The breeding ecology and habitat utilization of some freshwater marsh passerines

by

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I wish to state that this work is the result of my own investigation and that it has not been concurrently submitted in candidature for any degree.

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I certify that the above statement is correct.

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CHAPTER ONE

Introduction

In recent years, a great deal of interest has been shown in an apparent ecological expansion of some marshland passerines to breed outside their 'traditional' marshland habitats (Bell 1968, 1969, Catchpole 1974, Hornby 1971, Kent 1964, Prŷs-Jones 1977). Most attention has been directed towards the Reed Warbler *Acrocephalus scripaceus* and Reed Bunting *Emberiza schoeniclus* and has been concerned in the main with questions relating to their breeding success and habitat selection. In most instances the results have shown, not unexpectedly, that breeding success favours those in marshes rather than elsewhere

The other common British marshland passerine, the Sedge Warbler *Acrocephalus schoenobaenus*, is not suspected of any such ecological expansion and has been little studied during its breeding season.

As far as is known, no investigation of the breeding ecology of any marshland passerine between marshes of different 'quality' has been made, and the main purpose of this research was to undertake such a study at Oxwich marsh, Gower.

Marshes are environments which vary immensely in space and time, and a study of between-marsh variations in the breeding biology of the above species would be particularly interesting. Orians (1980) has recently demonstrated striking differences in the breeding biology of some new world Icterids breeding in various marshland areas in North and South America, identifying a variety of factors which influence the 'success' of particular species.

As far as is known, no such long term study has taken place in old world marshes, and the work reported here is in no way an attempt in this direction. The questions posed in this research are directed at within-marsh variations and concern various aspects of the breeding ecology of the three species mentioned.

Spatial patchiness of marshland environments vary in scale from, on the one hand, vast uniform expanses of pure Phragmites, to complex plant species rich marshes on the other. Oxwich marsh, which is essentially man-made (Chapter 2), contains both these extremes and consists of many discrete easily distinguishable habitat types. The variation between aspects of the breeding biology of Reed Warblers and Reed Buntings in relation to these distinct marshland habitats is the main concern of this thesis.

In a temperate climate marsh the major food source of small passerines during the breeding season is either emergent aquatic insects, spiders or caterpillars (Bell 1968, Havlin 1971, Henry 1977, 1978, Orians 1966). Apart from spiders, these are usually abundant for only a limited period of time and, especially in the case of many aquatic insects, will have populations varying according to e.g. habitat, weather and general lake productivity. The capacity of marshes to produce emerging aquatic insects clearly varies enormously. This productivity must also vary within a particular marsh and depend not only on the nutritional value of the associate lake or pond, but also on such factors as fish populations. A great deal of effort was therefore put into assessing the 'quality' of various marshland types in relation to insect abundance, whilst at the same time studying the breeding biology of the birds.

In the case of the Sedge Warbler, the work was directed purely towards habitat selection, with no reference to differential feeding ecology or breeding success. This work was an attempt to quantify the preferred breeding habitats for Sedge Warblers at Oxwich, but leaves aside the question of habitat utilization in terms of food resources.

Apart from the objectives already outlined, several other factors should be considered as relevant to the research.

(i) Oxwich marsh is well established, is probably extremely rich in nutrients, and as such makes an ideal comparison to Attenborough NNR, where a great deal of previous research has taken place. The latter marsh is of recent origin, being the result of gravel extractions.

(ii) During the last 30 years or so, Reed Warblers have increased in numbers at Oxwich from a few pairs in the early 1950's to the present population of several hundred pairs (Thomas 1977). The population is almost certainly still expanding and may be a reflection of the state of succession of the marsh.

(iii) The Reed Warbler colony is almost certainly not parasitised by Cuckoos _Cuculus canorus_, and as such the study is of particular interest.

(iv) Until very recently no attempt to sustain or reverse the vegetational succession at Oxwich has been made. The only physical management projects have been minor, and the present research is considered timely in this respect, and probably has important management implications.

Finally we point out that during the spring of 1975, an investigation into the populations and distributions of the three species was begun. In the case of Sedge Warbler and Reed Bunting this work proved to be quite straightforward, since both species respond well to a Common Bird Census (Bell et al 1973). An estimate of colony size in the case of the Reed Warbler is however far from easy to obtain in a large reed-bed, and work on this topic continued throughout the duration of this study. The results of this aspect of the work are not presented here, but a preliminary report was given to the Nature Conservancy Council (Thomas 1977).

CHAPTER TWO

Marshland habitats at Oxwich

2.1 History

The greater part of the Gower peninsula consists of a plateau 60-110m. above sea level, which can conveniently be divided into a southwestern portion of Carboniferous Limestone and a higher, northeastern portion of Millstone Grit and Lower Coal Measures, both of which are mostly covered by Boulder Clay.

Erosion by the sea has produced numerous bays and coves along the south coast, with the larger ones forming typical 'burrows' from blown sand, a fine example of which is to be found in Oxwich Bay.

There has been a marsh at Oxwich since the Middle Ages (Davies 1894), and probably for very much longer. Its formation is obscure, but it is likely to have been formed after the emergence of the present sand-dune system in the thirteenth and fourteenth centuries (Potts 1968). Initially, there would almost certainly have developed, behind the dunes, a tidal salt-marsh with an inlet, as there is today, at the eastern end of the bay.

A survey in 1632 (Gillham 1977) records 200 acres of fresh and salt-water marsh, some of which was grazed. In the eighteenth century, Thomas Mansel Talbot errected a seawall and sluice-gate to prevent flooding, and so improved the grazing. Many drainage ditches were also dug at this time so as to carry away the inflowing freshwater. The Serpentine Pond was subsequently constructed, presumably as a landscape feature, and the resulting 'improved' land was grazed until about 1945, when, as a result of a deterioration in the efficiency of the drainage channels and the sluice-gate, the water levels had risen too far.

The present day marsh has developed from this time by a natural succession, which has been essentially unchecked. It has been managed since 1962 by the Nature Conservancy Council under an agreement with the owners, but in fact until very recently little or no actual management has taken place.

The result of the succession has been the development of a complex marshland system due in part to the existence of the old drainage channels, and to the remnants of the Serpentine Pond, all of which have tended to create 'discrete' habitat types, often bounded by lines of Willow or Alder Carr. The now open sluice-gate must also have affected the plant regime by allowing salt water to penetrate freely into the marsh at its eastern end.

2.2 Marshland habitats

Little attention has been given to describing and comparing the breeding biology of marshland birds with respect to habitat differences between and/or within freshwater marshes. Catchpole (1974) considered habitat selection and breeding success in the Reed Warbler at Attenborough N.N.R. using a basic marsh, scrub, field, carr division. Bell (1968), working at the same place, addressed similar questions with regard to the Reed Bunting. Neither explored the question of 'habitat quality' as it relates to the breeding biology of marshland passerines.

At Oxwich, Reed Warblers breed exclusively in the marshes, Reed Buntings predominantly so and Sedge Warblers frequently. In order to consider within marsh variations of breeding success and habitat selection, three convenient habitat subdivisions were chosen, based on the known breeding locations of Reed Warblers and Reed Buntings and on their foraging behaviour. The range of habitats utilized by Sedge Warblers differed markedly from these two species, and an entirely separate habitat classification was chosen. This is described in Chapter 6. The divisions, chosen solely on physical and vegetational criteria were as follows:

Pure reed-marsh - PM

Areas consisting almost entirely of Phragmites communis Trin. Virtually all these areas are flooded throughout the year, but some small patches occasionally dry out during the summer.

Mixed reed-marsh - MM

Areas of flooded Phragmites, together with other marshland plants such as Iris pseudacorus L., Mentha aquatica L., Oenanthe fistulosa L., Rumex hybrolapathum Hudson, Solanum dulcamora L., Epilobium hirsutum L., Calystegia sepium (L), Filipendula ulmaria (L), Typha angustifolia L., Typha latifolia L., Scutellaria galericulata L., Lysimachia nummularia L., Lycopus europaeus L., Galium palustre L., Berula erecta (Hudson) and Carix sp. In some places the whole plant community grows from a floating mat over water 1 - 1½m. deep. In general the vegetation matrix is much denser than the PM just described.

Inferior reed-marsh - IM

Dominated again by Phragmites, but containing in the main poor quality, thin-stemmed plants, usually thinly spread and growing from a dry, or at most a damp base. Other plants present include Solanum dulcamora, Epilobium histutum, Oenanthe fistulosa, Typha angustifolia, Typha latifolia, Scutellaria galericulata, Galium palustre, Glyceria maxima (Hartman) and Carix sp.

Willow/Alder carr - W/A

Mainly Salix spp. and Alnus glutinosa (L) invading marshland areas. The early stages consist of scattered bushes, but large areas of maturing woodland are becomming established. Many Salix bushes have tended to spread along old drainage channels, resulting in areas of marsh being bordered or virtually surrounded by carr. Most developing bushes are less than 10m. high, but those in established areas are often in excess of 12m.

2.3 The study area

Apart from the Sedge Warbler study, where the entire marsh was utilized, a convenient study area (Fig. 2.1) around the Garden Lane was chosen containing some of the habitat types described above. The major areas were as follows:

Garden Lane Marsh

Almost all PM, but with an area of MM at its west end. The entire marsh was very wet, water levels varying from c¼ - 1m. Almost completely surrounded by W/A.

Triangle Marsh

Consisting entirely of PM. Water levels again c¼ - 1m. W/A along the length of the Garden Lane only.

West Marsh

MM with scattered small clumps of W/A. Bordered on the edge of the North Pond by a broken line of mostly tall established W/A. Water levels c½ - 1½m.

East Marsh

IM containing a few scattered W/A bushes. Virtually no W/A on its edge, but with an established Alder wood to the south.

Middle Marsh

A strip of IM running N-S along and to the east of the main road. Bordered on the east by established woodland. Little or no water.

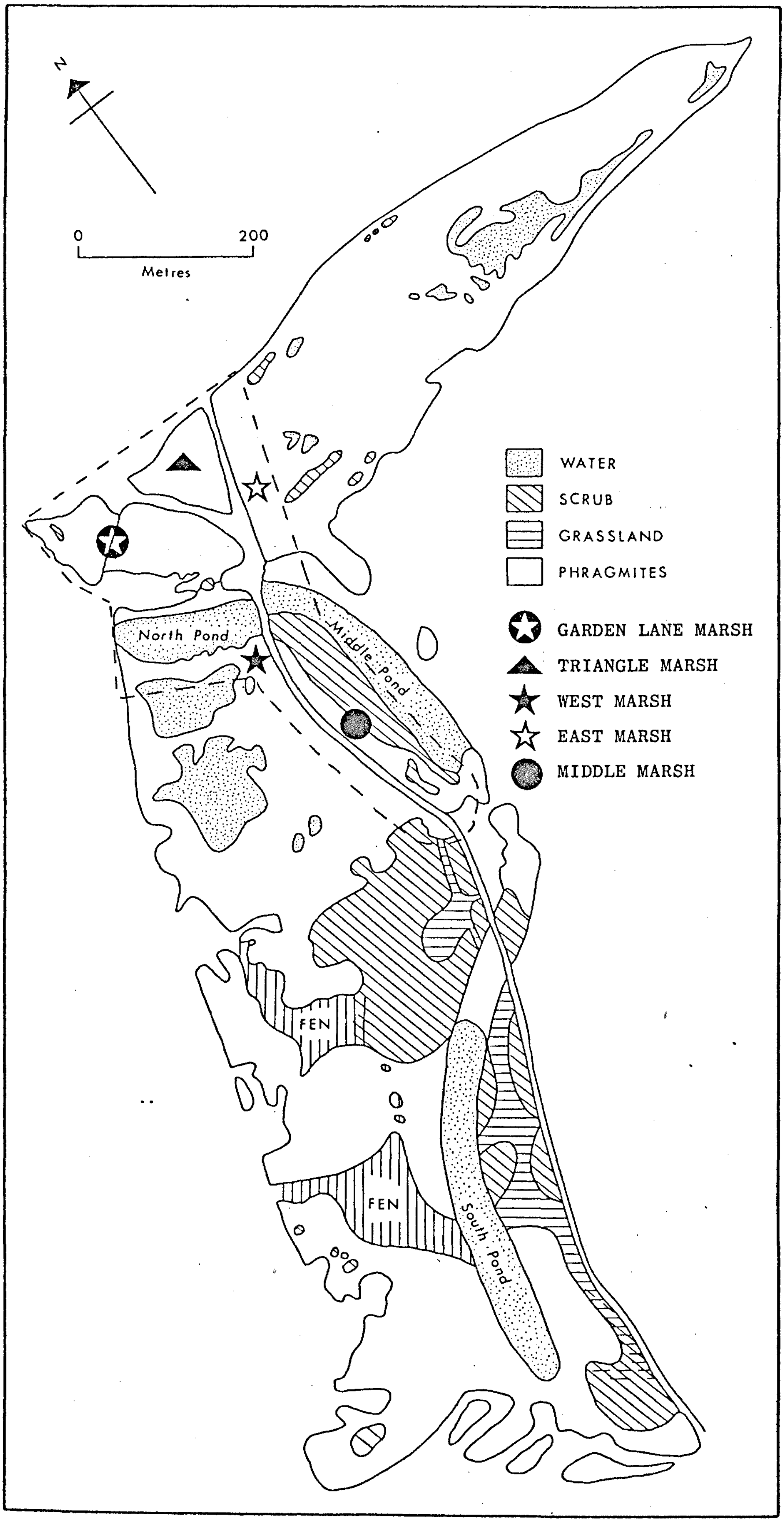

Fig 2·1 Study area

CHAPTER THREE

Marshland Invertebrates

Methods

Any method of sampling the invertebrate fauna in a freshwater marsh during the breeding season is fraught with difficulties, not only from the point of view of bias, but also because of the inevitable disturbance it causes to nesting birds.

A number of different collecting methods were tried but found wanting. Sweep netting was virtually impossible within the reed-beds since it caused a great deal of damage, created a lot of noise and caught very few insects. The use of sticky paper attached to reeds was also a failure since the paper became entangled in the reed-stems, often dried out and caught very few insects. A vacuum suction machine was tried and immediately abandoned because of the high noise level. Emergence traps were considered but were not tried.

Personal experience with water traps in European freshwater marshes (Bibby and Green 1981) had shown them to be quite successful in catching insects, easy to operate and to cause minimal disturbance. Since they could also be operated in a range of different habitats they were chosen as the method of sampling.

Ten sample sites were chosen, representing as wide a variety of habitats as possible in which Reed Warblers and Reed Buntings both nested and foraged. One site in dry bramble, was chosen since Sedge Warblers were known to nest there.

At each site, four stakes were driven into the ground, one at each corner of a 3m square. The height of each stake varied between about ½ - 1m above ground or water level (which of course also varied). A plant pot saucer 13 cm in diameter and 3·3 cm deep was nailed to the top of each stake. Another similar saucer was placed inside and almost filled with water containing a few drops of detergent.

The traps were emptied at weekly intervals for a one year period from 1st December 1977 to 23rd November 1978. We shall only be concerned here with the period 4th May to 17th August 1978 spanning sixteen weeks of the breeding season of the three species under consideration.

The invertebrates collected were placed in jars, sorted from the litter and stored in 70% alcohol on the day of collection. Subsequently samples were sorted into taxa (usually order or sub-order) and size classes. Any item less than 2 mm in length was ignored since it was assumed to be of little food value to the birds. In some instances, when a particular family was abundant, e.g. Chironomidae and Delphacidae, it was identified and separated. Chinery (1973) was used for most of the identification. The ten sampling sites chosen are shown in Fig. 3.1. In relation to the habitat types described in Chapter 2 they are as follows:

Site		Habitat type
Garden Lane East	(GLE)	PM
Triangle Marsh East	(TE)	PM
Triangle Marsh West	(TW)	PM
Garden Lane West	(GLW)	MM
West Marsh East	(WE)	MM
West Marsh West	(WW)	MM
East Marsh	(E)	IM
Garden Lane Willows	(GL)	W/A
North Pond Willows	(NP)	W/A
Bramble	(B)	B

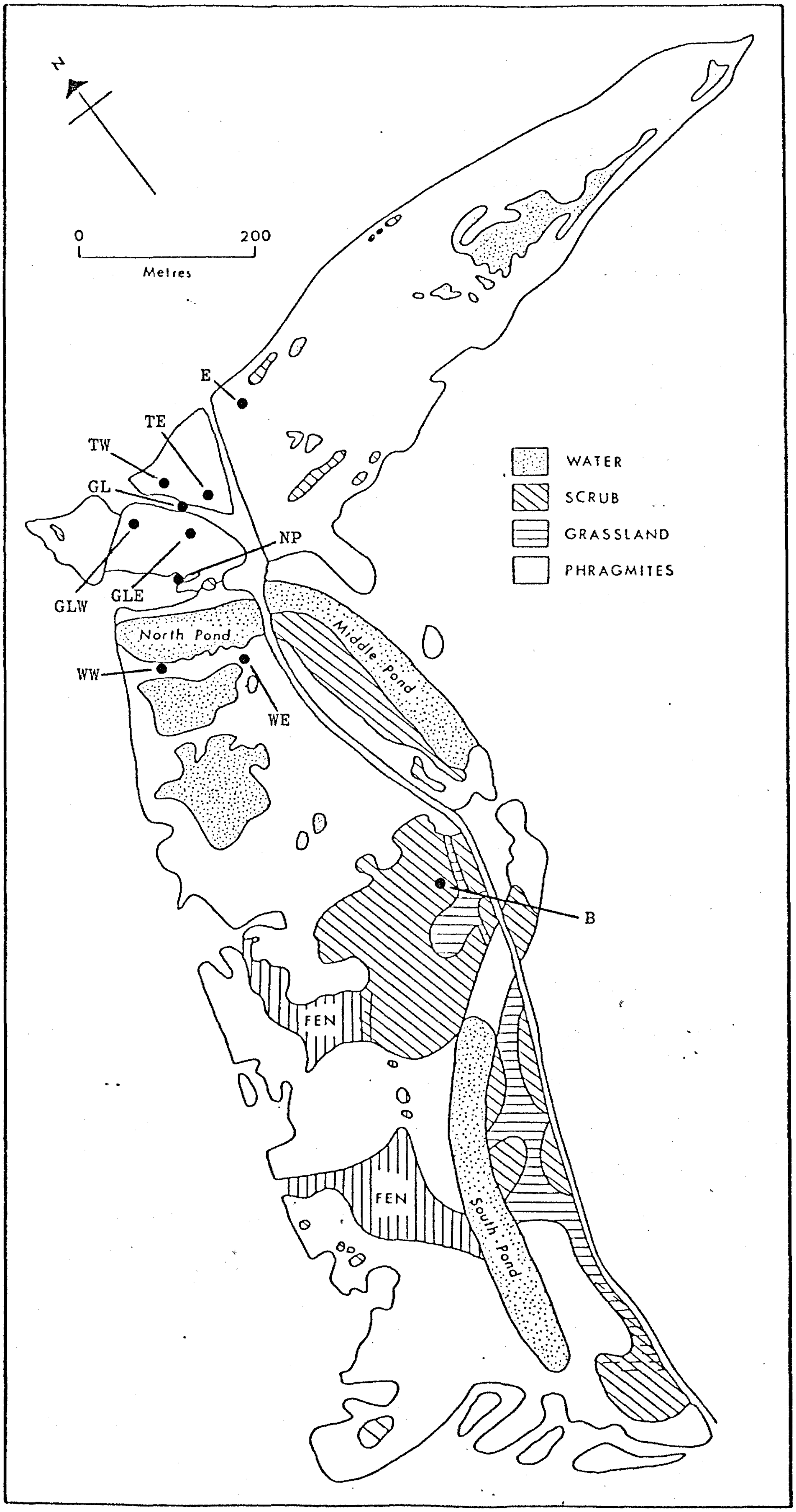

Fig.3·1 Positions of water trap sites.

Results

The results of the water trap samples are presented in Tables 3.1 to 3.1 Invertebrates were collected during one year only, and by just one method so that any conclusions drawn from the presented data are made with this proviso.

Tables 3.1 to 3.10 give the numbers of each taxon at each site divided in the size classes 2 - 4 mm, 4 - 6 mm, 6 + mm. Tables 3.11 to 3.14 combine these for the four habitat types PM, MM, IM and W/A. In order to make comparisons in a consistent way a standard non-parametric method of analysis, the W Kendall Coefficient of Concordance Test (Kendall 1970) was chosen and is used whenever possible in the following analysis.

3.1 Spiders

Spiders occurred throughout the period with no apparent seasonal trends (Fig. 3.2). Most were caught in the marshland sites with an average of 6·5/site/wk in PM, 7·2/site/wk in MM, 7·3/site/wk in IM and only 1·8/site/wk in W/A. Of the total 836, 534 (63·9%) were size 2 - 4 mm.

A Kendall Coefficient of Concordance Test gives W = 0·56 and a significant ranking PM > MM > IM > W/A (p < 0·01). A test between PM, MM and IM however gives a W = 0·03 and no significant ranking, indicating that most of the deviation from equality was due to W/A. It would appear therefore that the three marshland habitats contain significantly higher numbers of spiders than W/A. However, the obvious physical differences between these habitats could account for this, especially in view of the fact that spiders are terrestrial.

3.2 Odonata

Only Zygoptera were caught, these being represented by the three

Week ending

		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	4	8	3	7	8	7	6	5	2
	4-6	3	0	0	4	3	1	0	1	1
	6+	0	0	0	2	4	2	8	9	6
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	3	4	0	0	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	2	2	5	13	2	3
	4-6	0	0	0	0	2	11	8	4	8
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	1	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	2	1	0	0	0
	6+	0	0	1	2	2	1	2	3	4
Chironomidae	2-4	2020	1231	675	359	159	148	156	95	135
	4-6	3	7	13	7	5	10	8	7	4
	6+	129	45	21	13	2	3	7	2	1
Nematocera (other)	2-4	2	48	20	8	13	25	33	37	22
	4-6	53	165	125	14	6	13	3	7	7
	6+	2	1	0	2	3	4	4	4	2
Brachycera/ Cyclorrhapha	2-4	3	26	30	28	18	47	74	112	61
	4-6	8	2	7	8	19	904	1140	1097	599
	6+	8	16	13	10	3	14	16	5	10
Hymenoptera	2-4	0	0	0	8	4	10	10	5	5
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	1	0	1	0	0
Coleoptera	2-4	0	28	32	10	75	33	12	9	7
	4-6	0	1	0	80	38	23	1	1	0
	6+	0	4	0	1	2	4	2	4	3
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	3	0	0	1	1	1	0
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	1	0	2	0
Totals		2235	1583	943	568	375	1268	1505	1412	880

Table 3.1 Seasonal variation of numbers of invertebrates collected from water traps at site GLE. *(Ctd.)*

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	5	6	4	4	2	7	5	
	4-6	3	1	1	2	1	1	0	
	6+	8	3	1	4	6	0	2	160
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	7
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	1	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Aphididae	2-4	0	2	2	1	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	5
Delphacidae	2-4	3	1	2	1	0	0	0	
	4-6	2	1	1	1	3	0	0	
	6+	0	0	0	0	0	0	0	75
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	1	
	6+	0	0	0	1	0	0	0	20
Chironomidae	2-4	95	74	38	73	23	54	71	
	4-6	1	2	3	2	1	1	4	
	6+	3	5	9	7	1	4	14	5750
Nematocera (other)	2-4	27	15	60	87	37	29	48	
	4-6	18	3	9	2	6	0	1	
	6+	5	2	0	2	1	0	3	978
Brachycera/ Cyclorrhapha	2-4	55	109	75	84	60	147	94	
	4-6	1223	517	1411	891	312	258	300	
	6+	4	11	17	5	5	3	0	9859
Hymenoptera	2-4	2	2	2	18	29	51	51	
	4-6	0	2	0	0	1	0	0	
	6+	0	0	0	1	1	1	0	205
Coleoptera	2-4	15	7	16	17	9	5	14	
	4-6	1	1	0	4	0	0	0	
	6+	4	5	3	2	0	0	1	474
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	1	0	0	0	0	7
Miscellaneous	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	3	0	0	2	1	2	3	14
Totals		1477	769	1656	1211	499	563	612	17556

Table 3.1 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	1	9	2	5	0	1	3	4	1
	4-6	0	0	0	1	0	0	1	1	1
	6+	0	0	1	1	0	1	5	2	2
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	6	0	1	2	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	0	1
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	3	1	6	3	6	4
	4-6	0	0	0	0	0	24	17	7	2
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	2	1	3	1	1	0	1	4
Chironomidae	2-4	2594	2963	1093	496	434	505	498	371	234
	4-6	38	14	10	4	2	1	2	4	2
	6+	95	55	31	11	3	0	1	3	10
Nematocera (other)	2-4	46	21	26	18	20	30	10	27	14
	4-6	94	37	81	62	6	5	1	9	5
	6+	0	1	4	0	2	14	16	21	5
Brachycera/ Cyclorrhapha	2-4	17	6	37	32	35	98	86	192	87
	4-6	0	1	2	3	22	52	177	280	233
	6+	22	23	42	22	19	6	16	12	5
Hymenoptera	2-4	0	0	0	1	0	4	4	5	1
	4-6	0	0	0	3	0	2	0	1	0
	6+	0	0	0	0	2	3	3	2	0
Coleoptera	2-4	1	7	4	10	16	10	4	15	4
	4-6	1	7	1	8	5	9	2	1	0
	6+	2	4	1	1	0	0	2	3	1
Larvae	2-4	1	0	1	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	1	2	2	1	2	0	0
Miscellaneous	2-4	0	0	1	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	1	0	0	0	0	0	0
Totals		2912	3150	1340	686	576	773	854	969	616

Table 3.2 Seasonal variation of numbers of invertebrates collected from water traps at site TE.

(Ctd.)

Week ending

		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	0	0	4	0	1	3	0	
	4-6	1	0	1	0	0	0	0	
	6+	1	1	2	1	1	2	2	62
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	9
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	1	0	
	6+	0	0	0	0	0	0	0	1
Aphididae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Delphacidae	2-4	0	1	1	0	0	1	0	
	4-6	1	1	1	0	0	0	0	
	6+	0	0	0	0	0	0	0	79
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	6	0	2	4	1	6	8	40
Chironomidae	2-4	215	158	62	248	70	42	109	
	4-6	3	1	3	3	4	0	0	
	6+	6	2	7	5	3	0	20	10435
Nematocera (other)	2-4	21	20	68	73	58	85	44	
	4-6	2	4	4	4	3	1	0	
	6+	6	0	0	0	1	0	1	970
Brachycera/ Cyclorrhapha	2-4	61	93	112	244	110	140	173	
	4-6	139	117	367	77	132	57	83	
	6+	0	5	8	5	8	4	2	3464
Hymenoptera	2-4	1	4	5	23	31	83	56	
	4-6	0	0	2	6	1	5	0	
	6+	0	1	0	2	8	2	3	264
Coleoptera	2-4	6	4	6	14	5	3	2	
	4-6	0	0	0	0	4	0	2	
	6+	2	2	11	4	1	1	5	191
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	1	0	1	12
Miscellaneous	2-4	0	0	0	1	0	0	0	
	4-6	1	0	0	0	1	0	0	
	6+	0	0	0	0	0	0	7	12
Totals		472	414	666	714	444	436	518	15540

Table 3.2 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	2	1	7	5	1	9	5	4	1
	4-6	0	0	0	0	0	1	0	1	3
	6+	0	0	0	1	1	3	1	5	1
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	1	2	0	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	1	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	1	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	1	0	0	4	1	16	7	1
	4-6	0	0	0	0	2	13	3	6	3
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	1	0	0	0	0
	4-6	0	0	0	0	0	2	0	0	0
	6+	0	0	3	3	4	3	1	3	3
Chironomidae	2-4	452	365	568	209	113	206	302	186	585
	4-6	39	12	5	5	5	4	4	2	9
	6+	84	19	18	11	7	2	2	0	3
Nematocera (other)	2-4	16	52	9	13	37	51	88	34	90
	4-6	170	76	60	13	9	8	5	4	13
	6+	3	4	4	1	3	17	26	16	19
Brachycera/ Cyclorrhapha	2-4	14	6	46	22	28	128	85	121	89
	4-6	2	0	1	4	71	93	154	175	189
	6+	9	4	20	10	11	10	15	13	5
Hymenoptera	2-4	0	3	0	2	2	6	17	6	6
	4-6	0	0	0	0	0	1	0	0	0
	6+	0	0	0	0	0	3	0	2	0
Coleoptera	2-4	1	8	10	27	29	33	14	5	5
	4-6	0	9	2	2	35	17	1	0	0
	6+	0	3	1	0	0	2	0	6	1
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	2	2	1	2	0	3	0	0	1
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	1	0	1	1
Totals		794	565	755	331	364	620	739	597	1028

Table 3.3 Seasonal variation of numbers of invertebrates collected from water traps at site TW. (Ctd.

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	3	3	1	2	3	8	1	
	4-6	2	1	0	0	0	0	0	
	6+	5	1	4	1	0	4	1	92
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	3
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Aphididae	2-4	0	1	1	0	1	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	4
Delphacidae	2-4	0	1	0	0	0	0	0	
	4-6	1	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	59
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	2	0	0	2	1	8	7	43
Chironomidae	2-4	302	176	58	156	29	70	157	
	4-6	4	2	0	3	0	1	0	
	6+	3	1	5	2	3	1	8	4198
Nematocera (other)	2-4	42	34	67	211	37	99	95	
	4-6	4	1	5	2	0	2	2	
	6+	14	2	3	2	1	1	1	1466
Brachycera/ Cyclorrhapha	2-4	146	210	150	359	123	158	334	
	4-6	391	201	562	254	178	113	122	
	6+	21	10	32	20	3	1	8	4721
Hymenoptera	2-4	1	10	12	15	19	49	56	
	4-6	0	1	1	1	2	0	2	
	6+	0	0	1	0	0	0	1	219
Coleoptera	2-4	4	5	8	9	9	3	10	
	4-6	1	0	1	1	0	1	1	
	6+	0	3	8	9	3	0	2	289
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	1	0	0	0	0	1	13
Miscellaneous	2-4	0	1	0	0	1	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	1	2	6	8	22
Totals		946	665	919	1050	415	525	817	11130

Table 3.3 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	1	8	8	8	4	4	5	2	8
	4-6	0	0	0	0	0	1	0	0	2
	6+	1	2	0	1	1	1	2	5	4
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	1	3	1	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	0	2	0	5	3	0
	4-6	0	0	0	0	0	1	2	2	1
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	3	0	0	3	0	0
	6+	0	1	3	2	4	4	2	0	0
Chironomidae	2-4	386	246	456	475	158	77	220	236	144
	4-6	36	7	19	9	13	8	8	3	5
	6+	29	15	6	8	2	1	7	0	2
Nematocera (other)	2-4	24	24	14	14	16	14	15	16	22
	4-6	48	117	73	11	8	7	14	22	7
	6+	1	0	3	4	2	9	10	7	1
Brachycera/ Cyclorrhapha	2-4	38	13	19	19	15	33	79	109	75
	4-6	0	4	14	7	10	357	671	379	507
	6+	4	3	6	3	3	4	15	7	33
Hymenoptera	2-4	0	0	0	6	7	7	9	11	12
	4-6	0	0	0	0	1	0	0	0	1
	6+	0	0	0	0	2	3	1	1	0
Coleoptera	2-4	2	20	24	58	55	31	13	32	11
	4-6	0	0	2	2	42	39	7	0	0
	6+	1	0	0	0	4	3	6	12	5
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	1	0	0	0	0	0	0	0
	6+	0	2	2	1	1	4	4	1	1
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	1	0	1
Totals		571	463	649	631	351	611	1100	848	842

Table 3.4 Seasonal variation of numbers of invertebrates collected from water traps at site GLW.

(Ctd.)

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	1	3	2	1	8	5	1	
	4-6	0	3	0	0	1	0	0	
	6+	6	2	0	1	1	1	1	105
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	5
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Aphididae	2-4	0	2	0	0	0	0	1	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	3
Delphacidae	2-4	1	1	0	0	0	0	0	
	4-6	0	0	0	0	1	0	0	
	6+	0	0	0	0	0	0	0	19
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	5	2	2	9	6	1	1	48
Chironomidae	2-4	83	79	58	52	26	43	52	
	4-6	0	7	9	5	4	5	1	
	6+	1	3	3	6	4	7	5	3029
Nematocera (other)	2-4	9	9	34	72	38	24	22	
	4-6	4	6	4	7	7	1	0	
	6+	3	1	2	3	1	0	1	751
Brachycera/ Cyclorrhapha	2-4	59	89	87	150	104	111	79	
	4-6	776	650	762	777	300	170	182	
	6+	24	15	20	23	5	10	8	6828
Hymenoptera	2-4	8	7	2	18	30	43	29	
	4-6	0	0	1	0	4	2	0	
	6+	1	1	3	2	0	0	0	212
Coleoptera	2-4	9	19	19	36	21	27	25	
	4-6	0	0	1	3	2	0	0	
	6+	5	8	7	7	3	3	10	574
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	2	0	0	0	1	0	1	21
Miscellaneous	2-4	0	0	0	1	0	0	0	
	4-6	0	0	0	0	0	1	0	
	6+	2	0	0	1	0	1	12	20
Totals		999	907	1016	1174	567	455	431	11615

Table 3.4 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	1	8	11	14	5	4	3	3	1
	4-6	0	0	0	0	2	2	1	2	1
	6+	0	0	0	2	1	2	3	4	0
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	3	13	8	7	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	1	4	5	10	8	2
	4-6	0	0	0	0	3	11	7	0	2
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	10	0	2	0	0	0	0	0
	4-6	0	0	0	0	1	2	20	34	0
	6+	0	0	0	1	0	37	7	4	0
Chironomidae	2-4	8491	4054	1036	663	254	326	686	657	370
	4-6	7	29	11	23	15	13	12	8	6
	6+	267	185	105	67	20	7	3	6	10
Nematocera (other)	2-4	18	34	14	20	16	10	19	11	29
	4-6	40	84	40	16	12	2	13	11	12
	6+	3	2	4	9	14	16	15	13	10
Brachycera/ Cyclorrhapha	2-4	13	38	35	19	53	23	82	95	48
	4-6	6	21	13	0	33	659	2791	2336	4040
	6+	6	15	31	15	20	12	13	13	2
Hymenoptera	2-4	0	1	1	2	7	8	9	4	5
	4-6	0	0	0	0	1	0	0	0	0
	6+	0	0	0	1	0	2	1	0	0
Coleoptera	2-4	3	9	5	20	22	14	8	7	2
	4-6	0	1	1	6	11	6	1	0	1
	6+	0	1	2	1	1	2	2	8	11
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	1	1	2	0	0	2	1	0
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	1
Totals		8855	4493	1310	887	508	1171	3715	3225	4553

Table 3.5 Seasonal variation of numbers of invertebrates collected from water traps at site WE. *(Ctd.)*

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	0	5	4	5	7	5	5	
	4-6	0	0	0	0	1	0	0	
	6+	2	2	3	1	3	2	6	121
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	31
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	1	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Delphacidae	2-4	0	0	0	1	1	0	0	
	4-6	0	0	2	0	0	0	0	
	6+	0	0	0	0	0	0	0	57
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	1	0	0	
	6+	0	0	0	0	0	0	0	1
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	3	0	0	0	0	
	6+	3	0	1	2	0	1	1	129
Chironomidae	2-4	443	168	95	68	15	15	65	
	4-6	10	11	8	8	5	6	5	
	6+	18	9	12	13	7	4	19	18335
Nematocera (other)	2-4	116	38	37	56	20	44	24	
	4-6	46	8	6	3	6	5	2	
	6+	14	2	8	4	0	1	7	934
Brachycera/ Cyclorrhapha	2-4	46	59	53	124	98	76	74	
	4-6	3963	1609	1219	1228	368	278	175	
	6+	2	7	4	5	6	3	1	19830
Hymenoptera	2-4	5	7	9	26	44	64	45	
	4-6	1	0	0	1	1	0	0	
	6+	0	0	5	0	2	2	1	255
Coleoptera	2-4	4	11	25	16	0	10	5	
	4-6	1	0	0	0	3	1	2	
	6+	9	3	3	5	1	4	8	256
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	1	0	0	0	0	0	0	8
Miscellaneous	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	1	1	0	4	5	12
Totals		4684	1939	1499	1567	589	525	450	39970

Table 3.5 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	3	17	3	6	3	2	5	4	4
	4-6	0	0	0	2	0	4	2	1	0
	6+	0	1	0	0	0	1	2	0	3
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	6	19	26	33	55	23
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	1	1
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	1	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	2	11	6	1	1	0	0	0	0
	4-6	0	0	1	0	0	7	7	7	2
	6+	1	0	0	0	1	1	4	6	1
Chironomidae	2-4	687	283	299	478	223	321	345	321	193
	4-6	46	15	10	16	12	9	8	25	15
	6+	220	78	65	14	12	6	5	37	11
Nematocera (other)	2-4	44	33	60	52	43	28	54	50	43
	4-6	21	17	41	20	12	2	3	7	3
	6+	0	1	4	7	20	31	27	34	12
Brachycera/ Cyclorrhapha	2-4	14	3	7	4	17	23	45	101	56
	4-6	6	10	17	12	4	264	1928	2348	2875
	6+	14	12	11	8	8	8	28	29	9
Hymenoptera	2-4	0	1	4	2	3	5	3	1	2
	4-6	0	0	0	1	0	4	1	2	2
	6+	0	0	0	2	10	3	2	7	4
Coleoptera	2-4	1	2	10	5	3	5	4	4	1
	4-6	0	1	3	6	9	2	1	2	0
	6+	0	0	4	12	9	4	6	5	9
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	1	1
	6+	0	0	0	2	0	4	2	1	4
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	1	0	0	0	0	0	0	1	0
Totals		1060	485	545	657	409	760	2515	3050	3274

Table 3.6 Seasonal variation of numbers of invertebrates collected from water traps at site WW.

(Ctd.)

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	4	5	3	2	6	2	4	
	4-6	0	2	0	2	1	0	3	
	6+	2	10	2	2	0	2	5	120
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	3	0	0	0	0	0	0	165
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Aphididae	2-4	1	2	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	5
Delphacidae	2-4	2	0	1	1	0	1	0	
	4-6	0	0	0	2	0	0	0	
	6+	0	0	0	0	0	0	0	8
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	1	0	0	
	6+	0	0	0	0	0	0	0	1
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	1	0	0	0	1	0	0	
	6+	6	0	0	2	1	4	3	77
Chironomidae	2-4	112	77	44	61	13	15	23	
	4-6	5	6	4	6	3	3	1	
	6+	15	11	7	5	2	7	10	4184
Nematocera (other)	2-4	42	30	50	77	19	28	14	
	4-6	23	8	1	0	3	2	1	
	6+	28	9	15	7	5	7	11	1049
Brachycera/ Cyclorrhapha	2-4	79	74	42	175	126	35	98	
	4-6	3752	2543	944	1013	375	397	102	
	6+	16	14	16	18	7	10	6	17703
Hymenoptera	2-4	4	5	7	12	13	22	18	
	4-6	0	3	5	4	2	0	1	
	6+	0	1	1	1	0	0	3	161
Coleoptera	2-4	2	7	14	20	4	8	4	
	4-6	1	0	2	33	10	5	6	
	6+	20	16	25	27	8	12	11	343
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	4	5	3	6	1	0	0	
	6+	10	11	5	10	1	2	0	73
Miscellaneous	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	1	2	1	6
Totals		4132	2839	1191	1486	603	564	325	23895

Table 3.6 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	2	23	12	7	6	8	6	5	2
	4-6	0	0	0	0	1	1	1	0	0
	6+	1	1	0	0	1	0	0	4	2
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	1	1	1	16	4	1
Heteroptera	2-4	0	1	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	2	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	0	0	0	2	1	0
	4-6	0	0	0	0	0	0	0	0	1
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	3	0	0
	6+	0	1	3	4	3	4	1	4	1
Chironomidae	2-4	57	85	74	122	106	49	34	73	37
	4-6	4	6	6	6	10	3	0	1	1
	6+	7	5	6	5	8	0	0	0	0
Nematocera (other)	2-4	58	63	96	106	176	124	50	35	35
	4-6	7	2	26	5	28	1	1	2	2
	6+	10	11	11	10	17	30	20	24	6
Brachycera/ Cyclorrhapha	2-4	1	5	9	17	28	26	27	98	104
	4-6	4	2	14	11	16	10	46	89	359
	6+	2	5	10	7	6	9	12	31	31
Hymenoptera	2-4	0	0	0	2	1	3	3	4	4
	4-6	0	0	0	0	1	5	2	1	2
	6+	0	0	0	1	1	0	3	6	0
Coleoptera	2-4	4	22	8	19	30	13	4	15	3
	4-6	0	4	0	0	13	10	0	0	0
	6+	0	1	0	2	2	3	0	6	4
Larvae	2-4	1	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	1	0	0	0	4	2	3
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Totals		158	237	276	325	455	302	235	405	598

Table 3.7 Seasonal variation of numbers of invertebrates collected from water traps at site E. *(Ctd.)*

		Week ending							
		July				Aug			
	Site (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	4	3	1	1	2	1	2	
	4-6	3	2	0	1	1	0	0	
	6+	4	4	0	1	0	3	1	117
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	1	0	0	0	0	0	0	25
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Aphididae	2-4	0	2	0	2	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	6
Delphacidae	2-4	1	3	0	0	3	0	0	
	4-6	0	0	0	0	0	2	0	
	6+	0	0	0	0	0	0	0	13
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	1	1	0	0	0	2
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	1	0	0	0	0	0	0	
	6+	3	3	1	4	2	3	4	45
Chironomidae	2-4	32	32	32	24	11	23	27	
	4-6	3	1	4	2	1	2	2	
	6+	0	3	3	0	0	1	3	911
Nematocera (other)	2-4	36	29	71	76	68	18	34	
	4-6	2	1	3	0	1	2	0	
	6+	15	0	1	0	2	2	6	1323
Brachycera/ Cyclorrhapha	2-4	79	134	80	127	103	107	197	
	4-6	310	59	39	54	21	69	88	
	6+	31	49	90	64	38	18	44	2780
Hymenoptera	2-4	4	8	2	13	14	30	31	
	4-6	2	1	0	5	6	2	2	
	6+	0	2	1	0	3	14	7	186
Coleoptera	2-4	9	20	14	8	6	6	16	
	4-6	0	0	0	1	1	0	4	
	6+	4	8	34	25	8	7	13	347
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	2	0	0	0	0	0	1	14
Miscellaneous	2-4	0	1	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	6	7
Totals		546	365	377	409	291	310	488	5777

Table 3.7 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	2	6	3	4	4	4	2	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	1	0	0	0	1	0
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	1
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	1	1	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	0	0	0	1	4	3
	4-6	0	0	0	0	0	0	0	1	1
	6+	0	0	0	0	0	0	0	0	1
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	4	1	0	0	2	3	1
	6+	0	0	0	1	0	5	2	0	1
Chironomidae	2-4	185	333	204	737	473	286	211	66	95
	4-6	17	30	25	51	29	18	17	7	3
	6+	31	34	21	24	12	6	6	1	3
Nematocera (other)	2-4	36	42	26	69	77	107	149	54	73
	4-6	15	12	15	40	29	7	12	9	9
	6+	3	3	3	9	9	3	6	0	2
Brachycera/ Cyclorrhapha	2-4	20	3	8	4	16	6	11	28	25
	4-6	35	44	19	39	48	17	24	24	27
	6+	2	3	3	13	44	7	2	3	2
Hymenoptera	2-4	0	0	0	4	0	0	4	2	5
	4-6	0	0	3	1	0	2	0	0	0
	6+	0	0	0	0	0	2	0	0	2
Coleoptera	2-4	0	18	19	28	14	9	2	8	7
	4-6	1	1	1	0	0	0	0	0	0
	6+	1	2	0	1	1	3	1	0	2
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	1
	6+	0	0	1	1	1	1	2	0	1
Miscellaneous	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	1	0	0
	6+	1	0	0	0	1	1	0	1	0
Totals		349	531	355	1028	758	485	456	212	265

Table 3.8 Seasonal variation of numbers of invertebrates collected from water traps at site GL.

(Ctd)

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	7	2	0	1	2	1	0	
	4-6	0	0	0	0	0	0	0	
	6+	1	2	0	0	0	0	0	43
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	1
Aphididae	2-4	0	0	3	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	5
Delphacidae	2-4	1	0	1	0	0	0	2	
	4-6	0	1	1	0	0	0	0	
	6+	1	0	0	0	0	0	0	18
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	0	0	0	0	0	0	
	4-6	1	1	4	1	1	0	0	
	6+	0	2	0	2	2	1	0	35
Chironomidae	2-4	44	61	21	21	23	41	58	
	4-6	1	2	3	5	6	4	6	
	6+	5	7	6	4	10	14	14	3281
Nematocera (other)	2-4	103	98	121	66	58	53	27	
	4-6	5	3	6	1	1	5	5	
	6+	1	3	2	2	0	5	1	1385
Brachycera/ Cyclorrhapha	2-4	24	25	79	48	109	117	78	
	4-6	21	28	39	28	22	43	30	
	6+	3	5	5	10	2	9	7	1209
Hymenoptera	2-4	0	6	6	6	7	11	3	
	4-6	0	1	0	1	2	1	0	
	6+	0	0	1	0	1	0	2	73
Coleoptera	2-4	4	7	11	1	6	2	2	
	4-6	0	2	1	3	0	1	0	
	6+	0	0	3	0	1	2	0	165
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	1	0	0	0	3	12
Miscellaneous	2-4	1	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	1	0	1	1	2	1	2	14
Totals		224	256	315	201	255	311	240	6241

Table 3.8 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	3	0	3	1	1	1	1	2	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	1	0	0	0
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	6	9	9	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	1	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	0	0	1	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	0	1	0	0	1	3
	4-6	0	0	0	0	0	0	0	1	1
	6+	0	0	0	0	0	0	0	0	0
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	1	6	24	13	2	0	0	0	0
	4-6	4	0	0	0	4	2	32	112	54
	6+	1	1	0	0	1	74	10	2	0
Chironomidae	2-4	392	170	256	435	144	161	83	78	141
	4-6	60	10	16	33	6	10	2	4	7
	6+	64	50	28	30	8	8	2	3	8
Nematocera (other)	2-4	45	31	22	41	33	28	23	12	23
	4-6	22	10	7	16	13	2	0	2	1
	6+	8	3	3	7	6	7	1	6	2
Brachycera/ Cyclorrhapha	2-4	19	27	25	2	1	13	5	27	20
	4-6	76	327	131	42	19	9	15	50	31
	6+	22	14	10	32	28	48	16	19	7
Hymenoptera	2-4	0	0	0	0	0	1	2	2	2
	4-6	2	1	0	0	1	1	1	1	1
	6+	1	0	0	0	0	0	1	0	2
Coleoptera	2-4	2	2	12	23	30	14	2	6	0
	4-6	0	1	1	0	4	1	3	1	1
	6+	0	0	0	0	1	2	1	2	0
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	2	1	0	0	1	0	0
	6+	0	0	0	0	1	4	1	1	0
Miscellaneous	2-4	1	1	0	0	0	0	0	1	1
	4-6	0	0	1	0	0	0	0	1	0
	6+	0	0	0	4	0	1	0	2	1
Totals		723	654	542	680	310	397	211	337	306

Table 3.9 Seasonal variation of numbers of invertebrates collected from water traps at site NP. *(Ctd.)*

Week ending

		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	0	1	1	0	0	0	1	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	16
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	24
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	1	3	0	0	
	6+	0	0	0	0	0	0	0	5
Aphididae	2-4	0	0	0	0	0	2	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	3
Delphacidae	2-4	1	0	0	0	0	0	0	
	4-6	0	0	2	0	2	0	0	
	6+	2	0	0	0	0	0	0	14
Homoptera (other)	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	1	
	6+	0	0	2	0	0	1	0	4
Trichoptera	2-4	0	0	0	10	1	0	0	
	4-6	1	9	0	14	0	0	5	
	6+	29	3	27	44	10	6	0	502
Chironomidae	2-4	235	92	88	70	41	57	141	
	4-6	5	3	3	3	1	3	3	
	6+	8	5	2	8	4	3	9	2993
Nematocera (other)	2-4	187	48	74	48	28	17	12	
	4-6	2	0	2	0	0	1	4	
	6+	7	7	1	6	1	1	4	824
Brachycera/ Cyclorrhapha	2-4	13	59	117	119	74	87	73	
	4-6	20	18	64	45	26	50	89	
	6+	5	7	15	5	11	19	33	1984
Hymenoptera	2-4	6	4	7	10	8	7	2	
	4-6	0	0	0	1	1	0	1	
	6+	0	1	4	1	1	2	0	75
Coleoptera	2-4	2	3	7	4	3	3	1	
	4-6	0	0	1	0	2	0	0	
	6+	0	1	2	3	0	0	0	141
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	1	1	0	0	0	0	
	6+	0	0	1	0	1	0	0	15
Miscellaneous	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	2	2	4	1	0	2	0	25
Totals		525	264	425	393	218	261	379	6625

Table 3.9 *(Ctd.)*.

		Week ending								
		May				June				
	Size (mm)	4	11	18	25	1	8	15	22	29
Araneae	2-4	4	3	3	4	2	7	8	10	6
	4-6	0	0	0	1	1	4	1	2	3
	6+	0	0	0	2	1	2	1	2	6
Odonata	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	1	1	1	1	0	0
Heteroptera	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Aphididae	2-4	0	0	0	0	0	2	1	5	1
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Delphacidae	2-4	0	0	0	0	0	1	4	16	13
	4-6	0	0	0	0	0	0	0	2	0
	6+	0	0	0	0	0	0	0	0	4
Homoptera (other)	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Trichoptera	2-4	0	6	11	8	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	0	0	0	0	0
Chironomidae	2-4	10	3	7	3	4	4	5	2	2
	4-6	2	2	1	0	1	0	0	1	1
	6+	5	6	0	0	0	0	0	0	1
Nematocera (other)	2-4	6	13	5	4	2	2	3	0	1
	4-6	7	2	2	0	3	0	1	4	1
	6+	5	1	3	1	3	1	1	0	1
Brachycera/ Cyclorrhapha	2-4	19	10	1	2	4	4	4	11	20
	4-6	2	3	3	1	1	11	20	31	50
	6+	5	6	5	4	5	7	22	88	165
Hymenoptera	2-4	3	1	5	0	1	0	3	1	2
	4-5	2	1	0	0	0	1	0	2	6
	6+	0	1	0	3	2	7	4	3	6
Coleoptera	2-4	0	1	1	1	3	3	1	3	1
	4-6	1	0	0	3	2	1	0	0	1
	6+	0	1	1	0	2	0	3	2	1
Larvae	2-4	0	0	0	0	0	0	0	0	0
	4-6	0	0	0	0	0	0	0	0	0
	6+	0	0	0	0	1	1	0	1	1
Miscellaneous	2-4	0	0	2	0	2	5	0	0	0
	4-6	1	0	0	1	0	0	0	3	1
	6+	0	0	0	0	0	2	0	1	5
Totals		72	60	50	39	41	66	83	190	299

Table 3.10 Seasonal variation of numbers of invertebrates collected from water traps at site B.

(Ctd.)

		Week ending							
		July				Aug			
	Size (mm)	6	13	20	27	3	10	17	Totals
Araneae	2-4	6	7	7	3	6	0	4	
	4-6	1	2	0	1	1	3	1	
	6+	4	0	0	0	1	1	1	122
Odonata	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	4
Heteroptera	2-4	0	0	0	0	0	0	0	
	4-6	1	0	0	0	0	0	0	
	6+	1	0	0	2	1	0	0	5
Aphididae	2-4	0	0	2	0	1	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	12
Delphacidae	2-4	7	6	3	2	1	3	0	
	4-6	1	1	0	11	4	0	0	
	6+	0	0	0	0	0	0	0	79
Homoptera (other)	2-4	0	0	0	0	0	0	2	
	4-6	0	0	0	0	0	6	6	
	6+	0	16	10	9	14	7	3	73
Trichoptera	2-4	0	0	1	0	1	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	0	0	0	0	0	27
Chironomidae	2-4	2	4	0	3	1	0	1	
	4-6	1	0	2	0	1	0	1	
	6+	0	0	0	0	0	0	0	76
Nematocera (other)	2-4	26	35	3	5	0	3	4	
	4-6	1	1	1	1	0	0	1	
	6+	2	0	1	3	1	2	1	163
Brachycera/ Cyclorrhapha	2-4	31	9	17	38	28	24	3	
	4-6	7	7	15	20	21	12	9	
	6+	201	174	89	77	25	29	21	1361
Hymenoptera	2-4	1	4	2	0	12	10	9	
	4-6	1	3	4	1	1	2	2	
	6+	2	6	4	6	4	6	8	142
Coleoptera	2-4	1	1	5	2	2	5	2	
	4-6	1	1	0	1	0	2	0	
	6+	1	3	0	2	2	3	0	66
Larvae	2-4	0	0	0	0	0	0	0	
	4-6	0	0	0	0	0	0	0	
	6+	0	0	1	0	0	0	0	5
Miscellaneous	2-4	2	2	0	4	1	3	0	
	4-6	0	0	0	0	0	1	3	
	6+	4	7	2	7	0	1	3	63
Totals		305	289	169	198	129	123	85	2198

Table 3.10 *(Ctd.)*.

Week ending	Araneae	Odonata	Heteroptera	Aphid	Delphacidae	Other Homopterans	Trichoptera	Chironomidae	Other Nematocerans	Brachycera/ Cyclorrhapha	Hymenoptera	Coleoptera	Larvae	Miscellaneous
May 4	10	0	0	0	0	0	0	5454	386	83	0	5	3	0
11	18	0	0	0	1	1	2	4711	405	84	3	71	2	0
18	13	0	0	0	0	0	5	2434	329	198	0	51	6	2
25	26	3	1	0	5	0	8	1115	131	139	14	139	4	2
June 1	17	11	0	0	11	0	10	730	99	226	9	200	2	0
8	25	2	0	1	60	0	8	879	167	1352	29	131	5	2
15	29	1	0	0	60	0	3	980	186	1763	35	38	3	0
22	32	2	0	0	32	0	7	670	159	2007	21	44	1	3
29	18	0	0	1	21	0	11	983	177	1278	12	21	1	1
July 6	28	0	0	0	7	0	8	632	139	2040	4	33	0	4
13	16	0	0	3	5	0	0	421	81	1273	20	27	1	1
20	18	0	1	3	5	0	2	185	216	2734	23	53	1	0
27	14	0	0	1	2	0	7	499	383	1939	66	60	0	4
Aug 3	14	0	0	1	3	0	2	134	144	931	92	31	1	5
10	25	0	1	0	1	0	14	173	217	881	191	13	0	8
17	11	0	0	0	0	0	16	383	195	1116	169	37	2	18
Totals	314	19	3	10	213	1	103	20383	3414	18044	688	954	32	50

Table 3.11 Seasonal variation of numbers of invertebrates obtained from water traps in habitat PM (3 sites)

Week ending	Araneae	Odonata	Heteroptera	Aphid	Delphacidae	Other Homopterans	Trichoptera	Chironomidae	Other Nematocerans	Brachycera/ Cyclorrhapha	Hymenoptera	Coleoptera	Larvae	Miscellaneous
May 4	6	0	0	0	0	0	3	10169	199	101	0	7	0	1
11	36	0	0	0	0	0	22	4912	312	119	2	34	4	0
18	22	0	0	0	0	0	10	2007	253	153	5	51	3	0
25	33	9	0	0	2	0	9	1753	153	87	14	110	5	0
June 1	16	33	0	0	9	0	7	709	143	163	31	156	1	0
8	21	37	0	0	17	0	51	768	119	1383	32	106	8	0
15	23	41	0	0	24	0	43	1294	170	5652	26	48	8	1
22	21	55	0	1	13	0	51	1293	171	5417	26	70	4	1
29	23	23	0	1	5	0	3	756	139	7645	26	40	6	2
July 6	15	3	0	1	3	0	15	687	285	8717	19	51	17	2
13	32	0	0	4	1	0	2	371	111	5060	24	64	16	0
20	14	0	0	1	3	0	6	240	157	3147	33	96	8	1
27	14	0	0	0	4	0	13	224	229	3513	64	147	16	3
Aug 3	28	0	0	0	2	2	8	79	99	1389	96	52	3	1
10	17	0	0	0	1	0	6	105	112	1090	133	70	2	8
17	25	0	0	1	0	0	5	181	82	725	97	71	1	18
Totals	346	201	0	9	84	2	254	25548	2734	44361	628	1173	102	37

Table 3.12 Seasonal variation of numbers of invertebrates obtained from water traps in habitat MM (3 sites).

Week ending	Araneae	Odonata	Heteroptera	Aphid	Delphacidae	Other Homopterans	Trichoptera	Chironomidae	Other Nematocerans	Brachycera/ Cyclorrhapha	Hymenoptera	Coleoptera	Larvae	Miscellaneous
May 4	3	0	0	0	0	0	0	68	75	7	0	4	1	0
11	24	0	1	0	0	0	1	96	76	12	0	27	0	0
18	12	0	0	0	0	0	3	86	133	33	0	8	1	0
25	7	1	0	0	0	0	4	133	121	35	3	21	0	0
June 1	8	1	0	0	0	0	3	124	221	50	3	45	0	0
8	9	1	0	2	0	0	4	52	155	45	8	26	0	0
15	7	16	0	0	2	0	4	34	71	85	8	4	4	0
22	9	4	0	0	1	0	4	74	61	218	11	21	2	0
29	4	1	0	0	1	0	1	38	43	494	6	7	3	0
July 6	11	1	0	0	1	0	4	35	53	420	6	13	2	0
13	9	0	0	2	3	0	3	36	30	242	11	28	0	1
20	1	0	0	0	0	1	1	39	75	209	3	48	0	0
27	3	0	0	2	0	1	4	26	76	245	18	34	0	0
Aug 3	3	0	0	0	3	0	2	12	71	162	23	15	0	0
10	4	0	0	0	2	0	3	26	22	194	46	13	0	0
17	3	0	0	0	0	0	4	32	40	329	40	33	1	6
Totals	117	25	1	6	13	2	45	911	1323	2780	186	347	14	7

Table 3.13 Seasonal variation of numbers of invertebrates obtained from water traps in habitat IM (1 site).

Week ending	Araneae	Odonata	Heteroptera	Aphid	Delphacidae	Other Homopterans	Trichoptera	Chironomidae	Other Nematocerans	Brachycera/ Cyclorrhapha	Hymenoptera	Coleoptera	Larvae	Miscellaneous
May 4	5	0	0	0	0	0	6	749	129	174	3	4	0	2
11	6	0	0	0	0	0	7	627	101	418	1	24	0	1
18	6	0	1	0	0	0	28	550	76	196	3	33	3	1
25	6	0	0	0	0	0	15	1310	182	132	5	52	2	4
June 1	5	6	0	0	1	0	7	672	167	156	1	50	2	1
8	6	9	0	1	0	0	81	489	154	100	6	29	5	2
15	3	9	0	1	1	0	46	321	191	73	8	9	4	1
22	3	0	0	1	7	0	117	159	83	151	5	17	1	5
29	0	0	1	0	9	0	56	257	110	112	12	10	2	2
July 6	8	0	0	0	5	0	31	298	305	86	6	6	0	4
13	5	0	0	0	1	0	15	170	159	142	12	13	1	2
20	1	0	0	3	4	2	31	123	206	319	18	25	3	5
27	1	0	1	0	0	0	71	111	123	255	19	11	0	2
Aug 3	2	0	3	0	2	0	14	85	88	244	20	12	1	2
10	1	0	0	2	0	1	7	122	82	325	21	8	0	3
17	1	0	0	0	2	1	5	231	53	310	8	3	3	2
Totals	59	24	6	8	32	4	537	6274	2209	3193	148	306	27	39

Table 3.14 Seasonal variation of numbers of invertebrates obtained from water traps in habitat W/A (2 sites).

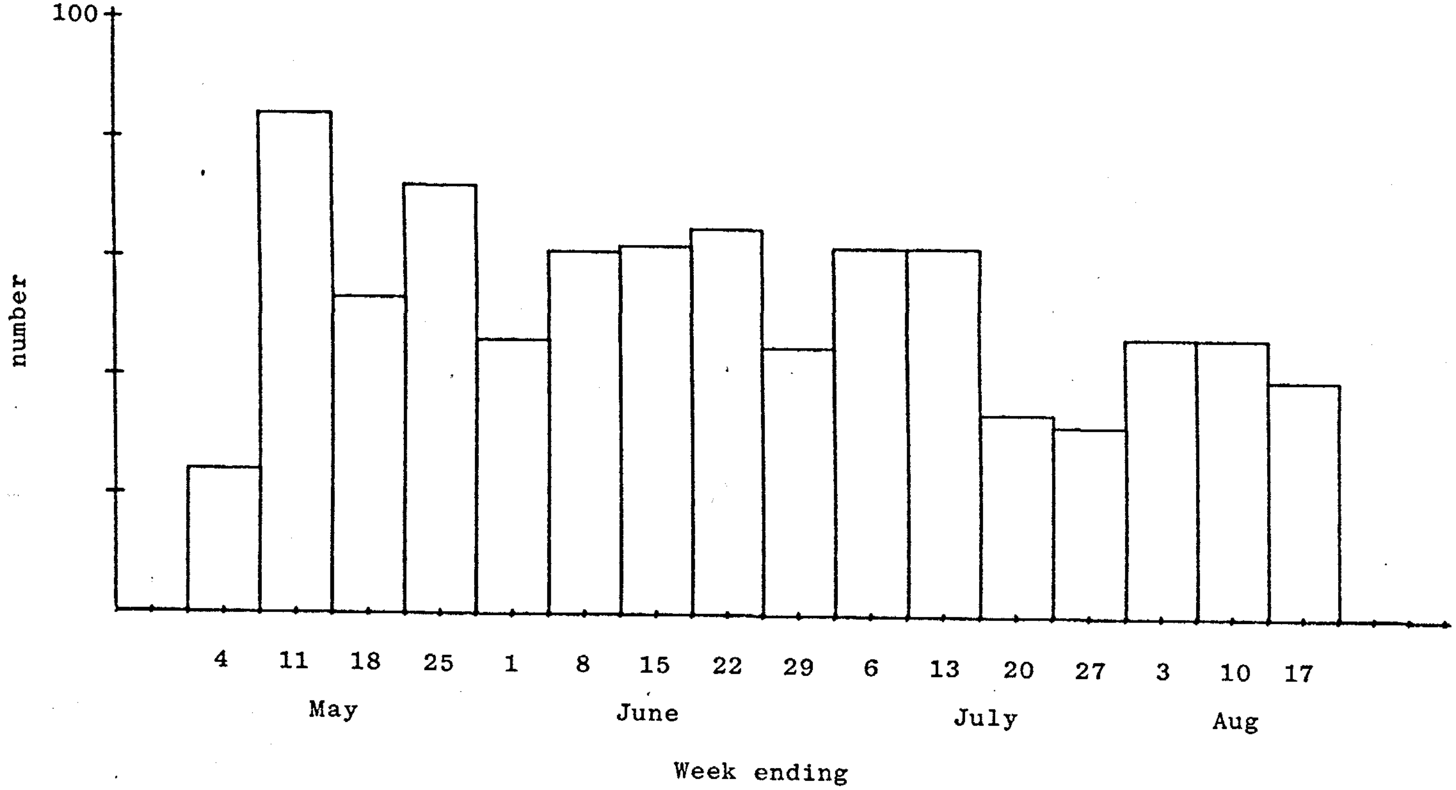

Fig.3·2. Seasonal variation of numbers of Spiders obtained from water traps (site B excluded).

species Pyrrhosoma nymphula (Sulzer), Coenagrion puella (L) and Ischnura elegans (van der Linden). Fig. 3.3 shows them to have a marked season, being caught only during weeks 4 to 10. Most were caught in MM with 4•2/site/wk and relatively few elsewhere viz 0•4/site/wk PM, 1•6/site/wk IM and 0•8/site/wk W/A.

A Kendall Coefficient of Concordance Test for weeks 4 to 10 gives $W = 0{\cdot}57$ and a significant ranking MM > IM > PM > W/A ($p < 0{\cdot}01$). Between IM, PM and W/A, $W = 0{\cdot}19$ with no significant association, indicating that MM holds more damsel flies than any of the other habitats.

3.3 Heteroptera

Only ten caught.

3.4 Homoptera - Aphididae

Only thirty three caught.

3.5 Homoptera - Delphacidae

Fairly common in both PM and MM, and, as Fig. 3.4 shows, markedly seasonal. Most were in PM with 4•4/site/wk and 1•8/site/wk in MM, 1•0/site/wk in W/A and 0•8/site/wk in IM. Only 4 individuals were > 6 mm with 169 (49•4%) 4 - 6 mm and the same number, 169, between 2 and 4mm.

A Kendall Coefficient of Concordance Test between the four habitats gives $W = 0{\cdot}22$ and a ranking PM > MM > W/A > IM significant with $p < 0{\cdot}02$. Again no significant association was found between the three lower ranked habitats ($W = 0{\cdot}05$), indicating that significantly more Delphacids were to be found in PM.

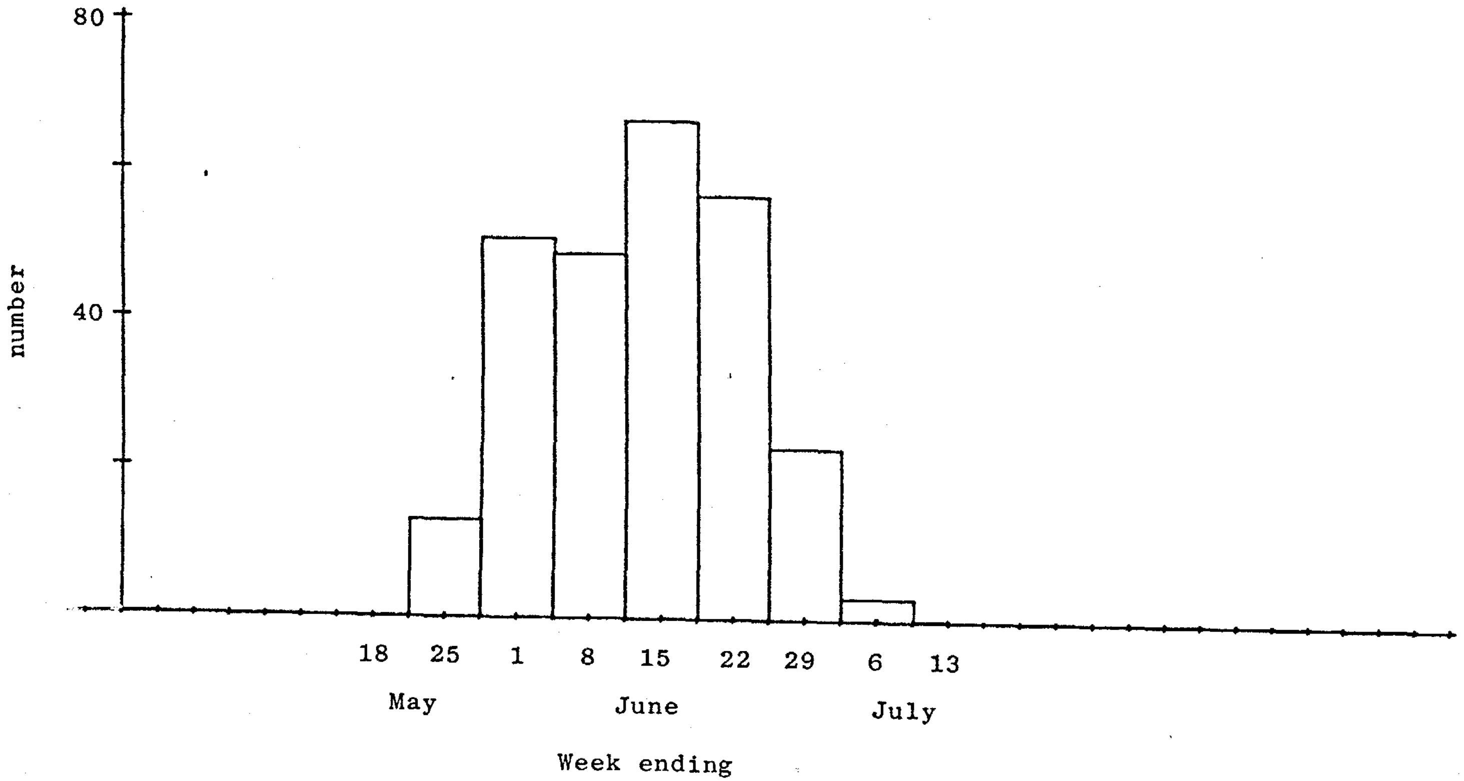

Fig.3·3 Seasonal variation of numbers of Odonata obtained from water traps (site B excluded).

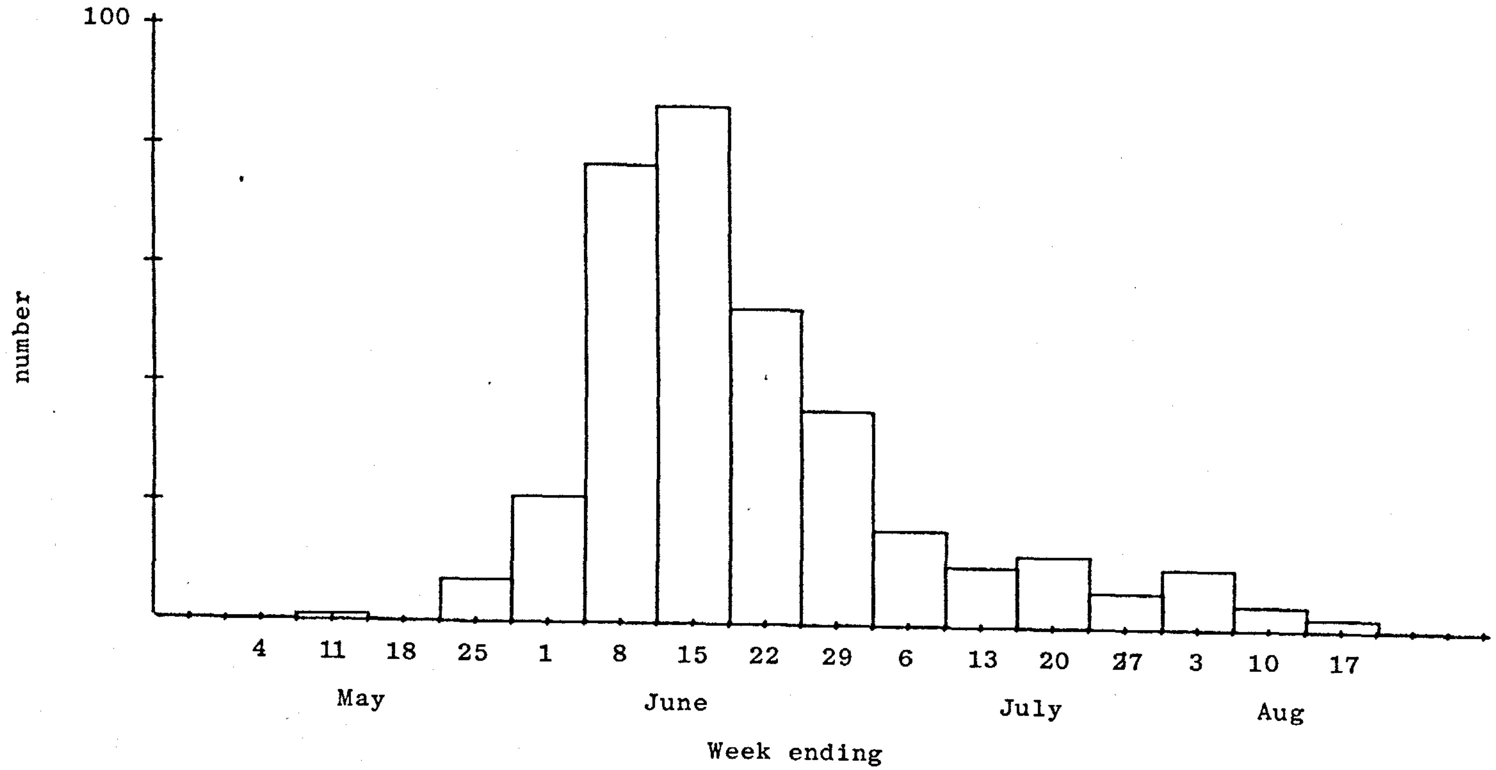

Fig.3·4 Seasonal variation of numbers of Delphacidae obtained from water traps (site B excluded).

3.6 Other Homoptera

Rarely found; (9 individuals caught).

3.7 Trichoptera

Particularly common in the W/A traps with 16·8/site/wk. Less common elsewhere with 5·3/site/wk in MM, 2·8/site/wk in IM and 2·2/site/wk in PM. Fig. 3.5 suggests that they were most common during weeks 6, 7 and 8 with another peak during week 13. This later peak was due almost entirely to individuals caught in the W/A traps. Of the 939 caught, 490 (52.2%) were of the large > 6 mm form and only 89 (9·5%) were between 2 and 4 mm.

A Kendall Coefficient of Concordance Test between the four habitats gives $W = 0 \cdot 48$ and a significant ranking W/A > MM > IM > PM ($p < 0 \cdot 01$). Excluding the Willow/Alder carr produces a $W = 0 \cdot 19$ and a significant ranking MM > IM > PM ($p < 0 \cdot 05$).

3.8 Diptera - Chironomidae

Abundant in the MM and PM traps and very common elsewhere. By far the commonest category of insect identified. The huge numbers caught at all sites were largely made up of the smaller 2 - 4 mm forms (93·0%). Even so, the numbers of individuals of the larger forms were high in comparison with other taxa.

Numbers caught were divided between habitats viz: 532·3/site/wk MM, 424·7/site/wk PM, 196·1/site/wk W/A and 56·9 IM. Excluding the 2 - 4 mm size, these figures become 38·7 MM, 26·0 W/A, 19·8 PM and 5·8 IM.

Fig. 3.6 shows that Chironomids were most common in the early part of the season, after which numbers rapidly decreased until about week 6, and then remained fairly steady throughout the rest of the period. The

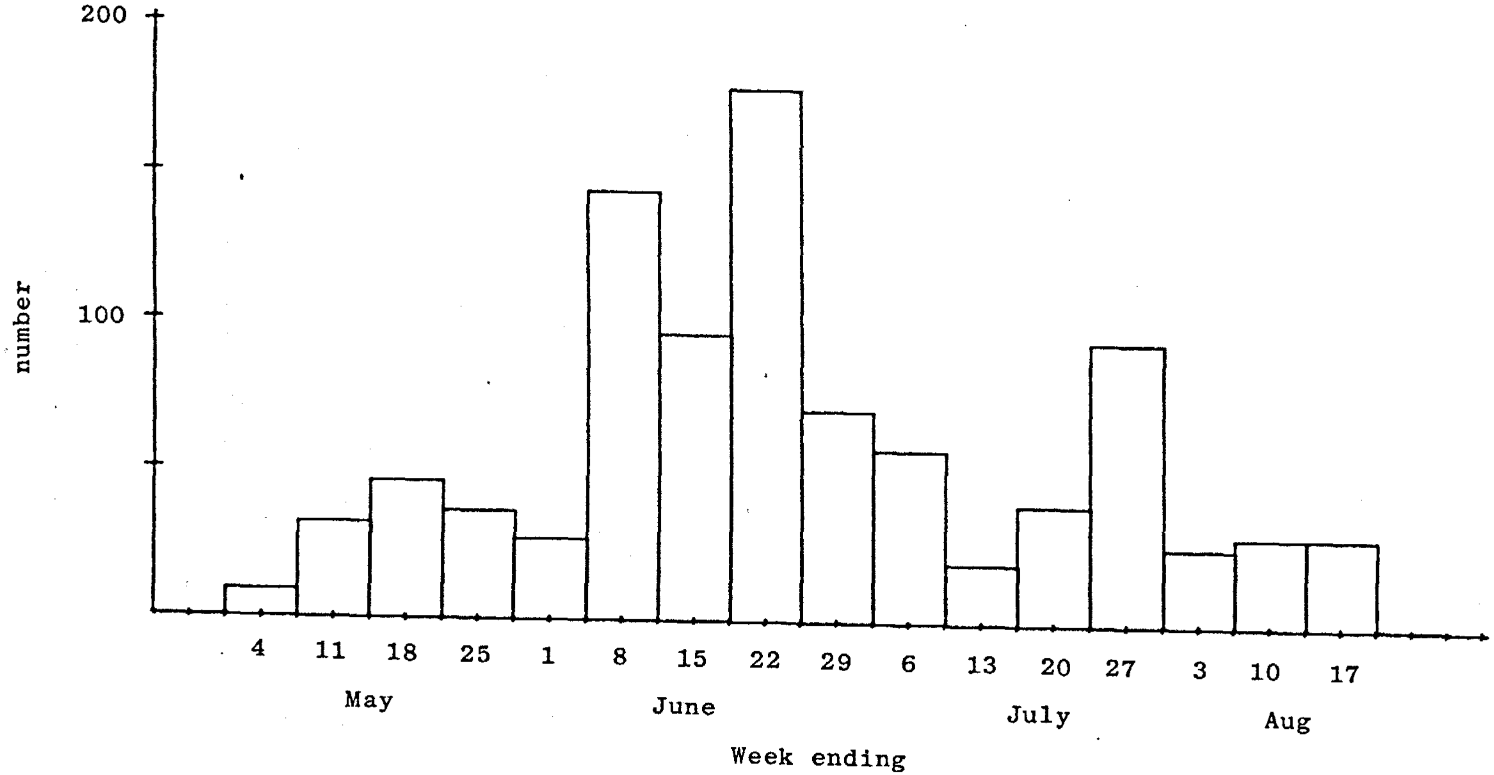

Fig.3·5 Seasonal variation of numbers of Trichoptera obtained from water traps (site B excluded).

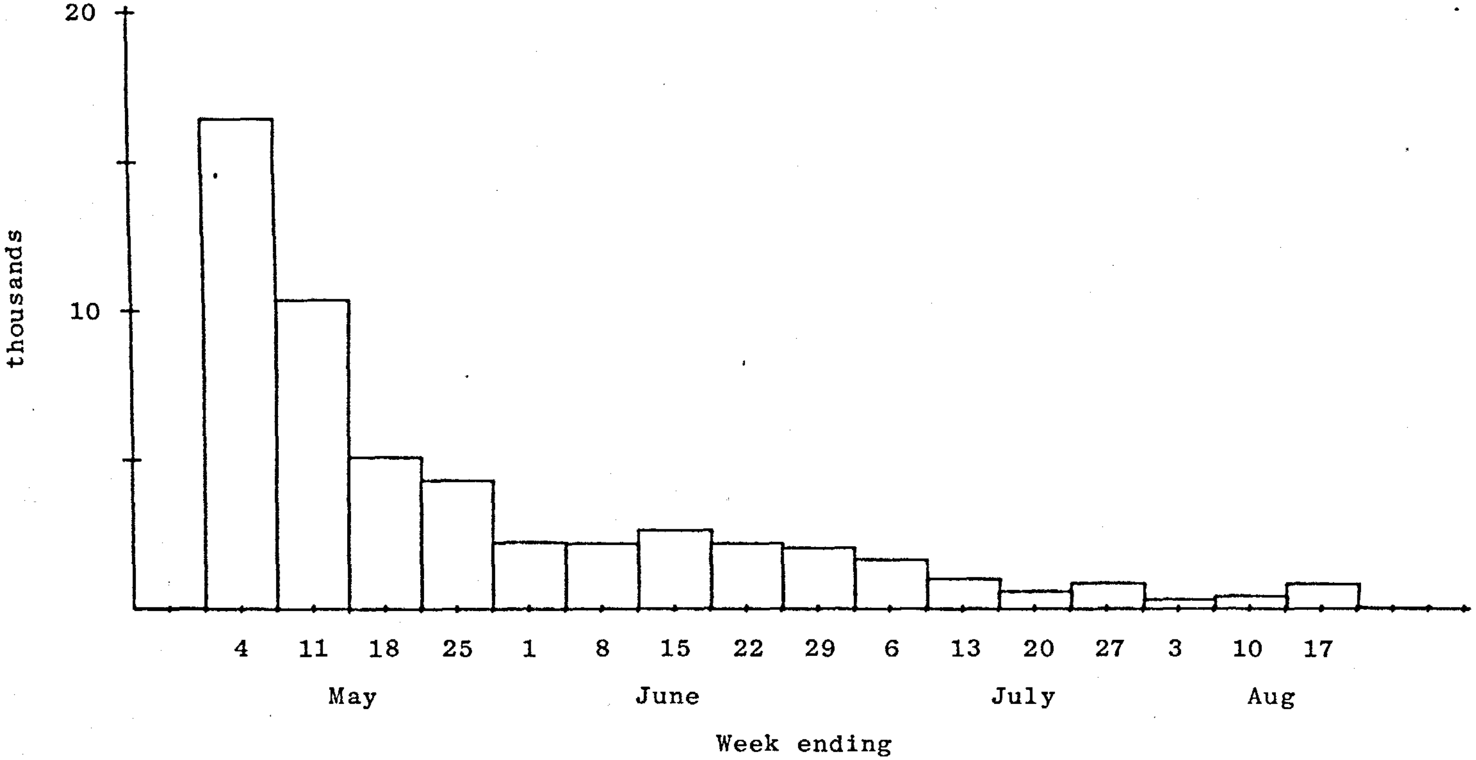

Fig.3·6 Seasonal variation of numbers of Chironomids obtained from water traps (site B excluded).

populations of both the small and the larger forms behaved similarly.

A Kendall Coefficient of Concordance Test between the four habitats gives $W = 0{\cdot}68$ and a significant ranking PM > MM > W/A > IM ($p < 0{\cdot}01$). Excluding the obviously poorer IM and repeating the test gives a $W = 0{\cdot}2$ and a significant ranking PM > MM > W/A ($p < 0{\cdot}05$).

Taking only the two larger size classes and repeating the test gives $W = 0{\cdot}69$ and a significant ranking MM > W/A > PM > IM ($p < 0{\cdot}01$). Finally, if we again exclude IM, $W = 0{\cdot}43$, the ranking MM > W/A > PM is significant ($p < 0{\cdot}01$).

3.9 Diptera - Other Nematocera

Fewer trapped than Chironomids but nevertheless very common, the most commonly represented families being Psychodidae, Tipulidae, Anisopodidae and Culicidae. Little variation between sites viz 82•7/site/wk IM, 71•1/site/wk PM, 69•0/site/wk W/A and 57•0/site/wk MM. Again relatively large numbers of the smaller 2 - 4 mm form were caught (67•3%) with the remainder having a similar distribution to Chironomids of the same size (23•5% 4 - 6 mm, 9•2% 6 + mm).

Fig. 3.7 shows that the numbers in the traps remained fairly constant throughout the period, although the larger 6 + mm form had a definite peak around weeks 6, 7 and 8.

A Kendall Coefficient of Concordance Test for the four habitats gives $W = 0{\cdot}07$ and no significant ranking. Applying the test to the 6 + mm forms gives $W = 0{\cdot}25$ and a significant ranking IM > MM > W/A > PM ($p < 0{\cdot}01$).

3.10 Diptera - Brachycera/Cyclorrhapha

Abundant, particularly so in the MM and PM traps. Most individuals (82•7%) were size 4 - 6 mm and were represented to a large extent by

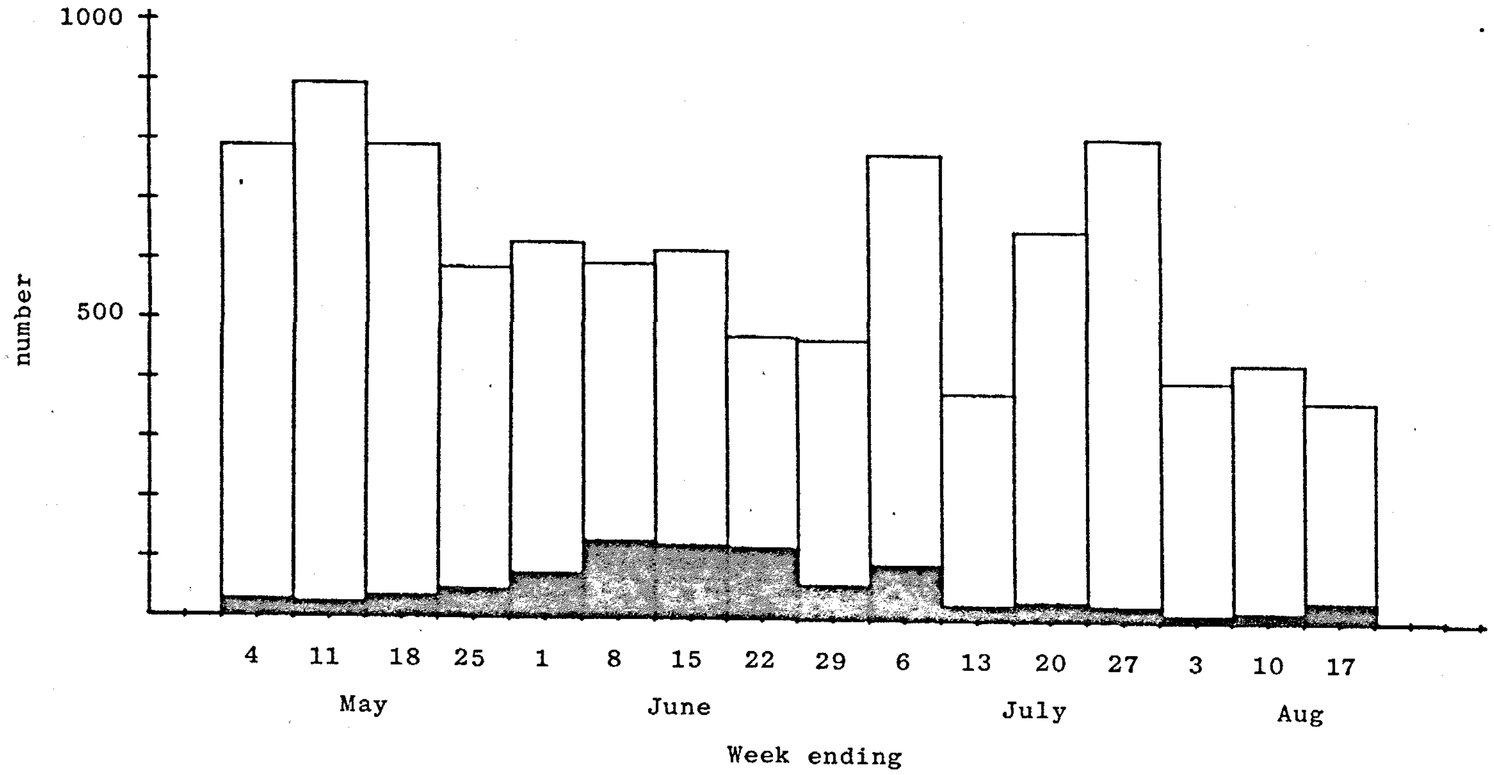

Fig. 3·7 Seasonal variation of numbers of other Nematocerans obtained from water traps (site B excluded). Shaded, 6+ mm form.

Empididae and Dolichopodidae. The breakdown of numbers by habitat is 924·2/site/wk MM, 375·9/site/wk PM, 173·8/site/wk IM and 66·5/site/wk W/A. A marked seasonal peak around weeks 9 and 10 is clear from Fig. 3.8 which indicates that, unlike Nematocera, they were relatively uncommon in the early part of the season.

A Kendall Coefficient of Concordance Test gives a $W = 0.31$ and a significant ranking MM > PM > W/A > IM ($p < 0.01$). Excluding the superior MM and repeating the test gives $W = 0.24$ and a significant ranking PM > IM > W/A ($p < 0.05$).

3.11 Hymenoptera

Fairly common in the three marshland habitats, uncommon in W/A, with 14·3/site/wk in PM, 13·1/site/wk in MM, 11·6/site/wk in IM and 4·6/site/wk in W/A. Overall, 83·1% were small 2 - 4 mm form. Fig. 3.9 shows that numbers of Hymenoptera built up steadily throughout the season reaching a maximum towards the end of the period.

A Kendall Coefficient of Concordance Test between the four habitats gives $W = 0.29$ and a significant ranking MM > PM > IM > W/A ($p < 0.01$). Omitting the poorer W/A gives $W = 0.13$ and no significant ranking.

3.12 Coleoptera

Fairly common in the marshland habitats, relatively uncommon in W/A. Numbers found in the traps were 24·4/site/wk in MM, 21·7/site/wk in IM, 19·9/site/wk in PM and 9·6/site/wk in W/A. The majority (60·7%) were the 2 - 4 mm form, the remainder being evenly divided viz 4 - 6 mm 19·1%, 6 + mm 20·2%. Overall, numbers tended to fluctuate during the period (Fig. 3.10) with no obvious seasonal trends.

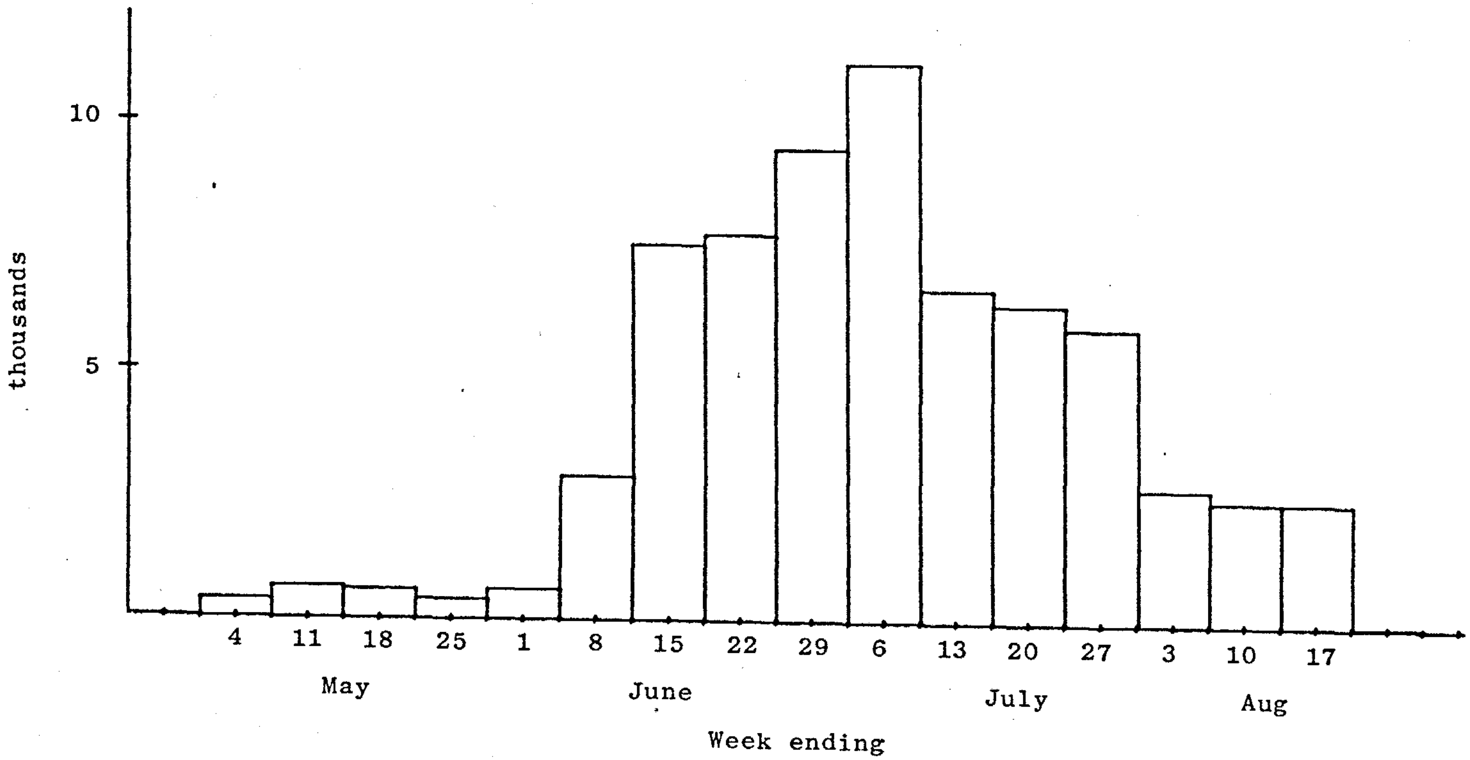

Fig.3·8 Seasonal variation of numbers of Brachycera/Cyclorrhaphans obtained from water traps (site B excluded).

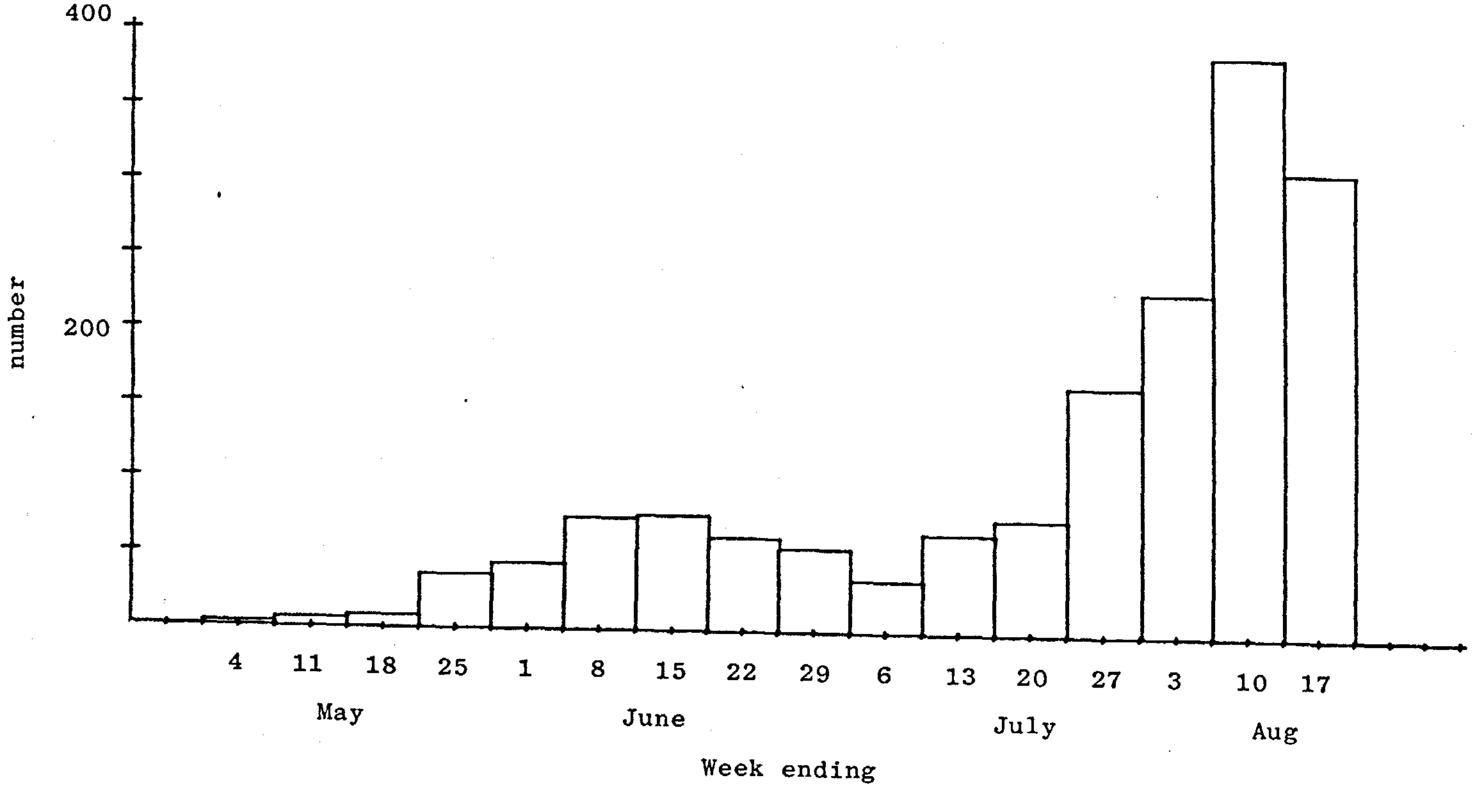

Fig.3·9 Seasonal variation of numbers of Hymenoptera obtained from water traps (site B excluded).

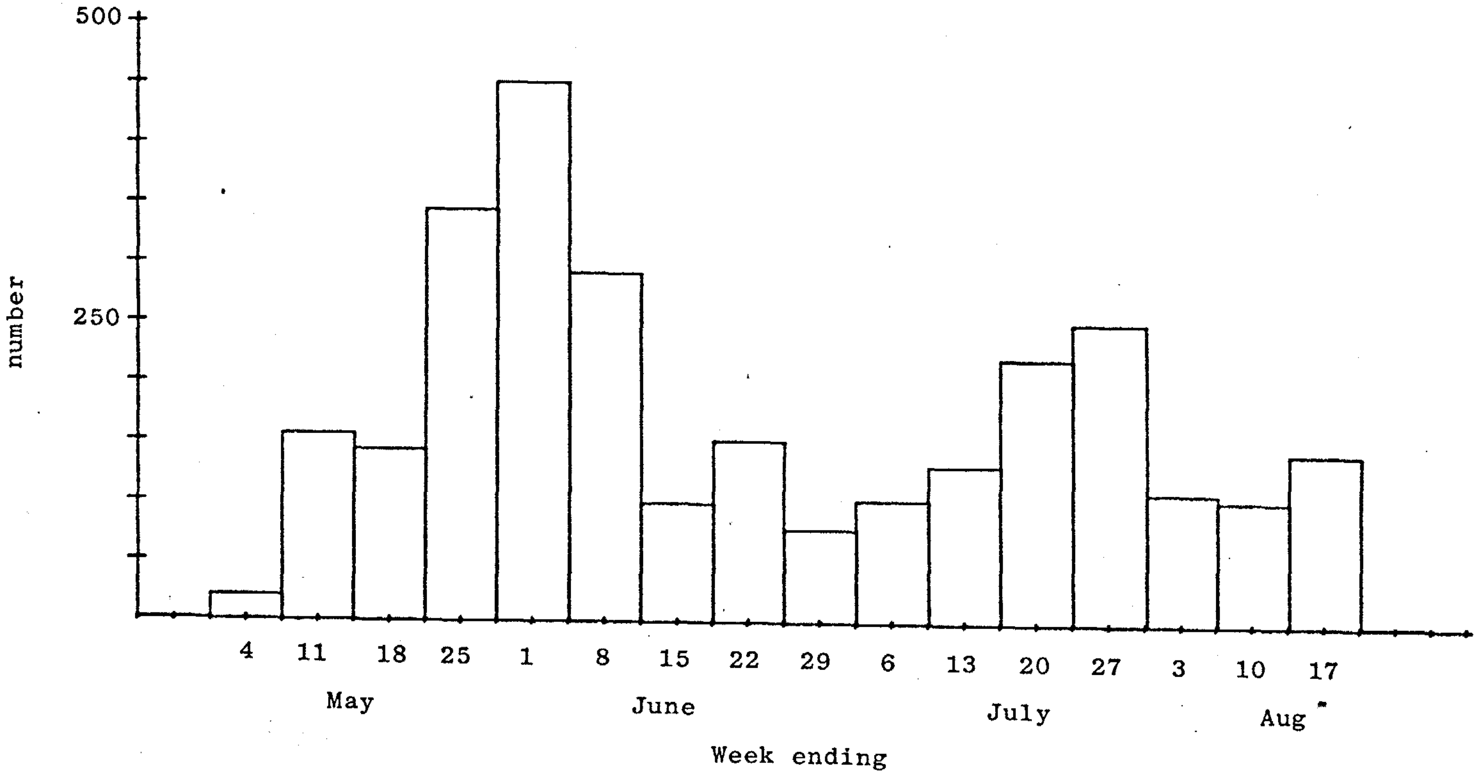

Fig.3·10 Seasonal variation of numbers of Coleoptera obtained from water traps (site B excluded).

A Kendall Coefficient of Concordance Test between habitats gives $W = 0{\cdot}44$ and a significant ranking $MM > IM > PM > W/A$ ($p < 0{\cdot}01$). Excluding W/A and repeating the test one obtains $W = 0{\cdot}15$ and no significant ranking, indicating that more beetles are to be found in the marsh habitats.

3.13 Larvae

The water traps almost certainly sampled larvae very poorly. Indeed, only 175 were caught during the sixteen weeks giving too few data for any reliable analysis. No convincing seasonal trends can be seen from Fig. 3.11, but most were caught in MM with 2·1/site/wk, 0·9/site/wk in IM, 0·8/site/wk in W/A and 0·7/site/wk in PM.

3.14 Other invertebrates

The only other invertebrates found in the water traps in any numbers were 91 moths and 15 mayflies. Most of the moths (58) were found in the last two weeks and so had a negligible effect on the study as regards potential food items. Other occasionals included Gastropods, Isopods, Millipedes, Scorpion flies, Lacewings and Collembola.

3.15 Diversity

In many situations, a measure of community structure in terms of a diversity index, identifies trends which might otherwise go undetected. It is usual to use 'species' as the unit of structure, but with the water trap samples, the best we can do is to use the subdivisions in Table 3.1 to 3.14. A variety of indices can be chosen (see e.g. Pielou 1977) but all tend to give the same basic information. The one used here is

$$S = \alpha \log \left(1 + \frac{N}{\alpha}\right),$$

where S is the number of 'forms', N is the number of individuals and α the index of diversity (see e.g. Lewis and Taylor 1967).

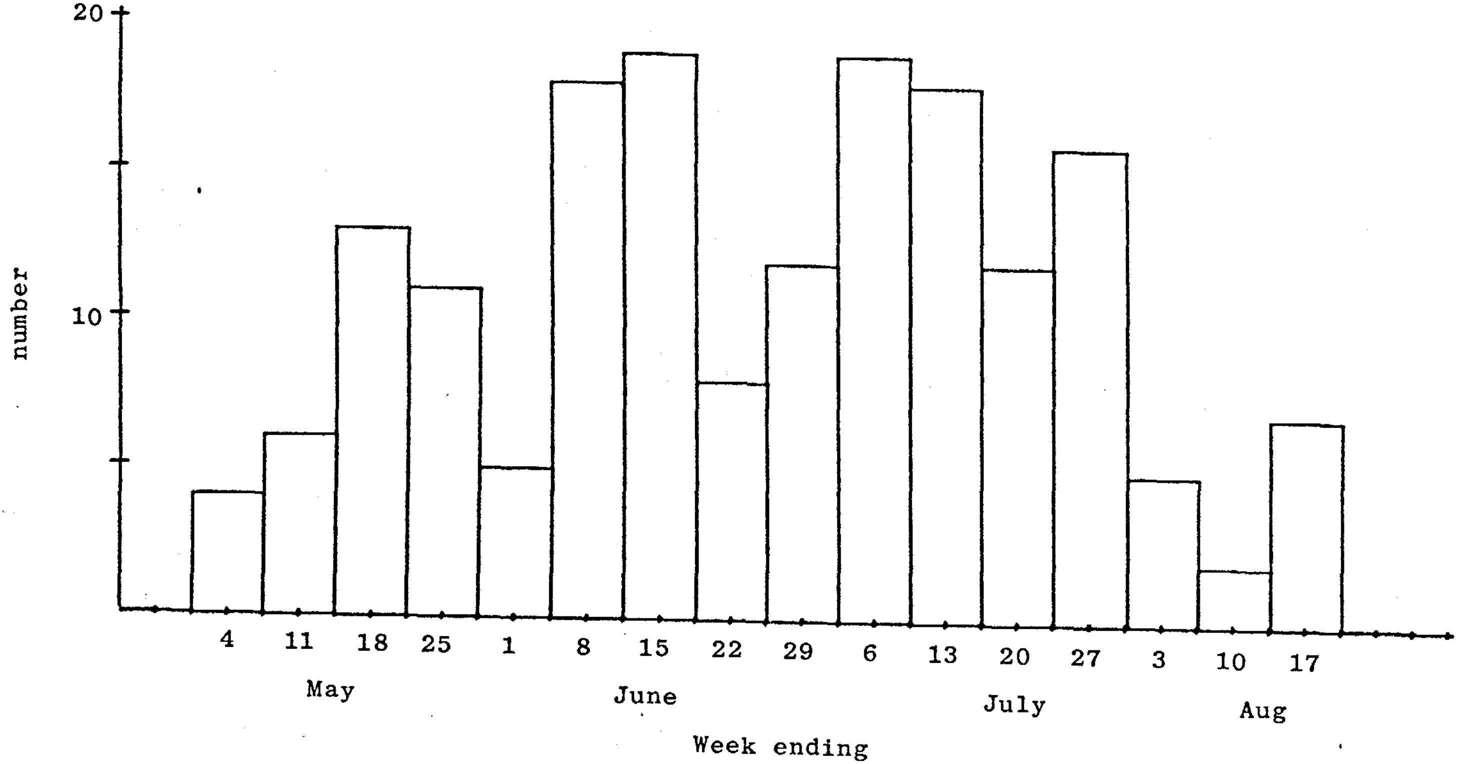

Fig. 3·11 Seasonal variation of numbers of Larvae obtained from water traps (site B excluded).

Table 3.15 lists α by week for each of the nine sites and Table 3.16 for each habitat. Little seasonal or between site/habitat variation of α is apparent. A precise interpretation as the the meaning of these results is difficult; not only is the subdivision of taxa rather crude, but the numbers of Diptera are relatively large. The net effect is to produce α values with little variation. In the case of IM and W/A, α values are somewhat higher, which is probably a reflection of the smaller Diptera numbers.

3.16 Invertebrate biomass

The preceeding analysis of the invertebrate fauna rests entirely on the numbers and size classes of the taxa found in the water traps. Another, albeit rough, measure of relative abundance is the biomass (dry weight) of invertebrates caught. Although dry weight is probably unsatisfactory as an absolute measure, taken en masse, it does provide a check on the relative abundance of potential prey items both seasonally and between habitats. Tables 3.17 and 3.18 list the total dry weights of all invertebrates caught by site and habitat and Fig. 3.12 shows the overall seasonal distribution. The results are comparable with those already obtained.

3.17 Conclusions

Fig. 3.13 shows the overall seasonal variation of numbers of invertebrates caught at all nine sites. Clearly the number of Diptera accounts for a very high proportion of all those present and in fact there is little variation in the totals of all other taxa. The relatively large numbers in the first two weeks are due almost entirely to the abundance of small 2 - 4 mm Chironomids. Thereafter, Nematoceran numbers decrease whilst

Week ending	GLE	TE	TW	GLW	WE	WW	GL	NP	E
May 4	0·47	0·72	0·88	0·75	0·51	1·01	1·03	1·26	1·24
11	0·79	0·72	1·32	1·17	0·95	1·16	0·76	1·10	1·35
18	1·03	1·30	1·07	1·10	0·97	1·13	1·45	1·53	1·31
25	1·52	1·46	1·71	1·29	1·58	1·67	1·18	1·47	1·48
June 1	1·67	1·51	1·67	1·92	1·55	1·41	1·07	1·98	1·38
8	1·48	1·43	2·11	1·70	1·33	1·43	1·78	1·86	1·74
15	1·27	1·40	1·25	1·70	1·25	1·17	2·03	1·91	2·12
22	1·45	1·37	1·50	1·22	1·13	1·44	1·91	2·69	1·86
29	1·22	1·49	1·54	1·41	0·94	1·27	1·80	1·74	1·71
July 6	1·11	1·58	1·20	1·55	0·94	1·37	1·88	1·54	1·74
13	1·25	1·20	1·67	1·39	0·77	1·01	1·57	1·80	1·90
20	1·42	1·28	1·03	1·01	1·44	1·15	1·97	2·06	1·44
27	1·50	1·26	1·18	1·33	1·26	1·27	1·67	1·42	1·63
Aug 3	1·35	1·60	1·85	1·52	1·31	1·70	1·57	1·89	1·52
10	1·13	1·60	1·34	1·59	1·34	1·94	1·50	2·06	1·50
17	1·30	1·55	1·42	1·83	1·38	1·48	1·85	1·43	1·57

Table 3.15 Seasonal variation by site of Index of Diversity α (see text) of invertebrates obtained from water traps.

Week ending	PM	MM	IM	W/A
May 4	0·66	0·73	1·24	1·35
11	1·19	0·92	1·35	1·15
18	1·14	1·03	1·31	1·58
25	1·59	1·36	1·48	1·41
June 1	1·47	1·48	1·38	1·71
8	1·78	1·32	1·74	1·96
15	1·28	1·27	2·12	2·08
22	1·59	1·41	1·86	2·62
29	1·48	1·37	1·71	1·93
July 6	1·30	1·35	1·74	1·83
13	1·39	1·18	1·90	1·76
20	1·42	1·40	1·44	2·03
27	1·44	1·37	1·63	1·51
Aug 3	1·81	1·57	1·52	2·02
10	1·43	1·77	1·50	2·15
17	1·22	1·49	1·57	2·11

Table 3.16 Seasonal variation by habitat of Index of Diversity α (see text) of invertebrates obtained from water traps.

Week ending		GLE	TE	TW	GLW	WE	WW	GL	NP	E	B	Totals
May	4	272	349	136	78	740	212	91	225	56	35	2194
	11	248	309	93	104	467	126	139	434	117	37	2074
	18	175	270	190	127	289	150	106	244	125	58	1734
	25	215	194	115	125	235	240	312	264	174	49	1708
June	1	193	261	220	145	283	287	326	268	214	122	2319
	8	881	171	318	459	888	636	144	437	183	106	4223
	15	1129	403	314	767	3074	2291	125	218	295	164	8780
	22	1020	479	330	503	2379	2587	74	274	381	372	8399
	29	615	300	320	694	3440	2956	125	123	531	663	9767
July	6	1081	216	568	934	3864	3737	99	113	558	641	11811
	13	453	168	276	649	1243	2122	90	106	303	508	5918
	20	1232	450	645	824	1212	1071	177	331	501	375	6818
	27	765	217	467	796	1066	965	101	170	469	434	5450
Aug	3	309	216	214	338	379	404	173	106	278	231	2648
	10	260	122	286	247	349	448	148	169	316	234	2579
	17	350	301	397	472	332	319	151	253	459	206	3240

Table 3.17 Seasonal variation by site of invertebrate biomass (mg dry weight) obtained from water traps.

Week ending	PM (3 sites)	MM (3 sites)	W/A (2 sites)	IM (1 site)	B (1 site)
May 4	252	343	158	56	35
11	217	232	287	117	37
18	212	189	175	125	58
25	175	200	288	174	49
June 1	225	238	297	214	122
8	457	661	291	183	106
15	615	2044	172	295	164
22	604	1823	174	381	372
29	412	2363	124	531	663
July 6	622	2845	106	558	641
13	299	1338	98	303	508
20	776	1036	254	501	375
27	483	942	136	469	434
Aug 3	246	374	140	278	231
10	223	348	159	316	234
17	349	374	202	459	206

Table 3.18 Seasonal variation by habitat of mean invertebrate biomass per site (mg dry weight) obtained from water traps.

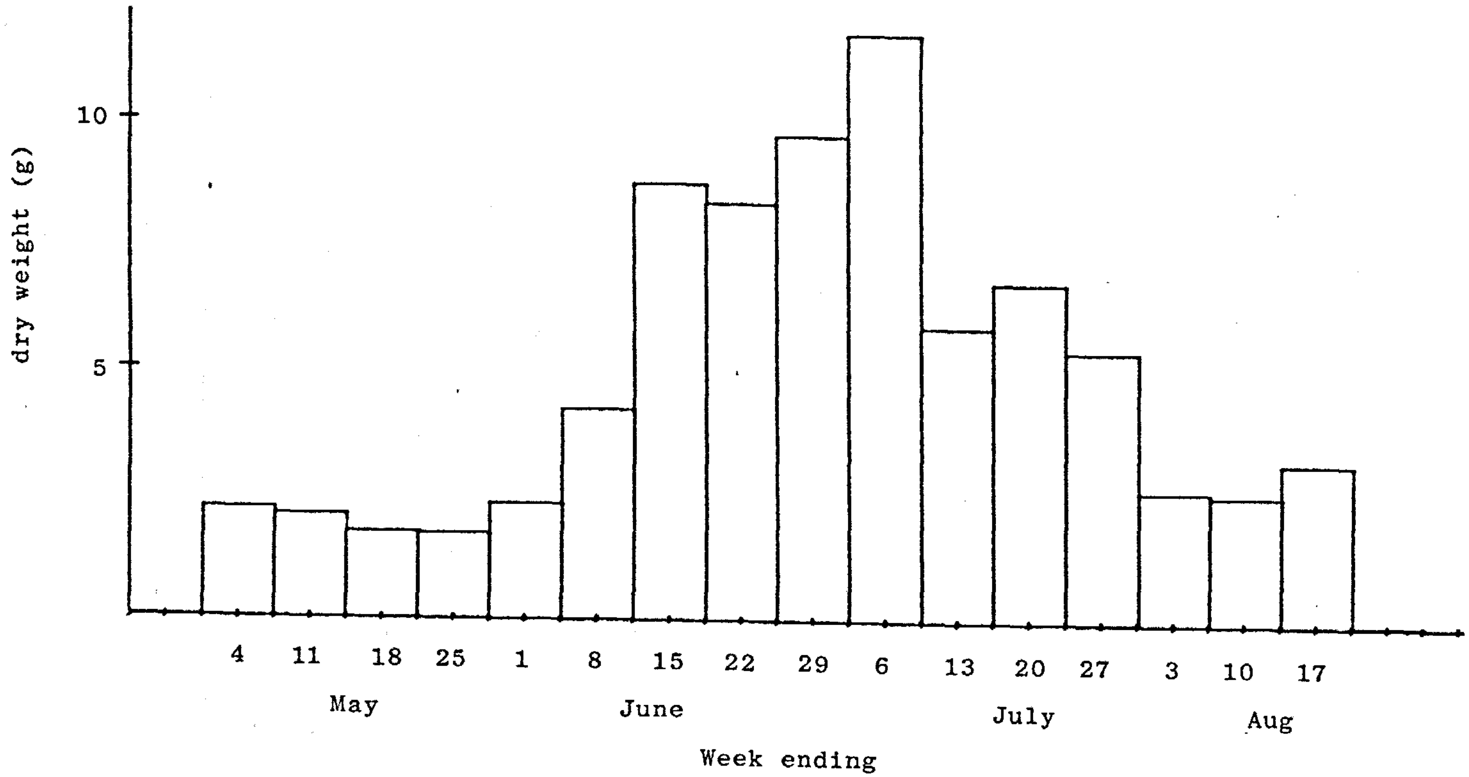

Fig.3·12 Seasonal variation of total biomass (gms dry weight) of all invertebrates obtained from water traps at all sites.

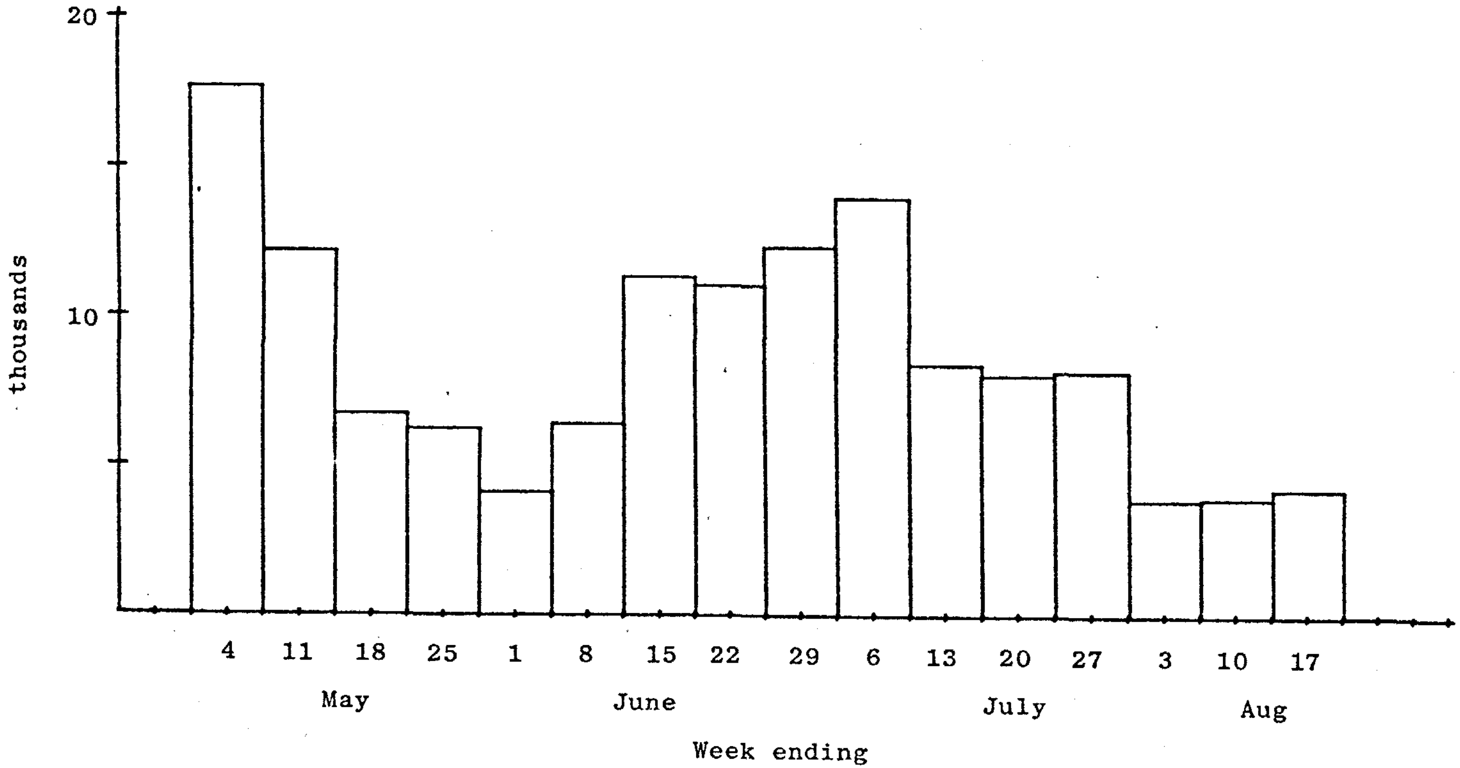

Fig.3·13 Seasonal variation of total numbers of all invertebrates obtained from water traps (site B excluded).

Cyclorrhapha/Brachycera increase. These too decrease from about week 10 but remain the commonest form until the end of the period.

The abundance of Chironomids in the first two weeks of May coincides with the period of maximum arrival at Oxwich of Reed Warblers and its significance will be discussed in Chapter 4. It is worthy of note at this stage, as is the second peak between mid-June and mid-July (together with the peak of Cyclorrohapha/Brachycera) since at these times, most Reed Warblers have young in the nest.

Overall between-site variation is given in Table 3.19. There is a marked contrast between PM and MM on the one hand, and IM and W/A on the other. The former habitats show distinct seasonal peaks (largely due to Diptera) whereas the latter appears to hold fairly constant numbers. A Kendall Coefficient of Concordance Test applied to Table 3.19 gives $W = 0{\cdot}51$ and a significant ranking $MM > PM > IM > W/A$ ($p < 0{\cdot}01$). The rank sums suggest however that both MM and PM are very much 'better' than the other two.

Week ending	PM	Rank	MM	Rank	IM	Rank	W/A	Rank	Mean
May 4	1980·3	2	3495·3	1	158	4	536	3	1961·9
11	1766	2	1813·7	1	237	4	592·5	3	1351·2
18	1012·7	1	834·7	2	276	4	448·5	3	746·1
25	528·3	3	725	2	325	4	854	1	643·7
June 1	438·3	3	422·7	4	455	2	534	1	456·2
8	877	1	847·3	2	302	4	441	3	709·7
15	1032·7	2	2443·3	1	235	4	333·5	3	1258·9
22	992·7	2	2374·3	1	405	3	274·5	4	1228·3
29	841·3	2	2889·7	1	598	3	285·5	4	1373·6
July 6	965	2	3271·7	1	546	3	374·5	4	1556·1
13	616	2	1895	1	365	3	260	4	935·3
20	1080·3	2	1235·3	1	377	3	370	4	896
27	991·7	2	1409	1	409	3	297	4	911·7
Aug 3	452·7	2	586·3	1	291	3	236·5	4	431·2
10	508	2	514·7	1	310	3	286	4	438·9
17	649	1	402	3	488	2	3095	4	473·3
Rank sums		31		24		52		53	

Table 3.19 Seasonal variation by habitat of mean numbers of invertebrates obtained from water traps.

CHAPTER FOUR

Breeding biology of the Reed Warbler

A basic account of the breeding biology of the Reed Warbler was given by Brown and Davies (1949), who found it to breed almost exclusively in Phragmites reed-beds. More recently Catchpole (1974) studied the species at Attenborough National Nature Reserve, and found, quite surprisingly, that field and scrub habitats were favoured and that the traditional Phragmites reed-beds were not optimal in terms of breeding success.

No Reed Warblers were found breeding outside the reed beds at Oxwich, although a considerable area of much suitable habitat, such as that described by Catchpole (1974) at Attenborough was available. This section considers the question of 'habitat quality' and breeding success, paying particular attention to the three marshland habitats described in Chapter 2.

Methods

All work was undertaken during the 1979 breeding season. As far as possible all Reed Warblers nests in the study area (see Chapter 2) were located and followed through to the fledging stage. It is possible that a few nests were missed, but enough time was spent nest-finding to ensure that this number was very small. 96 nests in all were found. This figure includes failures, repeats and second broods, but excludes those which were abandoned, moved or destroyed before an egg was laid. On completion, each nest was described and its height (rim to ground or water level) was measured. In almost all cases, nests were visited daily throughout their occupation, and when young were present, they were weighed to an accuracy of 0·1grms. using a Pesola balance. Weights were obtained from the hatching date (day 0) until about day 6 or 7, depending upon the state of the nest or the size of the brood etc. Thereafter the nest was visited daily until its outcome was known. In some cases nestlings were not weighed at all when the nest was considered unsafe (tilted e.g.). Unless observed, first egg dates were estimated either from the hatching date, or from nestling weights (assuming a period of 15 days for egg-laying and incubation, and 10 days for fledgling).

On handling, a large proportion of nestlings produced faecal sacs. These were collected and preserved in 70% alcohol for subsequent examination with a binocular microscope.

Hides were placed 1 - 2m. away from a selection of nests, which were observed for one hour periods during the nestling stage. Details of food items brought to the young and feeding rates and schedules were recorded.

Observations of the feeding locations of adults with young in the nest were made from the top of a 3m. step-ladder placed a suitable distance away from the nest. Journeys to and from the nest were noted. Occasionally, with the help of an assistant, simultaneous hide and step-ladder watches were undertaken.

The majority of observations were made in the period dawn to about 14.00 hrs. extending from late April to mid August.

Results

4.1 Timing of breeding

The build up of the spring arrival of Reed Warblers in a reed-bed is difficult to monitor, the standard Common Bird Census method giving very poor results (Bell, Catchpole et al 1973). The start of the breeding season was therefore taken as the mean first egg date. Since all nests were visited almost every day, subsequent nesting attempts after failure were usually easy to identify. Similarly, although perhaps not so easily, some second broods of individual pairs could also be identified.

The breeding seasons in the various habitats are shown in Fig. 4.1 and Table 4.1. By far the most realistic estimate of the start of breeding is Table 4.1 (b), which gives first egg dates of first attempts at first broods. The results show a difference of 8·24 days between the mean first egg date in PM and MM ($p < 0\cdot05$) and 12·35 days between PM and IM ($p < 0\cdot001$). The difference of 4·11 days between MM and IM is not significant ($p > 0\cdot2$).

4.2 Nest height

Catchpole (1974) found that nest height was correlated with season for Phragmites - nesting Reed Warblers but not so for those nesting in other habitats. Fig. 4.2 compares this correlation between the three habitat types at Oxwich. The results show that nests in PM are built higher more rapidly as the season progresses than in either MM or IM ($p < 0\cdot05$). Table 4.2 shows that in accordance with this, the mean height of nests from first breeding attempts is lower in PM than in MM and IM. Although these latter differences were significant, ($p < 0\cdot05$), they are rather small (< 2cm.).

4.3 Age and density of reed-stems

On arrival in spring, adult Reed Warblers find relatively few shoots of new Phragmites stems suitable for nest building, and must inevitably seek out areas where the old stems have survived the winter gales. It is probable that in large areas of pure reed, fewer reed-stems are broken by wind damage than in areas of mixed vegitation. Very few Reed Warblers,

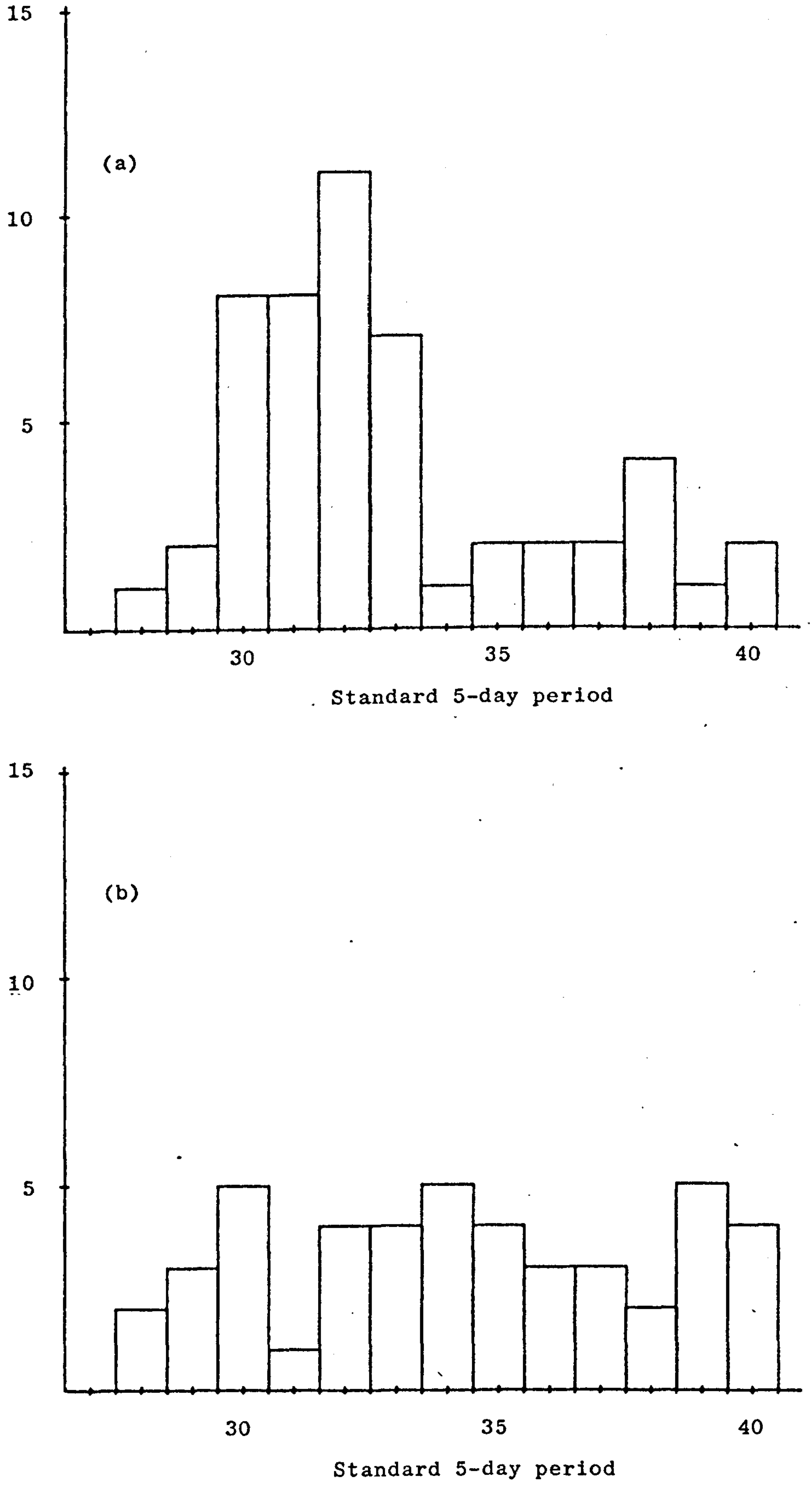

Fig.4·1 Frequency distribution of first egg dates of Reed Warblers in standard 5-day periods, (a) PM, (b) MM+IM.

		PM	MM	IM	MM + IM	All
(a)	n	51	26	19	45	96
Mean first egg date (June)		11·78	16·65	21·26	18·6	14·98
s.d. (days)		15·31	20·48	15·05	18·34	17·05
(b)	n	36	21	13	34	70
Mean first egg date (June)		4·19	12·43	16·54	14·0	8·96
s.d. (days)		7·37	19·73	14·37	17·75	14·24

Table 4.1 Mean first egg dates of Reed Warblers by habitat (a) all nests, (b) first attempts and first broods only.

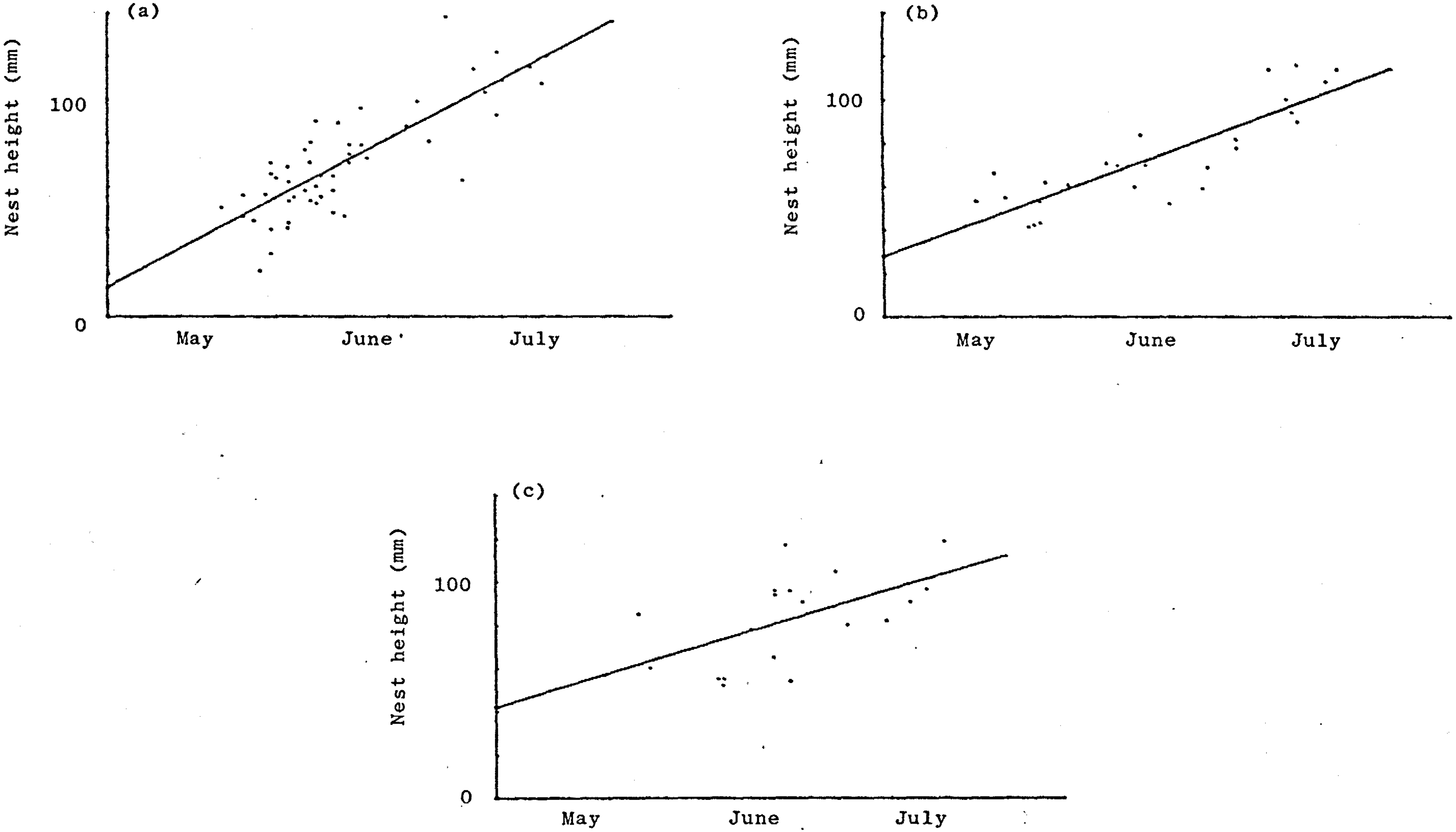

Fig. 4·2 Relationship between Reed Warbler nest height and season in (a) PM (y = 1·36x + 13·48), (b) MM (y = 0·96x + 27·68) and (c) IM (y = 0·78x + 41·96). (Day 1 = May 1st).

	PM	MM	IM
n	36	21	13
Mean height(mm)	60·83	68·90	78·15
s.d.	17·43	21·26	21·07

Table 4.2 Mean height(mm) of Reed Warbler nests (first attempts in first broods).

even those nesting in MM, used anything other than reed-stems around which to weave their nests, and Table 4.3 gives the number and proportion of nests built around old, new and a mixture of stems. No significant differences in the utilization of stems by age was found between the three habitats ($\chi^2 = 2 \cdot 93$, $p > 0 \cdot 3$, d.f. = 4).

The importance of old reed-stems in nest building can be further examined by considering the seasonal pattern of selection of old and new stems, and Fig. 4.3 shows this relationship in the three habitats. As is to be expected, in all cases selection of new stems is correlated with season, but is less strong in IM. (All slopes are significantly greater than zero ($p < 0 \cdot 001$) and the rate in PM is significantly greater than in IM ($0 \cdot 1 < p < 0 \cdot 2$)). The differences between the rates in PM and MM, and MM and IM are not significant ($p > 0 \cdot 2$). This suggests that in IM, fewer suitable old stems are available in the early part of the breeding season and agrees with the subjective description of IM given in Chapter 2 as 'thin-stemmed and thinly spread reeds'. The results are also consistent with the much later start of breeding in IM already described (§4.1).

Catchpole (1974) pointed out that one advantage of nesting in dense Phragmites is that nests suspended high off the ground are more stable the more suspension points per nest there are. Although vertical reed-stem density per unit area was not measured, Fig. 4.4 shows the number of stems used to support nests in each habitat. The mean number of stems used in PM (5·33) exceeds the numbers used in MM (4·66) and IM (4·68), the differences being significant at the 0·05 and 0·1 levels respectively. In Catchpole's 1974 study, the mean number of stems used was only 3·9, considerably lower than in any of the areas at Oxwich.

	Old	Mixed	New	Totals
PM	3	36	13	52
MM	3	15	9	27
IM	3	12	4	19
Totals	9	63	26	98

Table 4.3 Number of Reed Warbler nests built on old, mixed or new reed-stems.

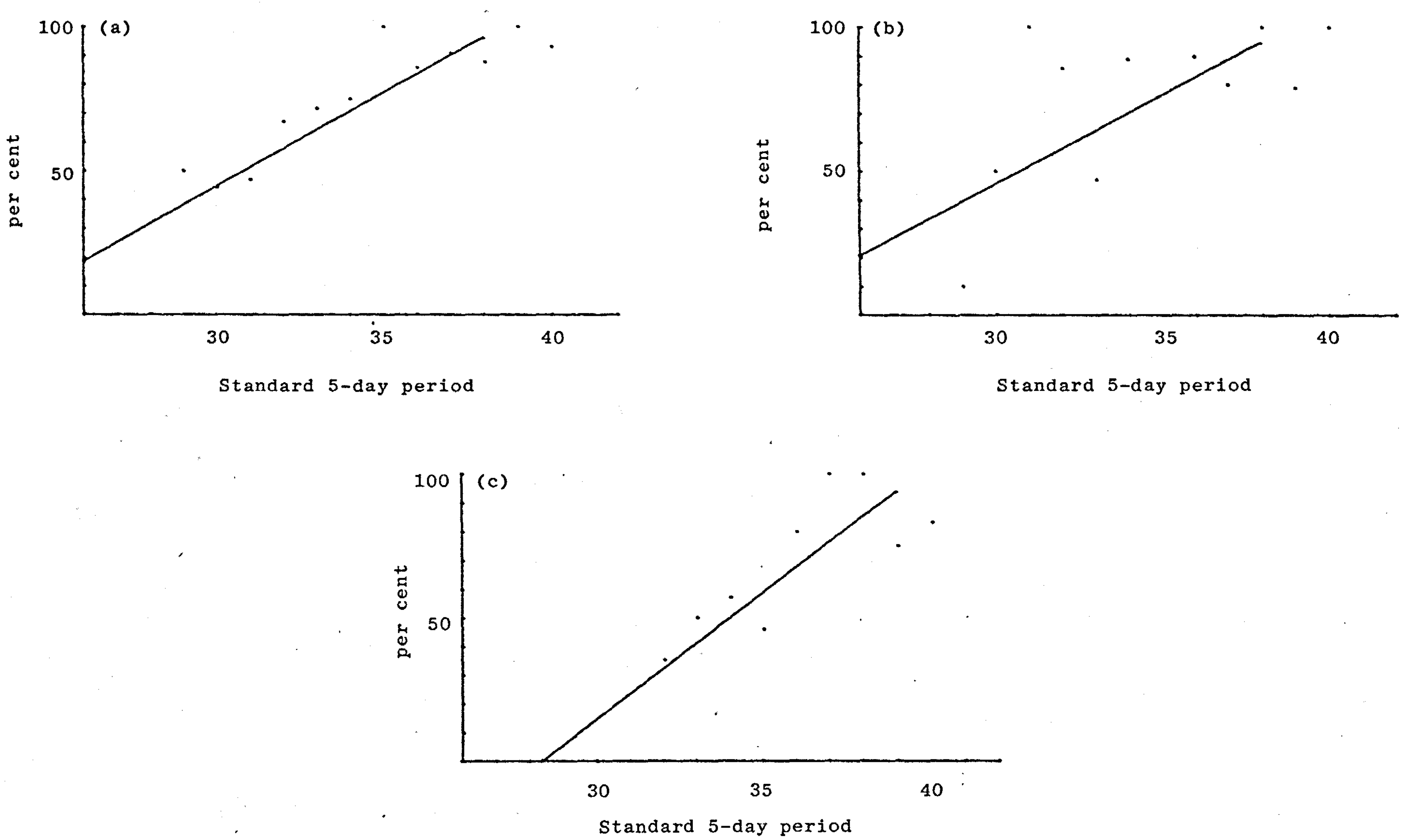

Fig.4.3 Percentage selection by Reed Warblers of new reed-stems by season (5-day periods) in (a) PM (y = 6·47x − 149·8), r = 0·88; (b) MM (y = 6·17x − 139·9), r = 0·72; (c) IM (y = 8·85x − 251·25), r = 0·91.

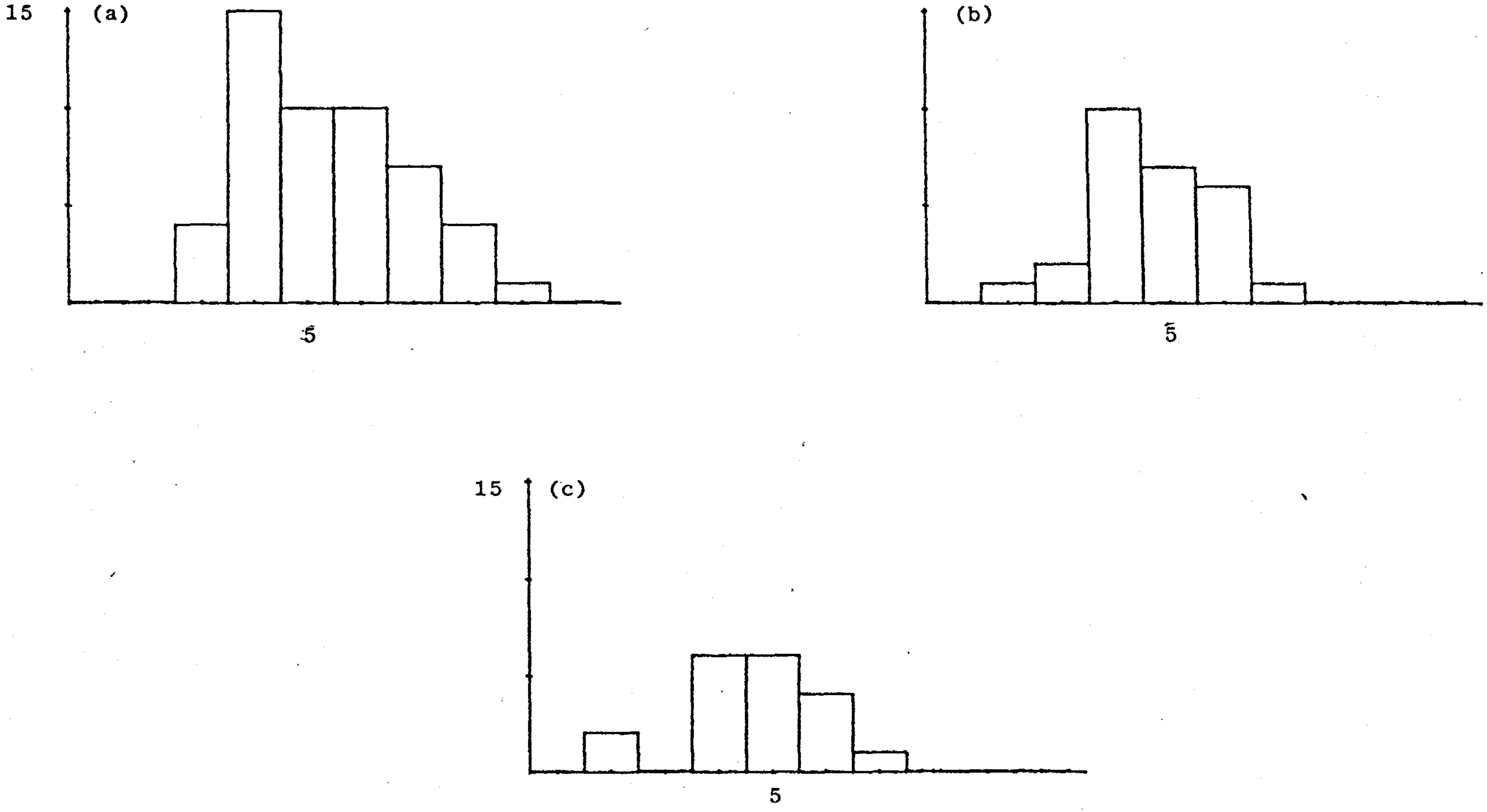

Fig.4.4 Number of stems used as nest supports by Reed Warblers in (a) PM, (b) MM, (c) IM.

4.4 Clutch size

The frequency distributions of clutch sizes in the three habitats are shown in Table 4.4. Only complete clutches are included, i.e. those in nests found either during the building stage or with eggs, and which were followed to a complete clutch by daily visits. The data includes clutches from subsequent attempts after failure, and second broods. The results show that Reed Warbler clutches were most frequently of four eggs and that overall mean clutch sizes varied little between habitat. (None of the differences are significant). The mean clutch sizes are comparable with Catchpole's (1974) findings, and also with those of Bibby (1978).

Fig. 4.5 shows the same data set out in standard five day periods of first egg dates. (Clutches in the MM and IM habitats are combined to give a reasonable sample). In both cases, the mean clutch size fell throughout the season, but significantly more in PM than elsewhere ($p < 0{\cdot}001$). The overall rate of decrease was very close to that found by Bibby (1978) using nationwide data.

4.5 Brood size

Since all nests were visited almost daily during their occupation, it was possible to determine brood sizes at fledging very accurately. Brood sizes in the various habitats are shown in Table 4.5, with seasonal variations plotted in Fig. 4.6. As with clutch sizes, there were no significant differences in mean brood sizes at fledging, which also declined throughout the season. In this case however, there were no differences in the rates of decrease ($p > 0{\cdot}2$).

A comparison between habitats PM, and MM and IM combined, shows no differences between mean clutch and brood sizes or by season ($p > 0{\cdot}2$).

	Clutch size					
	3	4	5	Total	Mean	s.d.
PM:						
number	10	27	7	44	3·93	0·63
percent	22·7	61·4	15·9			
MM:						
number	4	24	5	33	4·03	0·53
percent	12·1	72·7	15·2			
IM:						
number	1	9	-	10	3·9	0·32
percent	10·0	90·0	-			
MM + IM:						
number	5	33	5	43	4·0	0·49
percent	11·6	76·7	11·6			
All:						
number	15	60	12	87	3·97	0·56
percent	17·2	69·0	13·8			

Table 4.4 Frequency distribution of clutch sizes of Reed Warblers.

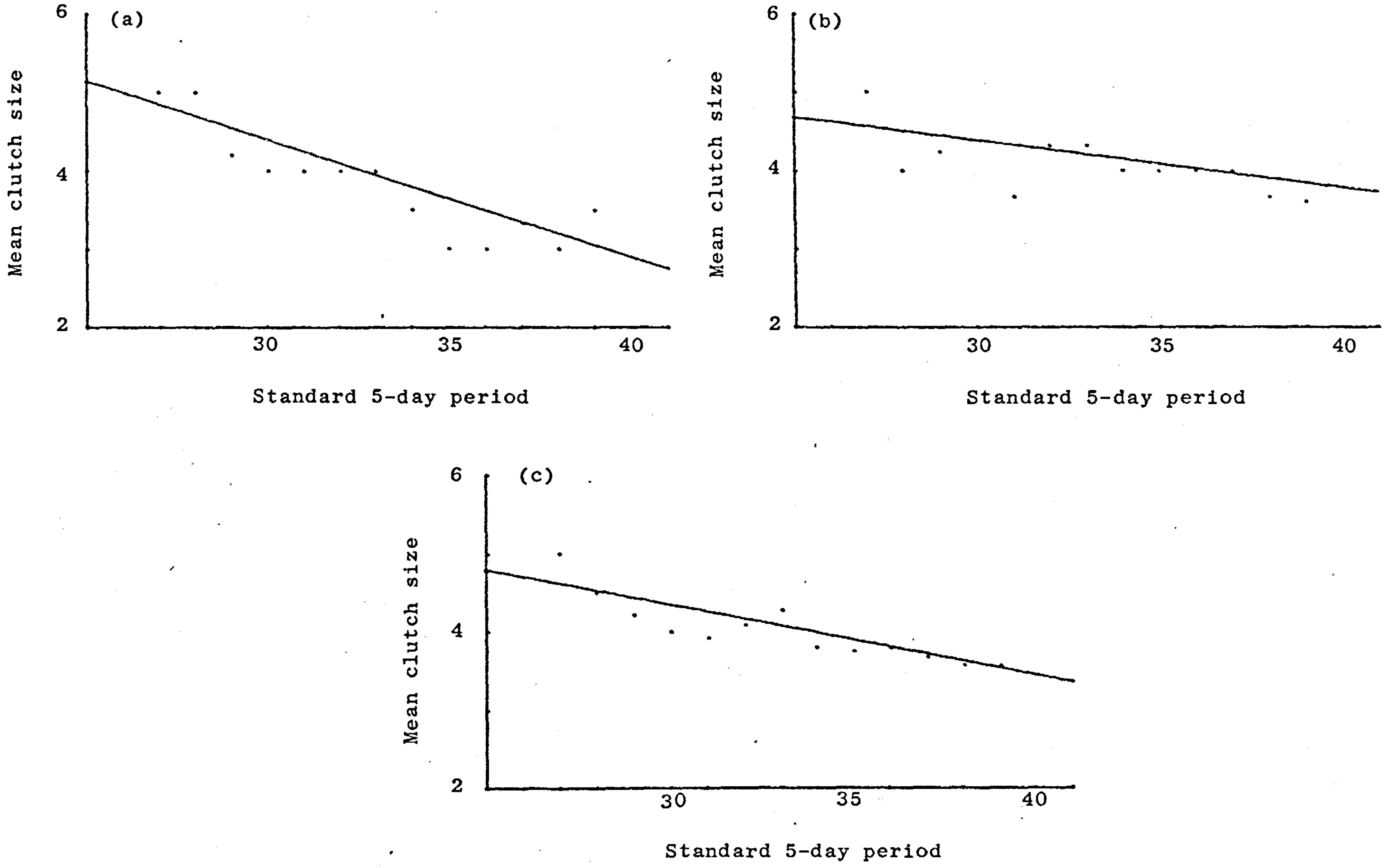

Fig. 4.5 Mean clutch sizes of Reed Warblers by standard 5-day periods of laying of first egg. (a) PM, (b) MM + IM, (c) All.

	Brood size							
	1	2	3	4	5	Total	Mean	s.d.
PM:								
number	-	3	12	14	2	31	3·48	0·77
percent	-	9·7	38·7	45·2	6·4			
MM:								
number	-	1	7	8	1	17	3·53	0·72
percent	-	5·9	41·2	47·1	5·8			
IM:								
number	2	-	-	6	1	9	3·44	1·42
percent	22·2	-	-	66·7	11·1			
MM + IM:								
number	2	1	7	14	2	26	3·5	0·99
percent	7·7	3·9	26·9	53·8	7·7			
All:								
number	2	4	19	28	4	57	3·49	0·87
percent	3·5	7·0	33·3	49·1	7·0			

Table 4.5 Frequency distribution of brood sizes at fledging of Reed Warblers.

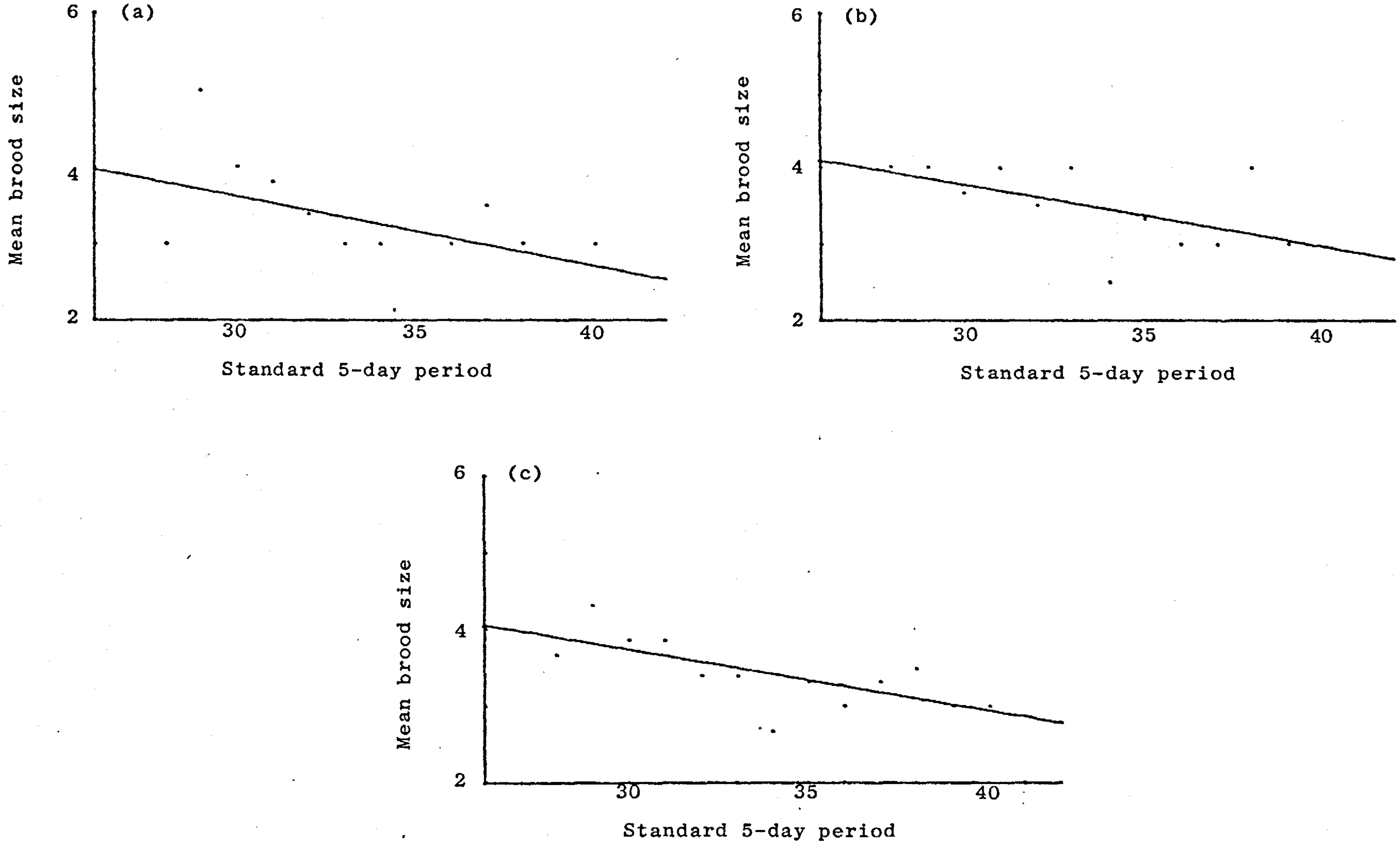

Fig.4·6 Mean brood sizes at fledging of Reed Warblers by standard 5-day periods of laying of first egg. (a) PM, (b) MM + IM, (c) All.

4.6 Nest success and clutch size

Bibby (1978) found that for both Reed and Sedge Warblers, the largest broods were reared, not as might be expected, from the most frequent, but from the largest clutches. Although Bibby's samples were very large (using British Trust for Ornithology data over 17 years), he was forced to measure successful brood sizes at about the seventh day, thus exagerating success to an unknown extent. The Oxwich sample measures brood size at fledging, enabling a more realistic estimate of the effect of clutch size on nesting success to be made.

Table 4.6 shows nesting succes of known clutch sizes in nests found during building, laying or incubation. All habitats are pooled and partial failures are not considered, so as to give as large a sample as possible. The results again show that the largest broods are reared from the largest clutches, contradicting Lack (1954).

4.7 Breeding success

The traditional straightforward method of calculating breeding success using simple proportions of eggs and young lost is not only fraught with obvious biases, but is extremely wasteful of data. A direct probability method, using virtually all the data collected has been available for some time (Mayfield 1975), but has been rarely used (Bibby 1978, 1979).

In calculating nest success, (the survival of any or all contents of a nest) we shall, for simplicity, ignore partial losses and proceed as follows:

For survival during incubation, we determine the number of (successful) nest-days and loss-days in the sample. Dividing the total number of loss-days by the total number of nest-days gives the probability of survival per nest-day. In the case of the Reed Warbler, egg-laying lasts 3-4 days and incubation 12 days. Using a total incubation period of

	Clutch size	n	Brood size of successes
	3	9	2·78
	4	34	3·47
	5	8	4·0
Total		51	3·39

Table 4.6 Outcome of Reed Warbler nests of known clutch size found during building, laying or incubation (All habitats combined).

15 days and multiplying daily probabilities provides an estimate of nest success during incubation. A similar analysis for the fledging period (10 days in the case of the Reed Warbler) provides an estimate of the probability that a nest will survive the fledging period. Finally, multiplying these two probabilities estimates the expected nest outcome or probability of nest success.

Bibby (1978) applied this method to great advantage using the B.T.O's nest record collection for Reed and Sedge Warblers. The present sample is very much smaller and is not suitable for a similar very detailed analysis. It is however easily large enough to consider overall and between-habitat variations in breeding success, consisting of a total of 1789 nest-visits.

Fig. 4.7 shows the daily probabilities of nests avoiding failure, plotted by standard 5 day periods, together with nest outcome i.e. prob. of success × mean brood size at fledging from Fig. 4.6. The overall survival probabilities by habitat are given in Table 4.7.

The outcome of Reed Warbler nests has two peaks, the first around the beginning of June, and the second towards the middle of July. This result fits reasonably well with the observed pattern of the breeding season (Fig. 4.1), with the model proposed by Bibby (1978), and with the observation of Catchpole (1974) and Naylor and Green (1976). It is interesting to note however that the seasonal variation of nest outcomes found by Bibby (1978) does not fit this pattern, and that in Bibby's analysis the expected nest outcome varied from about 1·4 to 1·8, whereas at Oxwich the figures are 1·03 to 2·98.

The survival probabilities by habitat set out in Table 4.7 show that overall, eggs are more prone to failure than are young. The probability of nest success is higher in MM than in PM and very low in IM, with a similar pattern of nest outcomes obtained from the mean brood sizes in Table 4.5.

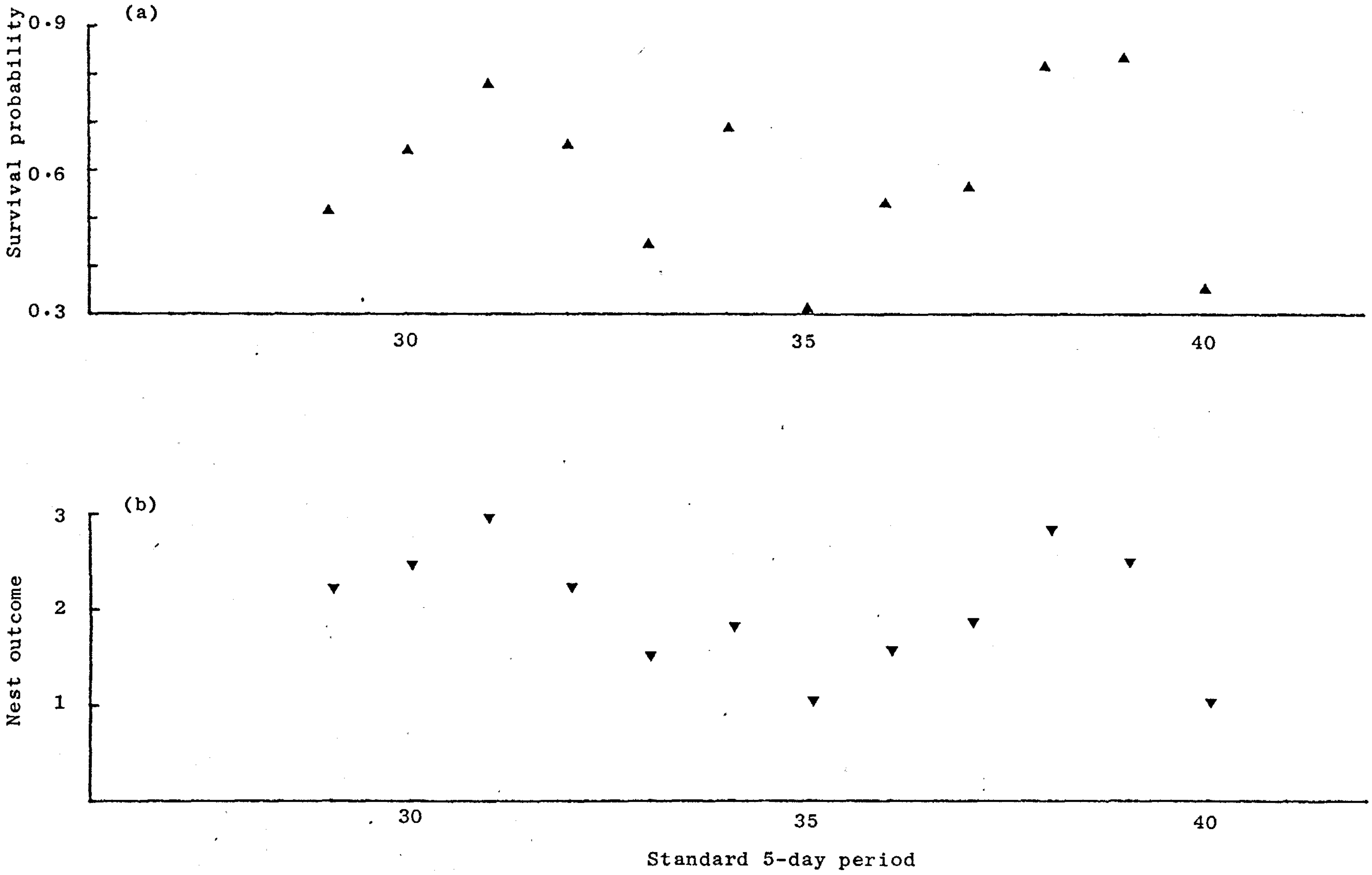

Fig.4.7 Overall survival probabilities (a) and nest outcomes (b) of Reed Warbler nests by standard 5-day periods for all habitats.

PM:	Days of survival	Days of failure	Prob. of daily survival
Nest with eggs	611	11	0·982315
Nest with young	399	9	0·977941

Probability of nest success $= 0{\cdot}982315^{15} \times 0{\cdot}977941^{10}$

$0{\cdot}765177 \times 0{\cdot}800067$

$0{\cdot}612195$

MM:			
Nests with eggs	296	3	0·989967
Nests with young	230	4	0·982906

Probability of nest success $= 0{\cdot}989967^{15} \times 0{\cdot}982906^{10}$

$= 0{\cdot}859628 \times 0{\cdot}841627$

$= 0{\cdot}723482$

IM:			
Nests with eggs	122	5	0·960630
Nests with young	97	2	0·979798

Probability of nest success $= 0{\cdot}96063^{15} \times 0{\cdot}979798^{10}$

$= 0{\cdot}547447 \times 0{\cdot}815390$

$= 0{\cdot}446382$

All:			
Nests with eggs	1029	19	0·981870
Nests with young	726	15	0·979757

Probability of nest success $= 0{\cdot}98187^{15} \times 0{\cdot}979757^{10}$

$= 0{\cdot}759993 \times 0{\cdot}815049$

$= 0{\cdot}619435$

Table 4.7 Probability of nesting success of Reed Warblers, calculated from the daily chance of avoiding total failure.

The overall probability of nesting success (0·6194) in Table 4.7 is very much higher than the 'national average' of 0·452 found by Bibby (1978). This suggests that either 1979 was in some way an 'above average' breeding season, or that Oxwich is a 'superior' breeding location. Evidence that the latter hypothesis is realistic is given in Thomas (1980). Here, breeding seasons at Oxwich from 1975-1979 were compared by measuring the ratio of the numbers of free-flying juveniles to adults caught in mist-nets placed around the study area during May, June and July (Table 4.8). The results show that breeding success by this measure was, if anything, below average during 1979.

When considering the population dynamics of any species, a most difficult, but important question to answer is 'how many breeding attempts are made by each pair?'. Using the enormous amount of data at his disposal, Bibby (1978) was able to give an estimate of the minimum number of attempts per pair, which when multiplied by nest outcome gives the number of young reared per pair. At Oxwich, although each pair was followed closely during its first brood, there was no way of reliably assessing how many of these were responsible for the assumed second broods found. Consequently no estimate of the number of attempts per pair can be made.

It is possible however to compare the Oxwich and B.T.O. data by considering how many attempts each pair must make in order to produce, say 4 young (Table 4.9). The results suggest a much less strenuous breeding schedule at Oxwich.

4.8 Causes of nest failure

Details of known nest failures are given in Table 4.10. The total of 36 includes two desertions which were not considered when calculating

	1975	1976	1977	1978	1979
Reed Warbler	0·57	1·38	0·87	0·39	0·49
Reed Bunting	0·44	0·46	0·38	0·33	-

Table 4.8 Juvenile/adult ratio (see text) of Reed Warblers and Reed Buntings caught around the study area during May, June and July 1975-79.

	Oxwich	BTO
Probability of success (p)	0·619	0·452
Mean brood size of successes (b)	3·49	3·44
Number of attempts required to produce 4 young $(= \frac{4}{pb})$	1·85	2·57

Table 4.9 Breeding statistics of Reed Warblers at Oxwich and elsewhere, and number of attempts necessary to produce 4 young per pair.

		PM	MM	IM
Eggs	Vanished - no trace	4	2	-
	Vanished - wet stain in nest	4	2	4
	Nest pulled out	3	-	-
	Deserted	1	-	1
	Totals	12	4	5
Young	Vanished	1	-	2
	Nest pulled out	4	1	-
	Nest fallen	3	2	-
	Young dead in nest	-	1	1
	Totals	8	4	3

Summary (percent)	Failure at egg stage	Failure at young stage
PM	33·3	22·2
MM + IM	25·0	19·4

Table 4.10 Causes of failure of Reed Warbler nests.

nest success in §4.7. More failures occured at the egg stage, when eggs either vanished without trace, or were presumed eaten in situ by virtue of a wet stain found at the bottom of the nest.

The identification of the predator responsible for eggs vanishing without trace is a mystery. Those presumed eaten at the nest must have been taken by a small mobile predator, since in all instances the nest was completely undisturbed. Cuckoos *Cuculus canorus* are well-known nest parasites of Reed Warblers (Lack 1963), but as far as is known remove only one egg from each nest. Apart from being too large, they also have never been observed in the reed-beds at Oxwich (pers. obs.) and probably parasitise the nearby population of Meadow Pipits *Anthus pratensis*.

The most likely explanation would seem to be a small rodent predator, and traps were set in a selection of reed-bed sites for a short period during June 1979. The traps, which were set both above water and on damp ground at the base of the reeds, caught several Woodmice *Apodemus sylvaticus*, suggesting these as a likely cause.

Small rodent predators of ground nesting birds have been recorded previously (Wynne-Edwards 1952, Sutton and Parmelee 1954-1955, Parmelle (in Bant 1968), Custer and Pitelka 1977, Maxson and Orinj 1978), mostly in arctic locations and in North America. Although Reed Warbler nests were never found on the ground, the dense nature of Phragmites would make passage from reed to reed possible for small rodents, which may also be good swimmers.

Predators definitely identified were as follows:

Moorhen *Gallinula choloropus*, Little Bittern *Ixobrychus minutus* (a rare chance occurrence) and Brown Rat *Rattus norvegicus*. Water Rail *Rallus aquaticus* was highly suspected but was never observed predating a nest.

Table 4.10 also gives the circumstances of failure of eggs and nests by habitat and shows no significant differences ($\chi^2 = 0{\cdot}35$, $p > 0{\cdot}2$, d.f. = 2).

4.9 Nestling growth

Results from many species have suggested that chicks from larger eggs grow faster and fledge at higher weights than those from smaller eggs (Skogland et al 1952, Parsons 1970, Schiffereli 1973). O'Connor (1975) showed that a high hatching day weight led to accelerated growth during the first week in the Blue Tit Parus caeruleus and House Sparrow Passer domesticus, and Perrins (1965), Perrins et al (1973) and O'Connor (1976) have given evidence that a heavy weight at fledging increases the post-fledging survival of the chick.

Growth patterns of nestling Reed Warblers are given in Table 4.11 (Day 0 = hatching day) and are divided by habitat. The results show that from the day of hatching, nestlings in PM nests are consistently heavier than those in other habitats (Table 4.12), and that apart from day 6, no significant differences exist between the weights of nestlings in MM and IM nests. In Fig. 4.8 MM and IM are thus combined showing that on each day young in PM nests are significantly heavier than elsewhere ($p < 0{\cdot}05$).

The pattern of nestling growth shown in Fig. 4.8 is common in birds and follows closely that found for Reed Warblers by Drycz (1974), who, using some undescribed technique, was apparently able to weigh young and replace them in the nest safely until day 11. Drycz's growth curves show the usual weight recession (Ricklefs 1968b) towards the end of the nestling period, which would pressumably have occurred at Oxwich had it been possible to obtain weights of older nestlings.

Although Fig. 4.8 shows clearly that nestlings from PM are, on average, heavier than those from other nests, it also suggests that growth rates

PM			MM		
Age (days)	Number of nestlings weighed	Mean weight (g) ± s.d	Age (days)	Number of nestlings weighed	Mean weight (g) ± s.d
0	26	1·80 ± 0·32	0	13	1·58 ± 0·19
1	98	2·42 ± 0·54	1	53	2·16 ± 0·44
2	110	3·48 ± 0·83	2	64	3·13 ± 0·72
3	112	4·95 ± 1·15	3	63	4·56 ± 0·98
4	112	6·70 ± 1·18	4	67	6·04 ± 1·18
5	98	8·31 ± 1·21	5	66	7·65 ± 1·15
6	52	9·30 ± 1·08	6	46	9·05 ± 1·34
7	8	10·69 ± 0·63	7	6	9·82 ± 0·55
8	2	11·45 ± 0·07	8	5	10·44 ± 0·15

IM			MM + IM		
0	-	-	0	13	1·58 ± 0·19
1	19	2·22 ± 0·42	1	72	2·18 ± 0·43
2	27	2·96 ± 0·94	2	91	3·08 ± 0·79
3	27	4·18 ± 1·13	3	90	4·45 ± 1·04
4	27	5·72 ± 1·46	4	94	5·95 ± 1·27
5	27	7·22 ± 1·61	5	93	7·53 ± 1·30
6	19	8·15 ± 1·76	6	65	8·78 ± 1·51
7	1	9·9	7	7	9·83 ± 0·50
8	-	-	8	5	10·44 ± 0·15

Table 4.11 Weights of nestling Reed Warblers by habitat.

Age (days)	PM v MM	PM v IM	MM v IM	PM v (MM + IM)
0	*	-	-	*
1	*	n.s	n.s	*
2	*	*	n.s	*
3	*	*	n.s	*
4	*	*	n.s	*
5	*	*	n.s	*
6	n.s	*	*	*
7	*	-	-	*
8	*	-	-	*

Table 4.12 Significant differences in mean weights of nestling Reed Warblers by habitat (* = $p < 0.05$).

	Number of nestlings in brood			
	2	3	4	5
Number of nestlings	8	39	124	15
Mean weight (g)	7·34	8·29	7·90	7·49
s.d.	2·09	1·20	1·29	1·19

Table 4.13 Mean weights (g) on day 5 of nestling Reed Warblers in various brood sizes.

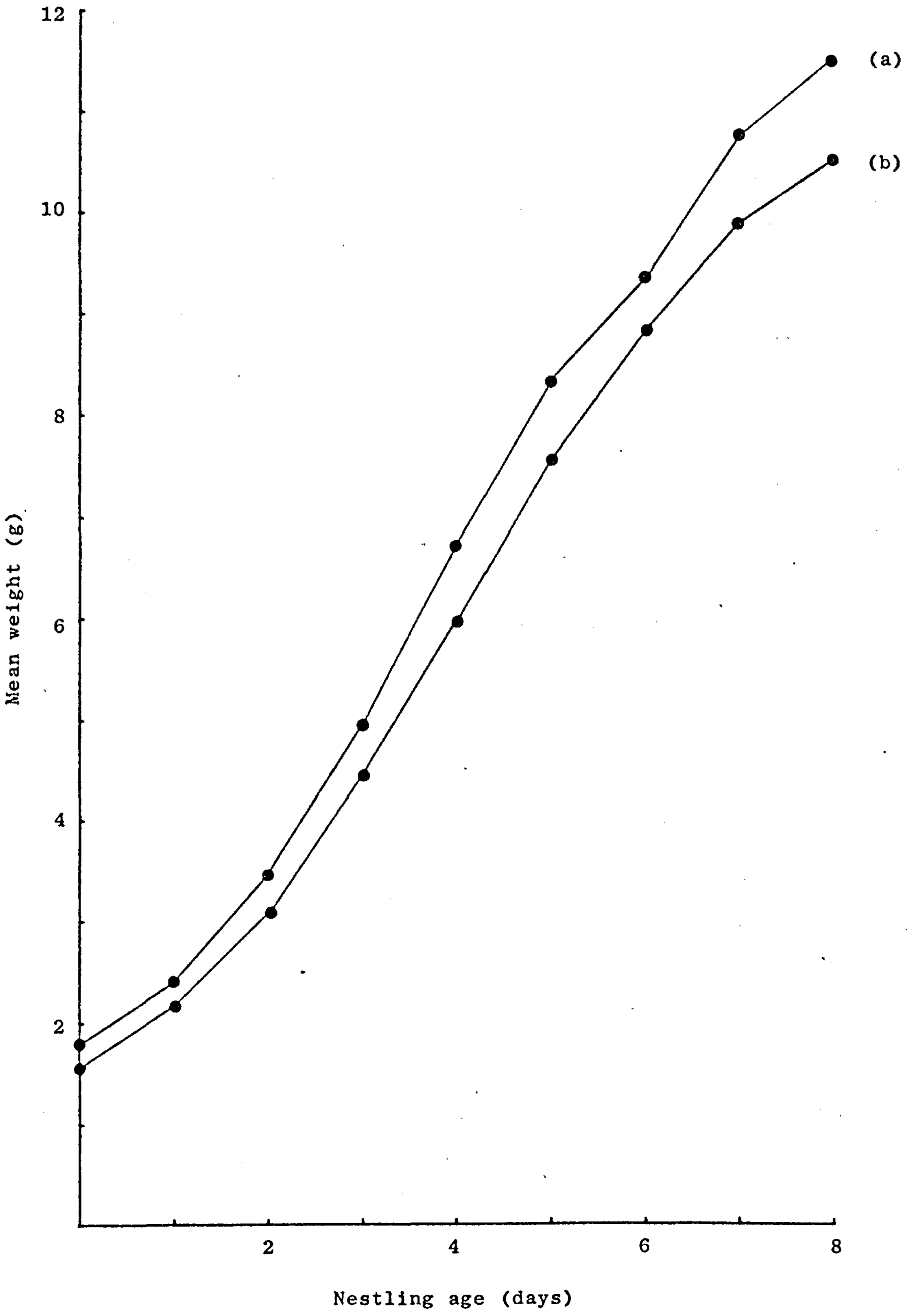

Fig.4·8 Mean weights of nestling Reed Warblers by age of nestling (a) PM, (b) MM+IM.

are similar in each habitat. Fitting the data in Table 4.11 to the logistic growth curve

$$\frac{dW}{dt} = KW(1 - W),$$

and calculating the growth constant K by the method of Ricklefs (1967), gives values of $K = 0{\cdot}505$ for PM nests (5 iterations, $r = 0{\cdot}9987$) and $K = 0{\cdot}53$ for other nests (4 iterations, $r = 0{\cdot}9987$), indicating little difference between growth rates. The results do show a slightly slower rate of growth in PM, but this difference is negligible as can be seen on calculating the predicted fledging weights (day 9) from the growth equation. The mean weights are consistent with those in Table 4.11, being 11•88g. for PM nestlings and 10•81g. for others.

4.10 Effect of brood-size on nestling weights

The weights of older nestlings more accurately reflect the potential fitness to survive after fledging (Perrins 1965, Perrins et al 1973). Drycz (1974) compared the effect of brood-size on nestling weights, but rather surprisingly did not choose the weights of nestlings he obtained immediately prior to fledging. No such weights are available at Oxwich, and day 5 is chosen since it represents the largest sample (Table 4.13). As might be expected (Lack 1954), the two most common brood-sizes at day 5 (and at fledging, Table 4.5) contain the heaviest young, but the only significant difference is between brood-sizes 3 and 5 ($p < 0{\cdot}05$). Drycz (1974) found no significant differences using day 7.

4.11 Seasonal variation in nestling weights

Table 4.14 shows that nestlings in early broods (first egg date before 5 day period 35 i.e. June 20) were on average heavier than those in later broods. The difference in mean weights are significant for days 2 - 6 ($p < 0{\cdot}05$)

Early broods †				Late broods			
Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.	Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.
0	39	1·79	0·34	0	-	-	-
1	130	2·34	0·52	1	40	2·22	0.47
2	144	3·39	0·81	2	57	3·07	0.88
3	150	4·85	1·06	3	52	4·38	1.21
4	151	6·50	1·17	4	55	5·95	1.48
5	137	8·15	1·11	5	54	7·37	1·62
6	87	9·35	0·86	6	30	8·03	1·96
7	12	10·37	0·77	7	3	9·97	0.31
8	6	10·78	0·53	8	1	10·4	-

Table 4.14 Mean weights (g) of nestling Reed Warblers in early and late broods,
(† first egg date before June 20).

The results agree well with §4.1 and §4.9. Drycz (1974) found that although young from early broods were heaviest in the Great Reed Warbler Acrocephalus arundinaceus, the opposite was true for the Reed Warbler, and proposed that this rather surprising result was due to interspecific competition for food during the early part of the breeding season.

4.12 Asynchronous hatching

Asynchronous hatching is generally considered to be an adaptation to a variable food supply, which in turn would tend to lower the number of young raised (Lack 1954). Since egg losses almost always involved the total clutch, the variation in weights between the heaviest and lightest nestlings in each brood is taken as a convenient means of assessing asynchronous hatching.

If, as might be expected, the food supply is more variable later in the season, the condition (weights) of late nestlings should be highly variable. Fig. 4.9 shows the variation of mean weight differences between the heaviest and lightest individuals in each brood by age of nestling and habitat.

The quadratic nature of the curve shows maximum differential weights towards the middle of the nestling period, coinciding with the time of maximum nestling growth (differential weights are less in PM than elsewhere, but not significantly so, $p > 0{\cdot}2$).

4.13 Feeding ecology of nestlings

(a) Faecal analysis

4.13a (i) General diet

The inherent errors in the various techniques used for collecting food samples in birds have been discussed by Hartley (1948). Apart

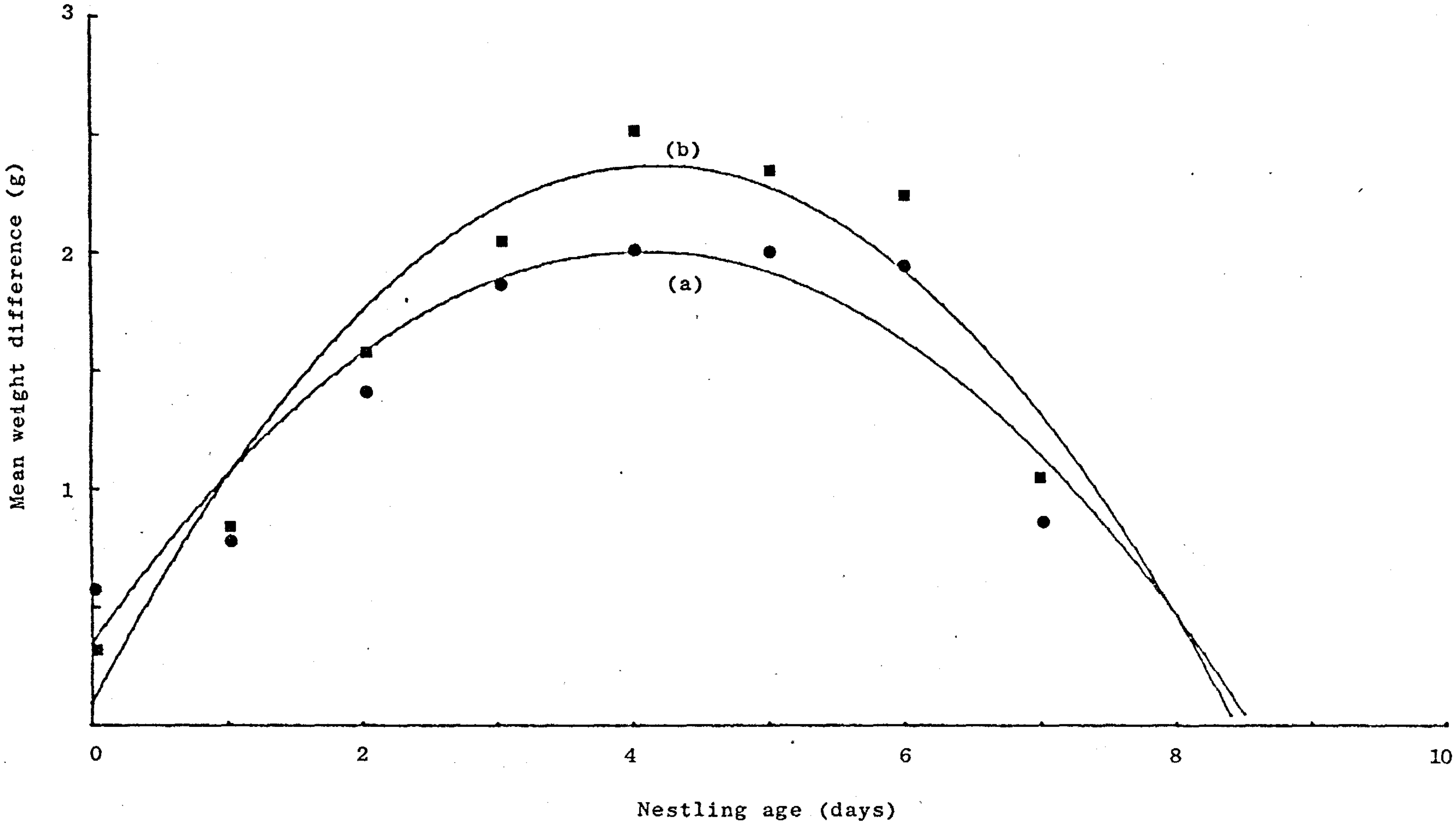

Fig. 4·9 Mean difference between lightest and heaviest young in Reed Warbler nests by nestling age, (a) PM ● ($y = 0{\cdot}34 + 0{\cdot}81x - 0{\cdot}1x^2$), (b) MM+IM, ($y = 0{\cdot}09 + 1{\cdot}09x - 0{\cdot}13x^2$).

from collecting the bird, only the use of an artificial nestling, placing a light collar around the neck of nestlings or collecting faecal sacs are viable alternatives with Reed Warblers. Although probably the least accurate, the latter was chosen, since it caused minimal disturbance. (An artificial nestling was made and tested, but proved totally useless).

The overall results of the analysis of 603 faecal sacs are shown in Table 4.15. The 3,913 items identified (mean of 6·5 per sac) represents the minimum number of prey detectable from the remains. It is impossible to assess relative detectability, since taxa such as spiders and flies were readily identified, but difficult to count, whereas beetles, bugs and damsel-flies could usually be counted fairly accurately.

The results illustrate the importance of spiders and flies in the diet, and to a lesser extent beetles, bugs and larvae. Table 4.15, which also gives the percentage frequency of occurrence of the taxa, supports the view that spiders and flies are underrecorded. Other important taxa include damsel flies, caddis flies and small Hymenopterans (usually Apocrita). The list of taxa in Table 4.15 compares well with those found in the water traps (Chapter 3), there being no notable omissions. Apart from spiders, which, as was pointed out in Chapter 3, were obviously sampled poorly by the water traps, there is a broad agreement between insect availability and prey taken, suggesting the Reed Warbler as a generalist feeder. This becomes more apparent when considering Figs. 4.10 to 4.18 which show the seasonal patterns (in 5 day periods) of the main prey items found in the faeces. With the exception of damsel flies, the trends are in line with the results of the water traps (Figs. 3.2 to 3.11). The two peaks in Fig. 4.11 as opposed to the one in Fig. 3.3, could well be attributed to the year difference in sampling this emergent aquatic insect.

	n	percent		percent with	
Araneae	834	21·3		70·5	
Nematocera	500	12·8	24·3	57·1	58·6
Brachycera/Cyclorrhapha	450	11·5		58·5	
Coleoptera	438	11·2		49·8	
Odonata	198	5·1		29·5	
Trichoptera	234	6·0		36·0	
Plecoptera	40	1·0		5·6	
Heteroptera	69	1·8		9·6	
Homoptera	498	12·7		36·5	
Aphid	35	0·9		5·8	
Hymenoptera	191	4·9		22·7	
Pscocoptera	3	0·1		0·5	
Gastropods	35	0·9		5·8	
Lepidoptera (imagines)	1	0		0·2	
Larvae	387	9·9		41·5	
Total	3913				

Table 4.15 Number of prey items identified from analysis of 603 faecal sacs collected from nestling Reed Warblers.

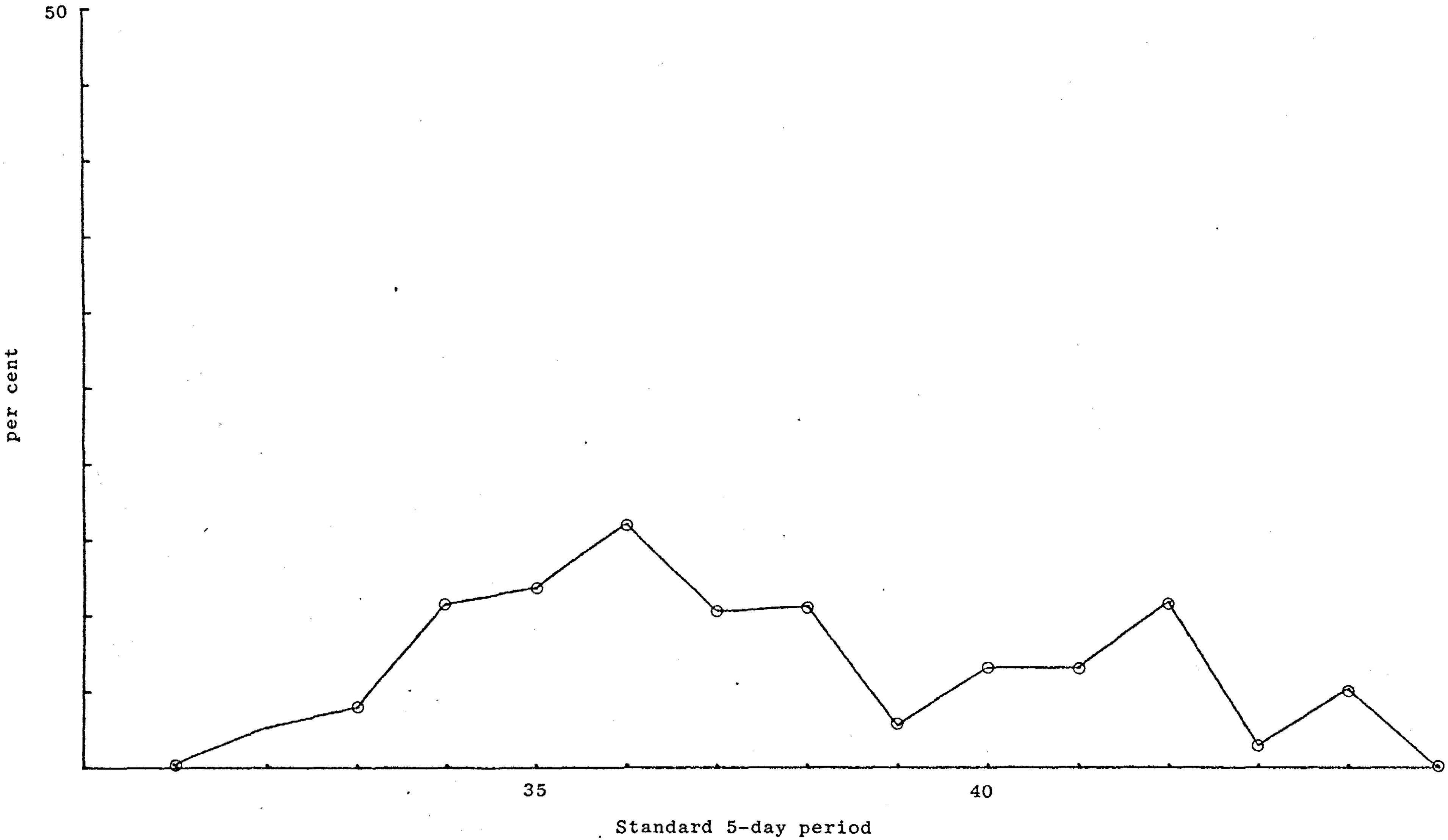

Fig 4·10 Percentages of the total number of Spiders detected in the faeces of nestling Reed Warblers by season.

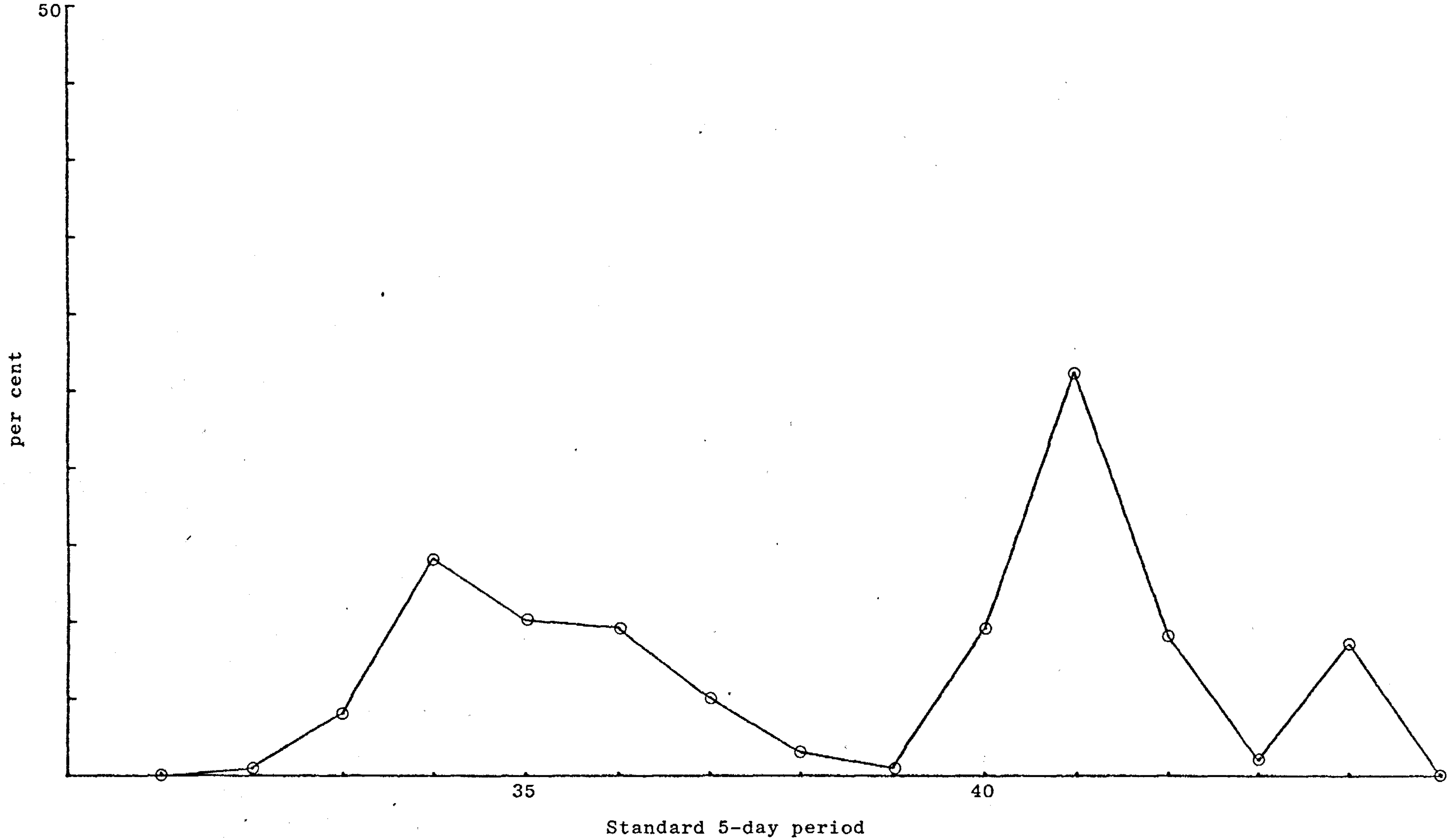

Fig.4·11 Percentages of the total number of Odonata detected in the faeces of nestling Reed Warblers by season.

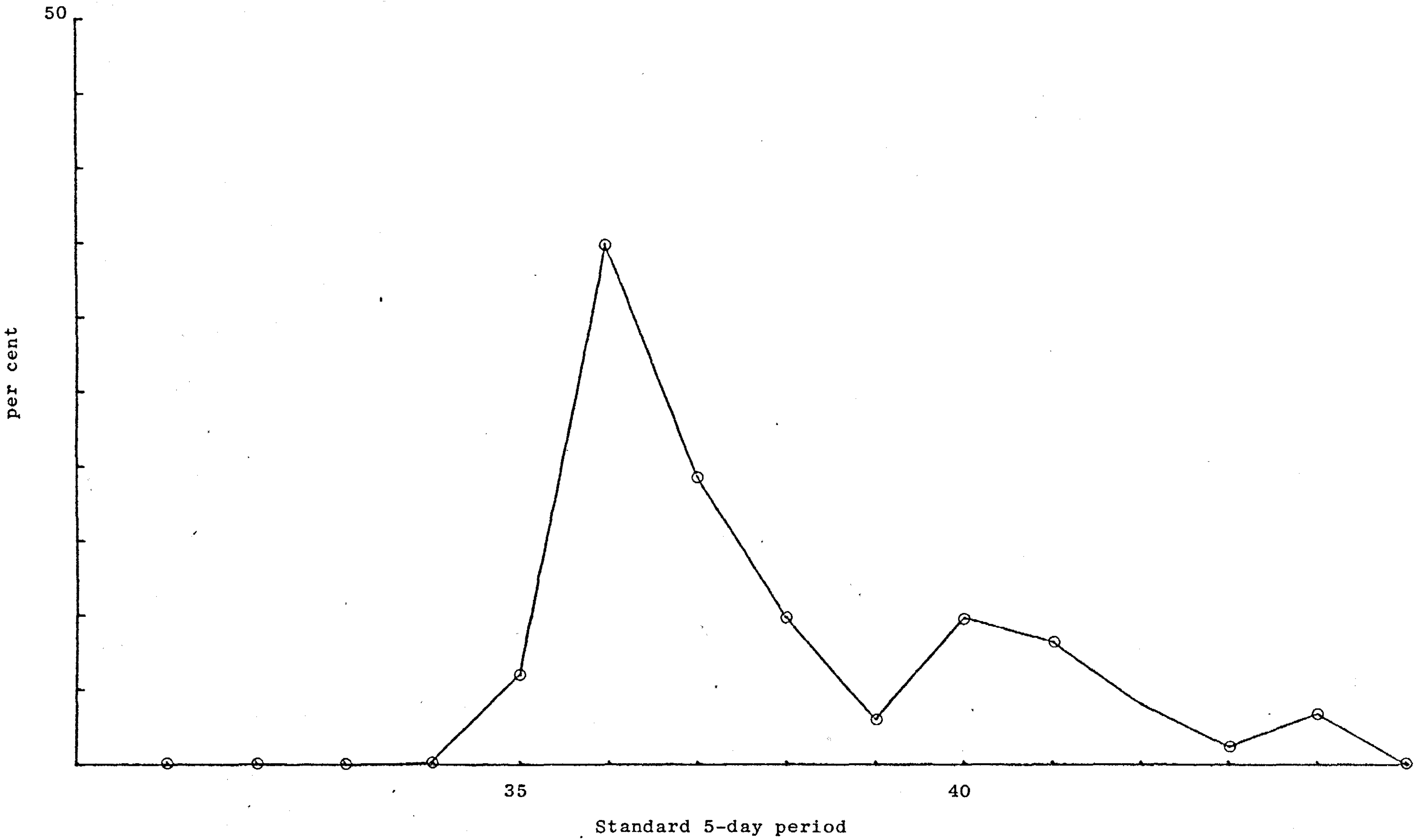

Fig.4·12 Percentages of the total number of Homopterans detected in the faeces of nestling Reed Warblers by season.

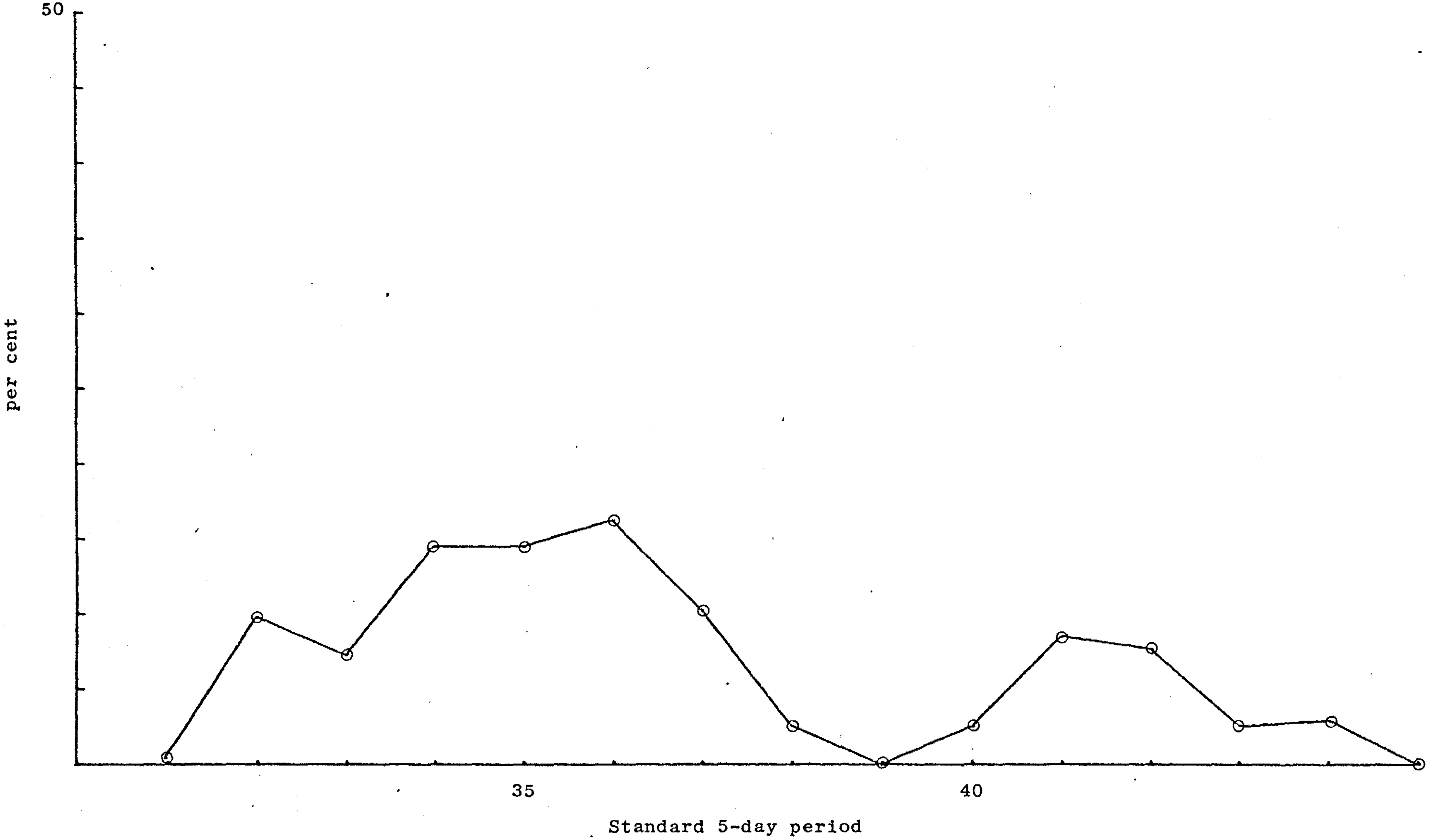

Fig. 4·13 Percentages of the total number of Trichopterans detected in the faeces of nestling Reed Warblers by season.

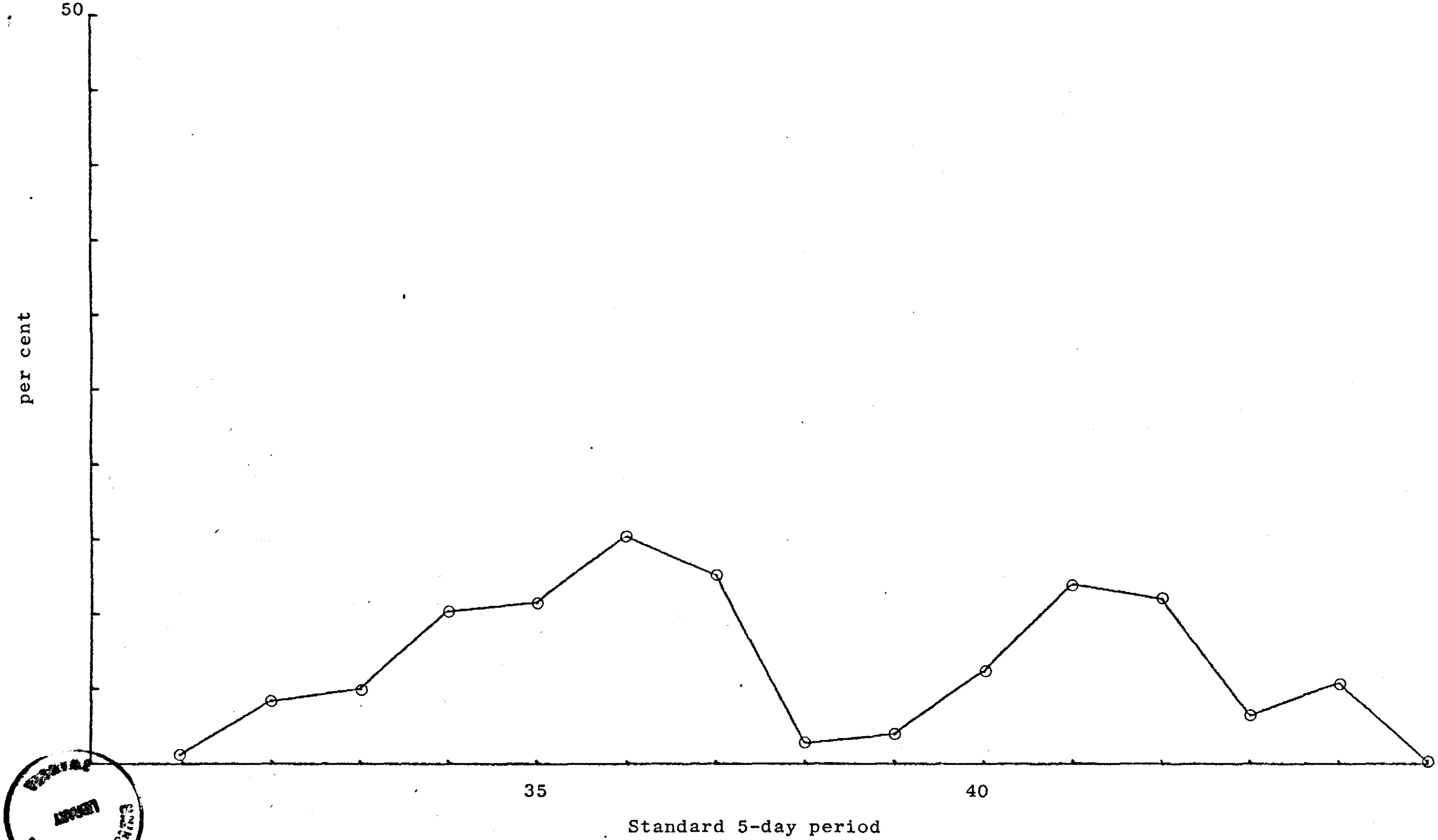

Fig. 4·14 Percentages of the total number of Nematocerans detected in the faeces of nestling Reed Warblers by season.

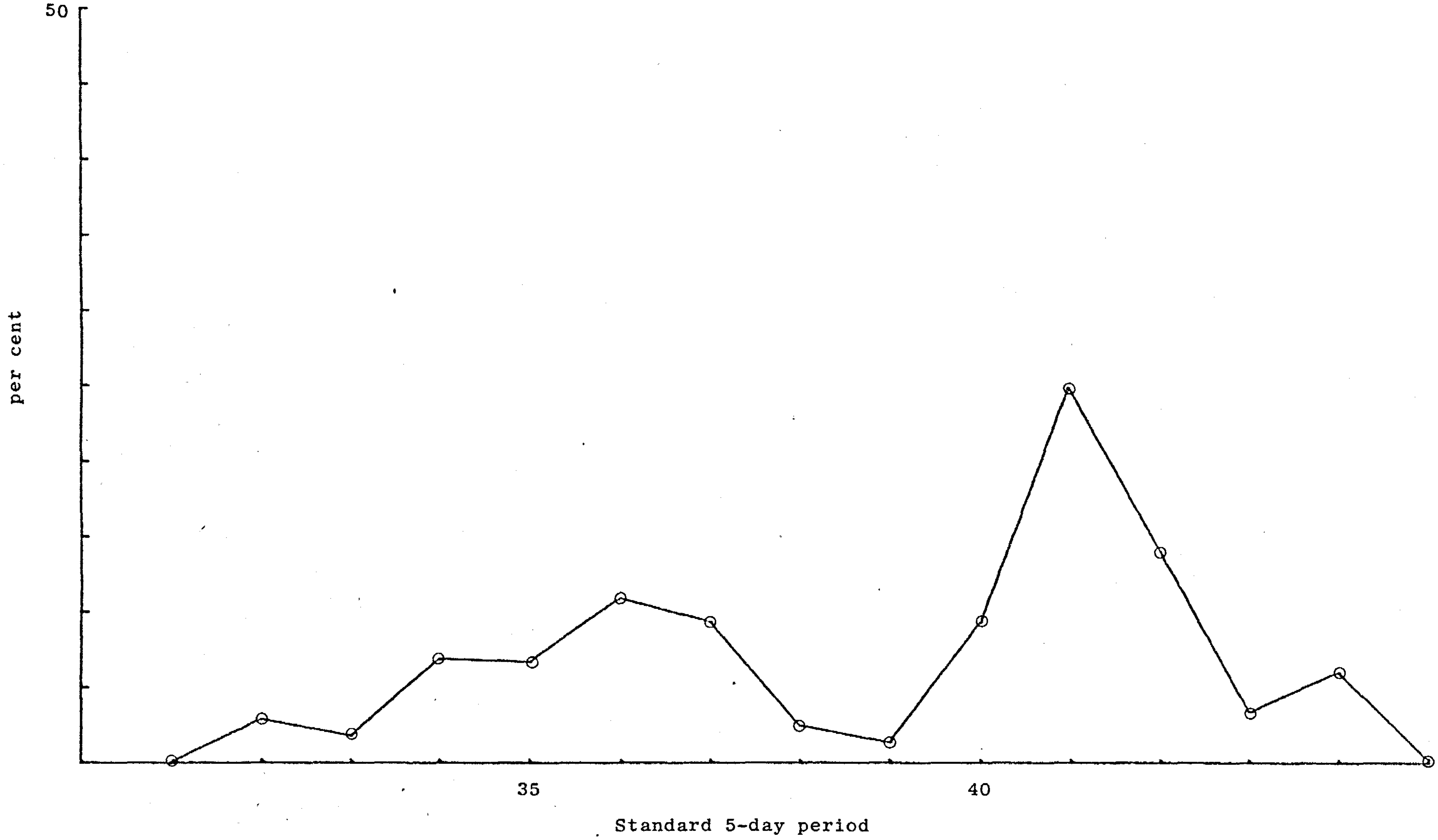

Fig.4·15 Percentages of the total number of Brachycera/Cyclorrhaphans detected in the faeces of nestling Reed Warblers by season.

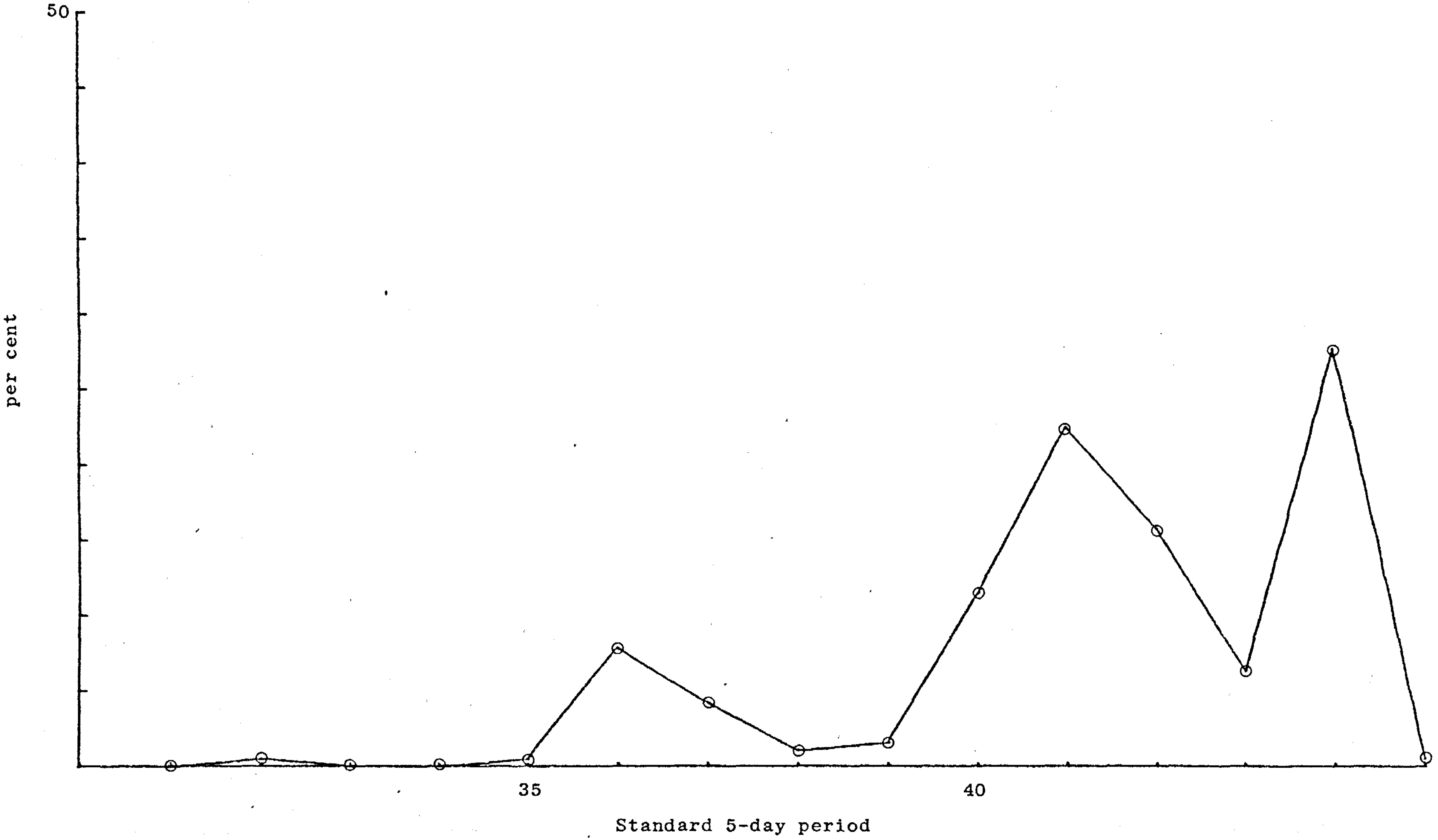

Fig.4·16 Percentages of the total number of Hymenopterans detected in the faeces of nestling Reed Warblers by season.

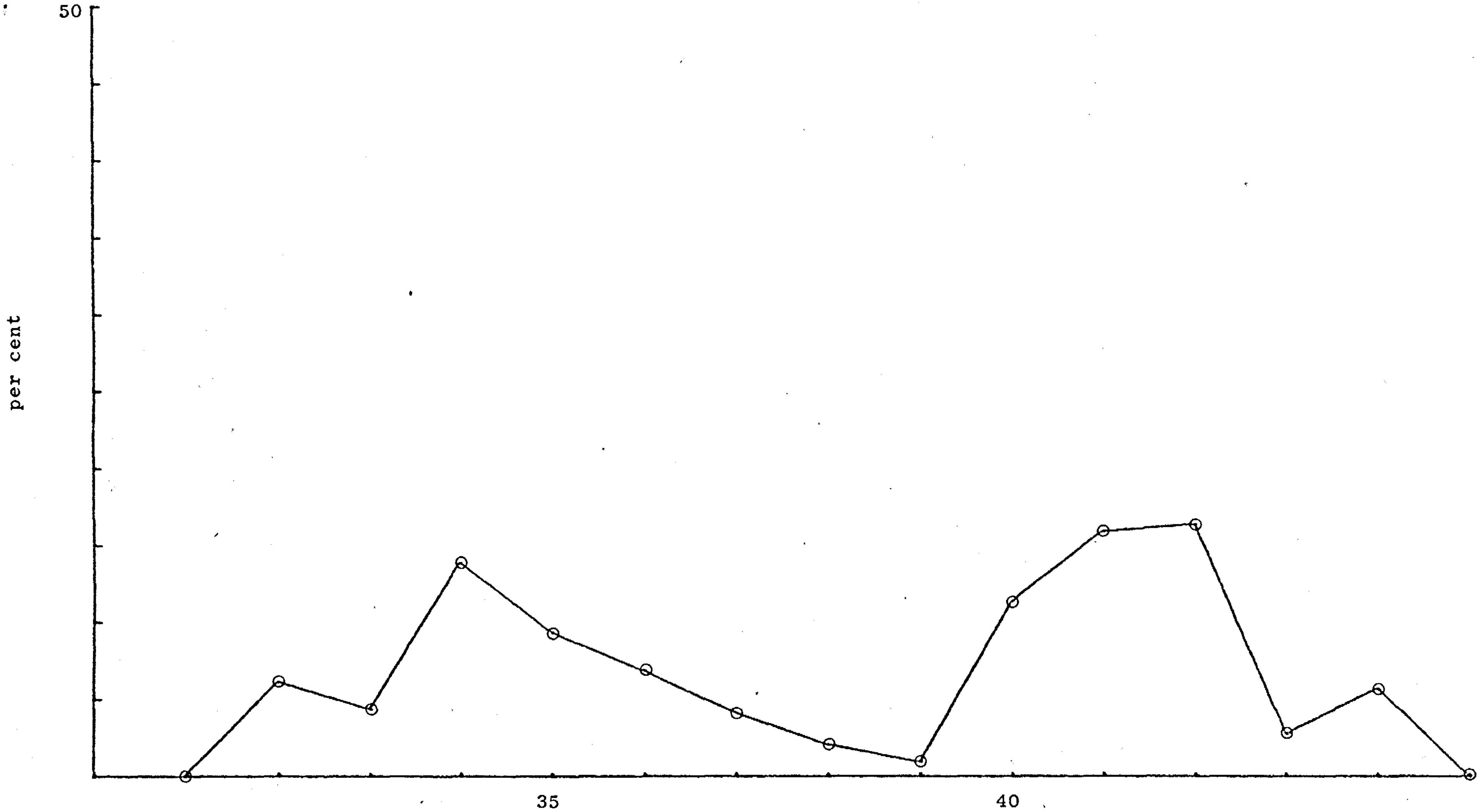

Fig.4·17 Percentages of the total number of Coleopterans detected in the faeces of nestling Reed Warblers by season.

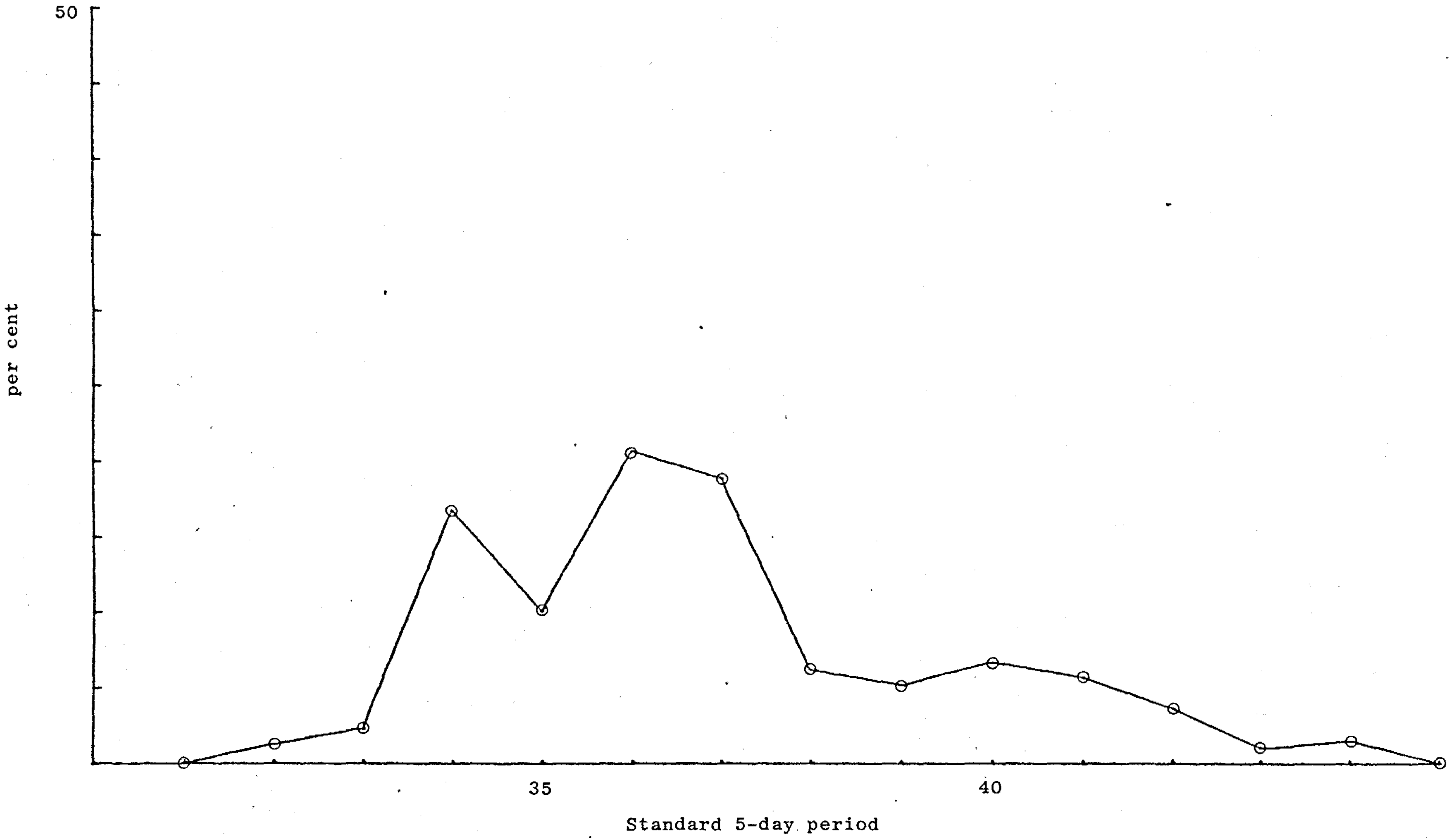

Fig. 4·18 Percentages of the total number of Larvae detected in the faeces of nestling Reed Warblers by season.

4.13a (ii) Variation of diet by habitat

Table 4.16 presents the faecal analysis results by habitat. The two main prey items, spiders and flies, contain approximately equal proportions within each habitat. In order to examine between habitat differences we omit these, together with the Psocoptera and Lepidopteran imagines (which contain zeros) and consider the remaining 10 × 3 contingency table. As might be expected, diets differ between habitats ($\chi^2 = 244{\cdot}5$, $p < 0{\cdot}001$, d.f. = 18), but with 66% of this variation being attributed to Trichopterans, Homopterans, Hymenopterans and larvae. This, together with Table 4.16, suggests that apart from a basic diet of spiders and flies, nestling Reed Warblers receive fewer caddis flies in IM, more bugs (Delphacidae) in PM and IM, more Hymenopterans in IM and few larvae in IM. The seasonal availability of these taxa (Figs. 3.3, 3.4, 3.5, 3.11 and the differences in the timing and breeding between habitats (Table 4.1) are likely explanations of this variation in diet.

4.13a (iii) Distribution of food according to nestling age

Table 4.17 lists the numbers of individual prey items identified per faecal sac for the major taxa according to nestling age. Spiders, although well represented, decreased in the diet as nestlings grew older, supporting Royama (1970) who suggested that they have special nutritional value in early nestling growth. Nematocerans similarly decreased in numbers, whereas Brachycerans/Cyclorrhaphans increased, the net result being a fairly constant dipteran diet. Beetles, and to a lesser extent damsel flies were more numerous in the diet of older nestlings, probably as a result of their relatively large size (most beetles being large Chrysomelidae). Except for the very young nestlings, caddis flies were fed at a steady rate. Bugs, mostly small Delphacidae, were common early in the nestling period, whilst Hymenopterans fluctuated erratically but generally increased in

	PM			MM			IM		
	n	% (within PM)		n	% (within MM)		n	% (within IM)	
Araneae	391	22·8		265	22·6		178	17·4	
Nematocera	231	13·4	22·7	163	13·9	25·2	106	10·4	25·9
Brachycera/Cyclorrhapha	160	9·3		132	11·3		158	15·5	
Coleoptera	150	8·7		151	12·9		137	13·4	
Odonata	71	4·13		51	4·4		76	7·4	
Trichoptera	133	7·7		70	6·0		31	3·0	
Plecoptera	27	1·6		11	0·9		2	0·2	
Heteroptera	11	0·6		26	2·2		32	3·1	
Homoptera	280	16·3		91	7·8		127	12·4	
Aphid	8	0·5		15	1·3		12	1·2	
Hymenoptera	40	2·3		56	4·8		95	9·3	
Pscocoptera	2	0·1		0	0		1	0·1	
Gastropods	6	0·4		13	1·1		16	1·6	
Lepidoptera (imagines)	0	0		0	0		1	0·1	
Larvae	209	12·2		128	10·9		50	4·9	
Totals	1719			1172			1022		
Number of samples	254			200			149		

Table 4.16 Number of prey items from analysis of 603 faecal sacs collected from nestling Reed Warblers by habitat.

Age of nestling	Araneae	Nematocera	Brachycera/ Cyclorrhapha	Coleoptera	Odonata	Trichoptera	Homoptera	Hymenoptera	Larvae
1	1·14	1·10	0·19	0·33	0	0·19	2·19	0·24	0·57
2	1·61	1·11	0·30	0·59	0	0·41	1·50	0·15	0·76
3	1·89	0·99	0·51	0·52	0·05	0·53	1·41	0·19	0·73
4	1·81	1·04	0·60	0·75	0·19	0·56	1·30	0·32	0·78
5	1·69	0·74	0·70	0·73	0·47	0·39	0·41	0·22	0·86
6	1·26	0·78	0·77	0·66	0·43	0·36	0·27	0·15	0·86
7	0·83	0·52	0·93	0·86	0·48	0·38	0·14	0·24	0·35
8	0·57	0·61	1·22	0·39	0·70	0·39	0·26	0·30	0·22
9	0·70	0·57	1·26	1·44	0·65	0·30	0·65	0·83	0·13
10	0·56	0·64	1·28	1·28	0·80	0·08	0·52	0·60	0·08
11	0·54	0·60	1·20	1·09	0·34	0·14	0·46	0·63	0·26
12	0·87	0·57	1·44	0·57	0·48	0·22	0·17	0·87	0·44

Table 4.17 Number of prey items identified per faecal sac from nestling Reed Warblers of known age.

numbers with increasing nestling age. Larvae, a most important constituent of the diet, were generally more common in the first half of the nestling period.

4.13a (iv) Effect of diet on nestling weight

The importance of a particular taxon in the diet can be assessed by comparing the number of each taxon per faecal sac with nestling weight. Day 6 was chosen as a convenient nestling age. Table 4.18 lists the linear regression results of the numbers of the various taxa found in the faeces by nestling weight. Although the correlations are rather poor, larvae, and to a lesser extent spiders and Nematoceran flies show highly significant rates of increase and would appear to be important constituents in the diet. Brachyceran/Cyclorrhaphan flies and damsel fly numbers also increase with increasing nestling weight, but the correlations are barely significant. The correlation for caddis flies is surprisingly poor and inexplicable, since as has already been noted (§4.14a(iii)), they were fed to the young consistently throughout the nestling period. On the other hand, beetles and damsel flies were fed more commonly to older nestlings, and bugs to younger ones (§4.14a(iii)), which could account for the poor correlations on day 6 in Table 4.18.

4.13a (v) Effect of diet on nestling weight according to habitat

Summing all taxa and dividing the above data by habitat (PM and elsewhere) gives regression equations

$y = 2{\cdot}47x - 16{\cdot}4$, $r = 0{\cdot}3201$ - PM (29 sacs)

$y = 1{\cdot}21x - 5{\cdot}69$, $r = 0{\cdot}3706$ - other (44 sacs)

The difference in rates is not significant ($p > 0{\cdot}2$).

	a	b	r	sig. level
Araneae	-2•91	0•46	0•2387	0•05
Nematocea	-1•74	0•28	0•2390	0•05
Brachycera/Cyclorrhapha	-0•82	0•17	0•1930	0•2
Coleoptera	0•05	0•07	0•0723	n.s.
Odonata	-0•91	0•15	0•1839	0•2
Trichoptera	0•28	0•01	0•0117	n.s.
Homoptera	-0•85	0•12	0•1235	n.s.
Larvae	-3•41	0•47	0•3371	0•01

Table 4.18 Linear regression statistics of the number of individual prey items identified per faecal sac (y) by mean nestling weight (x grms.) on day 6. (Data from 73 Reed Warbler sacs).

	Cal. value
Araneae	100
Odonata (Zygoptera)	50
Homoptera (Delphacidae)	25
Trichoptera (medium size)	50
Diptera (Nematocera)	15
(Brachycera/Cyclorrhapha)	15
Coleoptera (Chysomelidae)	55
Hymenoptera (Apocrita)	50
Larvae*	375

Table 4.19 Calorific values of various taxa found in faecal sacs of Reed Warblers (after Orians 1980).

*Mean value obtained by bomb calorimetry of samples taken from Oxwich.

4.13a (vi) Calorific value of diet according to nestling age

Apart from prey size, which could not be determined accurately from the faecal remains, differences in the nutritional value of the various foods must affect the diet of nestlings as they grow older. Although the calorific value of a prey item obviously varies with size, some indication as to the nutritional value of the diet can be found by combining Table 4.17 with a measure of the average calorific value of each taxon. A convenient table is given in Orians (1980). An omission from Orian's list is any value for Lepipopteran or Coleopteran larvae. A representative sample of larvae of the same general size as those fed to nestling Reed Warblers was collected and a mean calorific value obtained by bomb calorimetry (Table 4.19). Using these results, the total calorific value of the main food items by age of nestlings is easily calculated and is shown in Table 4.20. Although only a rough approximation, the results suggest that nestlings receive food of maximum calorific value on days 4 and 5, coinciding exactly with the period of maximum weight gain (Fig. 4.8). In terms of calorific value, larvae and spiders contribute most to the diet and their occurrence in the faeces falls off sharply after this period of maximum growth.

4.13 a (vii) Calorific value of diet according to season

Using again the calorific values in Table 4.19 and the numbers of items found per faecal sac in each habitat by 5 day periods (Tables 4.21-4.23), estimates of the total calorific value of the nestling diet by season for the various habitats are obtained (Table 4.24). Taking the first-egg dates in Table 4.1(a), allowing 15 days for the laying and incubation period, and a further 4 to 5 days up to the period of maximum nestling growth, one arrives at 5 day period 36 for PM, 37 for MM and IM, and 37 for all habitats. These time periods fit very well with the periods of maximum calorific food values in Table 4.24.

Age of nestling (days)	0	1	2	3	4	5	6	7	8	9	10	11	12
Calorific value of food	-	441·5	565·1	587·6	625·4	617·5	561·8	341·8	264·8	330·7	272·2	305·5	396·3

Table 4.20 Calorific value of food items found in faecal sacs of nestling Reed Warblers according to age of nestling (see text for explanation),

5 day period	Araneae	Nematocera	Brachycera/ Cyclorrhapha	Coleoptera	Odonata	Trichoptera	Homoptera	Hymenoptera	Larvae
33	1·27	1·18	0·27	0·64	0	1·00	0	0	0·18
34	1·22	0·63	0·42	0·88	0·44	0·63	0·02	0	0·90
35	1·80	0·98	0·55	0·75	0·36	0·62	0·55	0·02	0·71
36	1·94	1·02	0·59	0·43	0·25	0·52	2·57	0·18	1·06
37	1·46	0·97	0·83	0·34	0·23	0·46	2·00	0·14	1·34
38	3·00	0·20	1·20	0	0·20	0·40	0·60	0	0·40
39	1·00	0·50	0·50	0·17	0	0	0·50	0·17	1·00
40	-	-	-	-	-	-	-	-	-
41	2·67	2·67	1·33	0·67	0	0·33	0·67	1·00	0·67
42	1·14	0·71	1·14	0·86	0·36	0·36	0·14	0·36	0·36
43	0	2·00	1·33	0	0	0·33	0·33	0·67	0·33
44	0·70	0·90	0·90	1·10	0·30	0·20	0·40	1·20	0·10

Table 4.21 Number of prey items identified per faecal sac from nestling Reed Warblers by season (standard 5 day periods) - PM.

5 day period	Araneae	Nematocera	Brachycera/ Cyclorrhapha	Coleoptera	Odonata	Trichoptera	Homoptera	Hymenoptera	Larvae
32	0·77	0·73	0·42	1·00	0·04	0·81	0	0·04	0·19
33	1·00	0·63	0·26	0·63	0·42	0·32	0	0	0·37
34	1·29	0·81	0·45	0·81	0·32	0·26	0	0	0·90
35	-	-	-	-	-	-	-	-	-
36	1·00	1·00	1·00	0·25	0·25	0·42	1·00	0·33	1·08
37	1·84	1·53	0·68	0·32	0·11	0·42	1·37	0·16	1·37
38	3·90	0·32	0·26	0·47	0·11	0·21	2·42	0·11	1·16
39	1·31	0·54	0·23	0·23	0·08	0	0·92	0·15	1·08
40	1·29	0·71	1·00	1·19	0·45	0·14	1·12	0·52	0·62
41	0·56	0·62	1·29	0·81	0·62	0·23	0·46	0·48	0·24
42	1·56	0·94	0·98	1·25	0·27	0·27	0·38	0·52	0·19
43	0·86	0·71	0·79	0·86	0·14	0·36	0·36	0·71	0·21
44	1·64	0·82	0·82	0·64	0·64	0·23	0·59	1·86	0·23

Table 4.22 Number of prey items identified per faecal sac from nestling Reed Warblers by season (standard 5 day periods) - MM + IM.

5 day period	Araneae	Nematocera	Brachycera/ Cyclorrhapha	Coleoptera	Odonata	Trichoptera	Homoptera	Hymenoptera	Larvae
32	0·73	0·70	0·43	0·90	0·03	0·77	0	0·03	0·17
33	1·10	0·83	0·27	0·63	0·27	0·57	0	0	0·30
34	1·25	0·71	0·43	0·85	0·39	0·47	0·01	0	0·90
35	1·80	0·98	0·55	0·75	0·36	0·61	0·55	0·02	0·71
36	1·79	1·01	0·65	0·40	0·25	0·51	2·32	0·20	1·07
37	1·59	1·17	0·78	0·33	0·19	0·44	1·78	0·15	1·35
38	3·71	0·29	0·46	0·38	0·13	0·25	2·04	0·08	1·00
39	1·21	0·53	0·32	0·21	0·05	0	0·79	0·16	1·05
40	1·28	0·72	0·98	1·16	0·44	0·14	1·14	0·51	0·61
41	0·63	0·69	1·29	0·81	0·60	0·23	0·47	0·49	0·25
42	1·47	0·89	1·02	1·16	0·29	0·29	0·32	0·48	0·23
43	0·71	0·94	0·88	0·71	0·12	0·35	0·35	0·71	0·24
44	1·34	0·84	0·84	0·78	0·53	0·22	0·53	1·66	0·19

Table 4.23 Number of prey items identified per faecal sac from nestling Reed Warblers by season (standard 5 day periods) - All habitats.

5 day period	PM	MM + IM	All habitats
32	†	265·0	244·7
33	301·5	323·6	315·7
34	577·7	559·0	569·6
35	574·2	†	573·7
36	751·1	623·8	733·2
37	785·7	817·3	796·2
38	527·6	941·6	852·2
39	520·4	594·7	569·3
40	†	536·1	529·1
41	698·4	297·2	308·8
42	381·6	387·3	386·7
43	232·0	304·1	295·1
44	290·0	461·3	407·1

Table 4.24 Total calorific values of food items found in faecal sacs of nestling Reed Warblers by season (standard 5 day periods) - see text for explanation.

†small samples.

4.13a (viii) Calorific value of diet by habitat

Table 4.24 shows little consistency between habitats. The lower calorific values during the peak periods in PM are rather surprising, since these nestlings are heavier (Table 4.11). The higher peaks in the other habitats are equally inexplicable.

(b) Observations from hides

4.13b (i) Food items

Most feeds to nestlings consisted of several small items which were presented to the young as a tight 'ball' of food. The whole feeding operation was usually performed very rapidly and made identification beyond 'food-ball' virtually impossible. Even so, it was clear that these 'food-balls' contained spiders, flies, small beetles and probably some Hymenopterans. Other, larger taxon, could be easily identified e.g. damsel flies, caddis flies and larvae. The results of 59 hours of observations are shown in Table 4.25. Although there is some agreement with the 'percentage with' figures in Table 4.15, the results are imprecise and of little value.

4.13b (ii) Feeding rates

Feeding rates of nestlings by habitat are shown in Table 4.26 (no IM nests were watched). In both habitats the number of feeds per nestling per hour increases sigmoidally, following the pattern of nestling growth (Fig. 4.8). The small difference in feeding rates between habitats is not significant ($p > 0{\cdot}2$). The distribution of the age of nestlings observed (not shown) also shows no significant differences.

	PM (26 hrs)	MM (33 hrs)	All
'Food-balls'	255	330	585
Odonata	138	50	188
Trichoptera	29	39	68
Aphid	6	39	45
Hymenoptera	2	3	5
Gastropods	0	4	4
Lepidoptera (imagines)	6	23	29
Larvae	16	58	74
Unidentified	27	54	81
Totals	479	600	1079

Table 4.25 Food items of nestling Reed Warblers observed in 59 hrs from hides.

	PM			MM		
Nestling age	n	Mean	s.d.	n	Mean	s.d.
0	1	2·0	-	0	-	-
1	1	1·75	-	3	1·94	0·42
2	3	2·36	0·92	2	2·38	0·53
3	3	2·72	0·25	4	3·23	0·57
4	4	3·48	1·56	4	4·11	0·46
5	1	5·25	-	5	4·52	0·82
6	2	7·09	2·24	3	5·25	1·52
7	4	6·71	1·94	4	4·69	0·97
8	3	5·08	0·76	3	5·97	3·56
9	3	7·72	1·99	2	6·63	1·24
10	1	4·5	-	3	5·36	1·13
Totals	26			33		

Overall feeding rate = 4·70 ± 2·37

Overall feeding rate = 4·37 ± 1·74

Table 4.26 Feeding rates (per nestling per hour) of Reed Warblers in PM and MM by age of oldest nestling.

	'Food-balls'	Odonata	Trichoptera	Larvae	Others
Marsh	38(49)	13(7)	18(23)	3(4)	6(8)
Carr	16(46)	6(17)	4(11)	1(3)	8(23)

Table 4.27 Origins of food items given to nestling Reed Warblers.
Figures in brackets are percentages. (Others include Aphids, Neuroptera and Lepidoptera).

4.14 Simultaneous step-ladder and hide observations

Since the results from the hide observations gave rather poor data on the composition of the food given to nestlings, only 8 one hour simultaneous observation sessions were carried out. The results (Table 4.27) show little resemblance to those in Table 4.15 and are of limited value. They do perhaps suggest that more caddis flies are taken from Marsh than Carr and that damsel flies are obtained equally from both habitats.

4.15 Foraging behaviour

All observations relate to foraging for nestlings. Only two IM nests were studied and are not included. Table 4.28 summarises the feeding locations of adult Reed Warblers foraging for nestlings. Inward and outward journeys are combined, and habitat type is divided simply into 'Marsh' and 'Carr'. Thus, for a given nest, 'Marsh' means either PM or MM, but is in fact usually the same as the nesting habitat. The observations represent 1600 feeding locations obtained from 29 nests (18 PM, 11 MM) during a total time of 87·5 hours.

Adults from PM nests forage more in Carr than those from MM nests (adj $\chi^2 = 56{\cdot}7$, $p < 0{\cdot}001$, d.f. = 1), suggesting perhaps some overall deficiency in PM over MM. Although in no way conclusive, this does agree with the very general conclusions of food availability found in the water traps (Table 3.18). On the other hand Table 4.16 shows no gross difference in the diet of nestlings between the two habitats. The proximity of suitable Carr to a nest site may well influence its utilization, but no measurements were taken in this respect.

The distance travelled to and from foraging locations must indicate in some way the 'quality' of a nesting habitat in relation to food availability.

	Marsh (%)	Carr (%)	Totals
PM	464 (51)	438 (49)	902
MM	490 (70)	208 (30)	698

Table 4.28 Numbers of observed foraging locations of adult Reed Warblers collecting food for nestlings.

Fig.4.19 shows the relationships between the mean distances travelled from the nest by foraging adults according to the age of nestling for the two habitats. (The unit of distance is arbitrary and is merely that measured from the habitat maps used for plotting). Only in PM did adults forage further away from the nest as the age of nestlings increased ($0{\cdot}05 < p < 0{\cdot}1$).

The number of foraging trips to Carr also increases with increasing nestling age (Fig. 4.20). In this case, both rates of increase are significantly greater than zero ($p < 0{\cdot}01$, PM; $p < 0{\cdot}2$, MM). The difference in rates is however not significant ($p > 0{\cdot}2$).

4.16 Diurnal pattern of foraging activity

Although larvae and spiders are of prime importance in the food given to nestlings, emergent aquatic insects also make up a considerable proportion of the diet. The methods used made it impossible to assess accurately the exact composition of such prey within the diet. Nevertheless the data gathered on direct foraging can be used to infer the importance of aquatic insects, which from Table 4.28 would appear more important in MM than in PM.

The diurnal pattern of emergence of aquatic insects was not considered, but is generally known to occur most frequently in early morning or late evening (Orians 1980). Fig. 4.21 shows the diurnal pattern of foraging activity of adults. The pattern strongly reflects a typical insect emergence cycle given in Orians (1980).

The dispersion of recently emerged insects from the reed-beds towards the areas of Carr probably improves these areas as potential feeding places and could explain the rise in utilization of Carr during the morning. Thereafter, there is a return to reed-bed foraging, which appears, from the little data available, to last for the remainder of the day.

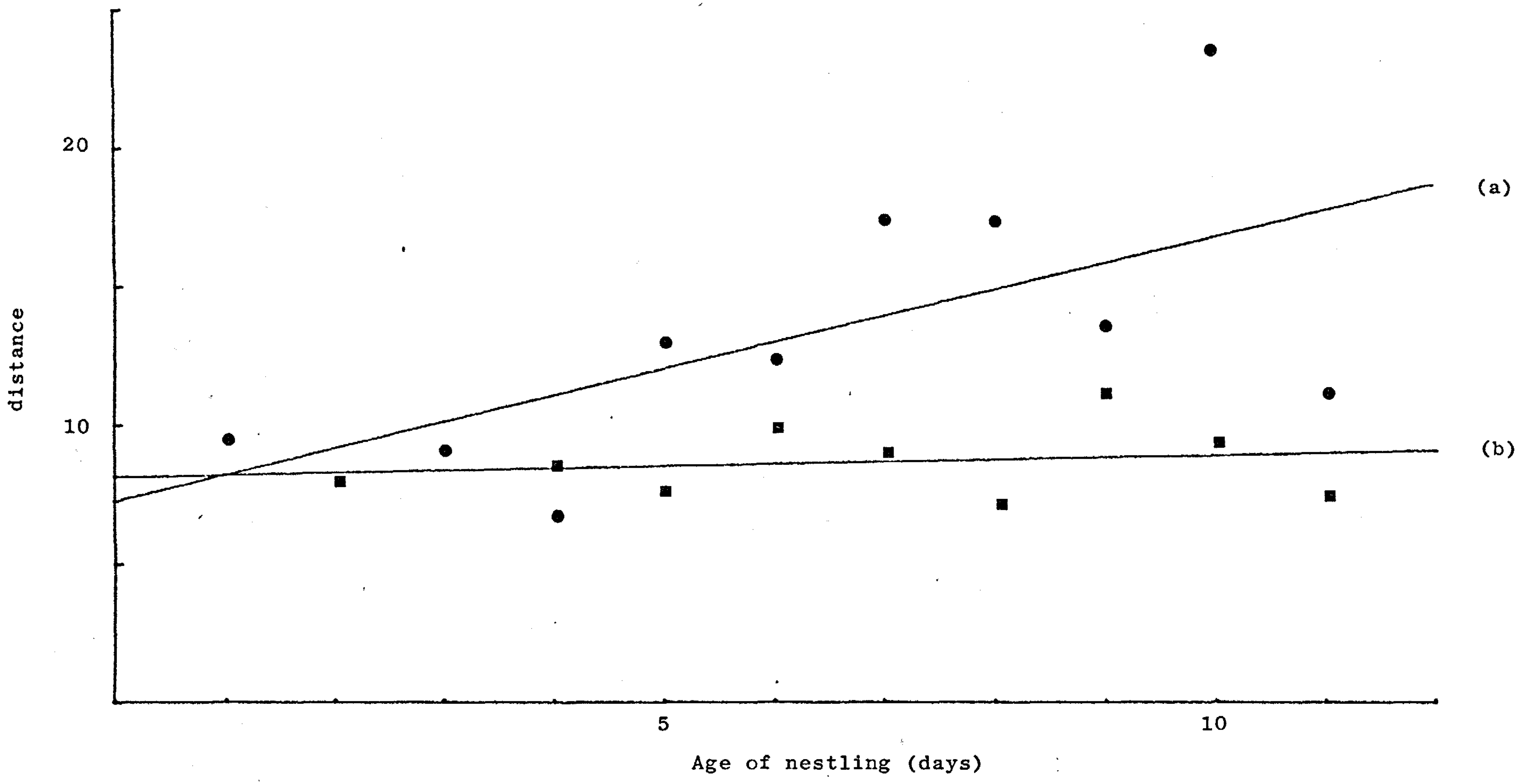

Fig. 4·19 Mean foraging distances of adult Reed Warblers collecting food for nestlings according to age of nestling. (a) ● PM, y = 0·96x + 7·25, (b) ■ MM, y = 0·08x + 8·16 (scale arbitrary).

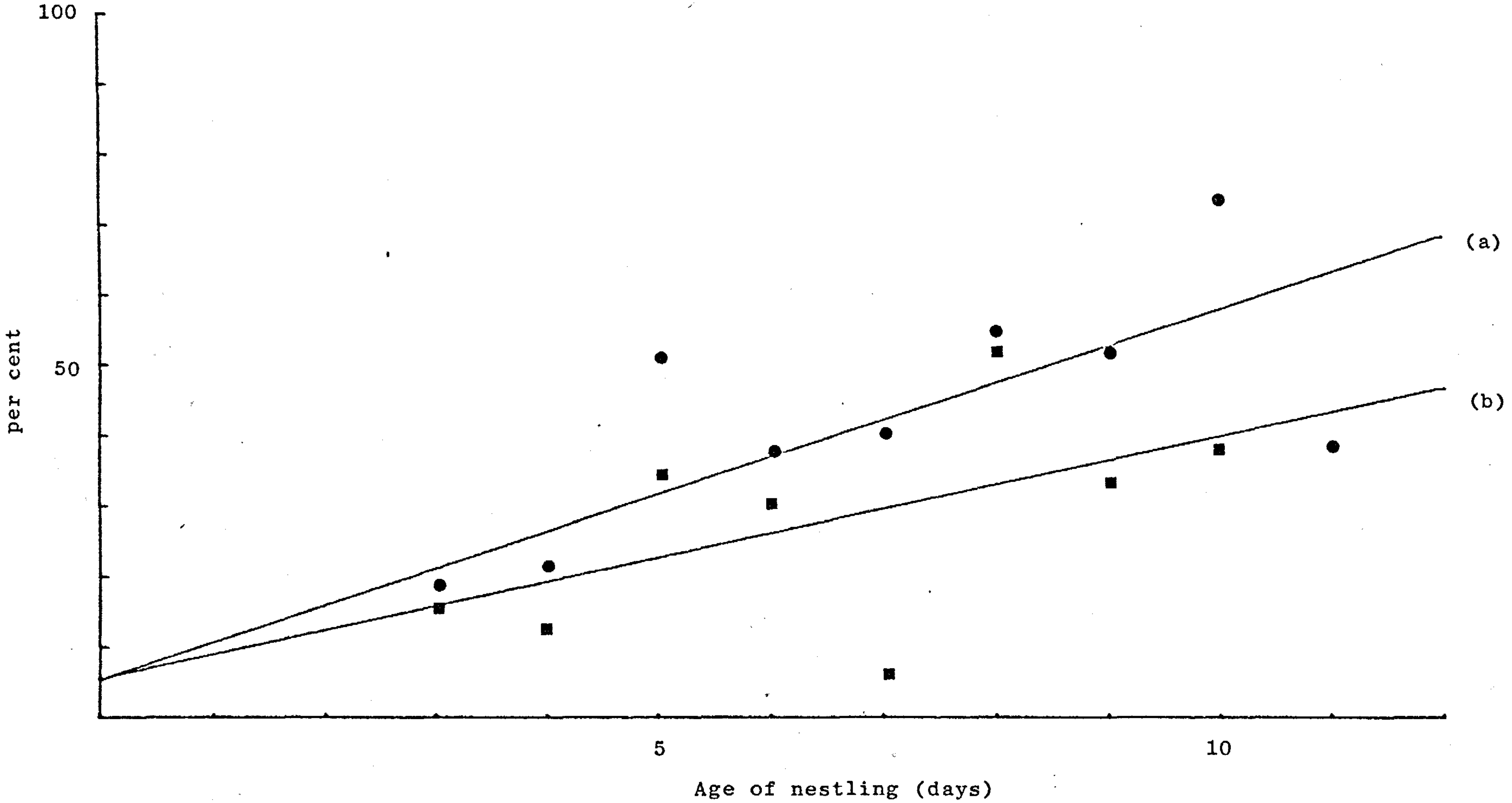

Fig. 4·20 Percentage of trips to Willow/Alder Carr made by adult Reed Warblers foraging for nestlings by age of nestling. (a) ● PM, $y = 5{\cdot}26x + 5{\cdot}36$, (b) ■ MM, $y = 3{\cdot}44x + 5{\cdot}51$ (scale arbitrary).

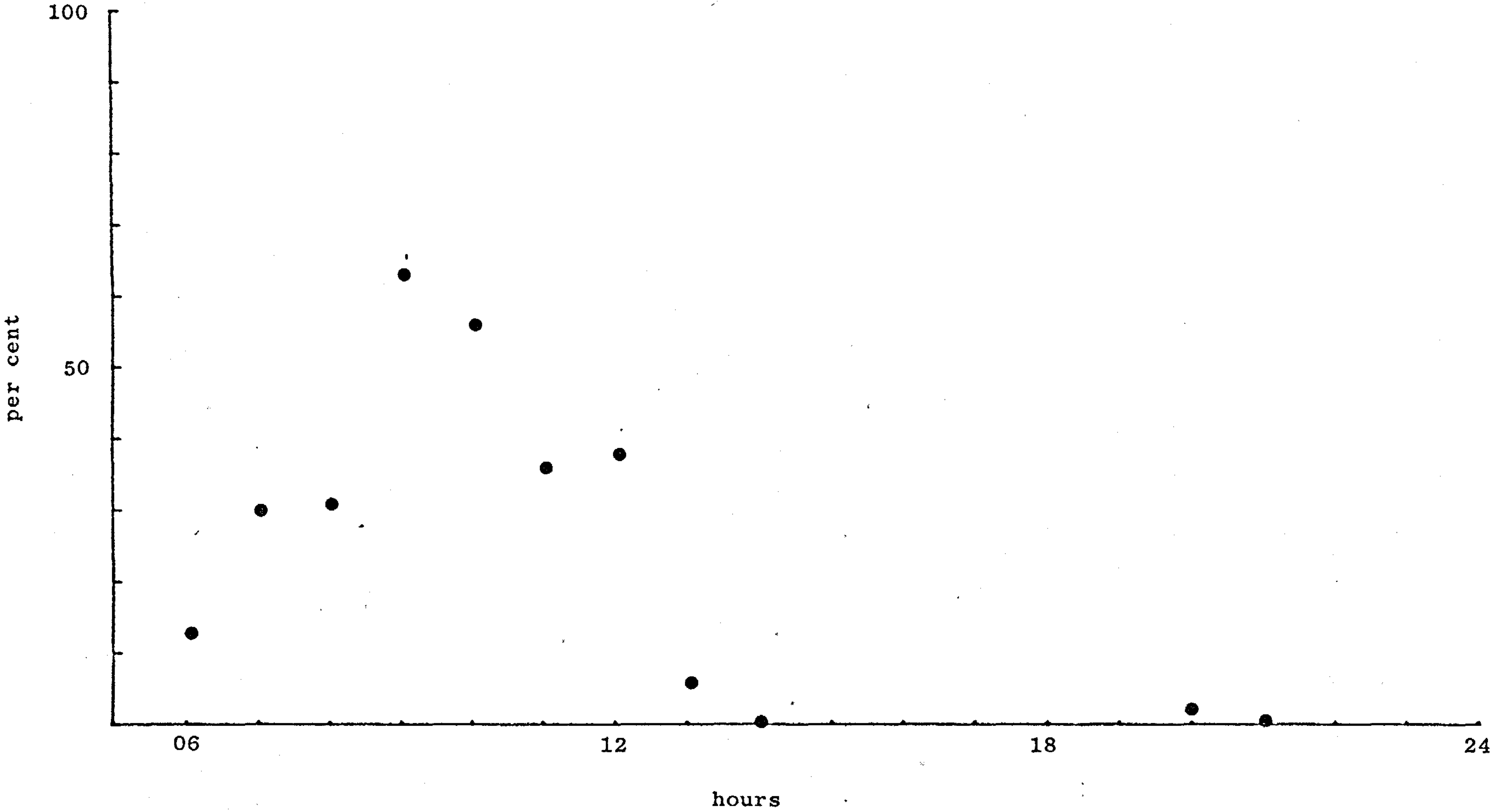

Fig. 4·21 Diurnal variation of percentage trips to Willow/Alder Carr by adult Reed Warblers foraging for nestlings.

Some insight into the feeding behaviour later in the day can be found by considering the observations gathered from a hide at one particular PM nest. The nest was watched from 19th - 29th June inclusive and from 19.18 - 20.18 hrs. on each day. It contained 4 nestlings throughout. As is to be expected, the feeding rate increased with the age of the nestlings, there being a total of 178 feeds during the 11 hours of observation. Damsel flies, which were readily recognised were very frequently brought from 23rd June onwards and totalled 98 in all. 88 feeds contained 'food-balls'. The only other items seen were 8 caddis flies, 2 lacewings and 2 larvae. Even though the 'food-balls' almost certainly contained some spiders, it is nevertheless clear that during this early evening period, a large proportion of the diet consisted of insects with an aquatic larvae stage.

An obvious explanation of these results is that emergent aquatic insects are most common in the early morning in the reed-beds and are easy to catch (being cold and inactive). As the ambient temperature rises, the insects disperse and are pursued by the foraging adults. The return to reed-bed foraging in the late morning is possibly a response to a lowering of prey capture rate, again as a result of increasing temperature. Finally the large numbers of aquatic insects taken during the evening may well be a result of their return to the reed-bed due to the fall in temperature and for egg-laying.

4.17 Discussion

In the introduction to this chapter, the basic question was raised as to whether Reed Warblers prefer to breed in reed-beds or, as Catchpole (1974) suggests, are perhaps undergoing some kind of ecological expansion away from this traditional habitat. Although we have followed a common course and concentrated solely on a population in its 'optimal' habitat

(Orions and Willson 1964), no Reed Warblers were found breeding outside reed-beds, and the results suggest strongly that reed-bed breeding, at least at Oxwich, is very profitable, even in the 'poorest' areas.

The breeding season begins 8 days earlier in PM than in MM and 4 days later still in IM (Table 4.1). These marked differences suggest in the first instance either differential feeding conditions between habitats, and/or structural variations in the vegetation resulting in differences in its suitability for nest-building.

Setting aside for the present differential feeding conditions, we recall that nest height was correlated with season (Fig. 4.2) in all habitats, with nests in PM being built higher, more rapidly, than elsewhere. No differences in the age of reed-stems used between habitats were found,but, as is to be expected, new stems are used more frequently later in the season (Fig. 4.3). The mean number of stems used to support each nest was higher in PM than elsewhere (Fig. 4.4) and much higher than in Catchpole's study, suggesting structurally safer nests.

Reed Warbler clutch sizes varied very little between habitats and were about the same as those found by Catchpole (1974) and Bibby (1978). Clutch size fell with season as is common in many species (Klomp 1970). However this fall was more dramatic in PM than elsewhere, suggesting that feeding conditions might deteriorate more here later in the season, a view supported by Table 3.18. Lack (1968) argued that this decline in clutch size was due to food availability being less as the season progresses, but Bibby (1978) suggested that this is probably not the case for Reed Warblers, since the major growth of vegetation occurs well after the start of breeding, resulting in an increase in insect abundance. Table 3.17 suggests that this is in fact not true, and that overall insect abundance peaks during the time most adults have young in the nest.

Brood size at fledging, like clutch size, did not vary much between habitats, and also fell with season. The differences in rates were slight and not significant. Bibby (1978) found to his surprise, that the largest broods are reared from the largest clutches contradicting Lack (1954). At Oxwich the same appears to be the case and is not easily explained. Bibby's sample (from the B.T.O's national nest-record collection) contained a bias towards success by excluding those nests which had already failed. As far as was known, this was not the case at Oxwich, and since brood size was determined at fledging (and not on day 7, as in Bibby's analysis) an explanation must be sought in the post-fledging period.

A direct probability method for estimating nesting success was employed (Mayfield 1974) since ample data was available to calculate overall and between habitat probabilities of success for the egg and young stages, and nest outcomes. Eggs were more prone to failure than young, and the probability of nest success was slightly higher in MM than in PM, and very low in IM (Table 4.7). Since brood sizes at fledging varied little between habitats, the net result was a slightly higher nest-outcome in MM and a low outcome in IM. All these results suggest much higher nest success at Oxwich than elsewhere, even in the IM. Seasonal variations of nest-outcomes (Fig. 4.7) fitted well with the model given by Bibby (1978).

Causes of nest failure were not easy to identify, but were mostly due to predators of some kind, and not from nests falling etc. There was circumstantial evidence that the contents of a great many nests were removed or eaten in situ by Woodmice. Havlin (1971) and Catchpole (1974) proposed the view that Reed Warblers breed more successfully outside reed-beds because of the greater risk of predation on reed-bed nests which tend to be grouped closely together (Catchpole 1972). Since none were found breeding outside the reed-beds, this is certainly not true at

Oxwich, and no evidence of mass plundering of nests was found, even though some nests were situated in 'loose colonies'. Catchpole (1974) also lists a variety of possible predators, but most of these would appear to be unnatural inhabitors of reed-beds, indeed only one, the Brown Rat was a definite predator at Oxwich.

In many reed-beds a major cause of nest-failure in Reed Warblers is the Cuckoo (Lack 1963), which was not a parasite at Oxwich. As far as is known, no comparisons have been made between Reed Warblers in reed-beds with and without Cuckoos, and the present study appears to be the first detailed account of Reed Warblers breeding exclusively in a Cuckoo-free reed-bed. In this respect, the very high nest-success rates are particularly interesting.

Nestlings from PM nests (i.e. the earlier breeders) were markedly heavier throughout the nestling period than those from elsewhere (the later breeders) (Fig. 4.8). Although this fits well with other aspects so far discussed, it is somewhat surprising, since many observers (e.g. Drycz 1963, 1974, Perrins 1970) have found that egg weights, and therefore presumably hatching weights increase with season. On the other hand, others have found the opposite to be the case (Coulson 1963, Dryčz 1974), so different factors must affect different species. Nevertheless, the mean weight of young at fledging was more than one grm. higher in PM nests, a weight advantage of almost 10%, which presumably gives these young a greater chance of survival in the post fledging period. Thus, even though slightly fewer young per nest are produced from the PM nests, they are of a 'higher quality' and were raised from pairs whose females are able to manufacture heavier eggs.

We are thus led to a consideration of the fledging conditions in the early part of the breeding season and in particular to the feeding ecology of females at this time. It was found in Chapter 3, that during this period Chironomids were abundant, but with many more caught in PM traps than elsewhere (Table 3.11 to 3.14). Even though no observations were made of adult feeding behaviour, this strongly suggests that a key factor in the breeding biology of Reed Warblers is the availability of a suitably abundant food source during this critical egg-laying period. The nature of this food supply probably varies from place to place, but Chironomids are generally abundant in wet places in spring (Street 1977) and could be a constant factor for the species as a whole.

Many observers have given superficial lists of the general composition of the foods of nestling Reed Warblers (e.g. Brown and Davies 1949, Catchpole 1973), but only Henry (1977) and, to a less extent Davies and Green (1976) have so far given any detailed account. Henry's technique involved the use of neck-collars, and he was therefore able to collect whole food items and identify families. Our methods used mostly the analysis of faecal remains, which necessarily gave less precise results, and only orders were recognised. A subjective comparison reveals however that the general compositions of the diets are similar.

The important findings of the faecal analysis results at Oxwich were that nestling Reed Warblers were fed mostly on 'food-balls' consisting usually of spiders, flies, beetles and bugs, together with a wide variety of other, larger, and important taxa e.g. damsel flies, caddis flies and larvae. The general composition of the food given to nestlings approximately matched the pattern of availability as found from the water-traps, supporting the view of Henry (1977) that Reed Warblers are generalist feeders. The diet varied according to habitat, with some taxa being important in one habitat but less so in others and vice versa. Diet also varied with nestling age (Table 4.18), larger taxa being fed more frequently to older nestlings, and more spiders to the younger ones. Evidence that the occurrence of larvae, spiders and Nematoceran flies increases the weight of nestlings was also found, but no overall between habitat effect of diet on nestling weight was apparent, indicating that to a very large extent, hatching weight strongly influenced fledging weight.

Good agreement was found between the total calorific food value given to nestlings and the period of maximum growth rate (Table 4.20), with a major proportion of this being attributed to larvae and spiders. Agreement was also found between calorific food values and season, but not between habitats (Table 4.24). In all these calculations, no account was taken of prey size and 'average' values were used (Orians 1980). The results hide any possible size selection within taxa, an adaptation commonly found in many animal groups (e.g. Henry 1977, Krebs 1978, Bibby 1979), and merely reflect the overall situation.

Feeding observations from hides proved to be of limited value, since food items were only identifiable when large. There were no differences in feeding rates between habitats. Observation of foraging locations on the other hand proved to be of great value and showed considerably more Carr feeding in PM than in MM, which, together with the dry weight figures from the water traps (Table 3.18), suggests that adults from PM nests find poorer feeding conditions there and are forced to forage elsewhere. This is further reinforced on considering the distances travelled by foraging adults as nestlings grow older. Fig. 4.19 showed that this was greater only in PM. This apparent 'deficiency' in habitat does not detract from the general picture of PM nests producing better quality young, it merely suggests that in order to maintain the advantage of heavier day 0 nestlings, adults must work harder, and this indeed appears to be the case.

Finally we point out that the availability of food for egg production has been put forward as a factor determining the start of the breeding season, but not as a factor likely to affect clutch size (Perrins 1965, 1970) and this appears to be the case for Reed Warblers.

CHAPTER FIVE

Breeding biology of the Reed Bunting

Introduction

In recent years, a great deal of attention has been given to the supposed ecological expansion of the Reed Bunting away from marshland habitats to open woodlands, dry wooded heaths and farmland (Kent 1964, Bell 1969, Gorden 1972, Prŷs-Jones 1977). It would appear that even though some proportion of Reed Buntings do breed in areas away from water, a very large proportion are still to be found in the traditional habitats.

This chapter reports on work carried out at Oxwich during the 1978, and to a lesser extent the 1979 breeding seasons, with the aim of investigating relationships between the species' breeding biology with respect to marshland habitats. As in Chapter 4, the results are designed to emphasise the variations of breeding success within a reed-bed, and not to consider these problems in relation to marsh, scrub, grassland etc. (Bell 1968, Hornby 1971).

Methods

As far as possible, the same methods were employed as for the Reed Warbler (Chapter 4). Most of the work was carried out during the 1978 breeding season, but some nests were found during the 1979 Reed Warbler study and data gathered from these (mainly nestling weights) is used.

Reed Buntings respond well to a Common Bird Census (Bell, Catchpole et al 1973) and so in order to identify breeding pairs, one was undertaken in the study area in 1978.

Unlike the Reed Warbler, the Reed Bunting is not in any way colonial, and breeds at a much lower density. Thus, in order to make sample sizes as large as possible, both years are combined whenever possible. Again in contrast to the Reed Warbler, nests were often very hard to find, and a great deal of effort was put into this. In spite of this, all nests in the study area were considered found in 1978, and about one half in 1979. A total of 22 nests was found in all. When found, nests were followed through to the fledging stage and nestlings weighed as before. Previous personal experience with the species had shown that adults were liable to desert nests with eggs if disturbed too often, and so some nests with 'nervous' females were not visited daily during this time. Also nestlings were difficult to replace safely in the nests after about day 6, and so few were weighed beyond this age.

The feeding ecology of nestlings was studied as before by collecting faecal sacs, observing nests from hides and plotting foraging locations from a step-ladder. Since Reed Buntings can easily be sexed in the field, feeding observations from hides and foraging locations were recorded separately for males and females.

The same habitat classification as described in Chapter 2 was used, but since the total number of nests found was relatively small, MM and IM are combined and are referred to throughout this chapter as 'other' marshland - OM.

Results

5.1 Timing of breeding

The results of the Common Bird Census are given in Fig.5.1 and show a fairly even distribution of territories, apparently completely 'filling' all the available marshland habitat. In fact the census extended beyond the study area and covered almost the whole marsh, and the results indicate

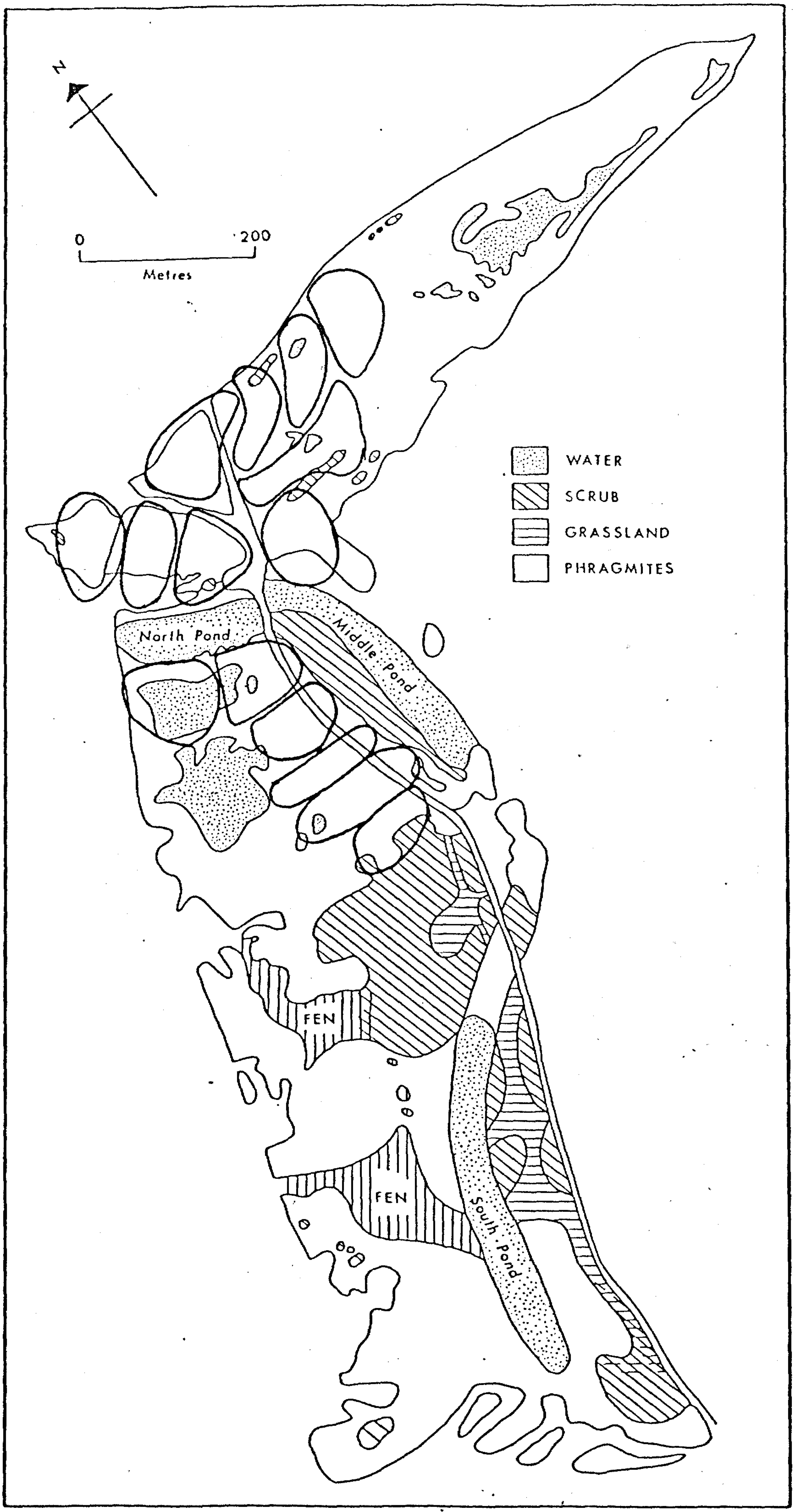

Fig.5·1 Positions of Reed Bunting territories in study area (1978) a possible complete occupation of the entire area. Exact territory boundaries were not plotted and are drawn in Fig. 5.1 in an arbitrary fashion. There nevertheless appears to be no obvious density difference over the marsh.

Territory occupation by males is not used to assess the timing of breeding, rather first egg dates are used as in §4.1. The start of breeding in PM and elsewhere is shown in Table 5.1 and Fig. 5.2. The results show that, taking both years together, Reed Buntings breed very much earlier (14·9 days) in PM than elsewhere ($p < 0{\cdot}05$), with a similar result for 1978 alone.

5.2 Nest sites

All nests were built on or very near to the ground and were constructed in typical fashion (Witherby et al 1940). In PM, nests tended to be built at the base of reed-stems, or amongst clumps of fallen reeds, which had the effect of raising them slightly above ground or water level. During April and May, water levels on the marsh were still fluctuating, and indeed one nest in PM was washed out. In MM (but not IM) several nests were built amongst fast growing vegetation such as Rumex hydrolapthum, Iris pseudacorus and Oenanthe fistulosa, resulting in these nests being gradually raised above the ground during their occupation. In spite of this, only one nest was ever in excess of one metre above ground or water level. In general, nests in PM were built on average slightly nearer the ground than elsewhere, but this was not measured.

5.3 Clutch size

As in the case of Reed Warblers, only complete clutches are included in Table 5.2, which gives the frequency distribution of clutch sizes according to habitat for both years combined. It is difficult to infer

		PM	OM	All
(a)	n	7	14	21
Mean first egg date		17·14 May	1·07 June	27·1 June
s.d. (days)		5·79	14·81	14·3
(b)	n	5	10	15
Mean first egg date		16·6 May	1·7 June	27·33 June
s.d. (days)		6·77	16·55	15·84

Table 5.1 Mean first egg dates of Reed Buntings by habitat (a) 1978 and 1979, (b) 1978 only.

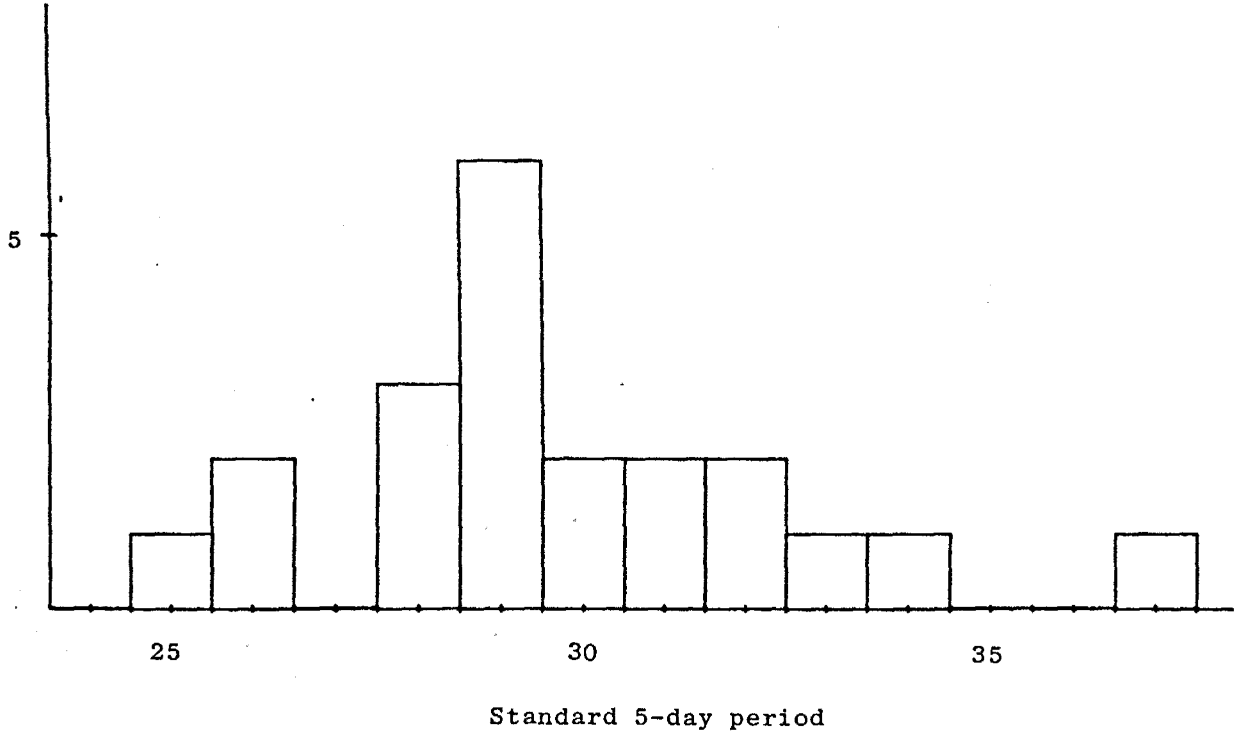

Fig.5·2 Frequency distribution of first egg dates of Reed Buntings in standard 5-day periods.

	Clutch size				
	4	5	Total	Mean	s.d.
PM:					
number	3	4	7	4·57	0·53
per cent	43	57			
OM:					
number	5	4	9	4·44	0·53
per cent	56	44			
All:					
number	8	8	16	4·5	0·52
per cent	50	50			

Table 5.2 Frequency distribution of clutch sizes of Reed Buntings.

much from such a small sample, but the results show no significant differences in mean clutch size between habitats ($p > 0{\cdot}2$).

Clutch size fell slightly with season (Fig. 5.3), but not significantly so ($p > 0{\cdot}2$), but again too few clutches were available to give reliability to the result.

5.4 Brood size

Brood sizes at fledging are shown in Table 5.3, and, since nests were visited almost daily during the nestling stage, are considered to be good estimates. Sample sizes are again small, especially in PM, but even so, PM nests produced significantly more fledged young than elsewhere ($p < 0{\cdot}2$). This result is somewhat surprising in view of the similarity of clutch sizes. It is possible that feeding conditions are superior in PM, but more likely that the differences are the result of small samples.

Fig. 5.3 shows that unlike clutch size, brood size at fledging decreased significantly with season ($p < 0{\cdot}01$), but again too few data points are available to consider between-habitat variations. It is possible however to obtain some information concerning this differential loss, by considering Table 5.4 which shows the percentage of young lost between hatching and fledging. The results indicate that the fall in brood size occurs mainly as a result of partial losses in OM.

5.5 Nest success and clutch size

Table 5.5 gives brood sizes of successful nests in relation to clutch size. It shows that slightly more young are produced from clutches of 4 eggs, but this is difficult to relate to Table 5.2 since clutches of 4 and 5 are equally divided in the small sample. On the other hand, Bell (1968) and Hankioja (1970) found that the most common clutch size was five, suggesting that perhaps for Reed Buntings, the largest brood

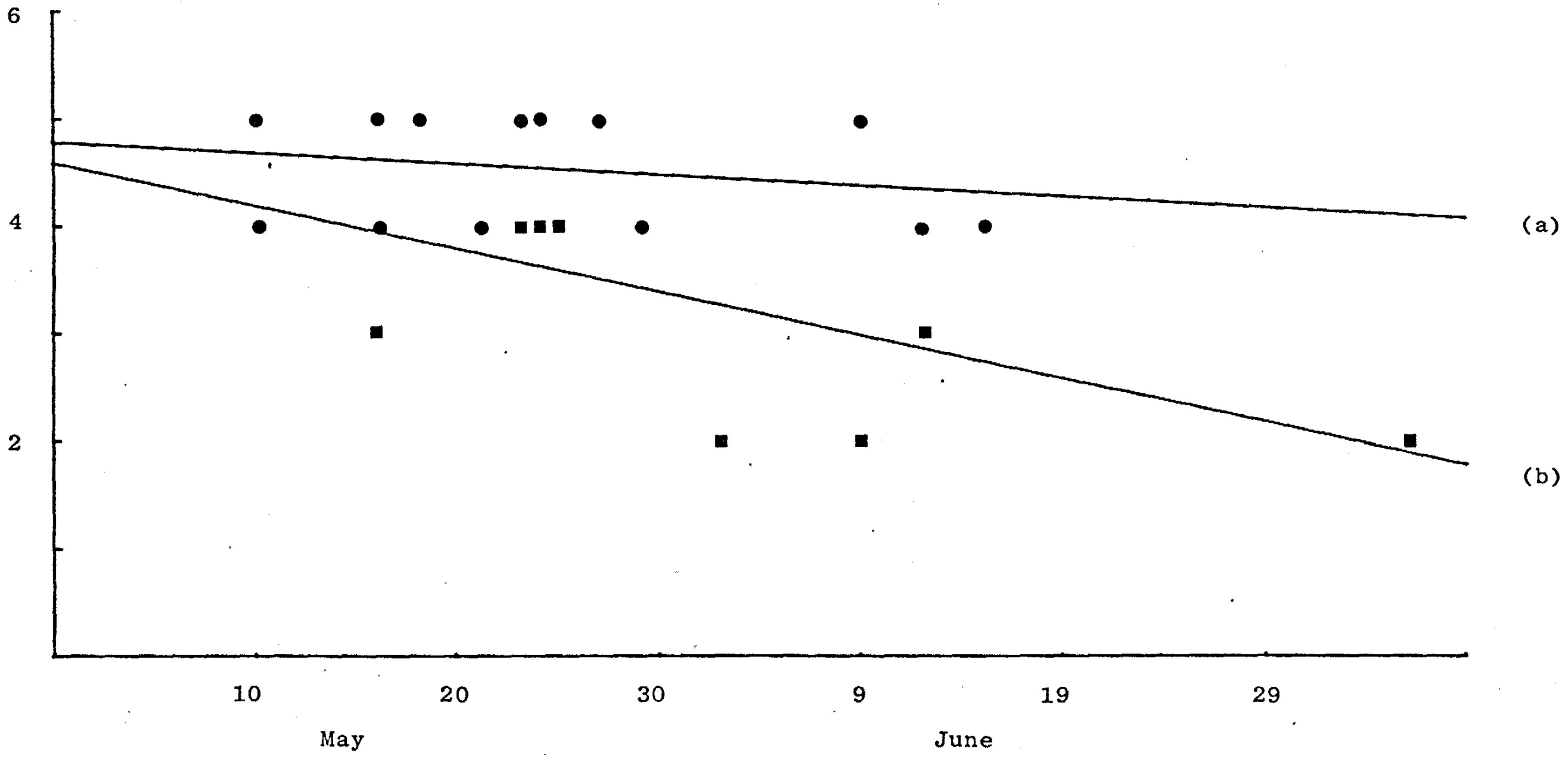

Fig.5·3 Seasonal variation in mean clutch sizes (a) and mean brood sizes at fledging (b) of laying of first egg of Reed Buntings. (All habitats). ● clutch, ■ brood.

	Brood size					
	2	3	4	Total	Mean	s.d.
1978	0	1	4	5	3·8	0·45
1979	3	1	4	8	3·13	0·99
1978 + 1979	3	2	8	13	3·38	0·87
per cent	23	15	62			

Table 5.3 Frequency distribution of brood sizes at fledging of Reed Buntings.

	Number of young hatched	Number lost	% lost
PM	20	1	5·0
OM	28	4	14·29

Table 5.4 Partial loss of nestling Reed Buntings by habitat. (Excluding predated nests).

Clutch size	number	Brood size of success
4	4	3·75
5	5	3·4
Total	9	3·56

Table 5.5 Outcome of Reed Bunting nests of known clutch size found during building, laying or incubation. (All habitats).

sizes are produced from the largest clutches (Lack 1954), in contrast to the results already obtained for the Reed Warbler in §4.6.

5.6 Breeding success

In calculating nest success, we follow the probability method described in §4.7. In the case of the Reed Bunting, egg-laying lasts 4 - 5 days, incubation 12 - 13 days and the fledging period extends for about 12 days. We therefore estimate nesting probabilities by taking 17 days for the egg stage and 12 days for the young stage. Both years are combined to increase the sample size.

Too little data is available for nest outcomes to be plotted seasonally, and so Table 5.6 sets out the overall survival probabilities divided according to habitat. In PM eggs are more prone to failure than are young, but elsewhere the situation is reversed, with nests standing a rather poor chance of surviving the young stage. The net result is that PM nests have a much greater probability of survival than elsewhere, with correspondingly higher nest outcomes (i.e. prob. of nest success x mean brood size at fledging from Table 5.3).

The overall probability of nesting success (0·4818) in Table 5.6 is rather low and, taken together with the mean brood size at fledging (3·38), suggests that in 1978, an average minimum of 2·46 nesting attempts per pair was necessary to produce four fledged young. This is consistent with the Reed Bunting as a double or triple brooder (Witherby et al 1940). However, evidence of multiple brooding was difficult to observe, the net result being that relatively few young were probably produced. Evidence to this effect can be seen from Table 4.8.

Bell (1968) also found that in his study relatively few pairs successfully reared more than one brood during the course of a season, and attributed this mainly to nest predations. His results show that during the summers

PM:	Days of survival	Days of failure	Prob. of daily survival
nests with eggs	65	1	0·984848
nests with young	61	1	0·983871

Probability of nest success = $0{\cdot}984848^{17} \times 0{\cdot}98371^{12}$

= 0·771401 × 0·822731

= 0·634655

Nest outcome = 0·634655 × 3·8 (from Table 5.3) = 2·41

OM:			
nests with eggs	53	1	0·981482
nests with young	98	5	0·951456

Probability of nest success = $0{\cdot}981482^{17} \times 0{\cdot}951456^{12}$

= 0·727773 × 0·550385

= 0·400555

Nest outcome = 0·400555 × 3·13 (from Table 5.3) = 1·25

All:			
nests with eggs	118	2	0·983333
nests with young	159	6	0·963636

Probability of nest success = $0{\cdot}983333^{17} \times 0{\cdot}963636^{12}$

= 0·751472 × 0·641148

= 0·481805

= 0·481805

Nest outcome = 0·481805 × 3·38 (from Table 5.3) = 1·63

Table 5.6 Probability of nesting success of Reed Bunting calculated from the daily chance of avoiding total failure.

1964 - 1966 the number of attempts per pair was 2·29 with a mean number of young raised per pair of only 2·7.

Although it is difficult to obtain an accurate estimate, the observation suggests that at Oxwich a minimum of 1·86 attempts per pair was made, which together with the probability of nest success, and brood size at fledging estimates gives a figure of 3·03 young raised per pair. This again falls short of what one should expect.

5.7 Causes of nest failure

From a total number of 22 nests found, 8 failed as a result of predation and Table 5.7 indicates that more were lost during the young stage, especially in OM nests.

Few clues as to the identification of predators were found, since in most cases the nests were little damaged and usually had had the contents removed. On two occasions the nestlings had clearly been eaten at the nest, possibly by a small mammal, and on another occasion the young were found dead in the nest after a night of very heavy rain. It is possible that Water Rails were a predator, since incubating Reed Buntings often became quite nervous on hearing them call close to the nest (personal observations from hides).

5.8 Nestling growth

The growth patterns of nestling Reed Buntings are shown in Table 5.8 (Day 0 = hatching day), and are divided by habitat. The results represent a total of 303 nestling weighings from 74 nestlings in 19 nests. As in the case of the Reed Warbler (§4.9), nestlings in PM nests are heavier than elsewhere, however these weight differences are smaller, and are not significant until day 4 (Table 5.9). The difference in day 6 weights is

	PM	OM
Number failing at egg stage	1	1
Number failing at young stage	1	5
Total number of nests found	7	15

Table 5.7 Failures of Reed Bunting nests by habitat.

PM				OM			
Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.	Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.
0	11	2·17	0·42	0	19	2·08	0·54
1	16	3·29	0·76	1	35	3·01	0·75
2	16	4·74	1·15	2	28	4·46	1·08
3	24	6·92	1·44	3	28	6·61	1·33
4	12	10·21	1·62	4	25	9·1	1·6
5	20	12·28	2·17	5	21	10·98	1·4
6	12	13·61	1·28	6	22	13·17	2·14
				7	7	14·37	2·33
				8	7	15·73	3·26

Table 5.8 Mean weights (g) of nestling Reed Buntings by habitat.

Age of nestling (days)	PM v OM
0	n.s
1	n.s
2	n.s
3	n.s
4	$0{\cdot}05 < p < 0{\cdot}1$
5	$p < 0{\cdot}05$
6	n.s

Table 5.9 Significant differences in mean weights of nestling Reed Buntings by habitat (n.s = $p > 0{\cdot}2$).

	Number of nestlings in brood			
	2	3	4	5
Number of nestlings	2	6	28	5
Mean weight (g)	12·75	10·52	11·89	10·94
s.d.	0·92	1·95	1·96	1·37

Table 5.10 Mean weights (g) on day 5 of nestling Reed Buntings in various brood sizes.

not significant, and it is difficult to speculate eventual fledging weights from Fig. 5.4. Fledging weights can be estimated by fitting the data in Table 5.8 to the logistic growth curve as in §4.9. The weights on days 7 and 8 are not included in the analysis so as to produce comparable estimates. The results give growth constants of $K = 0{\cdot}634$ for PM nests (10 iterations, $r = 0{\cdot}9966$) and $K = 0{\cdot}594$ for OM nests (4 iterations, $r = 0{\cdot}9966$), and predicted weights on day 12 of 15·67 and 15·17grms. respectively, showing that the differences in weights of nestlings after day 4 are maintained up to fledging age.

5.9 Effect of brood size on nestling weights

Following §4.10, Table 5.10 sets out the mean weights of nestling Reed Buntings on day 5 for various brood sizes. Ignoring the single broods of two and five nestlings, the heaviest young are found in broods of four, the most common size at fledging (Table 5.3). The difference in mean weight between brood sizes three and four is barely significant ($p < 0{\cdot}2$).

5.10 Seasonal variation in nestling weights

Table 5.11 shows nestling weights by age in early (first-egg date before five-day period 30, i.e. May 26), and late broods. Although very young nestlings are heavier in late broods, the results show this situation is reversed on about day 2 and thereafter young from early broods are heavier. In spite of this, weight differences are small, with only day 6 being significant ($p < 0{\cdot}1$). This again is possibly a result of small sample sizes of older nestlings.

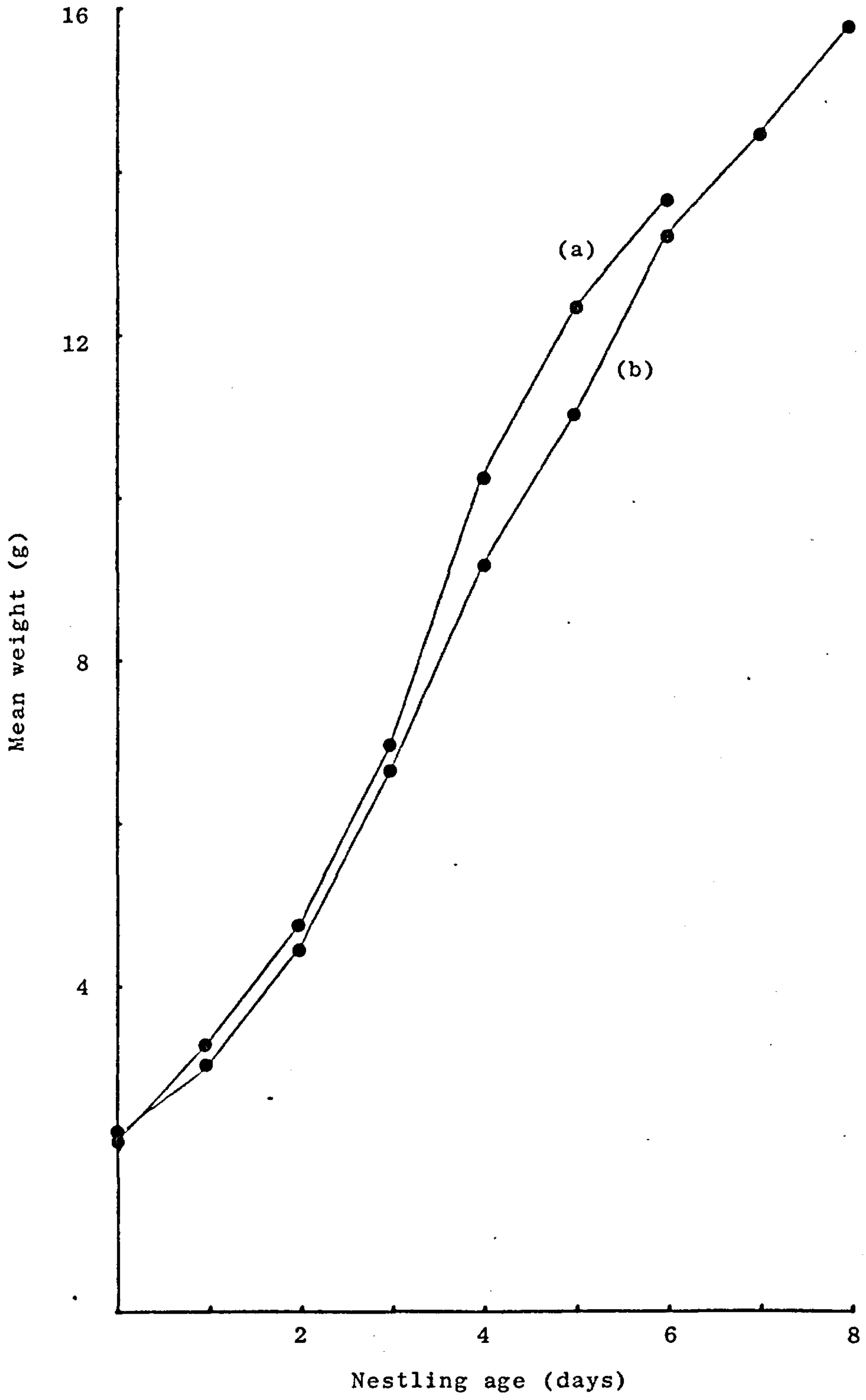

Fig.5·4 Mean weights of nestling Reed Buntings by age of nestling (a) PM, (b) OM.

Early broods †				Late broods			
Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.	Age (days)	Number of nestlings weighed	Mean weight (g)	s.d.
0	19	2·03	0·38	0	11	2·26	0·64
1	30	3·04	0·66	1	21	3·17	0·89
2	25	4·56	0·96	2	19	4·56	1·29
3	41	6·79	1·22	3	11	6·63	1·90
4	25	9·42	1·55	4	12	9·56	1·96
5	36	11·69	1·84	5	5	11·06	2·55
6	28	13·58	1·50	6	6	12·15	2·99
7	7	14·37	2·33	7	0	-	-
8	3	16·70	1·21	8	4	15·00	4·32

Table 5.11 Mean nestling weights (g) of Reed Buntings in early and late broods († = first egg date before May 26).

5.11 Asynchronous hatching

As was found for Reed Warblers (§4.12), mean weight differences between heaviest and lightest nestlings in each brood are correlated with nestling age and this is shown for each habitat in Fig. 5.5. In this case the relation is linear, and both slopes are significantly greater than zero (PM, $p < 0{\cdot}02$; OM, $p < 0{\cdot}001$) but the difference between slopes is not ($p > 0{\cdot}2$).

5.12 Feeding ecology of nestlings

(a) Faecal analysis

5.12a (i) General diet

Faecal sacs were collected during the 1978 breeding season only and a total of 44 was obtained. The overall results of the faecal analysis are given in Table 5.12, where the total of 315 items listed (mean 7·2 per faecal sac) again represents the minimum number of prey detectable from the remains. The results show the importance of larvae, and beetles (mostly large Chrysomelidae) in the diet, which together make up 74·6 per cent of the items identified. Both these prey items are relatively immobile, and if available must obviously attract the attention of a species like the Reed Bunting whose feeding behaviour is clearly not adapted for catching fast-moving flying insects. The same argument can also be applied to the two other important taxa in the diet i.e. spiders and damsel flies, although the latter is probably only a viable prey in early morning or late evening. Since the number of taxa listed in Table 5.12 is also quite small, the Reed Bunting, at least at Oxwich, is a more specialist feeder than the Reed Warbler, especially since the availability of food as measured by the water traps (Chapter 3) corresponds poorly with the diet given to nestlings.

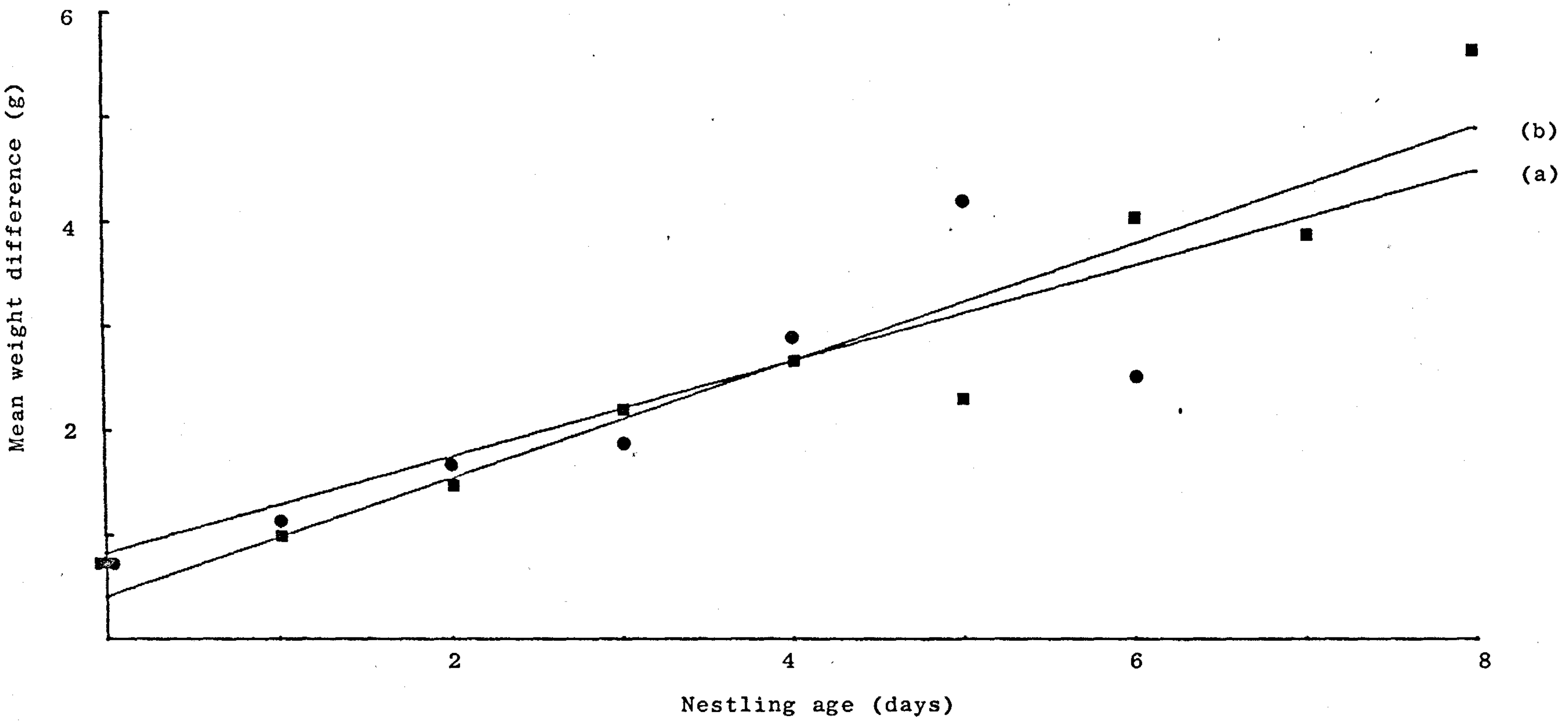

Fig.5·5 Mean difference between lightest and heaviest young in Reed Bunting nests by nestling age, (a) PM ● , (y = 0·82 + 0·46x), (b) OM ■ , (y = 0·40 + 0·56x). 1978 and 1979 combined.

	n	per cent	per cent with
Collembola	1	0·32	2·27
Araneae	20	6·35	34·09
Diptera	11	3·49	22·73
Coleoptera	131	41·59	90·91
Odonata	29	9·21	45·45
Trichoptera	8	2·54	13·64
Plecoptera	8	2·54	9·09
Hymenoptera	1	0·32	2·27
Gastropods	2	0·63	4·55
Larvae	104	33·02	81·82
Total	315		

Table 5.12 Number of prey items identified from analysis of 44 faecal sacs collected from nestling Reed Buntings.

5.12a (ii) Variation of diet by habitat

Table 5.13 shows the faecal analysis results divided according to habitat. More larvae and damsel flies are given to nestlings in PM, but more beetles elsewhere. On combining Collembola, Trichoptera, Plecoptera, Hymenoptera and Gastropods, and constructing a 6 × 2 contingency table these differences in diet are seen to be significant ($\chi^2 = 12{\cdot}61$, 5 d.f., $p < 0{\cdot}05$). Most of this variation arises from the comparison of beetle numbers, and can possibly be explained in terms of seasonal availability in the two habitats as shown in Tables 3.11 to 3.14. Although beetle numbers caught in the water traps increased in both habitats during the first part of the breeding season, numbers were maintained throughout the entire sample period in OM, but fell off in PM. This, together with the later nesting season in OM probably explains the greater numbers found in the diet of OM nestlings.

The difference in the numbers of larvae found in the faecal sacs from each habitat is not easily explained from the water trap results, but as has been pointed out, larvae were obviously sampled poorly by this method. It is however well-known that Lepidopteran larvae peak in spring (Perrins 1979), are common in wooded areas, and, as we have seen, are most frequently found in the diet of PM nestlings. We shall see later in this chapter that birds from PM nests forage more in Carr than elsewhere which probably accounts for the numbers of larvae in the diet.

5.12a (iii) Distribution of food according to nestling age

With so few samples available it is difficult to make comparisons with any degree of confidence. Table 5.14 lists the numbers of individual prey items per faecal sac for the five major taxa according to nestling age. Although samples from older young are absent, the

	PM		OM	
	n	% (within PM)	n	% (within OM)
Collembola	1	5·88	0	0
Araneae	9	35·29	11	33·33
Diptera	7	35·29	4	14·81
Coleoptera	44	88·24	87	88·89
Odonata	13	70·59	16	29·63
Trichoptera	4	11·76	4	14·81
Plecoptera	7	17·65	1	3·7
Hymenoptera	0	0	1	3·7
Gastropods	1	5·88	1	3·7
Larvae	52	94·12	52	74·07
Totals	138		177	
Number of samples	17		27	

Table 5.13 Number of prey items from analysis of 44 faecal sacs collected from nestling Reed Buntings by habitat.

Age of nestling (days)	Araneae	Diptera	Coleoptera	Odonata	Larvae
0	1	0	0	0	1
1	-	-	-	-	-
2	1	1	1	0	0
3	0·71	0·43	2·14	0·29	2·86
4	0·64	0·36	2·18	0·82	3·00
5	0·50	0·30	3·90	1·40	3·50
6	0	0	1·60	0·20	0·80
7	0	0	2·75	0	1·25
8	0·20	0	6·60	0·60	1·80

Table 5.14 Number of prey items identified per faecal sac from nestling Reed Buntings of known age.

results suggest that spiders and flies are more frequently fed to the youngest nestlings, whereas beetles become more important to older nestlings. Both larvae and damsel flies appear to drop off in the second half of the nestling period.

Apart from the fact that Reed Buntings concentrate on fewer taxa than Reed Warblers, the results are surprisingly similar to those found in §4.13a (iii), and suggest the possibility that both species are in some way reacting to the available food supply in a similar way.

5.12a (iv) Calorific value of diet

Only tentative conclusions are again possible to obtain with the data available. This is especially so in this situation, since, as Table 4.19 shows, larvae contribute a great deal to the calorific value of the diet, and so relatively small errors would induce gross errors in the total calorific value. It is nevertheless interesting to calculate the overall calorific values of the diet in each habitat. Using the results from Tables 4.19 and 5.13 and taking the five major food items listed, one obtains values of 1387 cals. for PM and 974 for OM (values per faecal sac).

(b) Observations from hides

5.12b (i) Food items

Unlike Reed Warblers, a great majority of the food given to nestlings was identifiable, mainly since relatively large items such as larvae, beetles, damsel flies and caddis flies were involved. 'Food-balls' were decidedly uncommon. The feeding operation tended to take place fairly slowly, which again aided identification of food items. There was often a moment or two when the adult paused at the nest before feeding the nestling. It was then possible to assess the length of larvae being fed in relation to the width of the adult's bill at its base, and this was done whenever possible.

The results of 36 hours observations are given in Table 5.15, and show good agreement with the faecal analysis results in Tables 5.12 and 5.13. The fact that these results show better consistency than those obtained for Reed Warblers is no doubt due to the relatively simple diet of the Reed Bunting and the fact that the main constituents of the diet are readily identifiable.

5.12b (ii) Feeding rates

The overall feeding rates per nestling per hour observed during the 36 hours were $3{\cdot}06 \pm 1{\cdot}36$ for PM nests and $2{\cdot}74 \pm 1{\cdot}76$ for OM nests. The difference in feeding rates is not significant ($p > 0{\cdot}2$). The observations cover nestling ages day 0 to day 10 inclusive and the distributions of age of nestlings observed are similar in each habitat (not shown).

5.12b (iii) Size of larvae fed to nestlings

As was pointed out above, the length of larvae given to nestlings was, whenever possible, estimated using the bill width of adults, and the results are shown in Table 5.16. Smaller larvae are fed to nestlings in PM nests than elsewhere ($p < 0{\cdot}01$), which is of considerable interest since we have already seen from the faecal analysis results and nest observations that more larvae are given to PM nestlings than elsewhere. Although at first sight this difference in the size of larvae is small, it is nevertheless important, since it represents larvae 13.4 per cent longer in OM than PM.

Adjusting the results of the faecal analysis in Table 5.13 to

	PM (22 hrs)	OM (14 hrs)	All
'Food-balls'	47	7	54
Ephemeroptera	3	0	3
Odonata	40	6	46
Trichoptera	19	0	19
Coleoptera	106	53	159
Larvae	160	97	257
Totals	375	163	538

Table 5.15 Food items of nestling Reed Buntings observed from hides.

Length of larvae (x bill width at base)	1	2	3	4	5	6	7	8	Totals
PM	4	41	51	27	10	2	1	2	138
OM	10	21	24	27	24	7	2	0	115

$$\left.\begin{array}{l}\text{Mean length (PM)} = 3{\cdot}13 \pm 1{\cdot}23 \\ \text{Mean length (OM)} = 3{\cdot}55 \pm 1{\cdot}46\end{array}\right\} \text{x bill width}$$

Table 5.16 Distributions of sizes of larvae fed to nestling Reed Buntings by habitat.

account for size of larvae and combining these results again with Table 4.19 gives better estimates of the total calorific food value viz 1387 cals. for PM, 1067 cals. for OM (values per faecal sac).

5.13 Simultaneous step-ladder and hide observations

A total of 9 one-hour simultaneous step-ladder and hide observations was made, but the results added little to the general picture of feeding ecology. They showed that there was good agreement in the feeding rates as observed from hides and step-ladders, the latter being only slightly under-recorded.

5.14 Foraging behaviour

As in the case of Reed Warblers, all observations relate to foraging for nestlings. Table 5.17 summarises the feeding locations of adult Reed Buntings (both sexes combined) foraging for nestlings. Inward and outward journeys are pooled and again, for simplicity, habitats are divided into 'marsh' and 'carr'. The observations represent 1130 feeding locations obtained from 11 nests (4 PM, 7 OM) during a total time of 77 hours.

The results show a remarkable difference in feeding behaviour, with birds from PM nests foraging to a very large extent in carr, and those from OM nests feeding mostly in marsh ($\chi^2 = 303{\cdot}9$, 2 d.f., $p < 0{\cdot}001$). These differences can possibly be explained in terms of feeding ecology as follows: Reed Buntings nesting in PM do so earlier and feed their young to a large extent on larvae, which, although not detectable from the results of the water traps, are probably more abundant at this time in the carr. The later, OM nesters take fewer (although bigger) larvae and more beetles, which, as was pointed out in §5.12a (ii), maintain

	Marsh (%)	Carr (%)	Elsewhere (%)	Totals
PM	107(18)	456(77)	29(5)	592
MM	371(69)	147(27)	20(4)	538

Table 5.17 Numbers of observed foraging locations of adult Reed Buntings collecting food for nestlings.

their numbers throughout the season in marsh, but drop off in carr. The net result is a marked difference in habitat utilization in response to this seasonal variation of the food supply.

The distance travelled to and from foraging locations would not appear to be an important feature in the foraging behaviour of Reed Buntings. Although actual territory boundaries were not deliniated, it appears that most foraging took place within, or on the edges of territories, the latter often being the lines of willows or alders at the edge of the marsh. This result agrees with Ghiot (1976), who found the Reed Bunting to be a type 'B' territory holder (Hinde 1956). Most foraging observations were by females, 71 per cent in PM and 63 per cent elsewhere and there was no obvious pattern of habitat utilization as the age of nestlings increased. Indeed, in only two nests did the utilization of marsh or carr increase with nestling age, whereas in all other cases the distribution was fairly uniform.

5.15 Discussion

In spite of the fact that only a few nests were studied, some of the objectives of the investigation were achieved. The entire study area was completely occupied by Reed Bunting territories, and quite possibly the entire marsh also. Bell's 1968 study compared breeding density in marsh, grassland, ruderal vegetation, open scrub and other miscellaneous sites. He found that only 34 per cent nested in marsh, but that breeding density was greatest in these areas. As far as it was possible to determine, all Reed Buntings at Oxwich bred in marshland areas, and it is clear that these areas are the preferred breeding habitats of the species. There was no evidence to suggest an ecological expansion of the Reed Bunting away from its traditional marshland habitats in the Oxwich Bay area.

The peak egg-laying period was found to be two weeks earlier in PM than elsewhere. Some of this variability could have been caused from a bias due to repeat layings after failure, but this is unlikely, since most failures occurred at the young stage and in OM nests. There appear to be two possible reasons for this striking temporal separation: (a) better prospects of nesting sites in respect of protection against predators exist in PM and (b) food availability for early egg production could be better there. The first possibility is unlikely, for the reasons already mentioned, and food availability is therefore a probable reason. There were however no obvious clues as to what adults were feeding on during this critical period. The main food given to nestlings (larvae and beetles) is probably not the same as that taken by adults at this time, and in any event showed no obvious seasonal pattern of availability (Chapter 3). Chironomids are however abundant during this period (Street 1977) (§3.8) and present an obvious food source. Unlike the Reed Warbler, the Reed Bunting is not particularly adapted to taking flies, but obviously can and does (Table 5.12). Prŷs-Jones (1977), studying the feeding ecology of Reed Buntings outside the breeding season, lists a variety of small arthropods (including Diptera) which are regularly taken. He also found that during March the birds responded to 'large hatches of small Chironomid midges, picking them off the ground at the rate of one or two per second'. Later in April he observed Reed Buntings taking 'large Diptera by flycatching, but making no attempt to catch the smaller Chironomids. It is very likely that as was reported in the case of the Reed Warbler (Chapter 4), the Reed Bunting takes advantage of this temporarily abundant food source during the early part of the breeding season, which at Oxwich is more pronounced in PM than elsewhere (Table 3.3). Temporary exploitation of patchily distributed food supplies has been observed in many species and has recently been synthesised by Krebs (1978).

Bell (1968) remarks that there is 'some evidence that the food supply in marshes is more suited to the species' and found that marshes were occupied earlier than elsewhere. Unfortunately even now, no quantitative study of the feeding ecology of Reed Buntings away from marshes appears to have been made and so comparisons are not possible.

Clutch sizes varied little between habitats and with season. The results are difficult to interpret because of the small numbers involved.

Brood sizes at fledging on the other hand gave significant results, with more young produced from PM nests than elsewhere. This, together with the clutch size results, suggests differential mortality during the nestling stage, with fewer dying in PM nests. Overall brood size at fledging decreased with season, with most of the fall being attributed to partial losses in OM. This result is somewhat curious, since the major food supply in these nests at this time consisted of beetles and, to a lesser extent larvae. Beetle numbers are still high in OM at this time, and larvae are by no means finished.

The probability method of calculating nest success (§4.7) was again employed and gave good results. Small sample sizes precluded any consideration of seasonal trends, but between habitat variations were possible. In PM, nests containing eggs were more likely to fail than those with young, but the reverse appeared to be the case in OM. Overall nesting success was 48 per cent but was much higher in PM than elsewhere.

The differences in success between habitats are interesting. In PM, total failure at both the egg and young stage was rare, as was also the case during the egg stage in OM. The major cause of failure was during the young stage in OM, and this, together with a degree of partial failure (expressed as a lower brood size at fledging), accounted for the much lower nesting success in OM. Total failures were again mainly the result of predators, which were apparently more successful in OM. This is a little surprising, since these nests were often built in a mixed vegetation matrix, and were perhaps more difficult to locate. On the other hand, I found nests in PM extremely difficult to find, as they were usually built on the ground and very well camouflaged.

Nestlings from PM nests were not significantly heavier at hatching (Table 5.8), but gained weight faster after about day 4. It is thus likely that egg weights were similar in both habitats (Schifferli 1973), which is surprising in view of the implications of the temporal separation in the start of breeding already discussed. Predicted mean fledging weights (day 12) differed by 0·5grm., suggesting that feeding conditions for PM nesters were 'better' during most of the nesting period.

Surprisingly little qualitative or quantitative data has been published concerning the feeding ecology of the Reed Bunting during the breeding season. In fact in most instances, only superficial lists have been given (Bell 1968, Prŷs-Jones 1977). In contrast to the Reed Warbler (Chapter 4), the diet of the Reed Bunting was found to be relatively simple (Table 5.12), with 75 per cent of the diet consisting of either larvae or beetles. The only other important taxa appeared to be spiders and damsel flies. All these taxa are relatively immobile (damsel flies being so in the early and late parts of the day), and are what one might expect from an Emberizidine finch.

The feeding ecology as determined by faecal analysis differed between habitats, with more larvae taken in PM, and more beetles in OM (Table 5.13). The results agreed with what one would expect from the observed feeding localities. The latter showed that PM nesters foraged mostly in carr, whilst OM nesters foraged to a large extent in marsh (Table 5.17). Assuming a spring abundance of caterpillars (Perrins 1979), the observed maintainance of beetle numbers in OM late in the season accounts for the different methods of exploiting the available food supply.

Feeding observations from hides at selected nests provided quite good information, since the main food items were easily identified, and 'food-balls' were relatively rare. Feeding rates were slightly higher in PM nests, where more larvae per nestling was given. On the other hand, it was possible to estimate the length of larvae involved, and significantly larger ones were fed to OM nestlings. Assuming an average of 16 hours daylight, the feeding rates imply that each PM nestling received 5·1 more feeds per day than those elsewhere and represented an increase of 11·7 per cent. However the bigger larvae fed to OM nestlings represented an increase of 13·4 per cent. Even though other taxa are involved in the diet their calorific value compares poorly with larvae (Table 4.19), and this difference in the size of larvae could easily account for the difference in feeding rates.

Apart from the points already discussed, the most important aspect concerning the breeding biology of the Reed Bunting appears to be whether one or more broods are reared. Without doubt, PM nesters have ample time to produce two and often three broods, but there was no evidence at all of genuine second brooding in PM. The probable reason is that in these areas the 'habitat quality' of the marsh in relation to the food supply necessary for Reed Buntings is never very high, and that as soon as the spring peak of caterpillars in the surrounding carr is over, there is little or no chance of a successful breeding attempt. In the OM nests, the situation is reversed, and the potential for successful later broods certainly exists. It is possible that some of the successful early brooders in PM bred later in the OM areas, but there was no evidence of this (a few individuals were colour-ringed).

CHAPTER SIX

Habitat selection in the Sedge Warbler

When considering habitat selection in birds, most authors have tended to relate habitat with plant species or communities. This rather superficial association, although identifying the overall characteristics of a particular habitat, probably masks the more subtle cues used by birds in 'choosing' a habitat. Hilden (1965), von Haartman (1971), Brown (1975) and more recently Partridge (1978), have each stressed the importance of defining habitat merely as 'the type of place in which an animal lives'. This definition allows for a wide range of factors to be considered as dominant features of habitat description e.g. humidity, shade, potential prey items, vegetation structure etc.

Although Sedge Warblers are almost always to be found breeding in dry scrub areas adjacent to rank vegetation, the proximate factors involved in this habitat preference are probably more precise than this vague description suggests. At Oxwich, Sedge Warblers are found breeding over a large proportion of the marsh, but some obvious superficial habitat preferences were apparent at the beginning of the study. Areas of pure reed did not appear to be occupied, especially when growing out of water, whereas a strong association with Bramble Rubus fruticosus agg. was clear. These bramble areas often consisted of a small clump, completely engulfed by reeds and/or Bracken Pteridium aquilinum, and were situated in dry, or at most damp areas of the marsh. They were however never far from rank vegetation. Bramble also occurred as a flat uniform ground cover, which invariably contained mature plants standing between one and two metres high.

This basic division of habitat was taken as a starting point and four habitats were identified:

(i) MB - mixed bramble; consisting of bramble with reed and/or bracken.

(ii) B - mature bramble.

(iii) MR - mixed reedmarsh; reed, together with a lower vegetation level e.g. Iris pseudacorus, Mentha aquatica, Oenanthe fistulosa, Rumex hybrolaparthum and Solanum dulcamora.

(iv) R - reed alone.

As was pointed out above, MB and B were essentially 'dry' habitats in contrast to MR and R which were always 'wet'.

Methods

Sedge Warblers respond well to a Common Bird Census (CBC), Bell et al (1973) and so from 1975-1979 a CBC was carried out to determine the breeding population level and to consider sumultaneously habitat preferences. The CBC was begun in each year immediately the first Sedge Warbler had returned to the marsh in mid-April. On each census visit, the locations of singing males, individuals present etc. were noted on a 25 inch vegetation map according to the established CBC rules (Williamson and Homes 1964). Habitat classifications of their positions were also made according to the categories (i) - (iv) above.

Regular census visits were undertaken during the period of arrivals and continued until the population had more or less stabilized. In each year, this period extended over about three to four weeks, with approximately ten census visits being necessary. Subsequent visits added little or nothing to the record. A few late arrivals were noted which often continued to sing well into June, suggesting they had failed to acquire a mate (Catchpole 1973b). Some apparent passage birds were also noted, but in general these were few. Almost all birds that appeared in a particular location remained there, the few exceptions have been included since they contributed to the habitat selection process.

It is important to point out that the song period of the Sedge Warbler is very short, and that about three weeks after the arrival of the first male, most had ceased singing. This is consistent with the findings of Catchpole (1973b). However this was by no means always the case. In some (rare) instances males continued to sing (albeit with reduced intensity) long after pairing. In some instances too, song was resumed in a particular territory, presumably due either to the loss of the female or to the failure of a nest.

Results

6.1 The CBC results

The results of the CBC are shown in Figs. 6.1 - 6.5. The positions marked are the approximate 'centres' of territories. Although exact territory boundaries were not determined, it is clear that most were small and often grouped closely together. Figs. 6.1 - 6.5 also show that the 339 territories identified over the five years were mostly situated on vegetation interfaces. However the mosaic nature of Oxwich marsh ensures that the chances of encountering an 'edge' within even a small territory are relatively high, and so little emphasis should be placed on this as a feature of habitat selection.

Table 6.1 lists the number of territories occupied by Sedge Warblers for the various habitat types in each year and also gives the estimated area of available habitat. In estimating these areas, a tape was used to measure the MB and B habitats. The marshland areas i.e. MR and R were measured from an aerial photograph (August 1976) supplied by the Nature Conservancy Council at Bangor. When estimating the area of MB habitats it was not always obvious where the boundaries lay, but in general the measurements are probably fairly accurate. The areas of mature bramble B were well defined and often isolated, thus giving accurate measurements.

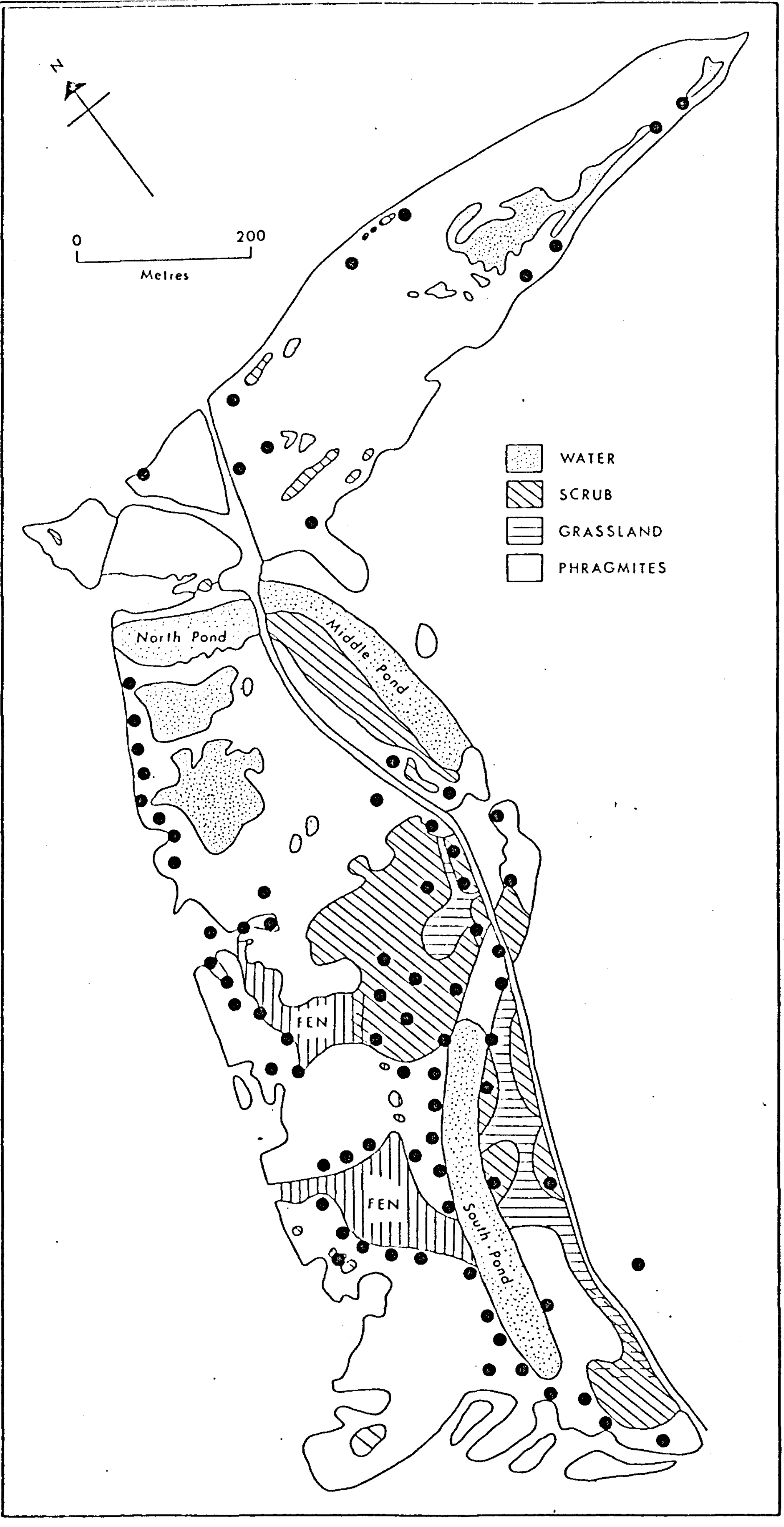

Fig.6·1 Positions of Sedge Warbler territories 1975.

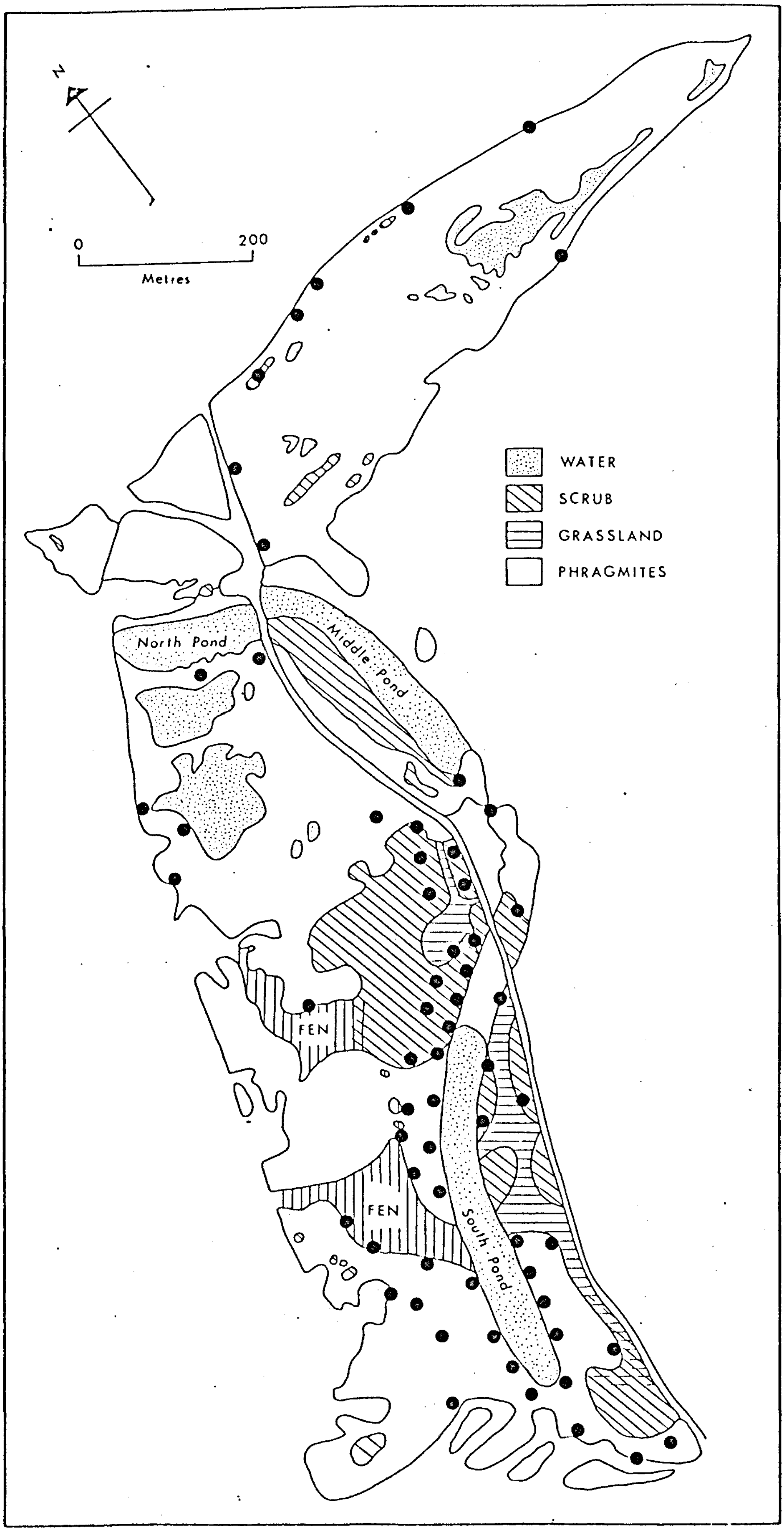

Fig.6·2 Positions of Sedg· ·arbler territories 1976.

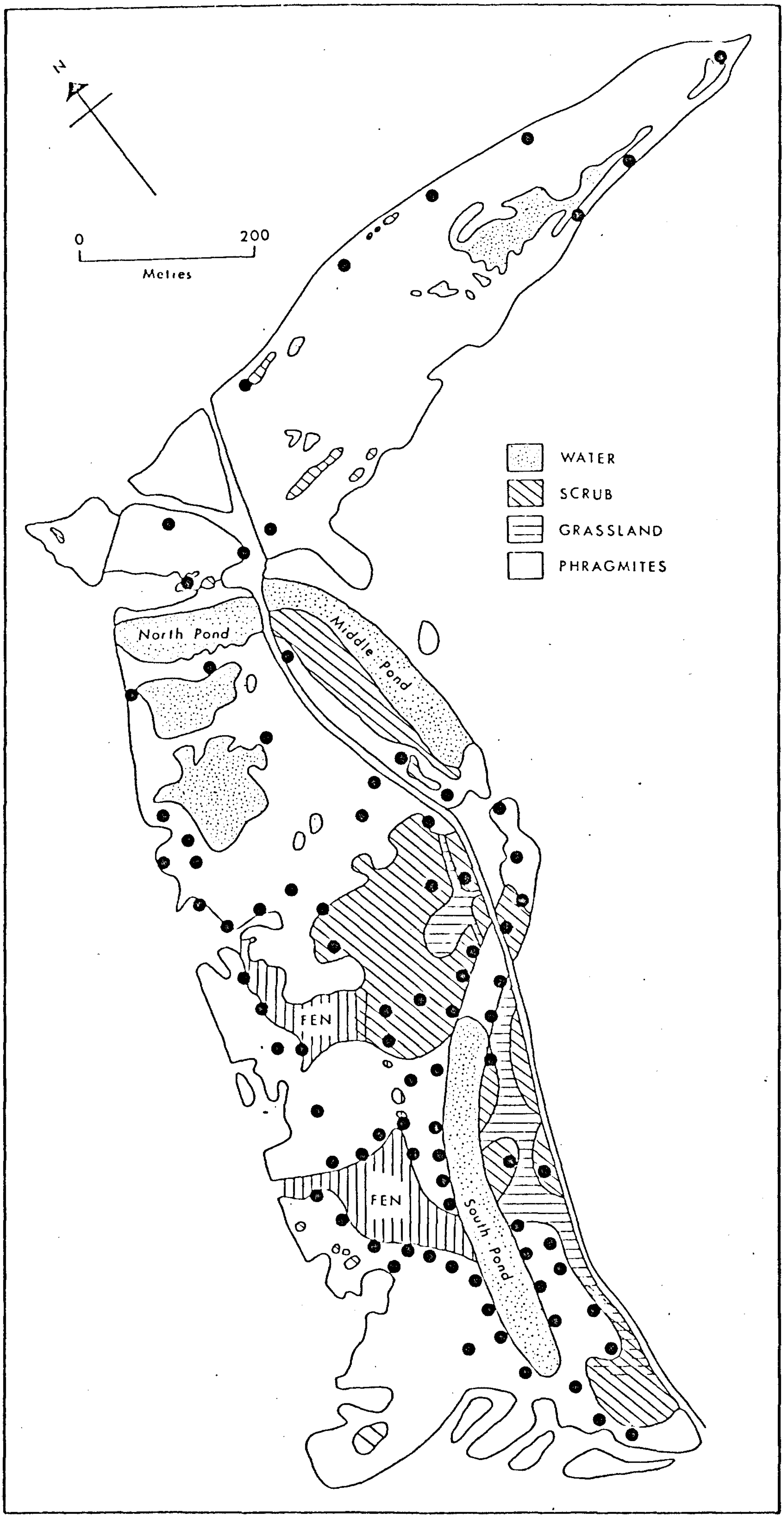

Fig.6·3 Positions of Sedge Warbler·territories 1977.

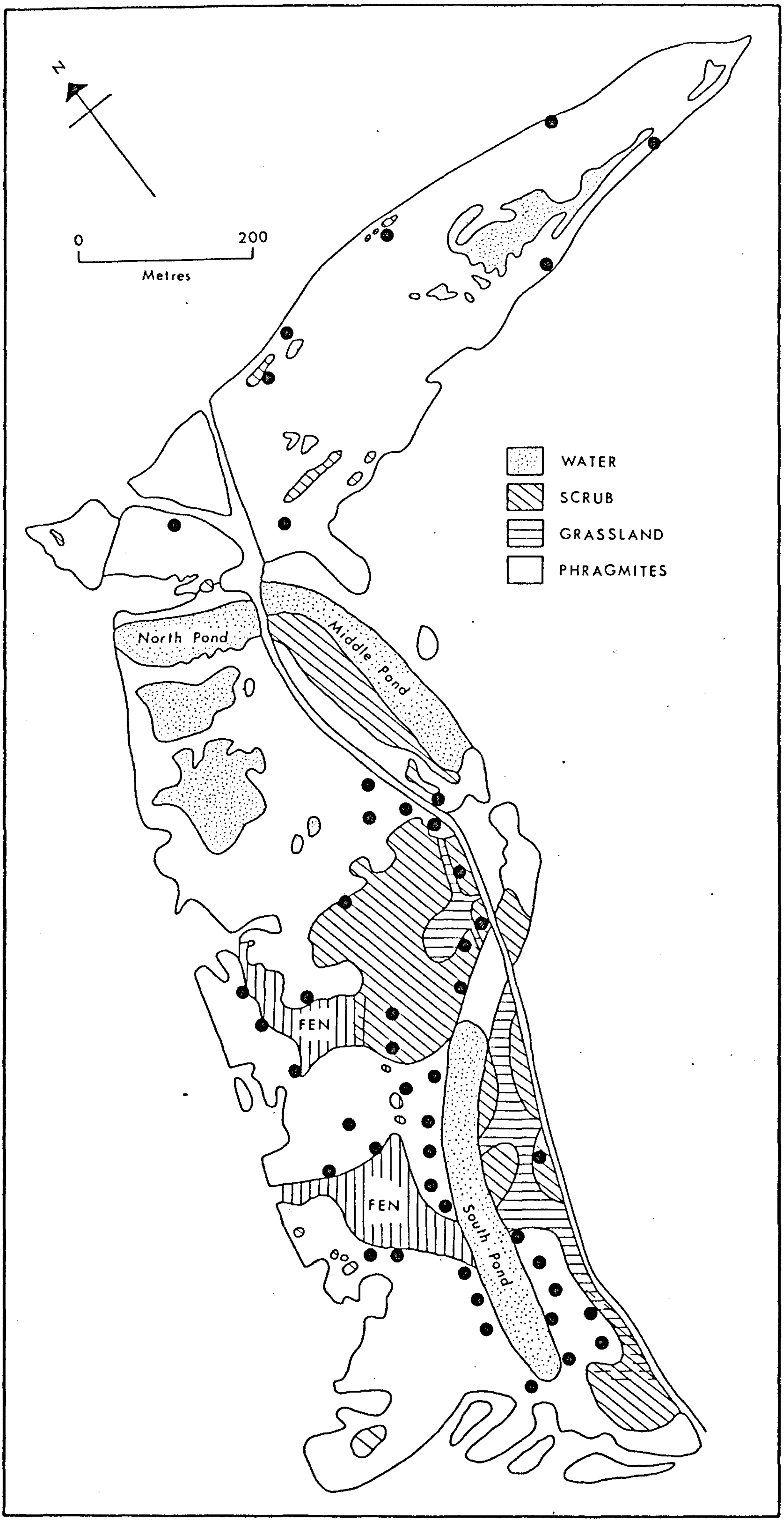

Fig.6·4 Positions of Sedge Warbler territories 1978.

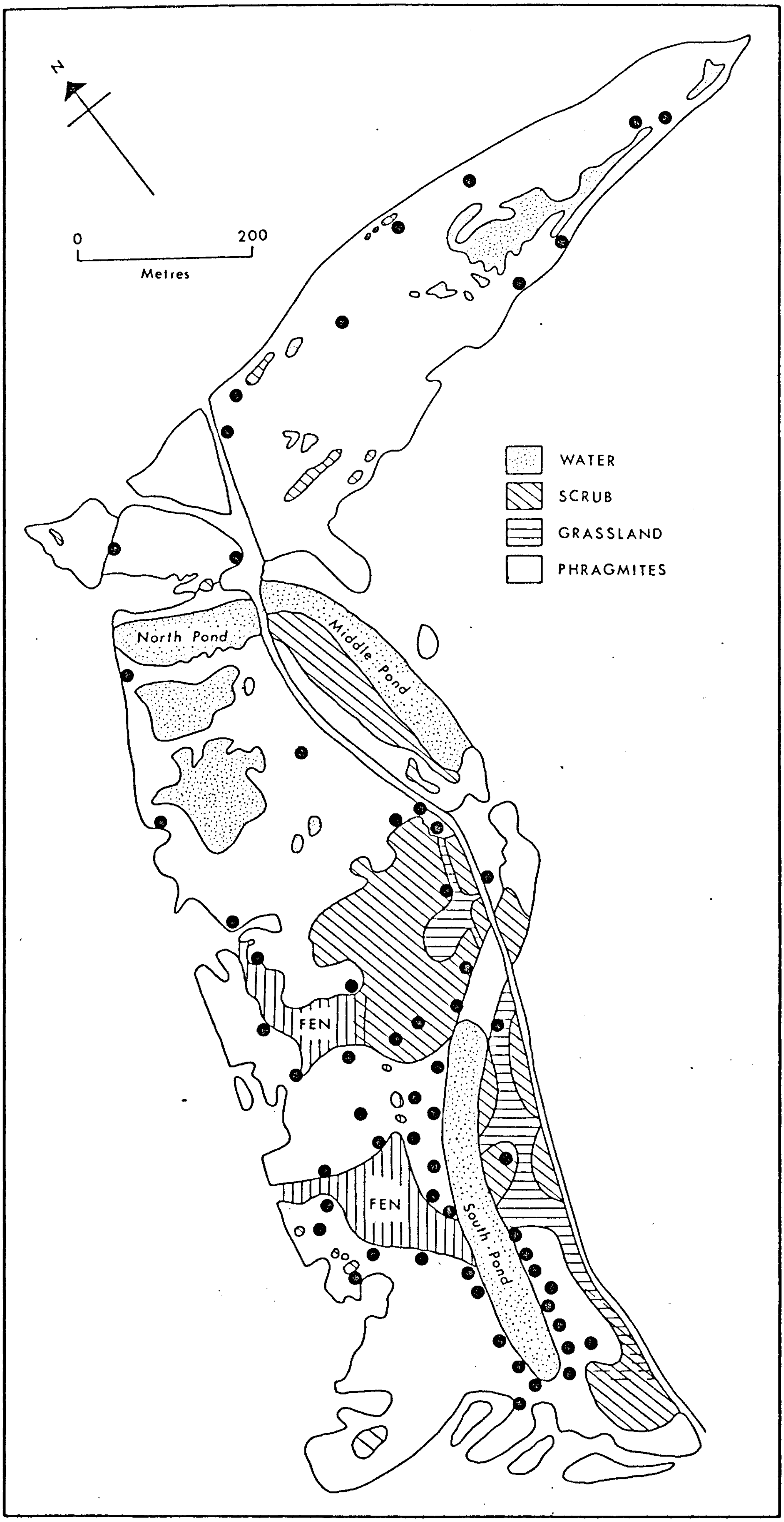

Fig.6·5 Positions of Sedge Warbler territories 1979.

	MB	B	MR	R	Totals
Area (ha)	3·86	0·86	34·75		
1975	29	11	39	1	80
1976	30	11	19	0	60
1977	36	9	38	4	87
1978	23	7	17	2	49
1979	23	4	31	5	63
Totals	141	42	144	12	339

Table 6.1 Number of territories occupied by Sedge Warblers in each year for various habitats.

Since exact territories were not plotted it is difficult to use Table 6.1 to determine realistic density estimates. However the data strongly suggests a preference from MB and B over MR and R.

6.2 The sequence of occupation

In order to look closer at these preferences it is necessary to consider the order of occupation of each habitat type. Habitat calendars were made up for each year listing the number of occupied territories in each category per census visit. In compiling the calendars the following rules were followed:

Occupation was counted if either

(a) a singing male was present;

(b) two birds were present in a position where a male had previously sung;

(c) a bird was apparently absent, but sang on both a preceeding and subsequent visit;

(d) a bird was apparently absent, but sang on at least three previous occasions.

Figs. 6.6 - 6.10 show the settlement pattern in each habitat type. In all years there is a clear order of occupation

$$MB > MR > B \text{ or } R.$$

Thus mature bramble appears in some way deficient, but when combined with other plant species becomes extremely attractive to Sedge Warblers. The MR habitat is obviously important (as was seen from Table 6.1). It is therefore clear that the initial subjective inclusion of bramble within the habitat is of secondary importance, and that the birds are probably responding to other cues in the make up of the vegetation.

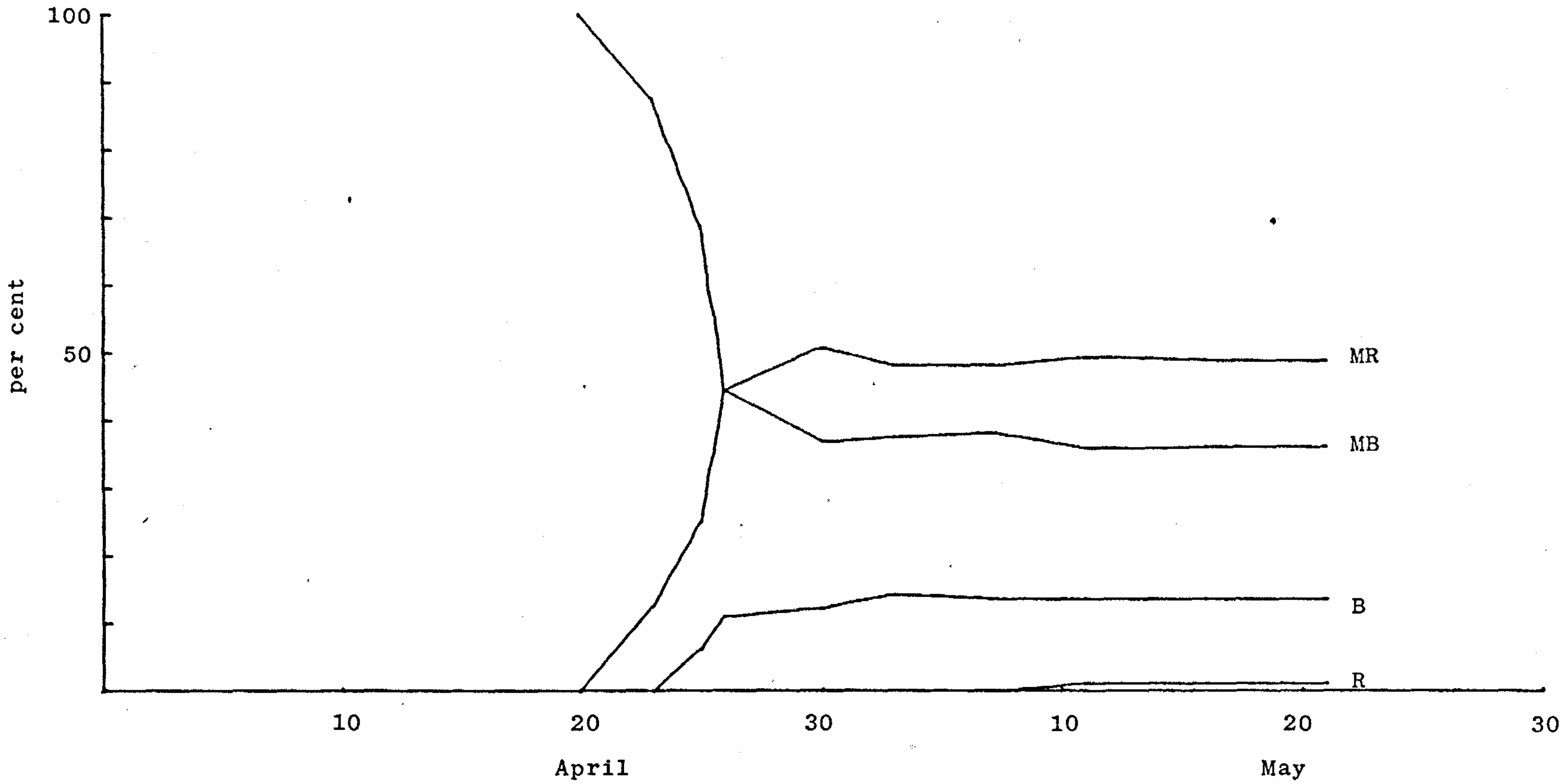

Fig. 6·6 Percentage per visit of number of occupied MB,MR,B and R Sedge Warbler territories (1975).

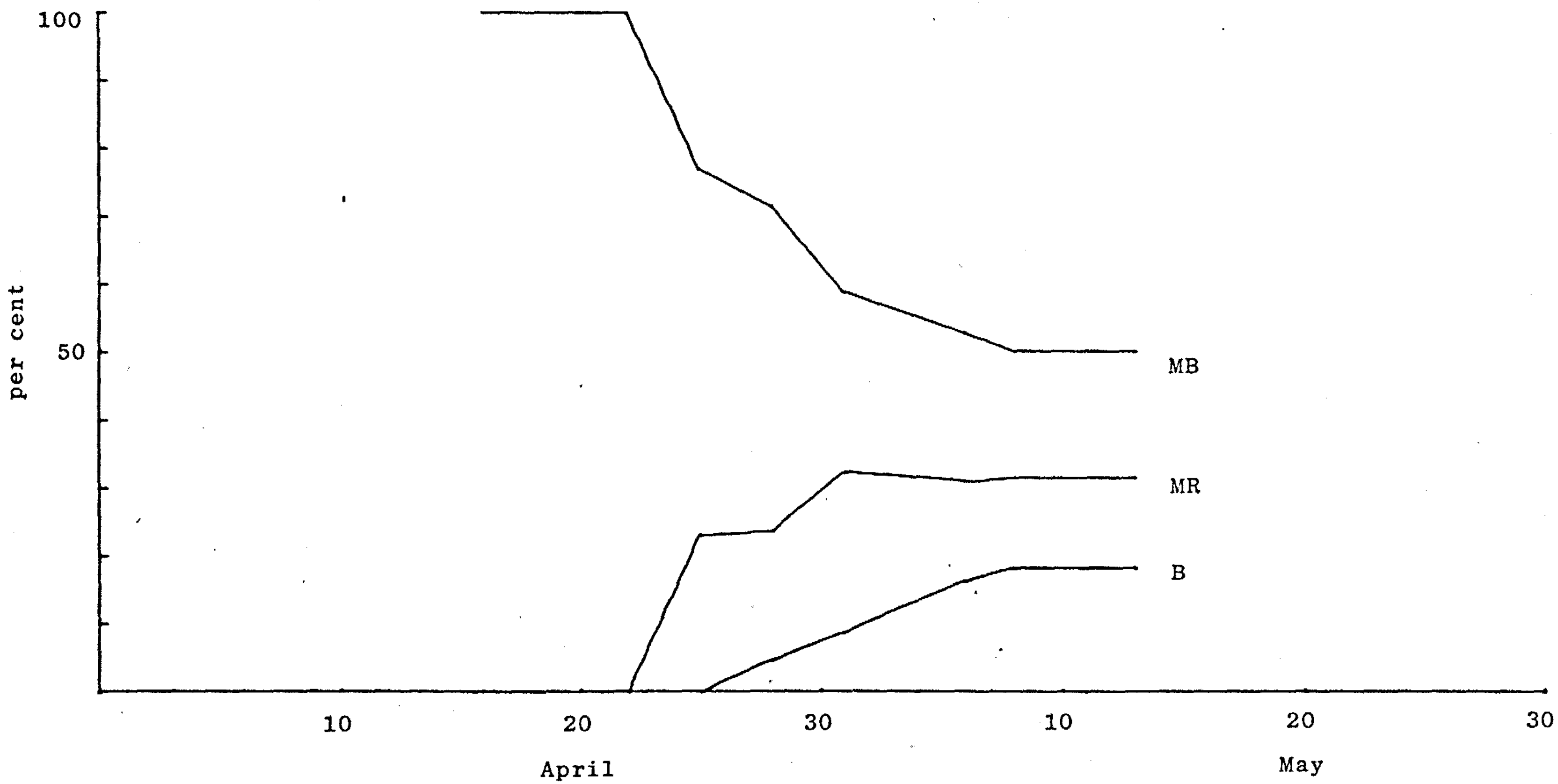

Fig. 6·7 Percentage per visit of number of occupied MB,MR,B and R Sedge Warbler territories (1976).

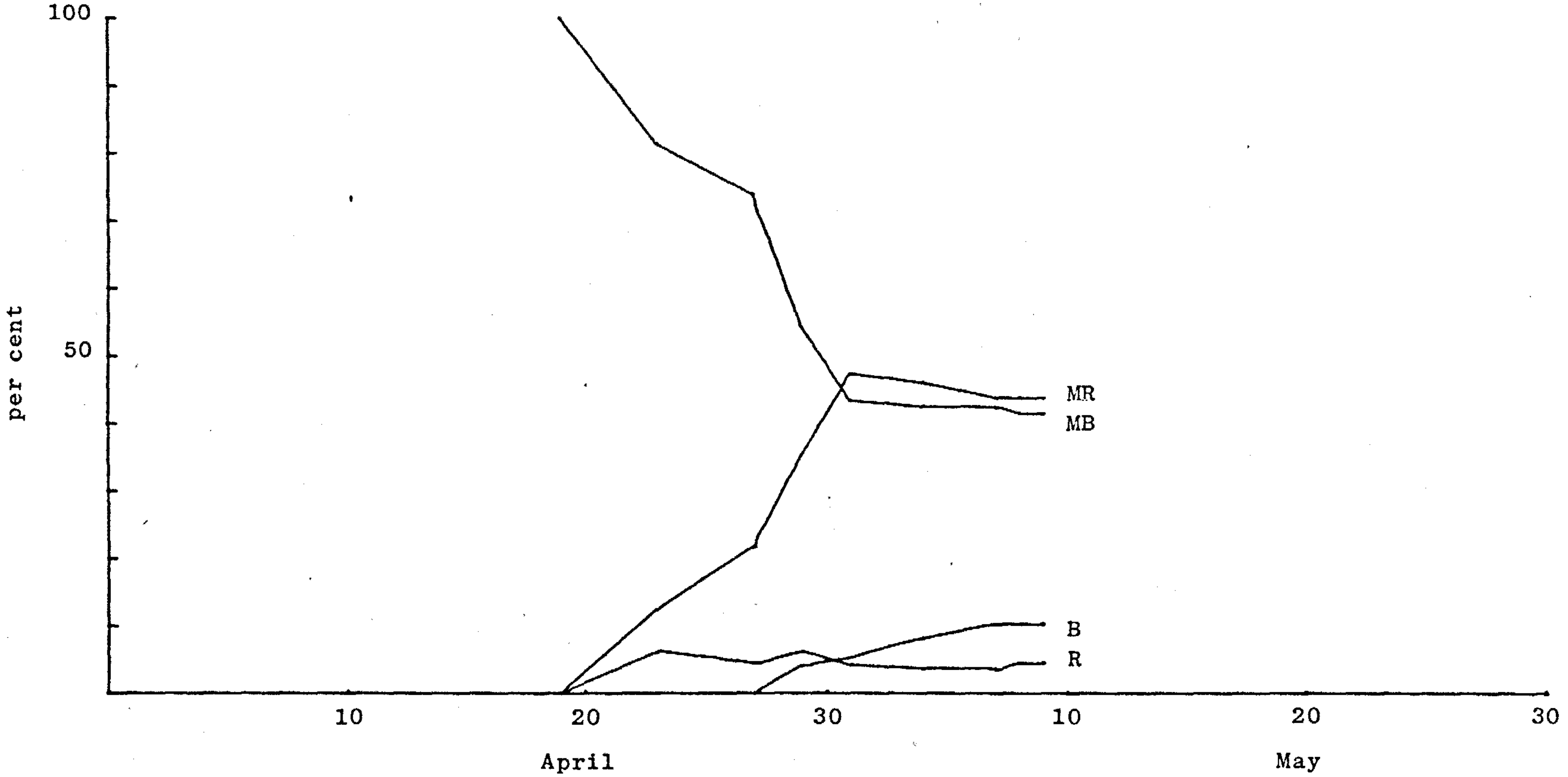

Fig. 6·8 Percentage per visit of number of occupied MB,MR,B and R Sedge Warbler territories (1977).

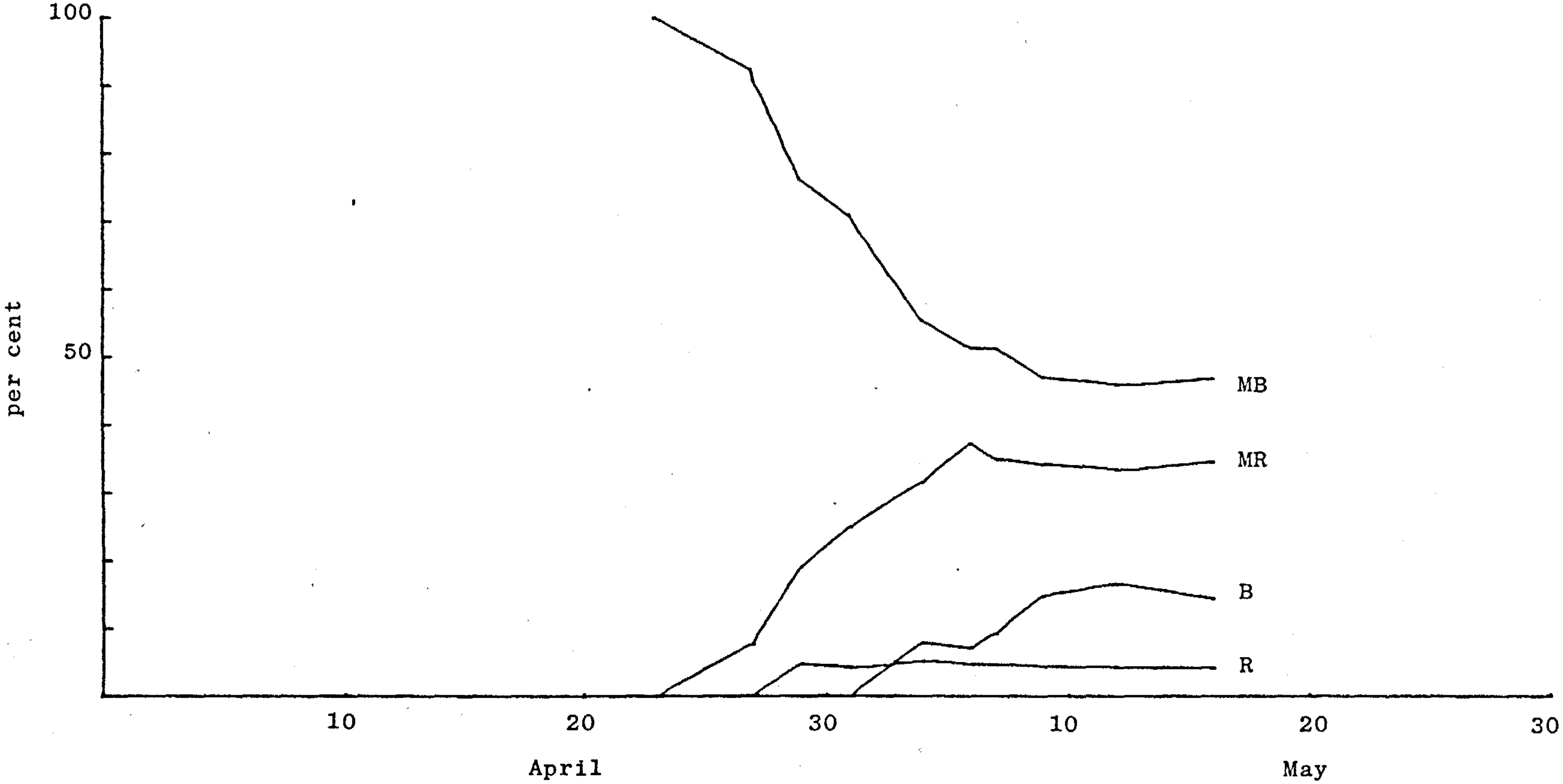

Fig. 6·9 Percentage per visit of number of occupied MB,MR,B and R Sedge Warbler territories (1978).

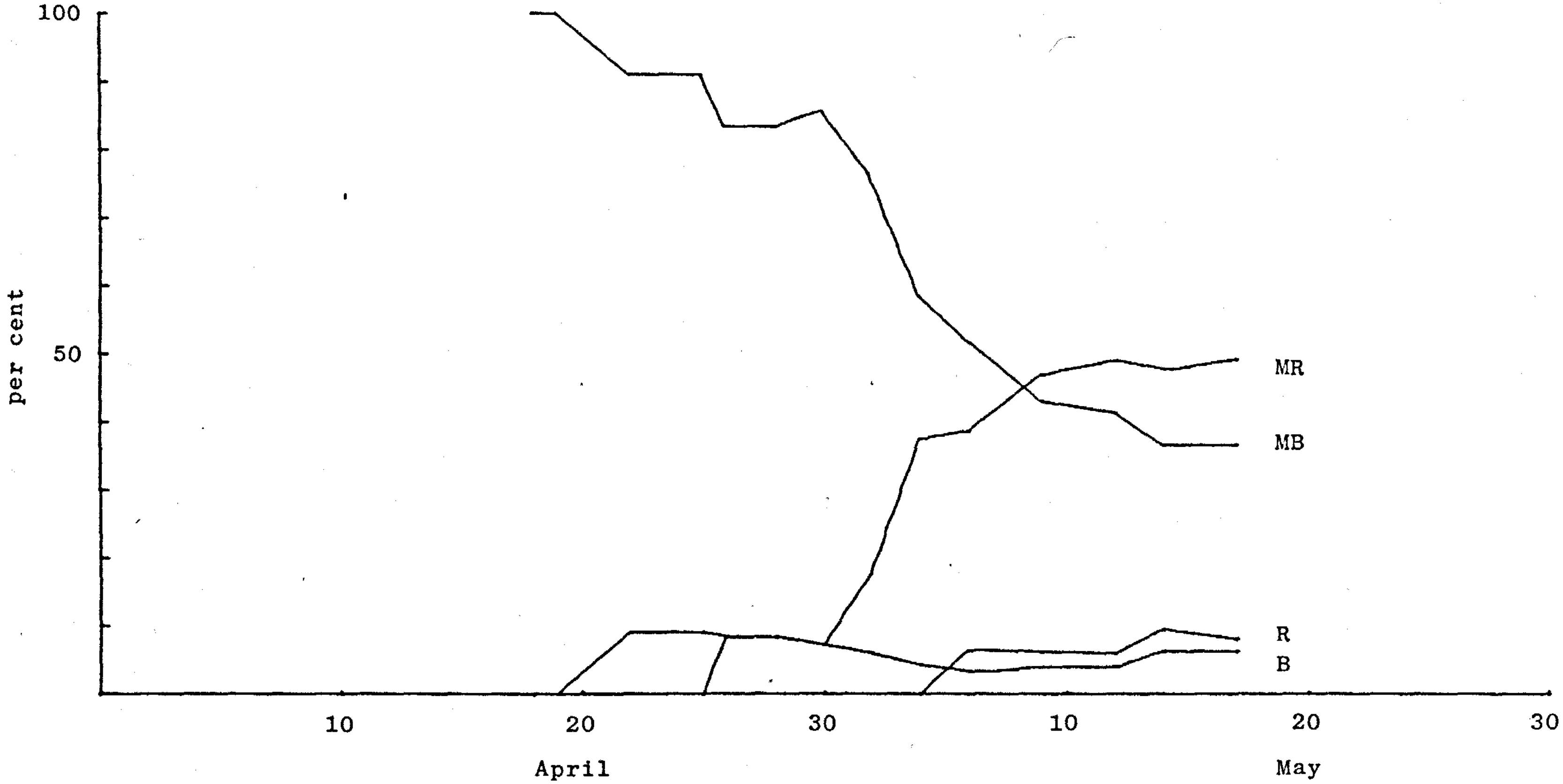

Fig. 6·10 Percentage per visit of number of occupied MB,MR,B and R Sedge Warbler territories (1979).

6.3 Vegetative structure

The above divisions of habitat are not sufficient to identify the proximate (and possibly ultimate) factors which influence habitat selection in the Sedge Warbler. The apparent preference for a mixture of vegetation strongly suggests that the structure and/or density of vegetation is the key to identifying the important features of the habitat. An attempt was made in 1979 to measure the vegetative structure of the four habitats. Zimmerman (1971) considered a similar problem in the Dickcissel *Spiza americana*, and demonstrated a strong correlation between breeding density and vegetation density. Unlike the Sedge Warbler, the Dickcissel has a relatively large territory, breeding in open fields and woodlands. In this context a natural measurement of this more open terrain is vegetation volume. We shall show that in the more compact world of the Sedge Warbler, it is the structure of the vegetation i.e. vegetative complexity that probably influences habitat selection. It is possible that vegetative volume is a factor, but we are unable to demonstrate this.

At Oxwich, two measurements were sought, (i) a measure of vegetative complexity, and (ii) its density (with respect to complexity) i.e. 'complexity × height'.

A translucent perspex 15 × 15cm. grid containing twenty five 3 × 3cm. squares was used as a convenient measuring device. The grid was purposely made translucent so as to obscure the vegetation more than a few cms. behind its surface. Having four years experience as to which sites Sedge Warblers were likely to occupy, 42 likely sites were measured during the first half of April 1979, before the birds arrived.

At each site five stations were measured, the aim being to choose as representative a measure as possible. At each station the grid was held in a vertical plane against the vegetation and the numbers of horizontal H, and vertical V intersections of plant stems with the grid were counted. (e.g. reed would register a high H and low V, whereas reed and bramble would register high H and V). The mean values of H and V were taken as the measure for the site. The height of the vegetation was also measured at each station and where this involved more than one profile, each was measured.

From these measurements an index I of vegetative complexity can be defined in a variety of ways. The one given below appears natural, and is sufficient for our needs:

$$I = \frac{HV}{H+V} .$$

It is worth pointing out that I behaves like the min (H,V) and is the reciprocal of the harmonic mean of H and V. A measure of density can be obtained by multiplying I by the mean height of the vegetation.

Table 6.2 sets out the mean values of I for the three main habitats. The differences between MB and both B and MR are significant ($p < 0{\cdot}01$, $p < 0{\cdot}001$) that between B and MR is not ($p > 0{\cdot}2$). Thus the habitat preferences exhibited in §6.2 are reflected in this measure of vegetative complexity.

Only in 1977 was all the MB habitat occupied. It is pertinent to ask therefore whether a higher value of I is found in occupied areas. In 1979, of the 22 measured, 14 were occupied. Comparing indices we find

$$I_{(occ)} = 49{\cdot}32 \pm 6{\cdot}76, \quad I_{(unocc)} = 44{\cdot}26 \pm 6{\cdot}7.$$

The difference in means is barely significant, ($p < 0{\cdot}2$), but sample sizes are quite small. Making the same comparison with all 42 values gives

$$I_{(occ)} = 44{\cdot}79 \pm 8{\cdot}5 \quad (n=25); \quad I_{(unocc)} = 39{\cdot}55 \pm 6{\cdot}96 \quad (n=17).$$

The difference in means is now significant with $p < 0{\cdot}05$.

6.4 Vegetative structure and settlement

In §6.2 we demonstrated a temporal pattern of settlement with regard

	Number of sites measured	I	s.d.
MB	22	47·78	7·04
B	8	38·3	6·21
MR	12	36·77	6·02

Table 6.2 Mean values of index of vegetation complexity I (see text) for various habitats used by Sedge Warblers

to habitat type. In order to support the view that the birds are responding to the structure of the vegetation we must show that the indix I is negatively correlated with settlement time.

Fig. 6.11 plots the date of first arrival in a particular territory against I. The resulting regression equation indeed shows a negative correlation, the low correlation coefficient ($r = -0{\cdot}3084$) being expected because of the non-uniform pattern of occupation. (Rate significantly greater than zero, ($p < 0{\cdot}02$)).

6.5 Vegetation density

No connections could be found between habitat selection and vegetation density (as defined in §6.3). That no relationship exists is certainly not proved; rather the techniques used in combining small variations in vegetation complexity with relatively large amounts of reedmarsh probably combined to produce large errors.

6.6 Discussion

The connections between population density, intraspecific competition and habitat selection are obviously complicated. Brown (1975) and von Haartman (1971) point to the following three possibilities.

(a) When the population is low, the preferred habitat may not be fully utilized and so other, less desirable habitats should not be occupied.

Table 6.1 shows that in 1978 when the population of Sedge Warblers only realized 49 pairs, many MB territories were indeed unoccupied. On the other hand, many other habitats were occupied, suggesting that within some of these at least, there was a satisfactory vegative structure.

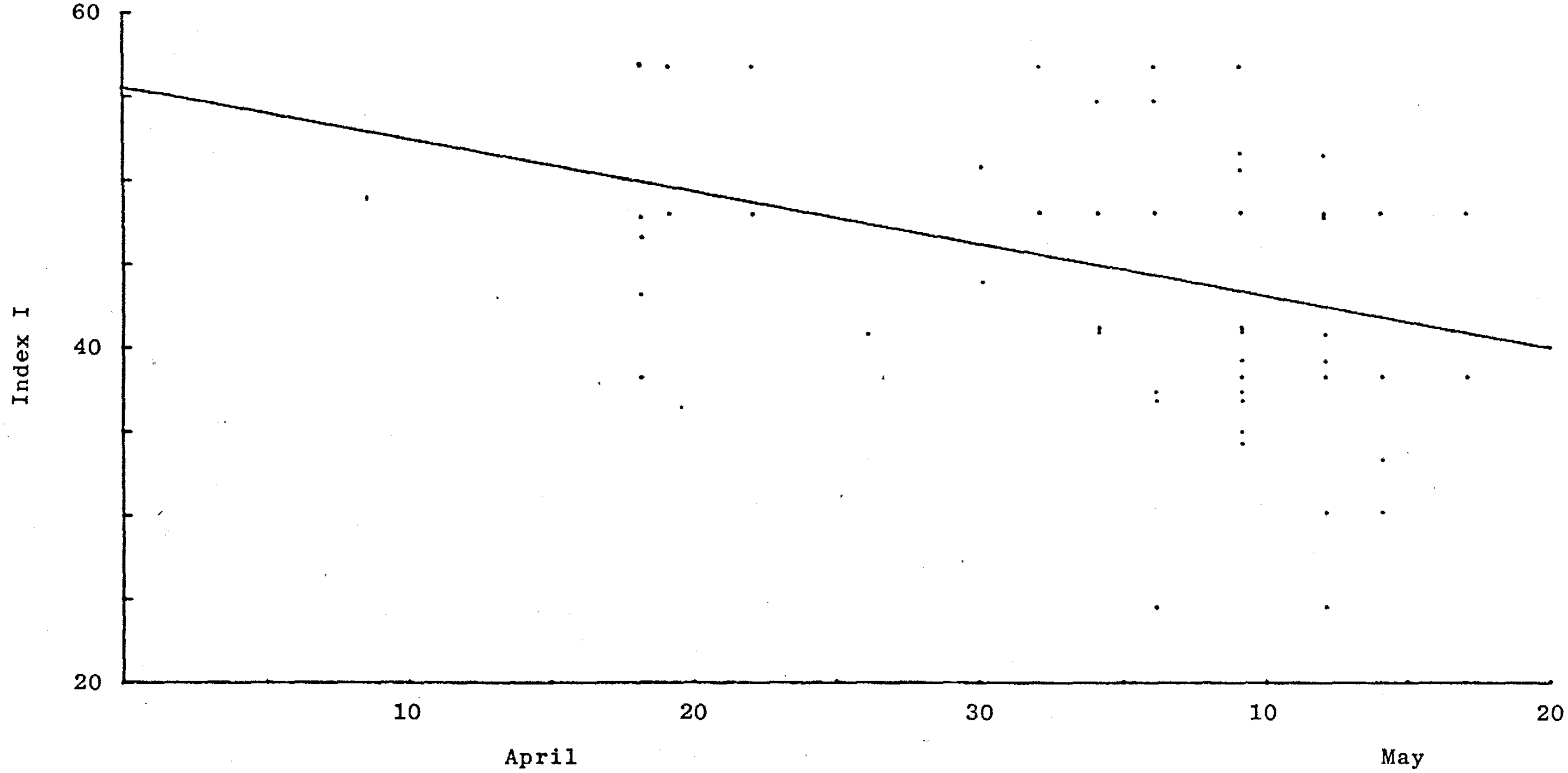

Fig.6·11 Index of vegetative complexity I according to date of arrival of Sedge Warblers for all years combined. (y = 55·49 - 0·31x).

(b) Yearly fluctuations in populations are greater in less preferred habitats.

This of course needs many years data to establish and is known to occur in the Chaffinch Fringilla coelebs (Glas 1960) and the Great Tit Parus major (Kluyver and Tinbergen 1953). Five years data for the Sedge Warbler is clearly inadequate, but the variation contained in the annual population levels given in Table 6.1 is less for the MB habitat than for the remainder.

(c) If the population is high, then a large proportion of the population may occupy less favoured areas.

This is not apparent from Table 6.1.

One can ask 'why are not all MB areas fully occupied in each year and before any other?'. The following density dependant explanation is offered.

On arrival, the first few Sedge Warblers establish territories in MB habitats. Since the amount of this habitat is relatively scarce, the density of singing males rises rapidly thus ensuring a high degree of territorial aggression towards later arrivals. These latter individuals may then prefer to settle in the less attractive MR habitats, which, although offering a poorer vegetation profile, are relatively free from competition. As the population level continues to rise, more individuals will opt for the less desirable habitat. At the same time the density in the MB habitat should increase until its attraction is offset by the repelling effect of the incumbant birds. The outcome of this process is to produce a critical level in the MB habitat beyond which the population density cannot increase. The situation described parallels that found in the Great Tit in Holland (Kluyver and Tinbergen 1953), where the habitat preference is for mixed rather than pine woodland.

Again emphasizing that only five years data is available, the maximum number of pairs found in the MB habitat was 36 (in 1977, when the population was also maximum). Taking the figure of 3·86 ha. as the area of available habitat, we see that a critical density figure corresponds to a territory size of 1072 m^2. This is considerably lower than the 1811 m^2 given by Catchpole (1972) as an average territory size for Sedge Warblers at Attenborough N.N.R. In order to calculate mean territory size, Catchpole used isolated areas of known size which were fully occupied. He also distinguished between 'dryland areas' and 'marshland areas', but it is not clear whether the territory sizes used in the calculations were taken from the preferred 'dryland areas'. Even so, since Catchpole's estimate was for mean territory size, smaller territories existed and were possibly smaller in the preferred habitat.

The minimum number of pairs found in the MB habitat was 23 (in 1978 and 1979) giving a territory size of 1678 m^2. However in both of these years, some MB remained unoccupied and the true figure is more likely to be in the order of 1300 m^2. Thus even in years when the population is low, the density in the preferred habitat remained quite high.

Territory size probably varies with the 'quality' of habitat, and the values given above possibly reflect this. Without detailed plotting, it is impossible to estimate the average territory size in MR. These did however appear considerably larger (song flights covered greater distances). The mature bramble B constituted only a very small amount of habitat and was rather fragmented. Thus any attempt at estimating territory size is fraught with problems.

Kluyver and Tinbergen (1953) remark that critical density levels must vary with habitat and demonstrated that for Great Tits mixed woodland contains smaller territories than pine woodland. Oxwich marsh is well established, containing a rich and diverse flora and fauna. Attenborough on the other hand is relatively new, having been created from recent gravel extractions. It is possible that at Oxwich, some territories are of such 'high quality' they can be compressed to a size far smaller than those at Attenborough. This could only be decided by a detailed study of habitat utilization with particular emphasis on feeding ecology. This topic was not considered for the Sedge Warbler.

CHAPTER SEVEN

Conclusions

At the end of each of the foregoing chapters a summary and discussion was given in relation to the particular topic under consideration. It is useful now to briefly summarise the main conclusions in these chapters, and to attempt to bring together the important results.

The work was concerned with the breeding biology of Reed Warblers and Reed Buntings in relation to marshland habitats, and with habitat selection in the Sedge Warbler. We first summarise these topics separately by enumerating the significant results.

Reed Warblers

1. The breeding season began earlier in PM than elsewhere.
2. Nests in PM were woven around more reed stems and were built higher than elsewhere.
3. Clutch size varied little between habitats, but fell quicker with season in PM.
4. Brood sizes at fledging showed no significant differences either between habitat or season.
5. Nest success (i.e. probability of a nest producing young) was high in PM and MM and very low in IM.
6. Most nest failures were due to predators (not Cuckoos).
7. Nestlings in PM were markedly heavier throughout the entire nestling period.
8. The diet of nestlings was similar in all habitats
9. Adults from PM nests foraged more in carr areas than those from MM nests and travelled greater distances.

Reed Buntings

1. The breeding season began very much earlier in PM.
2. Clutch size varied little between habitats and season.
3. Brood sizes were higher in PM and overall decreased with season.
4. In PM, nests containing eggs had a higher chance of failure than those with young. Elsewhere the reverse applied. Overall nest success was higher in PM.
5. Nestling weights differed between habitats, with predicted mean fledging weights in PM slightly heavier than elsewhere.
6. Nestling diet varied considerably between habitats.
7. Adults from PM nests foraged mostly in carr, whilst those from other nests foraged mainly in the marsh.

In order to fit these findings into some general picture of marshland utilization, we must recall the pattern of availability of potential prey as found in Chapter 3. We summarise this as follows:

1. Diptera accounted for a very high proportion of all potential prey items throughout the entire period.
2. Large numbers of Chironomids were present in the early part of each species' nesting season.
3. Overall peak prey abundance ocurred from mid-June to mid-July.
4. The distribution of available spiders was essentially uniform throughout the period.
5. Beetle numbers peaked at the beginning of June but remained steady throughout.
6. Larvae appeared uniformly distributed throughout the season (but probably peaked in the carr areas in late May).

The results obtained from both the above species demonstrate a clear advantage to those pairs nesting in PM. Both species nested earlier in PM and produced heavier young there. Reed Warblers laid heavier eggs in PM nests whereas Reed Buntings did not. It would appear therefore that both these species breed more successfully in PM but for different reasons. Reed Warblers probably take advantage of an early emergence of Chironomids in PM to produce larger eggs, whereas Reed Buntings clearly do not do so. Nest sites in PM are better suited to both species, Reed Warblers being able to build higher nests on more reed-stems, and Reed Buntings building nests which are highly camouflaged. The proximity of carr to nesting sites is probably an important factor in determining nesting success. Both species utilized carr to a greater extent when nesting in PM, particularly Reed Buntings. On the other hand, Reed Warblers nesting in PM travelled further on foraging trips than those nesting elsewhere, but Reed Buntings did not.

These basic differences in breeding biology in respect of habitat are reflected in the feeding ecology of both species as determined by faecal analysis and hide observations. As one might expect, Reed Buntings are more specialist feeders, the main food items being larvae, beetles and slow moving insects. The breeding season appears to be timed so that most young from first broods are in the nest towards the end of May when caterpillar numbers peak in the surrounding woodlands. This also coincides with the maximum number of available beetles found in the water traps.

Reed Warblers on the other hand are generalist feeders, taking advantage of virtually all available prey items during their particular season. There is strong evidence to support the idea that the Reed Warbler breeding season is governed to some extent by the availability of the abundant Chironomid supply in early spring, and that breeding commences earlier in those areas of high productivity. On the other hand, food of maximum calorific value is given to nestlings during their period of maximum growth, which also coincides with the overall peak in insect abundance. It is possible that these factors all contribute and are related in some way.

In conclusion we remark that in this discussion, apart from the vital question of how many young are produced per pair, the important factor in determining overall nesting success appears to be the ability of nestlings of both species to gain more weight in PM nests than elsewhere. Of course patterns of growth provide only one example of adaptation to ecological pressures. Lack (1968) has suggested the various patterns of nestling growth reflect an adaptation for optional breeding of parent birds. In contrast Ricklefs (1968) proposed that growth rates are predominantly determined by adult size and rate of development of mature function of the nestling. O'Connor (1978) on the other hand has argued that the predictability and stability of the food supply may also be an important factor in determining the growth of a species. From the results obtained in this investigation the latter hypothesis appears to be the most likely.

Sedge Warblers

Only habitat selection was considered. The results showed a marked preference for Sedge Warblers to nest in the areas of the marsh not favoured by Reed Warblers. In certain areas, particularly MM, Sedge Warbler and Reed Bunting territories overlapped as did their foraging locations. However virtually no observations of the feeding ecology of Sedge Warblers were made.

Sedge Warbler territories were most frequently found associated with a mixed dense vegetation matrix consisting of reed and bramble. These areas of the marsh were normally situated on 'dry land', but never far from a marsh/water interface. They contained by far the highest density of breeding pairs, and were occupied first in the habitat selection process.

Evidence was given to support the view that the plant species content within a breeding territory was less important than its vegetative complexity. The results were however superficial and much more work is needed to verify this.

Oxwich in relation to the national situation

In general terms, the breeding biology of each of the three species at Oxwich typifies the situation one might expect to find in any British marsh. On closer examination however, some important differences appear to exist.

In the case of the Reed Warbler the analysis of the B.T.O's data by Bibby (1978) is timely. Again stressing that the Oxwich results were obtained from only one year's work, we conclude that Reed Warblers have a much higher nesting success at Oxwich than elsewhere, this being the case even in the poor IM habitats.

An explanation is not obvious. However Bibby (pers. com.) studied the breeding biology of Reed Warblers at Fowlmere in Cambridgeshire during the same summer (1979), and employed identical methods to those at Oxwich. The results of the water trapping showed that considerably fewer potential prey items were available at Fowlmere, with some taxa e.g. Odonata being virtually non-existent.

The extensive work by Catchpole (1972, 1973a, 1974) at Attenborough NNR, Nottinghamshire led him to conclude that the Reed Warbler was possibly undergoing some kind of ecological expansion away from reed beds. Catchpole's arguments were based on his findings that breeding success was higher in those habitats outside the reed beds. The work did not however examine the 'quality' of the marsh which, being relatively recently formed, could quite possibly have had low insect productivity.

Since the diet of Reed Warblers is largely made up of emergent aquatic insects. The ability of the marsh to produce large numbers of insects must be of prime importance in determining overall nesting success. Oxwich and Leighton Moss in Cumbria (J. Wilson pers. com.) are two such marshes. Both have long histories, were formed in essentially the same way, have the same basic substrate and plant communities and sustain very large numbers of reed-nesting Reed Warblers. Such rich marshes are however probably uncommon in the British Isles, the total area of which must certainly have decreased in recent times. The resulting pressures on a locally abundant species such as the Reed Warbler to find these prime breeding marshes must be severe, and could explain the expansion into less productive habitats such as those described by Catchpole.

Although comparisons of breeding success in the Reed Bunting are more difficult to make, a similar argument to the one above is valid to some extent. At Oxwich there was strong evidence to suggest that the entire marsh was occupied. Bell (1968) and Hornby (1971) both found the species breeding at maximum densities in the marshland habitats at Attenborough, and that breeding success was highest there. There is substantial evidence to support a recent ecological expansion of the Reed Bunting away from marshes in Britain (Bell 1969, Batten 1971, Hornby 1971). This is not the place to reiterate these arguments but merely to add that at Oxwich no such expansion appears to exist, the reason possibly being again the 'high quality' of the marsh.

Very little can be inferred from the Sedge Warbler results. However most of the favoured habitat was occupied in each year, and most nests that were found were usually successful.

Further research

Many of the conclussions reached in this thesis are necessarily tentative and further research is desirable to verify them.

A major omission has been any consideration of the breeding success and feeding ecology of the Sedge Warbler in relation to its known habitat preferences. Particular attention could be given to studying this species in the vicinity of the South Serpentine Pond, where breeding densities are highest, and at the western end of the East Marsh where a few pairs usually breed near the road.

An understanding of the feeding ecology of all three species on their arrival at Oxwich in spring could be particularly rewarding, especially in the case of the Reed Warbler. This work would certainly present many difficulties, since it would ideally involve the watching of marked individuals, preferably of known sex, within the reed-beds.

More effort should be placed on trying to identify individual pairs of each species, so that an estimate might be obtained of the number of breeding attempts made per pair in each year. This is probably a feasible proposition in the case of the Reed Bunting, but more difficult for the other two species.

The survival of young during the immediate post-fledging period is of critical importance. Any information in this direction would be particularly valuable.

All the work reported in this thesis was concerned with breeding biology. The relationship between the dispersal and/or migration of the three species at Oxwich in late summer would be of great value, especially in connection with available food resources. Superficial evidence suggests that there is relatively little Acrocephalus movement through Oxwich during this time.

Ideally any of the above programmes should be undertaken for a minimum period of about three years, and should if possible be designed in such a way as to compliment the results reported in this thesis.

Management recommendations

Pressures on the traditional wetlands in Britain have increased enormously throughout this century and are very unlikely to be reversed. Such habitats are disappearing at an alarming rate, and at the same time few are being created (Bibby 1981).

At Oxwich, natural vegetative succession has already substantially changed the marsh over the last three or four decades, and if left unchecked, would probably eliminate it in a similar time span. Virtually no positive steps have been undertaken to check this succession, but ironically the marsh is probably more diverse now, both in flora and fauna, than at any period in its history. It would seem therefore that a strong argument can be made for maintaining the marsh in its present form. This involves eliminating to a large extent, the encroachment of Willow and Alder carr and maintaining the water table at its present high level.

Naturally any physical interference with the marsh must be a compromise, and the recommendations proposed here are made in the light of the research reported in this thesis. No direct consideration is given here to the implications of such interference on the flora of the marsh, but it is clear that some action is needed to maintain the rich plant communities that exist.

The following recommendations are considered urgent:

1. Repairing the sea wall.
2. Removal of the large area of Willow/Alder carr at the southwestern corner of the West Marsh and excavating to below the level of the water table.

3. Maintenance of the major drainage channels, particularly in the West Marsh.
4. The retention of small isolated Willow or Alder bushes within or along the edges of any of the marshland areas or ponds.
5. The maintenance of the Garden Lane Marsh in its present form by the careful elimination of any Willow or Alder encroachment, particularly along its southern boundary.
6. The maintenance of the Willows on either side of the Garden Lane.
7. The sluice-gate to be left in its present damaged state until an investigation of the breeding success of the substantial numbers of Reed Warblers at the eastern end of the East Marsh has been undertaken.
8. Continued elimination of the spread into the East Marsh of Alders from the Dead Wood.
9. Areas of IM to be cut (or burned) and the water levels raised by excavation.
10. All such work to be undertaken outside the breeding season.

We finally remark that the recommendations given by Elias (1979) are in broad agreement with those given here. Any differences are probably as a result of the present work concentrating on the three marshland passerines.

SUMMARY

The breeding biology of the Reed Warbler *Acrocephalus scirpaceous* and the Reed Bunting *Emberiza schoeniclus* was studied at Oxwich Marsh, Gower, primarily during the summers of 1978 and 1979. Three marshland habitat types were identified, and the utilization, feeding ecology and breeding success of both species in respect of these habitats was considered.

In 'pure reed marshes' both species bred earlier, produced heavier young, were predated less and had higher nesting success (i.e. probability of a nest producing young) than those breeding in 'mixed marshes' and other areas.

Invertebrates were collected in each habitat. Diptera accounted for a very high proportion of all potential prey items throughout the breeding season. Pure reed marshes produced more invertebrates than elsewhere, and overall peak abundance measured by numbers and biomass ocurred from mid-June to mid-July, coinciding with the time when most young of both species were in the nest.

The diet of nestlings based on faecal analysis and hide observations showed Reed Warblers to be generalist feeders, with a similar diet in all habitats. Reed Buntings proved to be more specialist feeders, with a diet varying considerably between habitat types.

Adults of both species foraged mostly in carr when nesting in pure reed marshes, whilst those from mixed marsh nests mostly utilized the marsh.

Habitat selection in the Sedge Warbler *Acrocephalus schoenobaenus* was studied. A separate habitat classification was used, which indicated a preference for nesting in areas with a mixed dense vegetation matrix, consisting mostly of reed and bramble. These areas contained the highest densities of breeding pairs and were occupied first.

Evidence was given to support the view that the plant species content within a breeding territory was less important than its vegetative complexity, which was measured and shown to be negatively correlated with settlement time.

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