible. On the other hand, newts were abundant (despite Grass Snakes, *Natrix natrix*, which first appeared in 1964) and may have been important predators of larvae. The Smooth Newt *(Triturus vulgaris)* was first seen in 1963 and by 1971 was present in all but one pond. The Great Crested Newt *(T. cristatus)* was first seen in 1970 and colonised all but three ponds by 1979 (COOKE et al., 1980). No frogs or toads were seen.

When full vegetation developed round the ponds an increasing number of birds was seen by the ponds. 15 species were recorded altogether, of which 11 nested within the banks surrounding the ponds. All the species observed are known to eat insects on occasion and the Sedge Warbler *(Acrocephalus schoenobaenus)*, Willow Warbler *(Phylloscopus trochilus)*, Grasshopper Warbler *(Locustella naevia)* and Reed Bunting *(Emberiza schoeniclus)* may well have been significant predators of teneral imaginal dragonflies.

Individuals of *Coenagrion puella* (L.), *C. pulchellum* (Vander L.) and *Lestes sponsa* (Hans.) were found caught in spiders' webs.

COLONISATION OF THE PONDS BY DRAGONFLIES AND THE SUBSEQUENT DEVELOPMENT OF ODONATE COMMUNITIES

Data on the colonisation of the Twenty Ponds, the three Heathfield ponds and the Swavesey pond are summarised in Tables II and II. Table II shows when mature insects were first observed on the different ponds. Table III shows when the first tenerals were seen or exuviae found and hence successful breeding was first recorded. The sequence of the species in the Tables is that in which the

Table II

Colonisation of new ponds at Woodwalton Fen and Swavesey by mature adult dragonflies — [Numerals underlined where colonisation of pond occurred in first season possible, i.e.season 1; — *: first recorded insect was a female]

	Pond	Season mature males and/or females first observed								
		I. elegans	*S. striolatum*	*L. quadrimaculata*	*C. puella*	*A. cyanea*	*P. nymphula*	*L. sponsa*	*S. sanguineum*	*A. grandis*
Twenty Ponds	1	2	2	5	5	10	4	3	5*	20
	2	1	1	3	2	3*	3	5	13	23*
	3	1	2	3	4	8	3	5	10	7
	4	1	1	3	3	5	4	5	10	7
	5	1	1	4	4	2	4	6	3	20
	6	1	1	5	5	7*	4	5	8	5
	7	1	1	3	3	7	5	5	17	21
	8	1	1	3	5	3	4	5	8	7
	9	1	1	4	5	10*	4	4	13	7*
	10	1	1	6	2	2	4	5	16	7*
	11	1	1	3	5	16	3	3	21	
	12	2	1	3	3	14*	4	5	18	23
	13	2	1	5	4	4	5	5	16	5
	14	1	1	2	4	7	5	5	3	10
	15	1*	1	3	3	4*	4	5	18	9*
	16	1	1	4*	3	10*	4	5	17	8*
	17	1*	1	3	5	8*	5	6	10	5
	18	1	1	3	2	3	5	5	13	5
	19	2	1	1	5	12	4	5	6	10
	20	2	1	2	3	3	3	5	17	7*
	$\bar{X}$	*1.25*	*1.10*	*3.40*	*3.75*	*6.90*	*4.05*	*4.85*	*12.10*	*10.30*
	SD	0.44	0.29	1.18	1.04	4.10	0.69	0.75	5.40	6.75
Heathfield Ponds	A	1	1	1	1	1		1	2	3
	B	1	1	1	1	9		1	1	2
	C	1	1	1	1	1		1	1	2
Swavesey	S	1	1	1	1	1	1	1	1	1
Earliest season adult could occur		1	1	1	1	1	1	1	1	1

species first appeared at one of the Twenty Ponds.

Most of the Twenty Ponds were colonised by adult male *Ischnura elegans* (Vander L.) and *Sympetrum striolatum* (Charp.) in the first year, and by *Libellula quadrimaculata* L., *C. puella*, *P. nymphula*, and *L. sponsa* in the third

Table III
Colonisation of new ponds at Woodwalton Fen and Swavesey, successful breeding — [Numerals underlined where colonisation of pond occurred in first season possible; — *: records for these species were based on exuviae]

		Season tenerals or exuviae* first observed									
	Pond	*I. elegans*	*S. striolatum*	*L. quadrimaculata*	*C. puella*	*A. cyanea**	*P. nymphula*	*L. sponsa*	*S. sanguineum*	*A. grandis**	*B. pratense**
Twenty Ponds	1	3	3	5	10	7		5	17		12
	2	3	4	4	18	8	5	6	13	25	10
	3	3	4	14	11	8		10	16	21	
	4	2	3	20	5	8	5	5	19	24	
	5	2	3	18	7	8		6	22		
	6	2	2	3	6	6	7	6	16		12
	7	3	15	11	17	7		18	14	22	12
	8	2	2	4	10	8	11	13	16		
	9	2	2	10	9	6		6	21	24	
	10	3	2	4	6	7		20			
	11	3	3	10	7	5		5	16	24	
	12	2	2	11	12	8		10	17	10	
	13	2	3	5	17	5		9		22	10
	14	3	3	19	6	5		5	13		
	15	2	6	14	2	7		9	17		
	16	2	2	6	14	5		7		22	
	17	2	2	13	17	8	4	20		10	7
	18	2	2	5	17	5	6	10			
	19	2	2	21	11	6	5	4			
	20	2	3	27	11	8	5	9			
	n	20	20	20	20	20	8	20	13	10	6
	X̄	*2.35*	*3.40*	*11.20*	*10.65*	*6.75*		*9.15*			
	SD	0.49	2.91	6.95	4.79	1.25		4.98			
Heathfield Ponds	A	2	4	5	3	4		2	4		
	B	7	3	4	5			4	2		
	C	3	2	5	6	4		2	2		
Swavesey	S	2	2		2	5	5	2	3	5	5
Earliest season teneral or exuviae could occur		2	2	3-4	2	3-4	3	2	2	3-4	3

to sixth years. The data for adults of *Aeshna cyanea* (Müll.) and *Aeshna grandis* (L.) give a misleading impression, because the ponds were too small to provide

Table IV

The Twenty Ponds: total number of mature males and tenerals on the days of their maximal abundance for the year indicated. — [(For each species the top line refers to mature males, the bottom to tenerals, or, to exuviae in the case of aeshnids. — Underlined: recording most reliable; — plain fount: recording of intermediate reliability; — (): recording least reliable see p. 207)]

Year	'62	'63	'64	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84	'85	'86	'87	'88
Season after construction	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Species																											
I. elegans	12	$\underline{26}$	$\underline{41}$	$\underline{14}$	$\underline{30}$	$\underline{33}$	$\underline{15}$	$\underline{25}$	18	$\underline{38}$	7	25	10	$\underline{25}$	13	$\underline{9}$	30	$\underline{27}$	$\underline{22}$	$\underline{27}$	$\underline{43}$	$\underline{45}$	$\underline{32}$	22	$\underline{15}$	(12)	16
		16	$\underline{35}$	20	$\underline{7}$	$\underline{14}$	$\underline{15}$	4	7	$\underline{7}$	0	$\underline{4}$	$\underline{5}$	$\underline{8}$	1	$\underline{2}$	$\underline{4}$	$\underline{4}$	$\underline{5}$	$\underline{8}$	6	$\underline{13}$	$\underline{5}$	2	$\underline{6}$	(0)	(3)
S. striolatum	19	$\underline{18}$	$\underline{16}$	$\underline{12}$	(16)	12	$\underline{17}$	7	$\underline{8}$	$\underline{4}$	(4)	9	8	2	(6)	(9)	$\underline{11}$	8	(4)	4	(6)	6	4	11	7	(12)	(19)
		(5)	18	$\underline{13}$	$\underline{7}$	7	$\underline{3}$	(1)	1	0	(1)	(1)	(1)	(4)	1	22	$\underline{20}$	3	(2)	5	14	5	$\underline{9}$	2	$\underline{2}$	(2)	(8)
L. quadrimaculata	(1)	1	$\underline{13}$	$\underline{2}$	$\underline{5}$	$\underline{1}$	$\underline{2}$	$\underline{3}$	$\underline{9}$	$\underline{2}$	$\underline{0}$	1	0	$\underline{2}$	$\underline{4}$	$\underline{4}$	$\underline{6}$	$\underline{13}$	$\underline{16}$	$\underline{20}$	17	$\underline{13}$	$\underline{15}$	12	$\underline{19}$	13	(14)
			$\underline{1}$	$\underline{1}$	$\underline{2}$	$\underline{1}$	$\underline{1}$	0	$\underline{0}$	$\underline{3}$	$\underline{1}$	(1)	(2)	10	0	0	1	(1)	$\underline{10}$	5	$\underline{11}$	$\underline{16}$	$\underline{2}$	3	16	25	11
C. puella		1	$\underline{9}$	14	$\underline{16}$	$\underline{3}$	$\underline{1}$	4	16	$\underline{30}$	$\underline{14}$	12	$\underline{19}$	$\underline{51}$	11	$\underline{7}$	$\underline{137}$	$\underline{204}$	$\underline{67}$	$\underline{197}$	183	$\underline{149}$	$\underline{102}$	$\underline{141}$	$\underline{147}$	178	(52)
		1	$\underline{0}$	$\underline{0}$	$\underline{1}$	$\underline{1}$	$\underline{2}$	$\underline{0}$	$\underline{1}$	$\underline{1}$	$\underline{5}$	(2)	(1)	4	$\underline{0}$	0	34	(24)	$\underline{36}$	22	$\underline{30}$	$\underline{155}$	$\underline{25}$	$\underline{119}$	$\underline{21}$	23	(32)
A. cyanea		$\underline{1}$	$\underline{2}$	$\underline{3}$	1	1	$\underline{2}$	3	$\underline{1}$	$\underline{5}$	1	2	$\underline{0}$	0	(0)	1	1	1	(0)	2	(1)	1	3	1	2	(2)	(2)
					9	10	$\underline{12}$	$\underline{425}$	$\underline{13}$	$\underline{48}$	$\underline{12}$	28	$\underline{158}$	(6)	3	0	(0)	12	5	10	19	$\underline{55}$	$\underline{3}$	34	20	(1)	2
P. nymphula			3	$\underline{20}$	$\underline{18}$	5	1																				
				$\underline{1}$	$\underline{4}$	2	1	(0)	0	$\underline{0}$	1																
L. sponsa			1	$\underline{1}$	36	16	57	(63)	(65)	111	(17)	(41)	(91)	21	15	61	(42)	31	(9)	155	$\underline{188}$	62	89	66	93	(69)	(92)
				1	4	4	2	2	7	7	(0)	4	(1)	5	1	3	(5)	3	2	8	12	21	$\underline{10}$	14	8	(6)	(4)
S. sanguineum			1	0	(0)	1	(0)	2	(0)	1	(0)	(0)	1	(0)	1	4	11	3	(0)	1	9	6	$\underline{10}$	4	9	3	4
													(2)	(2)	0	3	(3)	3	8	1	5	$\underline{3}$	$\underline{4}$	1	0	(0)	0
A. grandis					$\underline{4}$	0	$\underline{1}$	(1)	(0)	2	(0)	(2)	0	(0)	0	$\underline{1}$	$\underline{1}$	0	(1)	$\underline{2}$	1	0	$\underline{1}$	1	$\underline{4}$	(0)	(1)
										$\underline{1}$	0	0	0	0	0	0	0	$\underline{0}$	$\underline{0}$	0	$\underline{1}$	$\underline{13}$	$\underline{0}$	5	5	(0)	0
B. pratense																											
							$\underline{1}$	0	$\underline{0}$	$\underline{2}$	$\underline{0}$	(11)															

suitable territories for adult males of these species. As a result, males only made very brief visits and so could easily be missed during short visits to the pond by the observer. The records of exuviae in Table III show that in fact all ponds must have been visited by adult *A. cyanea* by the sixth year. Records of adult *A. grandis* show that at least half of the ponds had been visited by this species by the seventh year. Colonisation by adult *Sympetrum sanguineum* (Müll.) took place irregularly and over a much longer period of time.

Breeding followed colonisation by adults as follows. Tenerals of *I. elegans* and *S. striolatum* were recorded in most of the Twenty Ponds during the second and third years after their construction. *A. cyanea* emerged from all the ponds for the first time in the fifth to eighth seasons. There was much greater variation in the first recorded emergence of the other species.

By contrast to the Twenty Ponds, adults of most species colonised the Heathfield and Swavesey ponds in the first season of the ponds' existence. As in the Twenty Ponds, *I. elegans* and *S. striolatum* were among the first to breed, but in the Heathfield and Swavesey ponds most of the other species bred earlier than in most of the Twenty Ponds.

Table V

Number of ponds where mature males and tenerals were recorded in the year indicated. — [Stage I: Pioneer stage (3 species); — II: Developmental stage (5-9 species; — III: Climax stage (7-8 species). For each species the top line refers to mature males, the bottom to tenerals, or, to exuviae in the case of aeschnids. — Underlined: recording most reliable; — plain fount: recording of intermediate reliability; — ( ): recording least reliable (see p. 207). — IE: *I. elegans;* — SS: *S. striolatum;* — LQ: *L. quadrimaculata;* CP: *C. puella;* AC: *A. cyanea;* PN: *P. nymphula;* — LS: *L. sponsa;* — SA: *S. sanguineum;* — AG: *A. grandis;* — BP. *B. pratense*]

Year	'62	'63	'64	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84	'85	'86	'87	'88
Season after construction	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Stage	I						II													III							
Species																											
IE	13	19	20	16	19	20	19	19	19	20	6	17	19	20	14	14	19	20	19	20	20	20	20	18	18	(12)	13
		13	20	14	8	15	12	6	9	8	(0)	7	8	8	2	3	11	11	6	11	9	19	6	3	8	(0)	(3)
SS	18	18	17	17	(19)	14	14	10	12	7	(4)	15	12	2	(4)	(14)	15	10	4	5	(11)	10	11	12	12	(11)	(14)
		(9)	14	11	9	8	3	(2)	(1)	0	(1)	(1)	(1)	(2)	1	10	16	3	(3)	6	14	5	6	5	5	(3)	(5)
LQ	(1)	2	13	4	12	1	2	4	9	4	0	1	0	4	4	12	11	20	19	20	18	15	16	14	20	16	(11)
			1	3	3	2	1	0	0	3	3	(1)	(3)	8	0	0	1	(2)	8	9	9	13	2	4	8	9	5
CP		3	7	9	18	7	2	5	10	20	10	15	17	20	9	11	20	20	20	20	20	20	19	20	20	20	(19)
		1	0	0	1	3	2	0	1	2	6	(2)	(1)	5	0	0	15	(15)	16	14	20	20	16	20	13	13	(10)
AC		2	3	4	1	1	4	6	1	11	1	3	0	0	(0)	2	1	1	(0)	2	(2)	1	4	2	0	(3)	(2)
					5	4	7	20	8	14	9	12	17	(4)	2	0	(0)	5	4	5	7	12	3	10	10	(1)	2
PN			4	15	18	9	2																				
				1	4	1	1	(0)	0	0	1																
LS			1	1	18	14	20	(20)	(20)	20	(8)	(19)	(20)	(17)	7	20	(19)	16	(9)	20	20	17	19	20	20	(15)	(14)
				1	5	4	4	3	6	8	(0)	4	(1)	5	1	4	(4)	3	3	12	15	11	13	10	9	(2)	(3)
SA			3	0	0	2	0	(3)	(0)	4	(0)	(0)	(4)	(0)	1	8	(17)	7	(0)	2	13	11	15	8	9	4	6
													(2)	(1)	0	4	(4)	2	4	2	2	6	6	2	0	(0)	0
AG					4	0	3	(1)	(0)	4	(0)	(2)	0	(0)	0	1	2	0	(1)	2	2	0	3	3	5	(0)	(3)
										2	0	0	0	0	0	0	0	0	0	0	1	4	0	3	3	(0)	0
BP							1	0	0	2	0	(4)															

The subsequent development of the populations of the different species is summarised in different but complementary ways in Tables IV and V. In Table IV the numbers of mature males and tenerals/exuviae are recorded for the day of maximal observed abundance for each year. The values provide an index of abundance for each species in the year concerned.

The extent to which the Twenty Ponds were colonised is indicated in Tab. V. It shows the number of ponds which were shown to have adult males or produce tenerals/exuviae of each species for each year. The relationship between the colonisation of the Twenty Ponds and the odonate fauna of the surrounding area is shown in Table VI and is discussed later under Sources of Colonisation.

In the Twenty Ponds it will be seen that populations of *P. nymphula* and *Brachytron pratense* (Müll.) built up, and then became extinct by the thirteenth year after the construction of the ponds. No adult *B. pratense* was ever seen.

The development of populations of the other species appeared to be as follows. The pioneer species, *I. elegans* and *S. striolatum* maintained populations throughout the 27 year period. *L. quadrimaculata* maintained a population throughout the period; its breeding success appeared to improve from the eighteenth season onwards. The adult numbers of *C. puella* gradually increased in the 1960s and 1970s; there was a marked increase in breeding success from 1978 onwards. As already noted the ponds were suboptimal for adult territorial males of *A. cyanea* so the values for adult males have little significance. Breeding success appeared to be very erratic in this species. Nearly all the ponds were colonised by *L. sponsa* by the fifth season. There was some indication of an increase in breeding success during the 1980s. *S. sanguineum* was more often observed in the second half of the study than in the first. Breeding was not proven until ten years after the first adult males were seen at a pond. As with *A. cyanea*, the ponds were too small a habitat for territorial males of *A. grandis*. There were indications of a slight increase in breeding success of this species in the 1980s.

Data on the three Heathfield ponds are shown in Table VII. They show that the build-up in numbers of *C. puella*, *L. sponsa* and *S. sanguineum* was more rapid than on the Twenty Ponds.

Changes in the dragonfly community of the Twenty Ponds can be deduced from Tables IV, V, VI and VIII. Taking the site as a whole, the community went through three stages (see Tab. V):

(1) A pioneer stage in which the community consisted essentially of two species, *I. elegans* and *S. striolatum*. This lasted for one year.

(2) A developmental stage in which an increasing number of species colonised the site, but two of them, *P. nymphula* and *B. pratense*, disappeared after a few years. This lasted for eleven years.

(3) A climax stage in which the number of species remained stable, although populations fluctuated and the breeding success of *C. puella* and *L. quadrimaculata* increased after seventeen and nineteen years respectively from the construction of the ponds.

By contrast, at the Heathfield ponds (see Table VII) there was no clear distinction between stages: all seven of the breeding species appeared in the first season. In ponds B and C there were indications of a senescent stage, for there was a decline in the numbers of *I. elegans*, *L. quadrimaculata*, *C. puella* and *L. sponsa*

Table VI

Colonisation of the Twenty Ponds in relation to the odonate fauna in the surrounding area (cf. Fig. 1) — [( ): number of occasions adults seen (rare visitors only), [ ]: number of occasional tenerals or exuviae seen (rare breeders only)]

				Season by which:			Season by which:	
Category	Species	Distance from nearest population (m)	Adult first seen	Adult had been recorded on 10 ponds	Adult had been recorded on 20 ponds	Teneral first seen	Tenerals had been recorded on 10 ponds	Tenerals had been recorded on 20 ponds
Ponds apparently suitable, species numerous in area	*I. elegans*	30	1	1	2	2	2	3
	S. striolatum	30	1	1	2	2	3	15
	L. quadrimaculata	30	1	3	10	3	10	27
	C. puella	30	2	4	5	2	10	17
	L. sponsa	30	3	5	6	4	7	20
	A. cyanea	50	2	7	16	5	7	8
Ponds apparently suitable, species rare/local in area	*P. nymphula*	2,000	3	4		4 [6]		
	L. depressa	500	3 (2)			0		
Ponds apparently suboptimal, species numerous in area	*S. sanguineum*	30	3	10	18	13	19	
	A. grandis	50	5	10		10	25	
Ponds apparently suboptimal, species rare in area	*B. pratense*	≤2,000	0 (0)			7 [6]		
	C. pulchellum	≤2,000	7 (2)			0		
	A. imperator	500	0 (0)			0		
Ponds apparently unsuitable, species numerous in area .	*A. mixta*	50	1 (11)			0		
	E. cyathigerum	50	3 (7)			24 [1]		
	O. cancellatum	270	3 (3)			16 [1]		
	E. najas	270	22 (1)			0		
Ponds apparently unsuitable, species rare/local in area	*A. splendens*	800	0 (0)			8 [1]		
	A. juncea	6,200	22 (1)			0		
	L. fulva	800	0 (0)			0		

during the last few years of the twelve year study. The numbers of teneral insects observed were very small but they seemed to show a similar trend. Numbers of males were better maintained at pond A, except in the case of *L. sponsa* which appeared to decline about seven years after the construction of the pond.

Table VIII shows how the number of species per pond changed over the years at the Twenty Ponds. The records are confined to those years when the seasons were well covered by observations. The data show that in the earliest years most ponds had a fauna of only two species, but by 1964 most ponds had three or four species, and from 1966 most ponds held five or more species. However, there was considerable variation between ponds and the detailed data suggest that the fauna of individual ponds varied from year to year. Records of tenerals show that there was a clear progress from 1963, when no pond was seen to produce more

Table VII

Heathfield ponds B with C (1977-1988) and A (1974-1985): total number of mature males and tenerals on the days of their maximal abundance for the season indicated — [For each species the top line refers to mature males, the bottom to tenerals. — x = exuviae; — underlined: recording most reliable; — plain fount: recording of intermediate reliability; — ( ) recording least reliable (see p. 207)]

Species	Season after construction											
	1	2	3	4	5	6	7	8	9	10	11	12
	Ponds B and C											
I. elegans	6	6	4	10	4	12	4	2	1	1	(0)	0
			2	0	0	0	1	0	0	0	(0)	(0)
S. striolatum	(6)	4	4	(3)	1	(2)	3	2	1	3	(0)	(0)
		1	1	1	(0)	0	0	0	0	0	0	(0)
L. quadrimaculata	6	5	7	7	5	6	8	2	2	1	0	(1)
			(3)	5	1	4	3	2	1	0	0	0
C. puella	5	71	140	67	95	96	66	48	15	25	4	0
						1	63	4	12	10	0	0
A. cyanea	1	1	0	(0)	1	(0)	0	0	1	1	(0)	(0)
				1	0	0	4^x	0	0	0	(0)	(0)
L. sponsa	36	37	19	(37)	15	12	7	9	2	1	(0)	(0)
		(1)	3	2	6	2	4	2	0	0	(0)	(0)
S. sanguineum	3	7	5	8	3	4	3	2	1	2	(0)	(0)
		2	2	1	0	1	0	1	0	0	(0)	(0)
	Pond A											
I. elegans	5	3	5	4	6	1	8	4	9	2	2	3
		8	1	0	1	1	1	0	1	4	1	0
S. striolatum	4	2	4	3	2	1	(1)	1	(2)	2	1	1
		(0)	0	1	0	0	(0)	0	0	0	0	0
L. quadrimaculata	1	1	3	4	2	2	4	2	3	5	3	3
		0	0	0	2	(0)	1	0	1	1	0	0
C. puella	8	14	43	14	48	58	47	60	80	60	43	32
		0	1	8	4	1	2	3	2	117	2	22
A. cyanea	1	0	(1)	(1)	1	0	(0)	1	(0)	0	0	1
			0	5	(0)	0	1	0	0	0	0	0
L. sponsa	(20)	(10)	25	39	(14)	17	(10)	4	7	2	3	2
		2	2	1	2	0	0	2	0	2	1	0
S. sanguineum	(0)	(1)	1	4	(2)	1	(2)	1	2	1	1	0
		(0)	0	1	0	0	0	0	1	0	0	0

than two species, to the 1980s when most had records of three to five species emerging. As with adult males there appeared to be considerable variation between ponds and the situation at each pond appeared to vary from year to year. However, it must be emphasised that all records, especially those of tenerals, are likely to be underestimates as the rarer species must often have been missed. A more thorough investigation would almost certainly have shown less variation. The largest number of species — both adult and teneral — observed in one pond in one year was eight.

Table VIII

The Twenty Ponds: changes in the odonate community — [A: adult males; — B: tenerals + exuviae]

	Year	Season	Number of ponds with									species
			0	1	2	3	4	5	6	7	8	
A	1962	1	1	4	15							
	1963	2			16	3	1					
	1964	3			4	7	6	2	1			
	1965	4	1	2	2	3	7	5				
	1966	5					2	8	8	2		
	1971	10				2	7	9	2			
	1983	22			1	2	2	9	5	1		
	1984	23		1			2	3	8	5	1	
	1986	25				1	1	6	7	4	1	
B	1962	1	20									
	1963	2	6	5	9							
	1964	3		6	13	1						
	1965	4	1	8	11							
	1966	5	4	3	8	4	1					
	1971	10	1	5	7	6	1					
	1983	22			1	5	4	7		2	1	
	1984	23	2	2	6	4	4	2				
	1986	25	1	4	2	6	5	2				

SPATIAL AND SEASONAL OVERLAP OF SPECIES

Detailed records of teneral insects showed that larvae of all species occurred in the same pond as those of all other species on one or more occasions, except for the following: *B. pratense* and *P. nymphula* were never found in the same pond, and in addition *P. nymphula* was never found with *L. quadrimaculata, S. sanguineum* or *A. grandis. B. pratense* was never found with *C. puella* and *S. striolatum.*

The extent to which adult insects of different species were actually on the wing together depended on flight seasons. In this locality the seasons of all species were shown to overlap in at least one year during the period except *P. nymphula* never overlapped with *S. sanguineum* or *A. grandis* (elsewhere it often does).

Comparison of the periods when species were at peak numbers shows that the annual flight season fell into three distinct divisions:

(1) Spring, with *P. nymphula, L. quadrimaculata, C. puella* (and by inference *B. pratense*) at peak numbers. (May — second week in June)

(2) Summer, with *I. elegans, L. sponsa, S. sanguineum* and *A. grandis* at peak numbers. *I. elegans* could overlap with spring species, *A. grandis* with autumn species, and *L. sponsa* and *S. sanguineum* with both spring and autumn species. (Third week in June to last week in August)

(3) Autumn, with *S. striolatum* and *A. cyanea.* (First week in September to third week in October)

Periods of emergence overlapped for all species except that that of *P. nymphula* only overlapped with those of *L. quadrimaculata, C. puella* and *I. elegans,* and that of *A. grandis* never overlapped with those of *L. quadrimaculata, C. puella* or *P. nymphula.*

To conclude, all six species which successfully colonised the ponds had opportunities to interact with each other both at the larval and imaginal stages. Numerous interactions were also possible between these species and the transient species *P. nymphula* and *B. pratense.*

No observations were made on the interactions of larvae. Interspecific interactions were frequent between adults, but they were rarely seen to have significant results. On 1 August 1986 a male *S. sanguineum* was seen in copulation with a female *S. striolatum* at pond 5. On one occasion a male *L. quadrimaculata* was seen to expel a male *S. sanguineum* from a pond; on another a male *A. cyanea* drove out a male *S. striolatum,* and on another a male *L. sponsa* was seen to drive out a male *S. striolatum.* On the other hand, the relative abundance of adult males of different species at the ponds was largely determined by intraspecific encounters as is described below.

MAXIMAL NUMBERS OF EACH SPECIES PER POND

The simplest way to describe the specific differences in population size of adult males is to record the largest number of males of each species seen on an individual pond during the whole 27 year period. This is done in Table IX. The data show considerable differences between species, which are roughly, but not entirely, related to size of insect. The consistency of values within each species is remarkable and is discussed later.

The results can be attributed in most cases to territorial behaviour, because in all species studied except *C. puella,* aggressive behaviour by males was observed to result in the expulsion of the defeated male from the water's edge on occasions.

Territorial fights leading to the expulsion of one insect (usually the intruder) were most commonly observed in *L. quadrimaculata.* For this species the ponds

Table IX
Largest number of male dragonflies seen in each pond over 27 year period

Species	Pond																				Mean	SD	Range
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20			
A. cyanea	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1		1	1	1	1	0.0	1-1
A. grandis	1	1	1	1	1	1	1	1	1	1		1	1	1		1	1	1	1	1	1	0.0	1-1
S. sanguineum	1	1	2	1	1	1	1	2	1	2	2	1	1	1	1	2	1	1	1	1	1.25	±0.44	1-2
P. nymphula	1	2	2	2	2	1	1	2	2	1	1	3	1	1	1	2	1	2	1	2	1.55	±0.60	1-3
L. quadrimaculata	1	2	2	2	3	1	1	2	1	1	1	4	2	1	2	1	1	1	1	1	1.55	±0.83	1-4
S. striolatum	1	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	3	3	2.10	±0.45	1-3
I. elegans	6	5	4	5	4	4	5	4	6	4	5	5	5	4	4	6	3	4	4	4	4.55	±0.83	3-6
L. sponsa	8	14	14	18	10	12	17	15	13	9	10	13	12	11	10	14	10	8	10	7	11.75	±2.99	7-18
C. puella	14	15	15	22	16	23	15	25	11	16	12	19	18	12	12	23	16	13	14	15	16.30	±4.09	11-25

were too small to support more than one insect easily. Similarly, on the rare occasions when two aeshnas appeared on one pond simultaneously, one was always driven off. On the other hand most of the interactions between zygopteran males did not result in an insect leaving the pond. The maximal values for Zygoptera were rarely recorded: for most ponds only once or twice during the whole period of observation. This is not surprising because it was observed that expulsion of individual damselflies frequently occurred at densities below the maximal one for the species concerned. This type of behaviour was observed in *L. quadrimaculata, S. striolatum, S. sanguineum, I. elegans, P. nymphula* and *L. sponsa.* Male *C. puella* often confronted males of their own species, but were never seen to attack them and drive them from the pond.

INTERPRETATION OF THE DATA

Colonisation of new ponds depends on:

(a) the availability of colonists and hence on the nature and nearness of existing odonate communities in the vicinity
(b) recognition by potential colonists that the pond is a potential breeding habitat
(c) the ability of at least one fertilised female to oviposit in the new pond
(d) the successful development of larvae, and hence on the chemical, physical and biological characteristics of the pond at the time following oviposition.

The development of the odonate community over the years is the sum of colonisations and extinctions of breeding populations. It is determined by seral changes in the pond ecosystem and rare events such as droughts which affect the ecocsystem, and by changes in other populations of dragonflies in the vicinity. It is affected by predation and by the intra- and inter- relationships of the dragonflies themselves.

In this section an attempt is made to interpret the data by relating them to dragonfly populations in the vicinity, seral changes in the vegetation of the ponds, rare deleterious events, predation and territorial behaviour.

SOURCES OF COLONISATION

Three years before this study was started GARDNER (1960) made monthly visits to Woodwalton Fen. He recorded 14 species — *B. pratense, A. cyanea, Aeshna mixta* Latr., *A. grandis, L. quadrimaculata, S. striolatum, S. sanguineum, L. sponsa, Platycnemis pennipes* (Pall.), *P. nymphula, I. elegans, Erythromma najas* (Hans.), *E. cyathigerum* and *C. puella.* In addition he noted previous records of *Anax imperator* Leach (in 1939), *Calopteryx splendens* (Harr.) (in 1947) and *C. pulchellum* (in 1939). In 1958 the two meres and the broad New Drain on the southern edge of the Fen had not been constructed (see Fig. 1). *P. pennipes,* which was confined to the Great Raveley Drain (see Fig. 1) on the eastern margin of the Fen, became extinct shortly after Gardner's survey. When the New Drain and the meres were constructed in 1967, 1970 and 1978 respectively, they were quickly colonised by *Orthetrum cancellatum* (L.). As it has been abundant in Great Raveley Drain for many years it may have occurred there in 1958 but was overlooked. *Libellula fulva* Müll. appears to have colonised Great Ravely Drain about 1984. Both *P. nymphula* and *B. pratense* probably declined in the Fen in the years following Gardner's survey.

Thus, when the Twenty Ponds were dug in 1961 at least 16 species of Odonata occurred at Woodwalton Fen. In the following years three other species *(O. cancellatum, Libellula depressa* L. and *L. fulva)* were recorded at Woodwalton, and *Aeshna juncea* (L.) colonised a newly dug mere at the Holme Fen National Nature Reserve about 6,000 m away. Thus eventually there were 20 species breeding in the vicinity of the Woodwalton ponds. The data in Table VI show that the populations of these species varied in their proximity to the Twenty Ponds, in their abundance and in the degree to which they were localised. However, there is direct evidence that 18 out of the 20 species visited the Twenty Ponds, and *L. fulva* and *A. imperator* were seen within 500 m of them. Therefore, for the twelve abundant Woodwalton species, at least, availability of colonists cannot have limited the species which occurred at the Twenty Ponds.

Only six species *(I. elegans, S. striolatum, L. quadrimaculata, C. puella, L. sponsa* and *A. cyanea)* bred regularly at the ponds thus demonstrating that the ponds provided suitable habitats for them. It has to be explained why the others did not. *A. mixta, E. cyathigerum, E. najas* and *O. cancellatum* were extremely numerous at Woodwalton but were only rarely recorded at the Twenty Ponds. It must be concluded that these insects (like the human observer) could perceive that the ponds did not provide a suitable habitat: those insects that visited the ponds must have flown away after investigating them. The less numerous *C. splendens, A. imperator, A. juncea* and *L. fulva* probably did the same. Why *L. depressa* failed to breed in what appeared to be suitable habitat is not known. It is a rare species in Cambridgeshire and is at the northern edge of its range there: climate would affect both the availability of colonists and breeding success.

Most interest attaches to the four species, *P. nymphula, B. pratense, A. grandis* and *S. sanguineum,* which bred in some, but not all, of the Twenty Ponds. The data in Table V show that *P. nymphula* and *B. pratense* colonised ponds quite early in their development, but then disappeared. This suggests that the ponds were or became suboptimal habitats and since both species were rare and localised in the vicinity throughout the study period, there was not a large surplus of individuals available to recolonise the ponds when the original populations died out. By contrast, *A. grandis* and *S. sanguineum* were extremely numerous on the Fen, and although the ponds were clearly suboptimal for them, it appears that their abundance in the vicinity enabled some of the Twenty Ponds to support these species most years.

The Woodwalton Fen area produced similar opportunities for colonisation by dragonflies for the three Heathfield ponds. They were visited by the same species, except that *P. nymphula, B. pratense, C. pulchellum* and *C. splendens* were never recorded on them. However, *A. imperator* was seen on four occasions and *A. juncea* on two; and *O. cancellatum, E. najas* and *E. cyathigerum* were more frequent visitors than at the Twenty Ponds. *I. elegans, S. striolatum, S. sanguineum, L. quadrimaculata, C. puella, L. sponsa* and *A. cyanea* all bred as in the Twenty Ponds, but *A. grandis* was never proved to do so.

SERAL CHANGES IN VEGETATION

As shown above the vegetation of the Twenty Ponds went through three phases, two of which occurred in the first two years after construction. From the third season onwards most of the ponds contained submerged, floating and emergent aquatic plants. The striking difference between the dragonfly population of the first two years and subsequent years was presumably linked with seral changes in the vegetation. In other words only *I. elegans* and *S. striolatum* recognised the ponds as suitable habitat when they had little or no vegetation, and succeeded in breeding in them at that stage. This conclusion is supported by observations made at the Heathfield and Swavesey ponds. Emergent plants were planted round these ponds immediately after they were dug, and at Swavesey submerged and floating plants were introduced at the same time. Strict comparisons between these ponds and the Twenty Ponds cannot be made because they differed in size and substrate. However it seems highly probable that planting aquatic vegetation at the Heathfield and Swavesey ponds, and hence cutting out the bare edge stage in their development, was the reason why they were colonised by most dragonflies much more quickly than the Twenty Ponds, where development was natural and included a bare edge stage.

Differences in the means for the different species shown in the tables on colonisation (Tabs II and III) must, *inter alia,* reflect seral changes in the vegetation (as well as larval development time in the case of breeding success). The difference in the variance between species suggests that the vegetational differences of the ponds affected some species more than others. As was to be expected, colonisation by adults was less affected by these differences than breeding.

Nevertheless, detailed examination of individual ponds of the Twenty Ponds shows that the presence of aquatic vegetation was not all-determining. For example, *I. elegans, S. striolatum, P. nymphula, A. cyanea, A. grandis* and *L. quadrimaculata* all bred successfully in pond 17 when it lacked tall emergent plants of any kind. *I. elegans, S. striolatum, L. quadrimaculata, A. cyanea, C. puella* and *L. sponsa* all bred in ponds 1, 11 and 20 in which submerged vegetation was poorly developed, and even *A. grandis* bred in pond 11, *P. nymphula* in pond 20 and *S. sanguineum* in ponds 1 and 11. *I. elegans, L. sponsa, A. cyanea, S. striolatum* and *S. sanguineum* all bred in either or both of the peaty ponds B and C when they were entirely devoid of submerged weed. These observations do not show that aquatic vegetation is unimportant to these species, but they do show that its absence does not prevent breeding by several species.

The importance of submerged vegetation to *C. puella* is suggested by the fact that this species failed to breed in ponds B and C when they contained no submerged vegetation, but teneral insects were observed the year after *Sphagnum* was introduced into these ponds. The gradual increase in breeding success of *C. puella* and *L. quadrimaculata* in the Twenty Ponds probably reflects a gradual increase in aquatic plants and plant debris in these ponds.

The apparent declines of the populations of adult and teneral dragonflies in the Heathfield ponds B and C after seven or eight years coincided with the extensive development of reeds *(Phragmites)* in those ponds. The fact that the declines did not occur, or were much less, in the neighbouring pond A (see Table VII), where reed development was much less, suggests that the development of reeds in ponds B and C was the cause of the decline in their dragonflies. Casual observations elsewhere showed that other waterbodies covered by reeds were poor habitats for dragonflies. Several reasons for this can be suggested: the close stands of reeds make flight among them very difficult for Anisoptera, and reeds shade the water surface, which is thus made cooler and reduces the growth of submerged and floating vegetation.

RARE EVENTS

During the period under review three abnormal events occurred which theoretically could have had repercussions on the development of the dragonfly communities.

The floods of 1968 produced pools of standing water on the grassland between the Twenty Ponds in late summer. The data in Table IV do not suggest that this had any major effect that year or the following one.

The experimental spraying of ponds 5 and 13 with the herbicide diquat and ponds 6 and 7 with dichlobenil in 1972 had considerable effects on the higher plants and plankton (NEWBOLD, 1976) but none on the newts (COOKE et al., 1980). No significant difference was found between the populations of dragonflies in the four sprayed ponds and four unsprayed control ponds. This is not surprising since diquat and dichlobenil have rather low toxicities to insects, and as shown above, the absence of emergent and submerged plants does not prevent breeding in most of the species present. The herbicides probably did have some indirect effects on larvae but these could only be determined by much more extensive experimentation. The observations made here show that they had no major effect.

The drought of 1976 was the most extreme during the 27 year period. It was the only year when any of the Twenty Ponds dried out completely. Only ponds 5 and 8 retained water. The effects of the drought on breeding are indicated in Table X.

Table X

Breeding success in the 18 ponds which dried out in 1976, before, during and after that year. — [Underlined: recording most reliable; — plain fount: recording of intermediate reliability; — () recording least reliable (see p. 207); ^{X}: exuviae]

Species	Number of ponds at which teneral insects were observed in the year indicated				
	1975	1976	1977	1978	1979
S. striolatum	(2)	1	9	13	3
I. elegans	7	2	2	11	11
L. sponsa	3	0	2	(4)	3
S. sanguineum	(1)	0	2	(3)	2
C. puella	5	0	0	15	(13)
L. quadrimaculata	7	0	0	0	(1)
A. cyanea	(3)^{X}	1^{X}	0	(0)	4^{X}

S. striolatum, S. sanguineum, L. sponsa and *I. elegans* all emerged in the season following the drought in some ponds. *S. striolatum* might have developed from eggs laid in the autumn after the water had returned, but the other species must have survived the drought as eggs or larvae. *C. puella* and *L. quadrimaculata* and *A. cyanea* were apparently all exterminated by the drought, but emergence of individuals of these species from some of the ponds in 1978 and 1979 show that these ponds were successfully recolonised in the year following the drought, 1977. The difference in the year of appearance between *C. puella* and the other two species reflects the difference in development time of the species.

It is interesting that both *L. quadrimaculata* and *A. cyanea* were able to breed in ponds 5 and 8 which did not dry out, but were reduced to a depth of 15 cm.

data in Tables IV and V show that the effects of the drought were not long lasting: despite the fact that many ditches dried out at Woodwalton, enough dragonflies were produced on the Fen to recolonise the Twenty Ponds when they became filled with water again.

INTERSPECIFIC COMPETITION AND PREDATION

The data in Tables IV and V show that populations of the pioneer species *I. elegans* and *S. striolatum* were maintained. Throughout the period of observations, there is no evidence that colonisation of the ponds by other species had a marked effect on them.

The expansion of the population of *P. nymphula* occurred at a time when *L. sponsa* was virtually absent from the ponds, and it declined when *L. sponsa* was present on most of them. However, elsewhere these species often occur together and so it is unlikely that the decline of *P. nymphula* at Woodwalton was attributable to the increase of *L. sponsa*. The disappearance of *B. pratense* did not coincide with a major change in the population of another species.

Observations on adults suggested that interaction between adults of different species have little or no effects on their populations. Doubtless interaction among larvae, including predation, must have had effects on the size of larval populations, but this study provides no evidence that one species excluded another.

As the bushes grew up on the banks surrounding the Twenty Ponds, birds increased and so predation must have increased, but no evidence was obtained to suggest that birds had a significant effect on the odonate population of the ponds at Woodwalton.

CONCLUSIONS

The colonisation of the Woodwalton ponds by Odonata occurred quickly because there were numerous potential sources in the neighbourhood, and because aquatic vegetation developed rapidly. As a result, a fairly stable community developed within a few years. The one really deleterious rare event in the 27 year period was the drought in 1976. It had no permanent effect because other populations of dragonflies survived in the vicinity and these enabled rapid recolonisation of the ponds when water returned to them.

The eventual decline of odonate populations in two of the Heathfield ponds was almost certainly due to invasion of the ponds by reeds. The stability of the dragonfly populations, which was observed in the Twenty Ponds for a quarter of a century, was made possible by scrub control round the margins of the ponds. If scrub had not been controlled, declines in populations, and probably extinctions, would undoubtedly have occurred.

The actual numbers of male dragonflies of each species present on a pond on a particular occasion depends first on availability, and thus on the size of the population emerging from the pond (and perhaps from other sources) and on the stage of the season. Secondly, it depends on territorial behaviour; because when dragonflies are numerous, it is territorial behaviour which determines the number of males present. Thus an adult male population of two insects may indicate the maximum for that species allowed by territorial behaviour. But for a species which can live at higher densities, it either indicates that the day on which observations were made is early or late in the flight season, or that the breeding stock is too small to fill all the potential territories on the pond. Time of year, past breeding success and territorial behaviour together determine the communities of adult dragonflies which are observed in the field.

DISCUSSION

DRAGONFLY COMMUNITIES

To what extent were the Woodwalton Fen ponds typical? The odonate fauna of very small ponds has been little studied. The fauna of bomb holes in acid heathland in Dorset described by MOORE (1964) had some similarity with that of the Woodwalton Fen ponds. They differed in the presence of *Ceriagrion tenellum* (de Vill.), *Sympetrum danae* (Sulz.) and *A. imperator* and in the absence of *A. grandis* and *S. sanguineum.* Similarly the fauna of Belgian bomb holes described by DUMONT (1971) and German ones by RUDOLPH (1978, 1979) also had similarities. The presence of *E. najas* and the absence of *L. sponsa* in the Westfalian bomb holes described by RUDOLPH (1978) were striking differences and are not easily explained. However, in broad terms the odonate fauna of the Woodwalton ponds is probably fairly typical for Europe.

Rapid colonisation of new ponds by dragonflies has been recorded by several authors (e.g. YAMAGUCHI, 1974, 1975; MARTENS, 1983). In this respect the Woodwalton ponds are also typical. In Lower Saxony Martens showed that 28 out of the 31 species found in the area colonised the new ponds very quickly. Thus both there and at Woodwalton numerous species were able to co-exist in relatively simple habitats. MACAN (1974), McPEEK (1987) and others have demonstrated the complexity of the relationship between larvae of different species, yet there is little evidence that one species entirely excludes another, such is the catholicity of the habitat requirements of dragonflies which breed in ponds.

In larger waterbodies JACOB (1969) showed that the development of the odonate community was related to the development of the habitat. His first association of *A. imperator* and *E. najas* occurred under open water conditions and had no equivalent at Woodwalton, but his second with *O. cancellatum, L.*

depressa and *S. striolatum* was the equivalent of the pioneer stage with *S. striolatum* and *I. elegans* at Woodwalton. In England *O. cancellatum* and *E. cyathigerum* are characteristically early colonisers of gravel pits (MILNE, 1984). The mature stage at Woodwalton was similar to the third association described by JACOB (1969).

The odonate fauna of the complex of 12 ponds studied by DUMONT (1971) appeared to increase from 16 species in 1957 to 23 in 1969, but exact comparisons with the Woodwalton ponds cannot be made as the Belgian ponds were very varied, much larger and of different ages when observations were started. In one of the ponds studied by RUDOLPH (1979) a decline in species was recorded, and MARTENS (1983) showed that older ponds had fewer species than new ones. The results from Woodwalton are consistent with these findings because *P. nymphula* and *B. pratense* both disappeared from the Twenty Ponds after a few years, and there were gradual declines in ponds B and C following the growth of reeds in them. On the other hand, the continued absence of *P. nymphula* and *B. pratense,* both spring species, may be related to the deterioration of spring weather rather than to ecological succession.

The work of CLAUSNITZER (1983) and CLAESSENS (1989) emphasises the importance of anthropogenic factors in the development of an odonate community. Several authors (e.g.JOHNSON & CROWLEY, 1980; McPEEK, 1987) have shown that fish can be an important factor in modifying odonate communities. At Woodwalton fish were absent from most ponds and had no obvious effect in the two which they inhabited for a short time. CLAUSNITZER (1971) and VALTONEN (1986) have shown that several species can survive the drying out of ponds and that their recolonisation occurs quickly when water returns.

The study at Woodwalton shows how 23 very small ponds were colonised by dragonflies in an area with numerous odonate habitats and how their communities developed over a long period. In general it confirms previous studies on colonisation and the development of communities, but it draws special attention to related facts which are rarely emphasised:

(1) Despite known variations in the requirements of individual species, several species can co-exist in a wide range of very simple aquatic habitats.
(2) Dragonflies often breed in suboptimal habitats.
(3) The odonate community of a pond consists of autochthonous species for which the pond provides suitable habitats and other species for whom the pond provides suboptimal habitats.
(4) The fairly regular presence of species in suboptimal habitats depends on there being more suitable habitats for them in the neighbourhood.

These points are relevant to the conservation of dragonflies and will be discussed later.

HIGHEST STEADY DENSITY AND TERRITORY

The data in Table X show that the upper limit of population densities in the Twenty Ponds was remarkably similar within each species. In Table XI the values have been converted into highest steady densities (the number of males/100 m) and are compared with values obtained at the three Heathfield ponds and at the water-filled bomb holes at Arne in Dorset 225 km to the south west. The Twenty Ponds were dug in exposed grassland, the Heathfield ponds in peaty fen sheltered by woodland and the Arne bomb holes were in exposed acid heathland near the coast.

Table XI

Highest steady densities of male dragonflies at The Twenty Ponds and the three Heathfield Ponds at Woodwalton Fen, and the eight bombhole ponds at Arne, Dorset — [ ]: records based on less than three years observation and/or on fewer than half the ponds at each site; they are likely to give underestimates of highest steady density. Studies elsewhere (e.g. MOORE, 1964) show that the margins of all the ponds at Woodwalton and Arne were considerably less than the margins occupied by aeshnid males on larger ponds where more than one male was present. Studies on these ponds show that the highest steady densities of *A. cyanea* and *A. grandis* are about 2 and hence the pond margin patrolled by each is about 50 m. Arne records are from MOORE, 1964]

Species	Mean highest steady density (males per 100 m)			Metres per male dragonfly (means)		
	Twenty Ponds (20)	Heathfield Ponds (3)	Arne Ponds (8)	Twenty Ponds (20)	Heathfield Ponds (3)	Arne Ponds (8)
A. cyanea	< 6	< 4	< 3	16+	25+	18+
A. grandis	< 6	< 4	NP	16+	25+	NP
S. striolatum	13	13	11	8	8	9
L. quadrimaculata	13	17	13	8	6	8
S. sanguineum	13	16	NP	8	6	NP
P. nymphula	[13]	NP	33	[8]	NP	3
I. elegans	31	30	31	3	3	3
L. sponsa	75	110	[36]	1	1	[3]
C. puella	100	290	[78]	1	0.4	[1]

That habitat has some bearing on highest steady density is suggested by the higher highest steady density recorded in three of the territorial species at the Heathfield ponds: these ponds had much more marginal vegetation than the Twenty Ponds and the Arne ponds. Even so, considering the differences in habitat the values are remarkably similar and demonstrate that specific highest steady density depends primarily on the behaviour of the insects and not on type of habitat or location, in so far as England is concerned. It is therefore extremely interesting that far higher densities have been recorded for two of the Woodwalton species on the Continent. MOKRUSHOV (1982) states that two groups of males appear when population density exceeds 2-3 individual *L. quadrimaculata* per square meter — one is territorial and the other is not; and POETHKE (1988) rarely found fewer than six *A. cyanea* per 100 m and there were often up to 15 per 100 m. At Woodwalton *L. quadrimaculata* was once observed to occur at an unusually high density. On this occasion, instead of the usual one or two insects per pond, there were four. This was due to three females appearing at the pond simultaneously. Their pursuit by the territory holders enabled two other males to enter the pond and in the ensuing turmoil all four males were able to remain at the pond for some minutes, although later in the day only one male was present. Records of abnormally high densities have been recorded for other species, for example in *E. cyathigerum* by PARR (1976), *Orthetrum julia* Kirby by PARR (1980) and *Sympetrum parvulum* and *Leucorrhinia* by PAJUNEN (1980). Thus it seems that when population pressure is moderate, density is kept within the limit defined by highest steady density, but when it is very great a "new set of rules" takes over. It is to be expected that in suboptimal habitats like small ponds, densities at or below highest steady densities would usually pertain. More information is required to ascertain the frequency of densities above highest steady density in the optimal habitats of the species studied.

Highest steady density must largely be dependent on the behaviour of the male insects but it cannot be assumed that it results solely from territorial behaviour in the form of defending localities or the areas where the insects happen to be (MOORE, 1991). *C. puella* was never observed to chase another male from a pond, and it is generally supposed that it is not territorial (see for example BANKS & THOMPSON, 1985). Yet the large numbers of teneral insects emerging from the ponds suggest that if there had been no behavioural constraint the numbers of males could have been much greater. The range of the highest densities recorded was not very wide and did not differ greatly from that of *L. sponsa* (see Table IX), which was clearly territorial. *C. puella* has a distinctive threat display when perched. Also males make rigorous investigative flights towards other males, and although fights do not ensue, one insect may fly into vegetation away from the water after one of these encounters. Male *C. puella* also attempt to seize females of ovipositing pairs. It appears that all these activities together may have results on population density which are similar to those caused by true territorial behaviour. This could be tested by experiments in which individuals could be added to existing populations (see MOORE, 1964).

From an ecological point of view it is convenient to express the spatial relationship of dragonflies in terms of population density, but from an ethological point of view the significant fact is the territory size of the individual. The mean territory sizes of the Woodwalton species are given in Table XI. The new data confirm the earlier conclusion that territory is related to the size of insect (MOORE, 1964). It is generally accepted that for most species territory in dragonflies has nothing to do with feeding so why does this relationship exist? Presumably territory size is a compromise between mating with more females and not wasting energy. Are territory size differences related to differences in energy balance or powers of vision?

The low population densities which result from territorial behaviour have consequences for prey/predator relationships within the ecosystem. Even when several species are present the total numbers of adults are so low that they rarely attract more than an occasional avian predator. By contrast tenerals, especially those of species with synchronized emergence, often attract birds to ponds. Most dragonflies appear to feed rather little by water and so can have little effect on potential prey there. Territorial behaviour further reduces the effects of dragonflies on smaller insects by water.

CONSERVATION

This study supports the conclusions of MOORE (1960), DONATH (1980), KNAPP et al. (1983), WILDERMUTH & KREBS (1983) and others that man-made habitats are very important for dragonflies in Europe and can be improved by appropriate management.

SCHMIDT (1985) has emphasised the importance of excluding "accidental records" when building up an inventory of species at a given habitat. The present study gives strong support to this conclusion, because it shows that about a third of the species observed at the Woodwalton ponds only bred occasionally, a third were never recorded as breeding at all and only a third were autochthonous. Therefore, when carrying out surveys of dragonflies to determine their status in an area, or to select particular water bodies for conservation, it is important to recognise that the presence of adults of a species does not necessarily mean that the species is breeding there nor, if it is found to be breeding, that it could continue to do so unless supported by immigration from a stronger population in the neighbourhood. It would be extremely unwise to rely on a series of suboptimal habitats to conserve a species in a particular area. Occasional disasters, either natural or man-made, can destroy or seriously damage an odonate community but losses can be quickly made good if there are other habitats near at hand which have not suffered. Therefore several ponds with suitable habitat should be conserved in the same area. The need for this becomes important as habitats become increasingly isolated in urban areas and areas of industrialised farming and thus long range dispersal becomes more difficult.

This study shows that the conservation of the Odonata of natural waters can be supplemented easily by digging ponds. Newly constructed ponds provide habitats which are quickly colonised by the commoner species. The rate of colonisation can be accelerated by planting emergent and submerged plants as soon as the new pond has been constructed. Later, the seral change from open water to reeds growing in water is inimical to the species studied and therefore reeds should be eliminated if the aim is to conserve those species. When a dragonfly community has developed, it can be maintained at a constant level by controlling the scrub which tends to develop round the edge of the pond.

Finally, this long-term study would never have been embarked upon had there not been security of tenure at Woodwalton. Nature reserves, whose future is guaranteed by the State, have an important role in providing sites for biological monitoring and for the study of long-term phenomena. Predicted changes in climate are likely to make such work increasingly important in the future.

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