

**LARVAL DEVELOPMENT AND EMERGENCE
IN *PYRRHOSOMA NYMPHULA* (SULZER)
(ZYGOPTERA: COENAGRIONIDAE)**

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Larval development and emergence were studied over 3 years in a population in Yorkshire, England. Artificial substrates were used as emergence sites in the field to obtain quantitative data on various aspects of emergence. Development was thought to be completely semivoltine at this location, although the possibility of univoltine development is discussed. The proportion of the senior cohort overwintering in the penultimate (F-1) instar varied from zero to approximately 35% in the three cohorts studied. Emergence was synchronised but was interrupted by adverse weather conditions. In the year when F-1 larvae constituted a large proportion of the overwintering senior cohort, their emergence was signified by a small second peak in numbers. The larval sex ratio and the sex ratio at emergence did not differ significantly from unity. Mortality at emergence ranged from 3% to 5% and was mainly due to incomplete ecdysis, failure to expand the wings and predation by spiders. The reasons for the low emergence mortality in this population are discussed.

INTRODUCTION

Pyrrhosoma nymphula is a typical 'spring' species sensu CORBET (1954). It exhibits a synchronised emergence as a consequence of larvae entering diapause in the final instar in autumn, allowing larvae in earlier instars to catch up with faster growing members of the same cohort (CORBET, 1957a). Although *P. nymphula* is generally semivoltine in Britain (taking two years to complete one generation) (CORBET, 1957a; MACAN, 1964, 1974; LAWTON, 1970; CORBET

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& HARVEY, 1989), MACAN (1964, 1974) showed that an exceptionally large year-class resulted in some larvae taking three years to complete development and CORBET (1957a) discussed the possibility that a small proportion of *P. nymphula* larvae in the populations he studied in southern England were univoltine (taking one year to complete a generation). In this paper, larval life-history data and emergence data are used to investigate the pattern of larval development.

Emergence is a particularly 'useful' event in population studies of odonates. The emerging adults are visible but relatively immobile and it is possible to carry out an accurate census of the number emerging, thus providing a reference point for the larval and adult populations for which total counts cannot be made. The most common method of studying emergence is to make collections of exuviae and/or adults from emergent vegetation (CORBET, 1952; LAWTON, 1970, 1972; VAN NOORDWIJK, 1978; BANKS & THOMPSON, 1985; GRIBBIN & THOMPSON, 1990, 1991). Such collections are inevitably incomplete, however, as many exuviae and adults are not found, particularly if the vegetation is dense. Emergence traps have been used with limited success but generally do not provide quantitative information (MACAN, 1949, 1964; GOWER & KORMONDY, 1963; CRUMPTON, 1979). This study uses artificial substrates as alternative emergence sites for *P. nymphula* larvae in the field to obtain quantitative data on a number of aspects of emergence.

MATERIAL AND METHODS

This study was made in 1984, 1985 and 1986 on the population of *Pyrrosoma nymphula* inhabiting the drainage ditch on the disused airfield site at Skipwith Common, North Yorkshire, National Grid reference SE 655373 (Fig. 1). The ditch is an elongated horseshoe-shape, approximately 600m long (Fig. 2). It averages 2m in width, with a mean depth of around 0.7m (maximum about 1.2m). In summer, the ditch supports a very dense growth of bog pondweed (*Potamogeton polygonifolius* Pourr.). Other aquatic vegetation is mainly limited to occasional clumps of bulrush (*Typha latifolia* L.) and jointed rush (*Juncus articulatus* L.). Silver birch (*Betula pendula* Roth) and white willow (*Salix alba* L.) grow on both banks, partially shading the ditch.

Larvae were sampled monthly between April 1984 and August 1986. A pond net with a 1mm mesh and two types of sampler were used (Mill & Bennett, in prep.). The data were pooled since quantitative sampling is not necessary for life-history work. In the laboratory, samples were sorted by hand on a large white tray. The head width of each larva was measured using a digitiser in conjunction with a Wild dissecting microscope fitted with a drawing tube. The sex of larger larvae was recorded. Since males and females can only be distinguished reliably by external characteristics beyond a certain larval size (LAWTON, 1972), only *P. nymphula* larvae in their second year were used to calculate the larval sex ratio. All larvae were returned to the appropriate sampling point within five days.



Fig. 1. Location of the site.

In 1984, a 32m section approximately half way along the ditch (Site 1) was used for the study of emergence (Fig. 2). Lack of rainfall and high daily temperatures that summer left this part of the ditch without water for a number of weeks in late summer/early autumn, resulting in the death of most of the larvae and eggs there, as evidenced by the larval samples, the absence of emerging individuals in 1985 and the very low incidence of emergences in 1986. In these two years emergence was monitored at a 30m section close to the outlet of the ditch (Site 2) which had retained water during the drought. Field procedures were the same in all three years.

Artificial emergence sites were positioned on both sides of the ditch in early May before the onset of emergence. These consisted of screens made of plastic greenhouse shading, 30cm deep and with a mesh size of 1.5mm, attached to wooden stakes which were driven into the bottom of the ditch, keeping the screens pressed up against the steep banks. Grass and other vegetation overhanging the ditch were trimmed back to decrease the number of alternative emergence supports.

To test the effectiveness of the netting as an emergence support, some *P. nymphula* larvae were taken into the laboratory in December 1983 where, at the higher temperature, they emerged in early May 1984, before the onset of emergence in the field. All 12 larvae used emerged successfully on the netting.

Once emergence in the field had begun, the netting and surrounding vegetation were searched each day continuously from 0845 to 1300 GMT for exuviae and adults. A final check was made at about 1600 GMT. All exuviae were collected to prevent confusion between days. In almost all cases, adults were seen emerging, or the newly emerged adult was found before it could crawl far from its exuviae. On hot, sunny days when individuals emerged more rapidly, some exuviae were found on their own and it was assumed that the corresponding adults had already left on their maiden flight unless evidence of predation was seen. These exuviae were therefore included in the daily totals. The few newly emerged adults which could not be assigned an exuviae (a total of 12 over the three years) were excluded from the daily totals to avoid duplication of records.

The fate of each individual was recorded and all incidences of predation were noted. Thorough and continuous searching of the netting and vegetation meant that the progress of attacks by predators such as spiders could be monitored. Occasionally, on cold or wet days, one or two adults had not flown by the time we left the study site at 1600 GMT. Their location was noted accurately and, if they could not be found the following morning, predation was assumed.

RESULTS

Figure 3 shows monthly size-frequency histograms of larval head width for *P. nymphula* larvae collected between April 1984 and August 1986. Four year-classes (1982-1985) are represented. Instars two to twelve (counting the protonymph as instar one) separated readily on head width using a class interval of 0.025mm. The data show the typical two year life cycle of *P. nymphula*. By August, instars two, three and four are present in samples, indicating that eggs laid in May, June and July show direct development (i.e. no diapause). Larvae

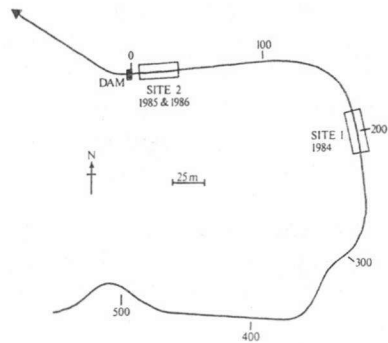


Fig. 2. Diagram of the ditch to show the sampling areas.

continue to grow until November, reaching instar five or six before overwintering. Growth is resumed in March and larvae reach instar eight or nine by the time they become the senior age group. The majority enter the final instar by their second November, and emergence occurs the following spring, as shown by the disappearance of the senior age group in June.

The first sample (April 1984) revealed three distinct size-groups of larvae. The two groups with the largest head width are larvae comprising the 1982 year-class (i.e. hatched from eggs laid in summer 1982). Consistent with other studies of larval development in *P. nymphula* (CORBET, 1957a; CORBET & HARVEY,

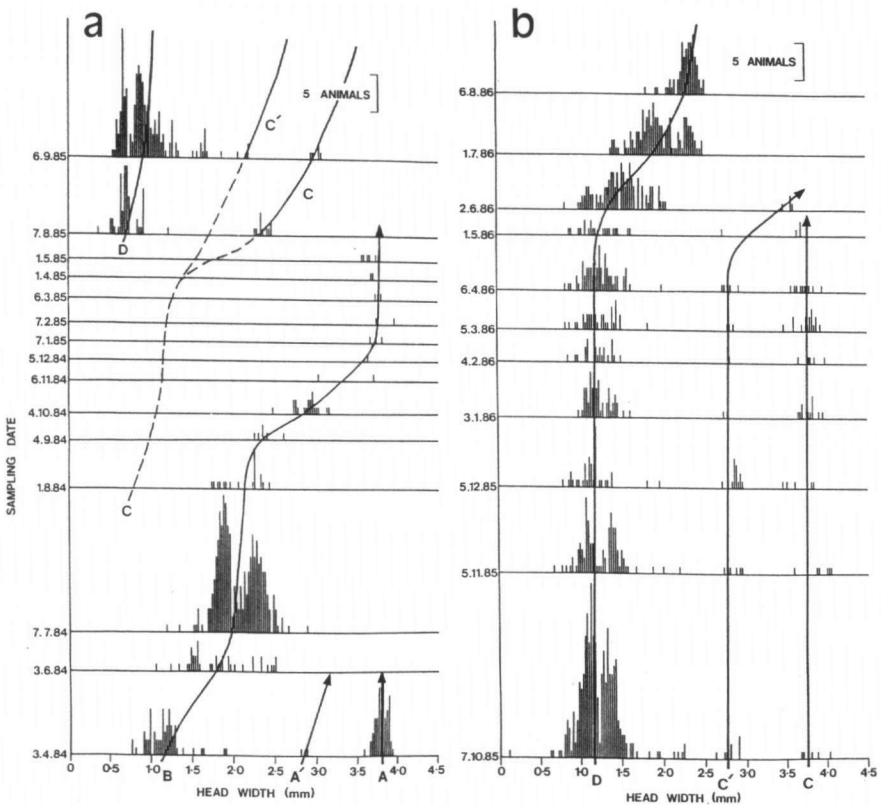


Fig. 3. Head width frequency histograms of larval samples. The lines are intended as guides to interpretation only and not as indicators of growth rates. Note that the Y-axis is not a continuous timescale and that samples were not taken in some months. Dashed lines indicate lack of small larvae due to the 1984 drought. Arrow heads indicate emergence. — (A) 1982 cohort larvae overwintering in F-0; — (A') 1982 cohort larvae overwintering in F-1; — (B) 1983 cohort larvae; — (C) 1984 cohort larvae overwintering in F-0; — (C') 1984 cohort larvae overwintering in F-1; — (D) 1985 cohort larvae.

1989), the data show that whereas the majority of the year-class overwintered in the final (F-0) instar (Fig. 3 - A), a small proportion of larvae spent the winter in the penultimate (F-1) instar (Fig. 3 - A'). That these F-1 larvae moulted to F-0 and also emerged in spring 1984, along with the rest of the year-class, is confirmed by the absence of a senior cohort in June 1984. Also present in April 1984 were 1983 year-class larvae just entering their first spring (Fig. 3 - B). These continued to grow through the summer, entered the F-0 instar in November 1984, and emerged the following spring. It appears from the samples that no larvae in this year-class overwintered in the penultimate instar.

Larvae comprising the 1984 year-class (Fig. 3 - C) were not found until August 1985, when they were already in their second year, probably due to a combination of low numbers resulting from the 1984 drought and the 'winter disappearance' of larvae also reported in other studies of larval *P. nymphula* (CORBET, 1957a; MACAN, 1964; LAWTON, 1970; CORBET & HARVEY, 1989). This winter disappearance is apparent in the data for the 1983, 1984 and 1985 cohorts; the samples were reflecting something other than mortality, since numbers apparently decreased during the winter and spring but increased again in summer. The general consensus of opinion is that the larvae probably retreat towards the bases of the vegetation to avoid unfavourable winter conditions, and consequently sampling efficiency decreases.

The 1985 year-class (Fig. 3 - D) shows an increase in numbers over those of the previous year. This newly-hatched year-class is a clearly separate group in August 1985. However, the subsequent three or four samples are confusing as the range of head widths of 1985 year-class larvae apparently increased markedly in September 1985, and it is not clear whether the larvae at the upper limit of the range belong to the 1984 or the 1985 year-class.

It is possible that a small proportion of the 1985 year-class larvae were univoltine and were therefore considerably larger and had a faster growth rate than their semivoltine peers. If so, their subsequent development is unclear since it is very unlikely they could have grown fast enough to enter F-1 in October 1985, only four to five months after hatching, which is the pattern of growth suggested by the frequency histograms. It seems more likely that these larvae represented the component of the 1984 cohort which overwintered in F-1. They appeared as a distinct group in the monthly samples from October 1985 through to May 1986 (Fig. 3 - C'), intermediate between their larger F-0 peers (Fig. 3 - C) and the 1985 year-class larvae (Fig. 3 - D). By June 1986, the majority of the 1984 cohort had emerged (Figure 4), but F-0 larvae were still present in the June samples. These were probably the overwintering F-1 larvae which had moulted to F-0 just prior to emergence, since no senior cohort larvae were found in subsequent samples. This is supported by the observation that the June F-0 larvae were slightly smaller than those in previous samples. In their study of seasonal development in *P. nymphula*, CORBET & HARVEY (1989) found that individuals

overwintering in the penultimate instar were smaller as F-0 larvae than those overwintering as F-0. It can be seen from the relative numbers of larvae collected that the proportion of the 1984 year-class overwintering as F-1 (about 30%) (Fig. 3 - C') was greater than that in 1982 (about 5%) (Fig. 3 - A'). Possible reasons for this are examined in the Discussion.

The artificial emergence sites proved extremely successful as 85-90% of all individuals emerged on the netting and were found easily. Exhaustive searches of the surrounding vegetation ensured that few if any of the remaining animals were missed. On hot, sunny days, emergence reached a peak between 0900 and 1000 GMT. Individuals emerging on dull or cool days, however, did not leave the water before about 0930 GMT and in some cases delayed emergence until the afternoon.

Table I
Emergence period, number emerging m⁻² and percentage of males at emergence in *P. nymphula*, 1984-1986

Year	Emergence period	No.m ⁻²	% Males
1984	14 May-24 June	22.3	51.6
1985	16 May- 3 June	4.7	50.9
1986	18 May-17 June	4.5	49.6

In 1984, 1426 individuals were recorded, 283 in 1985 and 272 in 1986. Table I gives the dates of the emergence period for each year, the number of individuals emerging per m² and the percentage of males. In 1985 and 1986, the densities at Site 2 were approximately

one fifth of those at Site 1 in 1984. Although the larval density at Site 2 before the 1984 drought was not known, it is likely that the small emerging populations in 1985 and 1986 were due to the inability of many eggs and larvae to survive the dry conditions in 1984. The sex ratio at emergence in each year did not differ significantly from unity (chi-square test, $p > 0.25$). Similarly, the ratio of the total number of male to the total number of female larvae collected did not differ significantly from 1:1 (97 males : 103 females, chi-square test, $p > 0.5$).

Figure 4 shows the percentage of the population emerging daily in each of the three years (sexes separate). There was no evidence that one sex emerged significantly earlier than the other (two sample t-test on log transformed data, $p > 0.05$ in each year). The timing of emergence and its degree of synchronisation, as illustrated by the skewness of the curves, show that *P. nymphula* is a typical 'spring' species. However, emergence was strongly influenced by the weather. In 1984, 83.1% of all individuals emerged between 19th and 31st May inclusive, but this main emergence period was split into three distinct peaks as cool, overcast and rainy weather on 21st and 22nd, and from 25th to 28th May suppressed emergence on these days. In 1985, the emergence curves were bimodal. By 18th May, 28.3% of the total population had emerged, but cold, windy weather and fairly heavy rain from 19th to 23rd May meant that few animals emerged on these days. Improved weather thereafter led to the build up of a second peak in

numbers. The total emergence period was considerably shorter than in 1984 and 1986 and was almost over by the end of May. In 1986, good weather prevailed throughout most of the emergence season, with the exception of rain on 20th and 21st May. Although the emergence lasted from 18th May to 17th June, 68.8% of the total population had emerged by 27th May. A particular feature of the 1986 curves is the small second 'peak' around 16th June, approximately 20-23 days after the main emergence peak. According to CORBET & HARVEY (1989), *P. nymphula* larvae which overwintered in F-1 emerged later in the season, and gave rise to smaller adults (HARVEY & CORBET, 1985), than those overwintering in F-0. This second peak can thus be attributed to the emergence of that fraction of the 1984 cohort which overwintered in F-1. Although a proportion of 1982 year-class larvae also spent their second winter in F-1, the percentage was much smaller, as noted earlier, and their presence was not signified by a second peak - the 1984 emergence histograms were simply drawn out into a long tail.

Mortality at emergence ranged from 3.0% to 5.2% over the three years of the study (Tab. II). The main causes were incomplete ec-

cdysis, failure to expand the wings and predation by spiders. The first two factors were assessed by examining and counting the number of disabled individuals left behind, unable to fly. Individuals were found at various stages of ec-

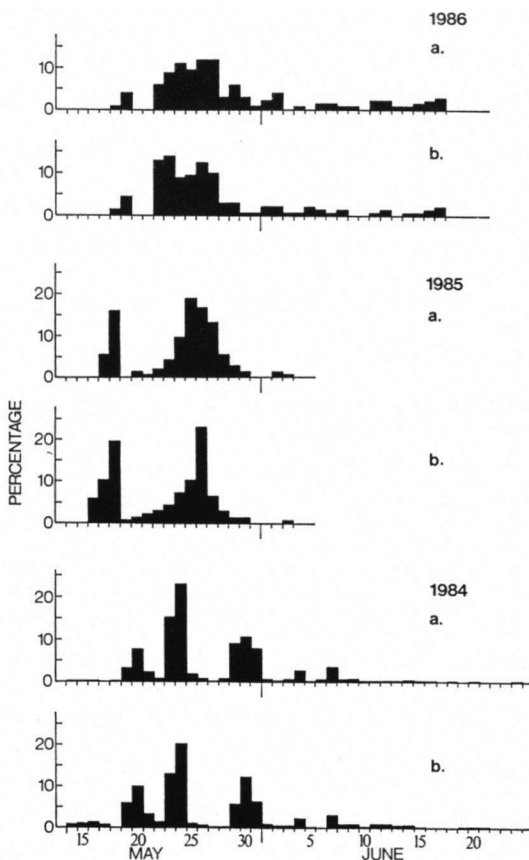


Fig. 4. Frequency histograms showing the percentage of the population emerging daily in 1984, 1985 and 1986: (a) males; - (b) females.

Table II
Mortality at emergence in *P. nymphula* expressed as a percentage of the total number emerging

Cause of mortality	Year		
	1984	1985	1986
Incomplete ecdysis	0.6	1.8	1.1
Incomplete wing expansion	1.2	2.1	3.3
Predation by spiders	0.9	—	0.4
Predation (unknown)	0.2	—	0.4
<i>Total</i>	<i>3.0*</i>	<i>3.9</i>	<i>5.2</i>

* Includes one death due to drowning

wings, which were often twisted. In all cases, failure was due to inability on the part of the individual and never to interference by other larvae.

The only instances of predation observed were those by spiders which constructed their webs on the bank and surrounding vegetation, or between the bank and the netting. Emerging adults were either attacked by spiders running over the banks or became entangled in webs when attempting their maiden flight. Newly-emerged adults still on the netting when we left the ditch but absent the next morning are included in Table II under 'Predation (unknown)' since we could not be sure that spiders had taken them. No other instances of predation were seen. Furthermore, no additional evidence of predation, such as discarded wings, could be found. The estimate of overall mortality for 1985 lacks a predation component and is therefore artificially low. In this year, adults were collected as soon as possible after emergence for a subsequent study of survivorship (Bennett & Mill, in prep.). Over the three years, only one individual was recorded as falling from its emergence support into the water.

DISCUSSION

Pyrrhosoma nymphula at Skipwith (latitude 53° 49.5'N) exhibits the same pattern of semivoltine development reported in previous studies of this damselfly in Britain, with latitudes ranging from 51°23'N (CORBET, 1957a) to 56°44'N (CORBET & HARVEY, 1989). MACAN's (1964, 1974) long-term study of *P. nymphula* at Hodson's Tarn (54°15'N) in the English Lake District also showed that the species was generally semivoltine, but an exceptionally large year-class resulted in some larvae taking three years to complete development. This work formed the basis for subsequent studies which showed that at high larval densities in the laboratory, odonate larvae interfere with each other's feeding (BAKER, 1980, 1981; ROWE, 1980), and consequently growth rates of some individuals may be so retarded that they cannot emerge in the same season as their faster growing peers (MACAN, 1977; BAKER, 1980). Within the time span of the

present study, development time for *P. nymphula* at Skipwith never exceeded two years. It is therefore suggested that the larvae were not food-limited nor that feeding-related interference was sufficiently important to influence larval life-history. It may be that this phenomenon only becomes important at very high larval densities. UTTLEY (1980) suggested that densities of at least $1,000\text{m}^{-2}$ in a 'useable' depth of only 8cm would be needed for aggressive interactions of larval *Ischnura elegans* (Vander L.) to have any effect on feeding. At Skipwith, the density of newly-hatched 1982 year-class larvae may have approached this, but the high early instar mortality rates postulated by us for *P. nymphula* (Bennett & Mill, in prep.) would result in a rapid decrease in density. In addition, the dense aquatic vegetation probably contributed to a reduction in feeding-related interference by increasing the habitat surface area (cf. CROWLEY et al, 1987).

The existence of univoltine development in the population at Skipwith seems unlikely. Univoltinism has not been demonstrated per se in any previous study of *P. nymphula* in Britain, although CORBET (1957a) discussed the possibility that some larvae in the populations he studied in southern England could have been univoltine. He suggested that univoltinism may be a feature of populations in shallow, productive ponds. The date of hatching may also be a critical factor in determining whether or not an individual can complete development in one year (HARVEY, 1985). It is significant that the only study to consider the possibility of univoltine development for *P. nymphula* (CORBET, 1957a) also reported the earliest hatching date (mid-June or earlier). The later dates of hatching given for the other, more northerly, study sites and the lower summer temperatures at these higher latitudes probably mean that the conditions for univoltine development cannot be met (HARVEY, 1985). In 1985, ovipositing females were first seen at Skipwith on 30th May. Considering the variation in hatching times recorded for *P. nymphula*, eggs laid around this date could have hatched well before the end of June, giving the larvae enough time to reach a sufficiently late instar to be able to emerge the next year. However, summer 1985 was not particularly warm and winter 1985/86 was not especially mild. Such conditions are probably necessary if larvae are to make use of their early hatching date.

It has been demonstrated that weather conditions, especially temperature, can also affect the proportion of the senior cohort overwintering as F-1, and thus influence the size of the second emergence peak. CORBET & HARVEY (1989) concluded from their own and previous studies of *P. nymphula* that it was rare for less than 90% of the senior cohort to overwinter in F-0. However, in one particular year-class of their population, close to 100% overwintered as F-1. They attributed this to an exceptionally cold winter at the time when these larvae were the junior cohort and its subsequent effect on larval growth the following spring and summer. At Skipwith, about 5% of the senior cohort overwintered as F-1 in 1983/84; no overwintering F-1 larvae were recorded in 1984/85, but the figure was as high as 35% in 1985/86. It is possible that the absence of overwintering

F-1 larvae in 1984/85 simply reflects the low sample sizes at that time, with the chance occurrence that no F-1 larvae were picked up. However, it is more likely that the unusually hot summer in 1984 promoted rapid growth rates, enabling all of the 1983 cohort to reach F-0 by December. The reasons for the high percentage of larvae overwintering in F-1 in 1985/86 are unclear. Winter 1984/85 was not exceptionally severe and spring/summer 1985 was not especially cool. It may be that the responses to factors governing this aspect of seasonal regulation in *P. nymphula* are more complex, with other factors such as date of hatching and prey availability also playing a role.

This work appears to be one of the most quantitative studies of odonate emergence to date. Not only was the study site visited on every day throughout the emergence period in all three years, but the use of a small area and the success of the emergence screens meant that the sex and fate of every individual could be recorded. The only other study in which artificial emergence sites have been used in a quantitative manner is that by INGRAM & JENNER (1976), but they limited their use to estimating the size of the season's total emergence.

The results of this study support WAAGE's (1980) conclusion that there is a general tendency towards an equal sex ratio at emergence in the Zygoptera. The emergence sex ratio in *P. nymphula* did not show a significant departure from 1:1 throughout the study. In addition, the overall larval sex ratio did not differ significantly from unity. This is at variance with other work on *P. nymphula*. Thus CORBET (1952, 1962) recorded significant excesses of male exuviae (63.0% and 53.7%) in two different years. However, 63.0% is probably not an accurate estimate as, in that year, collections of exuviae were made only during the peak emergence (nine days). LAWTON (1972) found a small but significant overall excess of males (52.0%) in *P. nymphula* larvae plus exuviae, but the larval ratios were considerable more variable than those calculated from exuviae, and the emergence sex ratios alone (50.3%, 50.7% and 51.5% male in three different ponds) did not differ significantly from unity throughout the study period (chi-square test, $p > 0.25$, recalculated from LAWTON, 1972, p.214, tab. I). Recently, GRIBBIN & THOMPSON (1991) demonstrated a significant male bias at emergence in *P. nymphula* at each of two adjacent ponds (54.6% and 53.1% male). They suggested that size-selective predation on larger female larvae could be one explanation for the excess of males in their own and previous studies. The data presented here do not follow the trend towards a male biased emergence sex ratio found in other studies of *P. nymphula* and thus offer no support for the occurrence of this phenomenon. The reasons for sex ratio differences between populations of the same species, and indeed for sex ratio imbalances in the Zygoptera in general, remain unclear.

Only one other quantitative estimate of emergence mortality for a zygopteran is currently available, and this is also for *P. nymphula*; GRIBBIN & THOMPSON (1990) recorded an overall emergence mortality of 27.9%, of which predators

accounted for 21.8% (birds, 7.4%; ants, 2.3%, spiders, 1.7%; unknown, 10.3%) and climatic factors 6.2%. The maximum emergence mortality recorded in the present study (5.1% in 1986) is considerably lower than this. It is also lower than that recorded by CORBET (1962) for *Anax imperator* Leach (8.5% to 15.8%), by MATHAVAN & PANDIAN (1977) for five species of tropical Anisoptera (8.35% to 16.8%) and by THOMPSON et al. (1985) for *Coenagrion puella* (L.) (about 30% in a year when horses were found to be a major cause of mortality), but comparable with that of UBUKATA (1981) for *Cordulia aenea amurensis* Selys (4.2%).

Mortality at emergence may be attributed to a number of causes and these are reviewed by GRIBBIN & THOMPSON (1990). There are three main reasons for the comparatively low emergence mortality recorded in the present study. Firstly, the incidence of predation was low. Obviously, the extent to which predation is important depends on the variety and numbers of predators present. It was not possible to determine conclusively whether birds preyed upon emerging *P. nymphula* as our presence naturally deterred them, but surprisingly low numbers of birds were observed in the vicinity of the ditch throughout the three years of fieldwork. There are records of ant predation for both Zygoptera (GRIBBIN & THOMPSON, 1990) and Anisoptera (UBUKATA, 1981) but ants were never seen to attack emerging *P. nymphula* at the ditch. Other potential predators were the smooth newt (*Triturus vulgaris*) and the common frog (*Rana temporaria*), of which only one or two were found, but no instances of predation were ever observed.

Secondly, mortality due to climatic factors was mainly limited to the effects of cold. It was evident that incomplete ecdysis and incomplete expansion of the wings occurred mainly on days when temperatures were unusually low for the time of year, suggesting that cold was directly impeding ecdysis (cf. CORBET, 1957b). Other individuals which emerged successfully on such days were unable to reach a sufficiently high body temperature to be able to fly and remained on the netting overnight, exposed to a high risk of predation. Fortunately, sudden or heavy showers were infrequent and rain was mainly limited to light drizzle in all three emergence seasons. This appeared to have little adverse effect, since adults were still able to fly successfully, if somewhat less rapidly. Similarly, windy days were uncommon, and no instances of mortality were seen which could be attributed directly to wind damage. Even the individual which drowned was not blown into the water - the larva must simply have failed to grip the netting sufficiently and the exuviae became detached and fell into the water as the adult was in the final stages of emergence.

Thirdly, although *P. nymphula* has a synchronised emergence, it does not exhibit the same 'mass' emergence shown by anisopteran such as *Anax imperator*, where overcrowding may increase mortality due to incomplete ecdysis and incomplete wing expansion to as much as 2.4% and 16% respectively on days of peak

emergence (CORBET, 1957b). The small physical size of *P. nymphula* and the abundance of emergence supports at the ditch meant that overcrowding and competition for supports did not occur even on days of peak emergence. Even without the emergence screens, supports would have been plentiful since long grass grew down to the water and there were trees on the banks. There was a tendency for some individuals to ascend much higher up the trunks of trees (anything up to three metres) in the year (1984) when emergence densities were high. However, emergence sites were still not a limiting factor and this phenomenon may have been due to the greater shading of Site 1, with individuals attempting to find warmer (sunnier) positions for emergence. Our results therefore support those of GRIBBIN & THOMPSON (1990), who also found no evidence for density dependent mortality at emergence in *P. nymphula*.

In contrast to previous work, this study has shown that, despite being the stage in the life cycle when odonates are probably most vulnerable, emergence is not always a time of high mortality. In the *P. nymphula* population at Skipwith, the combination of good weather, low predation pressure, abundance of emergence supports and the small physical size of the animals themselves resulted in a total emergence mortality of around 5% or less.

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