Ecology and Reproductive Behaviour

of Damselflies

Thesis submitted in accordance with the

requirements of the University of Liverpool

for the degree of Doctor in Philosophy by

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June 1989

Contents.

Ecology and Reproductive Behaviour of Damselflies.

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Abstract.

This thesis is concerned with intraspecific competition among damselfly larvae, and on the behaviour and ecology of adults. *Pyrrhosoma nymphula* (Sulzer) was the subject of the work on adult emergence and behaviour at two ponds in Cheshire, while larvae of *Ischnura elegans* (van der Linden) were used in laboratory competition studies.

An asymmetry was found in the way interference competition acts when small and large larvae of *I. elegans* were contained together with unlimited prey. Small larvae suffered significantly reduced development rates and size increases at the moult in the presence of large larvae, but similar reductions were not apparent when small larvae were combined with like-instar larvae, or when large larvae were combined with small larvae. In field populations, larvae which have been adversely affected by competition for food or fishing sites may be smaller and emerge later than competitively successful larvae. Adult size and seasonal occurrence may have a strong influence on both male and female reproductive success.

The emergence of *P. nymphula* was studied at two adjacent ponds. The emergence from both ponds appeared less well synchronised than might have been expected. There is likely to be a trade-off between the need to emerge around the same time as conspecifics in order to achieve a full reproductive potential, and the expression of temporal variation arising in part from competition. Newly emerged adults from one pond were significantly larger and emerged earlier than those from the other pond. This may have been due to differences in prey availability and distribution, and to temperature differences. A decline in size of newly emerged adults through the season was found at both ponds.

During periods of bad weather, numbers of individuals emerging were substantially reduced. Those individuals still attempting emergence presumably did so because of the progression of metamorphosis. Quantification of emergence mortality attributed to different factors was attempted. Mortality was found to be highest after a sudden deterioration in the weather. Mean daily mortality, expressed as a percentage of the total daily emergence, was calculated to be 27.93%. There was no evidence of density-dependent mortality at emergence.

Recovery of individuals marked at emergence and when mature was found to be low. For mature adults, this was attributed predominantly to dispersal to nearby water bodies. There was some indication that there was a higher mortality of smaller adults in the immature and reproductive stages of the life-history. Fewer females revisited the ponds than males which led to the estimation of female survivorship being considerably lower than that of males. A large increase in weight of females from emergence to maturity suggests that they may amass clutches of eggs over several days and thus not visit the ponds on every day of their reproductive life. In addition, mortality of females may be higher than that of males as a result of predation during oviposition.

For male *P. nymphula*, size was shown to have no effect on the outcome of territorial disputes,which were settled by a simple residency asymmetry. Size was also found to be unrelated to the total number of observed matings a male achieved, and the number of days a male spent at the ponds, although the latter may have been obscured by the low return of marked males. The relation of size to longevity could not be studied. Success in mating and in territorial disputes was found to be positively related for resident males. This was probably due to the amount of time spent at the ponds within a day.

Late emerging female *P. nymphula* visiting the ponds later in the season laid smaller clutches of smaller eggs than those arriving early in the season, irrespective of size. Clutch size is likely to be strongly related to the inter-clutch interval and thus the pattern of sunny and cloudy days through the season.

Chapter 1.   Introduction.

Damselflies (Odonata: Zygoptera) have complex life-histories. They have a relatively long-lived aquatic larval stage and a short-lived terrestrial adult stage. The direct metamorphosis from larvae into flying adults represents a transformation as dramatic as any seen in the animal kingdom with the adults living in a world totally unlike that of the larvae. An understanding of the population dynamics of such organisms is an important area of current ecological research. Of fundamental importance is the relationship between the two life-history stages, and in particular, how success as a larva influences success as an adult.

This thesis is concerned with intraspecific competition among larvae, and on the behaviour and ecology of adults. Two parameters consistently arose in the interpretation and discussion of results relating to adult behaviour and ecology; these were the size and seasonal occurrence of individuals. Both parameters relate directly to the larval stage of the life-history. Larvae that are forced into areas of low prey availability may suffer decreased development rates and reduced size increases at subsequent moults (see Lawton, Thompson & Thompson 1980; Baker 1982). Thus, larvae that have been successful in competition for food will not only emerge earlier than those adversely affected by competition, but they will also be larger.

The thesis has six data chapters. Chapter 2 is concerned with larval intraspecific competition. Chapters 3 and 4 deal with adult emergence and chapters 5, 6 and 7 present studies of the behaviour of mature adults. *Pyrrhosoma nymphula* (Sulzer) was the subject of the work on adult emergence and behaviour, while larvae of *Ischnura elegans* (van der Linden) were used in the competition studies.

Pyrrhosoma nymphula is a common damselfly with a wide distribution over almost all of the British Isles, occurring in a variety of habitats including slow-moving streams, canals, lakes, marshes, peat bogs and even brackish water (Hammond 1977). It is also found throughout Europe and extends as far as the Atlas Mountains of Morocco (d'Aguilar, Dommanget & Prechac 1986).

The life-history of *P. nymphula* has been investigated by Corbet (1952, 1957a, 1962), Gardner & McNeil (1950), Lawton (1970, 1971a) and Macan (1964, 1974). Typically, it has a two year life cycle which gives rise to two generations or year classes being present in any one year. It has been described as a characteristic spring emergence dragonfly with a well-synchronised adult emergence (Corbet 1957a, 1962). Eggs laid in May, June and July hatch after 2-4 weeks. Larvae usually reach instars 5 or 6 before overwintering and growth is resumed in the spring with the final instar being reached around October. Metamorphosis takes place in March and April of the following year with adult emergence commencing in early May.

Ischnura elegans is also a very commmom damselfly of canals, ponds, lakes and slow flowing streams. It is widely distributed throughout Europe and Asia (d'Aguilar, Dommanget & Prechac 1986). Larval development depends mainly on temperature and while in southern France *I. elegans* can have up to three generations per year, development generally takes one or two years in northern England (Parr 1970). The adult flight period tends to be longer than for other damselflies, usually lasting from mid May to early September.

Ecology of larvae and newly emerged adults.

The aggressive behaviour of odonate larvae towards conspecifics can have important consequences for population regulation. Baker (1980, 1981) showed that under laboratory conditions, smaller larvae of the damselfly *Coenagrion resolutum* (Hagen) may be excluded from profitable feeding sites by the aggressive behaviour of larger larvae. Under natural conditions such larvae may then suffer reduced growth and development rates or be at a greater risk from predators.

Evidence from field studies has shown that interference can result in growth suppression, injury, mortality and even cannibalism (Benke, Crowley & Johnson 1982; Merrill & Johnson 1984; Johnson *et al.* 1985; Pierce, Crowley & Johnson 1985; Baker & Dixon 1986; Crowley *et al.* 1987a).

In Chapter 2, a competition experiment is described between larvae of *Ischnura*

elegans. The experiment is designed to detect any asymmetries in the way interference competition acts between larvae belonging to small and large instars under conditions of unlimited prey. Such an investigation differs from other laboratory studies in two respects; firstly all larvae have at least the potential to maximise their feeding rates, and secondly, the time-span of the experiment runs over the entire duration of an instar, the parameters to be measured being the development rate (instar duration^{-1}) and the size increase at the moult.

Macan (1964) found that larvae of *Pyrrhosoma nymphula* took either two or three years to complete development in a study pond. When they were less abundant the entire population completed development in two years. This led him to conclude that the number of fishing sites was limited and that fast growing larvae remained in the optimal sites while smaller, slow growing larvae were forced into areas of little food. Similarly, Banks & Thompson (1987a) found that larvae of the damselfly *Coenagrion puella* (L.) in a high density population were smaller and more likely to be semivoltine than those in a low density population. Harvey & Corbet (1985) found that smaller adults of *P. nymphula* emerged late in the emergence period and Banks & Thompson (1985a) showed that the size of emerging *C. puella* declined through the emergence period. Presumably these smaller, late emerging adults had achieved low success in larval competition for food.

In Chapter 3, a study of the emergence of *P. nymphula* from two adjacent study ponds is described. The total number of males and females emerging daily through the entire season, together with size and weight measures, is presented. Such data, interpreted in different ways, provide information on the emergent sex ratio, differences between male and female emergence, and trends in size through the season. In addition, by studying the emergence at two adjacent ponds, factors which may determine the seasonal placement, duration and synchronisation of emergence within the emergence period can be investigated. Clearly, both study ponds will be subject to the same climatic conditions and photoperiod. Corbet (1962) stated that a photoperiod response functioned to place larvae in the right developmental stage at the

appropriate season, the actual date of emergence being determined by a response to temperature. The implications of such a statement are discussed in the light of the findings of this study.

In Chapter 4, a quantitative study of mortality at emergence is presented. Very few studies have attempted to quantify mortality during emergence. Previous investigations have largely been concentrated on the identification of either the predators seen to prey on newly emerged adults or the climatic conditions which result in increased mortality. In this study mortality is divided into two categories: that due to adverse climatic conditions and that attributed to predators (including birds, ants and spiders). In addition to estimating mortality levels and relating them to the prevailing weather conditions, the effects of climatic conditions on emergence are also investigated by comparing daily numbers of individuals emerging with various weather variables.

Behaviour of mature adults.

In recent years there have been a large number of studies on sexual selection and the behaviour of adult damselflies. Sperm competition, the significance of mate guarding, male territorial behaviour, and lifetime reproductive success of both males and females have all received considerable attention. Sperm removal has been shown to occur in many damselflies including *Calopteryx maculata* (Beauvois) (Waage 1979a), *Enallagma cyathigerum* (Charpentier) (Miller & Miller 1981) and *Enallagma hageni* (Walsh) (Fincke 1984a). All of the above studies have indicated that the secondary genitalia of males possess a variety of hooks and bristles which hold trapped sperm and, as a result, the last male to mate fertilizes 80-95% of a female's eggs laid after mating. It follows that postcopulatory mate guarding is a common occurrence in damselflies.

Although sperm removal may not directly benefit the female, she may gain subsequently by being guarded during oviposition (this may reduce the harassment from other males or reduce the risk of predation and drowning). The adaptive

significance of postcopulatory guarding is discussed by Alcock (1979, 1982, 1983) and Waage (1979b).

Territorial behaviour of male damselflies and dragonflies has also been widely studied, particularly in relation to mating success (e.g. Pajunen 1966a, 1966b; Waage 1973, 1979b; Robertson 1982; Fincke 1984b; Harvey & Corbet 1985). Males which defend oviposition sites that are attractive to females often achieve a higher mating success than non-territorial males.

Darwin (1859) made a distinction between selection for traits that enhance survival (natural selection) and selection for traits that increase an individual's success in acquiring mates (sexual selection). Studies of lifetime reproductive success of damselflies have attempted to quantify the intensity of natural and sexual selection. Fincke (1982, 1988) and Banks & Thompson (1985a, 1987b) studied lifetime mating success of the damselflies *Enallagma hageni* and *Coenagrion puella* respectively. Banks & Thompson (1985a) warned that it may be misleading to draw conclusions about the action of sexual selection from studies of daily, rather than lifetime, reproductive success. They found that smaller males had a higher daily mating rate than larger males, but larger males lived longer such that males at both extremes of the size distribution were more likely to fail to mate. Similarly, in female *C. puella* clutch size is inversely related to body size but because large females survive for longer than small females, selection should favour large size in females (Banks & Thompson 1987b).

For practical reasons, in this study only the short-term mating success of males and females is investigated. Thus, differences in, for instance, longevity which might favour individuals of a certain size are not addressed.

In Chapter 5, aspects of the life-history of adult *Pyrrhosoma nymphula* are presented which concern both males and females but do not relate directly to the studies of reproductive biology. Over one year's entire reproductive season all mature adults visiting two study ponds were caught, individually marked, measured and then released. Information on a diverse range of behavioural and ecological studies is

presented in this chapter.

Chapter 6 concerns male territorial and reproductive behaviour. Harvey & Corbet (1985) concluded that larger males of *P. nymphula* won more territorial disputes and enjoyed enhanced mating success. This is investigated further in this study. Males of *P. nymphula* neither defend oviposition sites nor display any type of obvious courtship behaviour. The territory simply consists of a perch site and the 'airspace' around it. From there they fly out to potential mates and chase other conspecific males that fly or attempt to settle near to them. In a detailed study the influence of male size on observed mating success and on the outcome of territory disputes is deduced. A comparison of the size of resident and interloper males and of the size of paired and unpaired males is undertaken, and the relationship between observed mating success and the outcome of territorial disputes is presented.

In Chapter 7, the reproductive biology of female *P. nymphula* is investigated. Banks & Thompson (1987b) found that females of *Coenagrion puella* maximised their lifetime egg production by minimising the interval between clutches, rather than by maximising the size of each clutch. They found that egg size and female size were not correlated and that clutch size was inversely related to body size. This study aims to investigate the factors affecting egg size and clutch size in female *P. nymphula*, and so provide a comparison with the results for *C. puella*.

In the final chapter, Chapter 8, the relationship between the larval and adult stages of the life-history is considered when the findings and conclusions from the preceding six data chapters are incorporated into a general discussion.

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Chapter 2.   Asymmetric, intraspecific competition among
larvae of the damselfly *Ischnura elegans*.

2.1   Introduction.

Several laboratory studies have shown that odonate larvae can interfere with each other's feeding, usually by means of some form of aggressive interaction (Baker 1980, 1981; Harvey & Corbet 1986; McPeek & Crowley 1987). The implication of these laboratory experiments is that some larvae (usually large larvae) exclude others from the best feeding sites, thus consigning the losers to some suboptimal site where growth and development may be suppressed, or to a more hazardous feeding site where individuals may risk greater exposure to predators in order to feed (see Heads 1986).

Field evidence of interference has come predominantly from enclosure experiments. Feeding interference, resulting in significant inhibition of growth, has been demonstrated by Pierce, Crowley & Johnson (1985) and by Crowley *et al.* (1987a). Interference can also result in mortality (Benke, Crowley & Johnson 1982; Crowley *et al.* 1987a) or injury (Baker & Dixon 1986). An extreme form of interference competition, cannibalism, has been found in studies by Benke (1978), Merrill & Johnson (1984) and Johnson *et al.* (1985).

The consequences of this interference at the population level have been shown by Macan (1964) and Banks & Thompson (1987a). They showed, in field studies, that when populations of zygopteran larvae were present at very high densities in relation to food supply and/or vegetation cover, cohort splitting could occur. Banks & Thompson (1987a) provided some evidence of density dependent larval mortality and suggested that most mortality was among the cohort destined to become semivoltine when the split occurred. In the laboratory, invertebrate predators have been shown to alter the behaviour of damselfly larvae and to be a significant cause of mortality to

those larvae that are forced by intraspecific interference to leave the best (safest) fishing sites (Heads 1985, 1986; Thompson 1987a).

When larvae are forced into areas of low prey density they can suffer decreased development rates, and reduced size increases at subsequent moults. The relationship between food abundance, growth and development rate has been studied by Lawton, Thompson & Thompson (1980), Baker (1982) and Pickup & Thompson (1984). The decreased development rates caused by long term feeding reduction may also extend the period of exposure to predators before the larvae reach maturity (Crowley *et al.* 1987b). Crowley *et al.* (1987b) pointed out that their model of population regulation in damselflies is particularly sensitive to the precise form of the relationship between growth rate and feeding rate (and therefore prey density). Clearly the aggressive behaviour of odonate larvae towards conspecifics can have important consequences for population regulation.

Most of these studies have been concerned with a relatively short time-span in relation to even the duration of an instar. The aim of this experiment was to study over the duration of an instar, the effects of the presence of large and small larvae on the growth and development rate of focal individuals. The experiment was performed with a superabundance of prey in order to remove any complicating and confusing effects due to exploitation competition. Any reductions found in growth or development rate could thus be attributed exclusively to interference competition. The experimental animals used were larvae of the damselfly *Ischnura elegans*, the same species that provided many of the parameter values for the model of Crowley *et al.* (1987b).

The results of this experiment underline an important consequence of interference competition among damselfly larvae on the lifetime reproductive success of damselflies.

2.2 Materials and methods.

2.2.1 Larval collection, identification and assignment to instars.

Larvae were collected from a number of local ponds at regular intervals over the course of the experiment. The site most frequently visited was at Caldy, Wirral (N.G.R. SJ 238846). This pond contained a semivoltine population of *I. elegans* and thus provided large numbers of larvae across a wide range of instars at virtually any time of the year. Such a range of instars was required at all times throughout a fifteen month period, while the experiment was in progress.

Larvae were collected simply by sweeping the vegetation around the pond periphery with a pond net. This served to dislodge some individuals as well as uprooting small amounts of the aquatic vegetation on which other larvae would be clinging. Since no quantitative measurements were required, the contents of several net sweeps could be emptied into a container and the samples sorted in the laboratory.

Larvae were placed together in glass bowls with fresh aerated pond water, in a 4°C constant temperature room until such time as they could be measured and identified. While at 4°C they were provided with a minimal food supply. Thompson (1978a) showed that growth of *I. elegans* ceases at temperatures below 8°C, and that at this temperature moulting is a rare occurrence even under conditions of an abundant food supply.

Larvae were assigned to instars by means of a plot of hind tibia length against head width, measured as the greatest head width across the eyes (Thompson 1975). All larvae from each sampling occasion were thus measured using a binocular microscope fitted with an eyepiece micrometer. They were then stored individually at 4°C in labelled glass bottles containing aerated pond water, a minimal food supply, and a wooden cocktail stick to provide a perch.

Such plots of hind tibia length against head width produce discrete clouds of points, each cloud corresponding to a particular instar. The instar clouds are only

discrete and separated when the measurements of larvae collected on one particular sampling occasion are plotted (Banks 1985). When samples are combined that have been taken in the same period but from different sites, or from the same pond over a longer period, instar clouds run into each other and the classification of larvae into instars becomes almost impossible. Instar maps were therefore plotted immediately larvae had been collected and measured on each sampling occasion.

Figure 2.1 shows the relationship between hind tibia length and head width for *Ischnura elegans* larvae obtained from a sampling occasion at Caldy on 12th October 1987. For the larger instars the corresponding points form discrete clouds. However, it is sometimes difficult to determine into which instar some of the smaller larvae should be grouped, particularly if they fall on the boundary of a cloud. Larvae falling outside the central mass of points within such clouds were not used in the experiment.

Arrows marked on the graph indicate the instar clouds and these have been labelled backwards from the final instar (N), the penultimate instar (N-1), antepenultimate instar (N-2) and so on. *Ischnura elegans* is known to have twelve instars although the smallest of these were never found in the samples, perhaps because they escaped through the mesh of the pond net, or because they were overlooked when sorting the vegetation. It is apparent by referring to Fig. 2.1 that the first four or five instars would all have had head widths of less than 1.0 mm. Hence, it would have been very difficult to assign these larvae to instars with confidence, and it is for this reason that the instar clouds have been labelled backwards from the final instar.

Three species of damselfly larvae were found in the pond samples. *Pyrrhosoma nymphula* occurred in very low numbers in a few of the ponds and could easily be distinguished from the other zygopteran larvae. The other two species found in all the samples were *I. elegans* and *Coenagrion puella*. The larger instars (from N down to N-4) could be distinguished under a binocular microscope with the aid of the key by Gardner (1954). *Coenagrion puella* has spotting over the head which is obvious in the final and penultimate instars. *Ischnura elegans* lacks this spotting, has differences
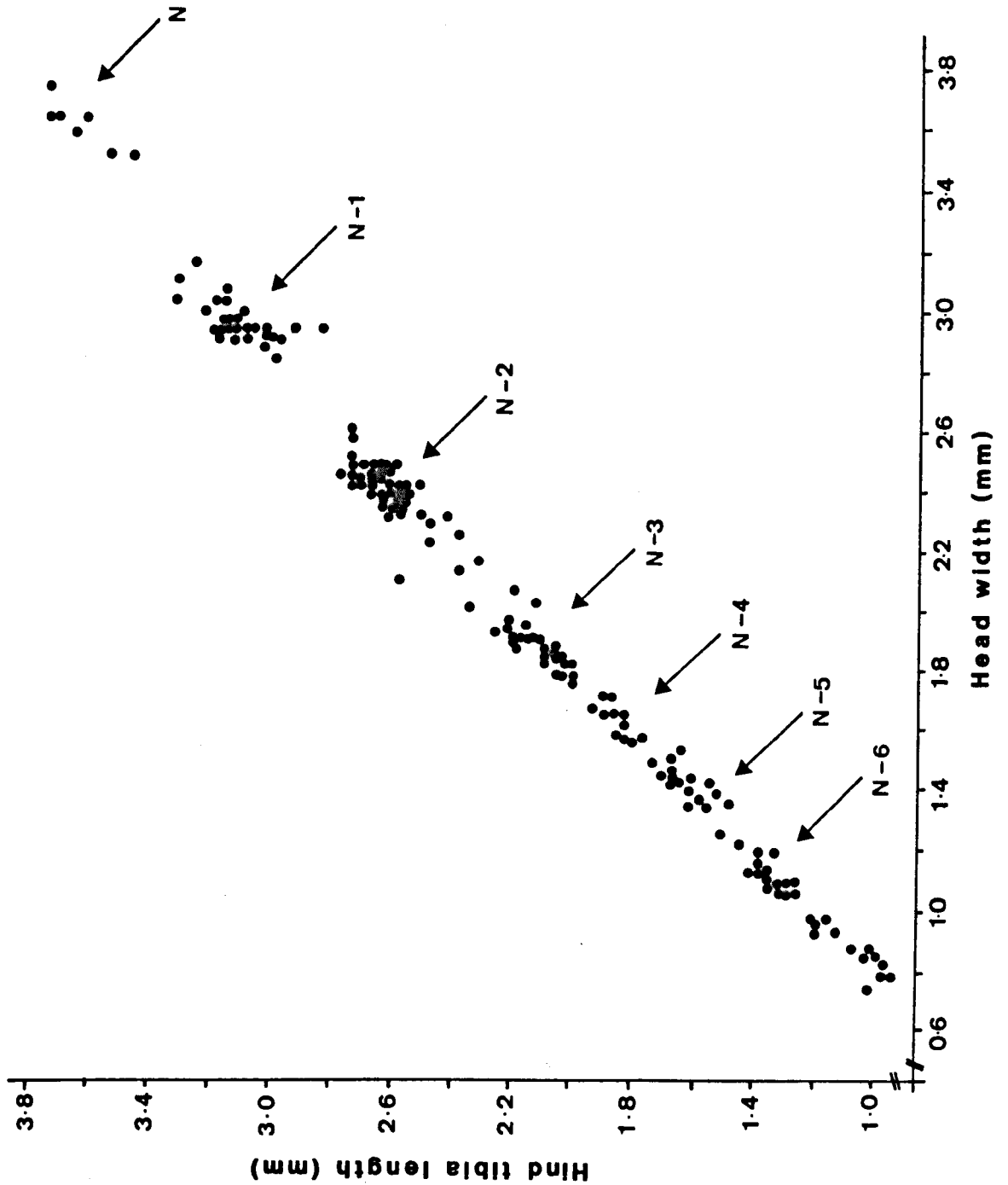
Fig. 2.1   The relationship between hind tibia length and head
width in I. elegans larvae (instar clouds indicated by
arrows).

in the shape of the caudal lamellae, and in addition, has four dark spots on the dorsal surface, one at the anterior end of each wing bud (Banks 1985).

Larvae belonging to smaller instars could not be distinguished this way since they lacked spots either on their heads or near their wingbuds. The ratio of hind tibia length to head width differs between the two species, with *I. elegans* having a relatively longer hind tibia (Banks 1985). Figure 2.2 clearly shows this and also demonstrates how such a relationship not only permits assignment of larvae to instars, as described above, but also provides a means to distinguish *I. elegans* from *C. puella*. The plot was obtained from a sample of larvae from a local pond on 9th December 1986. A best fit line drawn with the eye separates the two species with only a few exceptions.

Therefore, by plotting hind tibia length against head width and knowing the correct species identification of the larger larvae, a best fit line can be drawn on the graph between these points. This line can be extrapolated back to separate the points corresponding to smaller larvae, with the effect that only a limited minority of these larvae are wrongly identified.

2.2.2 Synchronisation of the stage of development of larvae within an instar.

Larvae from three instars were used in the experiment, these being penultimate or N-1 instar larvae, N-3 instar and N-4 instar larvae. One of the two parameters to be recorded was development rate. For the purpose of this experiment, development rate is equivalent to the inverse of the instar duration, which in turn was measured from the time a larva entered the experiment to when it moulted into the next instar. Therefore, to generate comparable results, it was necessary to synchronise all larvae entering the experiment with respect to their stage of development within an instar.

Such synchronisation was achieved as follows. Larvae that had been assigned to instars as described above were removed from the 4°C constant temperature room and transferred, first to 12°C for 24-48 hours and then to a 20°C incubator (a high mortality resulted if
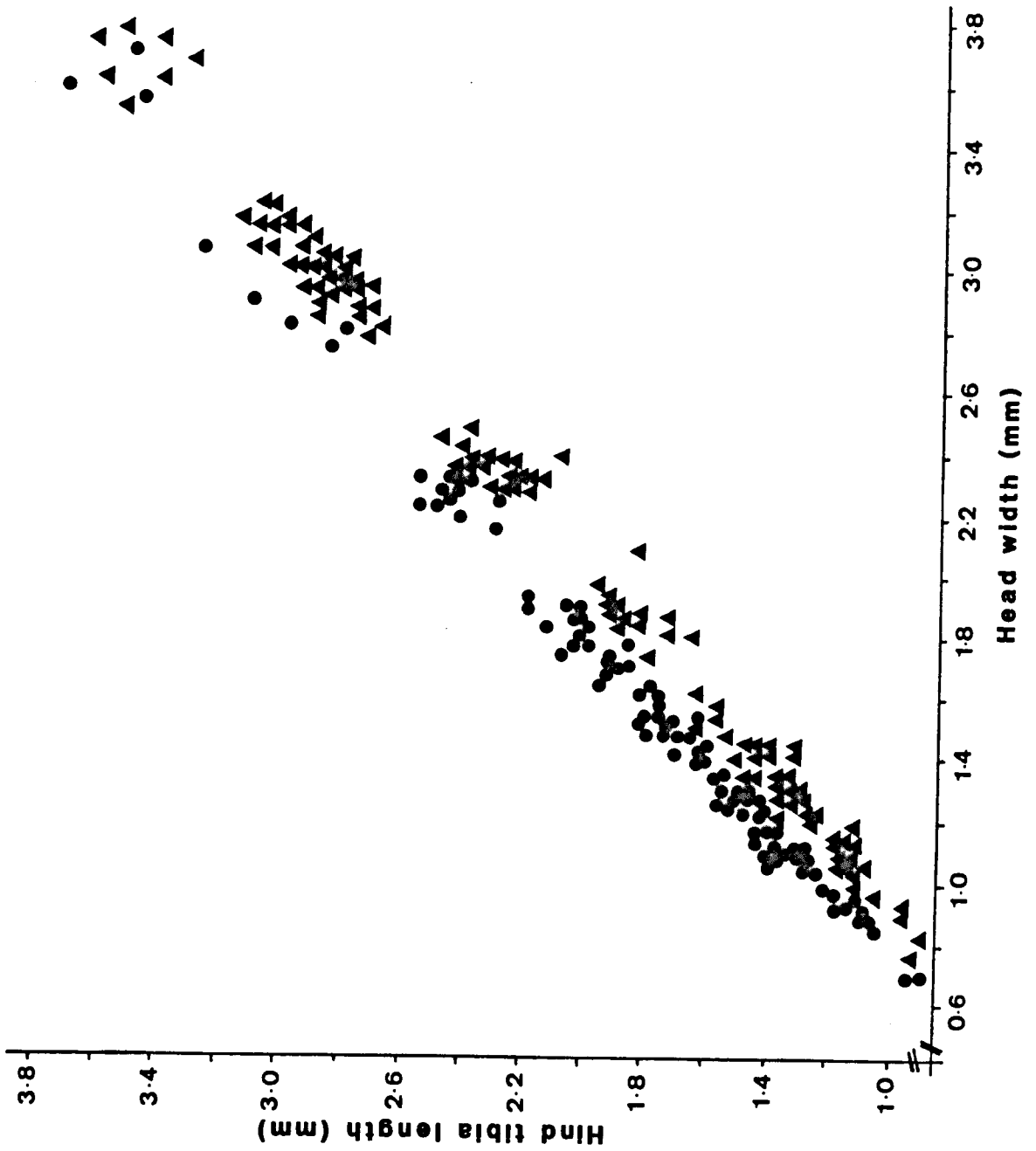
Fig. 2.2   The relationship between hind tibia length and head

width in I. elegans (●) and C. puella (▲) larvae.

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larvae were transferred directly from 4°C to 20°C). At 20°C they were provided with an *ad libitum* supply of food (*Daphnia magna* Straus) until they moulted. Thus, larvae of the desired instars for the experiment could be obtained simply by incubating individuals belonging to the preceding instars.

Once an incubated larva had moulted, the head width was measured and the date and estimated time of moult recorded. It was then included in the experiment. Incubated larvae were checked twice daily to see if they had moulted and the estimated time of moult was calculated as the middle point between the time of the last inspection and the time of the one in which they were found to have moulted. Since all larvae were checked twice daily, approximating in this way would lead on average to the actual time of moult being at the most six hours before or after the estimated time.

Clearly not all larvae that moulted into the penultimate instar or instar N-3 or N-4 in the incubator would do so at the same time. Entry of larvae into the experiment was therefore staggered over its entire course, with new replicates being set up as and when there were sufficient newly moulted larvae.

2.2.3   Experimental design.

The experimental containers used were transparent plastic cups filled with 80ml aerated pond water. Either one or four wooden cocktail sticks with 'plasticine' bases were provided in the cups as perches from which larvae could catch prey. The two types of cup were classified as having either low or high perch availability. Exactly the same larval combinations were studied using both types of cup but the results were analysed separately and then compared to expose any differences arising from the influence of perch availability.

As well as the experiment being split by differences in the provision of perch numbers, it was split additionally by the format of the combinations of larvae from the three different instars. Thus, N-3 instar larvae were observed alone, and in combination with like-instar and N-1 instar larvae at both levels of perch availability.

In exactly the same way, N-4 instar larvae were observed alone and in combination with other N-4 instar and N-1 instar larvae.

The larvae from instars N-3 and N-4 will be referred to as 'small larvae' or 'S' in the following figures and tables (the identity of these small larvae can be determined simply by reference to which of the two results sections they are under). Larvae from instar N-1 will be referred to as 'large larvae' or 'L' throughout.

Five different combinations of large and small larvae were set up in the containers (see Table 2.1). By including more than one experimental larva in the combinations (thus increasing the number of focal individuals) the actual number of experimental combinations studied could be increased to seven (the first mentioned larva being the focal individual). For instance, in cups containing one small larva and three large larvae, the experimental combinations '1S3L' and '1L1S2L' could both be studied by simply using an experimental larva from either one of the smaller instars (N-3 or N-4), or a larva from instar N-1, as the focal individual.

Each experimental combination, at both low and high perch availability and for both instars of small larvae, was replicated between four and sixteen times (see Table 2.2). Cups containing single larvae (either small or large) served as controls against which the other results could be compared. For all other cups the total number of larvae was always four.

Larvae in each of the experimental cups were fed daily with a superabundance of prey, *Daphnia magna*. One of the most important points in the design of the experiment was that this prey superabundance was maintained at all times to ensure that all larvae had at least the potential to maximise their feeding rates. Whether this potential was realized, or not, would then depend purely on interference effects arising from the presence of other larvae and not on there being a shortage of available prey.

Prey of an appropriate size (mean dry weight 0.033 mg) were obtained using graded Endecotts Test Sieves. As well as providing a superabundance of prey, it was clearly necessary to provide prey of a manageable size to ensure that all larvae (and in particular the smaller individuals) were not limited by prey items which they could not physically handle.

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Larval combinations in experimental containers	Experimental combinations
One small larva	1S
One small larva and three small larvae	1S3S
One small larva and three large larvae	1S3L 1L1S2L
One large larva	1L
One large larva and three small larvae	1L3S 1S1L2S

Table 2.1   The seven experimental combinations studied, arising from five different combinations of large and small larvae in the   experimental containers (the first mentioned larva in the experimental combination is the focal individual).

Experimental combination		Number of replicates	
		1 perch	4 perches
N-3	1S	16	12
	1S3S	13	12
	1S1L2S	9	9
	1S3L	7	7
N-4	1S	11	7
	1S3S	10	10
	1S1L2S	12	10
	1S3L	4	5
N-1	1L	10	9
	1L3S	4	4
	1L1S2L	14	11

Table 2.2 Number of replicates of each experimental combination.

Thompson (1978b) deduced the range of prey sizes consumed by each instar of *Ischnura elegans* in the field. He found that the minimum size consumed by a wide range of instars was very similar, while maximum prey size increased logarithmically with instar number. Appropriate sized prey were selected by reference to the above and by preliminary experiments carried out to monitor the feeding efficiency of smaller larvae.

Since the minimum prey size consumed by larvae from the three instars used was very similar, and because it was necessary, for comparison, to feed similar sized prey to each of the seven experimental combinations, it follows that mainly small-sized *D. magna* were used in the experiment. Considerable numbers of these small prey were often required each day and for this purpose sixteen large tanks containing cultures of *D. magna* were maintained throughout the course of the experiment.

Dead prey and prey remains were removed daily with a pipette and fresh aerated pond water added at the same time as the larvae were being fed. Throughout this procedure care was taken not to disturb the larvae from their current locations.

All experimental cups were maintained at 20°C in a 16 hour light : 8 hour dark photoperiod, and checked twice daily to see if any larvae had moulted. Moulted larvae were removed from the experiment, measured, and the date and time recorded. The estimated time of moult was calculated in the same way as described before, so enabling the total instar duration to be deduced by comparison of the two times.

In cups containing like-instar larvae a moulted individual could be distinguished easily using differences in colour and size. Its actual identity could be established without disturbing the other larvae by measuring the exuvium (efforts were made to ensure that such larvae, when placed together in an experimental cup, were of slightly different size).

Moulted larvae were replaced in the experiment with ones belonging to the appropriate instar from the stocks. When all the original experimental larvae in a cup had moulted the cup was removed from the experiment. For all larvae, development rate (the inverse of the instar duration in days) and percentage increase in head width at

the moult (actual increase in size as a percentage of the original head width) were recorded.

All statistical analyses regarding the results for percentage increase in head width were calculated using arc sine transformed data. Where necessary the values obtained were transformed back to percentages for the purpose of display. Non-integer degrees of freedom in the t-test analyses resulted from the use of a separate variance estimate in cases where the variances were not equal.

2.3   Results.

2.3.1   The effects of additional larvae on the growth and development rate of N-3 instar larvae.

The effects of the presence of large and small larvae on the development rate of other small (N-3 instar) larvae, for cups having low and high perch availability, are shown in Figs. 2.3a,b respectively. Regardless of the number of perches, the mean development rate decreases for small larvae in every combination with other larvae compared to that for small larvae in isolation. The difference is greatest, and significant (see Table 2.3), for the combination with three large larvae and least for the combination with three other small larvae where it is not significant. There is a significant difference between mean development rates of small larvae in the presence of like-instar larvae and small larvae in the presence of large larvae. Differences between other comparisons are also shown in Table 2.3. Together they support a hypothesis that small larvae suffer decreased development rates in the presence of large larvae, and that such a decrease becomes greater as the relative proportion of large larvae increases. However, small larvae are not significantly affected by the presence of like-instar larvae.

The mean percentage increases in head width are shown in Figs. 2.4 a,b. In

Fig. 2.3   Mean development rates (± standard errors) of small
(N-3 instar) larvae in isolation and in combination,
under conditions of a) low perch availability and b)
high perch availability.

Experimental Combinations Compared	Low Perch Availability			High Perch Availability		
	t	d.f.	P	t	d.f.	P
1S vs 1S3S	1.97	27	N.S.	1.30	22	N.S.
1S vs 1S1L2S	2.45	23	P< 0.05	1.74	19	N.S.
1S vs 1S3L	6.60	20.1	P< 0.001	4.10	17	P< 0.001
1S3S vs 1S1L2S	0.91	20	N.S.	0.89	19	N.S.
1S3S vs 1S3L	4.18	18	P< 0.001	4.70	17	P< 0.001
1S1L2S vs 1S3L	3.29	14	P< 0.01	3.70	14	P< 0.01

Table 2.3   T-tests comparing mean development rates between small (N-3 instar) larvae in different combinations.

Fig. 2.4   Mean percentage increases in head width (± standard errors) of small (N-3 instar) larvae in isolation and in combination, under conditions of a) low perch availability and b) high perch availability.

cups with only one perch there is a decline in the mean percentage increase for small larvae in all experimental combinations compared with isolated larvae. There is a significant difference (Table 2.4) in the mean percentage increase between larvae in combination with three like-instar larvae and those with three large larvae, whilst the difference between those combined with three like-instar larvae and those in isolation is not significant. In cups with four perches, the mean percentage increase for small larvae kept alone falls somewhat below that for small larvae in combination. The reason for this is unknown. However, a similar reduction to that above is found on comparing larvae combined with larger individuals and those in combination with like-instar larvae.

It is apparent from Fig. 2.4a that the reduction in the size increase at the moult for small (N-3 instar) larvae in the presence of large larvae can be very large. Such newly moulted larvae, when measured, would therefore have head widths falling short of the mean for N-2 instar larvae, taken from the original instar map. On several occasions these very small N-2 instar larvae were grown up in the incubator, being allowed to continue moulting to see if either correspondingly small adults emerged or new moults were added. A combination of what was expected occurred. That is, an extra moult was added to the larval life-history but this did not usually compensate fully for the size reduction. Therefore the corresponding adult not only emerged later than it would have done but also emerged smaller than the norm.

Tables 2.5a,b show the effect that perch availability has on the development rate and size increases of small larvae in isolation and in combination. There are no significant differences between the mean development rates of larvae in cups with low and high perch availability for any of the combinations with other small and large larvae, although in cups with more perches the mean rates are higher for all combinations. This implies that feeding interference is marginally reduced as the number of perches is increased. In cups with single perches the small larvae, when combined with three large larvae, were often found on the sides of the container where feeding efficiency almost certainly would have been reduced. It is likely that they were

Experimental Combinations Compared			Low Perch Availability			High Perch Availability		
			t	d.f.	P	t	d.f.	P
1S	vs	1S3S	0.39	28	N.S	−2.62	22	P< 0.05
1S	vs	1S1L2S	0.90	23	N.S.	−0.14	19	N.S.
1S	vs	1S3L	3.16	20	P< 0.01	3.25	17	P< 0.01
1S3S	vs	1S1L2S	0.72	21	N.S.	2.00	19	N.S.
1S3S	vs	1S3L	3.82	18	P< 0.01	5.36	17	P< 0.001
1S1L2S	vs	1S3L	2.33	13	P< 0.05	2.67	14	P< 0.05

Table 2.4   T-tests comparing mean percentage increases

in head width between small (N-3 instar) larvae

in different combinations.

a)

Experimental Combination	t	d.f	P
1S	-0.60	26	N.S.
1S3S	-1.50	23	N.S.
1S1L2S	-1.40	16	N.S.
1S3L	-0.43	12	N.S.

b)

Experimental Combination	t	d.f.	P
1S	-0.48	23.5	N.S.
1S3S	-3.41	24	P< 0.01
1S1L2S	-1.41	16	N.S.
1S3L	-2.38	11	P< 0.05

Table 2.5   T-tests comparing **a)** mean development rates and **b)** mean percentage increases in head width of small (N-3 instar) larvae, in combination, between conditions of low and high perch availability.

forced off the perch by the other larvae, or alternatively sought a safer feeding site away from the aggressive strikes of the accompanying larvae.

Table 2.5b compares mean percentage increases in head width between larvae in cups with one or four perches, and it shows that some of the differences between the results from low and high perch conditions are significant. The size increase remains about the same (see Figs. 2.4a,b) for the isolated small larvae, as expected, but is greater for larvae in all other combinations in cups with high perch availability, again indicating reduced interference as larvae are able to disperse to suitable fishing sites.

2.3.2 The effects of additional larvae on the growth and development rate of N-4 instar larvae.

The results presented in this section are, in essence, almost identical to those for the N-3 instar larvae in isolation and in combination with other small and large larvae. The experiment was repeated using N-4 instar larvae to make sure that the results obtained were repeatable, and also to see if any interference effects found in the previous section were stronger when combining N-1 instar larvae with smaller larvae. Because of their similarity these results will not be discussed in depth.

Figures 2.5a,b show the effect of the presence of small and large larvae on the development rate of other small larvae for cups having low and high perch numbers respectively. Irrespective of perch numbers, the mean development rate decreases for small larvae in every combination compared to that for small larvae in isolation. The difference between larvae in isolation and those with three like-instar larvae is not significant (see Table 2.6), although the difference between the latter and individuals combined with three large larvae is highly significant (P< 0.001).

The mean percentage increases in head width at the moult are shown in Figs. 2.6a,b. With the exception of the mean percentage increase for small larvae with three like-instar larvae, there is a decline in percentage increase for small larvae in all combinations compared with isolated larvae. Table 2.7 shows which of these
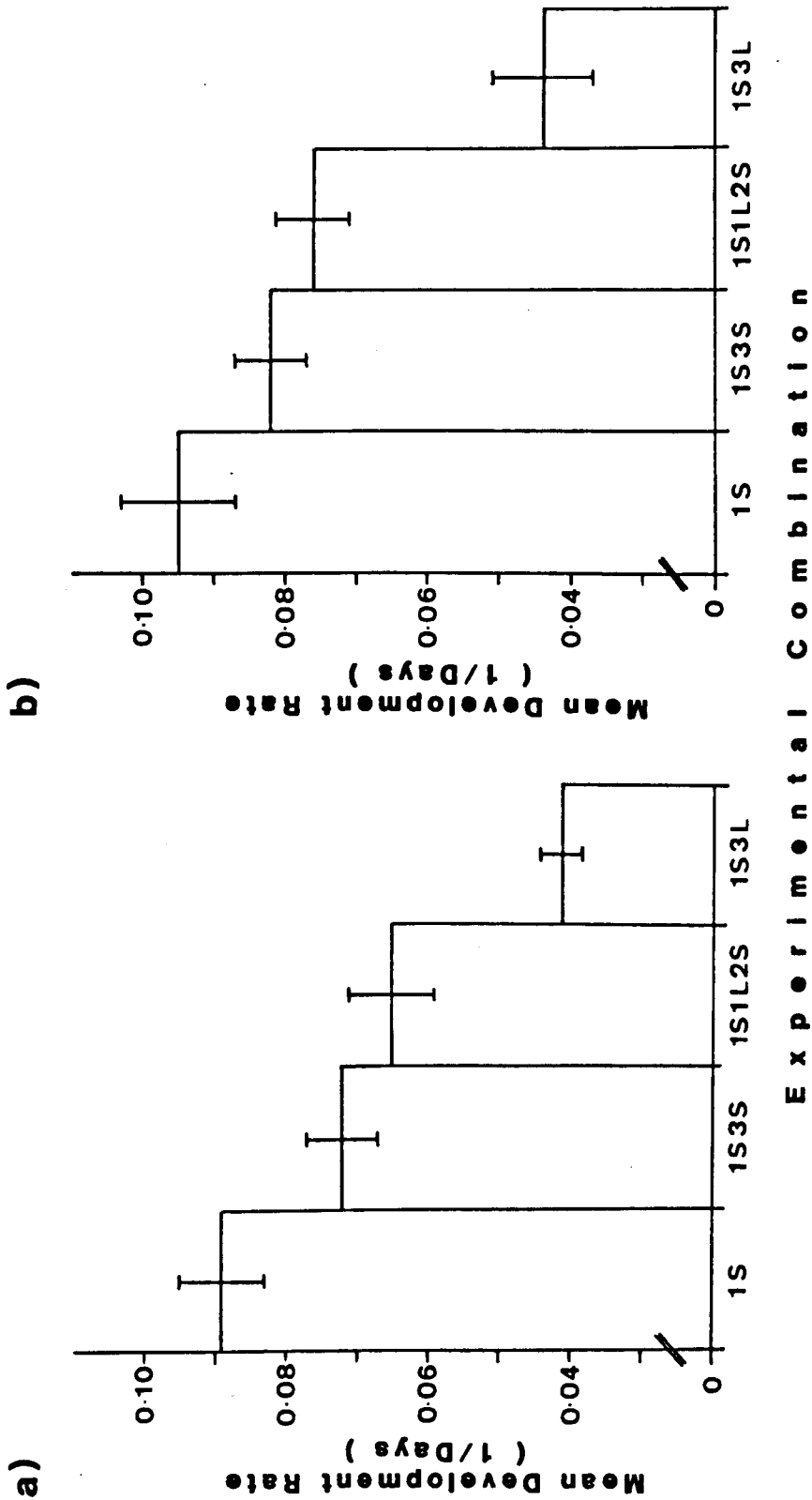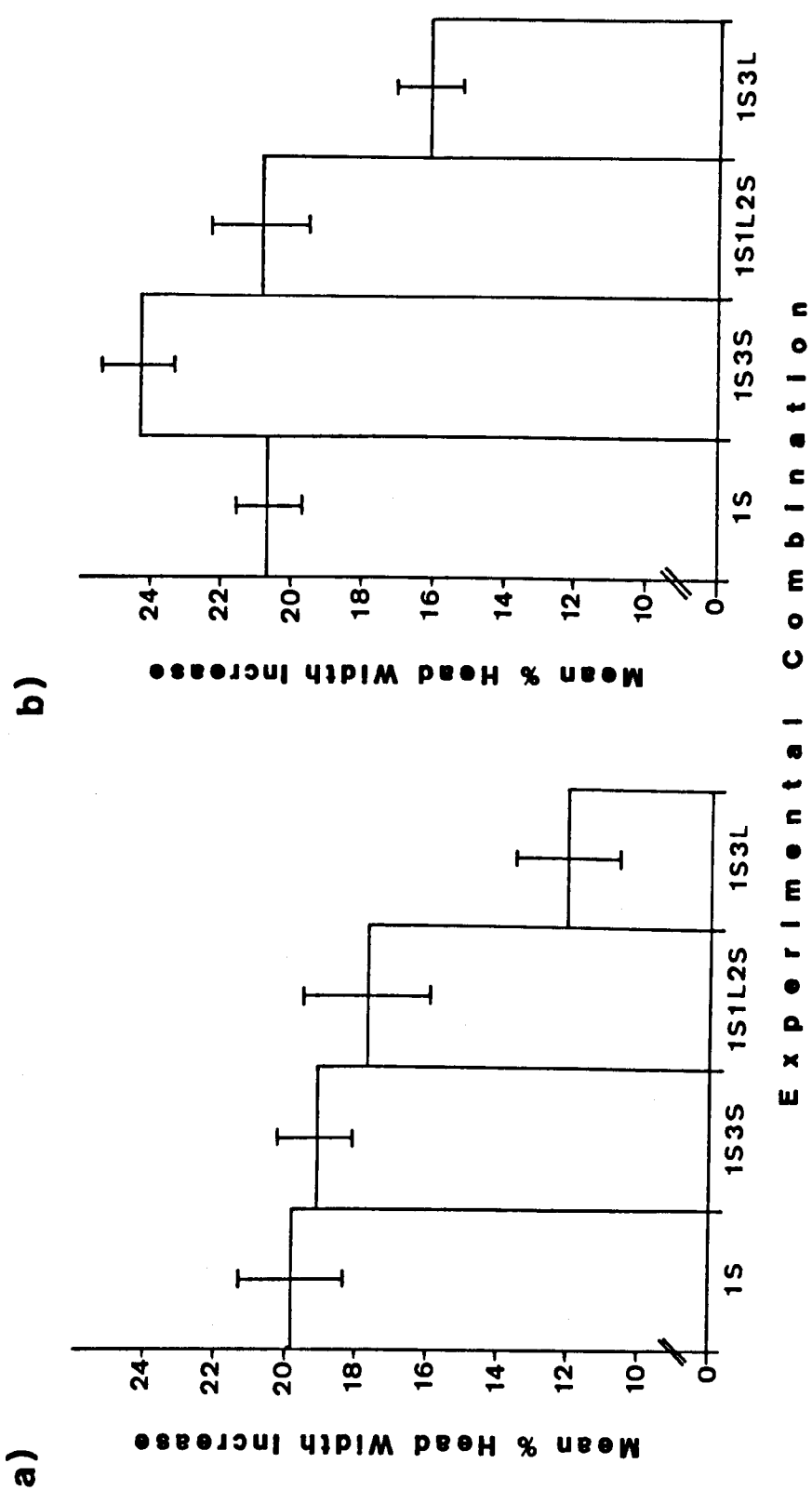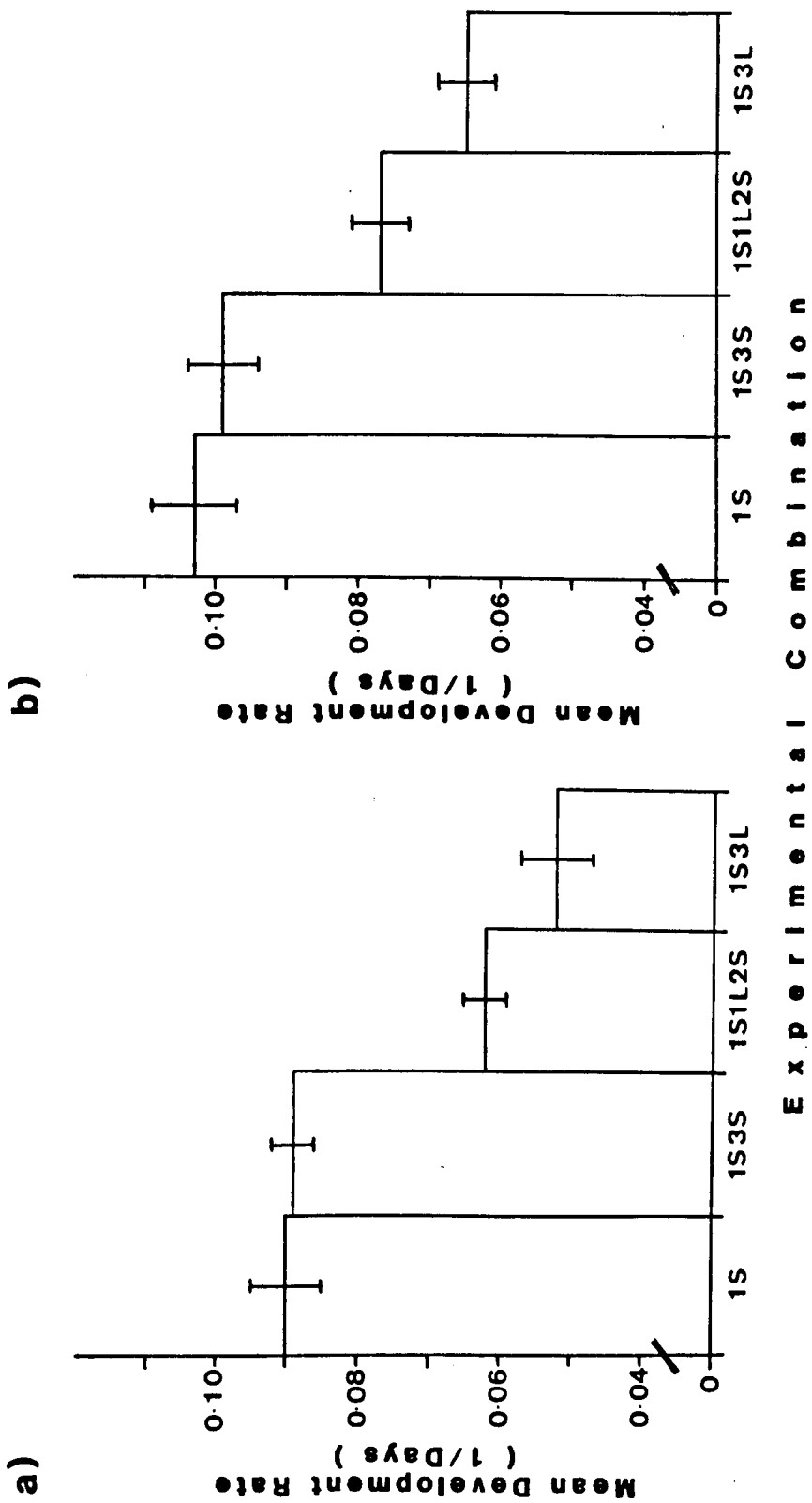
Fig. 2.5   Mean development rates (± standard errors) of small

(N-4 instar) larvae in isolation and in combination,

under conditions of **a)** low perch availability and **b)**

high perch availability.

Experimental Combinations Compared			Low Perch Availability			High Perch Availability		
			t	d.f.	P	t	d.f.	P
1S	vs	1S3S	0.30	19	N.S.	0.58	15	N.S.
1S	vs	1S1L2S	4.98	21	P< 0.001	3.71	15	P< 0.01
1S	vs	1S3L	4.40	13	P< 0.01	4.81	10	P< 0.001
1S3S	vs	1S1L2S	6.21	20	P< 0.001	3.50	18	P< 0.01
1S3S	vs	1S3L	6.66	12	P< 0.001	4.66	13	P< 0.001
1S1L2S	vs	1S3L	1.75	14	N.S.	1.82	13	N.S.

Table 2.6   T-tests comparing mean development rates between small (N-4 instar) larvae in different combinations.
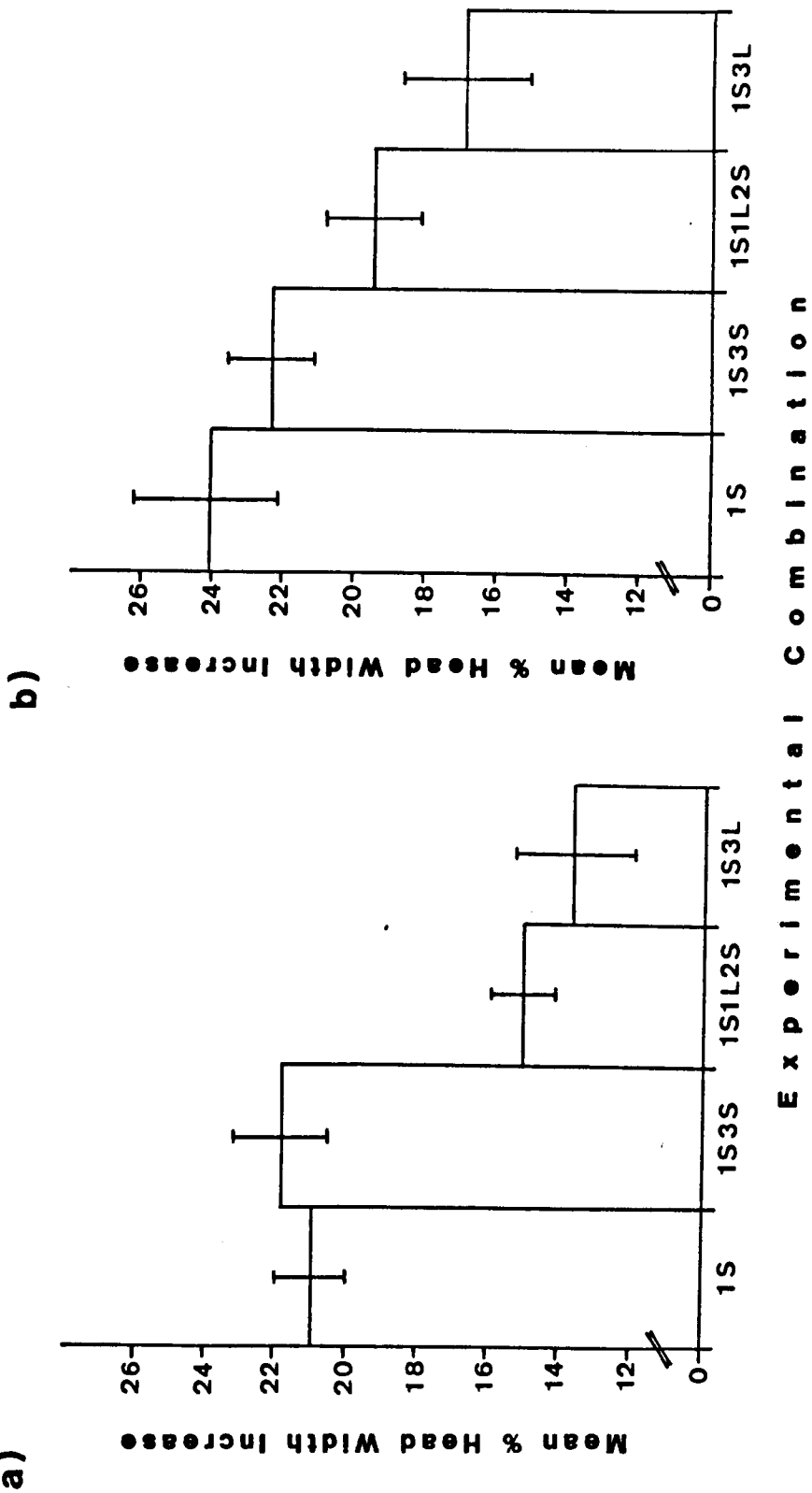
Fig. 2.6   Mean percentage increases in head width (± standard

errors) of small (N-4 instar) larvae in isolation and in

combination, under conditions of a) low perch

availability and b) high perch availability.

Experimental Combinations Compared			Low Perch Availability			High Perch Availability		
			t	d.f.	P	t	d.f.	P
1S	vs	1S3S	-0.54	19	N.S.	0.78	15	N.S.
1S	vs	1S1L2S	4.46	21	P< 0.001	1.95	15	N.S.
1S	vs	1S3L	3.94	13	P< 0.01	2.54	10	P< 0.05
1S3S	vs	1S1L2S	4.44	20	P< 0.001	1.58	18	N.S.
1S3S	vs	1S3L	3.65	12	P< 0.01	2.58	13	P< 0.05
1S1L2S	vs	1S3L	0.80	14	N.S.	1.11	13	N.S.

Table 2.7 T-tests comparing mean percentage increases in head width between small (N-4 instar) larvae in different combinations.

differences are significant.

Therefore, as for the N-3 instar larvae, it can be said that N-4 instar larvae show significantly reduced development rates and size increases when in the presence of large larvae but similar reductions are not evident when these smaller larvae are in the presence of like-instar larvae.

Tables 2.8a,b show the effect of perch availability on the parameters measured for larvae alone and in combination. For all experimental combinations, and with respect to both development rate and size increases at the moult, the interference effects are reduced when there are more perches available, although in only two cases is this reduction significant.

Tables 2.9a,b show the results of t-test analyses comparing the mean development rates and size increases of N-4 and N-3 instar larvae in the same experimental combinations. The mean development rate of N-4 instar larvae in isolation would be expected to be faster than that of the N-3 instar larvae in isolation. While this is true, the difference is not significant, although it is for larvae in some of the combinations (Table 2.9a). This indicates that the opposite to what was originally speculated might be occurring. That is, N-4 instar larvae are less adversly affected by the presence of accompanying larvae compared with N-3 instar larvae, perhaps because they are considered less of a threat, or are less conspicuous. The results are not conclusive enough to comment further.

In Table 2.9b the mean percentage increase in head width of N-4 instar larvae in isolation is also slightly higher than that for N-3 instar larvae, although, as before, the difference is not significant at either level of perch availability. For the other combinations, Some differences between the two instars are negative while others are positive, but in no cases are they significant.

a)

Experimental Combination	t	d.f.	P
1S	-1.63	16	N.S.
1S3S	-1.83	18	N.S.
1S1L2S	-2.86	20	P< 0.01
1S3L	-2.08	7	N.S.

b)

Experimental Combination	t	d.f.	P
1S	-1.53	16	N.S.
1S3S	-0.27	18	N.S.
1S1L2S	-2.88	20	P< 0.01
1S3L	-1.39	7	N.S.

Table 2.8   T-tests comparing **a)** mean development rates and

b) mean percentage increases in head width of small

(N-4 instar) larvae, in combination, between conditions

of low and high perch availability.

a)

Experimental Combination	Low Perch Availability			High Perch Availability		
	t	d.f.	P	t	d.f.	P
1S	0.18	25	N.S.	0.65	17	N.S.
1S3S	2.86	18.4	P< 0.05	2.41	20	P< 0.05
1S1L2S	− 0.39	19	N.S.	0.12	17	N.S.
1S3L	2.01	9	N.S.	2.36	10	P< 0.05

b)

Experimental Combination	Low Perch Availability			High Perch Availability		
	t	d.f.	P	t	d.f.	P
1S	0.55	25	N.S.	1.73	17	N.S.
1S3S	1.60	22	N.S.	− 1.25	20	N.S.
1S1L2S	− 1.48	19	N.S.	− 0.74	17	N.S.
1S3L	0.68	8	N.S.	0.41	10	N.S.

Table 2.9   T-tests comparing **a)** mean development rates and **b)** mean percentage increases in head width between N-4 instar larvae in combination and N-3 instar larvae in combination.

2.3.3   **The effects of additional larvae on the growth and development rate of N-1 instar larvae.**

Because there were no significant differences between them, the results for N-1 instar larvae contained with N-3 instar and N-4 instar larvae have been combined, thus giving results simply of N-1 instar larvae alone or combined with small or other large larvae.

The effects of the presence of small and large larvae on the development rate of other penultimate instar larvae are shown in Figs. 2.7a,b for cups having low and high perch availability respectively. The presence of small larvae has no significant effect on the development rate of the N-1 instar larvae (see Table 2.10a). However, there are significant differences when large larvae are contained with other large larvae, comparing this both to the mean development rate of isolated large larvae and those combined with three small larvae.

Figures 2.8a,b show the mean percentage increases in head width for large larvae alone and in combination. There are no significant differences between any of the combinations (see Table 2.10b).

As before, when comparing larvae in different conditions of perch availability, those in cups with more perches have higher mean development rates and mean percentage increases in head width (see Tables 2.11a,b). In only one case was the difference significant, this rather unfortunately being between the larvae in isolation which should clearly be unaffected by perch numbers.

Therefore, there is an asymmetry in the way interference competition affects damselfly larvae. That is, small larvae have significantly decreased development rates and size increases in the presence of large larvae but the reverse is not true : the development rate and head width increases of large larvae are not significantly affected by the presence of smaller larvae.
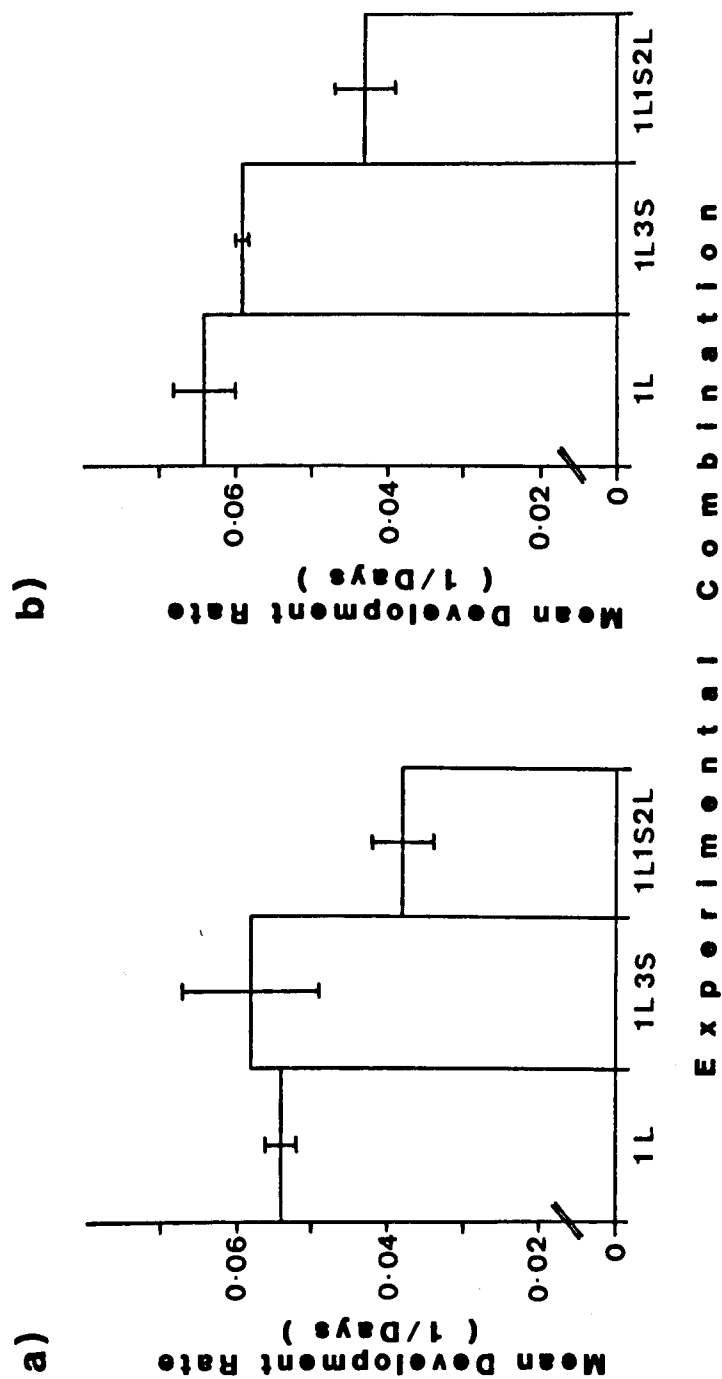
Fig. 2.7   Mean development rates (± standard errors) of large
(N-1 instar) larvae in isolation and in combination,
under conditions of a) low perch availability and b)
high perch availability.

a)

Experimental Combinations Compared		Low Perch Availability			High Perch Availability		
		t	d.f.	P	t	d.f.	P
1L	vs 1L3S	− 0.38	3.4	N.S.	0.87	11	N.S.
1L	vs 1L1S2L	3.25	22	P< 0.01	4.01	18	P< 0.001
1LS3	vs 1L1S2L	2.30	16	P< 0.05	4.05	12.2	P< 0.01

b)

Experimental Combinations Compared		Low Perch Availability			High Perch Availability		
		t	d.f.	P	t	d.f.	P
1L	vs 1L3S	− 1.08	11	N.S.	− 0.45	11	N.S.
1L	vs 1L1S2L	− 0.63	10.7	N.S.	1.12	10.8	N.S.
1L3S	vs 1L1S2L	1.19	16	N.S.	1.24	3.4	N.S.

Table 2.10   T-tests comparing **a)** mean development rates and

b) mean percentage increases in head width between

large (N-1 instar) larvae in different combinations.
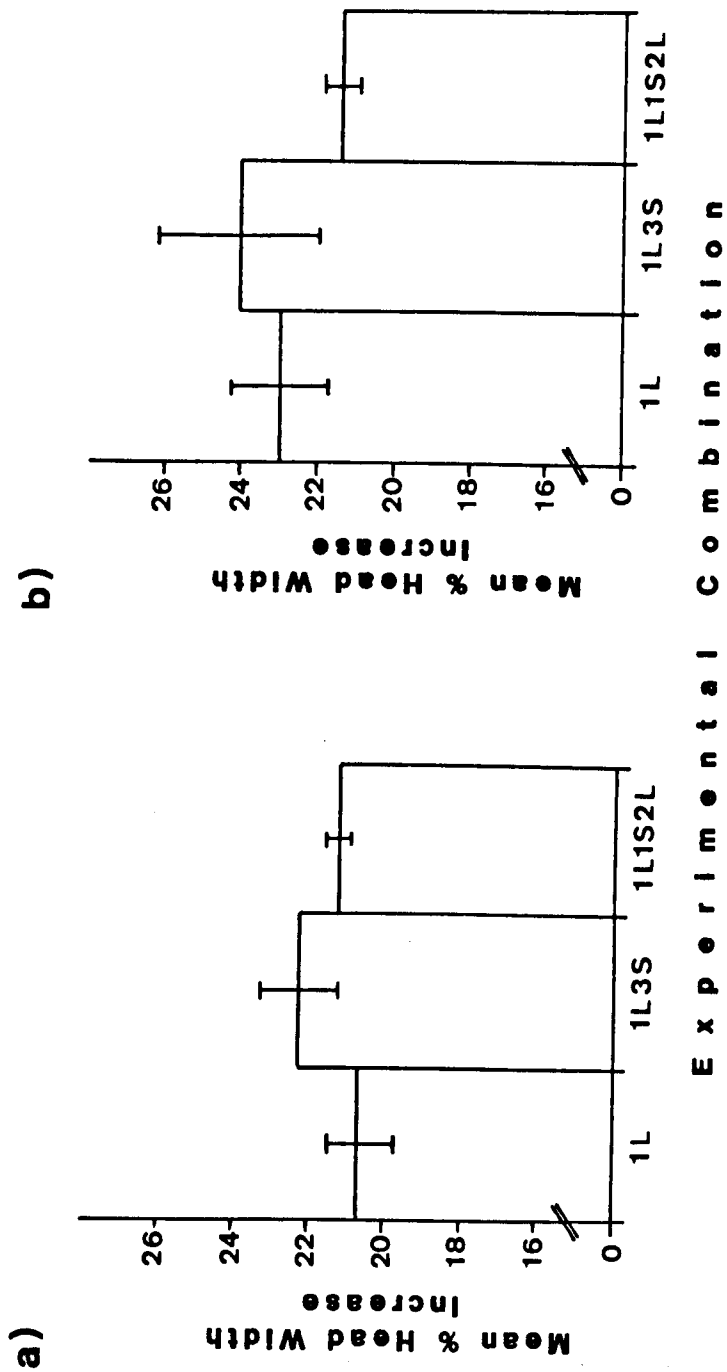
Fig. 2.8   Mean percentage increases in head width (± standard
errors) of large (N-1 instar) larvae in isolation and in
combination, under conditions of a) low perch
availability and b) high perch availability.

a)

Experimental Combination	t	d.f.	P
1L	-2.24	17	P< 0.05
1L3S	-1.00	3.1	N.S.
1L1S2L	-0.82	23	N.S.

b)

Experimental Combination	t	d.f.	P
1L	-1.50	16	N.S.
1L3S	-0.77	6	N.S.
1L1S2L	-0.28	23	N.S.

Table 2.11. T-tests comparing **a)** mean development rates and **b)** mean percentage increases in head width of large (N-1 instar) larvae, in combination, between conditions of low and high perch availability.

2.4 Discussion.

Several authors have shown that the availability of prey to damselfly larvae has a marked effect on their development rates and size increases at the moult (Lawton, Thompson & Thompson 1980; Baker 1982; Pickup & Thompson 1984). In this experiment, conditions of unlimited prey availability were maintained throughout, so that although each larva had the opportunity to maximise its feeding rate, those adversely affected by interference competition were clearly unable to. These smaller larvae suffered decreased development rates and size increases in the presence of larger larvae, presumably due to a decreased feeding rate. Reductions in development rate and size increases were not evident when smaller larvae were in the presence of like-instar larvae.

How the larger larvae interfere with the feeding rates of smaller larvae is not completely clear. In conditions of low perch availability small larvae were often seen on the side of the experimental container with the perch being occupied by the larger larvae. This is analogous with other evidence from laboratory studies demonstrating that smaller larvae may be excluded from profitable feeding sites by the aggressive behaviour of larger larvae (Baker 1980, 1981). Baker (1980) showed that under laboratory conditions, single larvae of *Coenagrion resolutum* found and remained at areas of high food concentration and that when several larvae were present some were excluded. Baker (1981) showed that large larvae excluded smaller larvae through aggressive interactions.

Heads (1986) showed in a similar experiment how the feeding rate of damselfly larvae was influenced by, in this case, potential predators. He found that the feeding rate of *Ischnura elegans* was depressed by the presence of detectable predators and that larvae fed in high prey density patches in the absence of predators but preferred patches with more cover and lower prey availability when predators were present.

Wilson, Leighton & Leighton (1978) and Hildrew & Townsend (1980) provided laboratory evidence of interference occurring in other insect populations. Wilson,

Leighton & Leighton (1978) found that a population of the ripple bug, *Rhagovelia scabra* (Bacon), was structured by interference competition into three components: optimal habitat users, suboptimal habitat users and non-users. This was done on the basis of dominance determined mostly by age, sex and disability. Hildrew & Townsend (1980) found a powerful behavioural mutual interference effect between larvae of the net-spinning caddis, *Plectrocnemia conspersa* (Curtis), at densities similar to those found in the field. The larvae contested ownership of nets and the outcome was determined mainly by body size.

The results of a field study provided by Macan (1964) compliment the laboratory evidence that some damselfly larvae aggressively exclude others from good feeding areas. He found that larvae of *Pyrrhosoma nymphula* took either two or three years to complete development, and that when they were less abundant in a study pond the entire population completed development in two years. Macan concluded that the number of fishing sites was limited and that fast growing (larger) larvae remained in the optimal areas while smaller, slow growing larvae were forced into suboptimal areas of little food. Similarly, Banks & Thompson (1987a) found that larvae of the damselfly *Coenagrion puella* in a high density population were smaller and more likely to be semivoltine than those in a low density population.

In this experiment, larger larvae were sometimes seen to make predatory strikes towards small larvae that were close by, despite there being no shortage of available prey. The threat of such aggressive encounters results in smaller larvae spending less time feeding and more time watching, even when perches are freely available. McPeek & Crowley (1987) found that larvae of *Ischnura verticalis* (Say) tended to reduce their involvement in aggressive interactions by increasing their vigilance of other larvae. Crowley (1984) and Crowley, Gillett & Lawton (1988) noted that, with respect to interference competition between damselflies, much time was spent watching and attacking other larvae when it clearly would have been mutually beneficial for them to ignore one another. They concluded that there was an ever present possibility of ambush which culminated in 'wars of attrition' or 'pre-emptive' aggression by one or

both larvae.

Hence, the feeding rate of smaller larvae might potentially be reduced by the need for increased vigilance. Additionally, such larvae might suffer a reduced prey encounter rate due to decreased mobility. Murdoch & Sih (1978) found that the feeding rate of juvenile stages of the bug, *Notonecta hoffmanni* Hungerford, was reduced by the presence of adults. Interference in this case resulted from the juveniles being less mobile and remaining longer at the edge of the habitat when adults were present. McPeek & Crowley (1987) found that larvae of *I. verticalis* showed decreased mobility and reduced responsiveness to prey when paired with successively larger instars and Heads (1985) showed that larval movement of *Ischnura elegans* was inhibited by the presence of vertebrate and invertebrate predators.

Such inhibition may result in a reduced feeding rate if, for instance, prey tend to aggregate in discrete patches. This may well be true in the field for prey populations such as cladocerans and chironomids whose distribution tends to be clumped, depending on water depth and the type of vegetation and substrate (Macan 1964; Baker 1980 and references therein).

In addition to the above inhibitions of feeding rate, a more extreme form of interference competition may affect smaller larvae under natural conditions. Benke (1978) and Merrill & Johnson (1984) found cannibalism occurring in the field where smaller instars coexisted with larger ones, and they concluded that such an extreme form of interference competition was an important consequence of the seasonal segregation of life-histories. Crowley *et al.* (1987a) found (by analysis of field collected faecal pellets) that large larvae of the semivoltine dragonfly, *Tetragoneuria cynosura* (Say), were responsible for some mortality of smaller conspecifics. They referred to such intra-odonate predation as interference mortality to distinguish it from feeding interference.

Wissinger (1988), in a laboratory experiment, studied naturally co-occurring size combinations of the dragonflies, *Libellula lydia* and *Libellula luctuosa* (Burmeister), to determine how inter-odonate predation varied as a function of larval size differences.

He found that for both intra- and interspecific combinations, little or no predation occurred between larvae of a similar size, but that the number of larvae consumed increased markedly as a function of instar difference. All larvae that he used had been starved for 48 hours and were not provided with prey during the experiment.

Baker & Dixon (1986), in a laboratory study, found that when smaller larvae of *Ischnura verticalis* were paired with larger individuals the smaller larvae were more likely to be wounded. Under field conditions the frequency of wounds was correlated with dispersal rates and wounded larvae were significantly smaller than non-wounded larvae.

The seasonal segregation of life-histories that is found in many odonate species may also be coupled with spatial segregation arising directly from the form of interference competition illustrated by this experiment. Thus, as well as the possibility of exclusion from good feeding patches, smaller larvae may migrate to other areas if the detrimental effects which arise from being in a suboptimal environment are equivalent to, or less than, those arising from being in the presence of larger larvae in an optimal environment (see Heads 1986).

Banks (1985) observed such spatial segregation of larger and smaller instars in a pond-dwelling semivoltine population of *Coenagrion puella*. Lawton (1970), in a study of *Pyrrhosoma nymphula*, was unable to find many smaller larvae of the junior year class in samples taken over the winter although their numbers were high in the autumn and they reappeared again the following spring. This implies that spatial segregation may be occurring between the two age classes of larvae over the winter.

In this experiment an unlimited food source was used to eliminate any effects of exploitation competition that would complicate the results. However, it is likely that in the field odonate larvae will not have access to a similar superabundance of prey. Crowley *et al.* (1987b and references therein) suggested that there is good evidence that larger larvae can be food limited in the field.

Lawton (1971b) was able to compare the maximum and actual field feeding rates for *Pyrrhosoma nymphula*. He found that the field feeding rates were never more than

70% of the maximum obtained in the laboratory, and fell as low as 20% of the maximum in the winter. Benke (1976) measured dragonfly production and prey turnover rates in the field and calculated that there was insufficient prey to satiate the larvae.

This being so, the interference effects found in this laboratory experiment can be expected to be exaggerated in the field. Sih (1981), in a study of *Notonecta hoffmanni*, showed that the interference effects that adults had on first instar conspecifics decreased with increasing prey density. In addition, larvae have been shown to move around more in the absence of food (see Crowley 1979; Heads 1985), and hence interactions with potential predators as well as conspecifics may increase and/or larvae may risk greater exposure to predators in order to feed.

The interference effects reported here were found to be reduced when there were more perches available, although in only a few cases was this reduction significant. In the field, perches are likely to be more abundant and complex than the simple cocktail sticks used in this experiment, thus acting as potential refuges where smaller larvae may avoid interactions with larger larvae.

Thompson (1987a) studied the effects of weed density on larval mortality due to predation. Using larvae of the damselfly *Coenagrion puella* as prey, and *Notonecta glauca* L. as predators, he found that for a given prey density the numbers of prey eaten declined as weed density increased.

Every effort was made to keep the design of this experiment as simple as possible in the hope of producing straightforward, clear results. It is to be expected that such laboratory experiments will be somewhat removed from what actually occurs in the field. By seeking simplicity and then deciding where it is not comparable to field conditions, such laboratory experiments can be put in perspective.

It seems likely, therefore, that the asymmetries in interference competition found in this experiment will, in the field, be exaggerated by reduced food abundance but lessened by habitat complexity and the availability of refuges. Unfortunately, because the experiment ran over a fifteen month period, larvae were obtained from ponds at

regular intervals over all four seasons. Ingram & Jenner (1976) found that, in a study of *Enallagma hageni* and *Enallagma aspersum* (Hagen), the development time from the middle instars to emergence decreased from a maximum for those larvae collected in August to a minimum for those collected in March. This was true irrespective of the temperature and photoperiod regime used. It is unknown if *Ischnura elegans* larvae are affected similarily, although any such effects arising from the use of larvae from different sampling occasions would be spread over all the experimental combinations studied.

In this experiment, small larvae which suffered considerably reduced size increases in the presence of larger larvae were found to add extra moults to their life-history, thus increasing their development time even further. It is unclear whether similar events would be repeated in the field since larvae were maintained in an incubator at a constant temperature and photoperiod, with an unlimited food supply. In such unnatural conditions, remaining longer in the aquatic stage to facilitate an extra moult may well be beneficial. However, in the field, temperature and photoperiod changes will provide information on the progression of the summer. There may be considerable selective pressure on larvae to emerge and begin their reproductive life while there are still potential mates in abundance, particularly if such larvae have already suffered decreased development rates from being in the presence of larger larvae.

Ingram & Jenner (1976) reported the occurrence of extra moults in larvae of the damselflies *Enallagma hageni* and *E. aspersum*. In a laboratory study, they found that extended or slow development was generally accompanied by extra moults, irrespective of photoperiod.

Paulson & Jenner (1971) suggested that extra moults were primarily a laboratory phenomenon. However, Ingram & Jenner (1976) found that it was apparently common in field populations of *E. aspersum*, occurring in late summer and autumn when there were similar conditions of photoperiod and temperature to those that produced the highest incidence of extra moulting in their laboratory experiments.

A number of studies have shown the occurrence of interference competition in field populations (eg. Benke 1978; Benke, Crowley & Johnson 1982; Johnson *et al.* 1985; Pierce, Crowley & Johnson 1985; Crowley *et al.* 1987a). Crowley *et al.* (1987a) looked for the occurrence of feeding interference and interference mortality in semivoltine populations of the dragonfly, *Tetragoneuria cynosura*. They found that colonization of large mesh cylinders by small larvae was inhibited by high densities of large larvae, and they suggested that such inhibition may result from interference mortality. Pierce, Crowley & Johnson (1985) found evidence of asymmetric interference competition between two species of *Enallagma* using field enclosure experiments and Benke (1978) found early emerging odonates had a highly significant influence on the abundance of smaller, late emerging larvae. Benke, Crowley & Johnson (1982) looked at interactions between two early species of dragonfly, *T. cynosura* and *Ladona deplanta* (Rambur), in small field enclosures. They found that the presence of *Tetragoneuria* reduced the total biomass of *Ladona* , but *Ladona* had no significant effect on *Tetragoneuria*. The two species were also found to reduce the biomass of late emerging Anisoptera which colonized the enclosures during the experiments.

Therefore, it has been shown that the development rates and size increases of small larvae are reduced when in the presence of large larvae, even with unlimited prey. Possible ways in which the feeding rate could be affected by the large larvae have been suggested with reference to other, predominantly laboratory, experiments (eg. reduced larval movement, increased larval vigilance, exclusion from good feeding areas by aggressive interactions). Further consequences of such interference competition have been given from both laboratory and field studies. Larvae may risk greater exposure to predators in order to feed; there may be risk of mortality from conspecifics, of cannibalism, and of injury, as well as the inhibition to growth and development shown in this experiment.

What are the consequences of interference competition for the reproductive success and fitness of adult damselflies ? Several authors have found odonates to be

excellent subjects with which to study lifetime mating success and/or reproductive success (eg. Fincke 1982; Banks & Thompson 1985a, 1987b; Koenig & Albano 1987). By marking individually and measuring almost all members of a population and watching which animals mate together, it has been possible to determine which factors (date of emergence, size effects, age effects etc.) are correlated with increased mating success.

For example, Banks & Thompson (1985a, 1987b) found that the major cause of variation in mating success in males and females of *Coenagrion puella* was longevity, which accounted for about 70% of the variation. Size had relatively little effect on lifetime mating success because although smaller males had a higher daily mating rate, this was offset by the increased longevity of larger males. Size of males and females declined through the breeding season, but date of emergence had no significant effect on mating success.

Lifetime mating success is some way removed from Darwinian fitness and the results of the present work underline some of the differences between the two for odonate populations. Clearly date of emergence is important . Those individuals which are successful as larvae emerge early in the breeding season. Their eggs are laid relatively early and hatch earlier than those of late emerging adults. The larvae of those adults that are present at the end of the breeding season are smaller than other larvae in their year class and suffer the interference competition described in this work and suggested by other shorter-term experiments and field studies described above.

The results of this experiment illustrate the dangers of disregarding the importance of size and date of emergence, especially in organisms with complex life-histories such as damselflies. Clearly, future considerations of individual fitness must take into account asymmetric competition in larval growth and development.

Chapter 3. The emergence of *Pyrrhosoma nymphula* from two adjacent ponds.

3.1   Introduction.

The aim of this investigation was to study the emergence of *Pyrrhosoma nymphula* from two adjacent ponds over the spring and summer of 1986. The total number of males and females emerging daily was accurately recorded, together with size and weight measures and mortality estimates from weather and predators. The effect of climatic conditions on emergence patterns and the relative contribution of climate and predators to emergence mortality are presented in Chapter 4. All other aspects of the emergence are presented here.

By studying the emergence at two adjacent ponds, factors which may determine the seasonal placement, duration and synchronisation of emergence within the emergence period could be investigated. This is reported to be constant for a given species in a given climatic situation (Corbet 1962, 1964). In temperate species, those which emerge earliest in the year, such as *P. nymphula*, usually have the shortest duration of emergence and the closest synchronisation. This is attributed to a diapause in the final instar allowing the majority of a year class to respond synchronously to rising temperatures which induce metamorphosis in spring (Corbet 1957a, 1962). Corbet (1962) stated that a photoperiod response functioned to place the maximum proportion of larvae in the right developmental stage at the appropriate season. The actual date of emergence within that season was determined mainly by response to temperature.

In this investigation, the two study ponds were subject to exactly the same photoperiod and climatic conditions. The lack of a highly synchronised emergence at either pond, and marked differences in the timing of emergence between the two ponds, indicate that additional factors must contribute to the seasonal regulation of

emergence in damselflies.

3.2   Materials and methods.

3.2.1   Location and characteristics of study ponds.

The study ponds were located in Risley Moss Nature Reserve, near Warrington, Cheshire (N.G.R. SJ 665915). Risley Moss covers roughly 220 acres and contains one of the few remaining areas of mossland in the northwest of England. The site was originally developed and managed as a country park and educational nature reserve, with the water table being deliberately raised to increase the area covered by mossland plant species. As well as this large area of mossland there are other habitats including substantial areas of scrubland, birchwood, grassland and mixed woodland. A large system of drainage ditches and as many as fifty ponds are found on the site, varying in size and occurring predominantly in the mossland habitat.

Risley Moss has a high diversity of dragonflies for such a northern site, with a total of thirteen species being recorded. Of these , two are fairly rare recordings, but the other eleven species are either common or abundant; there are five species of damselfly and six species of dragonfly.

Pyrrhosoma nymphula is one of the most abundant species at Risley Moss, breeding in virtually all of the ponds and ditches on the mossland and also in the woodland ponds. It is also the first species to be seen, the emergence beginning in late April in some instances, and it occurs through the summer until late July and August.

Figure 3.1 shows scale drawings of the two study ponds which will be referred to throughout as pond A and pond B. The ponds occurred in open mossland a distance of about 40 metres away from each other. About 200 metres to the northwest of the ponds, and 250 metres to the northeast, were areas of dense mixed woodland. It was in these areas that large numbers of teneral damselflies were found feeding

Pond A

N

0 1 2 3 4 5
metres

Pond B

N

raised
path

0 1 2 3 4 5
metres
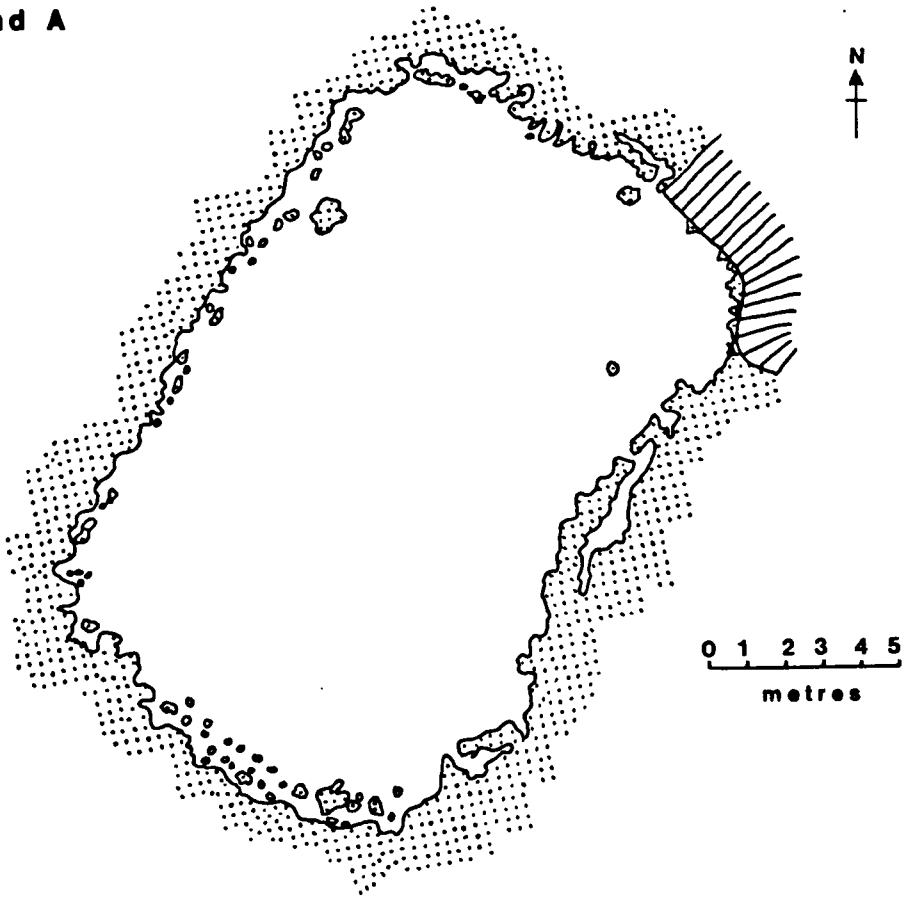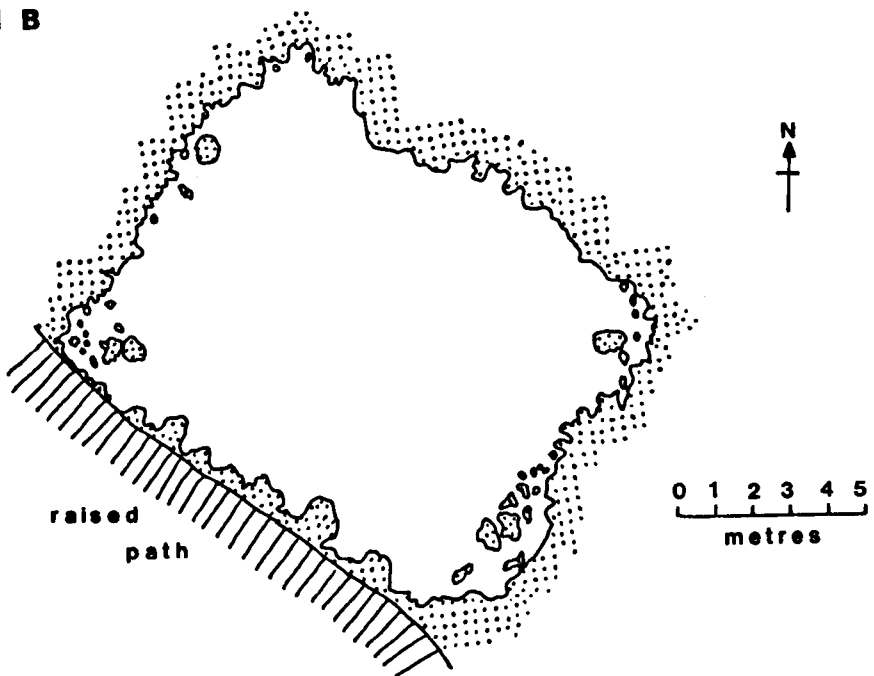
Fig. 3.1   Scale drawings of the study ponds.

during the maturation period immediately following emergence. Pond A was larger than pond B having an area of approximately 216.6m^2 compared to an area of approximately 126.4m^2 for pond B.

Figures 3.2 and 3.3 show the species composition of the emergent vegetation around pond A and pond B respectively. For both ponds it consisted predominantly of purple moor grass (*Molinia caerulea* (L.)) and common cotton-grass (*Eriophorum angustifolium* Honckeny), and around the periphery of pond B there were also some large clumps of reeds (*Juncus effusus* L.). Young saplings of birch (*Betula pubescens* Ehrh.) and willow (*Salix caprea* L.) were the only 'trees' present around the ponds, which as a result were fairly exposed and often subject to windy conditions.

3.2.2 Quantitative collection of newly emerged adults and exuviae.

Throughout the entire emergence period the vegetation around both ponds was searched twice daily for emerging adults or their exuviae. The ponds were visited from the beginning of May onwards although the first individuals to emerge were not recorded until 13th May. The lateness of the emergence period is attributed to an extended period of very cold weather following the winter months in that year.

The method of searching the vegetation was necessarily thorough to ensure that almost all of the emerging adults were noted. The four sides of both ponds would be covered in a main morning search which started on arrival at the ponds at about 9.30am. Once this was finished they would be searched again in the afternoon. Emergence predominantly occurred in the morning and consequently the second search was briefer. For each side of each pond the clumps and aerial stems of *Molinia, Eriophorum* and other plants with roots under the water were first carefully sorted through. Once all adults and exuviae from the periphery of the pond had been collected, the vegetation a little further back was searched. Finally, areas up to 2 metres back from the water were searched, particularly where there was an adjacent

Fig. 3.2   Species composition of the emergent
            vegetation around pond A.
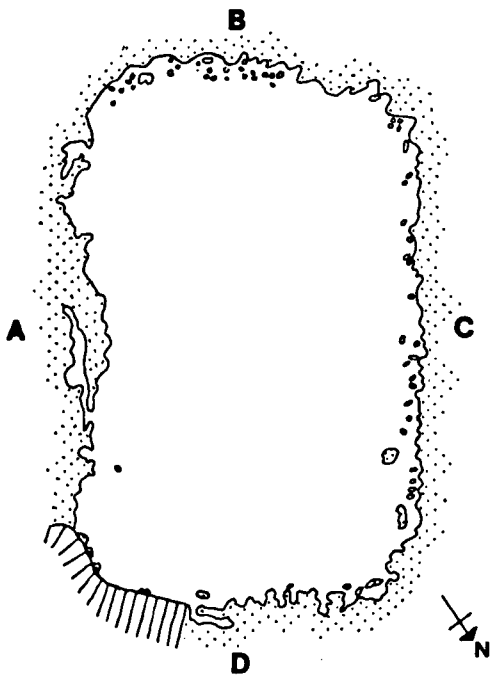
Molinia caerulea

Eriophorum vaginatum

Eriophorum angustifolium

E. angustifolium and
M. caerulea

Exposed peat

Betula pubescens

Calluna vulgaris

Floating, dead M. caerulea

0 1 2 3 4
metres

A

B

C

D
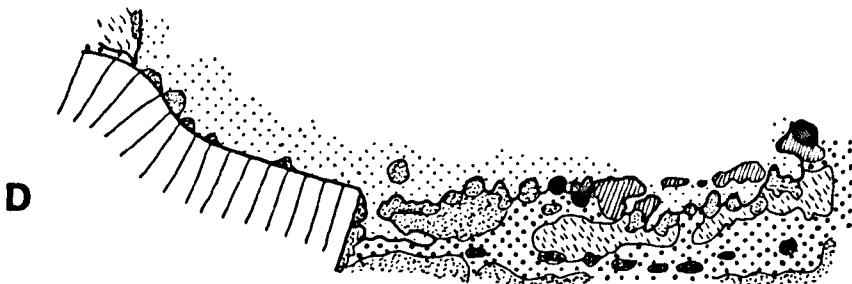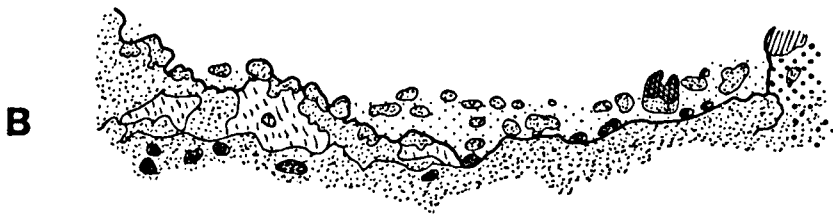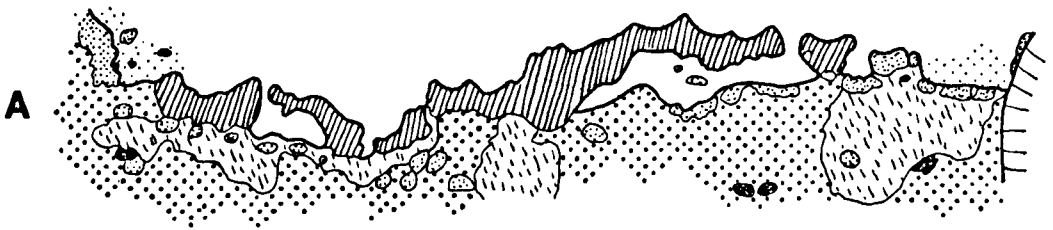
Fig. 3.3   Species composition of the emergent
vegetation around pond B.
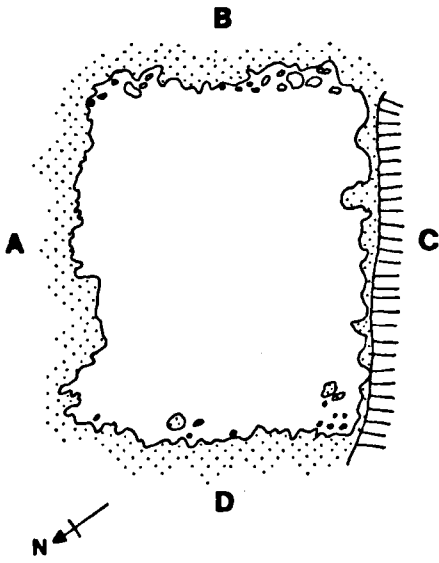
Molinia caerulea

Eriophorum vaginatum

Eriophorum angustifolium

E. angustifolium and M. caerulea

Exposed peat

Betula pubescens

Juncus effusus

Salix caprea

Sphagnum sp.

Phalaris arundinacea

Floating, dead M. caerulea

0 1 2 3 4
metres
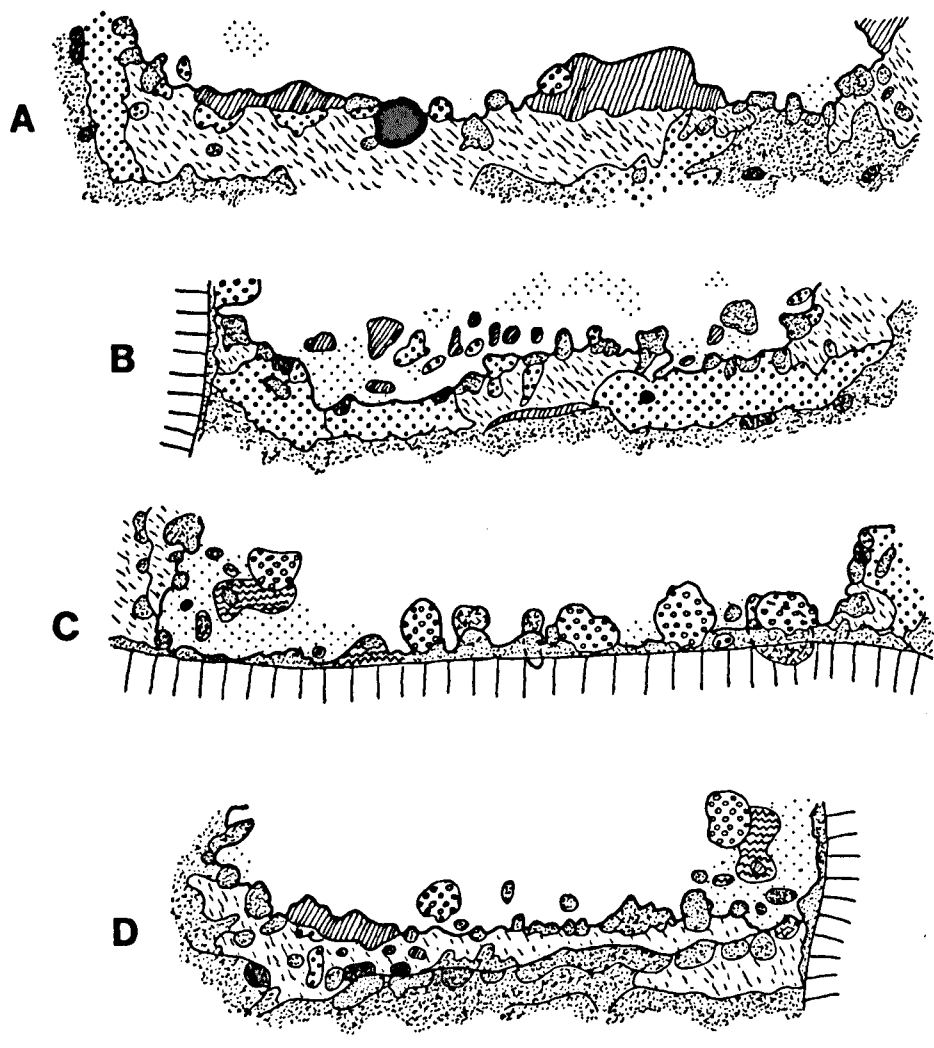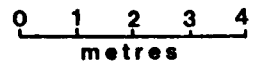
lack of emergent vegetation potentially forcing larvae to move a long way from the water to emerge.

While searching the vegetation around the ponds larvae could be found in all stages of emergence. Larvae found that were not yet fully emerged were left once their position had been noted. Newly emerged adults found near to exuviae were carefully placed in a small plastic container. This was most easily done by picking them up still attached to the stem on which they emerged since their wings and body were soft and delicate at this stage and could easily be damaged.

In almost all cases an exuvium would be found near to a newly emerged adult, the exception being when the adult had crawled some way from where it first emerged. The exuvium was placed along with the adult in the plastic cup. This ensured that it was not included again as part of the exuviae count and also it enabled a relationship between adult and exuvium weight to be computed.

Exuviae found on their own were retained and taken back to the laboratory to be counted, sexed and weighed. The corresponding adults were either assumed to have emerged and flown, to have crawled some way from that area, or to have been predated. On very hot days larvae could emerge and be ready to fly in a remarkably short time. In these conditions large numbers of exuviae were found without adults, especially by the time the last side of a pond was being searched. The exact time required before the adult is ready to fly is governed mainly by the weather. On cold or rainy days those larvae that do still emerge are unlikely to fly at all unless the weather improves throughout the day, while on hot days the time necessary for the wings to expand and dry out and the adult be able to fly may often be less than one hour.

It follows that teneral adults found without an exuvium, of which there were relatively few, were not included in the estimate of numbers emerging from the two ponds. As explained above, it was assumed that they were already accounted for by the recording of exuviae numbers. These adults were collected in plastic containers and taken back to the laboratory for marking and measuring.

Newly emerged adults that were badly damaged in some way were counted but

usually not collected. This included those individuals that had been attacked, or were in the process of being attacked, by spiders or ants. It also included individuals that had crumpled bodies and/or wings as a result of being caught in heavy rain, or from emerging in a windy exposed location, or simply from an error at emergence. Less badly damaged individuals (those with crumpled wings preventing flight), were usually collected, killed in an ether bottle, and used for dry weight analysis.

3.2.3 Measurements recorded and the relationship between them.

At the end of each day at the ponds, all newly emerged adults were taken back for measurement and marking. During this process the adults were lightly anaesthetised with either carbon dioxide or ether.

In an effort to make sure that the anaesthetic and the marking process had no effect on survivorship, a small experiment was set up to monitor the survivorship of adults subjected to three treatments. Fourteen adults (seven males and seven females) were used for each treatment. The first group was simply placed in a large plastic tank containing bits of vegetation to act as perches. Mesh netting was placed over the tank and it was transferred to a $12^{o}C$ constant temperature room set on a summer photoperiod. A small dish with water was placed in the tank and prey items (mainly small dipterans and hymenopterans) were added daily. The second group of adults were anaesthetised with CO_2, marked in the way that will be described below, and placed in an identical tank. The same procedure was followed for the third group, these having been lightly anaesthetised with ether.

Figure 3.4 shows the survivorship of the three groups of damselflies. The longest lifespan of any adult in the experiment was 16 days and Table 3.1a shows the mean lifespans of marked and unmarked adults. These values are likely to bear little resemblance to those of adults in the field, since the experimental animals were kept in unnatural conditions. They were unable to fly to any great extent and it is doubtful if

Fig. 3.4   Survivorship of **a)** unmarked adults, **b)**
marked adults anaesthetised with CO_2 and
c) marked adults anaesthetised with ether.
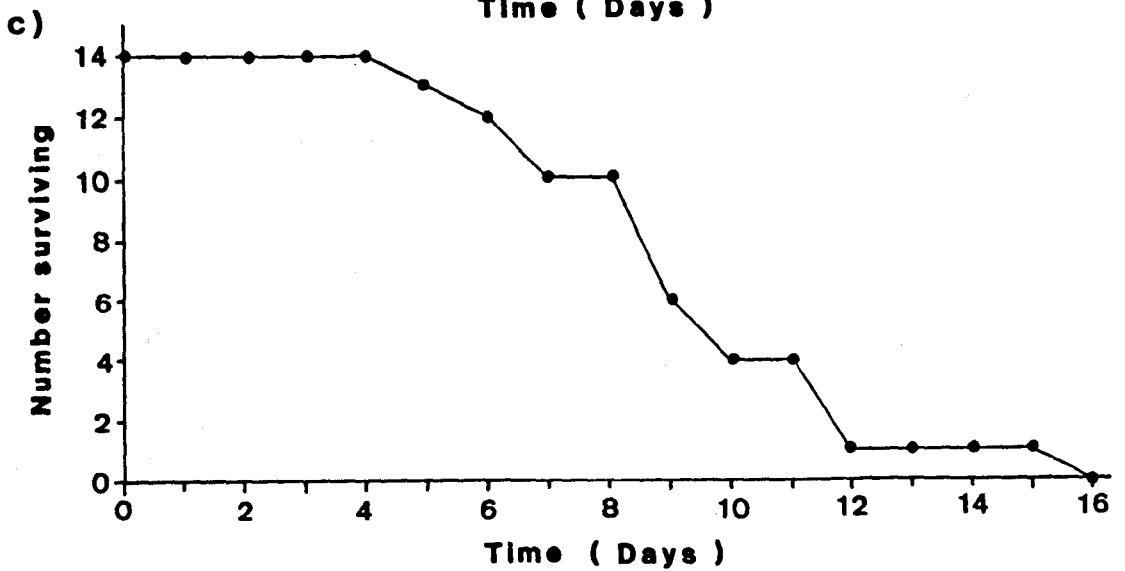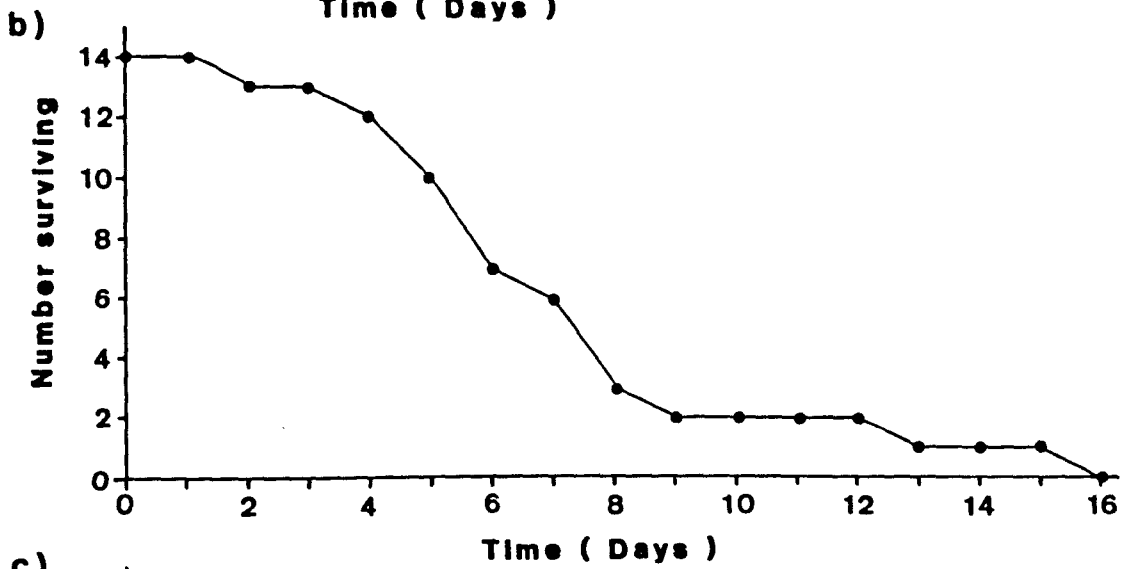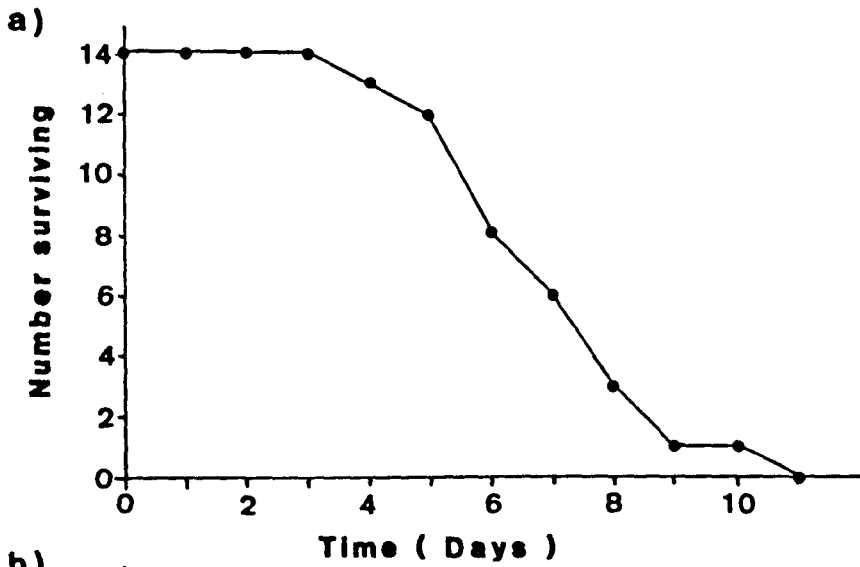
a)

	Mean lifespan (days)	Standard error	n
Unmarked adults	6.84	0.49	14
Marked adults anaesthetised with CO_2	6.86	0.96	14
Marked adults anaesthetised with ether	9.00	0.77	14

b)

	U	P
Unmarked adults vs Marked adults anaesthetised with CO_2	91.0	0.769
Unmarked adults vs Marked adults anaesthetised with ether	46.5	0.016
Marked adults anaesthetised with CO_2 vs Marked adults anaesthetised with ether	53.0	0.040

Table 3.1   **a)** Mean lifespans of marked and unmarked adults and **b)** comparisons of the lifespans by Mann-Whitney U-tests.

many of them fed, despite efforts to keep all the tanks well stocked with prey items.

Table 3.1b shows the results of Mann-Whitney U-tests comparing the lifespans of the three groups of adults; some of the differences are significant. The mean lifespan of adults anaesthetised with ether was longer than that for unmarked adults and those exposed to CO_2. This is likely to arise from variation resulting from the low sample sizes used rather than any positive effects attributed to the ether.

Therefore, there appears to be no evidence that the marking process and anaesthetic is detrimental to the survivorship of *P. nymphula*. Having said that, potential ways in which the marking might render individuals more susceptible to predation, or the anaesthetic might interfere with the sensory capabilities in the field, could be imagined, and these would not be apparent in this experiment. However, such detrimental effects were considered in reality to be unlikely occurrences. Banks & Thompson (1985b) anaesthetised and marked several thousand *Coenagrion puella* in the same manner and were able to follow a large marked population throughout an entire summer.

Once anaesthetised, the adults were weighed on a Cahn C29 electrobalance to the nearest 0.01mg. The head width was measured under a binocular microscope using an eyepiece micrometer and the left hindwing was measured to the nearest 0.05mm using dial callipers. Individuals were uniquely marked with a number on the left hindwing in waterproof felt- tip pen, and a dot of enamel paint on the dorsum of the thorax. The marking was necessary to record individuals returning to the ponds after the maturation period. Upon recovery from the anaesthetic the adults were kept in a $12^{O}C$ constant temperature room overnight and released the next morning near the edge of the ponds.

Those individuals that were slightly damaged at the ponds were weighed and measured and then killed and dried in an oven at $60^{O}C$ for at least five days and then weighed to the nearest 0.001mg. Exuviae were also dry weighed in the same manner.

Table 3.2 shows the results of Pearson correlations between the various measures of size for males and females combined. All variables are highly

	Adult wet weight (mg)	Head width (mm)	Hind-wing length (mm)	Adult dry weight (mg)
Head width (mm)	r= 0.659 n= 1155 P< 0.001			
Hindwing length (mm)	r= 0.709 n= 1093 P< 0.001	r= 0.419 n= 1132 P< 0.001		
Adult dry weight (mg)	r= 0.857 n= 119 P< 0.001	r= 0.529 n= 106 P< 0.001	r=0.588 n= 116 P< 0.001	
Exuvium dry weight (mg)	r= 0.533 n= 147 P< 0.001	r= 0.410 n= 65 P< 0.001	r= 0.458 n= 70 P< 0.001	r= 0.434 n= 78 P< 0.001

Table 3.2   Pearson correlations between various measures of size of newly emerged adults.

significantly correlated with each other, a result which is not surprising. Identical results are obtained if the same computations are calculated separately for males and females.

Wet weight and head width are used as the principle parameters in all the computations throughout the results. Wet weight is considered an accurate measure of adult size since individuals were collected as soon as they had emerged and so had no time to feed or begin reproductive maturation. In the case of mature adults, 'true' size measures such as head width or wing length would be more accurate since they remain constant over time.

3.3   Results

3.3.1   The emergence of *Pyrrhosoma nymphula* from pond A.

Figures 3.5a,b show the number of males and number of females emerging daily from pond A. The first male emerged on 19th May, and the first female on 20th May, with emergence being effectively completed by 27th June. After this date efforts were switched to recording reproductive behaviour of mature adults.

One of the most obvious features of the histograms is the large fluctuations in the number of individuals emerging from one day to the next (eg. day 21 followed by day 22). A consequence of these fluctuations is that there appears to be two rather separate peaks in emergence for both males and females. Variation in weather conditions over the same period is the most likely cause of the fluctuations. Evidence for this, from comparison of the emergence distributions with distributions of recorded weather variables will be given in Chapter 4.

The total number of adults to emerge from pond A was 1014 (554 male, 460 female). The sex ratio at emergence was therefore 1.204 male: 1 female (54.6 %

Fig. 3.5 Histograms showing **a)** distribution of males and **b)** distribution of females emerging daily at pond A.

a)

n = 554

TOTAL NUMBER EMERGING

DAYS (DAY 1 = 13th MAY)

b)

n = 460

TOTAL NUMBER EMERGING

DAYS (DAY 1 = 13th MAY)
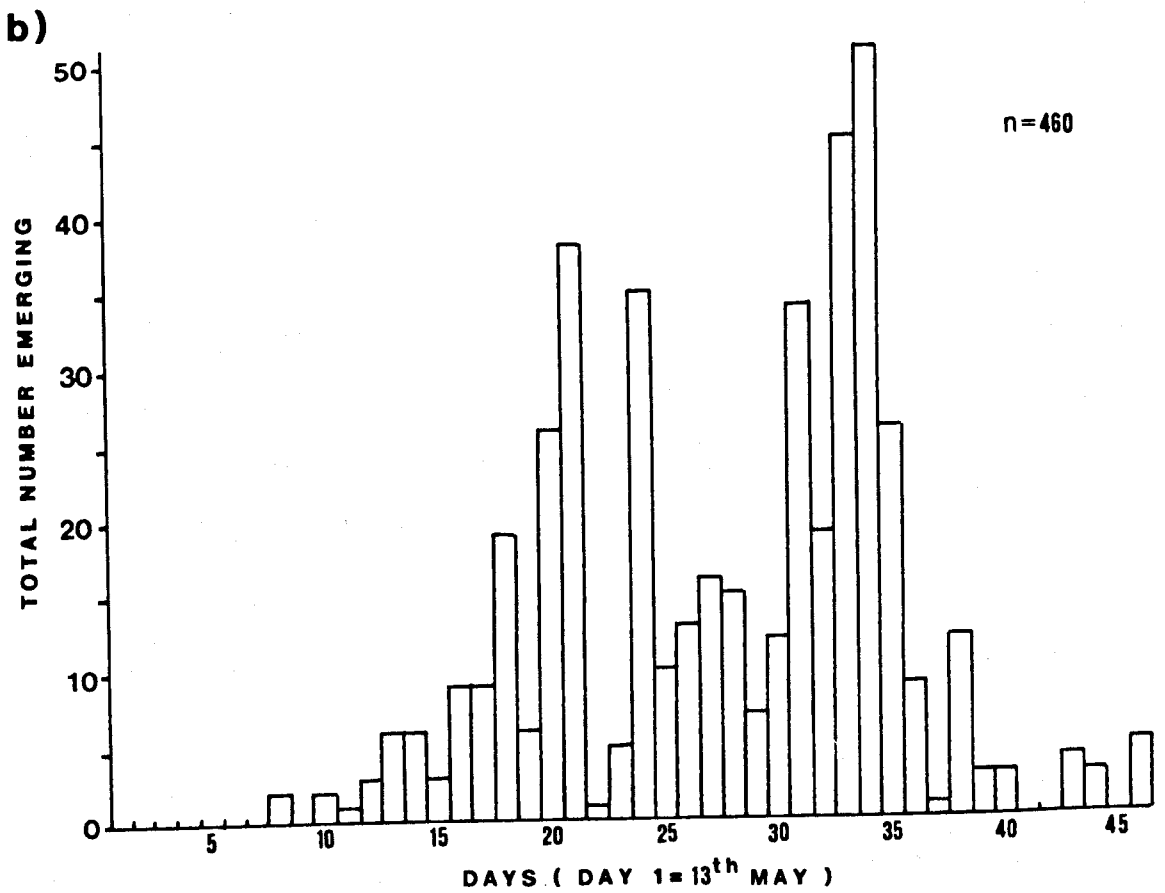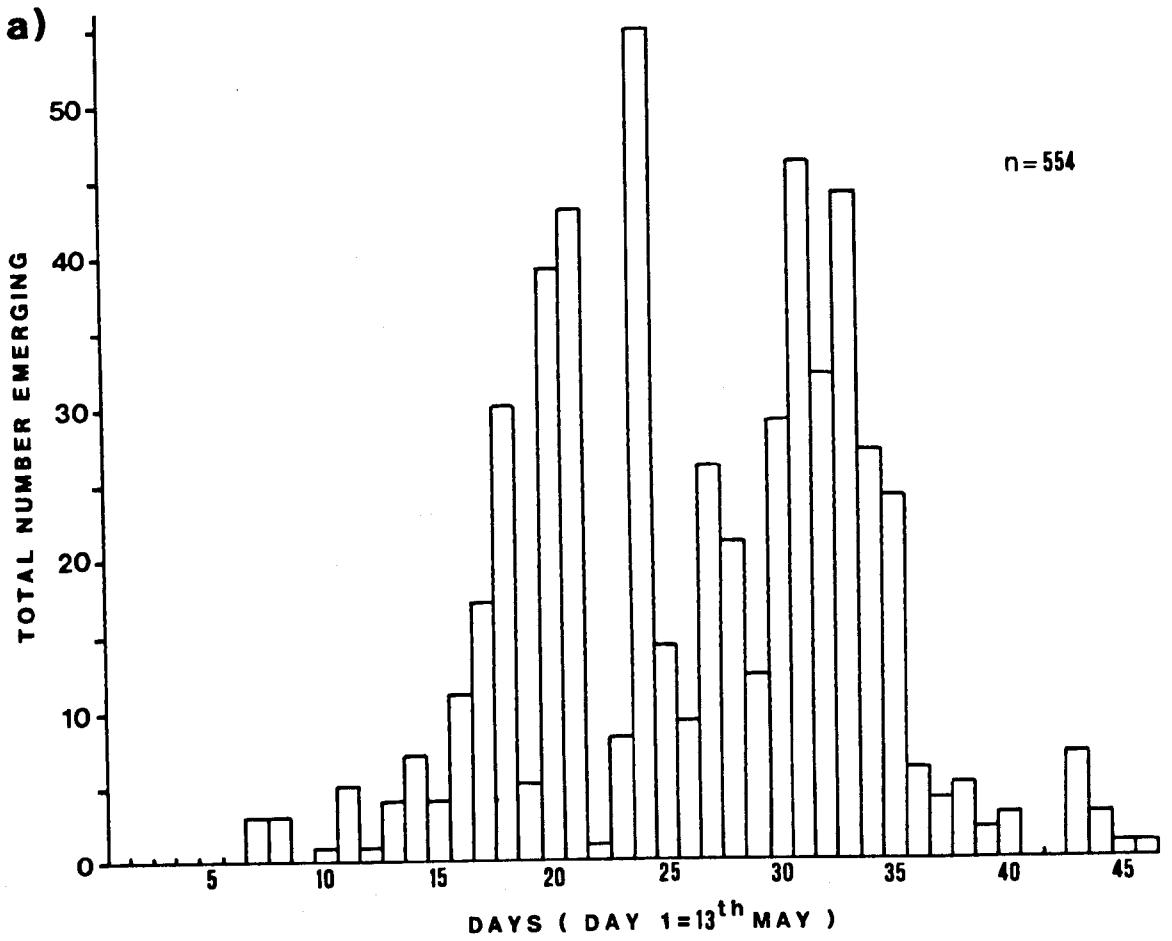
male), and is significantly different from equality ($X^2_{(1)}$ = 8.714, P< 0.01).

Both distributions in Figs. 3.5a,b were tested for skewness and were found to be symmetrical (using the t statistic, see Zar (1974)). However, the result of a Kolmogorov-Smirnov 2-sample test (see Table 3.3a) shows there is a significant difference between the male and female emergence distributions (this is a test of homogeneity of distributions and is sensitive to differences between the median, dispersion and skewness). In addition, there is a significant difference between the mean date of emergence of males and females from pond A, the mean for males being earlier than that for females (Table 3.3b). There is also less variation in the male mean date of emergence.

Comparison of the mean wet weights of males and females shows that females are significantly larger than males (male, mean 35.68mg, SE 0.19; female, mean 38.23mg, SE 0.27; t=7.98, 584 d.f., P< 0.001). Females also have a significantly larger mean hindwing length than males although there is no difference between mean or median head width.

3.3.2   The emergence of *Pyrrhosoma nymphula* from pond B.

Figures 3.6a,b show the number of males and females emerging daily from pond B. The first male emerged on 14th May, and the first female on 13th May, with emergence being effectively completed by 21st June for both sexes. As for the distributions from pond A, there are large fluctuations in numbers emerging which are also attributed to variation in weather conditions (see Chapter 4).

The total number of adults to emerge from pond B was 1099 (584 males, 515 females). The sex ratio was therefore 1.134 male: 1 female (53.1 % male) and this is significantly male biased ($X^2_{(1)}$ = 4.332, P< 0.05). Both the male and female emergence distributions are significantly positively skewed. The result of a Kolmogorov-Smirnov 2-sample test (Table 3.4a) shows that there are no significant

a)

K-S Z	P
1.983	P< 0.001

b)

	Mean	Standard deviation	Standard error	n
male	38.496	7.199	0.306	554
female	39.763	7.535	0.351	460

t	d.f.	P
-2.73	1012	P< 0.01

c)

Z	P
-3.081	P< 0.01

Table 3.3   Differences between the emergence of males and females from pond A, as shown by **a)** Kolmogorov-Smirnov 2-sample test and **b)** t-test analysis comparing mean date of emergence (day 1 = 1 st   May).

c) Mann-Whitney U-test comparing median emergence dates.

Fig. 3.6   Histograms showing **a)** distribution of males
and **b)** distribution of females emerging daily
at pond B.
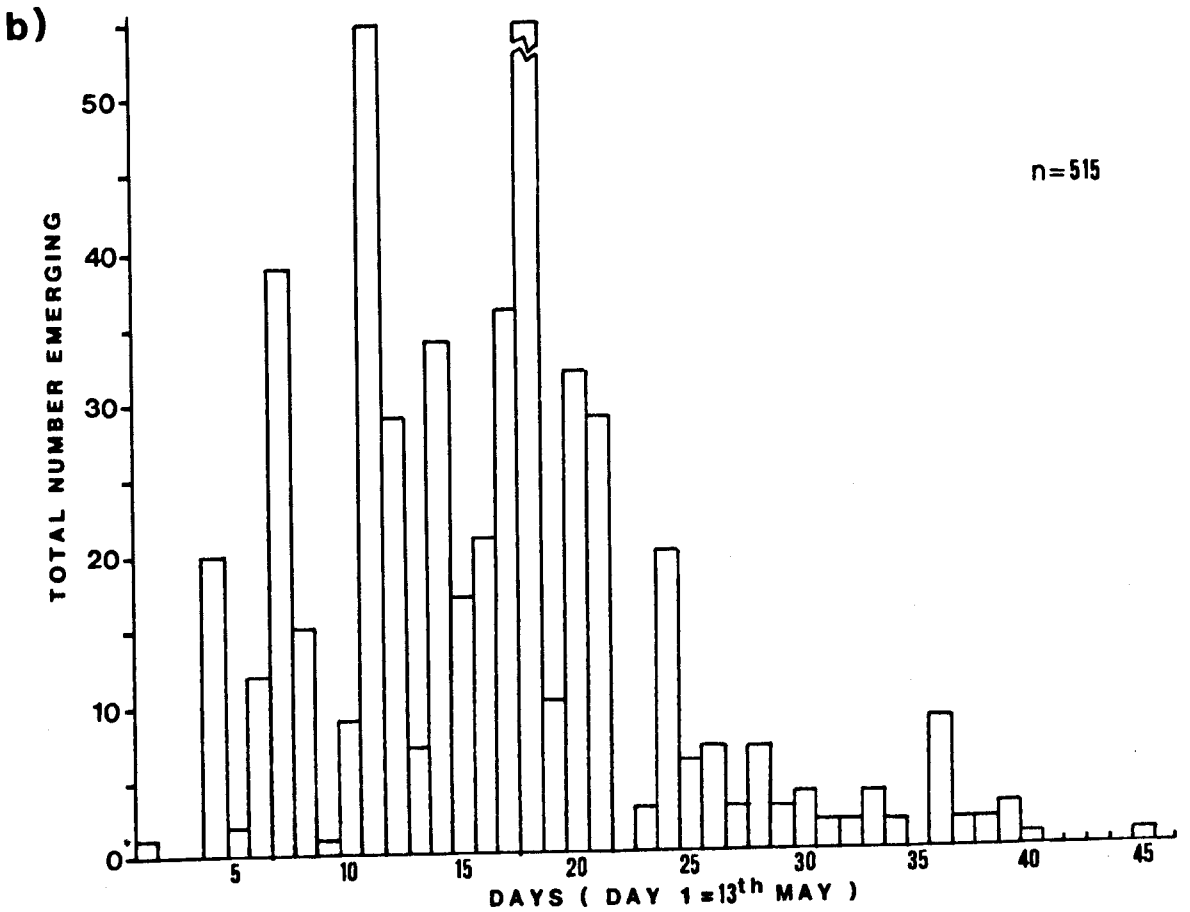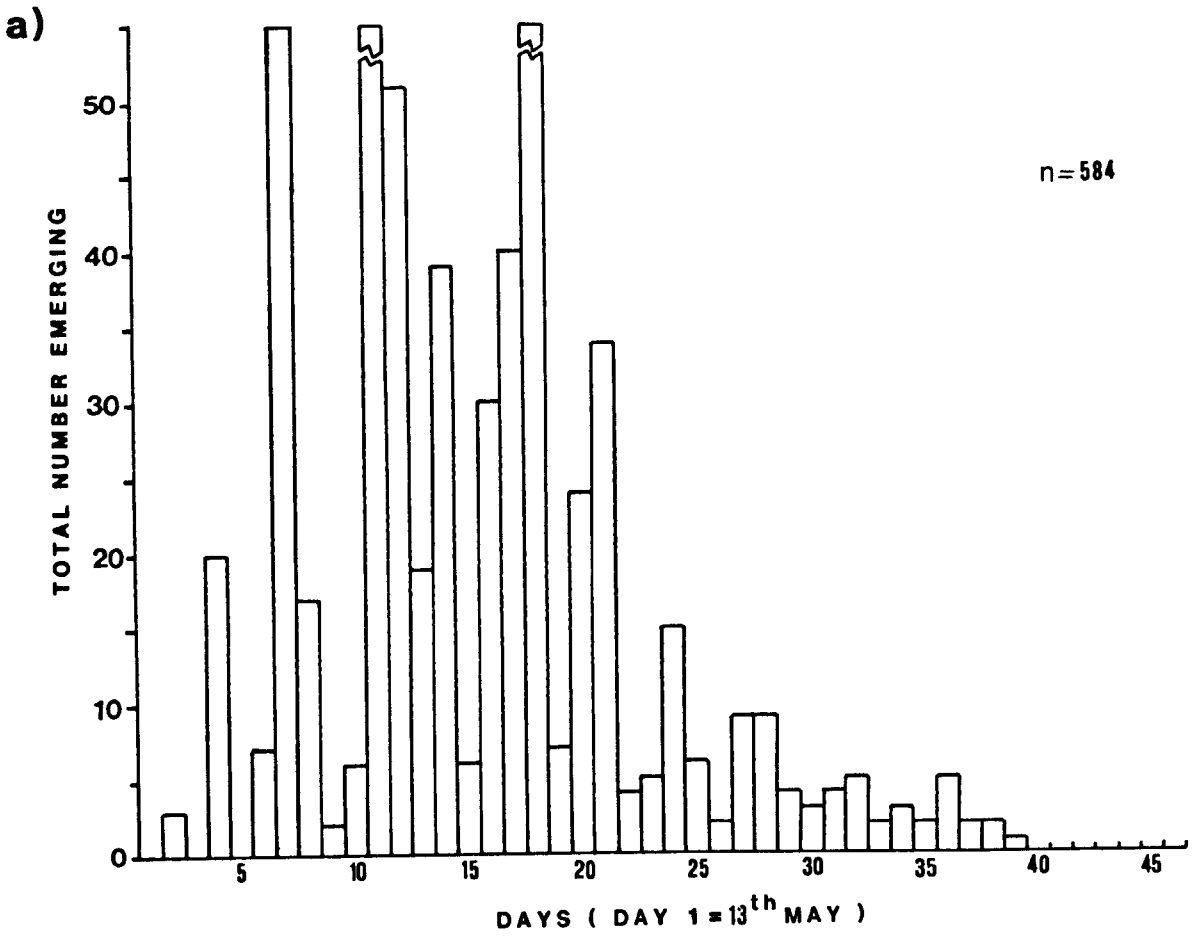
a)

K-S Z	P
1.153	N.S.

b)

	Mean	Standard deviation	Standard error	n
male	27.526	7.040	0.291	584
female	28.161	7.583	0.334	515

Z	P
-1.443	N.S.

Table 3.4 Differences between the emergence of males and females from pond B, as shown by **a)** Kolmogorov-Smirnov 2-sample test and **b)** mean dates of emergence (day 1 = 1 st May), and a Mann-Whitney U-test comparing median dates of emergence.

differences in the homogeneity of the distributions. The mean date of emergence of males and females, together with measures of the variation around the mean, and the result of a Mann-Whitney U-test are given in Table 3.4b. As before, there is less variation in mean date of male emergence compared to that for females. However, there is no significant difference between males and females with respect to the median date of emergence.

Females are significantly larger than males when the mean or median wet weights are compared (male, mean 37.94mg, SE 0.21; female, mean 41.23mg, SE 0.25; $t = 10.14$, 570 d.f., P< 0.001). Females are also significantly larger than males with respect to hindwing length, although there is no difference between mean or median head width.

3.3.3   Comparison of the emergence of *Pyrrhosoma nymphula* between pond A and pond B.

Figures 3.7a,b show the total number of individuals (males and females combined) emerging from ponds A and B respectively. There is no significant difference between the total number emerging from the two ponds ($X^2_{(1)} = 3.419$, N.S.), or between the sex ratios at emergence ($X^2_{(1)} = 0.475$, N.S.).

It is clear that not only are the shapes of the two distributions very different, but also the timing of the emergence differs between the two ponds. The median date of emergence for individuals from pond A is 28.0, which corresponds to 9th June, while the median for individuals from pond B is 16.0, which corresponds to 28th May.

There is a highly significant difference between the shape of the two distributions (Table 3.5a). In Table 3.5b the mean dates of emergence are given and the result of a Mann-Whitney U-test shows that there is a highly significant difference between individuals from the two ponds with respect to median date of emergence. Individuals from pond B emerge significantly earlier than those from pond A.

Tables 3.6a,b show the mean and median wet weights of males and females

Fig. 3.7   Histograms showing the distribution of individuals emerging from **a)** pond A and **b)** pond B.

a)

b)
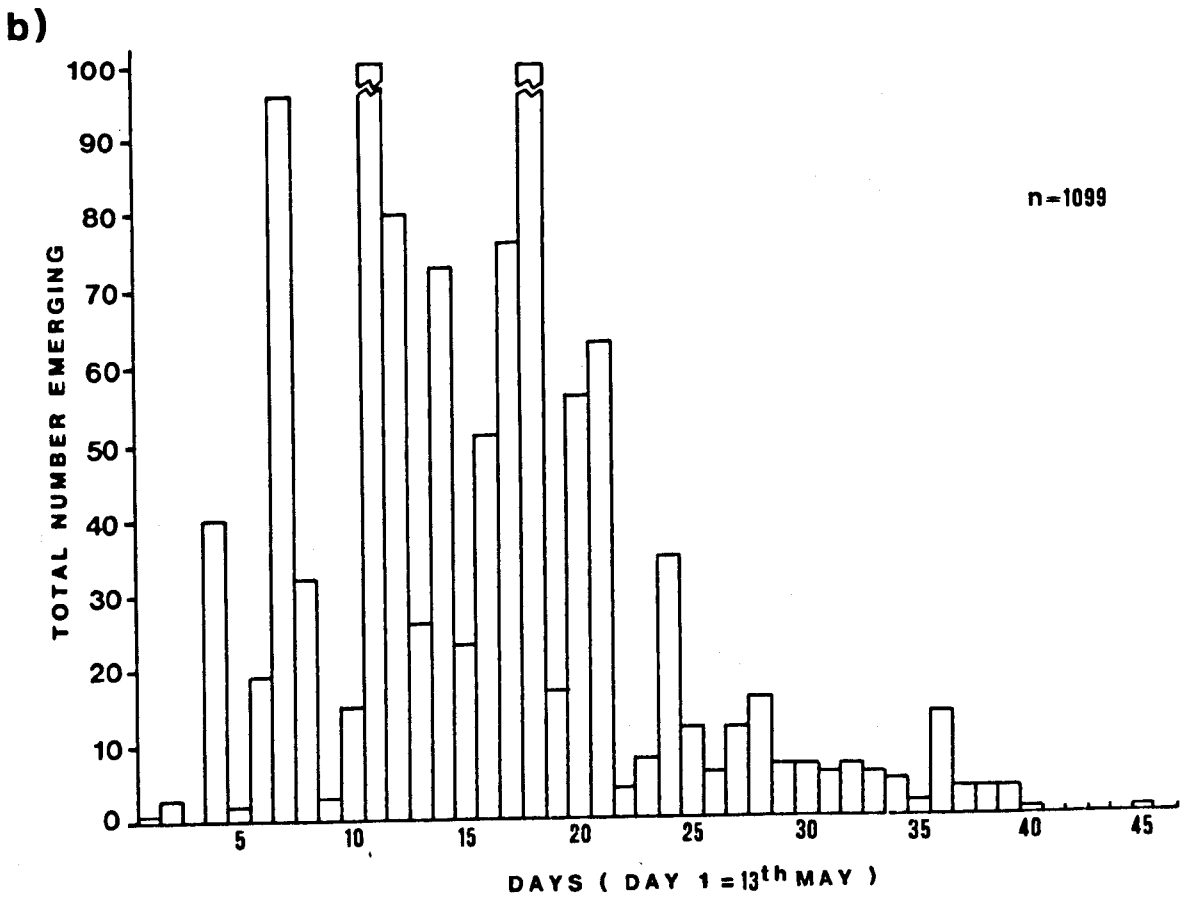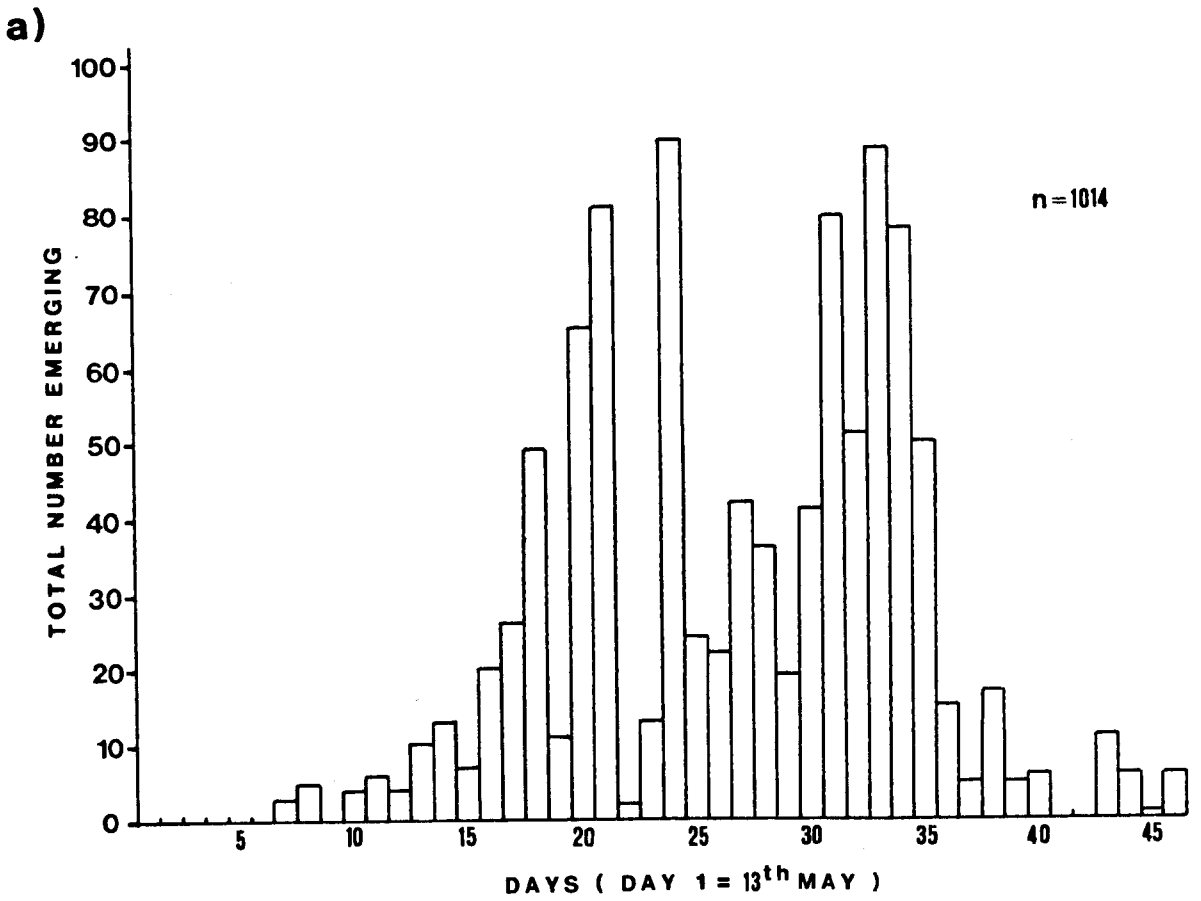
a)

K-S Z	P
13.473	P< 0.001

b)

	Mean	Standard deviation	Standard error	n
Pond A	39.071	7.377	0.232	1014
Pond B	27.823	7.303	0.220	1099

Z	P
-28.579	P< 0.001

Table 3.5 Differences between the emergence of individuals from pond A and pond B, as shown by **a)** Kolmogorov-Smirnov 2-sample test and **b)** mean dates of emergence (day 1 = 1 st May), and a Mann-Whitney U-test comparing median dates of emergence.

a)

	Pond A	Pond B
Mean wet weight (mg)	35.68	37.94
Standard error	0.19	0.21
n	343	303
Median wet weight (mg)	35.66	38.26

b)

	Pond A	Pond B
Mean wet weight (mg)	38.23	41.23
Standard error	0.27	0.25
n	243	269
Median wet weight (mg)	38.07	41.48

Table 3.6   Mean, standard error and median wet weight (mg) of **a)** males and **b)** females from pond A and pond B.

respectively, from ponds A and B. It is clear that for both males and females, individuals from pond B are larger. These differences are significant (Table 3.7) when wet weight are compared, and also when hindwing length and head width is compared.

Individuals emerge earlier at pond B, and early emergence in damselflies is often coupled with large size. It is possible, therefore, that the aforementioned size differences arise due to a small group of very large, early emerging adults biasing the results. Such a situation could occur in pond B, for instance, if a few competitively superior larvae managed to monopolise a good feeding area. For this reason, thirty-five males and thirty-five females were randomly chosen from the beginning, middle and end of the emergence distributions at each pond. Tables 3.8 and 3.9 show the results of t-tests comparing mean head width and mean wet weight respectively, for each group at each of the three stages of emergence.

At the beginning of emergence the mean head width of both sexes from pond B is significantly larger than that of pond A individuals. At the middle and end of emergence only one of the remaining four comparisons shows a significant difference. The mean wet weight of pond B males is significantly larger than that of pond A males at each of the three stages of emergence, and for females it is significantly larger at the beginning and middle of emergence but not at the end. However, the level by which the differences are significant declines from the beginning to the end of emergence for both males and females.

Therefore, it appears that the observed size differences result from a number of factors. There is evidence that individuals from pond B are consistently larger than those from pond A throughout the entire emergence period. There is also evidence that the differences are greatest at the beginning of the season, probably due to the emergence of some fast developing, competitively successful larvae.

3.3.4   Decline in size through the emergence period.

To reveal any size declines, the total emergence period at both ponds was split

	Male		Female	
	Z	P	Z	P
Wet weight (mg)	-7.990	P< 0.001	-8.024	P< 0.001
Hind wing length (mm)	-4.585	P< 0.001	-7.560	P< 0.001
Head width (mm)	-9.016	P< 0.001	-6.952	P< 0.001

Table 3.7   Results of Mann-Whitney U-tests comparing wet weight, hindwing length and head width of males and females between pond A and pond B.

			Mean	Standard error	P
Beginning	Male	Pond A	4.28	0.02	
		Pond B	4.41	0.01	P< 0.001
	Female	Pond A	4.31	0.02	
		Pond B	4.36	0.02	P< 0.001
Middle	Male	Pond A	4.39	0.01	
		Pond B	4.41	0.01	N.S.
	Female	Pond A	4.33	0.02	
		Pond B	4.42	0.02	P< 0.001
End	Male	Pond A	4.31	0.09	
		Pond B	4.30	0.12	N.S.
	Female	Pond A	4.25	0.02	
		Pond B	4.25	0.02	N.S.

Table 3.8   Results of t-tests comparing mean head width (mm) between groups of males and females from pond A and pond B at three different stages of emergence.

			Mean	Standard error	P
Beginning	Male	Pond A	36.31	0.63	P< 0.001
		Pond B	39.24	0.54	
	Female	Pond A	39.36	0.74	P< 0.001
		Pond B	43.11	0.58	
Middle	Male	Pond A	36.72	0.46	P< 0.05
		Pond B	38.26	0.45	
	Female	Pond A	39.41	0.57	P< 0.01
		Pond B	41.72	0.51	
End	Male	Pond A	33.38	0.47	P< 0.05
		Pond B	35.62	0.80	
	Female	Pond A	36.38	0.55	N.S.
		Pond B	38.01	0.86	

Table 3.9 Results of t-tests comparing mean wet weight (mg) between groups of males and females from pond A and pond B at three different stages of emergence.

into five day intervals, and the mean wet weight of all individuals within each interval was calculated. This was then plotted against the interval midpoint. The results for ponds A and B are shown respectively in Figs. 3.8a,b. At both ponds there is a significant decline in mean wet weight over the emergence period. For individuals from pond B the range is large, falling from a mean of 41.39mg in the first interval, to a mean of 31.18mg for individuals grouped in the last interval. For individuals from pond A there is a significant decline also in head width, but not in hindwing length, whereas for pond B individuals there is a significant decline in both of these parameters.

In Table 3.2 it was shown that exuvium dry weight is significantly correlated with other size measures. There is a significant decline in mean exuvium dry weight over time at pond B and there is also a decline at pond A although it is not quite significant (see Figs. 3.9a,b).

Therefore, a decline in size of *P. nymphula* over the emergence period can be detected either by measuring the newly emerged adults, or by measuring their exuviae.

3.4   Discussion.

The results presented here form a detailed study of the emergence of *P. nymphula*, and so compliment some of the previously undertaken larval and adult popuation studies (e.g. Corbet 1952, 1957a; Macan 1964, 1974; Lawton 1970, 1971a). The subsequent discussion will concentrate primarily on the following areas: the emergence of individuals through the day; the sex ratio at emergence; the emergence of males relative to females; the seasonal placement, duration, and synchronisation of emergence; factors responsible for differences between the emergence at ponds A and B and their relation to those determining the timing and duration of emergence; and the decline in size of individuals through the emergence period.

Fig. 3.8   Plots of mean wet weight of all individuals grouped within 5-day intervals with the interval midpoint, for **a)** pond A and **b)** pond B.

a)

MEAN WET WEIGHT (mg)

r = −0.865
p < 0.01

MIDPOINT OF 5-DAY INTERVAL (DAY 1 = 13th MAY)

b)

MEAN WET WEIGHT (mg)

r = −0.900
p < 0.01

MIDPOINT OF 5-DAY INTERVAL   (DAY 1 = 13th MAY)
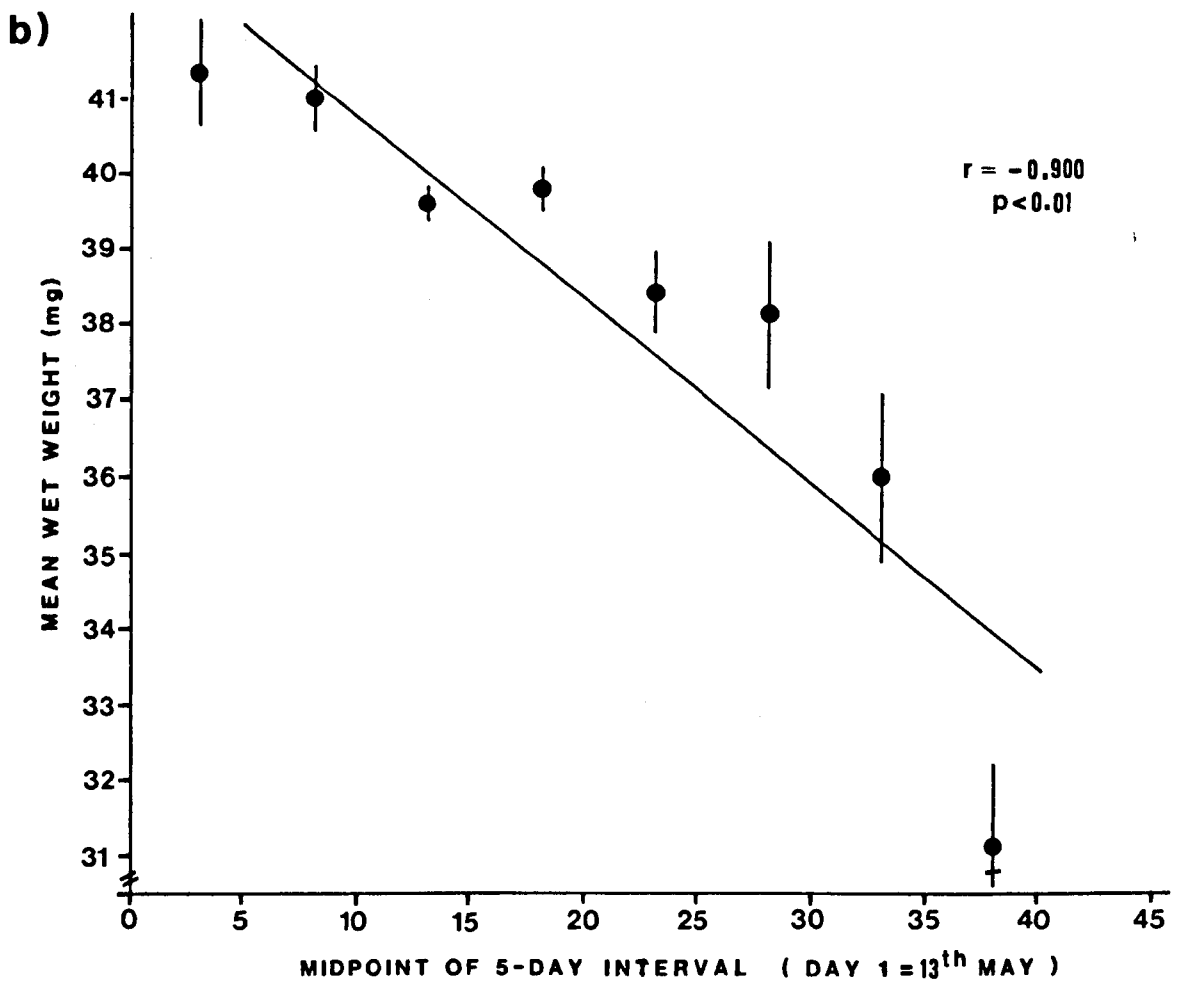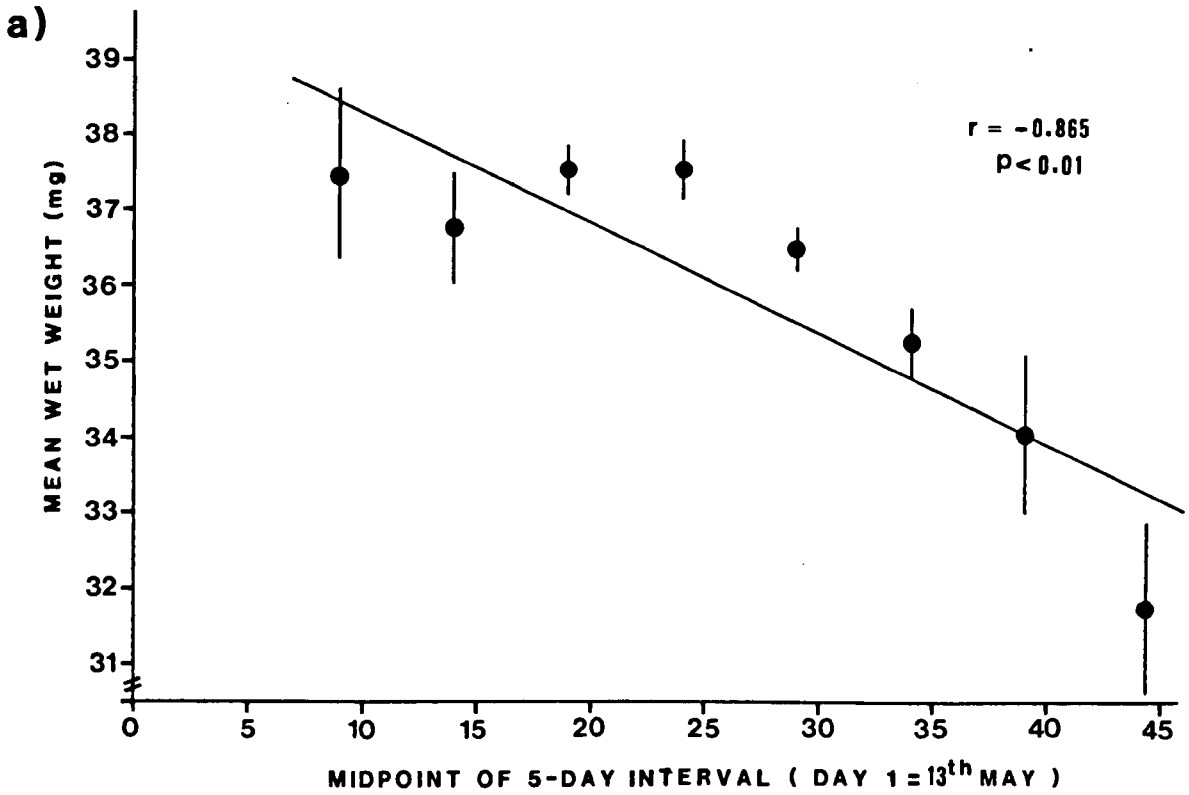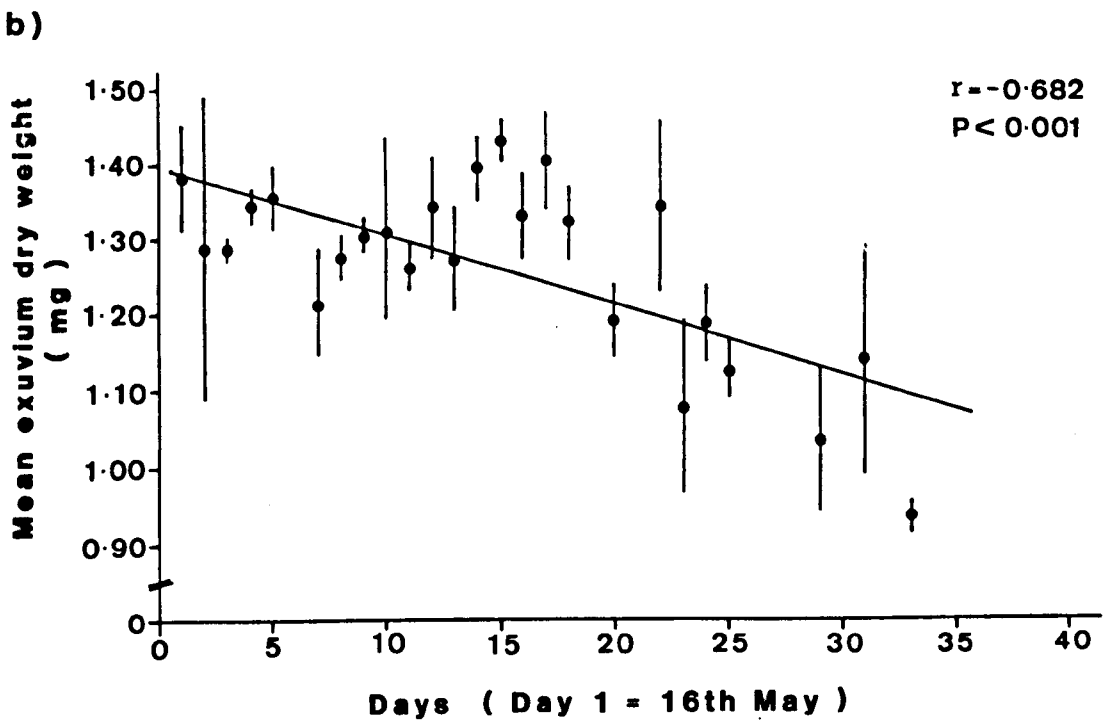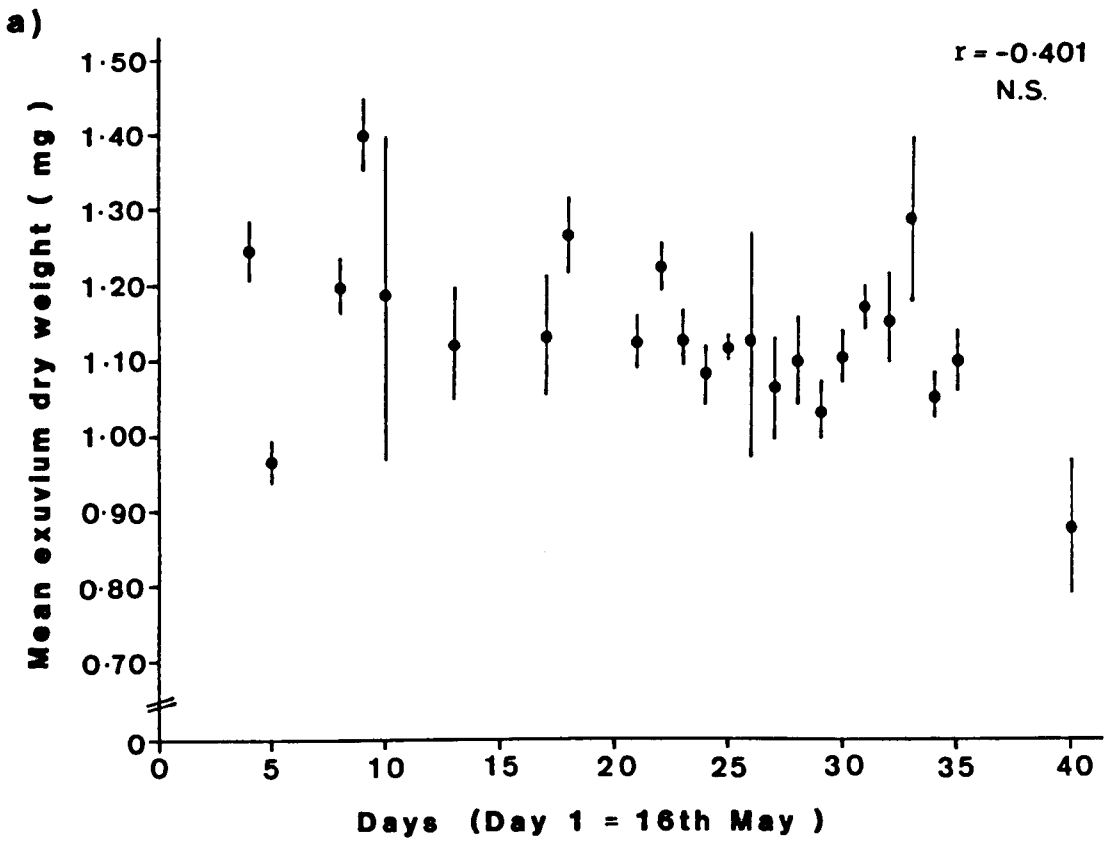
Fig. 3.9   Plots of mean exuvium dry weight through the
emergence period at **a)** pond A and **b)** pond B.

Corbet (1952) found that larvae of *P. nymphula* first began to emerge at about 8.30am with a daily peak occurring between 9.00 and 10.00am. He found that many larvae crawled some distance from the pond to emerge but that the majority did so only about half an inch above the water surface.

Fraser (1944) indicated that *P. nymphula* larvae, under some conditions, can crawl very large distances from the water to a suitable emergence support. He found exuviae on trees between 20 and 30 feet from a pond, and as high as 7 feet from the ground.

Differences between studies are likely to result from differences between pond characteristics, environmental conditions and predation pressures. In this study very few larvae crawled a long way from the water to emerge but this may be due to the generally abundant vegetation around the periphery of both ponds. In addition, while some larvae were found to emerge quite close to the water surface, if a suitable support was found, the majority climbed considerably more than half an inch above it. Lawton (1970) reported that *P. nymphula* exuviae in his study pond were usually found 10-20cm above the water surface.

This difference may be due to the avoidance of predators since frogs, spiders and ants were often seen to prey on newly emerged adults near to the water surface. Birds, and in particular reed buntings (*Emberiza schoeniclus* (L.)), which were frequent visitors to the site, would often concentrate on the clumps of *Molinia* at the very edge of the water.

In favourable weather conditions larvae first began to emerge at about the same time reported by Corbet (1952). However, the peak in emergence was often found to be later than he reported, especially on cold or cloudy days. It was clear that weather conditions, and particularly temperature, had a very marked effect on emergence and there may also be variation in timing due to the more southerly location of his study pond.

Banks & Thompson (1985b) warned that sampling only a part of the emergence period could give the impression of a biased sex ratio if the emergence patterns of the

two sexes were not identical. This was not a problem in this study because numbers of all newly emerged adults or exuviae were recorded daily at both ponds throughout the entire emergence period. Thus the estimates of male and female population size are likely to be very accurate.

A significant male biased sex ratio was found at both ponds. Lawton (1972) investigated larval sex ratios in populations of *P. nymphula* and *Coenagrion puella* through the later instars, up to and including emergence. He found that in both species there was a small (averaging 52.0% and 54.4% respectively) but significant excess of male larvae present. At emergence the adult sex ratio of *P. nymphula* (based on collections of exuviae) in three separate ponds was 50.7%, 50.3% and 51.5% male.

Corbet (1952) reported a biased sex ratio in *P. nymphula* of 63% male based on exuviae collections which were "carefully standardised but not exhaustive". In addition, collections did not continue throughout the entire emergence period, the sample size being only 97 exuviae. In a similar study but with a larger sample size, Corbet (1962) reported a male biased sex ratio of 53.7%.

Thus, all reported investigations, as well as this study, have found significantly male biased sex ratios at emergence in *P. nymphula*. Parr & Palmer (1971) studied the sex ratios of three coenagrionids : *Ischnura elegans, C. puella* and *Enallagma cyathigerum*. For *E. cyathigerum* the sex ratio at emergence was not significantly biased. Collections of exuviae were too small to estimate the sex ratio for the other two species and for this reason larval sex ratios were calculated. There was a slight excess of males for *I. elegans* but this was not significant, whereas for *C. puella* there was a very significant male biased larval sex ratio.

For all three species the imaginal sex ratio was significantly male biased. This is unsurprising and many studies have shown similar findings. Obtaining accurate estimates of the imaginal sex ratio is notoriously difficult because of the differential activity of the sexes. Females need come to water only briefly to lay their eggs and then depart to mature a new clutch, while males tend to remain near the water body throughout their reproductive life.

In a study of the emergence of *C. puella*, Banks & Thompson (1985b) found that the sex ratio was not significantly different from unity, being 50.96% male. They were able to collect very large numbers of newly emerged adults over the entire period.

Pickup, Thompson & Lawton (1984) studied larval growth in three populations of *Lestes sponsa* (Hansemann). They found that the sex ratio was close to equality initially, then it became male biased, but eventually was female biased at emergence. They suggested that the imbalances were the result of differential larval mortality in the later instars. Gower & Kormondy (1963) found a female biased sex ratio at emergence in *Lestes rectangularis* Say. Lutz (1968) found no significant departure from equality in *Lestes eurinus* Say in both larval collections and collections of exuviae at emergence.

There is therefore considerable variation in larval and exuviae sex ratios in damselflies. To an extent, the above studies indicate that different species may tend towards either male or female bias. However, Kormondy & Gower (1965) found wide annual fluctuations in population size and sex ratio of the same species of Zygoptera in the same ecosystem. By recording numbers of exuviae at emergence they found that the percentage of males of *Ischnura verticalis* increased from 34.4% in one year to 52.6% the following year. A similar increase was recorded for *Enallagma ebrium* (Hagen), which had a sex ratio of 43.6% male one year and 54.5% male the next.

Corbet (1962) and Lawton (1972) reviewed sex ratios in the Zygoptera and the Anisoptera. Lawton (1972) found that an excess of male larvae was reported in eight records for Zygoptera, the imbalance being significant in five of the records, involving two species. Another five records showed an excess of female larvae, with the imbalance being significant in two of the cases. Most of the records he reviewed are the same ones referred to above. In the Anisoptera a contrast is found. Each of twenty-one of the available records, involving fifteen species, showed an excess of female larvae. In the Zygoptera there was an indication that sex ratio imbalances involving an excess of females were larger than those involving an excess of males.

Lawton (1972) concluded that the reasons for the differences between the Zygoptera and the Anisoptera were uncertain, and the causes of sex ratio imbalances were not understood. In almost all cases, odonates are of the XO-XX type of sex determination mechanism, with the male being the heterogametic sex. Therefore, the ratio expected must be 1: 1, at least initially. Lawton (1972) stated that differential adult mortality between the sexes could not provide a means of selection for imbalance in the neonate sex ratio. Therefore, at some point in the development the observed imbalances must become apparent.

Because of the lack of explanation of this topic, differential larval mortality seems the only obvious suggestion to account for the male biased sex ratios found in this study. Since females are larger than males both as larvae and adults, there exists the possibility that differential predation of larger larvae may be occurring. Such predation would lead to a higher proportion of smaller (and therefore male) larvae surviving to emergence.

Comparison of the male and female emergence distributions from pond A show that males emerge slightly earlier than females and this is statistically significant. There is also less variation in the mean date of emergence of males compared with females, from both ponds.

Banks (1985) found similar results to these for *Coenagrion puella* and was able to use his data in a model formulated by Parker & Courtney (1983). The model concerns the timing of entry of individuals into a seasonal population in which there is competition amongst males for females. Information on the female emergence distribution, daily survival rate and probalility of remating is required in the model. Consequently, an evolutionarily stable probability distribution of male emergence dates is sought such that males emerging on all dates have equal fitness in terms of the number of matings obtained (Banks 1985).

The broad predictions of the model were that entry of males into the reproductive population should be earlier than that of females, and there should be less variance in the male entry date. These predictions were supported by his data.

In fact, Banks (1985) actually found that the female mean date of emergence was earlier than that of males, but he calculated the date of entry into the reproductive population as the emergence date plus the mean immature period, which was clearly shorter in males. Corbet (1952) estimated the immature period to be between 9-14 days for *P. nymphula*, but he did not give any indication of differences between the sexes. Corbet (1962) noted two species where information was available on maturation rates and in both cases males matured more rapidly than females.

Hence, according to Parker & Courtney's (1983) model, variation in the timing of entry of males into the population can be adaptive, because gains to each individual at a given stage are inversely related to population density. Other researchers have argued that such variation is maladaptive noise due to environmental effects (Fagerstrom & Wiklund 1982). By this hypothesis, selection on males will act only on the mean date of emergence maintaining it at the optimum with respect to the mean female date. However, confirmation of the Parker & Courtney (1983) model by Banks (1985), together with the similar end results found in this study, both support the suggestion that such variation is adaptive.

Having said this, Banks (1985) is quick to point out that there is undoubtedly variation imposed by environmental effects. Selection may have shaped the nature of that variation and there is no selective force acting to reduce it by favouring any particular optimal date. Further considerations, specific to this study, on the position of emergence within the emergence period, and variation in emergence date will be discussed later.

In common with many other zygopterans there is sexual dimorphism in the size of *P. nymphula*, with females being bigger than males (Hammond 1977). Banks & Thompson (1985a, 1987b) and Thompson (1989) investigated the nature of the different selective forces acting on the size of male and female *Coenagrion puella*. They were able to calculate the optimum sizes for each sex and found that the optimum size for females, with respect to lifetime egg production, was bigger than the optimum size for males, with respect to lifetime mating success. Thompson (1989) concluded

that it was the difference in the selective forces acting on the two sexes that would provide a full explanation of sexual dimorphism. This could best be investigated by studying selection on size in both sexes but unfortunately few such studies have been carried out.

Despite pond A being substantially larger than pond B, the numbers of individuals that emerged from each was not significantly different. Therefore, the density of emerging larvae was higher in pond B, being 8.69 m^{-2} compared to 4.68 m^{-2} in pond A.

Larval densities of *C. puella* were estimated by Thompson *et al.* (1985). Bin samples were taken just prior to emergence in two years and the mean larval densities calculated as 90 m^{-2} (S.E. 57) and 84 m^{-2} (S.E. 50). In a study of *P. nymphula*, Lawton (1970) found that mean numbers varied from a peak of as many as 400 m^{-2} in July and August (after eggs hatched), to around 20 m^{-2} prior to emergence. In one year the larval density prior to emergence was as little as 4 m^{-2} which is around the order found in this study. Initial larval densities may be very high indeed, but few larvae survive to emergence. Macan (1964) found *P. nymphula* densities of as many as 1400 newly hatched larvae m^{-2}, and Benke & Benke (1975) found a total odonate density of over 1700 m^{-2}.

Clearly there may be any number of factors that cause differences in larval density between ponds and between studies. Such factors may include the initial egg input into the pond, prey and predator density, perch and refuge availability, environmental conditions etc.

The values obtained in this study, however, do appear quite low, although they were obtained from emergence data, not larval sampling. Some investigations have shown that larval density prior to emergence may be substantially higher than density estimates obtained from recording emerging individuals. Benke & Benke (1975) found that mortality in three species of coexisting dragonfly larvae averaged 92% per annum from the time of hatching to the final instar. In a further comparison of larval estimates with emergence data, they found that at least 80% of the final instars died

just before leaving the water to emerge.

However, Lawton (1970) assumed that no mortality was occurring in a population of *P. nymphula* during the period from final instar to emergence. He used emergence numbers as an independent check of pre-emergence densities, although his results were by no means conclusive. Complete collections of exuviae yielded estimates of the number of emerging larvae that were 24% more in one year, and 34% less in another, than the calculated number of larvae present prior to emergence.

Lawton (1970) found an approximately constant mortality rate in *P. nymphula* within the same year class. Estimates for three years indicated annual mortalities of 78%, between 60 and 70%, and 99.5%. He was also able to recalculate Macan's (1964) data on *P. nymphula* and again obtained approximately constant mortality rates, these varying between 85% and 68% per annum with a mean of 75% per annum.

The emergence from pond A and pond B is synchronised only to a limited extent, lasting between 5-6 weeks in both cases. Corbet (1980) said that, with respect to temperate species, the shortest duration of emergence and the closest synchronisation is found among those emerging earliest in the year. For such species the annual duration of emergence would usually be less than a month. Corbet (1957a, 1962) referred to *P. nymphula* as a typical spring emergence dragonfly with a well synchronised adult emergence. This was attributed to a diapause in the final instar which allowed the majority of a year group to respond synchronously to rising temperatures which induced metamorphosis in spring.

The factors controlling seasonal emergence in dragonflies, and their relative roles in synchronising and positioning emergence in temperate latitudes, are complex. Corbet (1962) gave a detailed account of such factors, concentrating on the relative roles of temperature and photoperiod. He stated that the photoperiod response functioned to place the maximum proportion of larvae in the right developmental stage at the appropriate season, the actual date of emergence being determined mainly by responses to temperature.

There are two ways in which photoperiod may affect larval development. The

first has already been mentioned - many dragonflies have a diapause in the final instar and have so been classified as spring species (Corbet 1954). Tauber & Tauber (1976, and references therein) suggested that, in several species of Odonata, diapause was maintained through a quantitative response to daylength, the response gradually diminishing throughout the autumn. Corbet (1962) stated that at this point larvae are physiologically capable of metamorphosing but are prevented from doing so untill the spring because of the low temperatures.

In a study of the dragonfly *Anax imperator* Leach, Corbet (1954) found that emergence was restricted to a short period each year, although the larval population showed a wide measure of temporal variation. This was attributed to a diapause in the final instar. Corbet (1954) stated that the temporal variation accumulated in the long period of larval development was effectively erased in the final instar, such that more than 90% of the annual population emerged within the first 10 days of the emergence period.

The second response to photoperiod results in metamorphosis being accelerated by longer daylengths. This may provide a means by which temporal variation before emergence is reduced, both in spring and summer species. Such a response was reported by Corbet (1962) from personal communication with C.E. Jenner who found that larvae of several species of *Enallagma* showed accelerated development under longer photoperiods. Ingram & Jenner (1976) also reported similar findings.

It appears, therefore, that photoperiod and temperature interact to produce a highly synchronised emergence of short duration in spring species such as *P. nymphula*. In this study ,the lack of such a pattern and the relatively long duration of emergence may, in part, result from fluctuating weather conditions over that period. It is apparent, however, that additional factors must be contributing to the duration and spread of emergence.

The effects of interference competition on larval growth and development rate in *Ischnura elegans* have been shown in the previous chapter. Those individuals that are successful as larvae will emerge both earlier and bigger compared with other larvae.

Their eggs will be laid earlier, and thus hatch earlier in the summer. As a result, smaller, late emerging damselflies may suffer reduced lifetime reproductive success unless there is some, as yet, undiscovered phenomenon to offset the advantage of emerging early.

That there is a decline in size over the emergence period indicates that differences found between larvae in the senior year class, which may have arisen partly out of competition, are not erased, but are expressed in the adult population. There may well be selection acting on both sexes to emerge early in the season. However, from an evolutionary point of view, it is unreasonable to assume that temporal differences accumulated during the long larval period could simply be eradicated as a result of a 'synchronising diapause'.

In the light of the above, it is perhaps not so surprising that a highly synchronised emergence pattern is not apparent in this study. Whilst almost all larvae will be in the final instar by the winter preceding emergence, there will still be large size differences within the instar. Also, successful larvae will enter the final instar several weeks earlier than their smaller conspecifics. Such larvae will be that much more advanced when growth and development are arrested in the autumn, and also when development resumes in the spring. If resources are limited such that the effects and consequences of competition are intensified, it may be expected that emergence lasts longer and is less synchronised. In pond B the shape of the distribution is positively skewed. Although no more than speculation, asymmetric competition could provide an explanation for the presence of a few, very small, late emerging individuals skewing the distribution.

While it is true to say that the expression of differences in size and development arising from the larval stage of the life-history cannot be completely suppressed at emergence, they may well be modified. There is likely to be a compromise between the advantages of emerging early in the season and the disadvantages of a highly unsynchronised emergence where encounters with potential mates may be reduced. Corbet (1964) listed some possible consequences of a synchronised emergence.

These included an increase in both survivorship and mortality, depending on the environment, and coincidence of the sexes allowing the reproductive potential of individuals to be realized. The seasonal position of the emergence period will determine the physical and biotic environment the adults encounter. What is important, however, is that many factors undoubtedly interact with each other to determine the exact placement, synchronisation and duration of emergence.

For example, in a study of *P. nymphula*, Lawton (1971a) found that while over 75% of the senior year class moulted into the final instar within one month (September), it was not until early November that all larvae did so. A period of over 8 weeks therefore separated entry into the final instar. Initial differences in development arising from the timing of egg deposition may subsequently have been reinforced and increased by the effects of competition. However, the corresponding emergence in spring lasted under 5 weeks, perhaps indicating that larval development was later accelerated by longer daylengths.

Comparison of the emergence distributions between ponds A and B provides further evidence that additional factors contribute to the timing and duration of emergence. Individuals from pond B emerge significantly earlier than those from pond A, and yet the two ponds are close to each other and thus are subject to the same climatic conditions and photoperiod.

If photoperiod and diapause function to synchronise a species- specific temporal emergence, then larvae must either be exposed to very different temperatures in the two ponds or other factors are involved. The fact that pond B individuals are also consistently larger than those from pond A suggests the latter.

Gower & Kormondy (1963) studied the emergence of populations of *Lestes rectangularis* Say. They found that while more than 50% of a population emerged in the first 7 days of a 2-3 week period, the onset of emergence varied in different populations. These different populations occurred in nearby bodies of water and were therefore subject to the same photoperiod.

As already discussed, the density of emerging larvae is higher in pond B than in

pond A. Banks & Thompson (1987a) found that larvae of *Coenagrion puella* in high density populations were smaller than those in low density populations and were more likely to have a semivoltine life history. Macan (1964) showed that when initial densities of *P.nymphula* were high, a proportion of the larvae took three years to complete development, compared to the normal two.

If the population density was at such a level as to have a regulatory effect at either pond, those larvae in pond B would be expected to be smaller and have decreased development rates compared to larvae from pond A. Since this is the opposite to what was found, it is assumed that the difference in larval density is not a factor responsible for the emergence differences. However, the skewed nature of the emergence distribution from pond B may result from the higher larval density if competition is that much more intense there.

A possible explanation for the differences may be that the water temperature in pond B was higher than in pond A in the period between larvae coming out of diapause and emergence. However, this alone would not explain the differences in size. If water temperatures were consistently higher in pond B, larvae may develop faster throughout their entire life-history. With respect to size differences, Thompson (1978a) found that temperature had a marked effect on the functional response of *Ischnura elegans* larvae in the laboratory. Given the appropriate prey densities, larvae from pond B may achieve higher feeding rates and larger size increases at the moult. However, Baker & Feltmate (1987), in a laboratory experiment with *Ischnura verticalis*, found that temperature affected development rate but not size measures.

To decide whether water temperatures might vary between the two ponds, four depth measures were taken at regular intervals at each of nine transects across both ponds; Figure 3.10 shows the results. In the depth profiles, 5mm corresponds to 1m and thus it is difficult to detect any differences by sight, although pond B does appear the deeper of the two. The result of a t-test comparing mean depths shows that the mean for pond B is significantly greater than that for pond A (pond A, mean 39.14 cm, SE 2.11; pond B, mean 44.86 cm, SE 1.53; t = -2.19, 70 d.f., P<0.05).

Pond A

Depth

a
b
c
d
e
f
g
h
i

2
1
0

0 1 2 3
metres

Pond B

Depth

a
b
c
d
e
f
g
h
i

2
1
0

0 1 2 3
metres
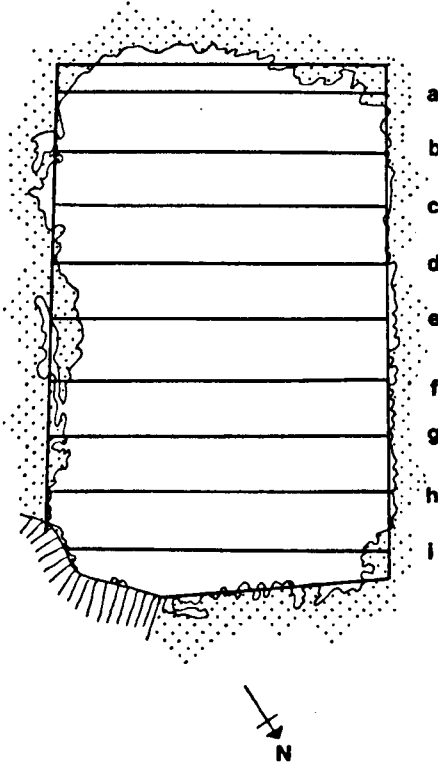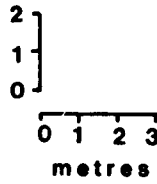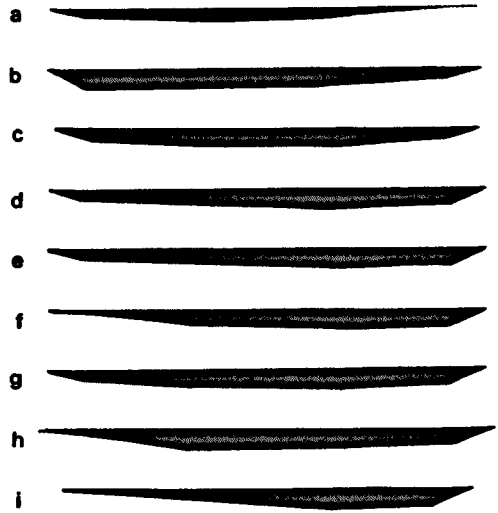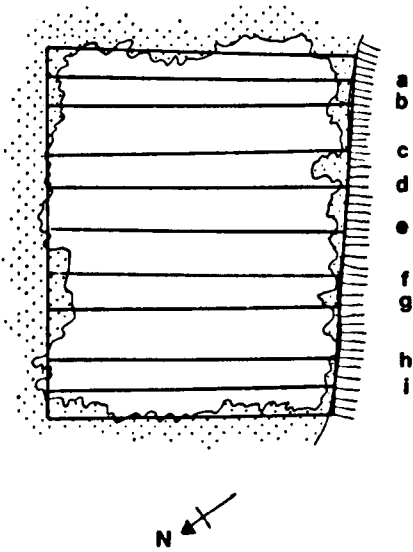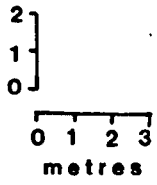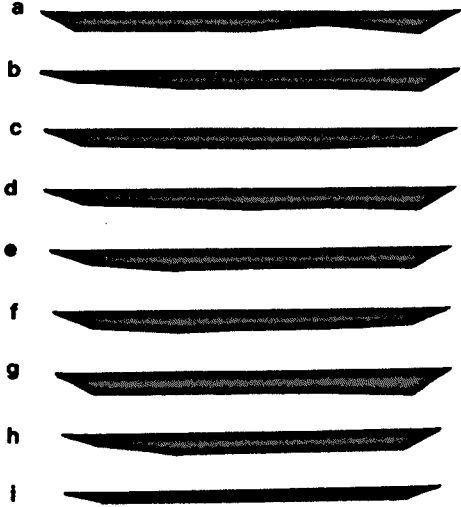
Fig. 3.10   Profiles of the depth at regular intervals in

ponds A and B.

Because pond B has a smaller surface area and is deeper than pond A, it may be less susceptible to slight fluctuations in temperature. During the winter months it is likely that there would be little difference in temperature between the two ponds. However, after the summer when the water temperatures are falling, pond B would probably take longer to cool down. Larvae there may be able to continue development longer, in either the final instar or instar 5 or 6, before overwintering. Having said this, the water temperatures in pond B would also probably take longer to rise again the following spring, compared to the larger, shallower pond A, so the differences may cancel each other out.

Parr (1973a) carried out a study on the emergence of *Ischnura elegans* from three neighbouring ponds over several years. He found that the populations differed with respect to the length of the flying season and the separation of the emergence peaks. The reason suggested was that since one of the ponds had a relatively large volume of water, the temperature might be expected to remain somewhat lower in the summer and higher in the winter. The cooling in the winter months would be quicker in the two smaller ponds. Hence the longer periods of relatively slow growth of larvae in the larger pond would result in less synchronisation in development than in the smaller ponds, where the active period of growth would be shorter.

Attempts were made to record the mean water temperatures at both ponds from the time when they first began to fall in the autumn until when they began to rise again. This was done using sucrose inversion tubes, with two tubes being placed at regular intervals on the bottom of both ponds. Unfortunately, inversion was very rapid due to a mild winter and the tubes were left too long in the ponds. No presentable data are available from the investigation, although there was some indication that the mean temperature at pond B was higher than that at pond A.

The only other evidence of temperature differences between the two ponds is shown in Fig. 3.11. These are the results of maximum and minimum recordings taken 10 cm below the water surface during the emergence period in the 1987 field season. While the minimum temperatures appear very similar, the maximum temperatures

Fig. 3.11   Maximum and minimum below water
temperatures recorded at pond A and
pond B from 10th May to19th June 1987.

Temperature (°F)

Days (Day 1 = 10th May)
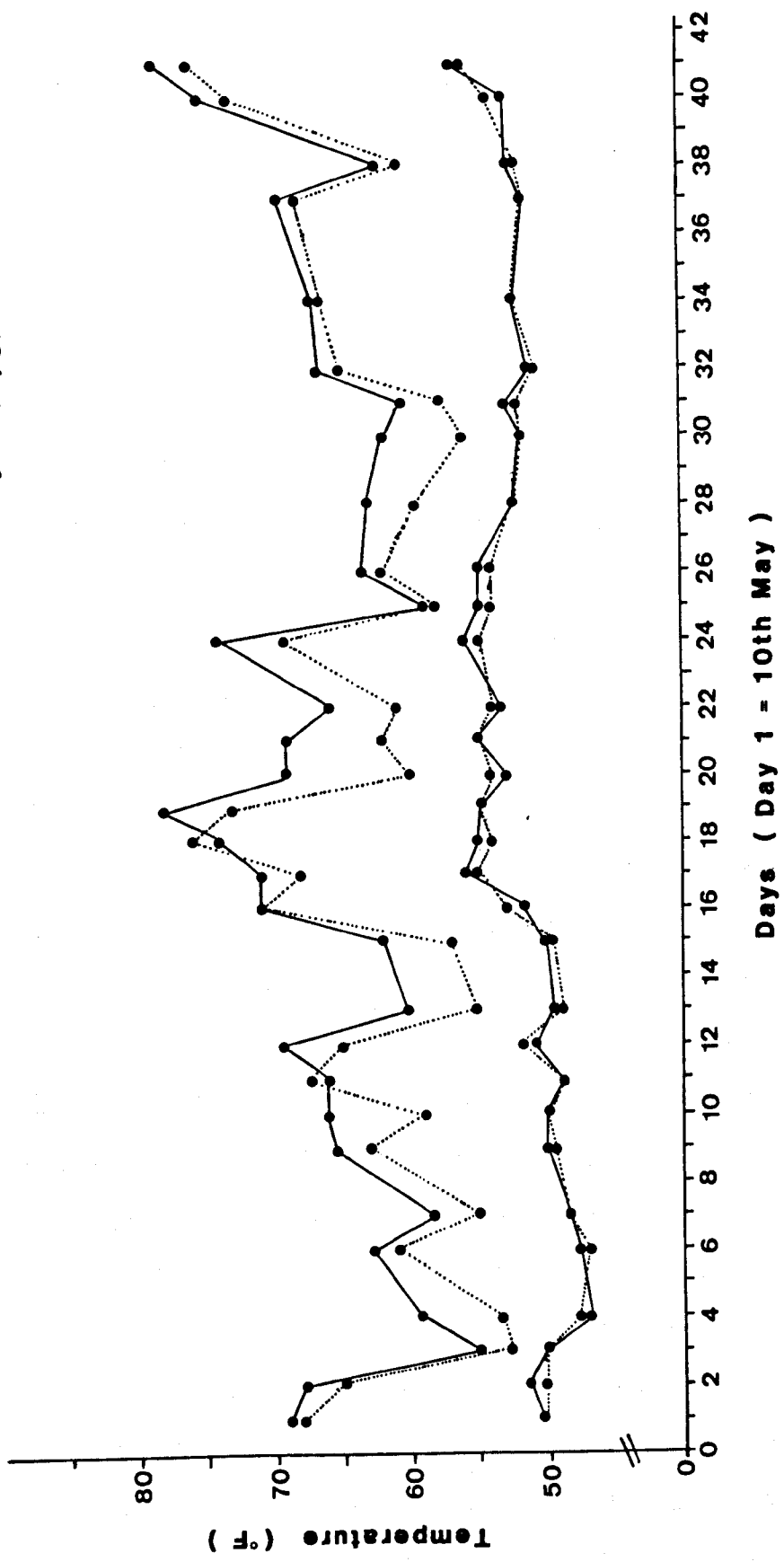
POND A
POND B

recorded are usually slightly higher in pond B. This is surprising given the differences in depth and size. It would be expected that the minimum temperature would remain higher overnight at pond B compared with pond A, and the maximum temperature, day to day, would be higher at pond A. The temperatures at depths greater than 10 cm were not recorded.

Data on temperature differences between the two ponds are therefore incomplete. What few results there are indicate, allbeit far from conclusively, that water temperatures may be higher in pond B than in pond A, at least at certain times of the year.

Given that individuals from pond B are bigger than those from pond A, prey density may differ between the ponds. Lawton, Thompson & Thompson (1980) showed that food availability in *Ischnura elegans* was correlated with increase in larval size at the moult. Poorly fed larvae take longer to develop to adulthood and may emerge as smaller adults compared to well fed larvae (Lawton, Thompson & Thompson 1980; Pickup & Thompson 1984). Attempts to quantify food availability from bin samples failed since very low numbers of chironomids were found in all samples. An alternative method was undertaken in which the mean dry weight of faecal pellets produced by isolated larvae from both ponds was compared.

Final instar and penultimate instar larvae were collected in the autumn of 1988 and placed individually in glass bottles containing filtered pond water. They were kept in a warm place and all faecal pellets produced were collected over a 10 day period. The mean head width of final instar larvae from pond B was significantly larger than that of larvae from pond A, although there were no differences between penultimate instar larvae. There was no relationship between faecal pellet mass and head width. Table 3.10 shows the results of t-tests comparing the mean faecal pellet dry weight between larvae from the two ponds. The mean dry weight for final instar larvae was higher for those from pond B, although it was not significant. Therefore, there is no conclusive evidence that prey density or larval feeding rate is greater in pond B than in pond A.

It is apparent that the ultimate and proximate factors controlling date and duration

	Mean (mg)	Standard error	n	t	d.f.	P
a)						
Pond A	0.032	0.006	4			
				0.04	22	N.S.
Pond B	0.031	0.005	20			
b)						
Pond A	0.028	0.005	8			
				− 1.30	22	N.S.
Pond B	0.042	0.007	16			
c)						
Pond A	0.030	0.004	12			
				− 0.84	46	N.S.
Pond B	0.036	0.004	36			

Table 3.10   T-test analysis comparing mean faecal pellet dry weight (mg) between larvae from ponds A and B for **a)** penultimate instar larvae, **b)** final instar larvae and **c)** larvae from both instars.

of emergence are complex. Photoperiod and temperature clearly interact to a large extent to govern the timing and synchronisation of emergence, but there must be other factors which act as fine tuning. The markedly different emergence distributions from two ponds subject to the same photoperiod illustrate this. Temperature differences alone are unlikely to account for such wide differences in timing or differences in size. Variation in prey density between populations and differences in prey availability , as a result of competition, within populations, are two factors that might affect the synchrony and position of emergence.

Crowley *et al.* (1987b) stated that size at emergence for a given population and sex probably varied little at a particular site or sampling date, but varied between sites and dates. Several studies have shown that size tended to decline through the emergence period (e.g. Banks & Thompson 1985a; Harvey & Corbet 1985; Thompson 1987b; Michiels & Dhondt 1989). Harvey & Corbet (1985) found that smaller adults of *P. nymphula* emerged late in the emergence period, and Banks & Thompson (1985a) showed that the size of emerging *Coenagrion puella* declined through the emergence period.

The larger adults that emerged earlier presumably hatched earlier from eggs that were laid earlier. Thus, there is an initial difference in stage of development between larvae of a given year class. In the previous chapter it was shown that asymmetric larval competition may increase any initial differences in size or development stage. With respect to other insect groups, a decline in size through the emergence period has been found in dungflies (Ward 1983) and fruitflies (Partridge & Farquhar 1983). In all these studies it was assumed that the smaller, late emerging adults had achieved low success in larval competition for food.

Chapter 4.   Mortality during emergence of *Pyrrhosoma nymphula*.

4.1   Introduction.

There were three aims in the investigation of mortality at emergence. The first was to study the effects of climatic conditions on emergence by comparing daily numbers of individuals emerging with various weather variables. Second, an attempt was made to quantify mortality during emergence. The third aim was to relate the estimates of mortality attributed to different factors to the prevailing weather conditions. The studies continued over three years, since the emergence of *P. nymphula* was confined to just a few weeks each year.

After the final moult, newly emerged adults are particularly vulnerable because they are unable to fly until their wings have expanded and the cuticle hardened. Corbet (1962) stated that mortality during emergence may be caused directly or indirectly in three ways : by physical factors, overcrowding and by predation. In this study mortality was divided into two categories : that due to adverse climatic conditions and that attributed to predators (including birds, ants and spiders).

Although knowledge of mortality during emergence is probably better than for any other stage in the life-history of dragonflies (Corbet 1962), very few studies have attempted to quantify it. Instead, investigations have concentrated on merely attempting to identify either those environmental conditions which resulted in increased mortality, or those predators seen to prey upon newly emerged adults. This lack of quantified data may well reflect the difficulties involved in such a study.

The accuracy of the estimates derived in this investigation will have been compromised, to an extent, by the need to collect a suitably large amount of data for analysis. Inferences often had to be made about the likely fate of emerged adults on the basis of previously acquired knowledge about emergence. However, the investigation provides a useful insight into factors which contribute towards mortality,

and the levels of mortality which may be expected under different environmental conditions.

4.2   Materials and methods.

4.2.1   Comparison of emergence with climatic conditions.

Mortality during emergence was studied at the same two ponds from which the emergence data presented in the previous chapter was obtained. In the spring and summer of 1987 and 1988, estimates of percentage mortality at emergence were derived. During the spring and summer of 1986 the emergence distributions obtained from ponds A and B were simply compared with distributions of climatic variables such as temperature, cloud cover and precipitation.

The formulation of the emergence distributions from both ponds (i.e. the daily location and collection of adults and exuviae) has been described in section 3.2.2. Accurate daily recordings of climatic conditions were obtained from weather records taken directly at Risley Moss Nature Reserve by the Pollution Control Services section of Warrington Borough Council. The daily recordings used for comparison were minimum, maximum and average temperature, average atmospheric pressure, precipitation and average wind speed.

In addition to these quantitative measurements, a qualitative estimate of the general weather conditions was made each day. This was based mainly on the degree of cloud cover, amount of sunshine and amount of rain throughout the day. Each day was assigned a score on a scale of 1 to 5. A score of 5 corresponded to a hot, sunny day with little or no cloud or wind, while a score of 1 corresponded to a cold, cloudy day with heavy or persistent rain.

4.2.2   Estimation of mortality at emergence : an introduction.

In order for the estimate of daily mortality to be reliable it was necessary to ensure that, as far as possible, all emerging adults were noted and followed through the day until they either flew from the ponds, were predated, or died as a result of unfavourable weather conditions. For such estimates to be highly accurate a study would have to be confined to a small area of one pond. That area would then have to be observed intensively, possibly over several days if adverse climatic conditions prevented flight of emerging adults. Clearly, such a focus of effort would yield few, albeit accurate results.

It follows that a compromise exists between obtaining a suitable amount of data for analysis and the corresponding accuracy of the derived mortality estimates.

Three separate sides of the two ponds were chosen for the study. These were side D of pond A, and sides C and D of pond B (see Figs. 3.2 and 3.3). These particular stretches were deliberately chosen because they represented different types and arrangements of emergent vegetation within the two ponds. Choosing a variety of microhabitats was important because of the possible occurrence of predators specific to certain areas or vegetation types. Also, the effect of climatic conditions such as wind and rain might vary according to the degree of protection offered by the vegetation.

On particularly hot days adults can often fly within an hour of emergence. On such days, working on a large area would likely give rise to inaccurate mortality estimates because large numbers of exuviae would be found without adults nearby. While many of these adults will have flown successfully from the ponds, an unknown number may have been predated. Working on a smaller area would permit more frequent checks of all emerging individuals. Thus, on fine days only one of the three sides was worked. On more overcast, cooler or rainy days, studies were made on two or sometimes all of the three sides.

The daily emergence was effectively completed by about 4.00pm. Any adults that had emerged would have either flown, have been accounted for in the mortality

estimates, or still have been at the pond. Individuals from the ____ category were almost always those that emerged on wet or cold days and they often remained at the same point overnight. The position of any remaining adults was marked at the ponds using white plastic labels so they could be checked again the following morning.

Before leaving the ponds, the sides that would be covered the next day were carefully searched and any exuviae found were removed and destroyed. This prevented any confusion arising over situations such as those when exuviae were found without adults on wet mornings. If exuviae had not been cleared from the study area these could represent individuals that successfully emerged the day before, perhaps in fine conditions. Alternatively they could belong to individuals that emerged that morning and, since they could not have flown in the rain, must have been predated.

On hot days it was necessary to arrive early at the ponds. An immediate and thorough search of the particular study area was made and the position of all emerging adults was recorded in a note book as well as on the ground using plastic labels. The study area was checked continuously through the day and the fate of the emerged adults was recorded . The positions of any additional adults emerging throughout the day were continuously added to the checklist.

The accompanying exuviae to these adults were destroyed when it was certain that their removal would not disturb any individual. Such removal prevented dual recordings being made.

As described in the previous chapter, extensive studies were carried out on the emergence of *P. nymphula* in the 1986 field season. During this time, such features as expansion of the body and development of colour were observed at all stages of emergence, from ecdysis to the point where flight was possible. Adults were also observed emerging in all types of weather conditions. Information gained at that time allowed an accurate estimate to be made, in this study, of the time necessary before an emerging adult could potentially fly. Subsequently, depending largely upon the weather conditions, more frequent checks could be made of those individuals that were

estimated to be close to flying.

The reduction in accuracy of the mortality estimates, resulting from concentration on a larger study area, relates mainly to individuals not always being seen successfully flying from the ponds, or being predated by, for instance, a bird. Under these circumstances it is inferred that such events are occurring on the basis of other evidence. It follows that there must be confidence in the validity of this evidence if the results of the study are to be of any value. Previous information gained on all aspects of the emergence of individuals in different climatic conditions was fundamental to this study of mortality at emergence.

For example, a newly emerged individual could be estimated to be a long way off flying, on the basis of colour or expansion of the body and wings. If, in the next check a few minutes later, it was found to have disappeared, then it would be assumed to have been predated. Other evidence may permit a more accurate inference to be made, for instance, the presence of fresh bird droppings at that point. Alternatively, if a missing adult was previously estimated to be close to flying, and the weather was fine, then it would be assumed to have successfully flown from the pond.

It is apparent that there is a rather ambiguous area where climatic conditions were neither poor nor fine. Under these conditions, presumptions about the fate of unobserved adults were difficult to make, although comparison of focal individuals with the general population often proved helpful.

Thus, where inferences were made they were usually derived on the basis of substantial evidence. However, occasionally assumptions could only be made exclusively on the basis of prevailing climatic conditions. Under these circumstances computations between the resulting mortality estimates and climatic variables would clearly be subject to a degree of bias. This is an unavoidable, although hopefully rare, source of error.

4.2.3   Estimation of percentage mortality at emergence
         due to climatic effects.

This form of mortality was usually confined to days when there was heavy rain or high winds, or it was unseasonably cold. However, even on warm, sunny days damage resulting from the wind was possible.

Mortality due to climatic conditions was split into two categories :- direct and indirect mortality. Direct mortality resulted in an individual's immediate death, for instance by being drenched in heavy rain or being blown into the water. Indirect mortality resulted in damage to an individual which prevented flight, but did not necessarily directly cause its death. A common example would be crumpled wings or a badly twisted abdomen as a result of a sudden shower or high winds (both ponds being situated in an open, exposed area of mossland).

Individuals that suffered directly from adverse climatic conditions were recorded and their bodies were removed from the study area. Those that suffered indirectly were recorded but not disturbed. Some individuals, being unable to fly, remained in approximately the same location for a number of days. Presumably they were either predated or eventually died.

The number of individuals suffering mortality as a result of climatic effects was expressed as a percentage of the total daily emergence.

4.2.4   Estimation of percentage mortality at emergence
         due to predators.

Mortality due to predators could also theoretically be caused directly or indirectly. In some instances, wounded adults were found which had almost certainly been attacked by predators. However, in most cases, attacks by ants, spiders and other common predators resulted directly in death. Therefore, no category was assigned for indirect mortality due to predators.

Mortality was split into four categories on the basis of predator type. Predation by birds was the first category. Reed buntings (*Emberiza schoeniclus*) were almost the only avian predators, although a greenfinch (*Carduelis chloris* (L.)) was occasionally seen at the ponds. Such predators could account for large losses of emerging adults as a result of their systematic searching of the emergent vegetation around the periphery of both ponds.

Mortality due to predation by ants was the second category. These occurred particularly amongst the purple moor grass and also in the clumps of reeds. Where such predation occurred, one or more ants would often be seen dragging the body away, this sometimes being chewed in two to enable easier transportation. Occasionally, this form of mortality was assumed to have occurred on the basis of characteristic 'chewed-off' parts of a body being found close to an exuvium .

The third category was mortality due to predation by spiders; in particular, *Pirata piraticus* (Clerck) and *Tibellus oblongus* (Walckenaer), and to a lesser extent other *Pirata* species. These species occurred in almost all types of emergent vegetation at both ponds. Accurate records of mortality due to spiders were possible owing to the time taken for the predator to kill, sometimes partially digest, and drag off its prey.

A final category of mortality included all those individuals assumed to have been attacked by an unknown predator. Cleary a category was required for those individuals that disappeared with there being no reliable evidence to indicate one of the above three predator types. Also included in this category was predation by the common newt (*Triturus vulgaris* (L.)) and common frog (*Rana temporia* L.). Although there was no means of recording actual numbers of damselflies taken by these predators, it was likely that they were accounting for some mortality.

The number of mortalities in each of the four categories was expressed as a percentage of the total daily emergence.

4.2.5   **Assumptions made about individuals remaining**

                  at the ponds overnight.

Individuals that successfully emerged on cold or wet days very often remained overnight at the ponds, and sometimes remained for several days and nights if there was continuous bad weather. Being unable to fly under such conditions, they usually managed to shelter from the worst effects of the wind and rain. As soon as conditions improved and the adults dried out they would fly from the ponds to complete maturation.

It follows that inferences would often be made about the fate of such individuals because of it being impracticable to continue checking the study area late in the evening or very early in the morning.

If conditions were unsuitable for flight, and individuals that remained overnight were not found the next morning, it would be inferred that predators had taken them. However, if weather conditions had improved the next morning then successful flight would be a strong possibility. Having already emerged, individuals under these conditions would require little time before they could fly.

Estimates of mortality and survivorship of individuals remaining overnight are likely to be less accurate than others because of the greater number of assumptions made. In particular, inferences had to be made about climatic conditions and the likelihood of flight during the period of absence from the ponds.

For this reason, estimates of mortality were sometimes not only calculated as a percentage of the total daily emergence, but also as a percentage of the number of individuals not remaining at the ponds overnight. This enabled those estimates which were considered more speculative to be ignored in the results. However, it was realized that this new percentage could also bias the results. For instance, on days when climatic conditions were adverse and flight was not possible, all those individuals not eaten, killed or damaged, would be forced to remain at the ponds overnight. Therefore, the mortality, expressed as a percentage of those individuals not

remaining overnight, would be 100%.

It follows that, under these conditions, mortality estimates of 100% will often correspond to, and possibly correlate with, poor weather conditions. Since a proportion of the day-group may survive by sheltering, these results may not be truly representative. Thus, there are advantages and disadvantages to applying this different mortality estimate, and its use was therefore limited in the results.

4.3   Results.

4.3.1   Comparison of the 1986 emergence with climatic conditions.

Figure 4.1 shows the 1986 emergence distribution of individuals from pond A and corresponding distributions of climatic variables. As mentioned in the previous chapter, there are large fluctuations in the daily numbers emerging. The distribution also appears bimodal.

There is a peak in the values of all three climatic variables around day 25 to day 29 which corresponds to one in emergence. There is a large amount of variation in atmospheric pressure over the entire period. Fluctuations in numbers emerging appear to follow quite closely these peaks and troughs, with the exception of the large number of individuals emerging on day 18. Similarly, there is a large amount of variation in the daily qualitative weather score and average temperature.

Table 4.1 presents the results of Pearson correlations between the total daily emergence and various climatic variables. The distributions have been compared only over the period, day 12 to day 29 (30th May to 16th June) inclusive. This period covers the main emergence, ignoring days at the very beginning and end of emergence when low numbers of adults emerged.

There is a significant correlation between the total daily emergence at pond A and the maximum and average daily temperature, and average atmospheric pressure. There

Fig. 4.1   Comparison of the emergence distribution at

pond A with corresponding distributions of

climatic variables.
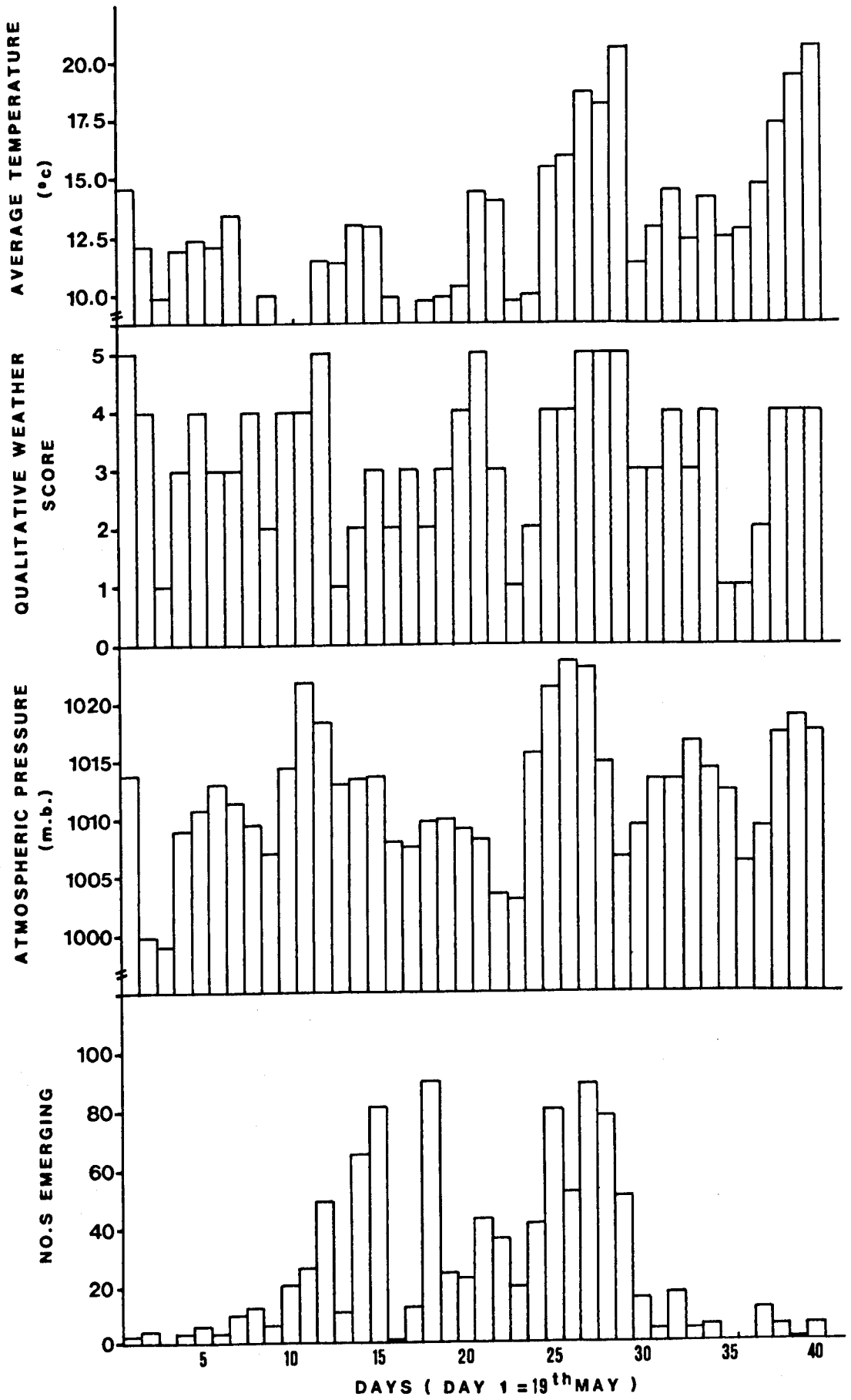
Correlation of daily emergence with :-	r	n	P
Average temperature	0.702	17	P< 0.01
Maximum temperature	0.663	17	P< 0.01
Minimum temperature	0.449	18	N.S.
Qualitative weather score	0.410	18	N.S.
Average atmospheric pressure	0.547	18	P< 0.05
Precipitation	− 0.095	18	N.S.
Wind speed	− 0.486	15	N.S.

Table 4.1 Pearson correlations of daily numbers emerging from pond A with various climatic variables over the period 30th May - 16th June inclusive.

is a negative, although just not significant, correlation between numbers emerging and average wind speed.

Figure 4.2 presents the 1986 emergence distribution from pond B. An initial peak in numbers occurs early on between day 6 and day 8. Referring to the other distributions, there is a similar increase, particularly in temperature and qualitative weather score, over the same period. There is a similar peak in numbers emerging around day 11, and also around days 17 and 18. In the latter case there is a well pronounced peak in atmospheric pressure and a high qualitative weather score.

Table 4.2 shows the results of correlations between daily emergence at pond B and the same climatic variables. As before, the distributions have been compared only over an 18 day period, from day 4 to day 21 (16th May to 2nd June) inclusive. There is a significant correlation between the total daily emergence at pond B and the daily qualitative weather score and average atmospheric pressure, although there was no correlation with temperature.

4.3.2   Relationships between overall mortality and
daily climatic conditions.

Data on mortality during emergence is presented from studies on a total of 20 days during 1987 and 1988. Because two pond sides were often studied on any one day, the total number of mortality estimates generated was 34. Of these, 16 were collected from side D of pond A, 8 were collected from side C of pond B, and 10 from side D of pond B.

It was decided not to attempt to analyse the results separately for each of the three sides. In practice, it was difficult to ensure that all sides were covered on an equal proportion of sunny, rainy or windy days. This, together with the low and unequal sample sizes, would make it hard to detect any potential differences between estimates taken from different pond sides. Combining the results not only produced a sample size large enough for analysis, but it also ensured that estimates had been obtained

Fig. 4.2 Comparison of the emergence distribution at pond B with corresponding distributions of climatic variables.
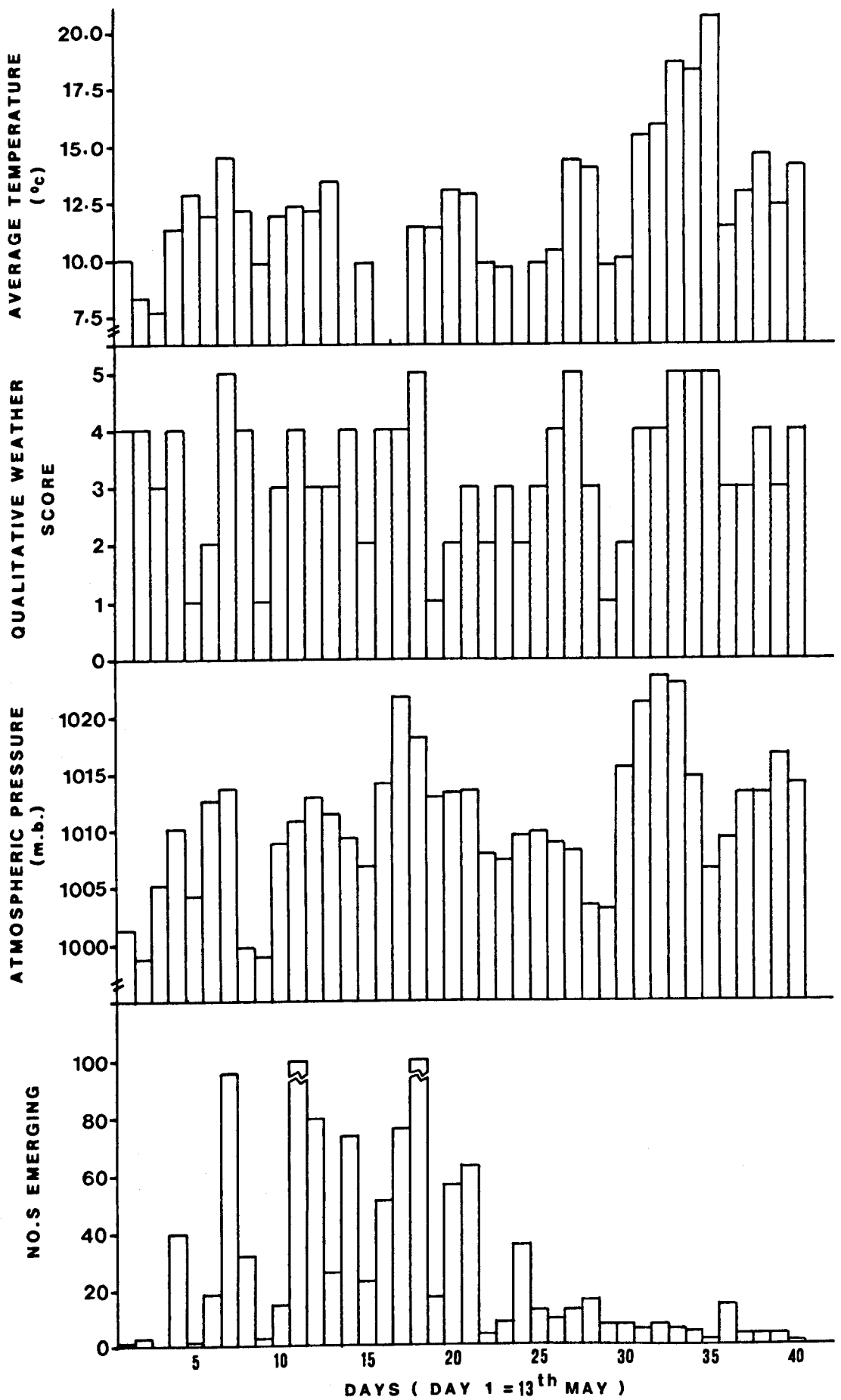
Correlation of daily emergence with :-	r	n	P
Average temperature	0.325	15	N.S.
Maximum temperature	0.463	15	N.S.
Minimum temperature	0.222	17	N.S.
Qualitative weather score	0.747	18	P< 0.001
Average atmospheric pressure	0.564	18	P< 0.05
Precipitation	0.287	18	N.S.
Wind speed	- 0.412	18	N.S.

Table 4.2 Pearson correlations of daily numbers emerging
from pond B with various climatic variables over
the period 16th May - 2nd June inclusive.

*

Percentage mortalities in Table 4.3 are derived by calculating the mean of the 34 separate mortality estimates and thus are subject to a degree of bias from high value estimates that were obtained on occasions where number of individuals emerging were low. Values in parentheses refer to mean percentage mortalities derived from the total number of affected individuals expressed as a percentage of the toal number of individuals emerging over the study.

from the wide variety of microhabitats and vegetation types that existed at both ponds.

The mean percentage overall mortality, calculated from the 34 separate mortality estimates, was 38.38% (SE 5.38). This is a higher value than was originally expected, although the weather, particularly throughout the 1987 part of the study, was generally very poor and atypical of previous summers.

Table 4.3 shows the values of mean percentage mortality attributed to all the various factors acting at the ponds. Of the overall value of 38.38% mortality, 30.35% is attributed to predators and 8.03% to climatic effects. There is a higher percentage mortality attributed to the direct effects of adverse weather than to indirect effects. Second to unknown predators, birds account for the highest mortality of newly emerged adults. ✳

Figures 4.3a,b show the distribution of overall percentage mortality and corresponding distributions of four climatic variables. For simplicity, throughout the results, the horizontal axis is labelled 'estimate number'. It follows from the above that there can be more than one estimate per day, and numbers 1-25 correspond to days between 13th May-10th June 1987, while numbers 26-34 correspond to days between 15th-27th May 1988. All estimates are in chronological order.

Mortality in Figs. 4.3a,b is calculated as a percentage of the total daily emergence. Sampling occasions where fewer than five individuals emerged are not included in any of the analysis. This prevented situations occurring where a large value of percentage mortality was derived from only one or two actual mortalities.

Comparing the distributions in Fig. 4.3a by sight, it appears that where there are periods of higher atmospheric pressure (e.g. corresponding to estimates 1-4, 11-12 and 26-29), there are periods of low percentage mortality. Conversely, over the range of estimates 15-23, when percentage mortality is high, average atmospheric pressure is low.

Likewise, comparing the distributions in Fig. 4.3b, where there are high levels of precipitation, there are corresponding high values of percentage mortality. However, with respect to average wind speed, few similarities can be detected.

Mortality	Mean	SE	
	(percentage)		
Overall	38.38	5.38	(27.93) *
Due to climate	8.03	1.91	(6.17)
Direct	4.96	1.88	(2.93)
Indirect	3.07	0.84	(3.24)
Due to predators	30.35	5.10	(21.76)
Bird	8.63	3.12	(7.41)
Ant	3.05	1.20	(2.31)
Spider	2.19	0.85	(1.70)
Unknown	16.49	3.56	(10.34)

Table 4.3 Mean and standard error % mortality, attributed
to various factors, calculated from 34 mortality
estimates. (Mortality expressed as a % of total daily
emergence.)

* Values in parentheses refer to mean percentage mortalities derived
from the total number of affected individuals expressed as a
percentage of the total number of individuals emerging over the
study.
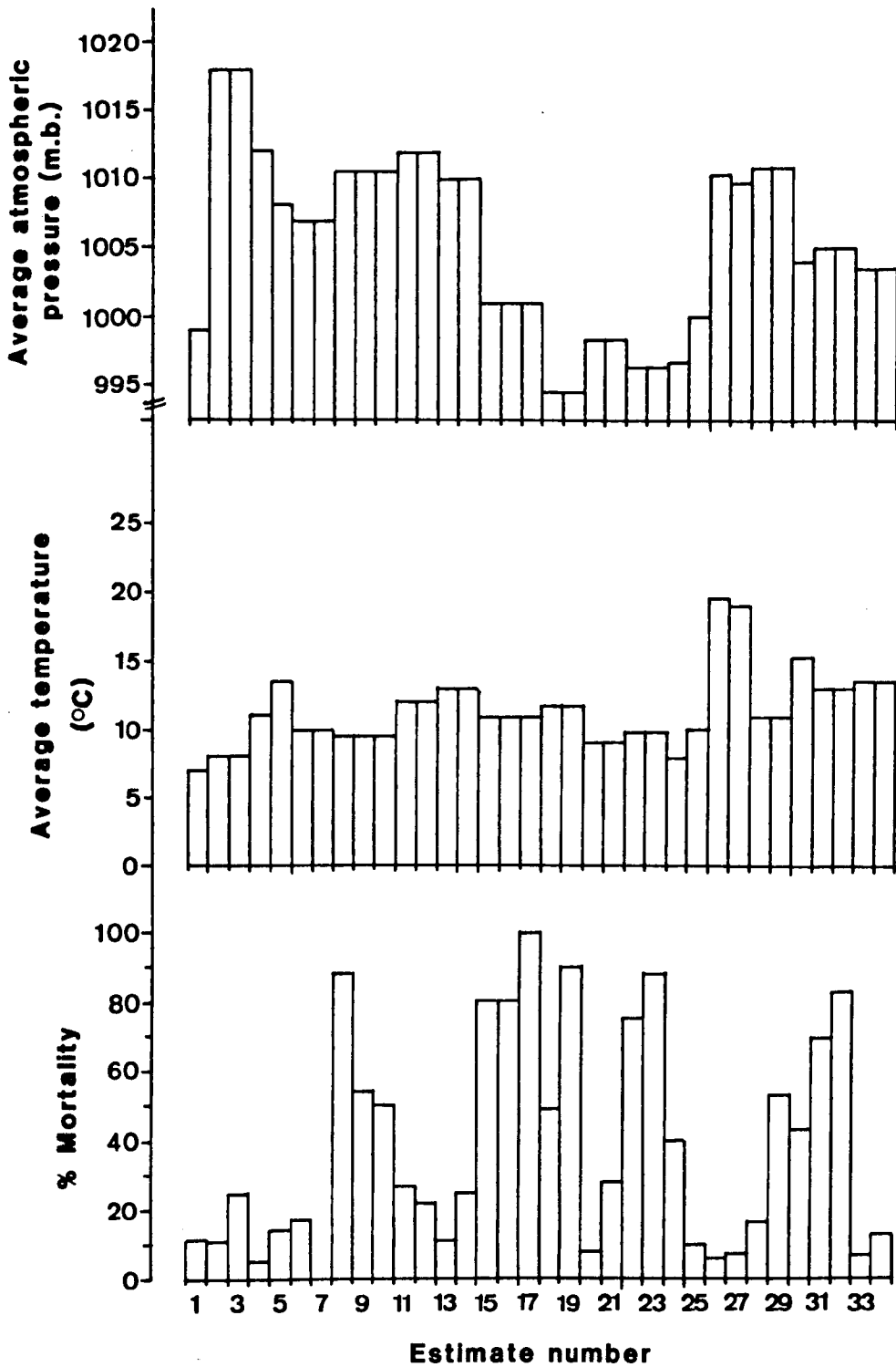
Fig. 4.3a   Distribution of overall % mortality (number of
mortalities expressed as a % of total daily
emergence) and corresponding distributions of
climatic variables.
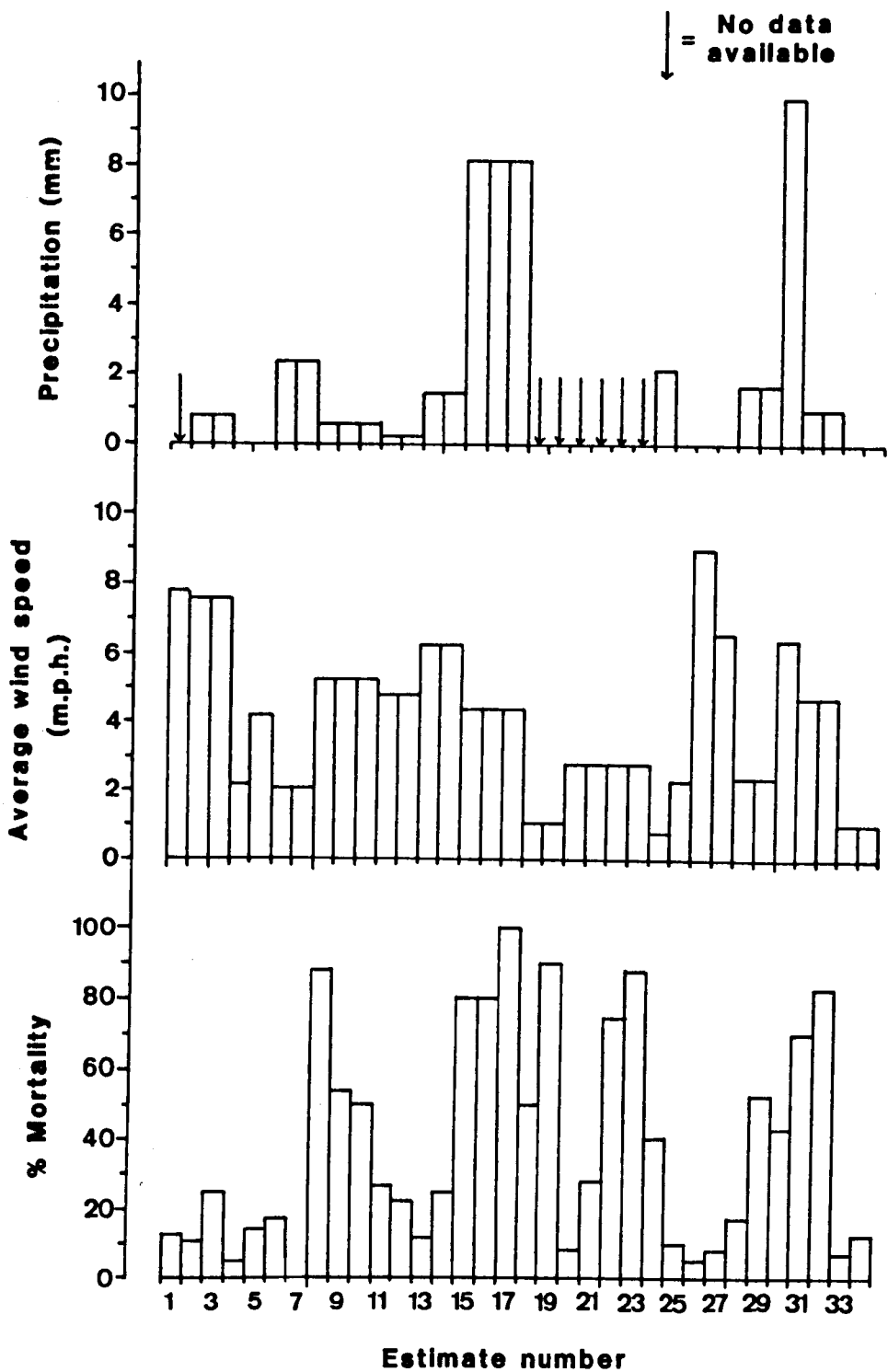
Fig. 4.3b   Distribution of overall % mortality (number of

mortalities expressed as a % of total daily

emergence) and corresponding distributions of

climatic variables.

Despite apparent similarities between the distributions of percentage overall mortality and those of climatic effects in Figs. 4.3a,b, percentage mortality is only significantly (positively) correlated with precipitation (Table 4.4a). The higher the level of rainfall, the greater the mortality of newly emerged adults. As expected, the coefficients are negative for the correlations with average temperature and atmospheric pressure, but they are not significant. (Because of incomplete data, the sample size for all correlations with precipitation is 27, rather than 34.)

In Table 4.4b, mortality is expressed as a percentage of the number of adults not remaining overnight at the ponds, rather than as a percentage of the total daily emergence. As mentioned earlier, there are reasons to be cautious about expressing mortality in this way, just as there are about inferences made concerning the fate of individuals remaining overnight. When such individuals are ignored the only difference to the above results is that percentage mortality becomes negatively correlated with average atmospheric pressure.

The mean value of each of the four climatic variables was calculated over the entire study period (ie. n= 34). The mortality estimates could then be divided into two groups on the basis of whether they were obtained on occasions when the values of the recorded climatic variables were less than, or greater than, the calculated study mean. For each group of estimates, the mean and median percentage mortalities could then be determined and compared.

Such results are presented in Table 4.5. Mean and median percentage mortalities are considerably higher on days when either average wind speed or precipitation is greater than the study mean, compared to occasions when it is less than the study mean. Similarly, mean and median percentage mortalities are lower on days when either average temperature or average atmospheric pressure is greater than the study mean, compared to days when it is less than the mean. Analysis of these results was carried out using Mann-Whitney U-tests. No significant differences were detected between the two groups of estimates in any of the four cases, this probably being due to the large spread of the data.

a)

	% Mortality	
	r	P
Average temperature	−0.159	N.S.
Average atmospheric pressure	−0.301	N.S.
Precipitation	0.515	P< 0.01
Average wind speed	0.003	N.S.

b)

	% Mortality	
	r	P
Average temperature	− 0.207	N.S.
Average atmospheric pressure	− 0.469	P< 0.01
Precipitation	0.595	P< 0.01
Average wind speed	− 0.106	N.S.

Table 4.4   Results of Spearman correlations between the estimate of overall % mortality and various climatic variables. Number of mortalities expressed as **a)** a % of total daily emergence and **b)** a % of number of adults not remaining at ponds overnight.

Average temperature			
Estimates less than mean	Estimates greater than mean		
n =20	n =14		
mean= 41.43	mean= 33.31		
SE= 7.47	SE=7.79		
median= 32.50	median= 23.45		

Average wind speed			
Estimates less than mean	Estimates greater than mean		
n =15	n =19		
mean= 32.43	mean= 42.54		
SE= 8.05	SE= 7.32		
median= 16.70	median= 27.30		

Average atmospheric pressure			
Estimates less than mean	Estimates greater than mean		
n =17	n =17		
mean= 50.79	mean= 25.34		
SE= 8.31	SE=5.61		
median= 48.30	median= 16.70		

Precipitation			
Estimates less than mean	Estimates greater than mean		
n = 20	n = 7		
mean= 29.85	mean= 51.37		
SE= 5.96	SE= 13.84		
median= 19.30	median= 42.90		

Table 4.5 Mean, standard error, and median % overall mortality derived from estimates where corresponding values of average temperature, wind speed, atmospheric pressure and precipitation were either less than, or greater than, the calculated mean value over the entire study.
(Mortality calculated as a % of total daily emergence.)

When daily percentage overall mortality is plotted against the number of individuals emerging then a significant, negative relationship is obtained (Spearman's r= -0.547, P<0.001). Thus, the greater the number of individuals emerging, the lower the percentage mortality.

4.3.3   Relationships between mortality attributed to climate and predators, and climatic effects.

Figure 4.4 shows how the overall mortality estimates break down into percentages attributed to the two categories of mortality due to climatic effects, and to those attributed to the four categories of predator mortality. Mortality is expressed as a percentage of the total daily emergence.

There appear to be few similarities detectable by sight when these results are compared with the distributions of climatic variables previously shown in Figs. 4.3a,b. It would be expected that there would be higher levels of direct mortality due to climatic effects on occasions when precipitation was heavy. This is found in estimate 15 but not elsewhere. The high values of mortality attributed to birds, found in estimates 19 and 23, may be related to heavy rain at this time. Unfortunately, no quantitative recordings of precipitation were available over this period.

The appearance of birds around the ponds may well be unrelated to patterns of climatic conditions. However, the degree of mortality they inflict could depend strongly on the weather at that time. On fine days, adults which emerge are able to fly after a short time such that a build-up of individuals around the ponds is avoided. However, on wet days, a concentration of adults which are unable to fly may occur. Consequently, a bird searching the emergent vegetation on such days might account for a much higher adult mortality. This is also applicable to other predators because the length of time that an emerged adult is exposed to a mortality risk will be greatly increased on wet days.

Apart from two occasions in the 1987 mortality estimates, predation by spiders
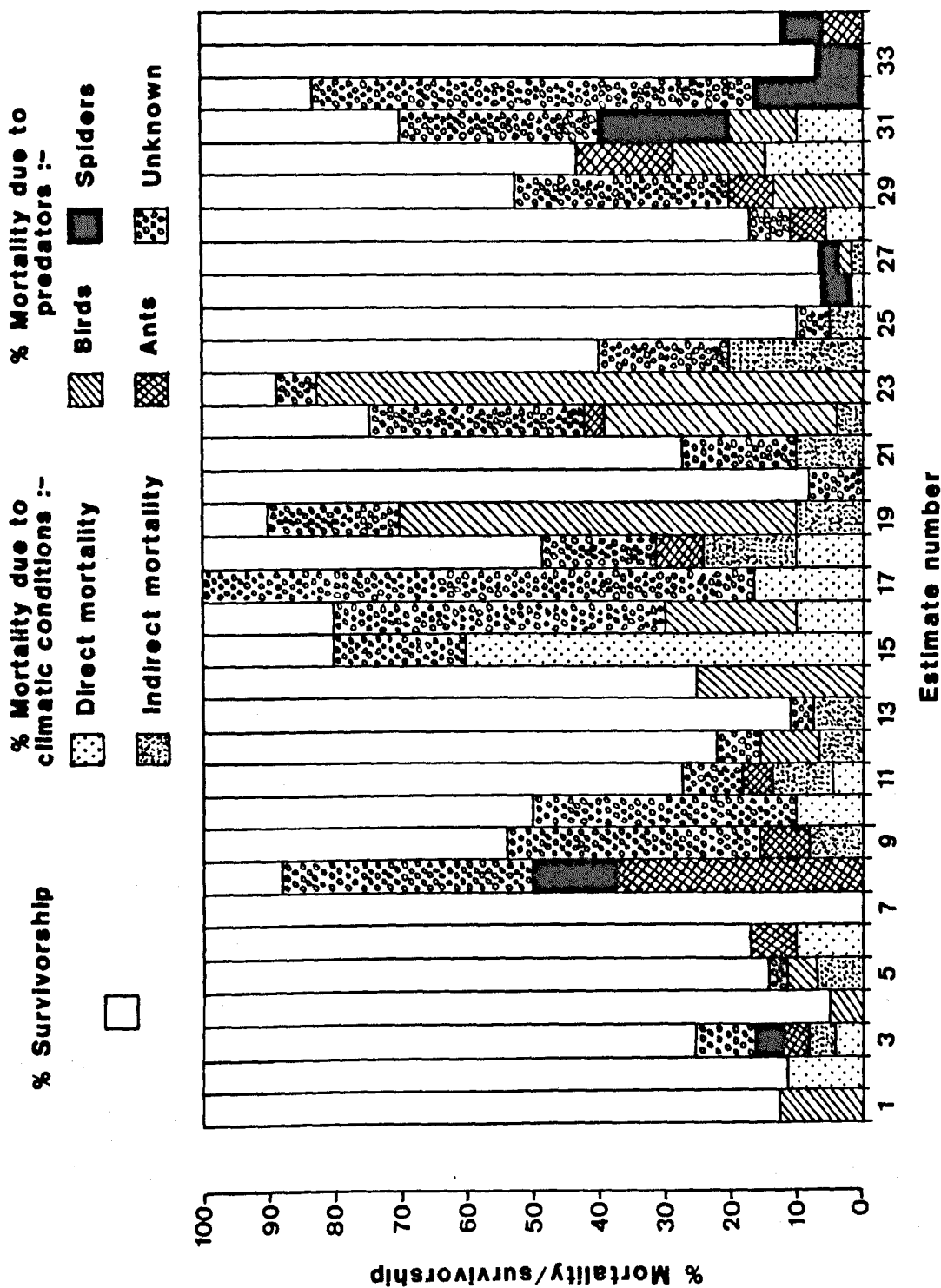
Fig. 4.4   Distribution of % survivorship and % mortality
attributed to climate and predators (estimates
expressed as a % of total daily emergence).

appears to be confined to the 1988 sample, occurring in estimates 26-34. The two common species of spider have a seasonal occurrence from spring to early summer. However, this cannot account for the differences because estimates from both years were taken over the same period in May and June. Average daily temperature appears slightly higher throughout the 1988 estimates, although these predators were commonly seen active under a wide variety of weather conditions, except heavy rain.

Table 4.6a presents results of correlations of mortality due to climate and predators with the four climatic variables. Mortality is again calculated as a percentage of the total daily emergence. With respect to percentage mortality due to climatic conditions, this is significantly positively correlated with precipitation, but with no other variable. There are no significant correlations between mortality due to predators and any of the climatic variables. However, there is a relatively high negative coefficient from the correlation with atmospheric pressure, and a high positive coefficient from that with precipitation, both of which are close to significance (P=0.059 and P= 0.054 respectively).

Figure 4.5 and Table 4.6b present data in exactly the same format as in Fig. 4.4 and Table 4.6a. However, mortality is expressed as a percentage of the number of individuals not remaining overnight at the ponds, instead of as a percentage of daily emergence. When those adults remaining overnight are ignored, 100% mortality is recorded in 11 out of the 34 estimates (see Fig. 4.5). For this reason, a degree of caution is required since this may weight the correlations towards significance.

From Table 4.6b, mortality due to climatic conditions is still significantly correlated with only one variable, precipitation. However, mortality due to predators is significantly negatively correlated with average atmospheric pressure and significantly positively correlated with precipitation.

In Table 4.7, the mortality estimates (calculated as a percentage of total daily emergence) have been divided into two groups, as they were in Table 4.5, on the basis of whether they were obtained on days when the recorded weather variables were less than, or greater than, the study means. The results in Table 4.7 refer only to mortality

	% Mortality due to climatic conditions		% Mortality due to predators	
	r	P	r	P
Average temperature	− 0.086	N.S.	− 0.115	N.S.
Average atmospheric pressure	−0.115	N.S.	−0.327	N.S.
Precipitation	0.480	P< 0.05	0.374	N.S.
Average wind speed	0.037	N.S.	− 0.010	N.S.

Table 4.6a   Results of Spearman correlations between estimates of % mortality and various climatic variables. Mortality is expressed as a % of total daily emergence.
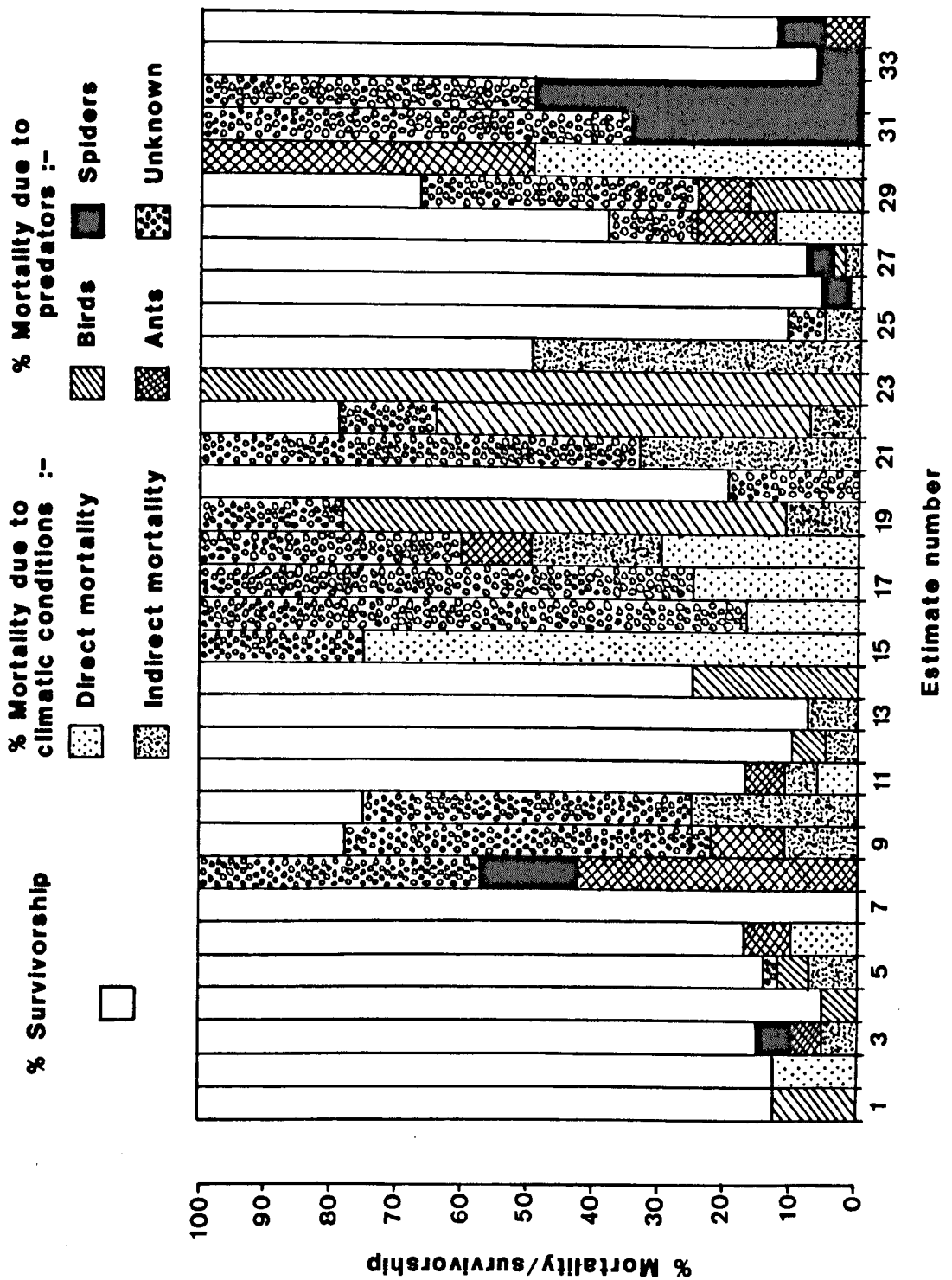
Fig. 4.5   Distribution of % survivorship and % mortality
            attributed to climate and predators (estimates
            expressed as a % of number of adults not remaining
            at ponds overnight).

	% Mortality due to climatic conditions		% Mortality due to predators	
	r	P	r	P
Average temperature	-0.167	N.S.	-0.149	N.S.
Average atmospheric pressure	-0.167	N.S.	-0.445	P<0.01
Precipitation	0.471	P< 0.05	0.383	P<0.05
Average wind speed	-0.013	N.S.	-0.125	N.S.

Table 4.6b   Results of Spearman correlations between estimates of % mortality and various climatic variables. Mortality is expressed as a % of number of emerging adults not remaining at ponds overnight.

Average temperature

Estimates less than mean	Estimates greater than mean
n =20	n =14
mean= 8.83	mean= 6.87
SE= 2.99	SE=1.90
median= 6.65	median= 6.65

Average wind speed

Estimates less than mean	Estimates greater than mean
n =15	n =19
mean= 5.80	mean= 9.78
SE= 1.98	SE= 3.03
median= 3.20	median= 7.70

Average atmospheric pressure

Estimates less than mean	Estimates greater than mean
n =17	n =17
mean= 10.73	mean= 5.32
SE= 3.60	SE= 1.11
median= 9.10	median= 6.30

Precipitation

Estimates less than mean	Estimates greater than mean
n = 20	n = 7
mean= 4.22	mean= 18.71
SE= 0.97	SE= 7.29
median= 3.45	median= 14.30

Table 4.7 Mean, standard error, and median % mortality due to climate derived from estimates where corresponding values of average temperature, wind speed, atmospheric pressure and precipitation were either less than, or greater than, the calculated mean value over the entire study.
(Mortality calculated as a % of total daily emergence)

due to climatic conditions. As before, mean and median percentage mortalities are higher on days when either average wind speed or precipitation is greater than the study mean, compared to occasions when it is less than the study mean. With respect to precipitation, the difference in percentage mortality between the two groups is substantial. It is also significant when tested using a Mann-Whitney U-test (U=20.0, P=0.004). Similarly, mean percentage mortality is lower on days when either average temperature or average atmospheric pressure is greater than the study mean, compared to days when it is less than the mean.

Table 4.8 presents results in exactly the same format, except that mortality is attributed only to predators. Whilst the values of mean and median percentage mortality are higher, the end results are very similar to those in Table 4.7. Percentage mortality, calculated from days on which average atmospheric pressure was less than the overall study mean, is significantly higher than that derived from days when atmospheric pressure was greater than the study mean (Mann-Whitney U = 76.0, P=0.018).

When percentage mortality attributed to predators is plotted against the total number of individuals emerging daily then a significant, negative relationship is obtained (Spearman's r= -0.524, P< 0.001). However, there is no relationship between percentage mortality attributed to climatic conditions and the number of individuals emerging.

4.3.4   Correlations involving mortality specifically
              due to climatic conditions.

Table 4.9 presents the results of correlations between estimates of direct and indirect mortality due to climatic conditions, and various climatic variables. Direct mortality remains significantly positively correlated only with precipitation, but there are no significant correlations between indirect mortality and any of the variables. There are no differences in the results when mortality is expressed as a percentage of

Average temperature		Average wind speed	
Estimates less than mean	Estimates greater than mean	Estimates less than mean	Estimates greater than mean
n =20	n =14	n =15	n =19
mean= 33.10	mean= 26.42	mean= 27.29	mean= 32.76
SE= 7.04	SE=7.39	SE= 7.77	SE= 6.88
median= 19.10	median= 14.60	median= 12.5	median= 20.00

Average atmospheric pressure		Precipitation	
Estimates less than mean	Estimates greater than mean	Estimates less than mean	Estimates greater than mean
n =17	n =17	n = 20	n = 7
mean= 40.68	mean= 20.02	mean= 25.63	mean= 32.66
SE= 7.78	SE= 5.77	SE= 5.98	SE= 11.99
median= 24.10	median= 11.10	median= 13.05	median= 20.00

Table 4.8 Mean, standard error, and median % mortality due to predators derived from estimates where corresponding values of average temperature, wind speed, atmospheric pressure and precipitation were either less than, or greater than, the calculated mean value over the entire study. (Mortality calculated as a % of total daily emergence.)

	% Direct mortality due to climatic conditions		% Indirect mortality due to climatic conditions	
	r	P	r	P
Average temperature	0.028	N.S.	−0.073	N.S.
Average atmospheric pressure	0.102	N.S.	−0.176	N.S.
Precipitation	0.532	P< 0.01	−0.282	N.S.
Average wind speed	0.215	N.S.	−0.146	N.S.

Table 4.9   Results of Spearman correlations between estimates of % mortality due to climatic conditions and various climatic variables. Mortality is expressed as a % of total daily emergence.

numbers not remaining overnight. There is also no relationship between either direct or indirect mortality due to climatic conditions and the daily adult emergence.

4.3.5 Correlations involving mortality specifically due to predators.

Table 4.10 presents results of mortality due to birds, ants, spiders and unknown predators, expressed as a percentage of the daily emergence, with the four climatic variables. The only significant correlation is betweem mortality due to spiders and average daily temperature, and the relationship here is positive. Thus, the higher the temperature, the greater the mortality due to spiders. The negative coefficient obtained from the correlation between mortality due to spiders and precipitation is close to significance (P= 0.059). No differences are found when mortality is expressed as a percentage of numbers not remaining overnight.

The correlation between daily percentage mortality due to unknown predators and the number of individuals emerging is negative and significant (Spearman's $r = -0.489$, $P<0.01$). There is no relationship between mortality specifically due to either birds, ants or spiders and the daily adult emergence.

4.3.6 Relationships between individuals remaining at the ponds overnight and daily climatic conditions.

Figures 4.6a,b show the distributions of the percentage of emerging adults that remain at the ponds overnight. In Fig. 4.6a, numbers remaining overnight are expressed as a percentage of the total daily emergence. Table 4.11a presents correlation results between these percentages and the climatic variables. The only significant correlation is with precipitation. More rain means more individuals remain overnight.

In Fig. 4.6b, numbers remaining overnight are expressed as a percentage of the

	% Mortality due to birds		% Mortality due to ants	
	r	P	r	P
Average temperature	0.176	N.S.	−0.036	N.S.
Atmospheric pressure	-0.206	N.S.	0.196	N.S.
Precipitation	0.118	N.S.	0.138	N.S.
Average wind speed	0.086	N.S.	−0.050	N.S.

	% Mortality due to spiders		% Mortality due to unknown predators	
	r	P	r	P
Average temperature	0.370	P< 0.05	−0.257	N.S.
Atmospheric pressure	0.152	N.S.	−0.120	N.S.
Precipitation	−0.368	N.S.	0.307	N.S.
Average wind speed	0.153	N.S.	−0.047	N.S.

Table 4.10 Results of Spearman correlations between estimates of % mortality due to predators and various climatic variables. Mortality is expressed as a % of total daily emergence.
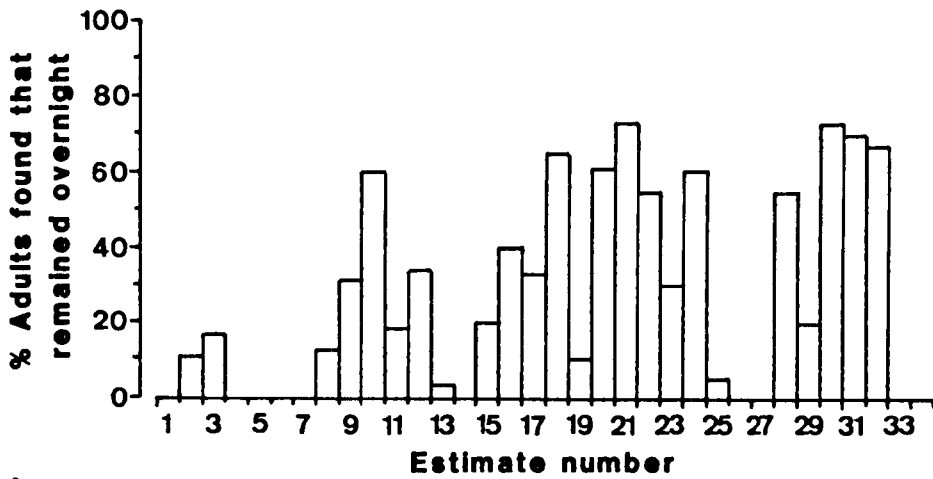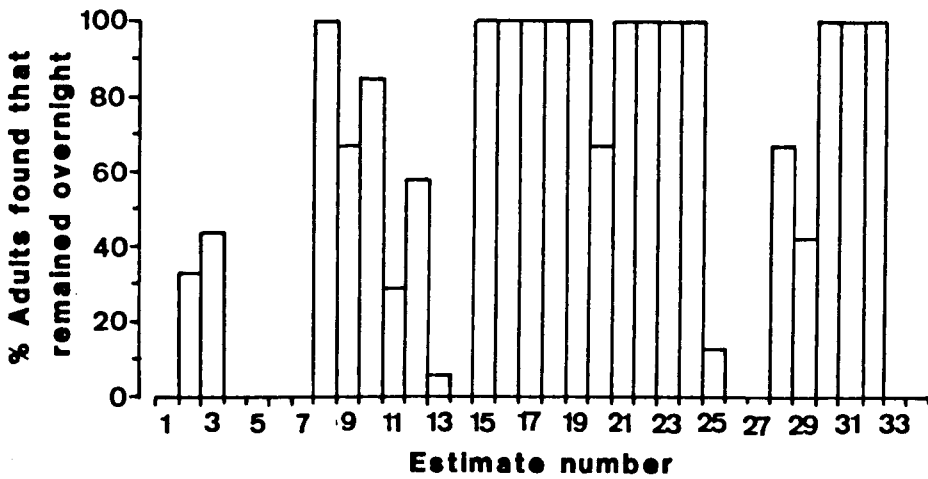
Fig. 4.6   Number of individuals remaining at the ponds overnight, expressed a) as a %/total daily emergence and b) as a %/number of individuals that could potentially fly.

a)

	% Emerging adults remaining at ponds overnight	
	r	P
Average temperature	-0.222	N.S.
Atmospheric pressure	-0.262	N.S.
Precipitation	0.493	$P < 0.01$
Average wind speed	-0.036	N.S.

b)

	% Emerging adults remaining at ponds overnight	
	r	P
Average temperature	-0.257	N.S.
Atmospheric pressure	-0.432	$P < 0.05$
Precipitation	0.554	$P < 0.01$
Average wind speed	-0.082	N.S.

Table 4.11 Results of Spearman correlations between % of adults remaining overnight and various climatic variables. Number of adults remaining overnight expressed **a)** as a % of daily emergence and **b)** as a % of number of adults that could potentially fly.

number of individuals that could potentially fly from the ponds. Thus, all those individuals that had been damaged such that they were unable to fly, or had been predated or killed, were left out of the analysis. In 13 of the estimates, 100% of adults that had successfully emerged and were able to fly remained at the ponds overnight. Table 4.11b presents correlation results between these percentages and the climatic variables. There is a significant positive correlation with precipitation and a significant negative correlation with average atmospheric pressure.

4.4   Discussion.

Corbet (1962) stated that mortality during emergence may sometimes be heavy, this being expected of a stage which is concentrated in space and time, and during which individuals are immobile and defenceless. In the main part of this study, an attempt has been made to quantify emergence mortality attributed to adverse climatic conditions and predators, and then relate this to prevailing weather conditions.

To an extent this was successful with various mortality estimates being generated and relationships being obtained between these and certain climatic variables, predominantly precipitation and atmospheric pressure. When placed in context, this study has provided some useful insights into the relative responsibility of various factors to mortality at emergence. It has also given an indication of just how high mortality can be during periods of continuous bad weather.

It is likely that the large amount of variation in numbers of individuals emerging daily from both ponds in 1986 arises mainly from weather effects. Histograms of various climatic variables show similar fluctuations over the same period and there are significant correlations between numbers emerging and daily temperature, atmospheric pressure and a qualitative weather score.

Lutz (1968), in a study of *Lestes eurinus*, found that comparisons could be made between the pattern of emergence and average daily temperature during the emergence

period. Lower emergence rates coincided with sub-normal average temperatures, and higher rates with above-normal average temperatures. It was assumed that changes in ambient temperature would quickly be manifested in changes in water temperature given the size and depth of the study pond.

The distribution of emerging adults at pond A appears almost bimodal. Harvey & Corbet (1985) found that the frequency distribution of male head widths in an emergent population of *P. nymphula* was bimodal. They concluded that some or all of the smaller adults derived from a minority of larvae that moulted into the final instar in spring, and thus emerged later in the season. In this study, frequency distributions of both head width and wet weight of males and females from both ponds showed no evidence of any bimodal shape. Generally, *P. nymphula* overwinters in the final instar (Corbet 1957a) and therefore a unimodal emergence distribution would be expected. For other species, such as *Ischnura elegans*, a bimodal emergence curve has been commonly reported (Parr 1970, 1973a). Parr (1970) suggested that a facultative diapause existed in the penultimate instar with emergence commencing in mid May. Those larvae still present as penultimate and antepenultimate instars in late May resulted in the second peak.

Corbet (1952), in a study of the emergence of *P. nymphula*, found that there were three distinct peaks in the emergence distribution. He concluded that these probably represented a dispersed single peak, since weather conditions on the days between these peaks were unfavourable, with thunderstorms and frequent heavy showers.

Therefore it is more likely that the bimodal appearance of the distribution from pond A is due to weather effects, rather than the emergence of individuals entering the final instar in spring instead of the previous autumn. The distributions of all the climatic variables shown in Fig. 4.1 have corresponding peaks in their values over the period where the 'second peak' in emergence occurred, and there is no evidence of any bimodality in the emergence distribution from pond B.

Corbet (1962) stated that mortality during emergence may be caused directly or

indirectly in three ways : by physical factors, overcrowding and by predation. He lists low temperatures and wind as the main physical factors causing mortality, and gives a review of a wide range of animals reported to be predators of dragonflies to varying degrees. Mortality due to overcrowding was not observed in this study, perhaps because of the abundant amount of emergent vegetation around both ponds. Newly emerged adults or exuviae were sometimes found very close together, but hardly ever so near that competition for emergence sites might lead to damage. This type of mortality is density-dependent and Corbet (1957b) found it could account for up to 16% of a day-group of *Anax imperator*.

To recall, estimates of overall mortality were found to range between being very high on some occasions and close to zero on others. These estimates were positively correlated with precipitation and negatively correlated with atmospheric pressure. The percentage of this mortality attributed to climatic effects was also (not surprisingly) positively correlated with precipitation.

Several studies have shown that the climate is an important factor in the survival of emerging adults. Corbet (1957b) found that low temperatures increased mortality of *A. imperator*, either by impeding or prolonging ecdysis itself, or by postponing emergence and thereby exposing more of a day-group to predation. Incomplete ecdysis and incomplete expansion of the wings, attributed to low temperatures, accounted for a high adult mortality (5-11% of the annual emergence).

In this study, there were few instances of unsuccessful ecdysis due to physical conditions. Any individuals found in such states were included in the estimate of either direct or indirect mortality due to climatic conditions. Much more often, individuals successfully emerged from their exuviae and were then damaged or killed as a result of the weather.

Tiensuu (in Corbet 1962) found that wind reduced survival of newly emerged adults by damaging their wings so as to prevent flight. On some occasions there were relatively high estimates of indirect mortality attributed to climatic conditions, and in particular, high winds. Under these circumstances, damage to the still delicate, soft

wings and body usually occurred either as a result of the wind directly, or by being blown against the vegetation. The only other studies reporting wind effects relate to the suppression of adult flight activity by high winds of *Ischnura elegans* (Parr 1973a) and *Coenagrion puella* (Waringer 1982).

Sudden showers also accounted for indirect mortality if the wings of newly emerged adults were physically damaged by the raindrops, or if they had only just emerged when it started raining. Corbet (1962) stated that the effects of rain were far less serious that those of the wind because many species chose shaded emergence sites. Newly emerged individuals, during periods of rain, would often be found taking cover under vegetation. Those with fully expanded body and wings would usually survive, even if caught in a shower out in the open. To these individuals, the adverse effects of the rain probably related more to exposing them to predation pressures for longer, rather than to physical damage. However, if ecdysis was actually occurring, or had only just finished, individuals caught in the open in the rain, being unable or less able to move to shelter, usually did not survive.

Corbet (1962) stated that predation may occur in any of three phases of emergence: during the final passage of the larva to the emergence support; at the site of emergence, after ecdysis; and during the maiden flight. In this study, mortality was only ever seen in the second of the three phases, although it is possible that frogs and newts may prey upon larvae as they crawl out of the water. Wright (in Corbet 1962) found that water spiders and water scorpions caught larvae as they left the water. Similarily, Corbet (1957c) suggested that land spiders might attack emerging *Crenigomphus renei* Fraser as they crawled to their emergence site.

Predation by birds, under certain conditions, can cause heavy mortality. There were several estimates in which this form of mortality was particularly high, and it has been suggested that this may be related to weather conditions if a build-up of individuals occurs on wet or cold days. Mass emergence of gomphid dragonflies along a river bank may attract large numbers of non-territorial birds to feed on them (Martin (in Corbet 1964)). Wolfe (1953) found that early morning mass emergence of

Uropetala carovei White attracted terns and gulls which were able to pick up large numbers of teneral adults still drying their wings. Jacobs (1955) also observed sandpipers preying on anisopterans during this phase.

However, depending on the environment, synchronisation may reduce as well as increase predation. Corbet (1957b) found that predation of *Anax imperator* by a pair of blackbirds (*Turdus merula* L.) was independent of density beyond a certain point. This was because the birds defended the pond as their territory and soon reached a capacity of predation, thus illustrating one benefit of dragonflies emerging more or less synchronously.

Kennedy (1950), in a long and comprehensive review, found that a very wide range of birds from many families were known to prey on dragonflies. Corbet (1962) stated that wagtails and chaffinches were sometimes seen taking small Coenagrionidae amongst marginal vegetation, and Ubukata (1981) included jays and wagtails as sources of mortality of emerging *Cordulia aenea amurensis* Selys.

Thompson *et al.* (1985) found a very large loss of adults of *Coenagrion puella* at emergence which was attributed to bird predation. Studying the emergence over two years, they found larval numbers prior to emergence in the second year were 93% of the first year figure. However, adult numbers successfully dispersing were 65% of the first year figure. In the first year, predation by house sparrows (*Passer domesticus* (L.)) was observed but accounted for less than 5% of emerging adults. However, in the second year the sparrows consumed about 30% of the population, this being due to the presence of two horses. The most important source of mortality caused indirectly by the horses was that, by prolonged grazing and gross thinning of the vegetation round the pond, the emergence sites became far more accessible to the sparrows. Grazing of the vegetation also meant that there were fewer sites on which larve could climb to emerge and thus some mortality may have arisen through individuals attempting emergence on poor supports.

Birds are also important predators of teneral and post-teneral adults. Parr & Parr (1972) and Parr (1973b) found that swifts (*Apus apus* (L.)) were common predators

of *Ischnura elegans*, taking the tenerals high in the air when they made their maiden flight after emergence.

Predation by the two common species of spider occurred predominantly in the second year of the study and was found to be positively related to temperature, with indications of a negative, though just not significant, relationship with precipitation. It is likely that spiders generally account for only a small, insignificant proportion of adult mortality, although such predation probably occurs in many populations. The only other record known is that of Calvert (in Corbet 1962) who found predation by spiders occurring in three species of dragonfly. Predation by ants has been reported by Ubukata (1981), where it accounted for 0.4% of emergence mortality of *Cordulia aenea amurensis*.

Given that the survival of individuals which emerge on cold, wet or windy days may be considerably reduced, why should emergence occur at all on such days ? The numbers emerging are usually quite low relative to fine days, but over the entire emergence period they could account for a significant proportion of the population.

The answer to this probably relates to the progression of metamorphosis prior to emergence. If metamorphosis has progressed to the point where ecdysis can begin, there may be little scope for postponing emergence until conditions are more favourable. While the majority of a day-group may be able to delay emergence on that day, it may be increasingly difficult if unfavourable conditions persist for several days. Alternatively, some individuals may be forced to attempt emergence if there has been a sudden overnight change in weather conditions.

Corbet (1957b) found that individuals of *Anax imperator* were very sensitive to air temperature when emerging, the cold greatly prolonging the process. This species usually emerged at night but occasionally some individuals emerged in the morning. Such a divided emergence was caused by a drop in air temperature after larvae had left the water. Those which had not already begun to moult returned to the water and emerged when temperatures rose again the following morning, although they were more vulnerable to predators at this time. Corbet suggested that emergence occurred in

the morning, rather than the following evening, because larvae had already changed over from aquatic to aerial respiration, and could therefore only spend a limited time under the water.

The consequences of emergence mortality are not well established. Clearly, the overall annual egg input into a population could be considerably decreased if the weather during the main emergence period was continuously poor. This may be more pronounced in species which have a very short duration of emergence. Periods of good and bad weather can be set against each other for those species having an emergence lasting several months.

Ubukata (1981) estimated emergence mortality of *Cordulia aenea amurensis* over several years. He inferred that populations were not regulated by density-dependent mortality at emergence. Previously described studies where birds are attracted to the synchronised emergence of anisopterans suggest that mortality can be density-dependent. Crowley *et al.* (1987b) suggested that, on available evidence, emergence mortality could be a contributing regulatory factor in some cases, but its generality is not established.

In this study there was no evidence of any density-dependent mortality. If such a process was occurring the outcome will probably have been obscured by the effects of climatic conditions. It is possible that predators such as birds may be attracted to the ponds during periods of bad weather due to the build-up of newly emerged individuals unable to fly. Under such conditions mortality may be very high. However, in fine weather, when equally high densities of tenerals may emerge through the day, the amount of mortality caused by an identical predator may be very much reduced because individuals will be able to fly shortly after emergence.

This is reflected in the relationships obtained between percentage mortality values and the total daily emergence. Instead of obtaining positive relationships between these variables, significant negative relationships were obtained. When high numbers of individuals emerge the weather is usually warm and sunny and thus they are able to fly very shortly after emergence and mortality is low. However, low numbers

emerging usually corresponds to cold, dull weather which results in individuals being prevented from flying from the ponds and therefore being more susceptible to predation and other mortality factors.

Clearly, there is evidence from this study and from previous investigations that emergence is a time of particularly high mortality. Mortality during emergence occurs as a result of aquatic and terrestrial predation, competition for emergence sites and the risk of damage from the wind, rain and other physical factors.

Chapter 5.   Aspects of the life-history of adult

Pyrrhosoma nymphula.

5.1   Introduction.

This chapter, together with the following two chapters, presents the results of studies on mature adult *Pyrrhosoma nymphula* at the two study ponds at Risley Moss Nature Reserve described previously. In Chapter 6, studies on male reproductive behaviour, mating success, and the outcome of territorial disputes will be presented. These studies were undertaken predominantly over the summer months of 1986. In Chapter 7, a study of female reproductive biology is presented, the results being collected over the summer of 1988.

This chapter is concerned with aspects of the life-history of adult *P. nymphula* which concern both males and females and do not relate directly to the studies of reproductive biology. All results were obtained over June and July 1986.

The studies uncovered many interesting features of the behaviour and ecology of *P. nymphula* adults. Although these could not often be attributed to some definite cause (usually as a result of high levels of dispersal of marked individuals away from the study area), they indicate areas which could be further investigated given a more enclosed, isolated study site.

5.2   Materials and methods.

5.2.1   Recording of activity at the study ponds.

The first mature adults were seen at the ponds on 8th June. From this date onwards until early July, an attempt was made to catch or record all individuals

visiting both ponds. To begin with the only marked individuals that visited the ponds would be those that returned after being marked at emergence. However, the proportion of these was expected to be low, relative to unmarked individuals, because there were so many other water bodies on the study site.

Recordings of individuals at the ponds differed according to whether they were marked or not. Unmarked males and females were caught using a butterfly net and were then transferred to plastic cups with gauze lids. These were kept in a cool, shaded place until transportation back to the laboratory. Males and females caught as a pair were kept that way until after measuring and marking.

Marked individuals were recorded by direct observation or sometimes through binoculars if they could not be easily identified. There was never any need to catch a marked individual, apart from when it was paired with an unmarked male or female. Under these circumstances the unmarked adult would be retained and the marked adult released at the pond in the same area where it was caught.

Each side of both ponds was divided into ten areas using wooden pegs and string. Referring to the sides as A-D (see Figs. 3.2 and 3.3), and the areas as 1-10, the location where an adult or pair was recorded or caught could be accurately noted.

In the field notebooks a number of details were taken for each individual or pair caught or recorded. Firstly, sex, status and any identification was noted. Secondly, the time of the recording was noted. For those unmarked individuals that were to be taken back to the laboratory, the time was also recorded on the plastic cup. This enabled size measurements of unmarked individuals from split pairs to be related to their marked partner that was released at the ponds. It also enabled the size of unmarked males involved in territorial disputes to be related to the known size of their marked opponents.

Finally, the area of the pond where the recording or catch was made was noted. Marked individuals that had been recorded earlier, and in one particular area, would only be re-recorded if they had moved to a different area or their status had changed (for example, from a lone patrolling male to a paired male).

There exists the possibility that the daily operational sex ratio and general male behaviour may be affected as a result of the immediate removal of unmarked individuals from the ponds. However, to be able to build up a record of the encounters (aggressive or reproductive) that an individual had with other males and females, it was clearly necessary to mark as many individuals as possible.

5.2.2 Quantification of field recordings.

All unmarked adults taken back to the laboratory in the evening were lightly anaesthetised with carbon dioxide or ether, and then measured and marked in exactly the same way as described for newly emerged adults in Section 3.2.3. Wet weight, head width and wing length were recorded and adult dry weight was calculated from the small number of individuals that were damaged on capture or during transportation. For both males and females, all weight and size measures were highly significantly correlated with each other ($P < 0.001$); head width and wet weight are used predominantly throughout the results.

Data on the cumulative number of days spent at the ponds, which ponds had been visited, daily and cumulative number of matings and the identity and size of partners, details of any territorial disputes (if male), times seen, areas of the ponds recorded in, etc. were stored on computer discs for subsequent analysis.

In many of the studies the results from ponds A and B have been combined. Under these circumstances it was considered irrelevant as to which pond was visited (for instance, when estimating survivorship of marked individuals or studying male territorial behaviour). In other investigations the results have been kept separate because of specific differences relating to the two ponds.

5.3   Results.

5.3.1   Estimation of the length of the maturation period.

A large number of individuals were marked at emergence in the hope that they would return and breed at the two ponds. In such instances it would be possible to obtain a fairly accurate estimation of the length of the immature period.

Of the 2113 individuals to emerge from both ponds, the number marked and released was 1067. The total number of mature adults visiting the ponds after being marked at emergence was 13 (1.22%). Because of the mortality likely to occur during the maturation period, and because the sample was concentrated on only a small area of the site, it is not possible to evaluate an overall population estimate from the above figures.

A rough indication of the length of the maturation period can be obtained from the 13 individuals that revisited the ponds, although the sample size is clearly very small. Also, there is no way of knowing whether any of these adults revisited the ponds as soon as they reached maturity, or whether they had been visiting other ponds on the site prior to their return. Nine males returned to the ponds to breed, the mean time between emergence and return being 11.22 days (SE 1.24). The mean time between emergence and return for the four females was 16.00 days (SE 4.02).

Tables 5.1 and 5.2 show differences (wet weight and head width respectively) between males and females measured at emergence and those captured as first-visit, mature adults. Not surprisingly, the mean wet weight of both mature males and mature females is significantly greater than that for newly emerged males and females (Table 5.1). With respect to females the difference is very great with an increase of 66.1% original mean weight (for males the increase is 14.6% original mean weight). The range in size of unmarked, mature males and females is also considerable. Male weight ranges over 24.94mg (30.90-55.84mg), and female weight ranges over 45.71mg (47.29-93.00mg). A wide range in weight would be expected for females

a)

	Mean	SE	n	t	d.f.	P
Mature males	42.10	0.16	691			
				24.77	1331.8	P< 0.001
Newly emerged males	36.74	0.15	646			

b)

	Mean	SE	n	t	d.f.	P
Mature females	66.10	0.35	486			
				65.87	766.9	P< 0.001
Newly emerged females	39.81	0.20	512			

Table 5.1   T-test analysis showing differences in mean wet weight (mg) **a)** between mature and newly emerged males and **b)** between mature and newly emerged females.

a)

	Mean	SE	n	t	d.f.	P
Mature males	4.441	0.005	682			
				16.27	1374	P< 0.001
Newly emerged males	4.340	0.004	694			

b)

	Mean	SE	n	t	d.f.	P
Mature females	4.439	0.006	480			
				11.19	976.5	P< 0.001
Newly emerged females	4.346	0.005	545			

Table 5.2 T-test analysis showing differences in mean head width (mm) **a)** between mature and newly emerged males and **b)** between mature and newly emerged females.

since some individuals will have matured more eggs than others, or they may have just laid a clutch of eggs.

Head width is a better measure of size to use since it remains fixed at emergence and does not vary with food intake, water loss or egg number as wet weight does. The mean head width of both mature males and mature females is also significantly greater than that for newly emerged males and females (Table 5.2). For newly emerged males, head width ranges from 3.95-4.68mm, while for mature males the range is from 4.11-4.84mm. The values for females are very similar. The differences between these ranges indicate that not only are the smallest newly emerged adults unrepresented in the mature adult sample, but also the largest mature adults are unrepresented in the emergence sample.

5.3.2 Recoveries of marked individuals.

The main period of reproductive activity at both ponds lasted from 8th June-3rd July 1986. After this there was a period of continuously bad weather. Following this, the ponds were revisited on ten occasions but very few adults were seen at either pond.

The total number of individuals caught at the ponds over this period was 1969 (1118 male, 851 female; $X^2_{(1)} = 36.21$, P< 0.001). Although it was not possible to catch every individual over the entire season, a very large proportion of the total population to visit the ponds will be represented in the captured sample. Of these, 174 individuals were not released back into the population as marked individuals. Some escaped after being caught in the nets, while others were either damaged during capture or transportation, or found dead or dying at the ponds (especially females that had been partially predated while ovipositing). Therefore the total number of mature individuals that were marked and released at the ponds was 1795 (1012 male, 783 female).

In attempting to build up a marked population at both ponds, all marked

individuals were carefully released low down in the vegetation, downwind of the ponds. Individuals were released around the pond they were previously caught at. However, upon release there was usually an immediate dispersal of marked adults. The mean percentage immediate dispersal for all individuals from both ponds was 72.3% (SE 5.1), with female dispersal being slightly higher than male dispersal.

Clearly, some individuals fly immediately from the ponds on release but may return the next day or several days later. Values of overall percentage dispersal were calculated to represent those mature adults that were released and then were never seen again on any day of the study. The mean percentage overall dispersal was 68.5% (SE 4.8); 64.9% (SE 4.9) males were never seen again compared to 72.6% (SE 5.1) females.

Figures 5.1a,b show the percentage overall dispersal, throughout the study period, for males and females respectively. Days without results correspond either to those where bad weather prevented adults from visiting the ponds, or to those where the number of males or number of females released was less than 10.

For both distributions, and in particular for females, the levels of dispersal appear to be lower after day 18 (25th June). Prior to this date there were several days of very bad weather (indicated as arrows in Figs. 5.1a,b), while after this the weather was warm and sunny with maximum weather scores being recorded on 6 consecutive days. Thus, dispersal may be affected by climatological factors.

Alternatively, the survivorship of mature adults may be greatly reduced by periods of bad weather. If so, adults from a particular day-group that would have been likely to revisit the ponds on later days might be killed. This would leave only those adults which remained at the ponds when first released as the sole representatives of that particular day-group. Unfortunately, there is no way of distinguishing mortality and dispersal in these circumstances, or indeed in any of the computations described above.
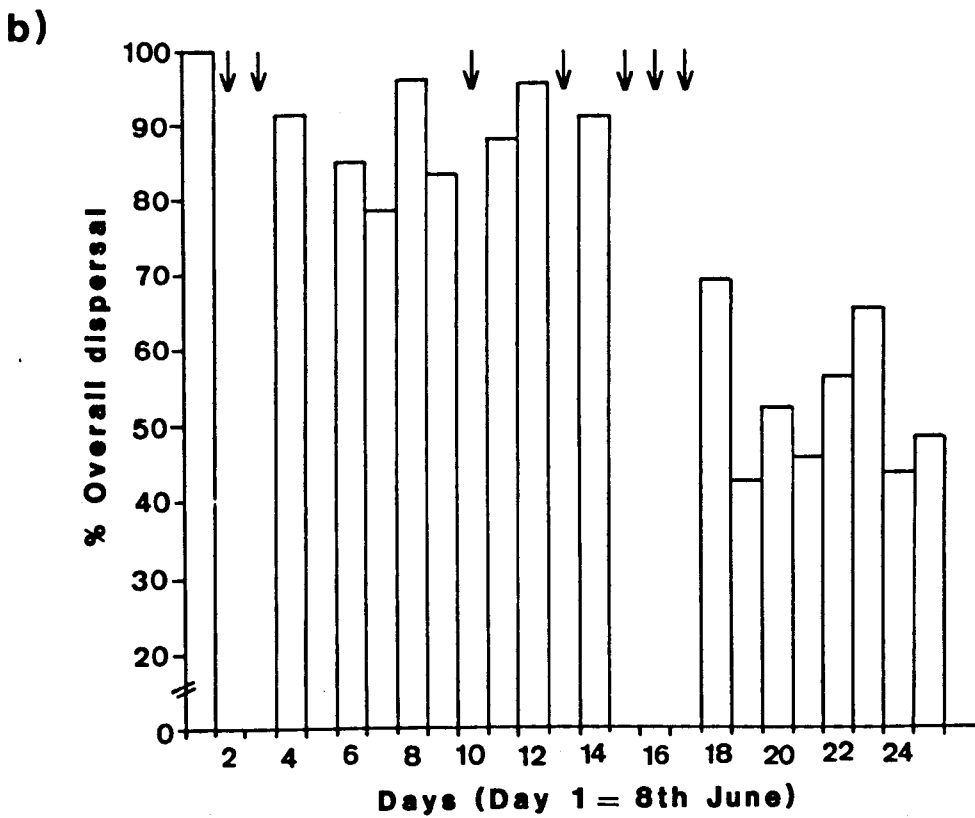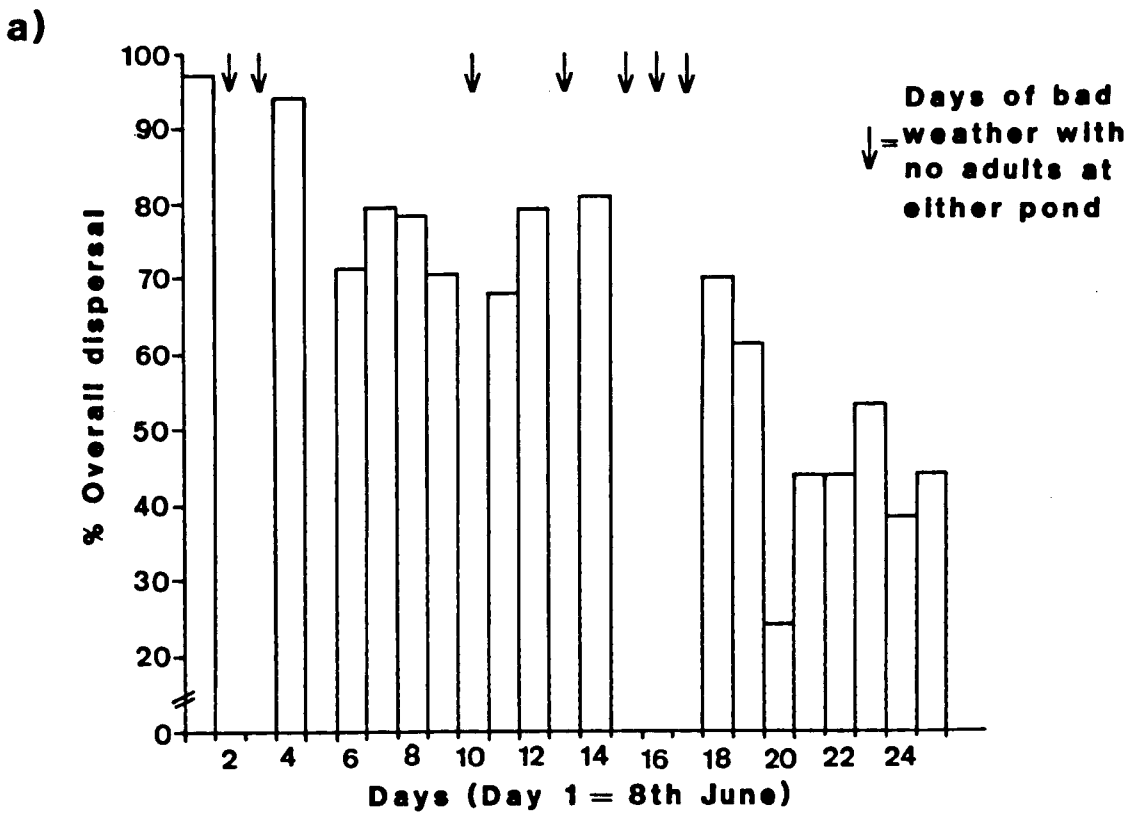
Fig. 5.1   Percentage overall dispersal of a) mature males and
b) mature females, marked and released at both ponds
over the study period.

5.3.3 Time of arrival at the ponds.

Figures 5.2a,b show the cumulative number of males and females arriving at the ponds through the day, on 27th and 28th June respectively. The results are representative of the trend found throughout the entire study period. While it would be possible to combine all the days of the study together, if this is done the distinct shape of the graphs is lost. This is because the time of arrival of adults to the ponds differed between days, probably as a result of weather conditions.

On both days, adults did not start arriving until about 10.30am. On some occasions the first adults were seen earlier than this, although even on particularly warm and sunny mornings there would be little reproductive activity before 10.00am. In Fig. 5.2a it can be seen that between 11.30am and 12.30pm the number of adults visiting the ponds increases markedly. After this time the arrival of females virtually ceases, and the arrival of males is very much reduced, although the graph still rises until about 3.00pm. In Fig. 5.2b the arrival of females is similar to before with only one or two 'new' females being recorded at the ponds after 1.00pm. However, recordings of males continue to rise until about 2.30pm, after which there were no new sightings.

5.3.4 Relationship between flight activity and weather conditions.

Figures 5.3a,b show the distribution of mature adults visiting pond A and pond B respectively, and Fig. 5.4 shows corresponding distributions of various climatic variables. Qualitative weather score was derived in the same way as described in Section 4.2.1. Not surprisingly, the two groups of distributions appear to be closely related when compared by sight. It is to be expected that climatic conditions such as rainfall, temperature and wind speed (not shown), will have a marked effect on the flight activity, and thus reproductive activity of dragonflies.
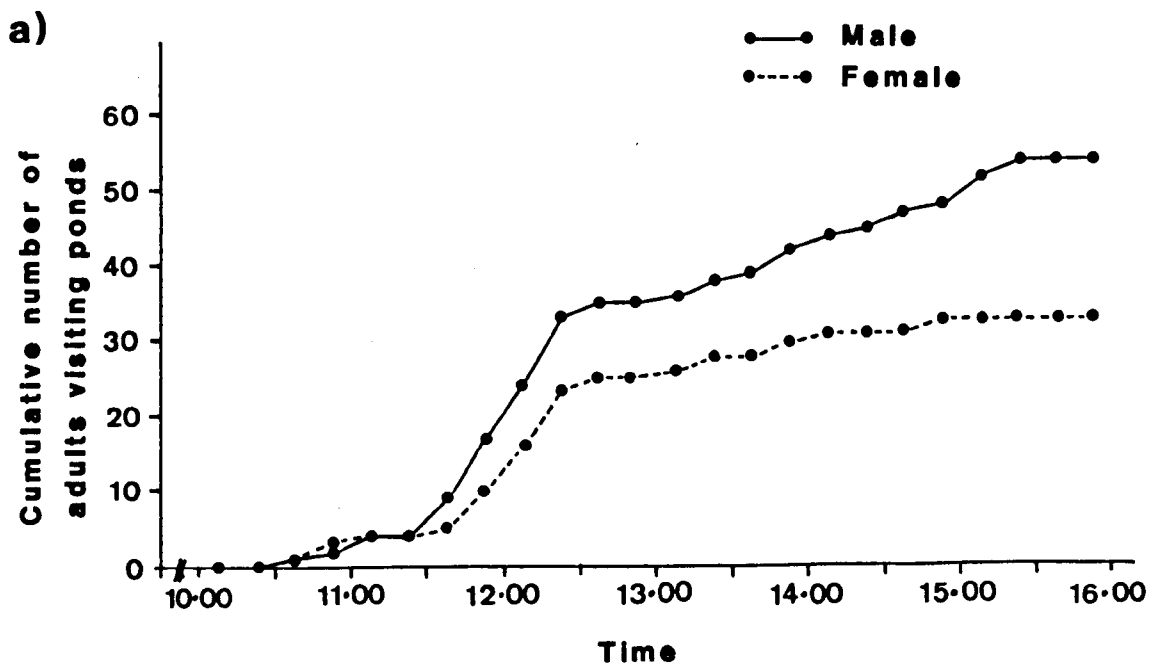
Fig. 5.2   Plots of the cumulative number of adults visiting both study ponds through the day on **a)** 27th June and **b)** 28th June.
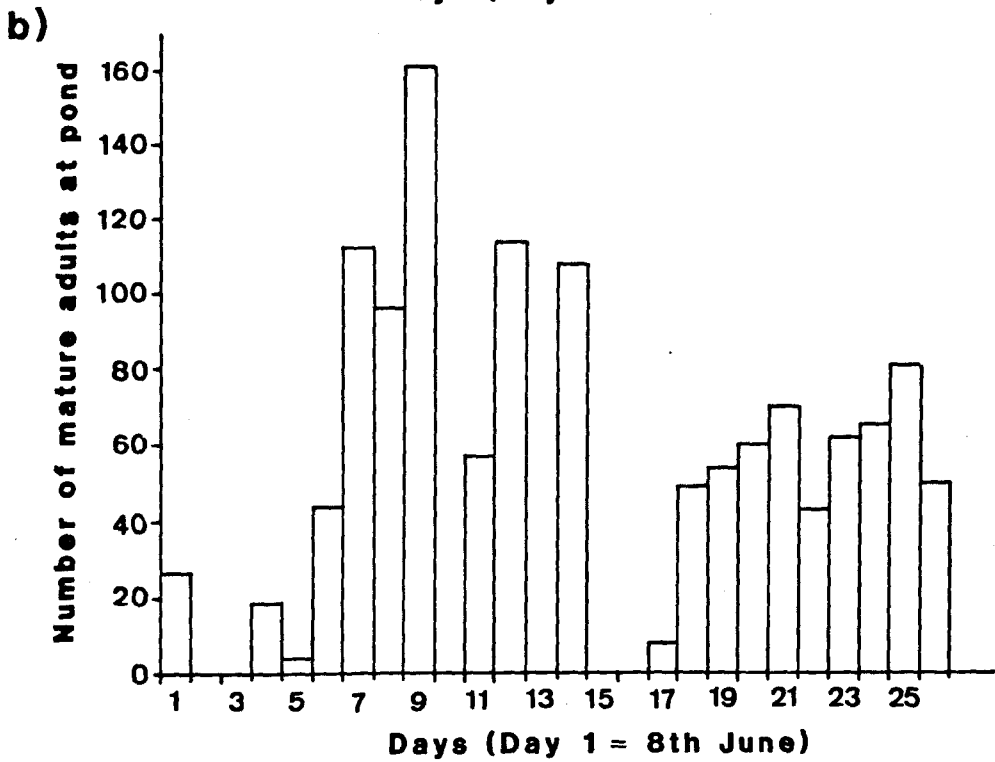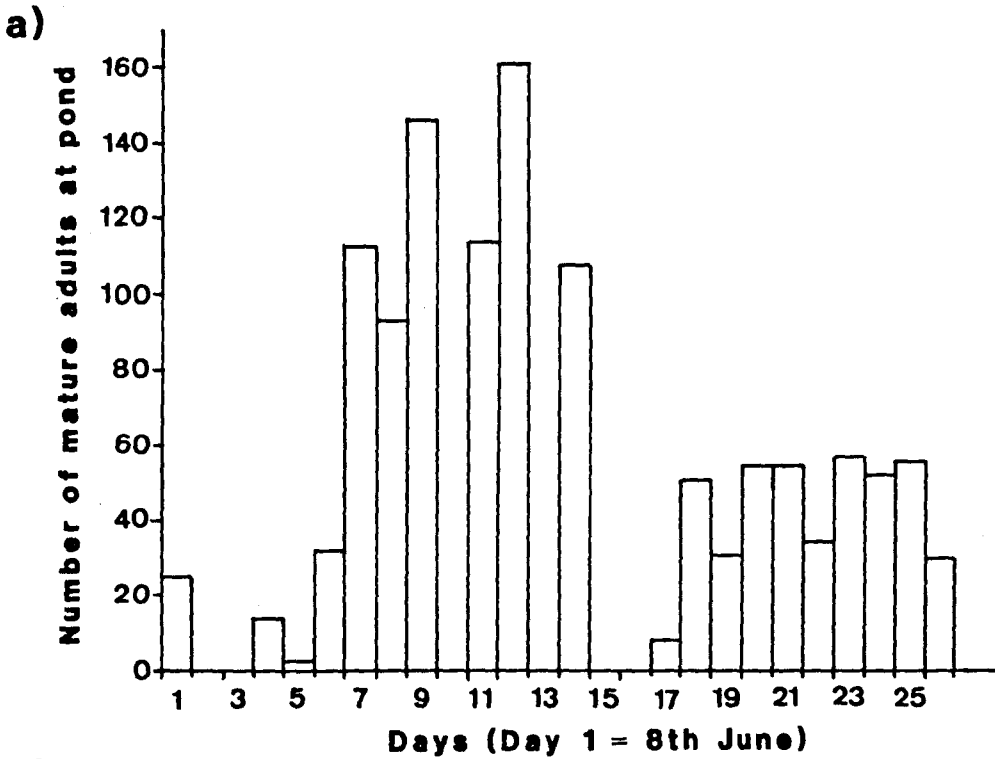
Fig. 5.3   Distribution of mature adults (males and females combined) visiting a) pond A and b) pond B over the study period.
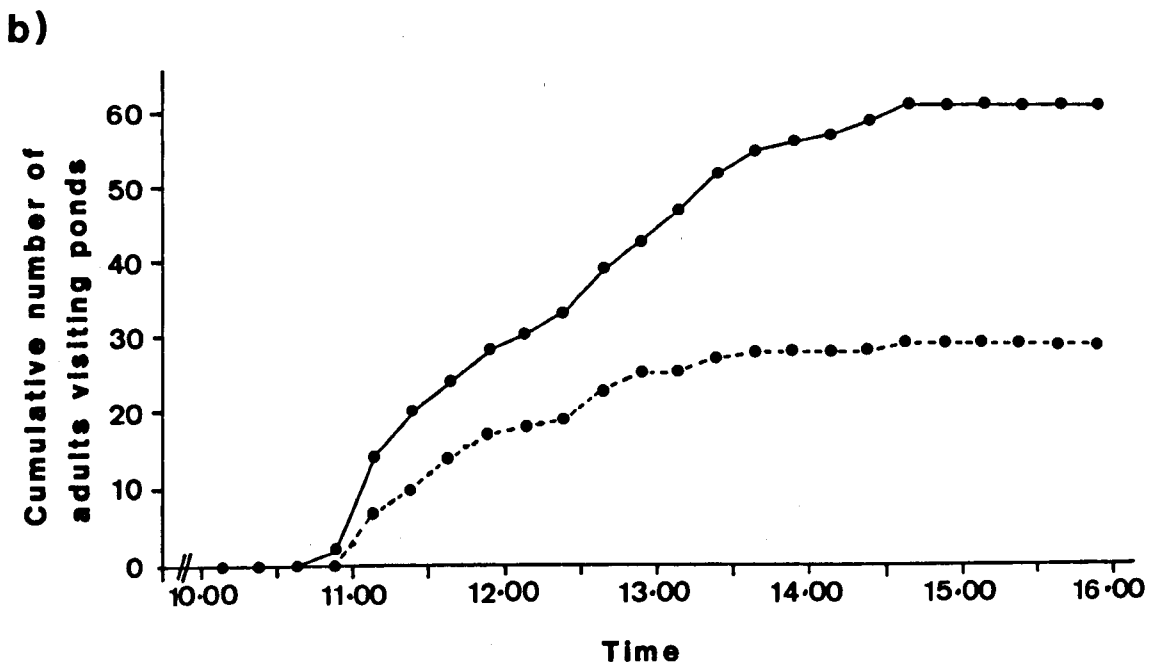
Fig. 5.4   Distributions of various climatic variables
over the study period.

Days (Day 1 = 8th June)

148
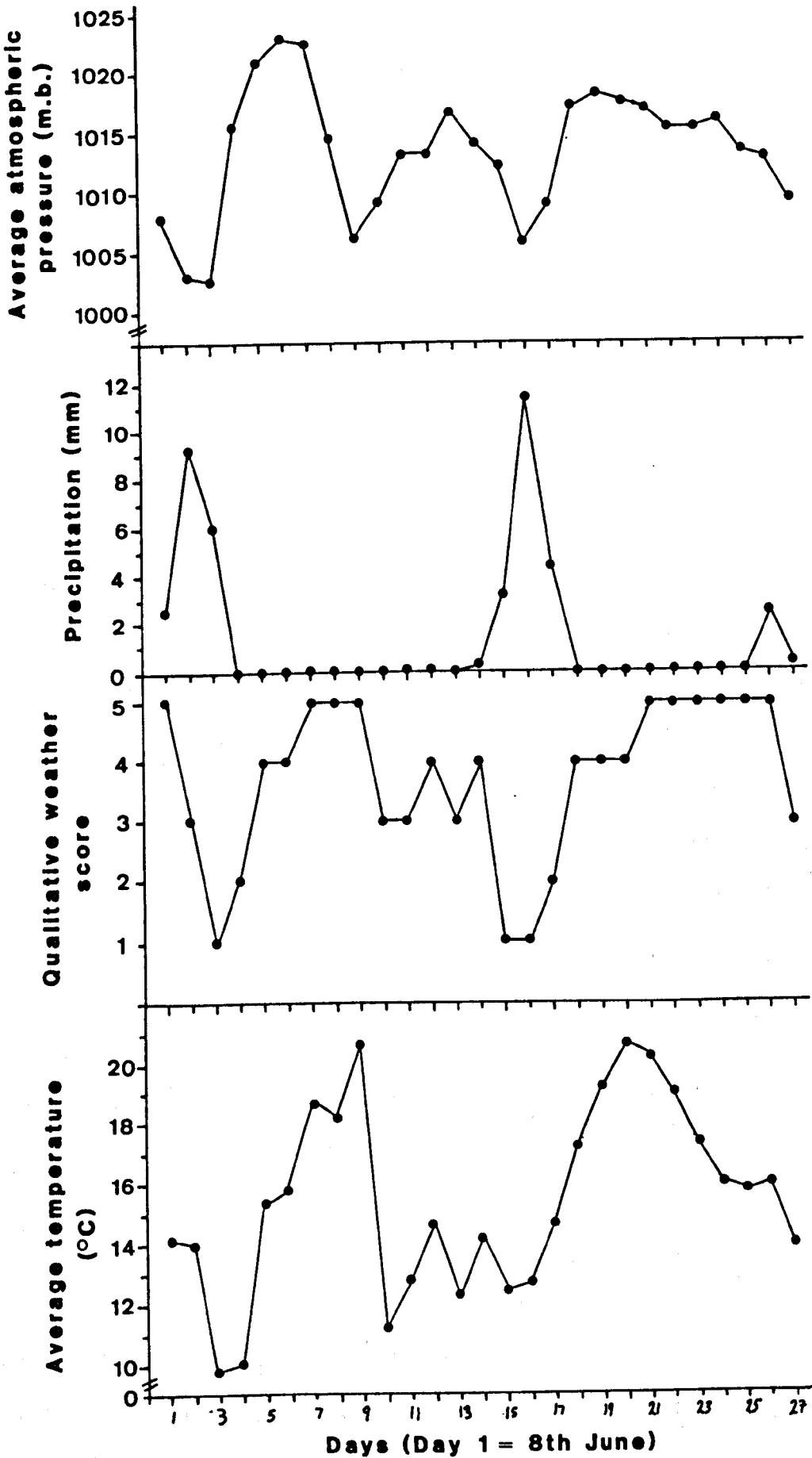
Tables 5.3a,b show the results of Pearson correlations between the daily number of adults visiting pond A and pond B respectively, and various climatic variables. The sample size for all correlations was 24, with the exception of those involving wind speed where the only available records were incomplete, the sample size being reduced to only 5.

There are significant positive correlations between number of adults visiting the ponds and average and maximum temperature, and qualitative weather score. There are significant negative correlations between numbers visiting the ponds and precipitation and average wind speed.

5.3.5   Distribution of visits to ponds.

In section 5.3.2 it was shown that a large proportion of marked adults, when released, were never seen again. However, some of the released adults did remain at the ponds that day, and a small proportion revisited on several occasions, sometimes consecutively and sometimes with long periods of absence separating two visits.

Tables 5.4a,b show the number of days spent at the ponds by males and females respectively. The most number of days spent there by any individual was 9, and 37 males visited the ponds on 4 or more days. The most number of days that a female was seen at the ponds was 3 days, with only 8 females falling into this category. Of the 151 females that visited the ponds twice, 134 did so on consecutive days (ie. the day of capture and the day of release). This leaves only 17 females that revisited the pond 'naturally' (ie. the second visit was not simply the product of being released at the water's edge). This figure is brought up to 25 when the 8 females that visited the ponds 3 times are included.

From these 25 females the interval between the two visits can be calculated. This is unlikely to represent the inter-clutch interval, since females probably visited other ponds on the mossland site during that period. On the basis of the total number of days between visits, the interval ranges from 2-11 days with a mean of 5.23 days (SE

a)

Correlation with :-	r	P
Average temperature	0.441	P< 0.05
Maximum temperature	0.575	P< 0.01
Minimum temperature	0.298	N.S.
Qualitative weather score	0.581	P< 0.01
Precipitation	− 0.460	P< 0.05
Wind speed	− 0.992	P< 0.001
Atmospheric pressure	0.162	N.S.

b)

Correlation with :-	r	P
Average temperature	0.622	P< 0.001
Maximum temperature	0.731	P< 0.001
Minimum temperature	0.429	P< 0.05
Qualitative weather score	0.716	P< 0.001
Precipitation	− 0.505	P< 0.01
Wind speed	− 0.993	P< 0.001
Atmospheric pressure	0.225	N.S.

Table 5.3 Results of Pearson correlations between the number
of mature adults visiting **a)** pond A and **b)** pond B,
and various climatic variables. Variables correlated
over the period 8th June-3rd July exclusive (n = 24).

a)

Number of days spent at ponds	Number of individuals	Cumulative percentage
1	699	69.3
2	225	91.6
3	47	96.3
4	19	98.2
5	11	99.3
6	4	99.7
7	1	99.8
8	1	99.9
9	1	100.0
	1008	

b)

Number of days spent at ponds	Number of individuals	Cumulative percentage
1	628	79.8
2	151	99.0
3	8	100.0
	787	

Table 5.4   The number of days spent at the ponds by a) males and b) females (data from ponds A and B combined).

0.62). However, on some days no mature adults were seen because of unfavourable weather conditions. If only those days when mature adults actually visited the ponds are counted, then the interval ranges from 1-8 days with a mean of 3.82 days (SE 0.48).

If the distributions are grouped separately for each pond, then it transpires that very few marked individuals visit both ponds on the same day, despite the ponds being only 40m away from each other. The total number of marked adults that visited the ponds on 2 or more days was 468 (309 males, 159 females; see Table 5.4). Of these there were only 28 individuals (18 males, 10 females) that were recorded at both ponds on the same day (equivalent to 5.98%). Nineteen of these were individuals released at one pond and recorded at the other, later in the day. If these are ignored, then only 9 individuals (7 males, 2 females) were seen 'naturally' at both study ponds on the same day.

An attempt was made to see if those males that visited the ponds on several occasions differed in any way from those that rarely visited. Unfortunately there was no way of deducing the age of any individual. Because there was a decline in size of captured individuals through the study period (see Chapters 6 and 7), it was necessary to compare approximately equal numbers of males marked over the same period. A grouped t-test showed that there was no significant difference between mean wet weight or mean head width of males that were recorded on 4 or more days, compared with males recorded on only 2 days.

5.3.6   Estimation of survivorship.

An attempt was made to estimate the survivorship of mature male and female *P. nymphula*. If the study ponds had been in an enclosed area with no other water bodies in the vicinity, then measurement of survivorship would have been straightforward. Individuals would only be able to visit those ponds, and their continual absence would imply mortality.

However, given the large number of nearby ponds and ditches, and the high levels of probable dispersal already described, it can be appreciated that the estimates of survivorship will only be rough approximations. The major assumption was that if a marked individual was never seen again at either pond, then it had died. The assumption is clearly not a valid one and this must be remembered when discussing the results.

Results from three day-groups were used for analysis, these being individuals marked on 16th, 19th, and 21st June. For each day-group the number of individuals definitely known to be alive on the days following marking and release was derived. For instance, on 16th June, 141 males and 121 females were caught at both study ponds, taken back to the laboratory to be measured and marked in the evening, and then released around the ponds the next morning. The total number of individuals of that day-group known to be alive on day 2 (17th June), was equal to all those individuals that actually revisited the ponds on day 2, plus all those (different) individuals that revisited on future days (in this case, 40 males and 19 females). Thus, even though an interval of, for instance, 10 days might elapse before an individual revisited the ponds, the fact that it eventually did, obviously proved that it had been alive during those 10 days.

Plots of the number of males and females known to be surviving against time are shown for two of the three day-groups, 16th and 19th June, in Figs. 5.5a,b respectively. In both cases there is an initial large drop in numbers from day 1 to day 2. After day 3, the numbers known to be alive decline more slowly, and at any particular time, female numbers are considerably lower than male numbers.

A linear relationship was obtained when the natural logarithm of the number of a day-group known to be surviving was plotted against time (days). Weighted regression analysis was then applied to the three plots, each point being weighted by the number of individuals that it represented. In each case the significance of both the correlation and the regression was high (P< 0.01).

Tables 5.5a,b present the results of the regression analysis, giving the gradient of

a)

b)
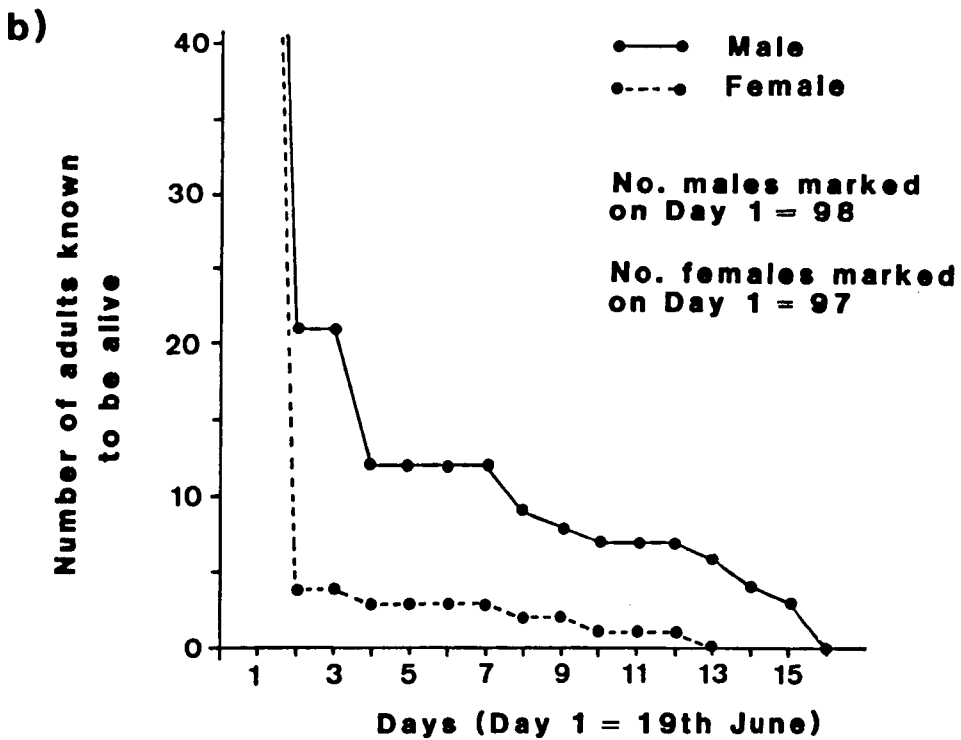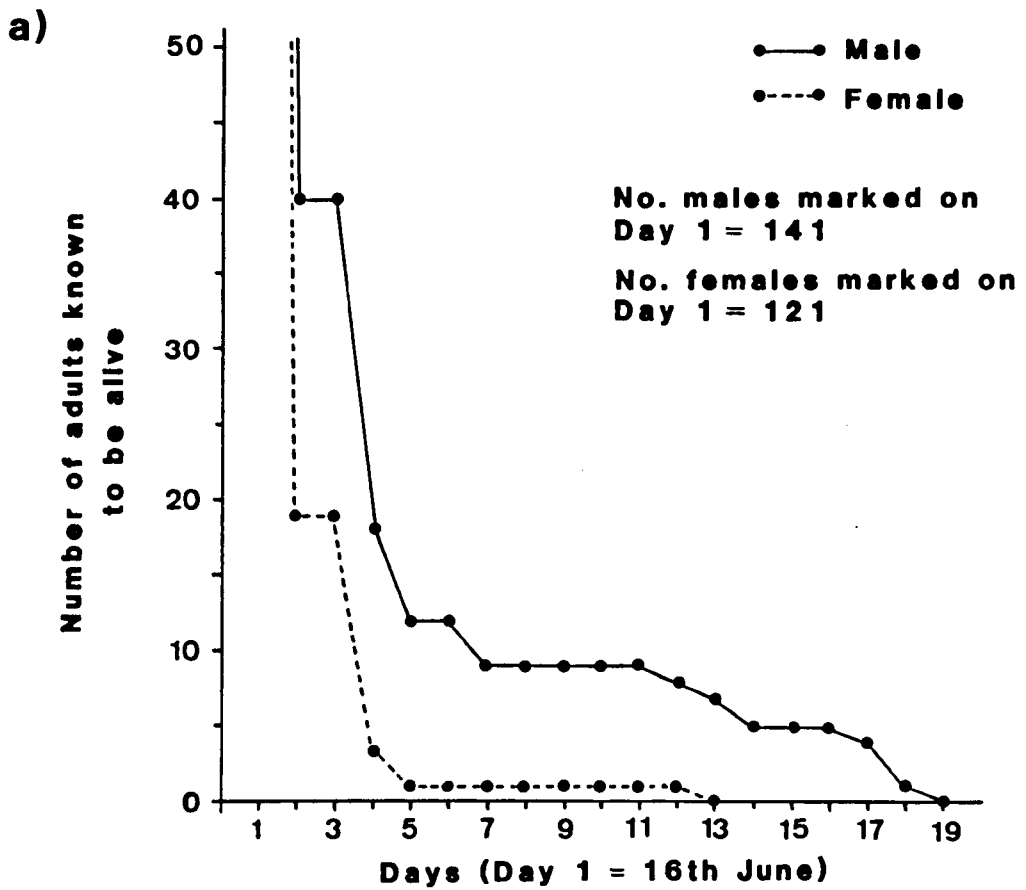
Fig. 5.5   Plots of the number of individuals **a)** marked on 16th June and **b)** marked on 19th June, that were known to be alive on following days.

a)

	Gradient of weighted regression line (x)	e^x
16th June	-0.252	0.777
19th June	-0.249	0.780
21st June	-0.283	0.753

b)

	Gradient of weighted regression line (x)	e^x
16th June	-0.649	0.523
19th June	-0.563	0.570
21st June	-0.733	0.480

Table 5.5   Results of weighted regression analysis of the logarithm of numbers known to be surviving against time (days), for **a)** males and **b)** females. Data from three day-groups is analysed. The antilog of the regression line gradient is an estimate of the daily survival rate.

the regression line for each of the three day-groups, and for males and females respectively. Estimates of the daily survival rate are obtained by taking the antilog of the regression line gradient. For males the three estimates range from 0.75-0.78 (mean 0.77, SE 0.01), while for females they range from 0.48-0.57 (mean 0.52, SE 0.02). In all cases these are likely to be underestimates of survivorship.

5.3.7   Non-random pattern of visits between and within the study ponds.

As already mentioned, a total of 1969 different individuals visited the two ponds over the study period, although a large proportion of these visited only once in their lifetime. Of this total, 1013 individuals were recorded at pond A on their first visit, and 956 were recorded at pond B. There is no significant difference between these values ($X^2_{(1)} = 1.65$, N.S.).

The total number of visits recorded for individuals that returned to the ponds after marking and release was 651. Of these, 270 were to pond A and 381 to pond B ($X^2_{(1)}=18.93$, P< 0.001). If these results are divided with respect to the two sexes, then the difference between males revisiting the two ponds remains highly significant, but there is no difference between females revisiting pond A and pond B. Therefore, those males that return to the ponds on two or more days, tend to revisit pond B significantly more often than pond A.

Irrespective of which pond was revisited, marked males that spent several days at the study ponds appeared to return to the same pond more than would be expected at random. Table 5.6 shows the sequence of visits to both ponds of males having been recorded between 5 and 9 times there. If a male's second recording at either pond occurred on the day of its release, then the first recording was ignored because of the possible manipulation involved.

Many of the sequences in Table 5.6 do not appear random. Runs tests would be the most appropriate form of analysis of these results but, unfortunately, the total

Number of valid recordings at study ponds	Number of males	Sequence of visits to both ponds
5	6	ABAAA, AAABB, AABBA AABBB, ABBBB, BBBBB
6	3	AAAAAA, BBABBB BBBBBB
8	1	ABBBBBBB
9	1	AAAAAAABB

Table 5.6 The sequence of visits to ponds A and B for males
having been recorded between 5 and 9 times there.

* Two or more points were used to represent those males visiting markedly different pond areas on any one day.

number of recordings of visits to the two ponds are not high enough for these to be applied.

Figures 5.6 and 5.7 show outlines of pond A and pond B respectively, each side having been divided into 10 areas. The points adjacent to these areas correspond to individual males either paired with ovipositing females, alone on a perch, or patrolling. Except where a males location changed markedly, each male is represented by a single point corresponding to the most frequently visited area.[*] For both pond A and pond B the results from 27th June-2nd July are shown, although there are no results available for 29th June at pond A.

Figure 5.6 indicates that on certain days, specific areas of pond A were particularly popular. Only one of the sides (side A) had recordings of males on each of the five days. On 27th and 28th June there were few recordings of males on side D, the number increased on 30th June, and on 1st July male visits were predominantly to that side of the pond. However, on the following day there were no recordings of males there. On side C of pond A there were virtually no recordings of males from 27th-30th June, but on 2nd July this was the predominant side on which male activity was recorded. Figure 5.7 shows similar events occurring at pond B, with side C being popular on all days, and with male activity being recorded elsewhere to differing degrees on the six consecutive days.

5.4   Discussion.

The estimates of the length of the immature period are likely to be inaccurate mainly because of the low number of returns of adults marked at emergence, but also because of the uncertainty that even these few individuals immediately returned to the ponds following maturation. Corbet (1952) estimated the length of the maturation period of *P. nymphula* to be about 15 days. This was calculated on the basis of correlation between peaks in emergence and those of adult arrival, rather than on

Fig. 5.6   Outline of pond A, with each side divided into

10 areas, and the location of individual males

being represented by closed circles.

Results are from :-

a) 27th June

b) 28th June

c) 30th June

d) 1st July

e) 2nd July.

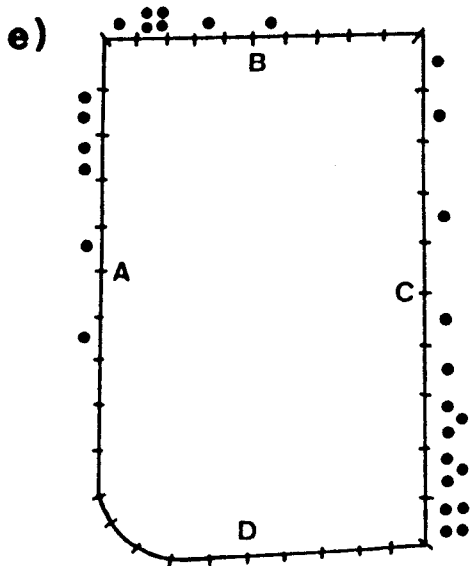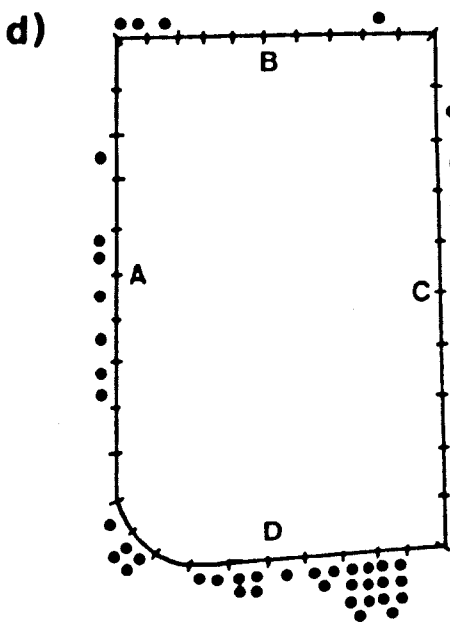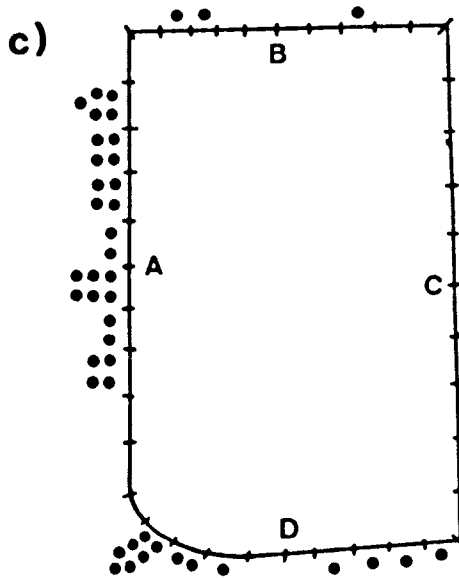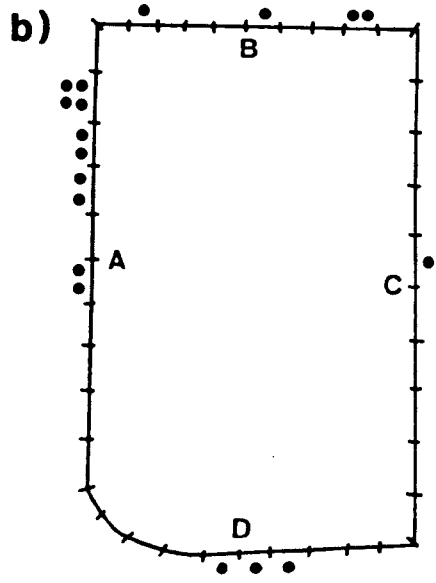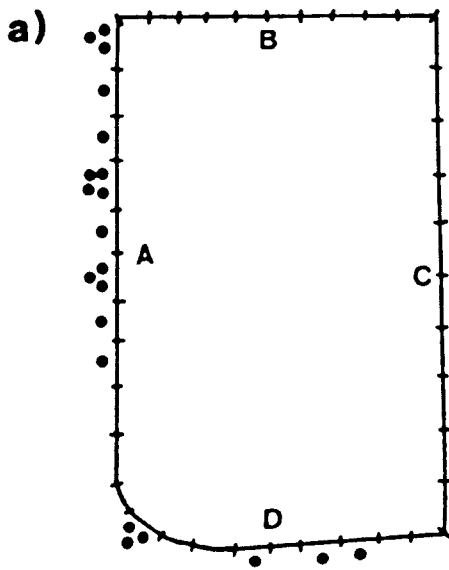Fig. 5.7   Outline of pond B, with each side divided into

10 areas, and the location of individual males

being represented by closed circles.

Results are from :-

a) 27th June

b) 28th June

c) 29th June

d) 30th June

e) 1st July

f) 2nd July.
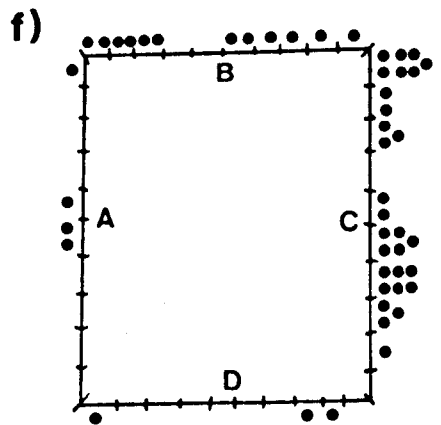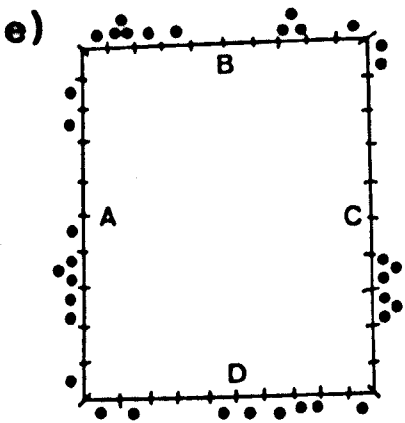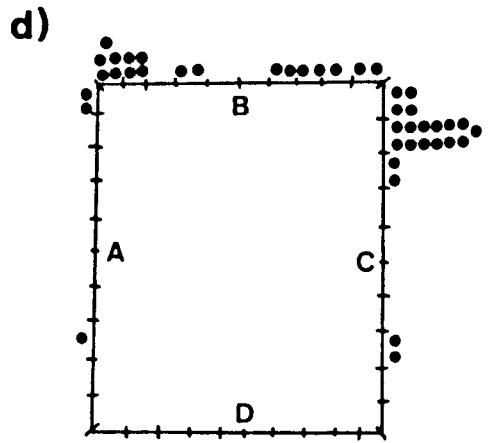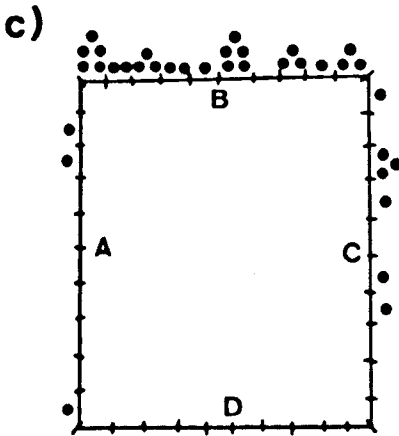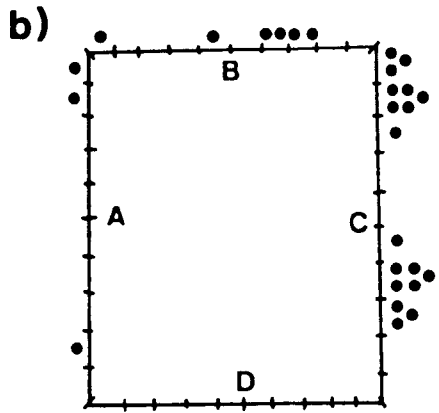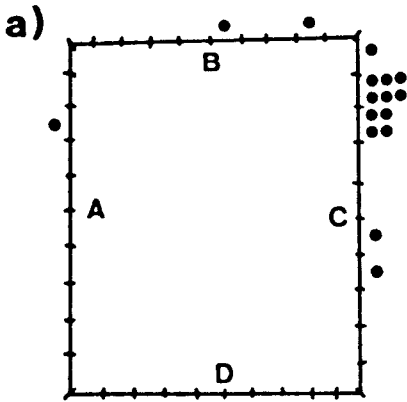
specific returns of marked individuals. Corbet, Longfield & Moore (1960) found that during one very warm spring, some *Pyrrhosoma* adults were mature only 9 days after emergence.

From the nine males and four females which returned after emergence in this study, the minimum interval between recordings was 6 and 9 days respectively. The maximum interval was 15 and 26 days respectively. The female immature period is likely to be longer because they have to mature a clutch of eggs before visiting the ponds, whereas males can visit the ponds immediately they are sexually mature.

Banks & Thompson (1985b), in a study of individually marked *Coenagrion puella*, calculated the immature period for females to be longer than that for males (a mean of 16.5 days compared with 13.2 days for males). Michiels & Dhondt (1989) found that in the dragonfly *Sympetrum danae* (Sulzer), males had a shorter maturation time than females. Parr & Palmer (1971) found the same for *Ischnura elegans*.

Corbet (1962), in a review of immature period length, found examples of it varying between 2 and 30 days in different species. Variation in length within and between species is likely because maturation can be accelerated by higher temperatures or longer feeding times (Corbet, Longfield & Moore 1960). Michiels & Dhondt (1989) found that the maturation time of *S. danae* was inversely related to emergence date. They assumed that this was under photoperiod control and resulted because the risk of bad weather increased rapidly towards the end of the season.

Corbet (1962, 1980) stated that the pre-reproductive period was usually spent away from the breeding site. In this study, during the immature period considerable numbers of teneral adults could be seen around the periphery of the mixed woodland adjacent to the main area of mossland. Actually within the woodland, very dense populations of *P. nymphula* gathered in sun spots where there were also large numbers of small flies and other insects. Teneral adults were very rarely seen around the ponds or even on the mossland areas.

Parr (1973b) found a different situation occurring in a study of *Ischnura elegans*. He found no evidence to indicate a general movement away from the water by teneral

adults. The characteristics of his study ponds are not known but they may have offered more protection or higher prey densities than normal. He also pointed out that *I. elegans* does not conform to what seem more general zygopteran characteristics.

The number of individuals visiting the ponds to breed that had been previously marked at emergence was very small. Bick & Bick (1961) found it difficult to recover individuals of *Lestes disjunctus australis* Walker marked at emergence. They obtained only a 21% recovery of 63 individuals marked when teneral. Bick, Bick & Hornuff (1976) found recoveries of marked individuals of *Chromagrion conditum* (Hagen) were also low (35% male, 9% female). Van Buskirk (1987) found that survival of *Sympetrum rubicundulum* (Hagen) was high for adults that had reached maturity, but it was very low during a 2-week maturation period from emergence to maturity (2-3% for both sexes).

Banks & Thompson (1985b) reported that of 1381 male, and 1333 female *C. puella* that were marked at emergence, only 23.2% and 12.7%, respectively, returned to the pond to breed. Having shown that the probability of an individual surviving to maturity was inversely related to the duration of the immature period, they attributed the difference between the sexes to a greater mortality of females during their longer immature period.

Although a 1.22% return of emerged adults is lower than ٠ll of the values referred to above, it should be remembered that there were many nearby water bodies to which individuals may have dispersed. Crowley *et al.* (1987b) stated that the immature stage appeared to be the primary dispersal stage. They also concluded that the common failure of studies to recover individuals marked at emergence suggested little or no site fidelity between emergence and reproduction, provided that suitable breeding sites were not widely scattered.

Mortality may also account for a low recovery of individuals marked at emergence. Parr (1973b) found the survival rate of *I. elegans* to be highly age-dependent, the heaviest losses occurring at the teneral stage. Teneral adults can be killed or seriously injured by severe weather and preyed upon by a variety of

vertebrate and invertebrates (Crowley *et al.* 1987b).

Mean head width of newly emerged adults and mature adults visiting the ponds was found to be significantly different. Bearing in mind that individuals emerging from pond B were larger than those emerging from pond A, it is perhaps not surprising that some of the mature adults measured had larger head widths than those measured at emergence. Such individuals presumably originated from other ponds having a reduced larval density, higher temperatures or higher prey densities.

However, at the other end of the scale, the smallest newly emerged individuals were unrepresented in the mature adult sample of 1795 individuals. This may suggest that there is a higher mortality of smaller adults in the immature and mature reproductive stages of the life-history. Banks & Thompson (1985a) found a weak effect of body size on the survival of *C. puella* adults, with larger males living longer. However, body size only accounted for 2% of the variance in lifespan. Michiels & Dhondt (1989), in a study of *Sympetrum danae*, found that larger, early emerging individuals lived longer than smaller individuals if they remained within the study area.

High levels of dispersal were found amongst those mature adults captured, marked and then released the following morning. Crowley *et al.* (1987b) pointed out that no studies have managed to completely disentangle dispersal of adults from mortality. While it is likely that mature adults will have a short reproductive lifespan (Corbet (1952) estimated this to be 6.7 days for *P. nymphula*), it is unlikely that the average 68.5% adults never seen again after daily release will have all simply died. It is also unlikely that the marking procedure was responsibe for increased adult mortality since this was tested for newly emerged adults in Section 3.2.3, and other researchers have used the same technique with success (e.g. Banks & Thompson 1985b).

Having said this, marking and release may influence immediate dispersal, firstly because adults would not have fed for 24 hours, and secondly because of the unnatural conditions under which adults had been stored and transported to the ponds.

Thus, it is assumed that a large proportion of those adults not seen after their first

visit disperse to the many other ponds on the site. Reference to other studies indicates that dispersal appears to be negligible. In a study of *C. puella*, Banks & Thompson (1985b) found that no individual (out of a possible 1442) that had been seen as a mature adult at their study pond was later seen at the nearest other pond, 800m away, despite the prevailing wind being in that direction.

Parr (1973b) found that a large proportion of teneral *Ischnura elegans* which were captured and marked were never seen again. He assumed that some might have moved permanently to other ponds while others would have died. However, in a different part of the study he found very little movement between colonies of mature adults at two ponds situated about 35m apart. By marking individuals, he estimated that only 1.5% of a total season's combined estimated population were likely to have moved from one pond to the other.

Mitchell (1962) found that a population of 10-20,000 *Ischnura verticalis* lost less than 2% dispersal to an adjacent pond about 100m away, durind 10 days of normal weather. However, there was a tenfold increase in dispersal during a two-day wind storm.

In this study there were indications that a large proportion of marked adults were never seen again during and following periods of bad weather. The proportion was lower at the end of the study when the weather was particularly fine. It is not known whether this was due to dispersal of individuals to other ponds or to mortality as a direct result of the adverse weather.

Several other features may contribute to the very low number of returns of marked individuals. Firstly, *P. nymphula* is somewhat larger than *C. puella* and the *Ischnura* species referred to above, and therefore may be capable of ranging over larger areas. This may also be related to a second feature, which is the nature of the habitat. The study ponds are situated in a very large open area of mossland, the nearest areas of woodland being some 200m away. If marked individuals leave the ponds late-afternoon to feed in areas some distance away, and given the number of other ponds in close proximity, then the expected return of these individuals to the

same pond the next day may well be unrealistic.

On several occasions, both in the afternoon when activity at the ponds had ceased, and in the morning before adults arrived, a search was made of the undergrowth some distance back from both ponds. No individuals were ever found, perhaps suggesting that most move away from the mossland area when not engaging in reproductive activity. However, it is likely that some individuals must remain closer to the ponds, for instance, those males that visited the ponds on many consecutive days.

To see if dispersal was influenced predominantly by the open, exposed nature of the study ponds, collections of marked *P. nymphula* were released on two occasions at a small, enclosed woodland pond. This was situated on the same site and large numbers of *P. nymphula* and *Coenagrion puella* were known to breed there. Although there is no quantifiable data available, it was found that a large proportion of marked individuals were seen at the pond on following days, and certainly a much larger number than would be expected on the open mossland.

Why fewer marked females should revisit the study ponds than marked males is not entirely clear. Males can visit the ponds daily whereas females have to mature a clutch of eggs before they return to breed. This could be a contributing factor given that the majority of individuals revisiting the ponds do so on the day immediately after release. Alternatively. if females could recognise ponds in which they had already oviposited, they might actively avoid returning to the same one. Such behaviour could be adaptive, although no known studies have reported this to occur.

In a study of *Lestes disjunctus australis*, Bick & Bick (1961) found that of 63 individuals marked when teneral 43% of the males and only 7% of the females were recovered. Of 91 males and 74 females marked when mature, 82% of the males and 58% of the females were recovered.

Not surprisingly, climatological conditions have been shown to have a marked effect on the activity of mature *P. nymphula*. The strongest relationships were found with wind speed, maximum daily temperature, and the qualitative weather score (based

largely on cloud cover and amount of sunshine).

Banks & Thompson (1985a,1987b) found that male and female *C. puella* only engaged in reproductive activity on warm sunny days. With respect to females, weather had a marked effect on egg production, with bad weather increasing the inter-clutch interval and thus lowering egg production. In two studies on male mating success, it was shown that the number of days on which an individual was present at the ponds accounted for 54% and 78% of the total variance in lifetime mating success.

Banks (1985) found that, for *C. puella*, the level of insolation was the major factor determining whether reproductive activity took place. Similarily, Warringer (1982) found that light intensity was the most important determinant of reproductive behaviour in *C. puella*, although he also found that no flight activity was observed on days when the wind intensity was greater than $8ms^{-1}$. Parr (1973b) reported that, in another coenagrionid, *Ischnura elegans*, weather conditions were far less limiting than for other species of Odonata, with a full range of activities being recorded in dull and cool weather. Parr (1973a) stated that only winds in excess of approximately $10.3ms^{-1}$, heavy rain, and a day temperature of less than $15^{o}C$ (especially in combination) completely suppressed flight in *I. elegans*.

Estimation of the average number of days between a marked females natural return to the ponds is unlikely to be equivalent to the inter-clutch interval. A mean of 3.8 sunny days separated visits by 25 such females. In a study of *C. puella*, Banks & Thompson (1987b) found that the maximum clutch size was reached after 3-4 days and was set by the physical size of a female's abdomen. However, most of their investigations concerned females that had matured clutches over 1-2 days, a one-day clutch having been produced between 19 and 27 hours after the previous clutch. The very large (66.1%) increase in mean wet weight between females marked at emergence and at maturity perhaps indicates that female *P. nymphula* differ from female *C. puella*, for instance, by not producing a clutch of eggs every day. This is discussed further in Chapter 7.

The fact that very few marked individuals were seen at both ponds on the same

day, despite their close proximity, indicates that most adults remain in one area throughout the day. More males were seen at both ponds on the same day than females. This is perhaps more likely, especially if they had been unable to find a mate or had been involved in many aggressive interactions with other males.

The daily survival rate was estimated to be 0.77 for males and 0.52 for females. These are likely to be underestimates because an individual from a marked day-group was assumed to have died if not seen again. The considerable initial drop in numbers of males and females known to be surviving from all three day-groups is unlikely to be solely attributable to mortality. A more constant decline in numbers is obtained after this.

Corbet (1952) estimated that an average daily survival rate of 0.85 gave the best fit with recapture data for a population of *P. nymphula*. The survival rate fell from considerably more than 0.90 at the beginning of the flying season, to less than 0.85 at the end. In his study, the average adult lifespan was 6.7 days. Recalculating Corbet's original data, the mean reproductive lifespan for males was 7.01 days, while for females it was 5.50 days. The maximum number of days between first and last capture of males and females was 31 days and 19 days respectively.

Banks & Thompson (1985b) found that *C. puella* had a mean reproductive lifespan of 5.6 days for males and 5.4 days for females, the daily survival rates being 0.83 and 0.82 respectively. In this study a difference between the survival and longevity of males and females was also indicated, although not conclusively shown. Some possible explanations for this have already been mentioned.

Actually at the ponds it was clear that mortality of females was considerably greater than males. Often, females would be found floating on the water surface having had their abdomens torn off by water beetles (*Dytiscus marginalis* L.) and dragonfly larvae (*Aeshna* spp.). On one particular day when reproductive activity was intense, within 2m of each other as many as 11 females were found partially predated whilst ovipositing. Because only the abdomens were eaten, the males were presumably able to escape.

Michiels (1989), in a study of oviposition site selection in *Sympetrum danae*, found that 14% of all females that started oviposition in tandem were predated by frogs, compared to only 3% of all males.

There is an indication that marked males which returned to the ponds on two or more occasions were more likely to visit pond B than pond A. This may be a feature of the prevailing wind, or the fact that pond B is more sheltered than pond A. Males remaining around that area for several days might then be less likely to be dispersed. There was no indication that female numbers were greater at pond B. One noticable difference between the ponds was that there were more small willow and birch saplings around pond B which may have made it more attractive to males. These were frequently used as perches from which males flew out to potential mates, and they also offered protection from the wind, and presumably predators.

Males which returned to the ponds on several occasions appeared to visit predominantly the same pond. This might suggest that those individuals remained close to the ponds overnight rather than feeding around the woodland areas. There was no evidence to suggest that males returning to the same pond over several days, returned to the same perch site or even the same area of the pond. However, certain pond areas did appear to be favoured on different days. This may be related to climatological factors, especially wind direction since this will influence the direction of incoming females. Temperature might also be involved. Michiels (1989) found that flight costs in *Sympetrum danae* were reduced behaviourally by using south facing sites at low ambient temperatures late in the season, and north facing sites at high ambient temperatures early in the season. Some sides of the ponds were popular on all days. This is likely to be related to the availability of perches and vantage points in those areas, as described above.

Males and females began arriving at the ponds between 10.00am and 10.30am. Usually, patrolling males would first be seen flying around the periphery of the ponds in search of receptive females. Initially, the first pairs arriving would have been formed away from the ponds, since few unattended females were seen early on (or

indeed at any time). However, through the day, some males originally recorded as unpaired patrollers at the ponds would later be seen in tandem. The few females seen ovipositing alone at the ponds would constantly be harassed by males. This indicates firstly that females are able to store enough sperm from previous matings to fertilize future clutches, and secondly that, by copulating, females gain the protection of a male from this harassment.

Arrival of females virtually ceases after about 12.30-1.00pm. However, male arrival at the ponds usually still increases. There are indications, unfortunately based only on observation, that while most males patrol around the pond periphery in search of incoming females or perhaps takeovers of existing pairs, other males remain in the vegetation back from the ponds. These males presumably attempt to intercept females before they reach the water. However, through the day, as the female input declines, males away from the pond may then have a higher chance of mating actually at the ponds, perhaps because of the presence of large numbers of females still ovipositing, and hence male numbers at the ponds increase.

It is unknown whether the above observations actually represent two different strategies or tactics of mate finding behaviour, the strategies themselves perhaps representing genetic polymorphisms or behavioural plasticity. Such alternative mating strategies (or intraspecific variation in male mating strategies) have been given considerable attention recently, both generally (e.g. Rubenstein 1980; Dunbar 1982; Thornhill & Alcock 1983), and specifically with respect to odonates (e.g. Waage 1973; Fincke 1985).

Although there is no evidence available, it seems unlikely that males are employing two distinct strategies to acquire mates near to the water's edge. Indeed, many individuals pair up some distance away from the ponds, this perhaps being true of the large number of pairs caught in which both individuals were unmarked. Because very few unmarked females were ever found in the vegetation surrounding the ponds, these pairs probably formed close to the roosting or feeding sites far away from the ponds. Lack of knowledge of the whereabouts of individuals before the start

of a day's reproductive activity prevents any further speculation.

At the beginning of a morning's reproductive activity, a male transfers sperm from a genital aperture on the ninth abdominal segment to accessory genitalia underneath the second abdominal segment. Sometimes this may actually occur after pairing with a female. When a male finds a female he lands on her and then clasps her prothorax with his anal appendages. If the female is receptive then she curls her abdomen upwards to bring her genitalia into contact with the male's accessory genitalia.

Copulation lasts about 30 minutes with conspicuous pumping movements occurring throughout, except in a brief, final phase (Corbet 1980). In *Calopteryx maculata*, these movements coincide with the removal of sperm (by the penis) already in the females spermatheca. Such sperm displacement, which in *C. maculata* is 88-100% effective, is then followed by insemination (Waage 1979a).

Identical sperm removal has been shown to occur in the damselflies, *Enallagma cyathigerum* (Miller & Miller 1981) and *Enallagma hageni* (Fincke 1984a). Miller & Miller (1981) found that dissection of the male secondary genitalia of *E. cyathigerum* showed that the penis head possessed a variety of hooks and bristles. These were seen to hold trapped sperm when pulled from females in copula. For *E. hageni*, Fincke (1984a) found that the last male to mate fertilized up to 95% of the eggs of the first clutch laid after mating. Dissection of females collected before, during , and after copula showed that a male removed a maximum of 87% of the sperm by volume of a previous mate.

When a male has inseminated a female, the female begins to oviposit, remaining in tandem with the male and depositing the eggs in the tissues of aquatic vegetation. When the female has finished laying her eggs the pair split. Given the potential for sperm displacement, postcopulatory guarding is advantageous to the guarding male since it assures him of fertilizing a substantial number of eggs prior to a subsequent mating by his mate (Waage 1979b).

Although sperm removal may not directly benefit the female, she may gain

subsequently by being guarded during oviposition (this may reduce harassment from other males, or reduce the risk of predation or drowning). Sexual selection and sperm competition in odonates is reviewed by Waage (1984a), and the adaptive significance of postcopulatory guarding to males and females is discussed by Alcock (1979, 1982, 1983) and Waage (1979b).

Chapter 6. Territorial and reproductive behaviour of male *Pyrrhosoma nymphula.*

6.1   Introduction.

The aim of this investigation was to study various aspects of male territorial and reproductive behaviour including the influence of size on the outcome of territorial disputes and on observed mating success.

While the territorial behaviour of *P. nymphula* is more obvious than that of many zygopterans, it is less characteristic than that of the Calopterygidae or the majority of anisopterans. For instance, males of *Calopteryx maculata* defend oviposition sites which are attractive to females. These territorial males increase their mating frequency by the exclusive occupancy of such an oviposition area, and by guarding mated females during their oviposition they increase the number of eggs fertilized (Waage 1973, 1979b). Additionally, there are usually specific courtship flights and displays by males and subsequent displays by females including rejection, invitation and neutral responses, which signal differences in their receptivity (Waage 1984b).

Males of *Pyrrhosoma nymphula* neither defend oviposition sites nor display any type of courtship behaviour. The territory simply consists of a perch site and the 'airspace' around it. From the perch, resident males presumably have a good vantage point and they make sallies out to patrolling males, pairs in tandem, and potential mates. However, their behaviour can be described as territorial because they usually chase other conspecific males that fly or attempt to settle near to them, and they return to the same perch site after winning a contest.

In a recent study of male *P. nymphula*, Harvey & Corbet (1985) concluded that larger males won more territorial disputes and enjoyed enhanced mating success. The results of this present study appear to contradict this, since a simple residency asymmetry appears to settle most territorial disputes.

6.2   Materials and methods.

6.2.1   Recording of activity.

Territorial and reproductive behaviour of male *P. nymphula* was recorded using the methods previously described in Chapter 5. Attention was largely focussed on marked males holding territories which interacted with either marked or unmarked males, females or pairs. As before, unmarked individuals were caught to be measured and marked, and then released the next day at the ponds. However, where possible, unmarked, single males were left until they had interacted with the marked individuals, since immediately removing them would decrease the amount of activity around the ponds and might affect normal male behaviour.

In the following computations, wet weight is the measure generally compared between different groups of individuals, although head width measures are sometimes used. Absolute size measures are usually favoured because they do not vary as weight measures tend to. Where weight is used it should be remembered that the correlation between male head width and wet weight is highly significant ($r = 0.665$, $n = 682$, $P<0.001$). Unless otherwise stated, all results were obtained from only those males involved in territorial disputes at the two study ponds.

6.3   Results.

6.3.1   The influence of male size on observed mating success.

Not surprisingly there is a highly significant relationship between a male's total number of observed matings and the total number of days it was seen at the ponds ($r=0.678$, $n =118$, $P < 0.001$). Both the number of observed matings and the number of days spent at the ponds were significantly negatively correlated with the day of

marking and measuring. This is again unsurprising because the study did not continue until the very last day on which there was adult activity. Thus, those males marked earlier on would have had a greater opportunity to return to the ponds during the study period and be re-recorded, whereas those males marked towards the end may have returned outside of the study period.

There was a significant decline in both head width and wet weight of mature, unmarked males and females through the study period (see Tables 6.1a,b).

Given the above intercorrelations, it is likely that spurious correlations will be generated when either the number of days spent at the ponds, or the total number of observed matings, is plotted against adult wet weight. For this reason, partial correlation coefficients of the two above correlations have been calculated, controlling for the day on which an individual was marked. There is no relationship either between the number of days spent at the ponds and male size (wet weight), or between the number of observed matings and male size, when the date of marking is controlled for (see Table 6.2).

In addition to size having no apparent effect on the number of matings achieved by males involved in territorial disputes, there is also no evidence of any size assortative mating occurring between all unmarked, first-visit males and females visiting the ponds over the entire season.

On 17 days of the study, numbers of unmarked pairs visiting the ponds were high enough to warrant analysis. With respect to head width, on none of these days was there any evidence of a correlation between male and female size. On only one of the 17 days was there a significant positive correlation between male and female wet weight. Plotting female head width or wet weight against the corresponding measures for males over the entire season, is complicated by the fact that there is a significant decline in size of males and females through the study period. Hence, a spurious positive correlation would be produced because large males would mate with large females early in the season, and small males with small females later in the season.

If female and male head width (or wet weight) are subjected to partial correlation

a)

Variable	Correlation coefficient	n	P
Head width	-0.251	682	P< 0.001
Wet weight	-0.335	691	P< 0.001

b)

Variable	Correlation coefficient	n	P
Head width	-0.400	480	P< 0.001
Wet weight	-0.380	486	P< 0.001

Table 6.1   Pearson correlations between head width and day of study, and wet weight and day of study, for **a)** mature, first-visit males and **b)** mature, first-visit females.

Variable	Controlling for :-	Partial correlation coefficient	n	P
Total number of days	Day marked	-0.152	115	0.102
Total number of matings	Day marked	-0.072	115	0.444

Table 6.2   Partial correlations between the total number of days
spent at the ponds and wet weight, controlling for day
marked, and between the total number of matings and
wet weight, controlling for day marked.

analysis controlling for the day on which an individual was measured, then no significant relationships are obtained (e.g. Pearson correlation of female and male head width: r= 0.131, n=388, P = 0.010; Partial correlation of female and male head width controlling for the day of the study : r= 0.018, n=385, P = 0.726).

6.3.2 Territorial behaviour and differences in size between resident and interloper.

The territory of a male *P. nymphula* consisted simply of a perch site (such as a reed or stem) from which the individual flew out to passing pairs, other conspecific males, and potential mates. Such perched males ('residents') usually attempted to drive away other patrolling males ('interlopers') that flew near, particularly if they attempted to settle nearby. Thus, a territorial dispute generally consisted only of a chase, with physical contact sometimes being involved, but usually without escalation. One or other of the males would then return to the same area, and often the same perch originally contested.

Although at any given time, males usually returned to the same perch site, they generally did not remain in the same area throughout the entire day. This might have been due to active movement in search of better perches, if for instance they had been unsuccessful in aquiring a mate, or it may have been the result of aggressive interactions with other males. Their site attachment was, therefore, not very high.

Unlike the territories of other species of dragonfly, the simple territories of *P. nymphula* do not contain an oviposition site to attract females. Pairs oviposited around the entire periphery of the ponds and one pair would often move around to many different areas. Quite often, considerable numbers of pairs would be seen ovipositing in very close proximity, and even along the same piece of floating vegetation.

A resident male's response to conspecifics differed according to their identity. As already mentioned, single patrolling males were almost always chased. However,

when a resident flew out to a pair it usually quickly returned to its perch without challenging them or attempting to drive them away (but see below). Often, pairs would oviposit undisturbed immediately below where a resident male was perched, the resident occasionally flying down to them when they moved position but, again, returning immediately to its perch. Under these circumstances the male, and sometimes the female, of the pair displayed a threat posture where the wings were flicked open rapidly. This is characteristic of the Coenagrionidae (Corbet, Longfield & Moore 1960), and for single males and females the abdomen is usually raised dorsally as well.

Occasionally single males were seen attempting to take over a paired female although a successful takeover was never observed. In the 1986 field season such behaviour was relatively rare. However, at the very beginning of the 1987 field season lone males appeared to be very much more aggressive, with some individuals constantly attempting takeovers. These individuals often tried to force the pair into the water, presumably so that the male's hold on the female was released. The differences in behaviour between the two field seasons may relate to differences in density, or to differences in the operational sex ratio. The latter is likely to be more male biased at the beginning of the reproductive season than at the end because males apparently have a shorter maturation period than females.

Resident males also made sallies out to males of *Ischnura elegans* and *Coenagrion puella,* which occurred in low numbers at both ponds. Unlike their response to conspecific males, residents made no attempt to drive off males of other species. Such behaviour, together with the similar response to passing pairs, suggests that residents do not immediately recognise the identity of an interloper until very close to it. Presumably, any shape moving near to it could be a potential mate and would thus necessitate an immediate response.

Towards the end of the day, male territorial behaviour changed and residents were less likely to fly out to males patrolling the sides of the ponds. With female numbers declining considerably through the afternoon, such patrolling males would

eventually no longer pose a threat to residents. Resident males at this stage were often seen to make the characteristic threat display mentioned earlier, raising or curving their abdomens and spreading, flicking, or fluttering their wings when interloper males flew near. Utzeri, Falchetti & Carchini (1983) reported very similar threat displays in another coenagrionid, *Coenagrion lindeni* (Selys).

At the ponds there was a bale biased operational sex ratio. At pond A this ranged between 51.6% - 70.2% male (mean 59.9% male, or 1.495 (SE 0.092) male: 1 female). At pond B the sex ratio ranged between 50.0% - 69.2% male (mean 62.3% male, or 1.654 (SE 0.097) male: 1 female). Combined, the mean operational sex ratio was 61.1 % male, or 1.574 (SE 0.067) male: 1 female, which was significantly male biased ($X^2_{(1)} = 86.88$, P < 0.001). Over the entire study period the mean daily number of males and females was 43.0 and 31.2 respectively at pond A, and 45.7 and 29.1 respectively at pond B.

The highest number of territorial disputes that an individual was observed to have been involved in was 7. Figure 6.1a shows the distribution of males involved in between 1 and 7 disputes at both ponds. Data are presented for the 118 males for which size and weight measures are available. There is no relationship between the observed number of disputes an individual was involved in and individual wet weight. There is also no relationship between the observed number of disputes either as a resident or an interloper and individual weight.

The total number of recorded territorial disputes was 120. Paired t-test analysis of all these disputes showed that there was no significant difference between the mean wet weight of the resident male and the interloper male.

Figure 6.1b shows the number of disputes an individual was involved in when it was the resident male, plotted against the total number of disputes the resident was involved in. The broken lines drawn on the graph represent two distinct groups of males. The first are those that were residents in all disputes they were involved in (R), while the second were interlopers in all disputes they were involved in (I). Ignoring those individuals only ever involved in one dispute, there are 7 males belonging to the

Fig. 6.1   **a)** Distribution of males involved in between

1 and 7 territorial disputes at both ponds, and

 b) the number of disputes an individual was

involved in as a resident male, plotted

against the total number of disputes involved

in (see text for explanation).

a)
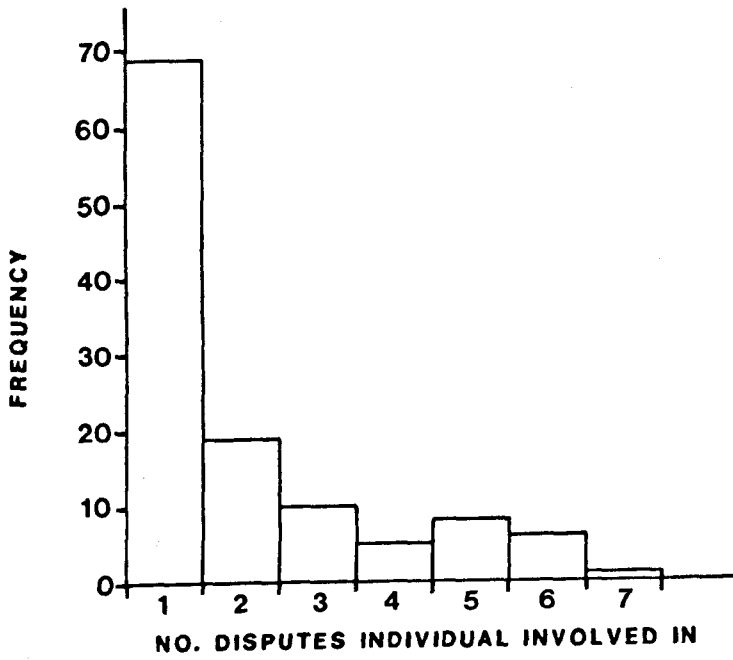
b)
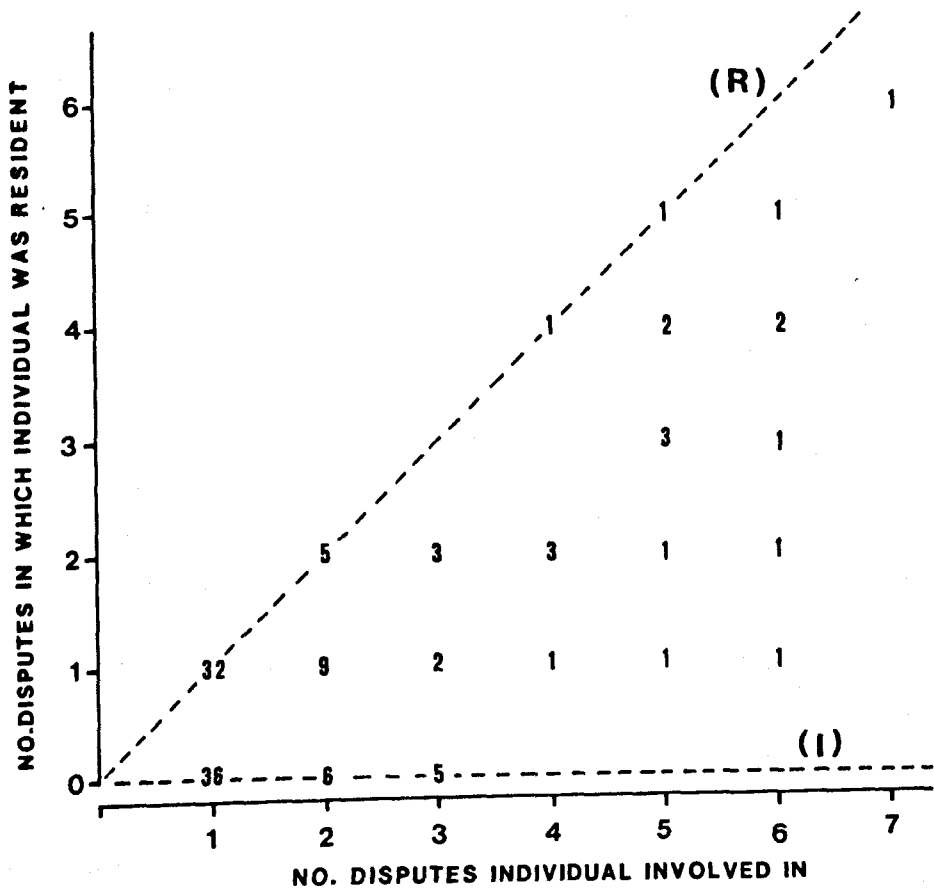
resident group, and 11 males to the interloper group.

Using t-tests these two groups of males were compared with respect to mean wet weight, mean number of observed matings, mean number of days spent at the ponds, and mean day first marked. For all of these there were no significant differences between males that were always recorded as residents in disputes and males that were always seen as interlopers.

6.3.3 The influence of male size on the outcome of territorial disputes.

Of the 120 recorded territorial disputes, resident males won 117 and lost 3 (residents were assumed to have won a dispute if they drove the interloper away from the area and then returned to the same perch, and they were assumed to have lost if they were displaced by the interloper). Of the 117 disputes in which the resident won, there were 61 cases where the resident weight was greater than the interloper weight and 56 cases where it was less than the interloper weight. In all 3 of the disputes where the resident lost, the resident weight was greater than the interloper weight. Therefore, in the total 120 disputes, resident males were heavier than interlopers on 64 occasions, and interloper males were heavier than residents on 56 occasions.

Chi-squared analysis of the above can be undertaken using a Null Hypothesis which states that the expected number of wins by a resident will equal the number of disputes in which weight of the resident is greater than weight of the interloper. If this is computed then the Null Hypothesis is firmly rejected ($X^2_{(1)} = 94.05$, N.S.). Resident males win almost all territorial disputes with size having no apparent effect on the outcome.

On the three occasions on which interlopers displaced resident males, the disputes were escalated and aggressive. There was a much greater degree of physical contact, each male attempting to force the other into the water. Several males were found struggling or even drowned in the water throughout the study, and may have

been the victims of such escalated disputes. There were a few disputes which were not recorded because neither the resident nor the interloper returned to the original area. These again were escalated disputes with both males flying high into the air, spiralling round each other, and then moving out of sight. Unfortunately, times of disputes were not recorded.

The above disputes generally arose because of confusion over residency. This usually happened if two males had settled in the same area without at first noticing each other, or if an interloper male settled near to the perch of a resident while it was absent.

Table 6.3 shows the mean wet weight, mean number of observed matings, mean number of days seen at the ponds, and mean day first marked, for 11 males having won 3 or more disputes as resident, and 11 males having lost 3 or more disputes as interloper. T-tests comparing the means in each case showed no significant differences between the two groups of males.

6.3.4   The relationship between observed mating success and the outcome of territorial disputes.

When an individual's total observed number of matings is plotted against its observed number of territorial disputes a positive, significant correlation is obtained (r= 0.471, n=118, P < 0.001). However, both of these variables are correlated with the total number of days an individual spent at the ponds. If a partial correlation coefficient is calculated, controlling for the number of days spent at the ponds, then the result is not significant (r=0.089, n =115, P = 0.340).

If the number of matings is now plotted against the number of disputes won as a resident male (or the number of disputes lost as an interloper male), then the correlation is again positive and significant (Fig. 6.2). As before, because all of these variables are significantly correlated with the number of days spent at the ponds, it is necessary to compute partial correlations. If this is done the relationship between

	Males having won 3 or more disputes as resident	Males having lost 3 or more disputes as interloper
Mean wet weight (mg)	40.18	39.37
(SE)	(1.11)	(1.15)
Mean number observed matings	2.55	1.82
(SE)	(0.51)	(0.42)
Mean number days seen at ponds	4.09	3.91
(SE)	(0.46)	(0.37)
Mean day first marked (Day 1 = 1st June)	27.64	27.18
(SE)	(1.21)	(1.21)

Table 6.3   Mean wet weight, mean total number of observed matings, mean total number of days seen at the ponds, and mean day marked, of 11 males having won 3 or more disputes as resident, and 11 males having lost 3 or more disputes as interloper.
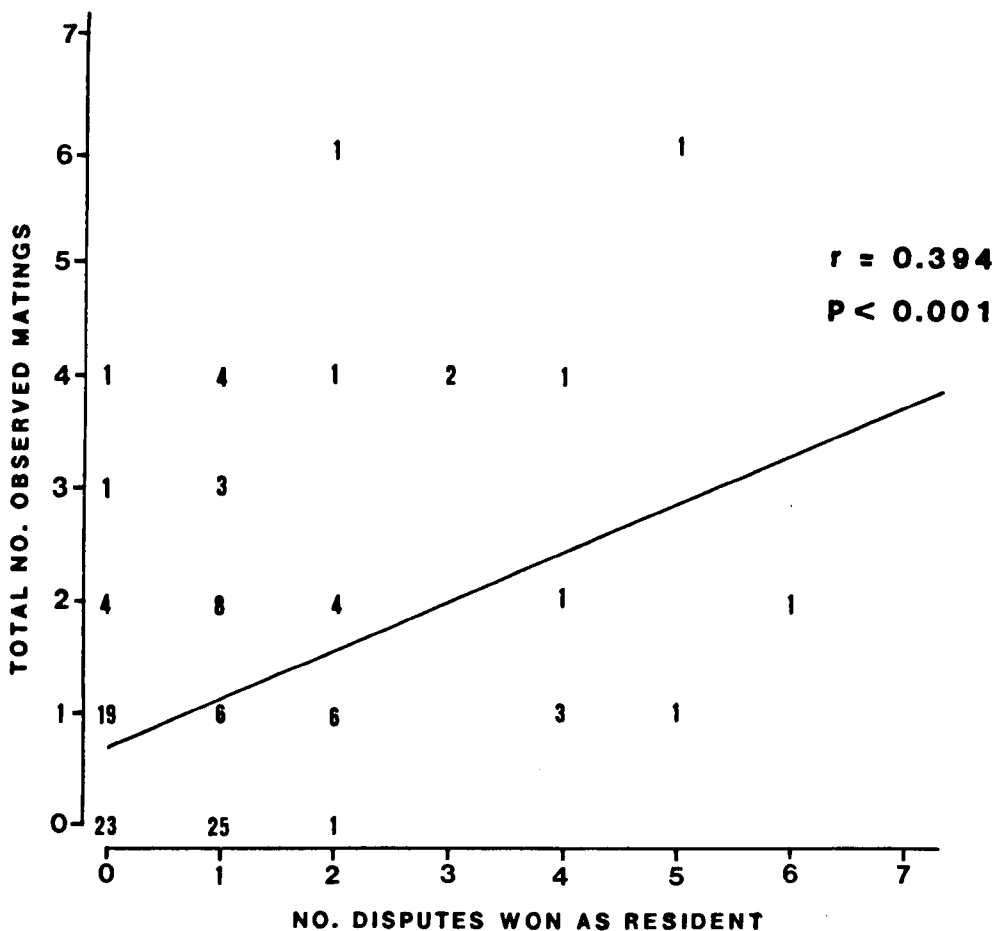
Fig. 6.2 Plot of observed number of matings against the number of territorial disputes won as a resident male.

observed mating success and number of disputes lost as an interloper does not remain significant. However, the relationship between observed mating success and number of disputes won as a resident remains positive and significant (see Fig. 6.2).

6.3.5   Comparison of paired and unpaired males.

If all first-visit, unmarked, paired males captured at the ponds are compared with first-visit, unmarked, single or patrolling males, then differences with respect to size can be detected. Males in pairs have a significantly larger mean head width than single males, but there is no significant difference with respect to wet weight.

However, the ratio of the number of patrolling males to paired males changes through the season, with there being relatively higher numbers of patrolling males later on. There is a decline in size of males and females through the season and so it follows that the above differences may simply be the product of this size decline.

For this reason equal numbers of paired and single males were chosen at random from each daily sample. There were 15 days throughout the study period when numbers of both paired and single males were high enough to allow comparison. With respect to head width, on 14 out of the 15 days the mean for paired males was greater than that for unpaired males, although on only one occasion was the difference significant. With respect to wet weight, the number of days on which the mean for paired males was greater than, or less than, that for unpaired males was almost equal, and there were no significant differences between the means.

Combining the data from all 15 days, the mean head width of paired males was significantly larger than that of unpaired, patrolling males, but there was no significant difference between mean wet weight (see Tables 6.4a,b).

6.4   Discussion.

Territorial behaviour in *P. nymphula* differs from the many examples of

a)

	Mean	SE	n	t	d.f.	P
Paired males	4.461	0.008	209			
				3.32	416	P< 0.001
Single males	4.423	0.008	209			

b)

	Mean	SE	n	t	d.f.	P
Paired males	41.74	0.28	209			
				−0.83	416	P= 0.407
Single males	42.08	0.30	209			

Table 6.4   Grouped t-tests comparing **a)** mean head width (mm) between unmarked paired and unpaired males and **b)** mean wet weight (mg) between unmarked paired and unpaired males. (Equal numbers of paired and unpaired males selected at random throughout study period)

'classical' dragonfly territoriality relating to the Anisoptera (e.g. Jacobs 1955; Wolf & Waltz 1984) and to the Zygoptera, and particularly the Calopterygidae (e.g. Pajunen 1966a, 1966b; Waage 1973, 1979b, 1984b). In the latter studies there were usually specific courtship displays by males and subsequent displays by females signalling differences in receptivity. Male territories contained an oviposition site and females usually exchanged matings for guarding and undisturbed oviposition.

In the course of several investigations the patterns of behaviour leading to a male being considered territorial have been defined. Robertson (1982) studied mating behaviour and its relationship to territoriality in *Platycypha caligata* (Selys). Territories were centred around oviposition sites, with a perch in the sunlight nearby. He considered the males to be territorial because they often remained in, or returned regularly to, the same area and maintained exclusive use of this area by active exclusion of intruders.

Corbet (1980) stated that odonate males were termed territorial when a male 'localizes in a more or less fixed area within which he behaves in a way that evokes escape and avoidance among intruders'. He also stated that among species of Odonata a gradient existed from simple, aggressive behaviour without either site attachment or residentiality, at one end, to ritualized display with site attachment and pronounced residentiality, at the other.

Male *Pyrrhosoma nymphula* do not defend oviposition sites and they could not accurately be described as having high site attachment since they often occurred in different areas through the day. However, at any particular point in the day, a male on a perch may repeatedly return to exactly the same position after sallies out to interlopers. Occasionally such males were seen at more or less the same location throughout the day, and very occasionally they were seen likewise on two consecutive days. Corbet (1980) stated that even among species showing pronounced territoriality, a male seldom occupies a territory for more than a few consecutive days, although some more persistent individuals may remain without interruption for some weeks (see Fincke 1984b).

The fact that a male will continuously return to, and defend, the same area over a finite amount of time, indicates that it is valid to refer to *P. nymphula* as showing a degree of territorial, rather than simply aggressive, behaviour.

Territorial male *P. nymphula* are typical 'perchers' making sallies out to interlopers or potential mates and only occasionally embarking on longer patrolling flights or cruises along the edge of the pond.

Bick & Bick (1961) found a similar situation with *Lestes disjunctus australis*, where males seemed to maintain tenure merely by passive occupancy, remaining perched for long periods of time and spending very little time making patrolling flights. Other species may spend much more time cruising, and when perching hardly ever do so repeatedly at one spot (Corbet 1980).

Several studies have investigated the influence of population density on the occurrence of territoriality (e.g. Pajunen 1966a, 1966b). In *Leucorrhinia rubicunda* L., as the male density increases, individual flight areas become obscured and there are fewer aggressive encounters (Pajunen 1966a). In *Calopteryx virgo* L., increased density leads to increased disturbances of stationary territorial breeding and necessitates a change in behaviour, involving an active search for females and the abandonment of their protection during oviposition (Pajunen 1966b).

Because *P. nymphula* males do not defend such a territory containing an oviposition site it is unlikely that similar behaviour would occur. However, with increasing density there might be a change in the number of aggressive interactions and males might spend more time patrolling rather than remaining stationary in one particular area. An attempt to investigate density effects at the ponds was made although it proved largely unsuccessful and is not presented here.

For males involved in territorial disputes there was no relationship, firstly between size and the total number of days spent at the ponds, and secondly between size and the total number of observed matings achieved. With the lack of a complete known life-history of each individual and the potential level of movement between ponds, few conclusions can be confidently drawn from these particular results.

In a study of *Coenagrion puella*, Banks & Thompson (1985a) found that the number of days a male spent at the breeding site was mostly determined by a male's mature lifespan, and that larger males lived longer. They also found that smaller males had a higher daily mating rate (hence the overall effect of size on lifetime mating success was that males at both extremes of the size distribution were more likely to fail to mate). Van Buskirk (1987) found that daily mating success of *Sympetrum rubicundulum* was not influenced by size.

The fact that paired, first-visit males were significantly larger than unpaired males may appear to contradict the above finding that observed mating success is apparently unrelated to size. Why exactly males in pairs should be larger than those patrolling is not entirely clear, especially since size has been shown to have no effect on the outcome of territorial disputes, and also since there was no difference in size between residents and interlopers. However, because there is a decline in size of unmarked adults through the study period, larger males will generally have reached maturity earlier than smaller males and therefore may have spent more time at the breeding site and achieved more matings. Thus, these larger (older) males, with more acquired experience, may be more likely to succeed in mating on a given day compared to smaller males.

Hence, differences between age and experience might explain the size differences found between paired and unpaired males. In a similar manner, such differences may also account for the apparent discrepancy between this and the previous conculsion that size is unrelated to mating success. In the comparison of paired and unpaired males, unmarked individuals were sampled at only one point in time (i.e. at that point the male was either paired or single, its future status being irrelevant), and thus experience may be important. However, with respect to the 118 territorial males, mating success was recorded over the entire time thay were seen at the ponds, and thus initial differences or advantages in mating experience might fade away.

One of the problems with this study was that due to the need to mark individuals so they could be followed, unmarked males and females were constantly being

removed from the breeding site through the day. Thus, marked territorial and patrolling males may have achieved a higher number of matings than normal. Such males, having been caught with unmarked partners and subsequently released, could immediately mate with another female whereas before they would have been prevented doing so by postcopulatory guarding. Unfortunately, there is no way of avoiding this problem and it is assumed that the consequences of removing individuals from the ponds does not inherently alter the behaviour observed or the results obtained.

The sex ratio at emergence was significantly male biased (54.6% male at pond A, and 53.1% male at pond B; see Chapter 3). The operational sex ratio was also found to be significantly male biased (the mean for the two ponds combined was 61.1% male).

Waage (1980) stated that in contrast to a general tendency towards an equal sex ratio at emergence, zygopteran adult sex ratios appear to be strongly male biased when censuses are taken at the water. He found a significant excess of male *Calopteryx maculata* at the water and concluded that it could be explained by either differential mortality or differential behaviour of the sexes. He pointed out that many studies on zygopterans have failed to provide evidence for a consistently higher female adult mortality that might account for the general male excess. The fact that males are potentially able to visit a breeding site constantly from the point of maturation onwards, whereas females have to mature a clutch of eggs before visiting, is one of the most obvious differences in behaviour between the sexes which would limit female numbers relative to males.

Parr & Palmer (1971) calculated the adult sex ratios of three coexisting coenagrionids. They found the sex ratio of *Coenagrion puella* to be 70.0-89.6% male, that of *Enallagma cyathigerum* to be 80.0-92.9% male, and that of *Ischnura elegans* to be 51.3-74.8% male.

Corbet (1952) found that 80% of the total captures of *Pyrrhosoma nymphula* were males. However, he pointed out that owing to differential activity and habitat choice of the sexes, a high proportion of males was to be expected near to the water

even though the true sex ratio may be unity. By analysis of recapture data he was able to show that the sex ratio was influenced by differential activity of the sexes and males actually comprised about 70% of the population.

In the present investigation, if the adult sex ratio is calculated on the basis of the total number of males and females caught and marked throughout the entire study, rather than daily proportions, then the value is lower than before (56.8% male).

No relationship was found between observed number of matings and number of territorial disputes involved in, when controlling for the number of days spent at the ponds. However, when the analysis was taken a step further there was a (just!) significant, positive relationship between observed mating success and number of disputes won as a resident.

In many studies, male dragonflies which defend oviposition sites that are attractive to females have been shown to achieve a higher mating success than non-territorial males (Waage 1973, 1979b; Fincke 1984b; Harvey & Hubbard 1987). In a study of *Calopteryx maculata*, Waage (1979b) found that 15 territorial males, which represented 32% of the males observed, accounted for 74% of matings seen. In a study of *Orthemis ferruginea* (Fabricius), Harvey & Hubbard (1987) found that 35 matings near water were obtained by territorial males, 7 by non-territorial males, and 11 by males of unknown status.

The territories of *P. nymphula* only represent air space around a perch site, so in themselves they are not attractive to females. Given the amount of vegetation around the study ponds and its structural complexity there does not appear to be any shortage of these territories. However, it is possible that perch sites in particular areas (e.g. high up, near to the water) may provide better vantage points to fly out to incoming females. The fact that these simple territories seem to be so abundant may explain why interlopers do not usually attempt to escalate contests. In addition, escalated contests will be energetically expensive and males may avoid them whether territories are rare or common.

There is only a limited amount of data available on the number of matings

resident males obtain relative to interlopers. This is partly because most individuals were both residents and interlopers in different disputes, and partly because interlopers tended to be unmarked males which were caught immediately after a dispute and were therefore removed from the mating arena. However, for those males that were either residents or interlopers in all disputes they were involved in, there was no significant difference in mean number of matings. There was also no significant difference in the mean number of matings between those individuals having won 3 or more disputes as a resident, and those having lost 3 or more disputes as an interloper.

Given this, it is surprising that observed mating success was positively correlated with the number of disputes won as a resident, especially since observed mating success was unrelated to the total number of disputes an individual was involved in. It is possible that the correlation arises from differences in reaction to stimuli, due perhaps to energetic differences, or variation in visionary capabilities. Hence, those males that were more likely to fly out to interlopers (and thus win more territorial disputes) would also be more likely to fly out at potential mates.

However, it is perhaps more likely that the males which won more territorial disputes and achieved more matings were simply those that spent more time at the ponds. While it was possible to calculate partial correlations controlling for the number of days spent at the ponds, it is not possible to control for the amount of time spent there within a day.

Perhaps the major finding of this study was that size had no effect on the outcome of territorial disputes. There was no significant difference in mean size between resident and interloper male (i.e. larger males do not exclusively hold territories), and in almost all disputes the resident won. Those disputes in which the resident did not win arose because of confusion over residency.

Game theory models for asymmetric contests usually predict a quick resolution to a contest using conventions involving display and recognition of an asymmetry between the opponents. Such an asymmetry may be size, experience, or simply residency (Maynard Smith & Parker 1976; Maynard Smith 1982). Escalated contests

are expected only if a second asymmetry outweighs the first, or if the value of the contested resource is sufficiently high and perceived to be so by both contestants, or if there is confusion over, or incomplete information about, the normal contest settling asymmetry (Maynard Smith & Parker 1976; Waage 1988). Thus, both quick resolution and escalation of contests can occur by means of a simple residency convention that may not be correlated with fighting ability or resource value (Maynard Smith & Parker 1976; Waage 1988).

In studies of *Calopteryx maculata*, Waage (1983, 1988) found that territorial contests between males normally involved one or a few short persuits of an intruder by a resident, a situation very similar to that occurring in *P. nymphula*. However, in a 3-year sample of 2005 bouts, 18.5% involved escalated, spiralling, aerial chases that were significantly longer, some lasting several hours. Waage concluded that escalation was probably due to situations in which two males accidently became residents in the same territory, the same explanation given here for *P. nymphula*. Waage was actually able to test the 'confusion over residency' hypothesis for escalation by using moving territories (oviposition sites).

Thus, among male *P. nymphula* a simple residency asymmetry appears to settle most territorial disputes. In this respect it is similar to that found by Davies (1978) in the speckled wood butterfly (*Pararge aegeria* L.). He found that the rule for settling contests was 'resident wins, intruder retreats'. Individuals could be made winners or losers simply by reversing their status as resident and intruder in a sun spot. Escalations only occurred when two males were made residents simultaneously. It seems likely that the reason *P. nymphula* interlopers accept defeat immediately without a serious fight is the same as that given by Davies. That is, that contests may be costly and territories abundant.

Harvey & Corbet (1986) studied the behaviour of final instar larvae of *P. nymphula* during laboratory-staged territorial interactions. They attempted to determine the relationship between outcome and any asymmetries which existed during the contests. They found that occupants won 72%, and intruders 22%, of encounters.

Size differences between larvae did not affect the outcome of the interactions.

Harvey & Corbet (1985) claimed that the territorial behaviour of *P. nymphula* larvae enhanced short-term mating success in adult males. They found that larvae which obtained more food became larger in the final instar, and that larval and adult size were positively correlated. Field observations were then carried out which, they suggested, demonstrated that larger males won more territorial disputes and obtained more matings near to the water.

The results of this present study appear to contradict this. Size was not found to affect the outcome of territorial disputes, and it has been argued that there is no firm, conclusive evidence to suggest that males which won more territorial disputes obtained more matings.

The way in which Harvey & Corbet (1985) arrive at their conclusions is by first plotting a frequency distribution of male head widths in the population at emergence. They then plotted two similar frequency distributions, one of head widths of males winning territorial disputes, and another of males caught copulating. The mean head widths of the three groups of males were then compared.

There is, however, a fairly obvious flaw in their analysis. Finding that the mean head width of males winning territorial disputes was greater than the mean head width of males measured at emergence does not necessarily imply that larger males win more territorial disputes. The mean head width of males winning disputes was not compared with that of males losing disputes, and the losers were not compared with the original emergent population. There may have been size-dependent mortality occurring during the maturation period such that fewer small individuals were represented in the mature population, or some other factors may have affected the distribution of small males relative to larger males.

Therefore, unless the disribution of small males is known, or alternatively the size of the losers of the territorial disputes, it is not valid of Harvey & Corbet to conclude that larger *P. nymphula* males won more territorial disputes and enjoyed enhanced mating success.

Chapter 7. Reproductive biology of female *Pyrrhosoma nymphula*.

7.1 Introduction.

The aim of this study was to investigate factors affecting egg size and egg numbers/clutch size in female *P. nymphula*. Potential factors which could affect egg size were female skeletal size, egg numbers, date of sampling through the season, and the length of time since a previous clutch was laid (the inter-clutch interval). The last of these could not be estimated in this study owing to the lack of site attachment of marked females. Similarly, egg numbers could potentially be related to female skeletal size, egg size, sampling date, and the inter-clutch interval.

In a recent study of another coenagrionid damselfly, *Coenagrion puella*, Banks & Thompson (1987b) found that females maximised their lifetime egg production by minimising the interval between clutches, rather than by maximising the size of each clutch. They found that egg size was not correlated with female size, and that clutch size was inversely related to body size. This study provides indications that the reproductive biology of female *P. nymphula* differs in several instances from that of *C. puella*.

7.2 Materials and methods.

7.2.1 Determination of clutch size and mean egg size.

At regular intervals throughout May and June 1988, six samples of mature females were taken around ponds A and B. Between 10 and 20 females were caught on each occasion (mean 15.8), either unpaired, in tandem, or ovipositing. Females were caught as early in the day as possible to ensure that few eggs, if any, had been

deposited.

In the laboratory, females were anaesthetised with ether, the head width measured under a binocular microscope, and the abdomen length measured to the nearest 0.05mm using dial callipers. They were then weighed to the nearest 0.01mg, killed by prolonged exposure to ether, and then preserved in 70% alcohol until such time as they could be dissected.

The females were dissected under 70% alcohol and the total number of eggs inside the abdomen was counted under a binocular microscope. Mature eggs could easily be distinguished from immature eggs by their larger size. Often the abdomens would be packed with large numbers of mature eggs, with immature eggs of all sizes occurring in 'strings' towards the anterior of the abdomen.

There were indications that almost all mature eggs are laid during an oviposition bout. Two females caught towards the end of a day after a natural separation from their partners, were found to possess very low numbers of mature eggs relative to similar sized females caught earlier in the day (between 20-30 eggs compared with a mean of around 350 eggs for females caught early in the day). This suggests that mature egg numbers are equivalent to clutch sizes.

Thirty eggs were measured under the binocular microscope fitted with an eyepiece micrometer. Each egg was selected at random, the length was measured to the nearest 0.01mm. The mean egg length corresponding to each female was then computed.

Finally, a sample of eggs was removed to be weighed. Using the tip of a scalpel blade, eggs were individually picked up and placed in a drop of alcohol on a small piece of aluminium foil. The average number of eggs taken from each female was 79. The eggs were dried at $60^{\circ}C$ for at least 7 days and were then dry weighed on a Cahn C29 electrobalance to the nearest $0.1\mu g$. The eggs and foil were first weighed, then the eggs were removed with a scalpel blade under a binocular microscope, and finally the foil was weighed to give the weight of the eggs by subtraction.

The three measures of female size were all highly significantly correlated with

each other. Because wet weight was likely to vary with egg number and egg weight this measure was not used in the following computations. Head width was generally used as the measure of female size, although abdomen length was used where it was considered appropriate.

7.3   Results.

7.3.1   Factors affecting egg weight.

There was no relationship between egg weight and egg length. This result is perhaps not surprising considering the potential for variation in egg length and weight. For instance, slender eggs of a given length could weigh the same as shorter, squat eggs, or they could weigh differently from eggs of the same length which were broader.

The first sample of females was taken on the 15th May and the last on 23rd June. Over this period, mean egg weight ranged over 7.8μg from 11.6-19.4μg (mean 14.3, SE 0.2, n=92). Egg length ranged over 0.18mm from 0.96-1.14mm (mean 1.07, SE 0.01, n=95).

Data analyses were carried out separately for both egg weight and egg length. However, because the end results were the same for both variables, only those using egg weight are presented. Weight gives a better indication of overall egg size compared with length which is a measurement in only one direction.

For both head width and abdomen length there was a significant decline in size over the study period. Figure 7.1 shows the relationship between head width and date.

There is a significant decline in mean egg weight through the study period (Fig. 7.2a), and a significant positive relationship between mean egg weight and female head width, but not abdomen length (Fig. 7.2b). It is likely that one or other of these
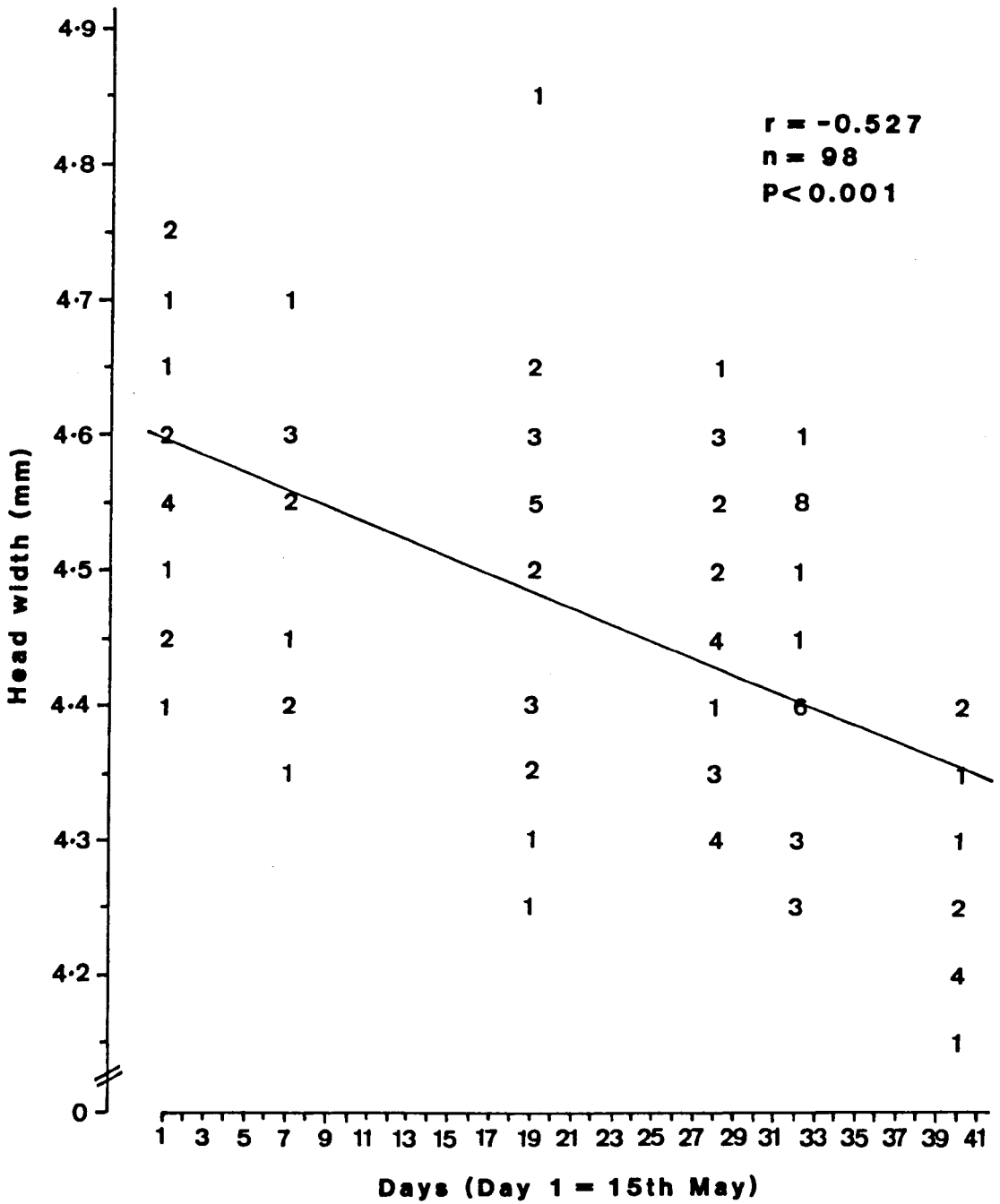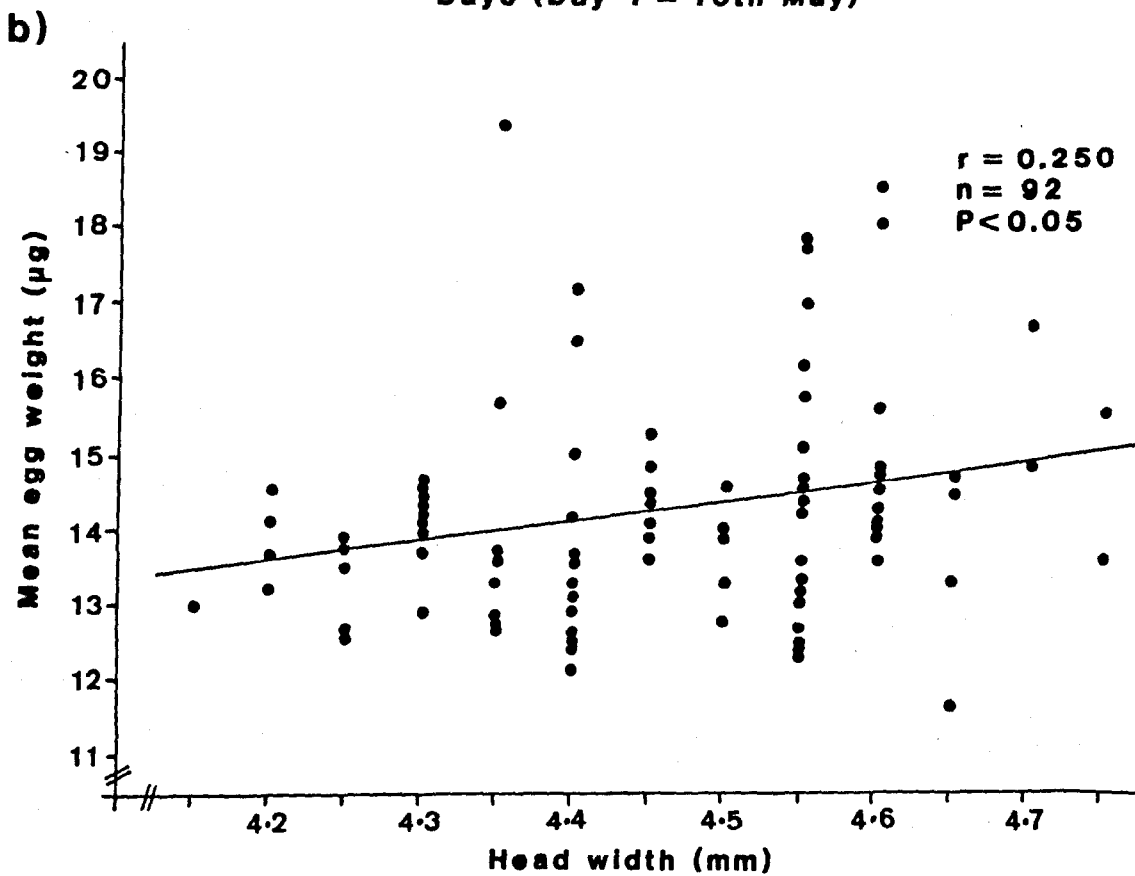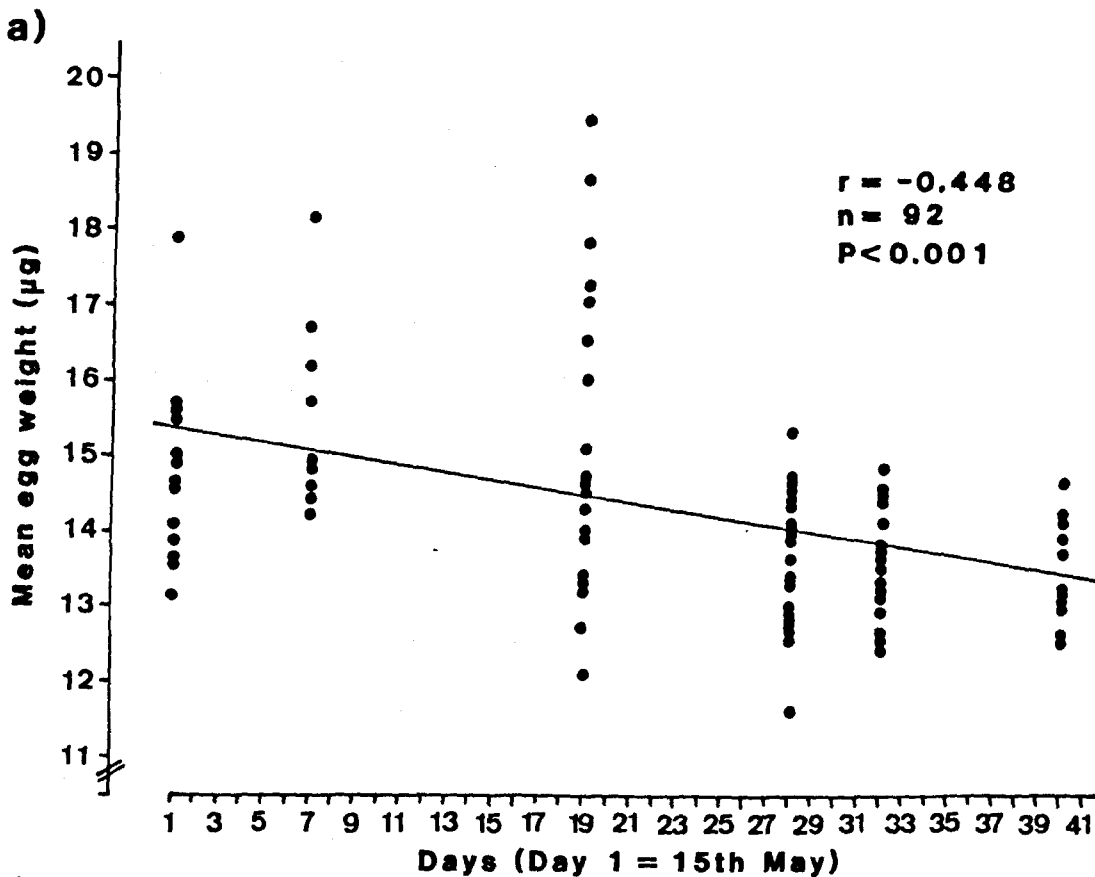
Fig. 7.1   The decline in female head width through the season.

Fig. 7.2   **a)** The relationship between mean egg weight and date of sample, and **b)** the relationship between mean egg weight and female head width.

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relationships is a spurious correlation generated by intercorrelations between egg weight, female head width, and sample date. The decline in mean egg weight with date could have arisen because of the real relationship between head width and date and the relationship between mean egg weight and head width. Alternatively, the increase in mean egg weight with head width could have arisen out of the genuine decline in head width with date and the relationship between mean egg weight and date.

To determine which of the two relationships in Figs. 7.2a,b is genuine it is necessary to calculate partial correlation coefficients controlling for head width and date respectively. Table 7.1 presents the results of this analysis. The relationship between mean egg weight and female size is lost when date is controlled for, while the relationship between mean egg weight and date remains significant when head width (or any other size measure) is controlled for. The same conclusion is arrived at if correlations between mean egg weight and date are computed for groups of females having identical head widths.

Figure 7.3 shows the relationship between mean egg weight and clutch size. There is a significant positive correlation between the two variables. However, egg size has already been shown to decline with date of sampling, and clutch size also declines with date (see section 7.3.2). Both of these correlations appear to be genuine. Spurious correlations can be generated between both mean egg weight and clutch size when these are plotted against skeletal size measures. When the complicating effects of date and female size are held constant using partial correlation analysis the significant relationship between mean egg weight and clutch size is lost (see Table 7.2).

Therefore, it appears from Pearson and partial correlations that the only factor having any effect on mean egg weight is the date on which a sample of females was caught. This is further supported by multiple regression analysis which showed that date was the only significant variable accounting for variation in egg weight (contributing to 20.1% of the total variation).

Correlation of mean egg weight with :-	Controlling for :-	Partial correlation coefficient	n	P
Date of sample	Head width	-0.388	87	P< 0.001
Head width	Date of sample	-0.017	87	P= 0.878

Table 7.1 Partial correlations of mean egg weight with date, controlling for female head width, and of mean egg weight with female head width, controlling for date.
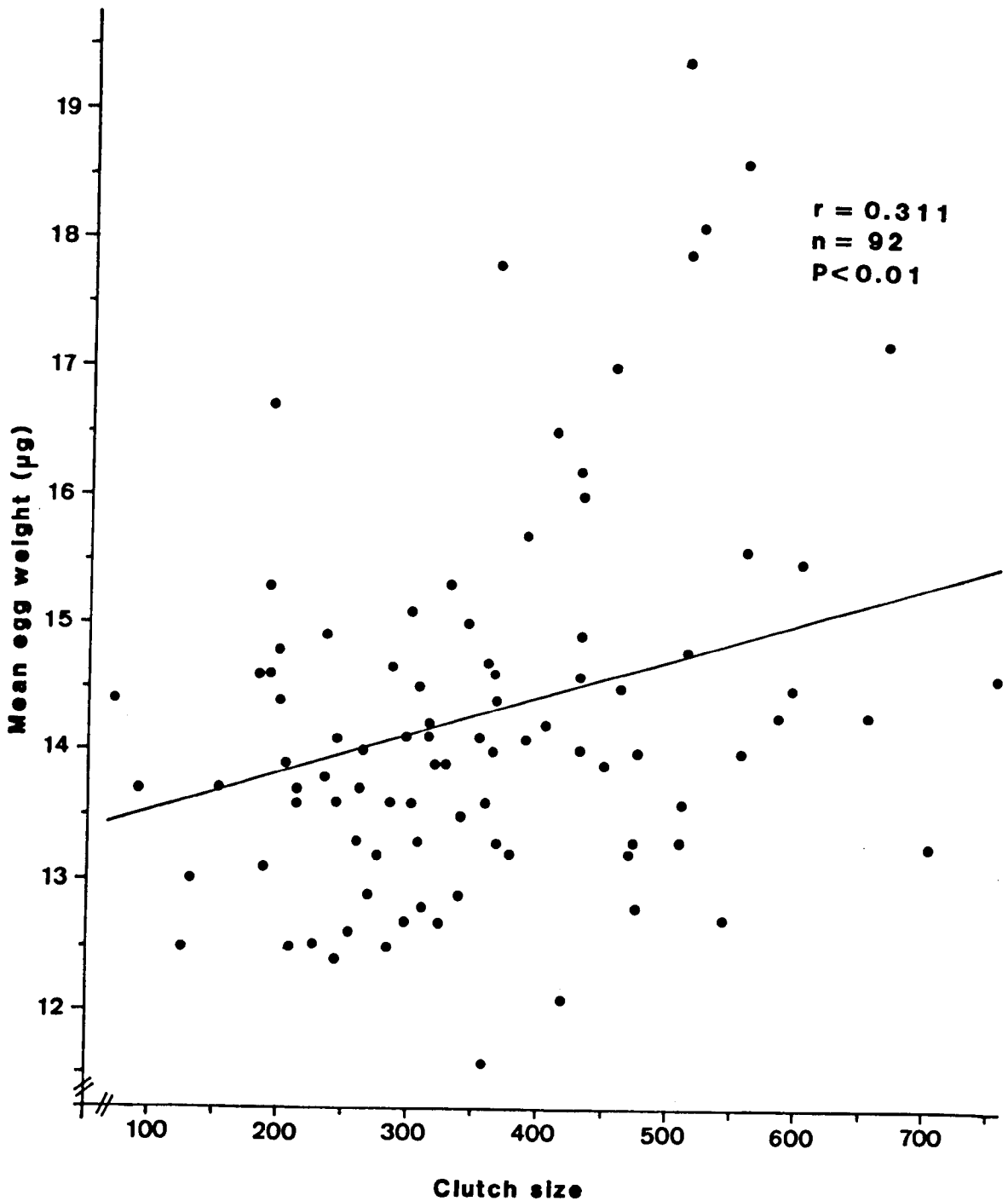
Fig. 7.3   The relationship between mean egg weight and the
             total number of mature eggs (clutch size).

Partial correlation controlling for :-	Partial correlation coefficient	n	P
Date of sample	0.174	89	0.098
Date of sample and head width	0.176	88	0.098

Table 7.2 Partial correlations between mean egg weight and clutch size, controlling for sample date, and for sample date and head width.

7.3.2   Factors affecting clutch size.

Egg numbers dissected from a total of 95 females ranged from 68-754 with a mean of 350.6 (SE 14.5). Figure 7.4 shows that there is a significant negative relationship between clutch size and date of sample, and Fig. 7.5 shows that there is a significant positive relationship between clutch size and female head width. As before, it is necessary to calculate partial correlation coefficients to determine which of the two is a genuine relationship.

The relationship between clutch size and female size is lost when date is controlled for, while the relationship between clutch size and date remains significant when head width (or any other size measure) is controlled for (Table 7.3). Multiple regression analysis also showed that sample date was the only significant variable accounting for variation in clutch size (contributing to 13.8% of the total variation in egg numbers).

It might be expected that when clutch sizes are particularly high, the physical size of a female's abdomen might limit the maximum number of eggs in a clutch. Having said this, is has just been shown that the relationship between clutch size and female head width disappeared on applying partial correlation analysis, and identical results can be obtained when head width is replaced by abdomen length. However, if only those females having clutch sizes greater than 400 are included in the analysis then the results are different. As expected, a significant positive relationship is generated between clutch size and abdomen length ($r=0.414$, $n=32$, $P=0.019$), but this relationship remains significant when a partial correlation coefficient is calculated controlling for sample date ($r=0.403$, $n=29$, $P=0.024$). Thus, there are indications that beyond a certain clutch size female skeletal size may be important.

It is likely that the decline in clutch size over the study period is mainly due to the pattern of sunny and cloudy days. For instance , on the third sampling occasion (day 19 or 2nd June) egg numbers were generally higher than might be expected, and this followed four days of overcast, dull weather on which there was little or no
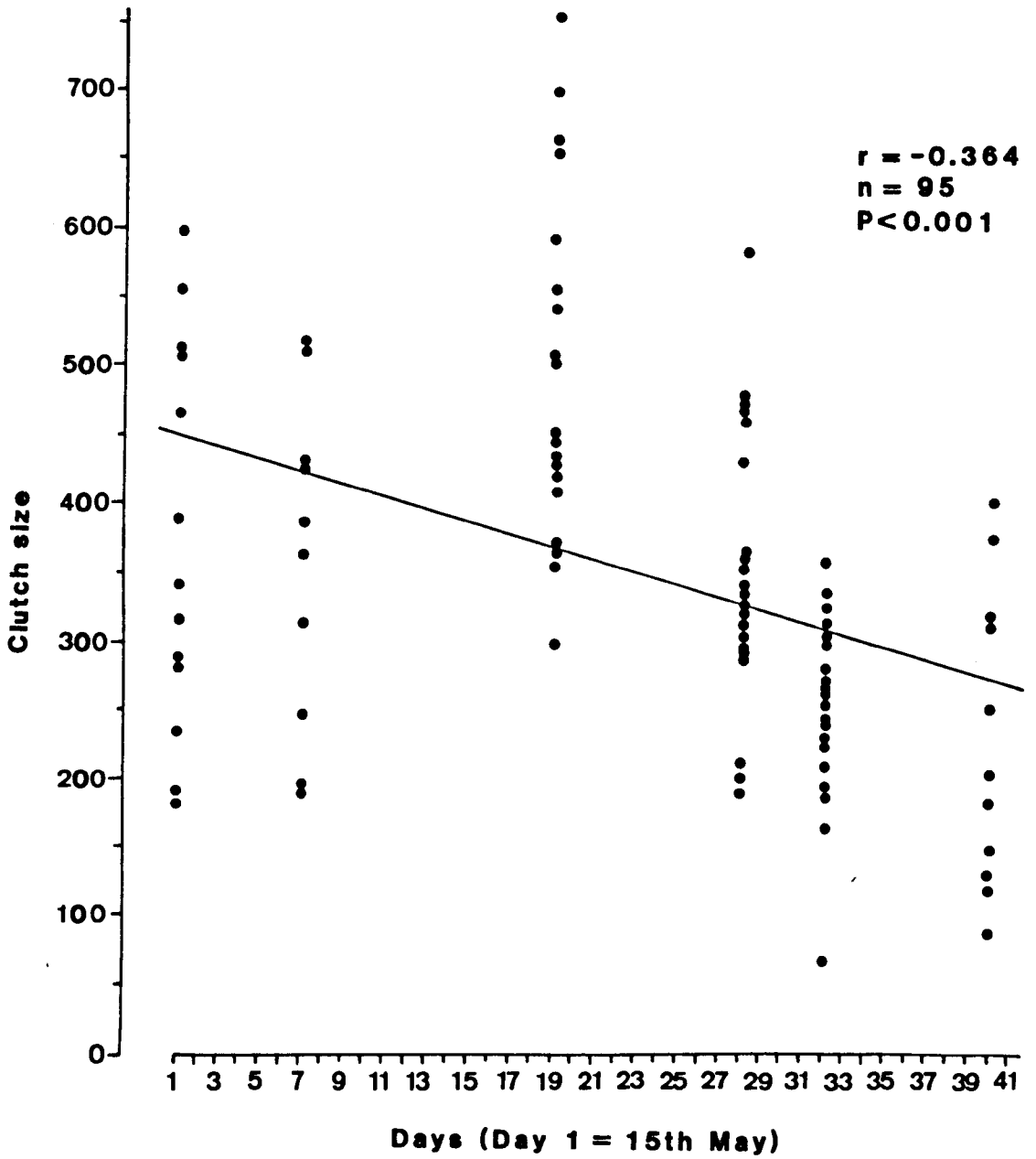
Fig. 7.4   The relationship between clutch size and
           date of sample.
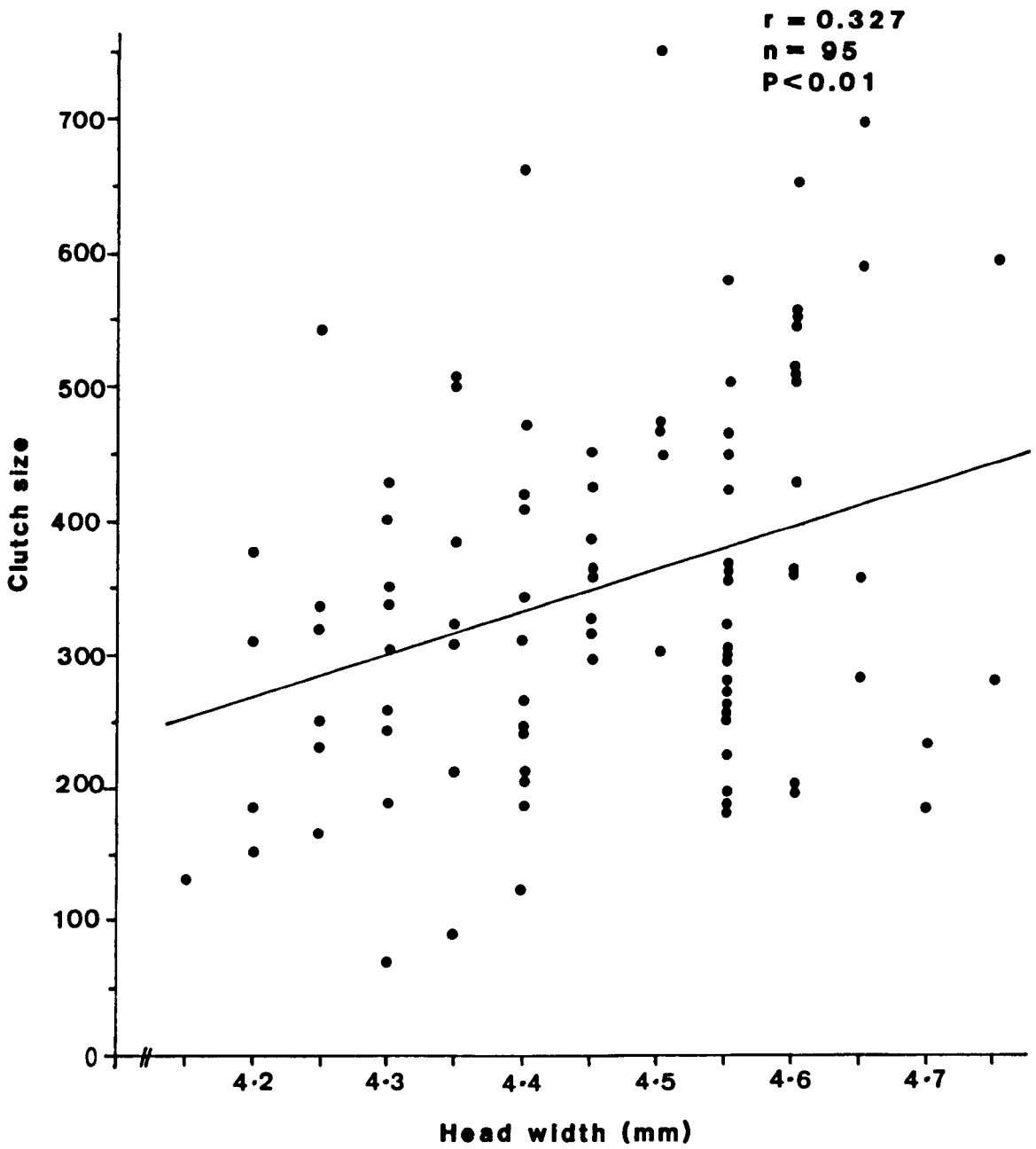
Fig. 7.5   The relationship between clutch size and head width.

Correlation of clutch size with :-	Controlling for :-	Partial correlation coefficient	n	P
Date of sample	Head width	− 0.217	90	P < 0.05
Head width	Date of sample	0.185	90	P= 0.078

Table 7.3 Partial correlations of clutch size with date,

controlling for female head width, and of clutch

size with head width, controlling for date.

reproductive activity. Females unable to visit the ponds over this period presumably would have been able to mature large clutches of eggs. Towards the end of the study period the egg numbers on the fifth and sixth sampling occasions (day 32 and day 40, or 15th and 23rd June) fell towards the lower end of the range. The weather prior to these days was warm and sunny and thus suitable for reproductive activity.

If the range in clutch size corresponding to each sampling occasion is allocated to one of three qualitative groupings (small, medium and large) then this agrees closely with predictions based on the pattern of cloudy and sunny days prior to a particular sampling date.

This might suggest that if the weather patterns had been considerably different, then the relationship between clutch size and sampling date may have been positive or unsignificant, rather than negative. Further investigation would be required to deduce whether or not variation in clutch size arises only from differences in the inter-clutch interval.

7.4   Discussion.

Despite the large amount of variation in mean egg weight (ranging between 11.6-19.4µg), no relationship was found between this and female size, when controlling for sample date. Similarly, in a study of *Coenagrion puella*, Banks & Thompson (1987b) found that mean egg weight was not correlated with female skeletal size.

Clutch size was also uncorrelated with female size when sample date was controlled for. However, there were indications that abdomen size may genuinely limit clutch size at high enough levels. The fact that such a relationship only applies when egg numbers are high indicates that a physical size limitation is a more likely explanation than, for instance, larger females being more successful in competition for food.

Banks & Thompson (1987b and references therein) reported that positive relationships between female skeletal size and clutch size have been reported for several insect groups including butterflies, mayflies and dung flies. However, they found an inverse relationship between female size and clutch size for those clutches taking one day to mature (the majority of clutches) in *Coenagrion puella*. They suggested that clutch size would be a decreasing function of body size because of the way in which the energetic cost of flight scales with body size. There was no such relationship in clutches taking longer to mature, and they found that overall, lifetime egg production was positively correlated with female body size because larger females produced a greater number of clutches.

Clutch size was found to vary between 68-754, despite females being caught as early in the day as possible. It is likely that even when egg numbers are high almost all will be laid during a days oviposition. Female *Coenagrion puella* contained an average of 12.7 eggs as they flew away from a breeding site at the end of oviposition, whereas initial clutch sizes ranged between 110 and 250 eggs (Banks & Thompson 1987b). In a study of *Chromagrion conditum*, Bick, Bick & Hornuff (1976) found that eggs were deposited at a rate of 5.5 per minute, resulting in an expected average complement of 200 eggs being deposited for each sequence of oviposition. Waage (1978) found that egg deposition rates for *Calopteryx maculata* averaged 7-10 eggs per minute for four common plant species. Multiple bouts for marked females showed that an average of 230-328 eggs may be laid per day, while maximum duration of oviposition per day was 75 minutes which would correspond to between 525-700 eggs being deposited.

Both mean egg weight and clutch size were found to be significantly negatively correlated with sample date. That is, females visiting the ponds later in the season tended to lay smaller clutches and smaller eggs than those arriving early in the season, irrespective of size. Because reproductive lifespan is likely to last only a few days, those females caught later in the season are likely to be individuals that emerged later and reached sexual maturity later than those caught early on.

The decline in clutch size may be closely related to the weather pattern (and thus the inter-clutch interval), and this will be discussed further below. Alternatively, or additionally, the decline may be related to fundamental differences in females' physiology or behaviour.

A decline in egg size and egg numbers in late emerging females may arise because these females have a shorter maturation period. It is unknown whether there is variation in the length of the maturation period in *P. nymphula*, but Michiels & Dhondt (1989) found maturation time to be inversely related to emergence date in the dragonfly *Sympetrum danae*. They suggested that this arose due to photoperiod cues and attributed it to the need to speed up maturation as the risk of bad weather increased rapidly towards the end of the season. If late emerging *P. nymphula* females are also maturing faster, they may be unable to produce as many eggs or as large eggs as females which have been able to spend longer in the teneral stage.

Late emerging females will have suffered reduced development rates and size increases as aquatic larvae, resulting from competition with larger, early emerging adults. An alternative explanation for the above results could be that the detrimental effects of such competition may directly affect a female's egg producing capability.

It is also possible that the decline in mean egg weight and clutch size through the study period may be related to female age. Because of the lack of recaptures of females marked at emergence or when mature, information on longevity could not be collected. However, it is likely that a sample of females caught towards the end of the season would contain a higher proportion of older females relative to one caught at the beginning of the season. Begon & Parker (1986) devised a model in which female insects gathered resources for eggs in a pre-reproductive phase, and then were subject to mortality during the production of successive clutches of offspring in a reproductive phase. The broad predictions of the model were that if clutch size was constrained, egg size should decline with maternal age. Similarly, if egg size was constrained, clutch size should decline with maternal age. They were able to find support for their model in a variety of species, particularly in butterflies.

Date of sampling was the only variable found to account significantly for any variation in clutch size. It has been suggested that sample date has a stong effect on clutch size via the pattern of sunny and cloudy days prior to it, and thus the time since females last oviposited. Banks & Thompson (1987b) found that the most important determinant of clutch size in *Coenagrion puella* was the time since the previous clutch was laid. They found that the longer the inter-clutch interval, the larger the subsequent clutch, with the maximum being reached after 3-4 days. However, females would maximise their lifetime egg production by minimising the period between clutches. This is because a clutch that took two days to mature was less than twice as big as one that took one day to mature, and because the shorter the period between clutches, the higher the propability of actually surviving to lay another clutch.

The inter-clutch interval for females in this study is not known, but it is likely that it too would have been an important determinant of clutch size. However, comparison of the results found for *P. nymphula* with those of Banks & Thompson (1987b) for *C. puella* indicates that female *P. nymphula* probably do not come to the water every day to breed. It is not known whether this is because they are prevented doing so due to adverse weather, or because they actively avoid the ponds even on fine days.

During a period in which over 85% of days were sunny, most (60%) clutches of *C. puella* were produced on the day following the previous clutch (Banks & Thompson 1987b). The mean weight of newly emerged females was 39.2mg while the mean weight of mature females was 50.5mg, the range for mature females being 33.2mg (M. J. Banks unpublished). For female *P. nymphula*, the mean weight at emergence was 39.8mg and the mean weight of mature females was 66.1mg, the range being 45.7mg (see section 5.3.1). Thus, female *C. puella* show a 28.8% increase in original mean wet weight from emergence to maturity, while female *P. nymphula* show a 66.1% increase in original mean weight.

Such a substantial difference in weight increase between the two coenagrionids might suggest that female *P. nymphula* build up large clutches of eggs over comparatively long inter-clutch intervals, and thus visit the ponds only on occasions.

Fincke (1988) found that female *Enallagma hageni* visited a study pond on average once every 6 days. Female *E. hageni* submerge completely to oviposit and suffer a fixed probability of failing to escape from the water at the end of each bout of oviposition, which is independent of the duration of the oviposition bout. They minimise the risk of mortality by minimising the number of oviposition bouts, and thus by producing large clutches with long inter-clutch intervals (O. M. Fincke, personal communication with Banks & Thompson 1987b).

It has already been mentioned that *P. nymphula* females are at risk from predation from water beetles, dragonfly larvae, and frogs and newts during an oviposition bout. Unfortunately, no quantitative data was taken on female mortality during oviposition but on occasions considerable numbers of females were found with abdomens consumed.

Therefore, it is possible that females might reduce the risk of mortality by reducing their total number of oviposition bouts. However, the probability of predation is likely to increase with the duration of oviposition. Banks & Thompson (1987b) indicated that a higher risk of mortality during oviposition would not favour longer inter-clutch intervals unless the rate of egg laying during oviposition increased with the inter-clutch interval.

Further evidence that females do not visit the ponds every day is provided from comparison of the operational, absolute, and emergent sex ratios. Fincke (1988) estimated an absolute sex ratio of 1.3 males: 1 female for *Enallagma hageni*. As stated above, females visited the pond on average once every 6 days. Males visited the ponds nearly twice as frequently, and this resulted in an operational sex ratio of 2.6 males: 1 female.

In this study the sex ratio at emergence averaged 1.17 males: 1 female, the absolute sex ratio (calculated from the total number of males and females visiting both ponds over the summer) was 1.31: 1, and the average operational sex ratio was 1.57: 1. Thus, it would appear that males visited the ponds between 1.20 and 1.34 times as frequently as females. Since it is unclear whether all males visit the ponds on every

available fine day during their reproductive lifespan it is not possible to speculate further about the length of the inter-clutch period of female *P. nymphula*.

To conclude, for female *P. nymphula*, egg size and clutch size decrease with sample date. This may be related to the need for faster maturation later in the season, or to differences in adult fitness or longevity. Clutch size is likely to be strongly related to the inter-clutch interval, and there are indications that females may not visit the ponds every day to breed. Studies of other zygopterans have indicated that females would maximise their lifetime egg production by minimising the period between clutches. If the reasons behind this also apply to female *P. nymphula*, then some stronger, opposite force must be preventing females from ovipositing daily. This may be related to mortality risks or perhaps to climatic limitations. Not only will bad weather prevent reproductive activity, but it is also highly likely that egg production is related to temperature. Clearly a more detailed study, preferably at an isolated water body, is necessary to unravel the inter-relationships between factors affecting the reproductive biology of female *Pyrrhosoma nymphula*.

Chapter 8.   General Discussion.

Each preceding chapter includes a detailed discussion of the results within it. This chapter contains a synthesis of the work together with general conclusions that may be drawn from it, and particular areas where further investigation is required. In particular, the following topics will be covered: a discussion of the results of the competition experiment in relation to larval population dynamics; the relationship between the larval and adult stages of the damselfly life-history with particular emphasis on how size and seasonal occurrence may affect adult longevity and reproductive success; the vulnerability of individuals at emergence and when mature, and their dependance on fine weather conditions for survival and expression of reproductive potential; and the reproductive biology of female *P. nymphula*.

In Chapter 2 it was shown that there is an asymmetry in the way interference competition acts when small and large larvae are contained together with unlimited prey. Small larvae suffered significantly reduced development rates and size increases at the moult in the presence of larger larvae but similar reductions were not apparent when small larvae were combined with like-instar larvae, or when large larvae were combined with small larvae. The instars used in the experiment were within the range found to occur naturally in field populations. However, in natural populations such interference effects are likely to be reduced by the availability of refuges and by habitat complexity, but also intensified by food limitation. The effects of density were not investigated in this experiment. Larval density may affect survival, development and size in field populations (Banks & Thompson 1987a).

Adults which emerge early in the season will lay eggs that will hatch several weeks earlier than those of late emerging adults. Thus, at the end of the summer initial size differences between larvae will already be established. Whether such larvae are in a uni- or semi-voltine population, these initial differences will be maintained or even exaggerated by such interference competition found in this experiment. Thus, larvae that are successful in competition will emerge both earlier and larger than their

less successful conspecifics.

Size and date of emergence may have a strong effect on adult longevity and reproductive success. This will be further discussed below. A more direct consequence of such competition may be that some larvae do not even survive to emergence. In the laboratory larvae may interfere with each other's feeding usually by means of an aggressive interaction (Baker 1980, 1981; McPeek & Crowley 1987). Several field experiments have shown that interference can result in mortality, injury or cannibalism (Benke, Crowley & Johnson 1982; Merrill & Johnson 1984; Johnson *et al.* 1985; Baker & Dixon 1986; Crowley *et al.* 1987a).

In a field study of *Coenagrion puella*, Banks & Thompson (1987a) found that larvae in high density populations were smaller than those in low density populations and were more likely to have a semi-voltine life-history. They also found that in the high density population there was a constant rate of larval mortality, while in the low density population there was no detectable mortality. Not only will the intensity of interference competition increase with density, but the likelihood of exploitation competition will be greater as food supplies are diminished. If female lifetime fecundity is correlated with female size (as it is in *C. puella* (Banks & Thompson 1987b)), then female fecundity will depend on larval density. Hence, a density-dependent reduction in larval (and thus adult) size or larval survivorship may have important implications for damselfly population dynamics (Crowley *et al.* 1987b).

The dynamics of damselfly populations have been modelled by Crowley *et al.* (1987b). They simplified the life-history into six stages, these being eggs, small larvae, large larvae, final instar larvae waiting to emerge, immature adults and mature adults. Their theoretical study indicated several areas where data are lacking, and suggested potential studies which would test the understanding of damselfly population dynamics. With respect to larval population dynamics, they suggested that more field experiments capable of detecting and measuring both feeding- and mortality-related interference are required. In their model, density-dependent predation

and interference mortality are of central importance because they supply the regulation, although other factors also help determine densities. More field experiments on the potential for prey depletion by damselfly larvae, and additional laboratory studies on the relation between growth rate and feeding rate are also needed. Finally, they suggested that quantitative data on the relative spatial distributions of larval instars in the field is essential to a better assessment of the potential of interference between larval stages, which is a key determinant of the model's behaviour.

The overall conclusion that may be drawn from the above is that larvae which have been adversely effected by interference competition for food or fishing sites, given that they survive, will be smaller and emerge later than competitively successful larvae. However, before simply extending the findings obtained with *Ischnura elegans* and assuming that *Pyrrhosoma nymphula* will be likewise affected, it should be remembered that *I. elegans* is essentially univoltine in the north of England while *P. nymphula* has a semi-voltine life-history. Thus, for *P. nymphula* larvae, not only will there be size differences within an age-class, but there will also be greater size differences between the junior and senior age-classes. The effect of this may be that not only may small larvae of one age-class be forced out of profitable feeding areas, but in addition, the majority of the junior age-class may either be forced into a different area, or may disperse to a different area to avoid aggressive interactions with larvae of the senior age-class. Spatial segregation of small and large larvae has been demonstrated in semi-voltine populations of *Coenagrion puella* (Banks 1985) and *P. nymphula* (Lawton 1970).

In Chapter 3 it was shown that the emergence of *P. nymphula* from pond B was earlier than that from pond A and adults were larger than those from pond A, thus illustrating that there may be differences between, as well as within, populations. In this case these were likely to be related to variation in prey density, differences in prey availability and distribution, and perhaps temperature differences. Also in Chapter 3, a decline in size of emerging *P. nymphula* adults through the season was found at both ponds. Similar size declines through emergence have been shown in both zygopterans

and anisopterans (e.g. Banks & Thompson 1985a; Thompson 1987b; Michiels & Dhondt 1989).

Adult size and seasonal occurrence may have a strong influence on reproductive success of both males and females. Having said this, it is also possible that selection might favour, for instance, large size in larvae because it may increase the chances of surviving to maturity, but size may have little or no effect actually within the adult stage of the life-history.

Examples of fairly obvious advantages of large size to adult males can be obtained from studies of strongly territorial dragonflies. Fincke (1984b) found that territorial male *Megaloprepus coerulatus* were larger than non-territorial males and achieved a higher number of matings. Contrary to what might be expected, in Chapter 6 it was shown that size appears to have little influence on male mating success in *P. nymphula*, at least in the short-term. Size was shown to have no effect on the outcome of territorial disputes, and was found to be unrelated to the number of days a male spent at the ponds, and a male's total number of observed matings. There was an indication that paired, first-visit males were larger than unpaired males but this was assumed to have been due to the larger males being older and having more mating experience at that point in time. Over a mature adult's lifespan such advantages would be cancelled out.

It would, however, be unwise to conclude that there are no benefits of large size to adult male *P. nymphula*. Perhaps the major problem with this study was the lack of an enclosed, isolated field site, and therefore the low recapture of marked individuals. As a result of this it is unknown whether size is important with respect to longevity. Size was shown to be unrelated to the number of days spent at the ponds by males, but this may have been affected by the high levels of dispersal. There were indications, from comparison of mature and emerging adults, that the smallest newly emerged individuals were unrepresented in the mature adult sample. This may suggest that there is a higher mortality among smaller adults in the immature period. Michiels & Dhondt (1989) found that larger, early emerging *Sympetrum danae* lived longer than

smaller individuals if they remained within the study area, and Banks & Thompson (1985a), in a study of *Coenagrion puella*, found that the number of days a male spent at the breeding site was mostly determined by its mature lifespan, and that larger males lived longer.

Similarly, in Chapter 7 it was shown that there was no relationship between female skeletal size and either mean egg weight or clutch size. However, there were indications that for larger clutches the total number of eggs may be limited by the physical size of a female's abdomen. Banks & Thompson (1987b) found an inverse relationship between clutch size and female size in *C. puella* for those clutches taking one day to mature. However, because larger females lived longer, they concluded that selection should favour large size in females.

Larvae suffering adversely from competition will suffer decreased development rates as well as reduced size increases and therefore may emerge later in the season than other larvae. There is likely to be a trade off between the expression of temporal variation arising in part from competition, and the need to emerge around the same time as conspecifics in order to achieve a full reproductive potential. Date of emergence may be important in the adult stage of the life-history for a number of reasons. Early emerging males will mate with larger, early emerging females which may, under certain circumstances, lay larger clutches of eggs (see above).

In Chapter 7 it was shown that females visiting the ponds later in the season tended to lay smaller clutches of smaller eggs than those arriving early in the season, irrespective of size. The mature females caught early in the season would have emerged earlier than females caught later on. It was suggested that late emerging females may have laid fewer, smaller eggs because of an incomplete or accelerated maturation period. Michiels & Dhondt (1989) found that maturation time was inversely related to emergence date in *Sympetrum danae*. They concluded that there was a need to speed up maturation as the risk of bad weather increased towards the end of the season. Deterioration of the weather later in the summer would clearly favour early emergence in dragonflies. It was also suggested that if the adverse effects

of competition as larvae in some way affected the normal physiological development of females, then this may in turn affect the capacity to produce eggs in mature adults. The lack of isolation of the study ponds and low returns of marked females made it impossible to determine whether the decline in clutch size through the season represented genuine biological differences between females, or was the product of the pattern of sunny and cloudy days through the season.

The results presented in Chapter 4 illustrate how vulnerable newly emerged adults can be during periods of bad weather. Although the numbers emerging on such days are considerably reduced, some individuals still attempt emergence. This is presumably due to the progression of metamorphosis. Mortality is particularly high when there is a sudden change in the weather from fine, dry conditions on one day, to wet, windy conditions the next. Adults which emerge on cold, wet or very windy days are usually unable to fly from the ponds and are therefore exposed to the risk of predation there for longer. In the study of mortality during emergence, mean overall mortality, expressed as a percentage of the total daily emergence, was calculated to be 38.38%.

The difficulties involved in such a study of emergence mortality have been outlined. Assumptions often had to be made about the fate of individuals, particularly those remaining overnight or over several days during periods of continuously bad weather. However, being aware of these drawbacks, the quantification of mortality attributed to different factors does provide a useful insisight into an important area of damselfly population dynamics, and an area which has clearly lacked study until now. In their model of damselfly population regulation, Crowley *et al.* (1987b) stated that more studies of emergence mortality were required and, in particular, of mortality in relation to density. During bad weather fewer individuals emerged from the ponds. At the same time these individuals were rendered more at risk because flight from the ponds was not possible. In some instances this caused an inverse relationship to be produced betweeen density and mortality. Although it was realized that predation by, for instance, birds could potentially be density-dependent, this particular study found

no evidence of density-dependence of mortality at emergence.

In Chapter 5 it was shown that mature *P. nymphula* adults may also be severely affected by periods of bad weather. Dispersal may increase after bad weather and adults only engage in reproductive activity on fine, sunny days. Banks & Thompson (1985b) calculated the mean mature adult lifespan of *Coenagrion puella* to be 5.6 days in males and 5.4 days in females. Even if these values are higher for *P. nymphula* it is clear that bad summers will drastically limit the reproductive potential of a year group. For *C. puella*, Banks & Thompson (1985a) found that the number of days that a male was present at the breeding site accounted for up to 78% of the variance in lifetime mating success. Reproductive lifespan accounted for 70% of the variation in female reproductive success (Banks & Thompson 1987b).

Concerning *P. nymphula* specifically, one particular area of research where further study would prove useful and interesting is that of female reproductive behaviour and, in particular, the determination of the inter-clutch interval and mortality during oviposition. An investigation undertaken at an isolated water body could accurately determine whether females visited every day to oviposit or whether they amassed large clutches of eggs over several days. Such a study would also indicate whether there was a genuine lower survivorship of females relative to males. Fewer females returned to the ponds after release, so producing a reduced survivorship estimate of 0.52 compared to 0.77 for males. If males visited the ponds on every day of their reproductive life but females only did so at intervals, then this in itself would lead to the survivorship of females being lower than that of males. There were indications that, on occasions, very high numbers of females may suffer partial predation by dragonfly larvae (*Aeshna* spp.), water beetles (*Dytiscus marginalis*), and possibly frogs and newts. Large numbers of females were often seen ovipositing in the same area and even on the same piece of aquatic vegetation. The presence of ovipositing females may attract others since they might indicate an area of reduced risk of predation. The construction of shoreline pens either stocked with appropriate aquatic predators or free from predators could be attempted.

What is clear from these studies of both larvae and adults is that damselflies are an excellent taxon with which to study insect ecology and behaviour. They provide ideal subjects with which to study reproductive behaviour and reproductive success since they are large enough to be uniquely marked and easily identified, they usually breed in large numbers and in distinct places such as ponds or streams, and they are short-lived enough to be followed throughout their entire reproductive life. In addition, because they have a complex life-history they provide a challenge to the determination of the mechanisms of population regulation.

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