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THE INFLUENCE OF LARVAL DENSITY ON LARVAL GROWTH, AND THE CONSEQUENCES FOR ADULT SURVIVAL AND REPRODUCTIVE SUCCESS IN THE DAMSELFLY CALOPTERYX VIRGO (ODONATA)

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THE INFLUENCE OF LARVAL DENSITY ON LARVAL GROWTH, AND THE CONSEQUENCES FOR ADULT SURVIVAL AND REPRODUCTIVE SUCCESS IN THE DAMSELFLY CALOPTERYX VIRGO (ODONATA)

by

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A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences
Faculty of Science

In collaboration with
the Devon Wildlife Trust

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ABSTRACT

THE INFLUENCE OF LARVAL DENSITY ON LARVAL GROWTH, AND THE CONSEQUENCES FOR ADULT SURVIVAL AND REPRODUCTIVE SUCCESS IN THE DAMSELFLY *CALOPTERYX VIRGO* (ODONATA)

by Claire L. Lambert

This study of a population of *C.virgo* at Burrator, Dartmoor looks for signs of a population regulation mechanism acting through the effects of larval density on larval growth. The consequences of adult body size and emergence time for survival and reproductive success are also examined to look for further regulation mechanisms, and opportunities for natural and sexual selection; in particular the importance of body size to territorial males.

Although there were significant differences in patterns of growth and body size within and between year classes of larvae, the differences were were not related to density. Smaller, later developing larvae were present, and the possibility that this was related to late hatching is discussed. Smaller, later developing larvae emerged later as smaller sized adults. Survival to maturity was not influenced by body size. Density-triggered bird predation was a regular feature of the population, and could result in early emergers experiencing higher survival to maturity. The advantage of early emergence could, however, easily be countered by adverse weather patterns.

A field experiment showed that ovipositing females were highly aggregated, and that mature males were able to predict and profit from the aggregated distribution of females. Consequently male daily reproductive success was very variable, and was by far the most important component of their lifetime reproductive success. A large body size was an advantage to mature males when levels of competition were high, but not when competition was reduced as a result of bird predation and poor weather. Mature females produced between 85 and 1,615 eggs in their lifetime. The number of sunny days females survived to see was the most important component of their lifetime reproductive success, and was influenced by random predation and weather patterns. Body size was not related to either survival or clutch size. Early emerging females had higher lifetime reproductive success, but only as a result of the timing of the density-triggered bird predation, and this advantage could easily be lost through random weather patterns.

The lack of evidence for density dependent feeding competition in larvae, and for a relationship between female body size and fecundity in adults, suggests that feeding competition is not a regulatory mechanism in this population. The difficulties of detecting density dependence in short term studies is discussed. The strong influence of environmental variables on the importance of adult body size and emergence time indicates that the opportunity for selection of these characteristics would be variable and hence weak in the short term. Over the long term, however, there would be a persistent selective pressure, and the possible consequences for larval growth are discussed.

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AUTHOR'S DECLARATION

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(i) Department of Biology (Plymouth) seminars
(ii) British Ecological Society conferences
(iii) British Dragonfly Society conferences

signed: Claire Lambert

date : 29th March 1994

CHAPTER ONE

INTRODUCTION

Since the 1930s laboratory studies of insects have shown that density dependent larval competition can influence larval growth and mortality, and the size and fecundity of adults (Peters and Barbosa 1977 and references therein); these studies continue (Peckarsky and Cowen 1991). Larval competition can therefore be expected to play an important part in insect population dynamics and in influencing reproductive success, but determining if similar phenomena are important in natural populations is proving to be a difficult task. In Odonata the importance of density dependent competition in natural populations of larvae, and its subsequent influence on adult populations is, as discussed below, currently a matter of keen debate.

The development of dragonflies and damselflies through the one to four year aquatic larval period is strongly influenced by temperature and photoperiod (Corbet 1980). In addition to these environmental constraints, however, there is evidence to suggest that density dependent processes may be important. From 1955 to 1975 Macan carried out one of the few long term field studies of damselfly population dynamics (Macan 1964, 1977). He found that in years when Pyrrhosoma nymphula larval densities were high, mortality increased and some larvae took longer to develop. He hypothesised that territorial behaviour led to stability in the numbers emerging, and that the slower developing larvae were those which were less competitive. Since then numerous laboratory

studies have shown strong behavioural interactions between the aquatic larvae of the Odonata. These sometimes involve overt aggression (Baker 1980, 1981, 1983 and Harvey and Corbet 1986) distraction (McPeek and Crowley 1987, Crowley et al 1988) or a reduction in movement (Blois-Heulin 1990). In the laboratory such behaviour, known as mutual interference, leads to larvae becoming regularly spaced (Rowe 1980) and, more importantly, reduces their feeding rate (Uttley 1980, Crowley and Martin 1989) as density increases. Anholt (1990) has challenged the presumption that the detrimental effects of high density are entirely due to interference competition, and showed that exploitation competition, where larval density reduces or locally depresses prey density, may also be involved. Whatever the cause, larvae which experience food shortage take longer to develop (Wissinger 1988, Hassan 1976) and can also put on less growth from one instar to the next (Lawton et al 1980). These effects may have important implications for larval population dynamics. Where food limitation through competition lengthens the duration of development total mortality during development will be increased. Such an effect will be density dependent, and therefore it has the potential to be an important mechanism of population regulation (Crowley et al 1987b).

Recent work has concentrated on ascertaining whether larval competition occurs in natural populations. Field enclosure experiments, using realistic larval densities, provide a halfway house between the laboratory and natural populations. In such experiments it has been found that as density increases body size decreases (Pierce et al 1985) and

also that development time can increase and survival decrease (Van Buskirk 1987a). Given the strong evidence for larval competition affecting feeding rate, growth and survival, it was surprising when Crowley et al (1987b), in the first 'working hypothesis' of a model of damselfly population dynamics, found both interference and exploitation competition to be unimportant in population regulation. This inconsistency led the authors to suggest that more work is needed on the role of competition in larval growth, and it is now important to find out if the potential for competition evident from enclosure experiments is realised in natural populations. Enclosure experiments differ from the conditions of natural populations in several important respects: enclosures are small and larvae are unable to move in response to high densities, habitat complexity may be oversimplified and natural predators will be excluded so that high densities may be maintained for an unrealistically long time. To date there are few studies of competition within natural populations of larvae, and the results are inconsistent (Banks and Thompson 1987a, Baker 1989).

Where feeding competition influences larval growth it may also influence the body size and time of emergence of adults. Harvey and Corbet (1985) found that the body size of emerging adults of laboratory reared P.nymphula depended on the prey intake of final instars. In natural populations a decline in the body size of adults emerging later in the season has been reported (Banks and Thompson 1985, Fincke 1986 and Michiels and Dhondt 1991), and Gribbin and Thompson (1991) note that this is often presumed to be a competitive

effect. There have been few studies of the consequences of larval density for the body size and emergence time of adults in natural populations, however, and the cause of the smaller body size of later emerging adults has yet to be identified.

The body size and time of emergence of adults may have important consequences for the adult population. It has been suggested that the influence of larval competition on adult female body size may act as a further population regulation mechanism (Harvey and Corbet 1985, Banks and Thompson 1985). For example density dependent larval growth could result in all, or a greater proportion, of females emerging at a smaller body size when larval densities are high. If body size influences female reproductive success fewer eggs would be produced in years of high larval density. Crowley et al's model of damselfly population dynamics did not allow for the effect of larval competition on adult body size. They recognised, however, the need for more work on the influence of larval density on adult body size and consequently on reproductive success.

The importance of adult body size to breeding behaviour in Odonata has been researched in an attempt to understand the nature and extent of sexual selection. Work has concentrated on males, where a large body size may confer a competitive advantage, and in particular on species with territorial males where competition for territories may be high (Koenig and Albano 1987, McVey 1988, Koenig 1991 and Fincke 1992). An inconsistent picture has been revealed however, with some studies finding a large body size confers

advantages to breeding behaviour (Fincke 1992, Tsubaki and Ono 1987) while others find that it confers no advantage (Van Buskirk 1987b, McVey 1988). Further work may help to understand the causes of this inconsistency.

Where natural or sexual selection acts on adult characteristics which are the result of larval competition rather than genetic predisposition, such selection may influence larval growth and behaviour. For example Harvey and Corbet (1985) suggest that territorial behaviour in larvae of P.nymphula may enhance the reproductive success of adult males, and Koenig and Albano (1987) suggest that early emergence in larvae may be encouraged by the higher reproductive success of early emerging adults. An understanding of the selective pressures faced by adults may therefore also assist in understanding patterns of larval growth and behaviour.

Banks and Thompson (1985) have highlighted the fact that studies of short term reproductive success may not reflect the selective forces operating through body size, since they may not relate to reproductive success achieved over an individual's lifetime. Lifetime reproductive success will be influenced by additional factors relating to survival, breeding rate and weather conditions, and these may even conflict with selective pressure on short term reproductive success. In looking for signs of a population regulation mechanism acting through female fecundity, and for evidence of selection, it is necessary to look at the importance of body size and emergence time to lifetime

reproductive success. Although the number of studies on lifetime reproductive success is growing, they are still uncommon, particularly for females, and again give conflicting results. For example Banks and Thompson (1987b) and Michiels and Dhondt (1991) report that a large body size is important to females and males respectively, whereas Koenig and Albano (1987) find that body size is unimportant in either sex.

Most studies looking for an influence of body size and time of emergence on the adult population concentrate on the reproductive success of mature adults. Survival to maturity will be important in determining which individuals breed, however, and as such could also be important in both the population regulation mechanism and selection processes. Further work on immature survival and adult reproductive success will therefore help build a picture of the circumstances (species and environmental characteristics) under which body size and time of emergence may be important to selection processes and population regulation.

This study of a natural population looks at the effects of larval density on larval growth and hence survival, and the consequences for adult survival and reproductive success. The work is the first on a stream dwelling damselfly, Calopteryx virgo, a useful species in which to look for the effects of competition since interference behviour has been observed in the laboratory (Ryazanova and Mazokhin-Porshnyakov 1985), and the larvae are relatively large and inhabit a very restricted linear habitat, the banks of fast

flowing streams (Zahner 1959). The relatively simple stream bank habitat of this species also enables realistic estimates of density to be made, and this is further facilitated by the selection of a man-made water course, the Devonport Leat as the study site.

Chapters Two to Four describe the selection of a discrete study population, and look at the influence of significant differences in larval density on the pattern of growth and body size achieved during the full two year development period of the 1985 year class. Comparisons of growth pattern and body size are also made between year classes which developed at significantly different densities. The way in which larval growth patterns are manifest in the timing of emergence and the size of emerging adults is described in Chapter Five, and the influence of these factors on the survival to maturity is explored in Chapter Six.

The remaining Chapters look at the importance of body size and time of emergence to the reproductive success of males and females. Calopteryx males are strongly territorial, and females come down to male territories to oviposit into vegetation at the water's edge (Pajunen 1966). The breeding behaviour and distribution of territorial males and ovipositing females along the Devonport Leat in 1986 gives clues to the factors which may influence reproductive success. These are used in the design of a field experiment to look at the influence of territory quality on the daily reproductive success of males, estimate daily clutch size in females, and to enable the entire reproductive lifespan of

males and females to be monitored. A full analysis of the relative importance of the various components of lifetime reproductive success follows, allowing the importance of body size and time of emergence to be assessed.

Throughout the thesis descriptions are given of the general behaviour of C.virgo, both for the interpretation of ecological effects and to ensure that valuable observations of Calopteryx behaviour are formally recorded.

CHAPTER TWO

THE STUDY POPULATION

2.1 Calopteryx virgo

The Calopterygidae (Zygoptera, Odonata) are widely represented throughout the world, although only one genus Calopteryx is represented in Europe (d'Aguilar et al 1986). Calopteryx is a very homogenous group, known commonly as 'demoiselles', and differs from other damselflies in having large body size and often brilliantly coloured wings. C.virgo is found throughout Europe except for the extreme north, and its distribution also extends to the Near East and northern Asia.

Larvae of C.virgo inhabit streams with clear, well oxygenated water. They are usually found clinging to undercut stream banks, although they will colonise clumps of aquatic plants where these occur (Zahner 1959). Larval development takes place over two years, and adults start to emerge in the spring (Corbet 1957). The adults are often noted for fluttering, unsustained flight which results in their remaining close to their site of emergence (Hammond 1983, Zahner 1960). On reaching maturity the males become territorial, defending areas of floating vegetation along the stream bank where females come to oviposit. Breeding behaviour is complex, with elaborate coutship displays and ritualistic territorial defence flights (Pajunen 1966).

2.2 SELECTION OF THE STUDY POPULATION

2.2.1 Introduction

The Devonport Leat is a manmade watercourse, constructed in 1793 to collect water from Dartmoor and carry it to the city of Plymouth. For much of its length the Leat runs across open moorland, but as it descends towards Burrator reservoir it runs through areas of conifer plantation and semi-natural deciduous woodland. The walls of the Leat were constructed of stone, and the bed of clay and gravel. In many places the bank stones have now gone, and there are long stretches of undercut mud bank. The flow rate through the Leat is sufficiently high in most places to prevent colonization of the gravel bed by aquatic macrophytes. The Leat vegetation therefore consists mainly of algae and aquatic mosses, together with the roots and trailing leaves of bank vegetation which trap fallen leaves.

The aquatic invertebrate fauna of the Leat is diverse and abundant, with many species of stonefly, mayfly and caddisfly among others. The main groups occuring in the bank habitats are shown in Table 2.1. C. virgo larvae are known to occur at various localities above and east of the Burrator reservoir, and it is the only species of Odonata recorded in the Leat apart from the rarely occurring Cordulegaster boltonii. Brown Trout (Salmo trutta) are also abundant.

In order to select and define a study population the Devonport Leat above and east of Burrator reservoir was

ORDER	FAMILY	TROPHIC STATUS
ODONATA	Calopterygidae	Predators
	Cordulegastridae	Predators
PLECOPTERA	Perlidae	Predators
	Perlodidae	Predators
	Nemouridae	Herbivores
	Leuctridae	Herbivores
MEGALOPTERA	Sialidae	Predators
TRICHOPTERA	Rhyacophilidae	Predators
	Hydropsychidae	Omnivores
EPHEMEROPTERA	Ephemerellidae	Herbivores
	Leptophlebiidae	Herbivores
DIPTERA	Tipulidae	
	Chironomidae	
	Tabanidae	Scavengers
	Simuliidae	
	Ceratopogonidae	
COLEOPTERA	Dryopidae	
NEMATODA		
ARACHNIDA	Hydracarina	

TABLE 2.1 THE AQUATIC BANK FAUNA OF THE DEVONPORT LEAT.

sampled to determine the distribution of C.virgo larvae.

2.2.2 Method

From March to May 1985 approximately 3,000m of the Leat was sampled at 50m intervals. The first sample point was at SX550 684, 250m above sea level, where the Leat is diverted through a pipe to the Burrator reservoir. Samples continued until the Leat leaves a conifer plantation at SX569 709, 300m above sea level. The approximate positions of selected sample points are shown in Figure 2.1.

At each sample point the bank on each side and the leat bed were sampled using a Freshwater Biological Association 25*25 cm mouth net with 2 mm mesh. Two metre lengths of bank were sampled by sweeping the net through the vegetation at the leat edge. Sometimes this meant pushing the net under the undercut bank, and sometimes scraping it across moss covered stones. The Leat bed was sampled by kicking a 2m length of gravel to disturb sheltering animals, and catching them in a net held immediately downstream. Samples were sorted in the field, and numbers of C.virgo counted.

2.2.3 Results and discussion

Only three larvae were found in samples taken from the Leat bed. The concentration of larvae in the stream bank rather than the stream bed is typical, and has been noted by Zahner (1959) for C.virgo.

The distribution of larvae along the Leat banks was very uneven, and appeared to be influenced by both bank

FIGURE 2.1 SELECTION OF THE STUDY POPULATION: NUMBERS REPRESENT 50m SAMPLE POSITIONS ALONG THE DEVONPORT LEAT. POSITIONS 16-21 WERE SELECTED AS THE STUDY AREA.

conditions and the adjacent land use (Figure 2.2). No larvae were found at sample positions 0-15, where the leat was completely shaded by a mature conifer plantation which ran right up to its banks on either side, and the Leat banks were mainly bare stone with short stretches of mud. A group of larvae were found at sample positions 16-21, where a younger plantation to the north was set 4-5 metres back from the Leat edge, and the southern aspect was largely free from shading. Here also the banks were undercut mud for most of their length with overhanging vegetation. The Leat ran across open wood-pasture and moorland from samples 23-29, but for most of this section the banks were stone with no overhanging vegetation, and no larvae were found on the mossy stone sides.

Larvae were found almost continuously from sample 30 to 60, always in the frequent patches of undercut mud banks or in dense mats of overhanging vegetation. The Leat continued through open wood-pasture to sample 40, after which it ran through a second conifer plantation to the end of sampling. There was never complete shading by this second plantation however, since the trees to the south were set several metres back from the Leat edge, allowing dappled sunlight to filter through. In summary, the larvae were largely confined to areas with undercut mud banks and overhanging vegetation. It is also possible that the degree of shading influenced the distribution of larvae through its effect on adult oviposition sites (Chapters Seven and Eight).

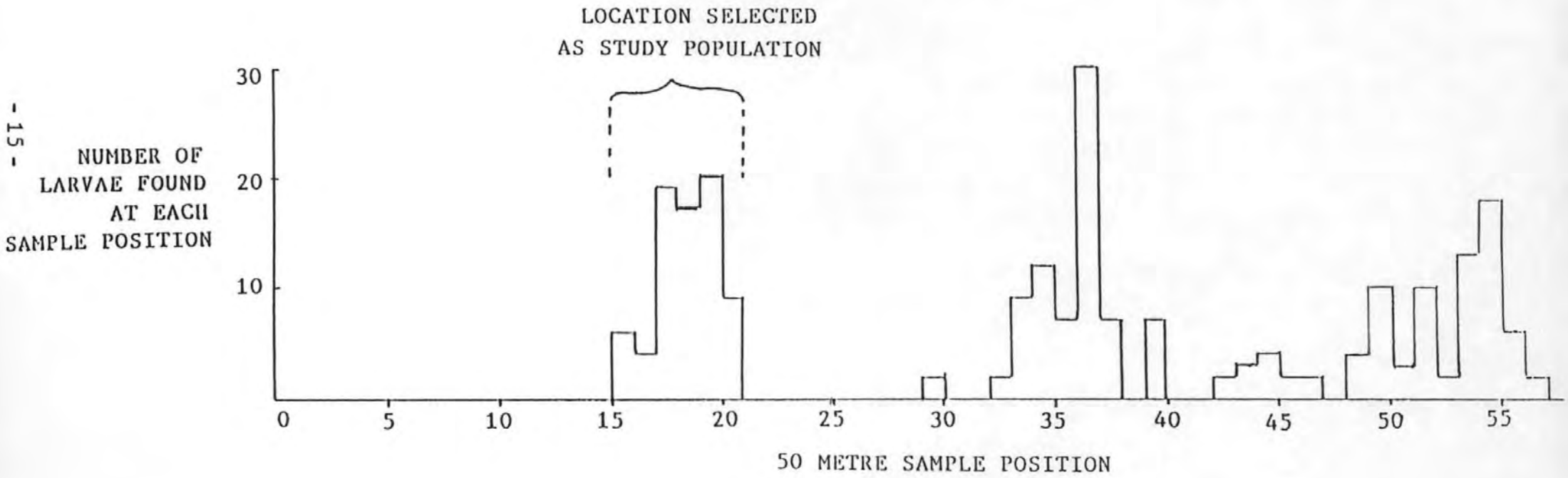


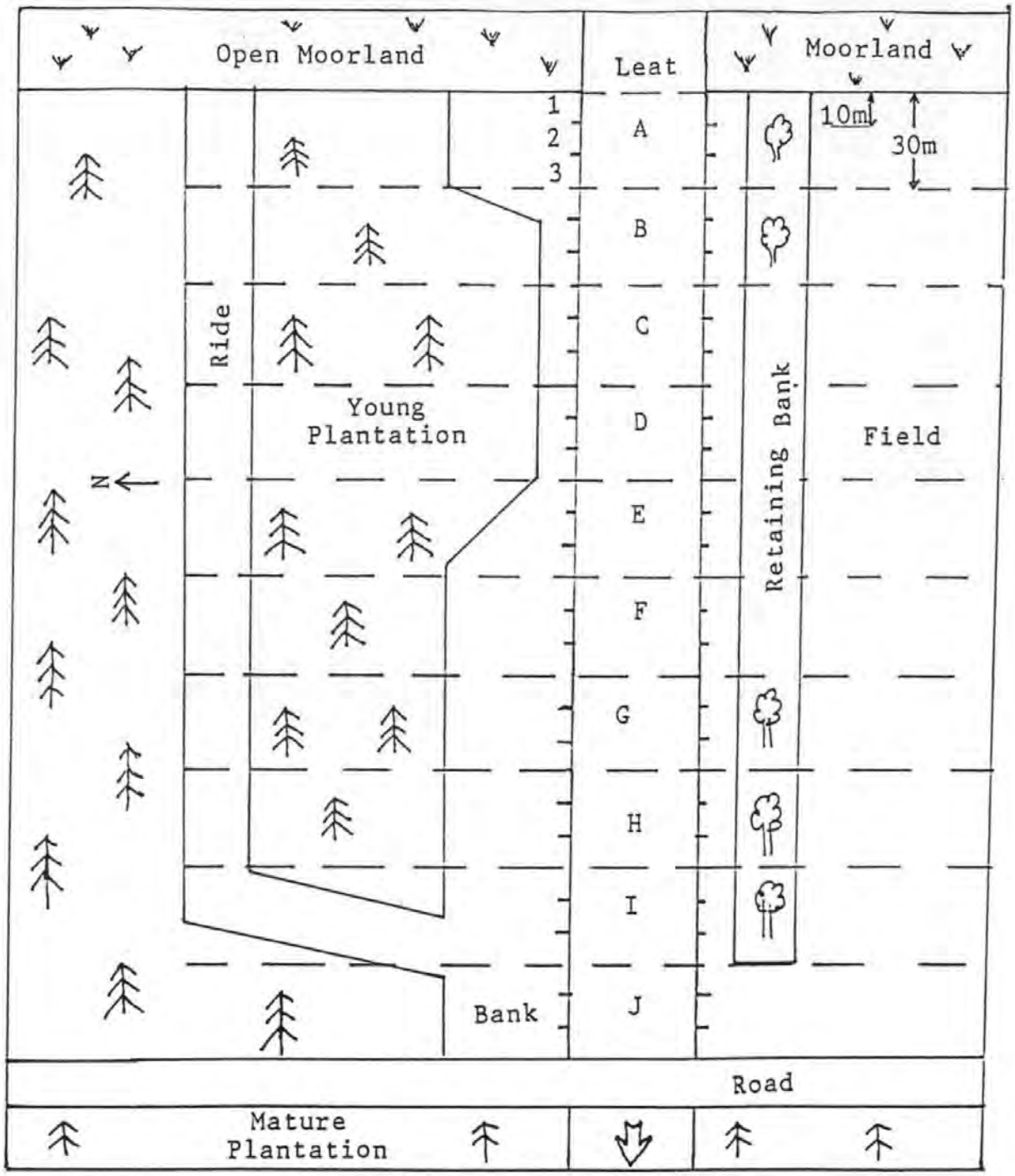
FIGURE 2.2 THE NUMBER OF LARVAE FOUND AT 50 METRE SAMPLE POSITIONS ALONG APPROXIMATELY 3000 METRES OF THE DEVONPORT LEAT (FOR LOCATION OF SAMPLES SEE FIGURE 2.1)

The group of larvae found at sample sites 16-22 was considered to be an ideal study 'population'. It was confined to a relatively small stretch, 300m, which would be easy to monitor, and was separated by 600m of unfavourable larval habitat from the only neighbouring group of larvae (there were no natural streams nearby). The distribution of breeding adults along the Leat broadly matched the distribution of larvae, and confirmed the level of isolation of the study population. Movement of larvae and adults between the study population and upstream groups was likely to be limited by the level of isolation, and could be easily monitored. There was also easy access to the site, but the level of public disturbance was low.

2.3 DESCRIPTION OF THE STUDY SITE.

The study site was comprised of 300m of the Devonport Leat above Burrator Reservoir, running from the Lowery Road at SX692 553 to the end of the conifer plantation at SX694 556, around the south facing slope of Peak Hill at 260m above sea level. In the summer of 1985 the Leat within the study area (which will now be referred to as the Leat) was divided into ten 30m sections using red marker posts (Figure 2.3). The sections were labelled A to J, starting upstream and working down. Within each 30m there was further division into 10m sections, and finally into 1m sections using cane markers. A system of rings and dots was used to define the exact position of each 1m marker post, and these marks could be read from any angle.

a) DIAGRAMATIC PLAN OF THE STUDY SITE (Not to scale)



b) CROSS-SECTION OF THE STUDY SITE (Not to scale)

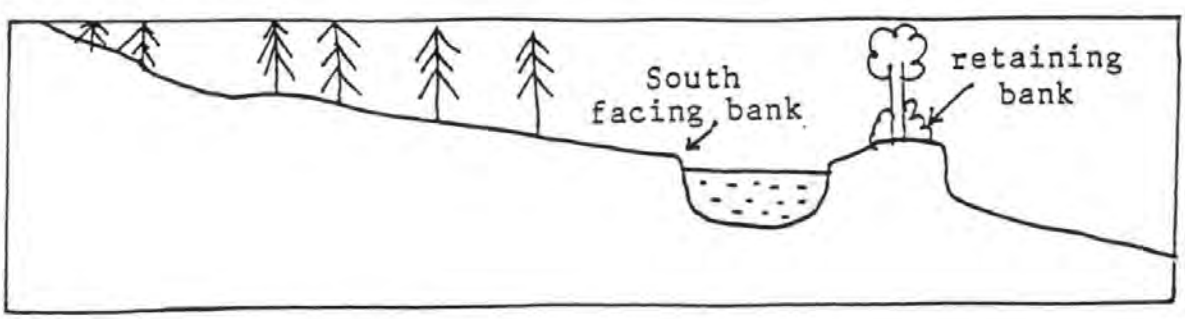


FIGURE 2.3 DIAGRAMATIC PLAN AND CROSS-SECTION OF THE STUDY SITE

The Leat runs from east to west, resulting in a south facing and north facing bank. Since the aspect of the Leat banks influenced the distribution of adults and larvae they will be referred to according to this criterion. A young conifer plantation bordered the south facing bank, set 4-6m back from the bank at sections A and E to J, but within 2m of the water from sections B to D (Plates 2.1-2.3). A woodland ride ran through the conifer plantation parallel with the Leat and about 50m from the southern edge of the plantation. The north facing Leat bank comprised a large retaining earthwork, and to the south of this the ground fell some 2-3m to a pasture below, where the ground continued to slope down the south facing valley side (Figure 2.3b). The north facing bank was topped by a deciduous hedge and trees of varying heights, about a metre back from the water's edge.

The ground flora surrounding the Leat was mainly ferns and grasses. Ferns closest to the water's edge started to topple into the water in summer, particularly after heavy rain, and by autumn large areas of the bank were covered in a mass of decaying vegetation (Plate 2.1b). In spring the south facing bank between the Leat and conifers was dominated by bluebells (Hyacinthoides non-scripta (L.) Chouard ex Rothm.), but by midsummer it was dense bracken (Pteridium aquilinum (L.) Kuhn) (Plate 2.2). The varying height of the deciduous hedge on the north facing bank and proximity of conifers on the south facing bank resulted in a patchy distribution of sunny habitat along the Leat in summer. The south facing bank of sections A and E to F contained large areas of bracken

a) Looking downstream from section A to sections B and C in early spring.

b) Ferns fallen into the water in section A.

PLATE 2.1 LEAT SECTION A

a) Looking upstream towards section E in spring. The one metre marker posts can be seen at the Leat edge.

b) Looking downstream towards section G in August.

PLATE 2.2 LEAT SECTION F

a) Looking downstream from the start of section G in spring. The red marker posts can be seen on the extreme right hand side.

b) The same view of section G in August.

PLATE 2.3 LEAT SECTION G

which received full summer sunlight, while sections B to D only received dappled sunlight.

The Leat sides were 0-15cm above the water level from sections A to F, but from G to J the banks rose 1-1.5m above water level, being particularly high in G. From sections A to F the Leat was around 2m wide, after which it narrowed considerably through the tall banks of G to around 1 metre, widened slightly to around 1.5m through H and I before reaching its greatest width of 3m in J. The water depth was usually around 20-30cm, although the water level rose significantly during the frequent winter spates. The water temperature was generally between 5-11^{0}C in winter and 12-21^{0}C in summer. On hot summer days temperatures could rise from 15^{0}C in the cool of early morning, to 21^{0}C by early afternoon as ground water sources warmed. The flow rate of the Leat varied from 1.01-1.23 m.sec^{-1} in the centre of the flow, but fell to only a sluggish 0.15-0.30 m.sec^{-1} at the Leat banks. There was little variation in flow rate down the Leat, and the flow was sufficiently high to prevent the colonization by aquatic macrophytes.

In August 1985 each metre of Leat bank was categorised into one of four bank habitat types for the purposes of future sampling programmes:

1) undercut mud beneath overhanging fern
2) undercut mud beneath short grass
3) rock beneath overhanging fern
4) rock beneath short grass

The extent of each habitat was then measured. Figure 2.4 shows that the north facing bank had more stone than the south facing bank. The south facing bank was largely undercut mud apart from long stretches of stone at sections G H and I. Large stretches of both banks were covered in overhanging fern.

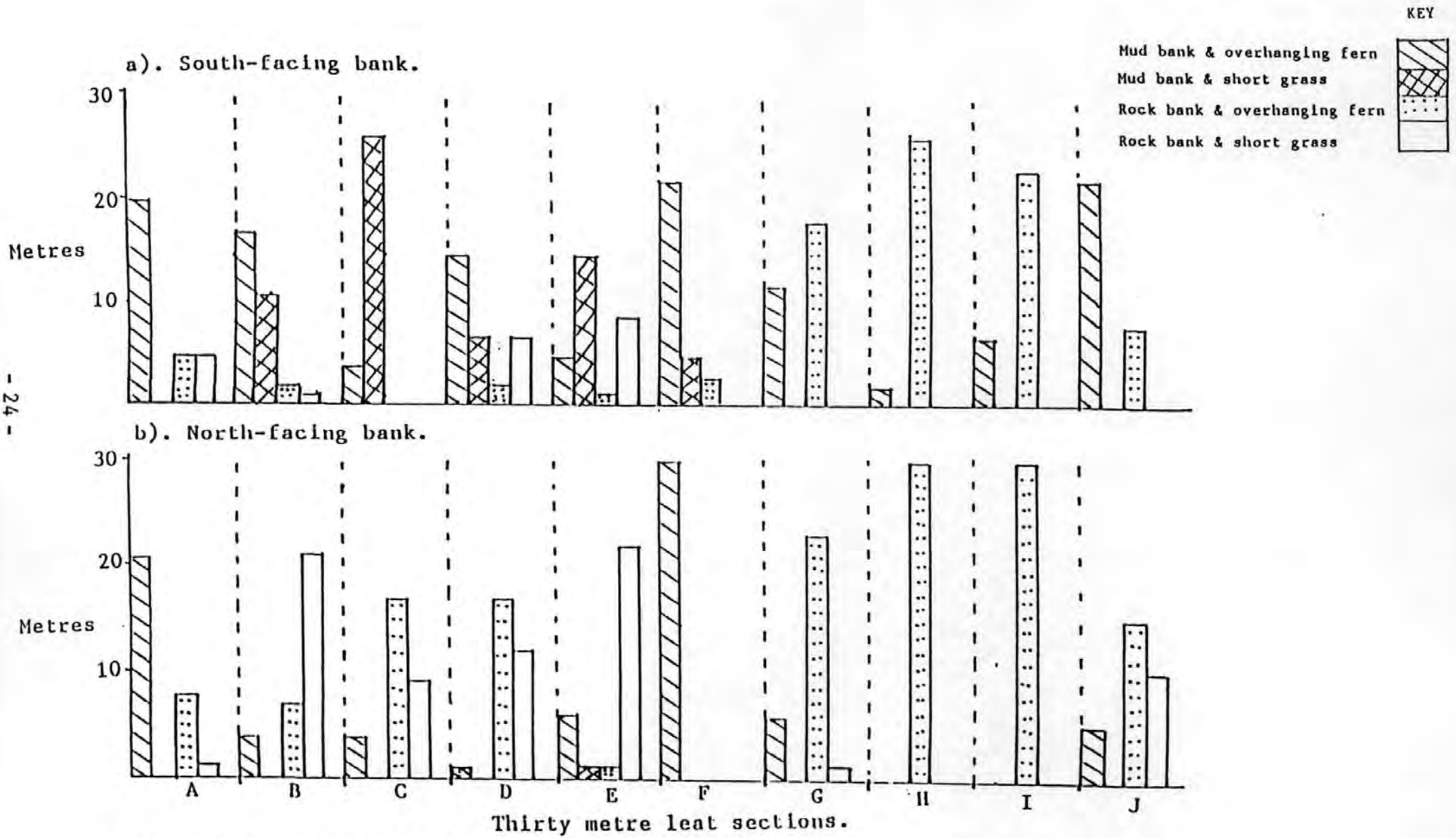


FIGURE 2.4 THE DISTRIBUTION OF BANK HABITAT TYPES ALONG THE LEAT

CHAPTER THREE

THE DISTRIBUTION OF LARVAE IN THE STUDY AREA

3.1 INTRODUCTION

Chapter Two identified a section of the Leat for further study and the distribution of possible larval habitats within it. In this chapter the distribution of larvae between different habitat types, and along the Leat study area are examined to identify areas of high and low density. Large areas of the north facing bank were stone and unlikely to be favourable larval habitats, and experimental sampling revealed that larval densities were generally low along this bank. Consequently the south facing bank was chosen as the sampling site, and sampling took place in September 1985.

3.2 METHOD

The four bank habitat types identified in the last chapter resulted in six habitats where larvae could be found, since in some areas two habitats were provided: overhanging vegetation and the bank itself. Five samples were taken in each habitat in each 30m section of the south facing bank. Uncommon habitat types (less than 4m in a section) were not sampled.

The different habitats, the sections of the Leat where they were found and the number of samples taken are listed below. Differences in the number of samples taken reflect the

proportion of each habitat type along the south-facing bank. Overhanging vegetation was predominantly ferns and has been described as such. An abbreviation of the description of each habitat is shown in brackets, and the habitats will subsequently be referred to in this way.

Leat Sections A-J

1)50 samples: undercut mud bank beneath overhanging fern (mud/fern)

2)50 samples: fern hanging over undercut mud bank (fern/mud)

Leat Sections B-F

3)25 samples: undercut mud bank beneath short grass (mud/grass)

Leat Sections A, G-J

4)25 samples: stone bank beneath overhanging fern (stone/fern)

5)25 samples: fern hanging over stone bank (fern/stone)

Leat Sections D and E

6)15 samples: stone beneath grass (stone/grass).

Samples were taken with a FBA net with a 25*25cm mouth and 1mm mesh size, in order catch recently hatched larvae whose body length was around 3mm (Corbet 1957). Experience from the previous sample had shown that the best method for sampling undercut mud and stone banks was to brush and agitate the surface with the hand while holding the net immediately underneath and downstream. Similarly fern samples

were best taken by slipping the net over a mass of fern, with the mouth pointed upstream, and agitating the fern. The current then carried dislodged larvae and material into the bottom of the net.

The area sampled at any one time, whether bank or fern, was the area of the rectangular net mouth, 25*25cm, and the duration of sampling was ten seconds (determined by tests of eficiency which are described below). The presence of plant roots and debris under the bank meant that the vegetation sampled there was three dimensional. Densities of larvae can therefore be compared between bank and fern sample types. Sample positions were selected within each habitat type within each Leat section using random number tables, and fern samples were taken at the same position as bank samples.

Samples were sorted in the field. Large and small larvae were separated and taken back to the laboratory to be measured. Body lengths were determined by placing larvae in a petri dish over graph paper, and recording the distance, viewed immediately overhead, from the front of the labrum (the most forward point of the head) to the rear end of the 10th abdominal segment. After having been measured larvae were returned to the exact position on the Leat from which they were taken. Larvae were placed, with great care, in a sheltered nook in the vegetation using a teaspoon, from where they could be seen quickly dispersing under the bank.

Before the full sampling programme began the efficiency of the sampling method was tested. Tests included increasing

the bank/fern agitation time from 5 to 10 to 15 seconds; holding a second net (1mm mesh) close to the bank 1m downstream to determine how many larvae were being lost in the drift during sample collection; sorting through samples a second time in the laboratory; and holding the net against the bank 1m downstream while larvae were being returned to see how many were lost downstream.

3.3 RESULTS

3.3.1 Tests of sampling efficiency

Increasing the mud bank sampling time from five to ten seconds during seven trials resulted in a further five out of a total of sixty three larvae (8%) being retrieved. Increasing sample time further to fifteen seconds during the same trials resulted in only one extra larva (2%) being found. During five test samples five out of sixty two larvae (8%) were lost downstream, although it is likely that these came from the edge of the sample area and did not form part of the sample. During a second sorting of five samples in the laboratory eight out of a total of seventy eight (10%) larvae were retrieved, and most of these were early instars. Finally in six out of nineteen trial samples eight out of a total of 137 larvae (6%) were not successfully returned to the bank after measuring.

Sampling will not therefore seriously underestimate densities or bias the age structure, although field sorting will have resulted in the younger year class being slightly underestimated. Larvae dislodged in the sampling process are

not likely to travel far, because there was a general tendency for material to settle out in the slower current next to the bank.

3.3.2 The distribution of larvae

Larvae ranged in body length from 3 to 20mm (Figure 3.1). An approximate division between the two year classes was taken to be 11mm. Larvae below 11mm were judged to be mostly those which hatched that summer and were due to emerge in 1987 (the 1985 year class), and 12-20mm larvae those which hatched in the summer of 1984 and were due to emerge the following year (the 1984 year class). Surprisingly a Mann-Whitney U test showed that the median density of the older 1984 year class was significantly greater than that of the 1985 year class ($U=30589$ $n=190$, $P<0.01$). The overall distribution of larvae along the south facing bank was very skewed in both year classes (Figure 3.2) possibly reflecting aggregation within or between habitats.

It was not possible to use a two way analysis of variance to look at the distribution of larvae along the Leat and between habitats because there was an uneven distribution of habitats. Comparisons of density between pairs of habitats were made in Leat sections where both occurred using Mann-Whitney U tests (Table 3.1). Although some larvae were found on areas of rock bank, in both year classes there were significantly fewer there than on mud banks, whether or not the banks were covered with fern. The main difference between the year classes was found in the fern habitat. While there were just as many large year class larvae in the fern/mud as

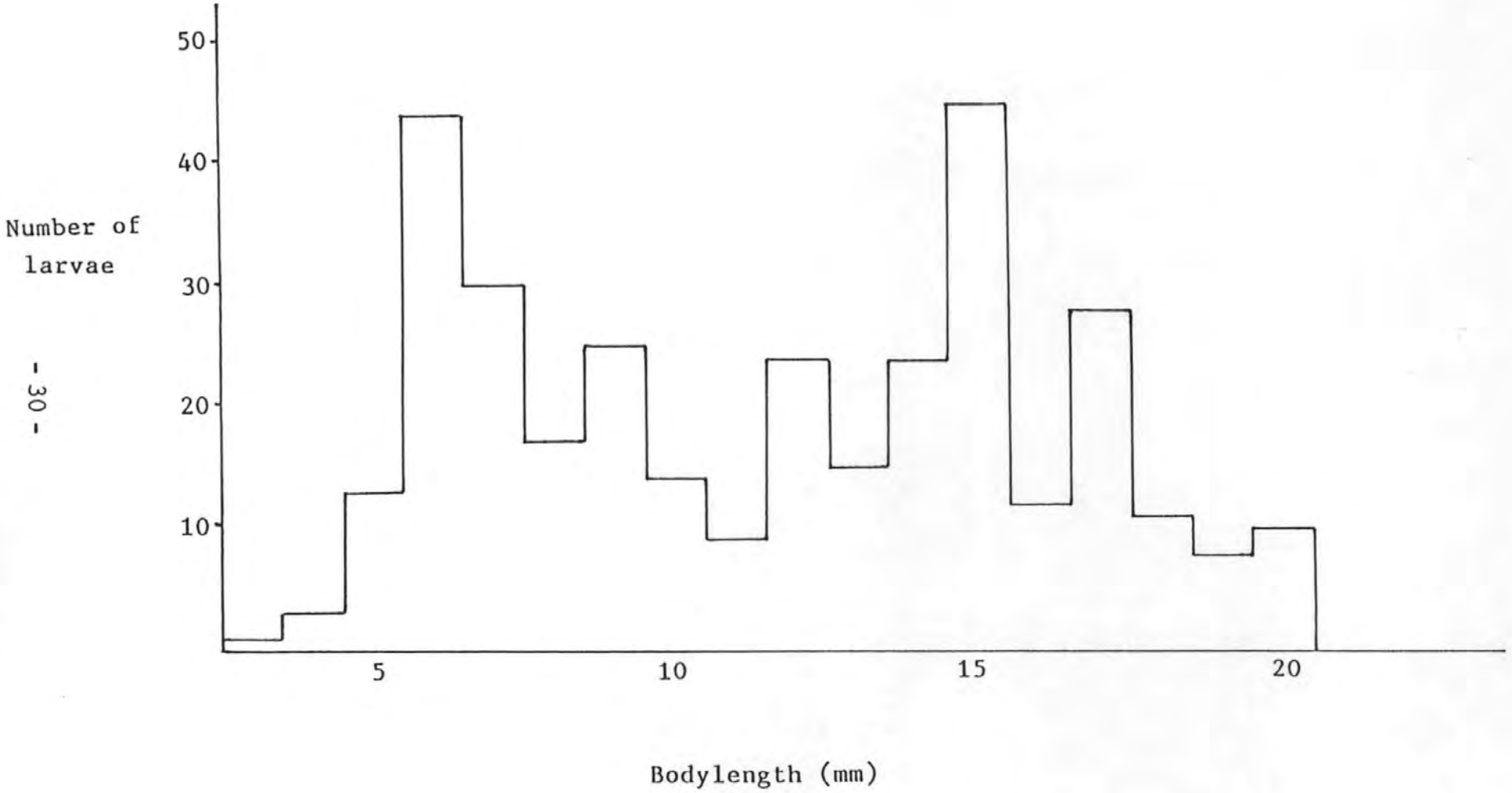
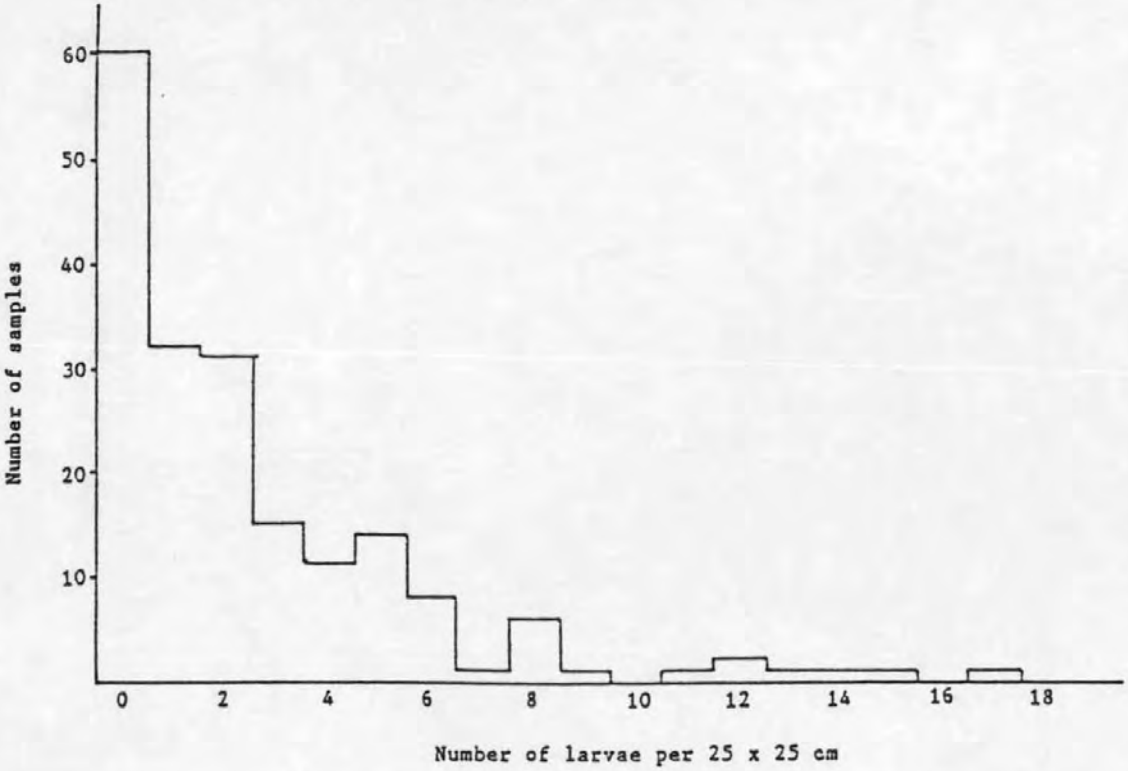


FIGURE 3.1 THE BODY LENGTHS OF LARVAE FOUND ALONG THE SOUTH-FACING BANK IN LEAT SECTIONS E AND F IN SEPTEMBER 1985.

a) The 1984 Year Class.



b) The 1985 Year Class.

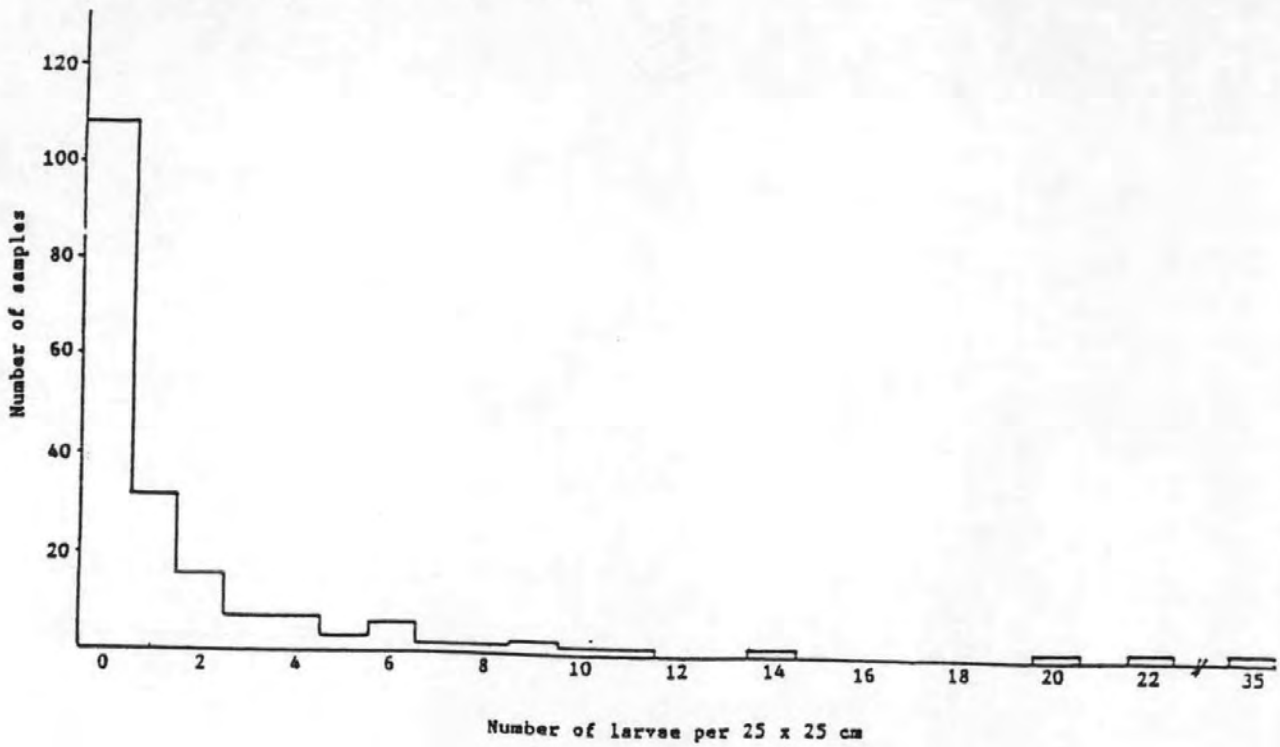


FIGURE 3.2 THE DISTRIBUTION OF LARVAE ON THE SOUTH FACING BANK OF THE LEAT.

Habitats and Leat sections	Density per 25x25 cm median	mean	range	U	P
a) The 1984 Year Class					
Rock/Grass	10	1	0.8	0-2	16	0.0089_c
Mud/Grass (D&E)	10	2	2.0	0-3	
Rock/Fern	25	0	0.76	0-5	167.5	0.0033
Mud/Fern (AGHIJ)	25	2	2.2	0-6	
Mud/Fern	50	2	2.72	0-9	1237	0.925
Fern/Mud (A-J)	50	2	3.32	0-17	
Fern/Rock	25	0	1.52	0-13	22.3	0.063
Fern/Mud (AGHIJ)	25	1	2.56	0-17	
Mud/Fern	25	3	3.24	0-9	304	0.862
Mud/Grass (BCDEF)	25	3	3.96	0-16	
b) The 1985 Year Class					
Rock/Grass	10	0	0.6	0-2	11.5	0.0029_c
Mud/Grass (D&E)	10	2	5.3	0-22	
Rock/Fern	25	0	0.28	0-3	206	0.0136
Mud/Fern (AGHIJ)	25	1	1.4	0-7	
Mud/Fern	50	2	2.6	0-35	745.5	0.003
Fern/Mud (A-J)	50	0	0.54	0-6	
Mud/Fern	25	2	2.87	0-10	282	0.557
Mud/Grass (BCDEF)	25	2	4.28	0-22	

c = ties present and not corrected, p is conservative.

TABLE 3.1 MANN-WHITNEY U TEST OF THE DIFFERENCES IN LARVAL DENSITY PER 25 x 25 cm BETWEEN BANK HABITATS.

mud/fern, the small year class was rarely found in fern/mud and numbers there were significantly lower than in mud/fern. There was no significant difference between the number of large larvae in fern/rock and fern/mud, but a strong trend towards there being higher densities over mud banks. The densities of small larvae in the fern habitat were not compared because numbers in both types were so low. Finally in both year classes there was no difference in the number of larvae found in mud/fern or mud/grass habitats.

Behavioural interactions between year classes were not responsible for the distribution of the younger year class between the mud/fern and fern/mud habitat. The proportion of the younger year class in the fern at any one sample site was not correlated with the density of the older year class there (Spearman rank correlation=0.217, n=40, P=0.173).

Differences in average density along the Leat within each habitat are shown in Table 3.2, and differences within the most widespread habitats along the Leat were examined using a Kruskal-Wallace test (Table 3.3). The density of the older year class rose in one or more habitats in sections E, F and H. Similarly the density of the younger year class rose in section E and F.

Leat Section	Mud/ Fern	Mud/ Grass	Fern/ Mud	Fern/ Rock	Rock/ Fern	Rock/ Grass
a) The 1984 Year Class						
A	1.8	-	4.0	0.2	0.8	0.35
B	3.0	4.0	1.2	-	-	-
C	2.2	3.2	2.6	-	-	-
D	2.0	2.0	1.4	-	-	0.6
E	3.6	1.6	9.6	-	-	1.0
F	5.4	8.0	5.8	-	-	-
G	4.0	-	2.0	1.2	1.6	-
H	2.4	-	5.6	5.4	1.2	-
I	1.6	-	0.6	1.0	0.2	-
J	1.2	-	1.4	0.2	0.2	-
b) The 1985 Year Class						
A	1.8	-	4.0	0.2	0.8	0.2
B	1.4	3.0	0.2	-	-	-
C	0.6	1.4	0.2	-	-	-
D	4.0	1.2	0.4	-	-	0.4
E	11.4	9.4	1.4	-	-	0.8
F	3.4	6.4	0.6	-	-	-
G	1.8	-	0.4	0.2	0.2	-
H	0.8	-	0.2	0.2	0.4	-
I	0.4	-	0.2	0.2	0.2	-
J	0.6	-	0.2	0.2	0.2	-

TABLE 3.2 AVERAGE LARVAL DENSITY PER 25 x 25 cm, WITHIN EACH HABITAT IN LEAT SECTIONS A TO J. FOR DESCRIPTION OF HABITATS SEE SECTION 3.2.

Habitat	No. of leat sections	Total no. of samples	H (adjusted for ties)	df	P
a) 1984 Year class					
Mud/Fern	10	50	15.22	9	ns
Fern/Mud	10	50	24.64	9	0.01
Mud/Grass	5	25	5.9	4	ns
b) 1985 Year class					
Mud/Fern	10	50	24.5	9	0.01
Fern/Mud	10	50	11.17	9	ns
Mud/Grass	5	25	11.82	4	0.02

TABLE 3.3 A KRUSKAL-WALLIS TEST OF THE DIFFERENCE IN LARVAL DENSITY BETWEEN LEAT SECTIONS DOWN THE SOUTH FACING BANK.

3.4 DISCUSSION

The density of 1984 year class was higher than the 1985 year class even though the older year class had experienced mortality over a far longer period. Either the mortality of the 1984 year class had been comparatively low, or it started at a much higher density than the 1985 year class. Since the number of breeding adults along the Leat in 1985 was very low (see Chapter Seven) it is probable that the 1984 year class spent the entire larval period at higher densities than the 1985 year class. The consequences of differing densities for the development of the two year classes are examined further in the next chapter.

Within each year class significant differences occurred in the density of larvae between habitat types and along the Leat. Larvae of all ages showed the expected preference for mud banks rather than moss covered stone, probably reflecting the greater amount of vegetation there resulting in increased prey abundance and protection from predators. The absence of the young year class from the fern samples is unlikely to be due to biased sampling. Samples from fern habitat which were taken back to the laboratory for a second search revealed no further small larvae, although small larvae occurred at high density in adjacent mud banks.

The results therefore suggest either behavioural interactions or behavioural differences between the year classes. Crowley et al (1987a) found that larger larvae of the dragonfly Tetragoneuria cynosura inhibited the

colonization of smaller ones in a field experiment. The proportion of small instars in the fern/mud here, however, was independent of the density of larger ones, suggesting that behavioural differences rather than interactions were responsible.

Since eggs are laid in vegetation at the water's edge, the absence of small larvae in fern samples represents an active response rather than a passive lack of movement. Because the fern habitat protrudes into the Leat it is subject to greater currents and higher light levels, and the smaller larvae may be moving away from one or both of these factors. The movement towards the bank may be a response to predation. It has been found that the presence of predators can strongly influence the behaviour of Odonata larvae; they may hide in inaccessible habitats when predators are present (Wellborn and Robinson 1987), and differing levels of predation between larval instars can result in behavioural differences between them (Dixon and Baker 1988). C.virgo larvae of all instars show a response to light levels, generally moving away from bright light and being active only in low light levels (Zahner 1959 and casual observations during this study). Such behaviour suggests a response to visual predators such as fish. While most size classes of the very numerous Brown Trout usually fed along the centre of the Leat, very young trout (2-3cm in length) were frequently seen amongst the overhanging fern and were often inadvertently caught in fern samples. Such small fish would be unable to take larger instars of C.virgo, but could take small ones. Small larvae may therefore move under the bank because of a

greater response to light levels which enables them to avoid the greater risk of fish predation.

The peak in numbers in both year classes in sections E and F, in habitats that occurred the length of the Leat, suggested that these sections were more suitable for adult oviposition sites, and this was confirmed in later studies (see Chapter Seven). The peak in only the older year class in section H may reflect an annual variation in the distribution of oviposition sites, or that the smaller larvae were somehow inaccessible in this mainly stone bank section (perhaps hiding deep in crevices), or that larger larvae had migrated there.

CHAPTER FOUR

THE INFLUENCE OF LARVAL DENSITY ON THE PATTERN OF GROWTH WITHIN AND BETWEEN YEAR CLASSES

4.1 INTRODUCTION

In Chapter Three it was shown that there was significant variation in larval density down the south facing bank of the Leat, and this was attributable to the distribution of adult oviposition sites rather than differences in larval habitat. The aim of this chapter is to compare the growth of larvae in selected areas of high and low density. Comparisons will be made primarily within year classes, but since the 1984 and 1985 year classes were likely to have experienced different densities during their development, comparisons can also be made between year classes. The degree of aggregation shown by larvae, the relative densities of potential prey and the movement of final instars were also examined since they may have a bearing on the influence of larval density.

4.2 METHODS

4.2.1 Larval sampling

With the September 1985 sample described in Chapter Three being the starting point, the growth of the 1984 year class was followed until emergence in June 1986, and the 1985 year class until emergence in 1987. The south facing bank of Leat sections CD (excluding the last half of D where densities were higher), AB and EF were chosen to represent

low, medium and high densities in September 1985, but the low number of larvae that were later found in all habitats in sections AB and CD resulted in these areas being subsequently pooled as one low density area. Sections A to F encompass most of the variation in density seen along the south facing bank, and were largely mud bank and fern habitat where larvae were most commonly found.

Mud/fern, mud/grass and fern/mud habitats only were included in the sample, since stone habitats were very limited in extent. In order to supply approximately fifty larvae from each year class in each density area, around twenty samples were taken in both CD and AB, and ten samples in EF. These samples were divided between the different habitats present according to their representation in the sections. The position of samples was decided by selecting half metre positions within each habitat type using random number tables. Fern habitat was sampled at the same position as the appropriate mud bank samples. Samples were taken every 1-3 months. The method of sampling was that described in Chapter Three, with the exception that all samples were taken back to the laboratory for sorting in order to avoid under-recording small instars. Both head width and body length measurements were taken. Body lengths of larvae over 9mm were measured using the petri dish method already described, but smaller larvae were measured using a binocular microscope with an eyepiece graticule. Head widths were measured as the greatest distance across the eyes using the binocular microscope.

When sorting and measuring were complete, sample material (which was full of invertebrates) and C.virgo larvae were returned to the Leat banks. C.virgo larvae were returned to the exact positions they were taken from using the method described in section 3.2.

4.2.2 Sampling for prey and predators

On three sample occasions, from December 1986 to May 1987, numbers of potential prey and invertebrate predators in each sample were estimated. Counts of mayflies, stoneflies, other prey items (eg nematodes), and predators were made using tally counters as the sorting tray was quickly searched. The potential prey items counted all had body lengths of around 5-10mm, and penultimate and final instar C.virgo larvae readily fed on them in the laboratory. The potential predators of C.virgo counted were those with body lengths of around 10-20mm.

4.2.3 Monitoring the movement of final instar larvae

The mobility of larvae was assessed by marking eighty one final instar larvae from samples taken from December 1986 to May 1987. The method of marking was that devised by Rowe (1979). A mixture of 'perspex' solution and coloured powder was painted around leg segments using a fine needle. A hard plastic ring soon formed, which was held in place mechanically rather than relying on adhesion. Rowe reports the rings remaining in place for the whole three month period of his study. During tests here it was found that marked limbs were very occasionally rejected within 12 hours of the mark having been applied. When legs were not lost the rings

remained in place for several weeks, and it was assumed they would last the four months until emergence. By using different colours and marking different legs a unique mark was allocated to each of the positions sampled. Initially red marks were used, but this colour was so conspicuous in the field that only blue, brown and black were subsequently used. Marked larvae were kept for at least twenty four hours, to check that the marks had taken, before they were returned to the Leat. Final instars in subsequent samples were checked for marks and exuviae were checked for marks during the monitoring of emergence in 1987 (see Chapter Five)

4.2.4 Monitoring larval drift

In order to monitor movement of larvae in the drift two drift nets were moved between four sample positions as follows:

1) Up stream of the study population area at the start of section A.
2) Down stream of the medium and low larval density areas at the end of section D.
3) Down Stream of the high larval density area at the end of section F.
4) Down stream of the study population area at the end of section J.

One drift net was placed in the centre of the Leat, and one close to the south facing bank without actually touching it. The single pair of nets was moved in succession from one site to the next every week, from July 1986 to July 1987. The

nets were still actively filtering the drift at the end of each week. The rectangular frame holding the mouth of the nets measured 25*30cm and was secured to the leat bed by stakes, so that most of the depth of water was sampled. The 2mm pore size net tapered to a point 40cm behind the mouth. Drift net samples were taken back to the laboratory for sorting, and the body length of any larvae measured.

4.3 RESULTS

4.3.1 The density and distribution of larvae in Leat sections A-D and EF

Two aspects of larval density may be important to levels of competition: average density and local densities. Local densities may vary considerably for a given average density dependent upon the pattern of larval distribution, and the following measures of distribution and local density were employed:

A measure of the pattern of distribution is given by I, the Index of Dispersion (Southwood 1978) where:

$$I = S^2(n-1)/\overline{X}$$

and $\overline{X}$ = mean density, S^2 = the sample variance and n = the number of samples. If the distribution of larvae is random (as described by the Poisson distribution), the variance to mean ratio will be close to unity, but will decrease as distributions become more regular, and increase as they become aggregated. I is distributed as chi square, and can

therefore be used to determine if the distribution differs significantly from a random distribution.

A measure of local density is given by the Index of Mean Crowding, M^* (Lloyd 1967). This is a simple descriptive index which combines the level of aggregation with mean density to enable comparisons of average levels of individual crowding to be made between different populations. It is calculated as follows:

$$M^* = \bar{X} + ((S^2/\bar{X}) - 1)$$

where S2 and $\bar{X}$ are as described above. If a population is randomly distributed $M^* = \bar{X}$, but M^* increases with the degree of aggregation and decreases as the distribution becomes more regular.

All habitats were pooled for analysis, with the exception that fern/mud was excluded from the September 1985 sample for the 1985 Year Class, because very small larvae were virtually absent in fern/mud habitat. The low and high density Leat areas each contained similar numbers of samples from each habitat type.

a) The 1984 Year Class

In September 1985 when 1984 Year Class larvae were twelve to fifteen months old and were beginning to molt to the penultimate instar (Figure 4.5b), average densities in EF were two to three times higher than in A-D (Figure 4.1, Table 4.1). Larvae in EF and AB were significantly aggregated but

those in CD were randomly distributed. The combination of mean density and degree of aggregation resulted in larvae in EF experiencing two or three times the level of mean crowding than those in A-D.

When all larvae were in the penultimate and final instar in February and April 1986 overall densities in A-D and EF had fallen, but mean density in EF was still around double that in A-D. A Mann-Whitney U test shows that densities in EF at this time were still significantly higher than in A-D (Table 4.2). The distributions in the two areas were still significantly aggregated, and larvae in EF were experiencing over three times the level of mean crowding than those in A-D. Indeed, although the mean densities in EF had fallen since September 1985, the aggregation had increased, with the result that the level of mean crowding had hardly changed since that time although larvae were five to seven months older.

b) The 1985 Year Class

In September 1985 the pattern of density of small larvae was similar to that shown by the older year class at the same time, where mean densities were at least two to three times higher in EF than in the other Leat sections (Figure 4.2. Table 4.1). The combination of differences in mean density and degree of aggregation resulted in larvae in EF experiencing more than double the level of mean crowding than those in A-D, and levels in CD were very low.

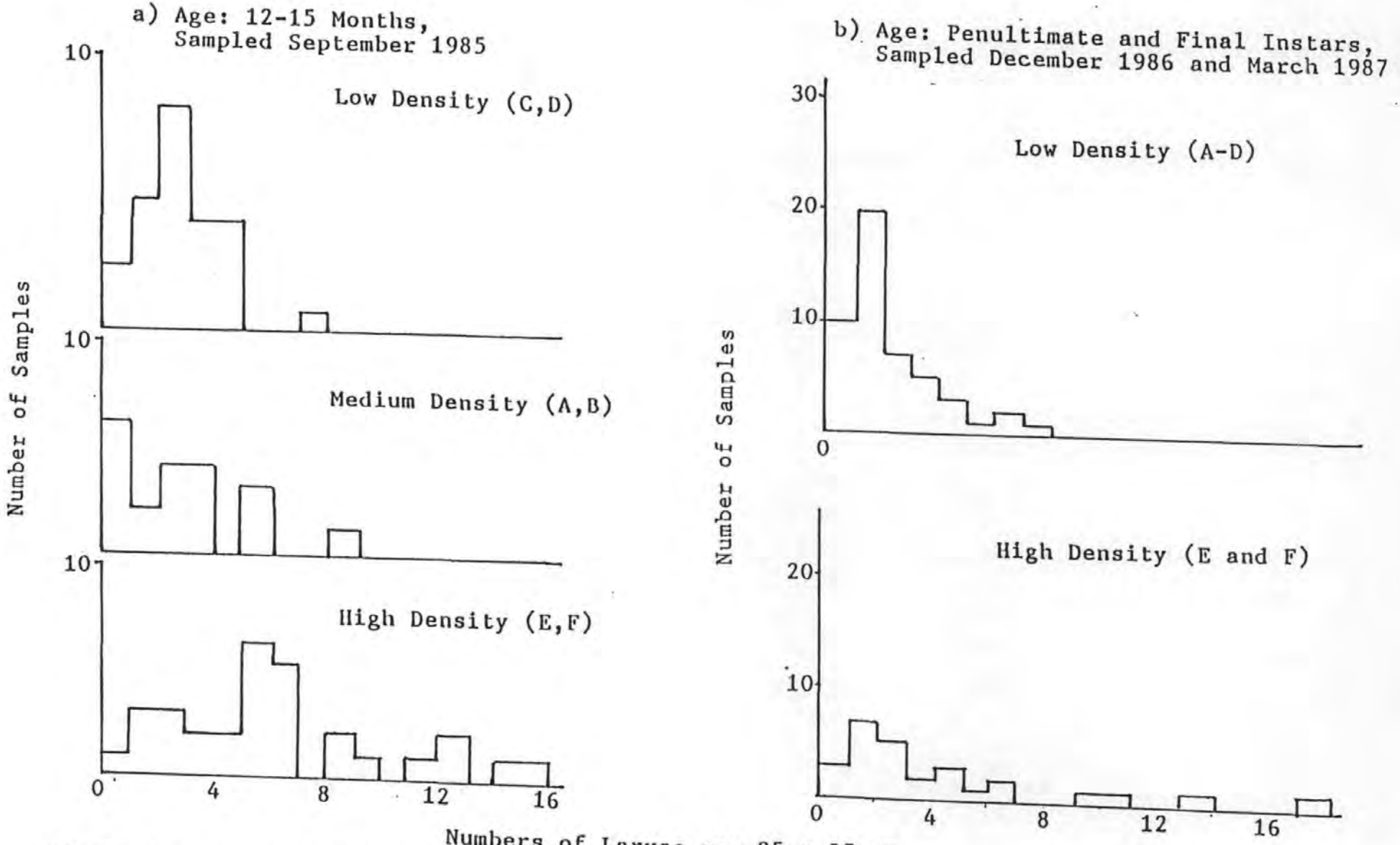


FIGURE 4.1 THE FREQUENCY DISTRIBUTION OF LARVAL DENSITY OF 1984 YEAR CLASS LARVAE IN HIGH (E F) AND LOW (A-D) DENSITY AREAS.

Year Class	Age and Sample Date	Leat Section	Density Area	n	mean density per 25x25 cm	S^2	$S^2/\bar{x}$	I	P	m^*
	12-15 months sampled Sep. 1985	CD	Low	30	2.267	2.28	1.005	29.167	ns	2.273
		AB	Medium	20	2.105	4.653	2.210	41.998	<0.05	3.315
		EF	High	30	5.733	15.445	2.694	78.127	<0.05	7.427
1984										
	Penultimate and Final Instars Sampled Dec 1986, Mar 87	A-D	Low	49	1.735	2.91	1.677	80.507	<0.05	2.412
		EF	High	27	3.741	17.356	4.639	120.614	<0.05	7.380
	0-3 months Sampled Sep. 1985	CD	Low	15	0.928	0.504	0.543	7.603	ns	0.471
		AB	Medium	15	2.6	9.12	3.508	49.107	<0.05	5.107
		EF	High	20	7.05	40.158	5.696	108.22	<0.05	11.75
1985										
	Penultimate and Final Instars Sampled Feb. & April 1986.	A-D	Low	61	0.705	2.846	3.972	242.2	<0.05	3.74
		EF	High	44	1.886	6.477	3.434	109.4	<0.05	4.356

I = Index of Dispersion, m^* = Index of Mean Crowding

TABLE 4.1 LARVAL DENSITY AND DISTRIBUTION IN HIGH AND LOW DENSITY AREAS.

Year Class	Density Area	n	Median Density/ 25x25 cm	U	P
a) Comparisons within year classes.					
1984	High Density (EF)	27	2.00	1245.5	0.0218
	Low Density (A-D)	49	1.00		
1985	High Density (EF)	44	1.00	3096.0	0.0001
	Low Density (A-D)	67	0.00		
b) Comparisons between year classes.					
1984	High Density (EF)	27	2.00	1178.0	0.012
1985		44	1.00		
1984	Low Density (A-D)	49	1.00	3722.5	0.000
1985		67	0.000		
1984	Low Density (A-D)	49	1.000	2382.0	0.546
1985	High Density (EF)	44	1.000		

1984 Year Class: Samples pooled from February and March 1986.

1985 Year Class: Samples pooled from December 1986 and April 1987.

P is adjusted for ties.

TABLE 4.2 MANN-WHITNEY U TESTS COMPARING THE DENSITIES OF PENULTIMATE AND FINAL INSTAR LARVAE WITHIN AND BETWEEN YEAR CLASSES AND LEAT AREAS.

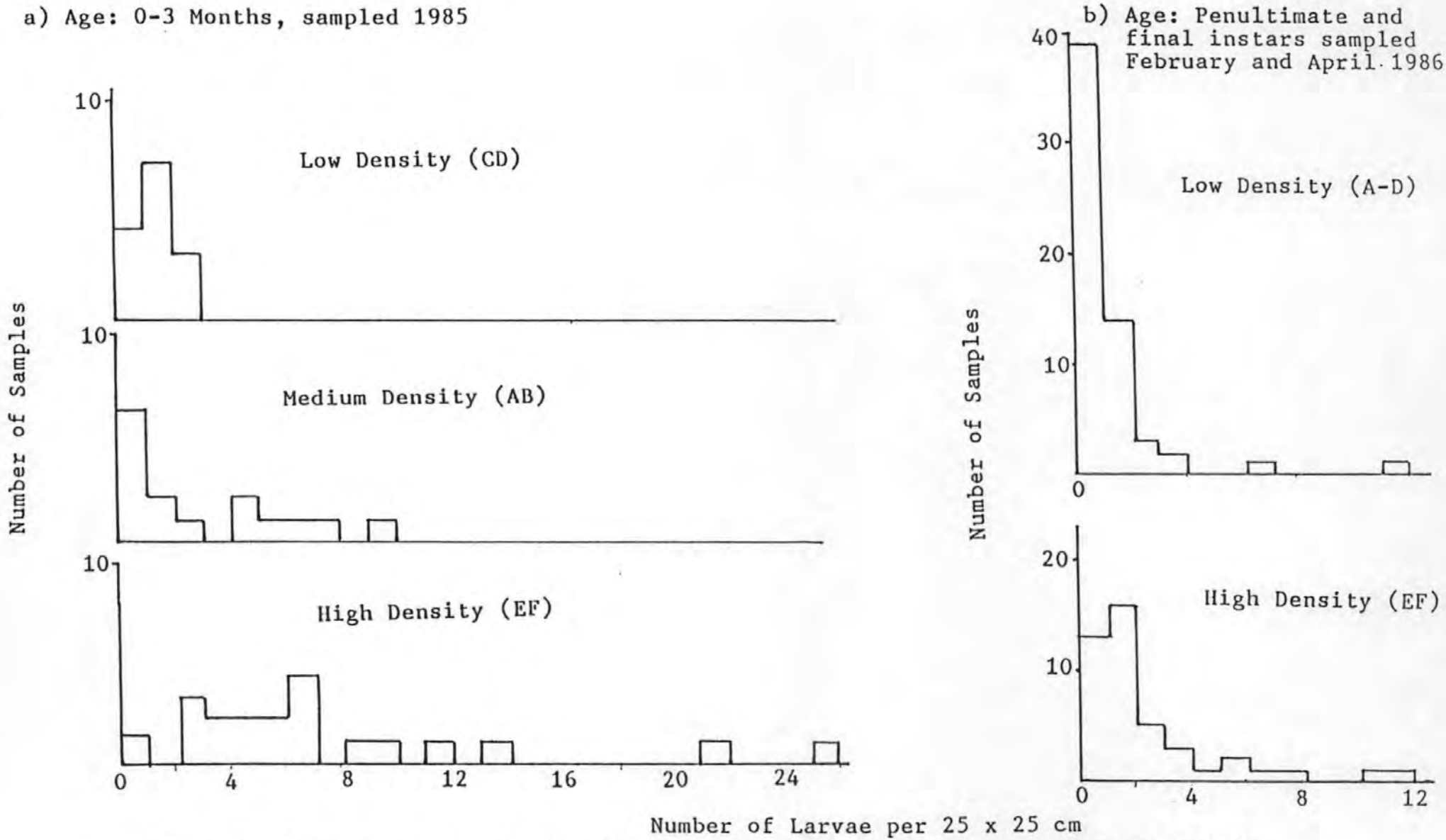


FIGURE 4.2 THE FREQUENCY DISTRIBUTION OF LARVAL DENSITY OF 1985 YEAR CLASS LARVAE IN HIGH (EF) AND LOW (AB, CD) DENSITY AREAS.

When in the penultimate and final instar in December 1986 and March 1987 all densities had fallen by about a third, but mean densities in EF were still around double those in A-D. A Mann-Whitney U test showed that the densities in EF were still significantly higher than in A-D (Table 4.2). Distributions in both EF and A-D were significantly aggregated, but the lower degree of aggregation in EF meant that there was now little difference in the levels of mean crowding between the two areas. The level of mean crowding had fallen since September 1985, particularly in the high density area, but larvae were now considerably larger.

c) A Comparison Between the Year Classes

In the previous Chapter it was discovered that in September 1985 there was no significant difference between the densities of the two year classes in Leat sections A-J, despite the age difference between them. There is no merit in comparing levels of mean crowding at this time however, because larvae from the different year classes were of very different sizes. When in the penultimate and final instar, mean densities of the 1984 year class in both EF and AD were around double those of the 1985 year class (Table 4.1). A Mann-Whitney U test shows that the differences in densities between year classes were significant (Table 4.2). A comparison of the level of mean crowding at this time indicates that the 1984 year class experienced greater levels than the 1985 year class in the high density areas, but less in the low density areas.

The mean densities of penultimate and final instars from the 1984 year class in AD appeared similar to those from the 1985 year class in EF, and a Mann-Whitney U test confirms that there was no significant difference between the densities of these groups (Table 4.2). A comparison of the level of mean crowding indicates that 1985 larvae in EF were experiencing almost double the level of 1984 larvae in AD.

4.3.2 The Numbers of Potential Predators and Prey

By far the most numerous prey were stoneflies (mainly Leucridae), followed by 'others' such as nematodes and dipterans, with mayflies being very uncommon (Figure 4.3). During the sample period potential prey items were very numerous compared to the number of C.virgo larvae, with the average number of all prey being forty times greater than the average number of damselfly larvae (Table 4.3). The density of the commonest prey item, stoneflies, and all prey were compared between the high and low density damselfly areas using a Mann-Whitney test, and no significant differences were found (Table 4.4). The number of potential invertebrate predators large enough to tackle the last few damselfly instars were scarce, with their average density being half that of C.virgo (Figure 4.4, Table 4.3).

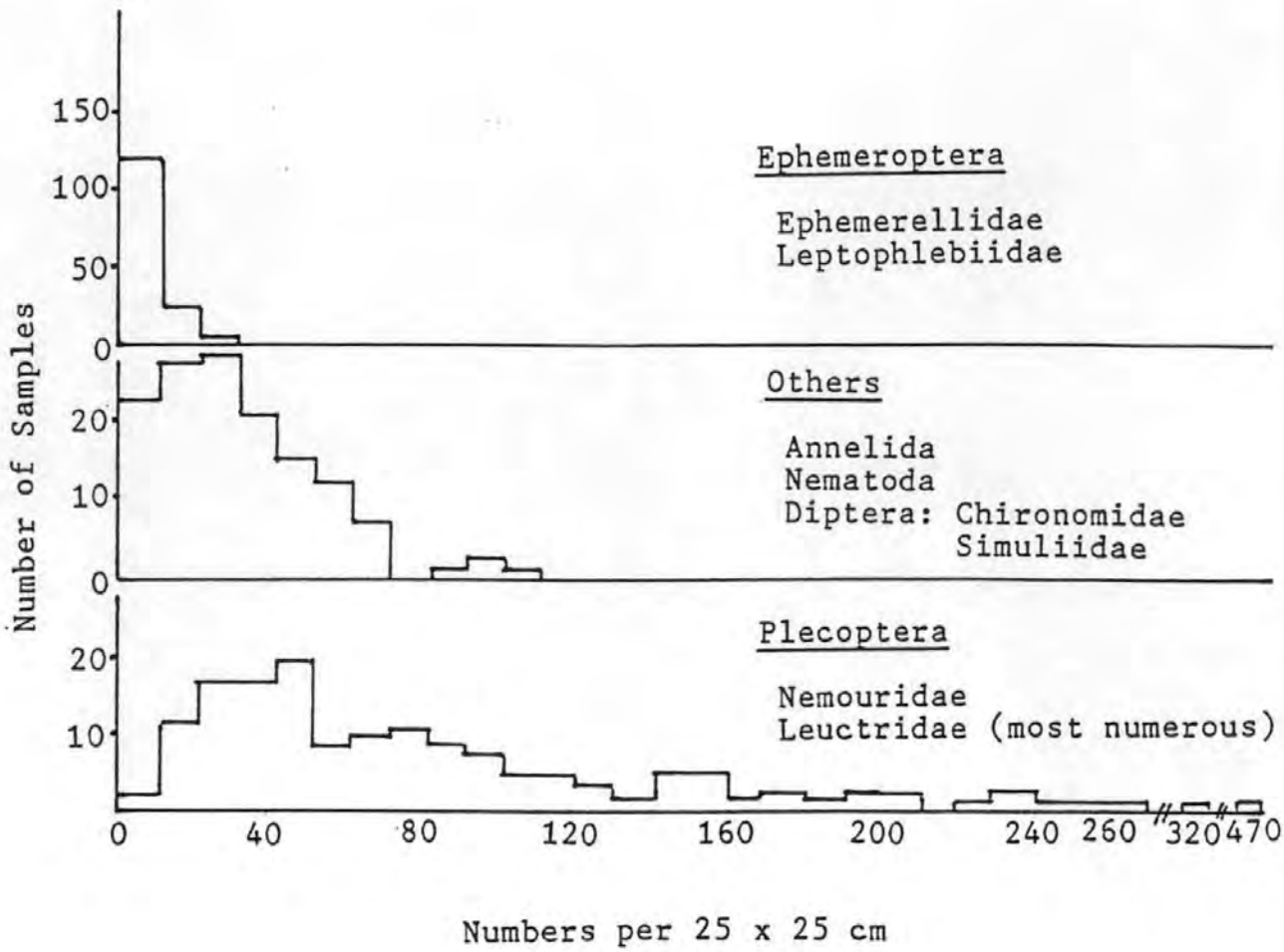


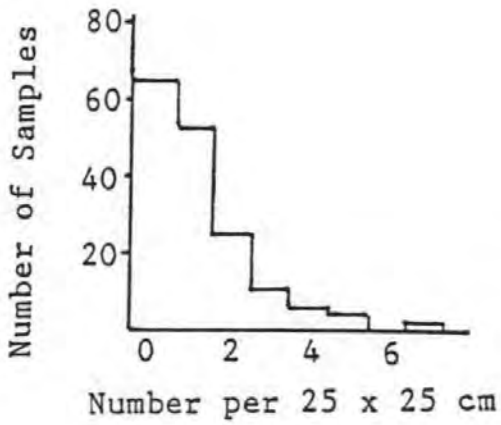
FIGURE 4.3 THE FREQUENCY DISTRIBUTION OF POTENTIAL PREY ITEMS IN SAMPLES. DATA POOLED FROM SAMPLES TAKEN DEC.86, MAR.87 AND MAY 87.

Group	n	Mean	Median
C. virgo	144	2.556	1
Predators	144	1.153	1
Prey: Plecoptera	144	75.91	54.5
Ephemoptera	144	2.396	1
Others	144	24.44	21
All Prey	144	102.75	83

TABLE 4.3 THE MEAN AND MEDIAN NUMBERS OF POTENTIAL PREDATORS AND PREY COMPARED TO *C. virgo*

Potential Prey	C. virgo Larval Density Area	n	Median	U	P
Plecoptera	High	60	46.5	4011.0	0.1702
	Low	84	64.0		
All	High	60	85	4540.5	0.4413
	Low	84	81.5		

TABLE 4.4 A MANN-WHITNEY U TEST OF THE DENSITY OF POTENTIAL PREY IN HIGH AND LOW C. virgo LARVAL DENSITY AREAS



Plecoptera: Perlodidae

Megaloptera: Sialidae

Trichoptera: Rhyacophilidae

FIGURE 4.4 THE DISTRIBUTION OF POTENTIAL PREDATORS. BODY LENGTH 10-20mm. SAMPLES POOLED DEC,86, MAR.87 AND MAY 87.

4.3.3 The Growth pattern of Larvae in High and Low Density areas.

In order to look for any effects of larval density on growth it is first necessary to determine overall growth patterns and size trends.

a) The growth pattern of the two year classes in combined high and low density areas (Leat sections A-F).

Figure 4.5 a and b shows the head widths and body lengths of larvae from each sample occasion (on the first sample occasion in September 1985 body lengths only were measured). The 1984 year class lagged behind the 1985 year class in its final development stages. In the last half of April 1986 47% of the larvae emerging that year were still in the penultimate instar, while in 1987 all the larvae due to emerge that year were in the final instar by the beginning of May.

A t-test of the size of male and female 1985 year class final instars showed that there was no significant difference between them (head width $t=0.36$, 50df, $P=0.72$, body length $t=0.61$, 42df, $P=0.54$). Males and females were therefore pooled to compare the size and variance in size of final instar larvae from the two year classes. Although the timing of samples in 1986 and 1987 were not exactly synchronised, comparable months could be selected, omitting May 1987 when final instars had bimodal body lengths as half of them had swollen prior to emergence. Table 4.5 shows that final instars from the earlier developing 1985 year class were significantly larger in both head width and body length than

the 1984 year class. There was, however, no significant difference in the variance of body size between the two groups.

There is asynchronous growth within the 1985 year class. While the majority of larvae overwinter at head widths of 1.0-1.7mm, very early instar larvae (head widths 0.5-0.7mm, body length 3mm) were also present. These two groups are referred to as 1985a and 1985b larvae respectively. By July the two groups are very obvious since the 1985b larvae have increased in number to form 32% of the year class. At this time the 1985a larvae are beginning to molt to the penultimate instar, but the 1985b larvae form a separate group of much smaller larvae (body length 5-8mm). This smaller body size group does not include newly hatched 1986 year class larvae. The first oviposition in 1986 took place at the end of June, and had the eggs taken around a month to hatch as previously observed for this species in the New Forest (Corbet 1957) then hatchlings with a body length of 3mm would just be starting to appear. The 1985b group are therefore too numerous and have too large a body size to include such newly hatched larvae. It is also estimated in Chapter Eight (section 8.4) that at this site hatching took seven to eight weeks, considerably longer than in the New Forest. In addition, as a result of unsettled weather there was very little oviposition in July, and most was seen in scattered sunny spells in August (see Chapter Six). This is likely to account for the fact that the first newly hatched 1986 year class larvae are not seen until the end of September.

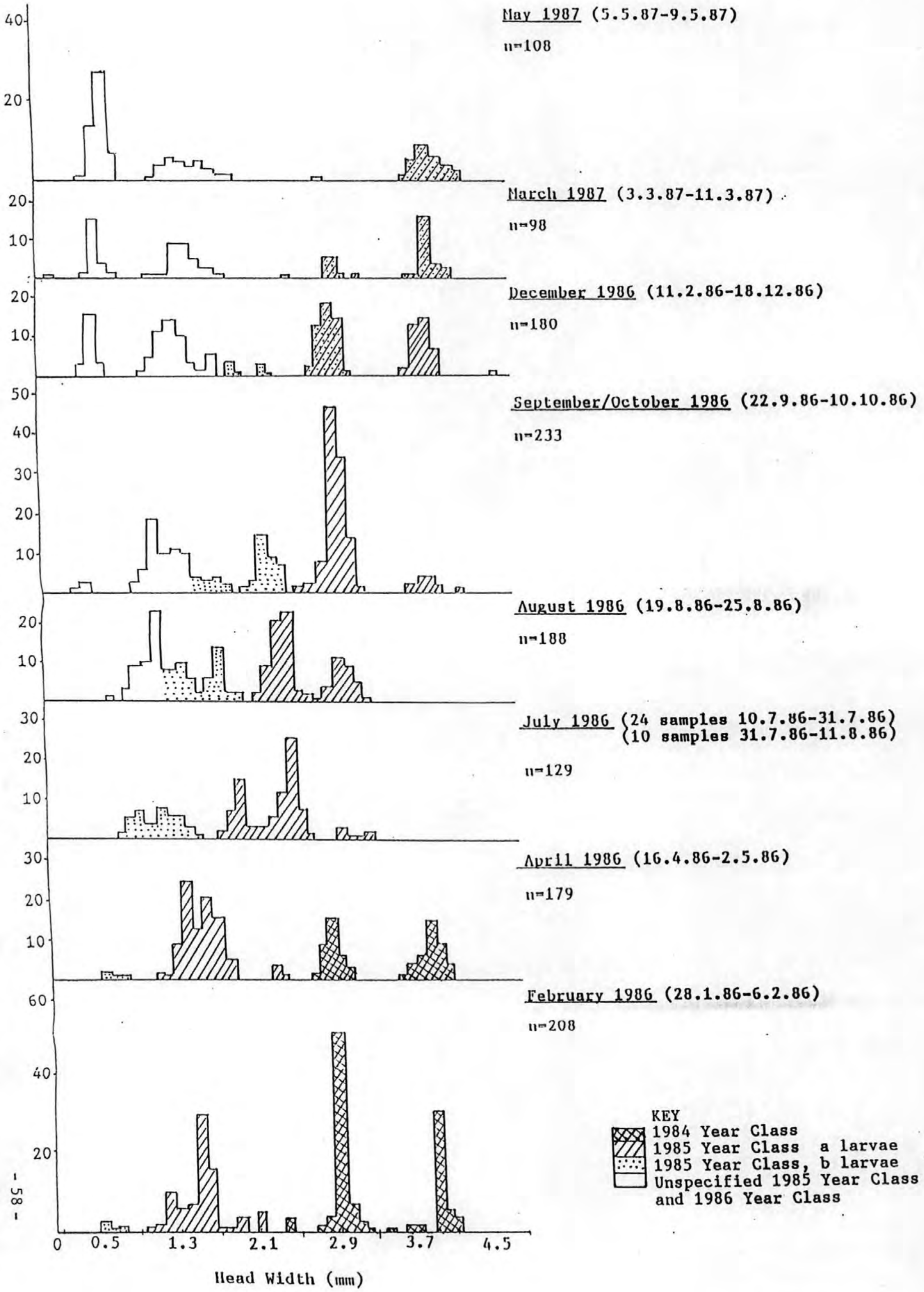
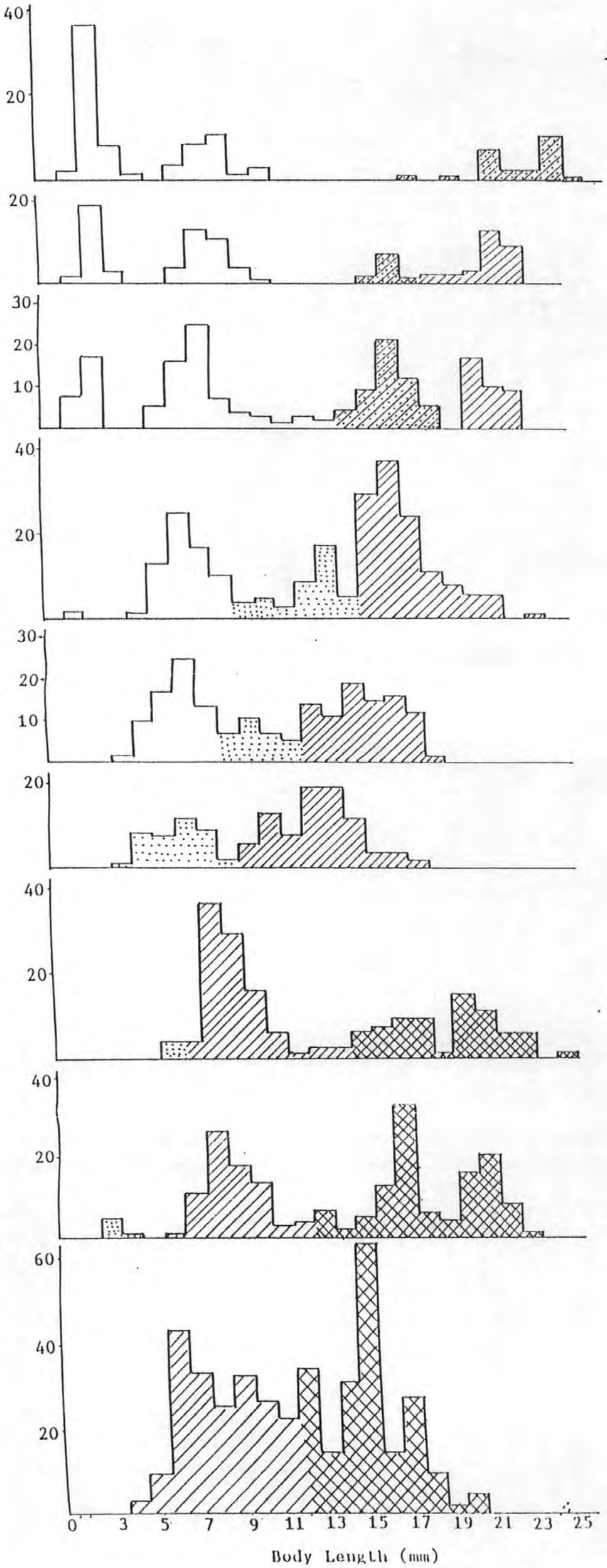


FIGURE 4.5a THE PATTERN OF GROWTH OF 1984 AND 1985 YEAR CLASS LARVAE IN ALL DENSITY AREAS: HEAD WIDTH



May 1987 (5.5.87-9.5.87)

n=105

March 1987 (3.3.87-11.3.87)

n=97

December 1986 (11.2.86-18.12.86)

n=179

September/October 1986 (22.9.86-10.10.86)

n=233

August 1986 (19.8.86-25.8.86)

n=186

July 1986 (24s 10.7.86-31.7.86)
(10s 31.7.86-11.8.86)

n=128

April 1986 (16.4.86-25.5.86)

n=171

February 1986 (28.1.86-6.2.86)

n=201

September 1985 (23.8.85-20.9.85)

KEY
1984 Year Class
1985 Year Class a larvae
1985 Year Class, b larvae
Unspecified 1985 Year Class and 1986 Year Class

FIGURE 4.5b THE PATTERN OF GROWTH OF 1984 AND 1985 YEAR CLASS LARVAE IN ALL DENSITY AREAS: BODY LENGTH

	Year Class	n	Mean	SD	SE	df	t	P	S^2	F ratio	P
Head Width (mm)	1984	85	3.893	0.106	0.011	136	5.75	0.000	0.011	1.375	ns
	1985	59	3.986	0.0895	0.012				0.008		
Body Length (mm)	1984	84	20.93	1.02	0.11	136	5.65	0.000	1.04	1.4	ns
	1985	59	21.827	0.862	0.11				0.743		

1986 larvae sampled February 86, March 86.
1987 larvae sampled December 86, April 87.

TABLE 4.5 THE DIFFERENCE IN AVERAGE SIZE AND VARIANCE IN SIZE BETWEEN 1984 AND 1985 YEAR CLASS FINAL INSTAR LARVAE

The presence of this numerous 1985b group of larvae would seem to indicate a later developing group. Through the summer the 1985b group develop rapidly and some have clearly caught up with the 1985a group in the penultimate instar in December, and will go on to emerge with that group in the summer of 1987. The relative size of 1985a larvae, and the later developing 1985b larvae which subsequently 'caught up', was examined by comparing the size of larvae which molted to the penultimate instar before the August 1986 sample with those still in this instar in the December 1986 sample. Table 4.6 shows that the later developing larvae were significantly smaller in both head width and body length.

The continuous presence of a 0.9-1.7mm head width group through late summer and autumn, when the first 1986 year class hatchlings were found is a puzzle, since there is no obvious origin for these larvae. It is possible that they represent slower developing 1985b larvae and possibly some early 1986 year class larvae that were not detected as hatchlings.

The first newly hatched larvae after summer 1986 were seen in the September/October sample, and numbers had grown by December. The size distribution of larvae over-wintering in 1986-7 is similar to that in 1985-6, except that the 'recently hatched' group is much more numerous in 1986-7 probably due to the late oviposition in the summer of 1986. In May 1987 there is a dramatic increase in the number of very early instar larvae relative to other groups.

	Penultimate Instar Group	n	Mean	SD	t	P
Head Width (mm)	Sampled Aug 86	30	3.058	0.0978	2.8	0.001
	Sampled Dec 86	49	2.995	0.0946		
Body Length (mm)	Sampled Aug 86	30	17.287	0.796	2.3	0.05
	Sampled Dec 86	49	16.751	1.271		

TABLE 4.6 A T-TEST OF THE DIFFERENCES IN SIZE BETWEEN 1985 LARVAE IN THE PENULTIMATE INSTAR IN AUGUST, AND THOSE STILL IN THIS INSTAR IN DECEMBER 1986.

b) A comparison of the growth of larvae from high and low density areas.

Patterns of growth in head width and body length of larvae in different density areas can be compared by superimposing histograms from high and low density (Figure 4.6 a and b). All the trends seen in the overall pattern of growth were equally represented from both density areas. Although in February 1986 a greater proportion of the 1984 year class were still in the penultimate instar in the high density areas compared to the low density areas, this difference had disappeared by April 1986. There was no sign, therefore, that in low density areas the abundant 1984 year class was at a similarly advanced stage of development as the 1985 year class. When the sizes of final instar larvae from different density areas were compared, there was no difference in either head widths or body lengths within either year class (Table 4.7). Similarly there was no difference in the variance in body size of larvae from high and low density areas (Table 4.8).

The later developing 1985b larvae were present in both high and low density areas, and equally small in both areas (Table 4.9).

4.3.4 The sex ratio of larvae and the development of males and females

The sex ratio of larvae in successive months in successive instars was examined to see if there were any overall differences, or, bearing in mind that adult females are significantly larger than males (Chapter Five), if there

was any sign of males and females developing at different rates. Table 4.10 shows that the overall sex ratio for each month's sample from July 1986 to May 1987 is remarkably close to a 1:1 ratio, and the proportion of males and females in each instar gives no indication of different rates of development between the sexes.

4.3.5 The Movement of Marked Final Instars and The Number of Larvae Found in the Drift.

Of the eighty one final instars marked only nineteen, around a quarter, were recovered (Figure 4.7). Six of those marked in December and January samples were later found in April or May samples. Five of these had only moved 1-3 metres, although one had moved 12 metres. Larvae which had not moved at all will have been under-represented in bank samples since the same bank area is unlikely to have been sampled twice. Of the forty marked final instars released in section F, thirteen marked exuviae were recovered during the monitoring of emergence (see Chapter Five). Ten of the exuviae were within 0-1 metre of the release site of the final instar larvae, and no marked exuviae were found on the opposite north facing bank.

In the 48 drift net samples taken only four larvae were found. Stoneflies and mayflies were commonly found though, at densities of 27.1±6.5 and 9.7±2.2 respectively (means given with one standard error).

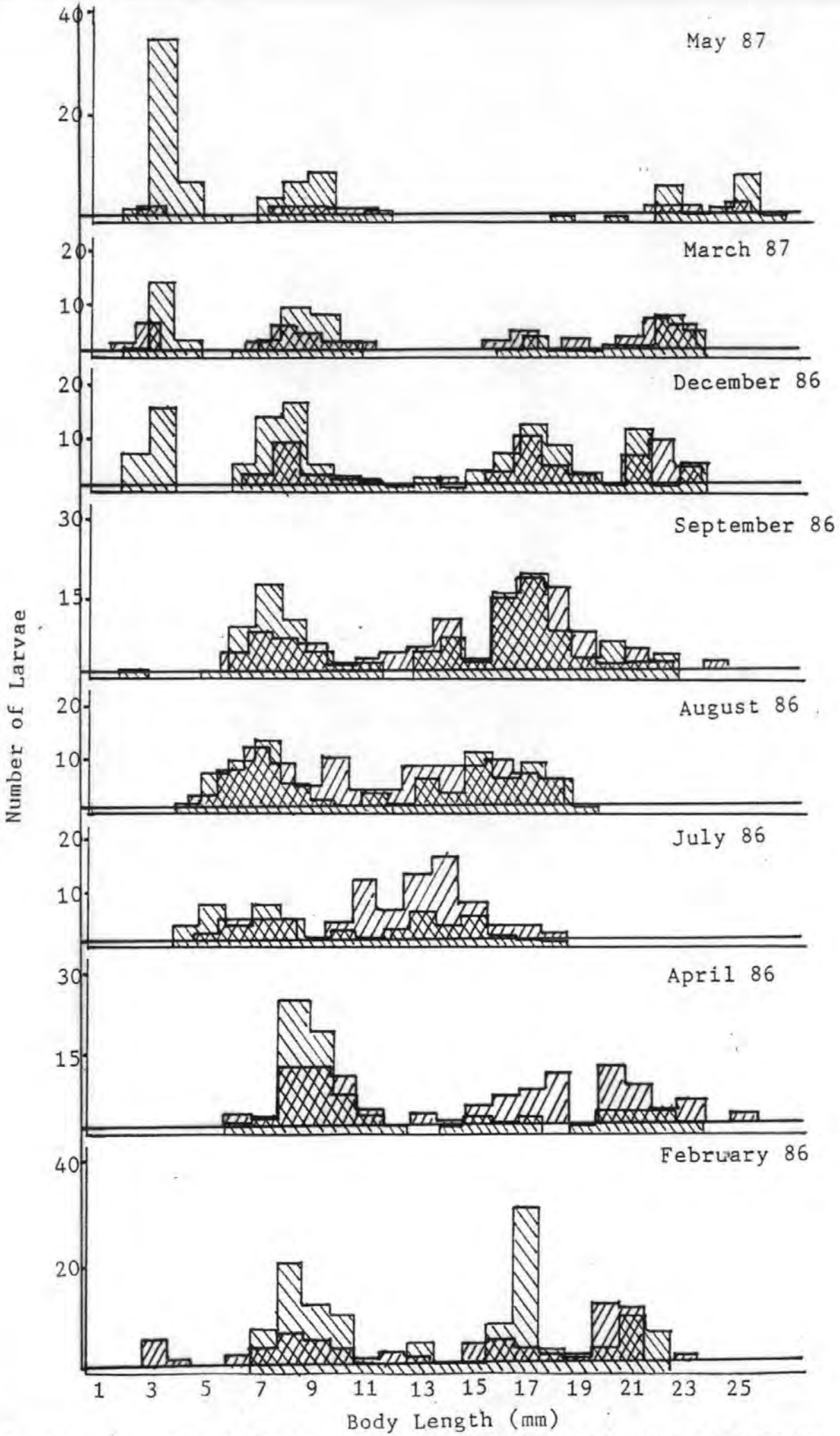


FIGURE 4.6a THE PATTERN OF GROWTH OF 1984 AND 1985 YEAR CLASS LARVAE IN HIGH AND LOW DENSITY AREAS: BODY LENGTH
High Density Area Low Density Area

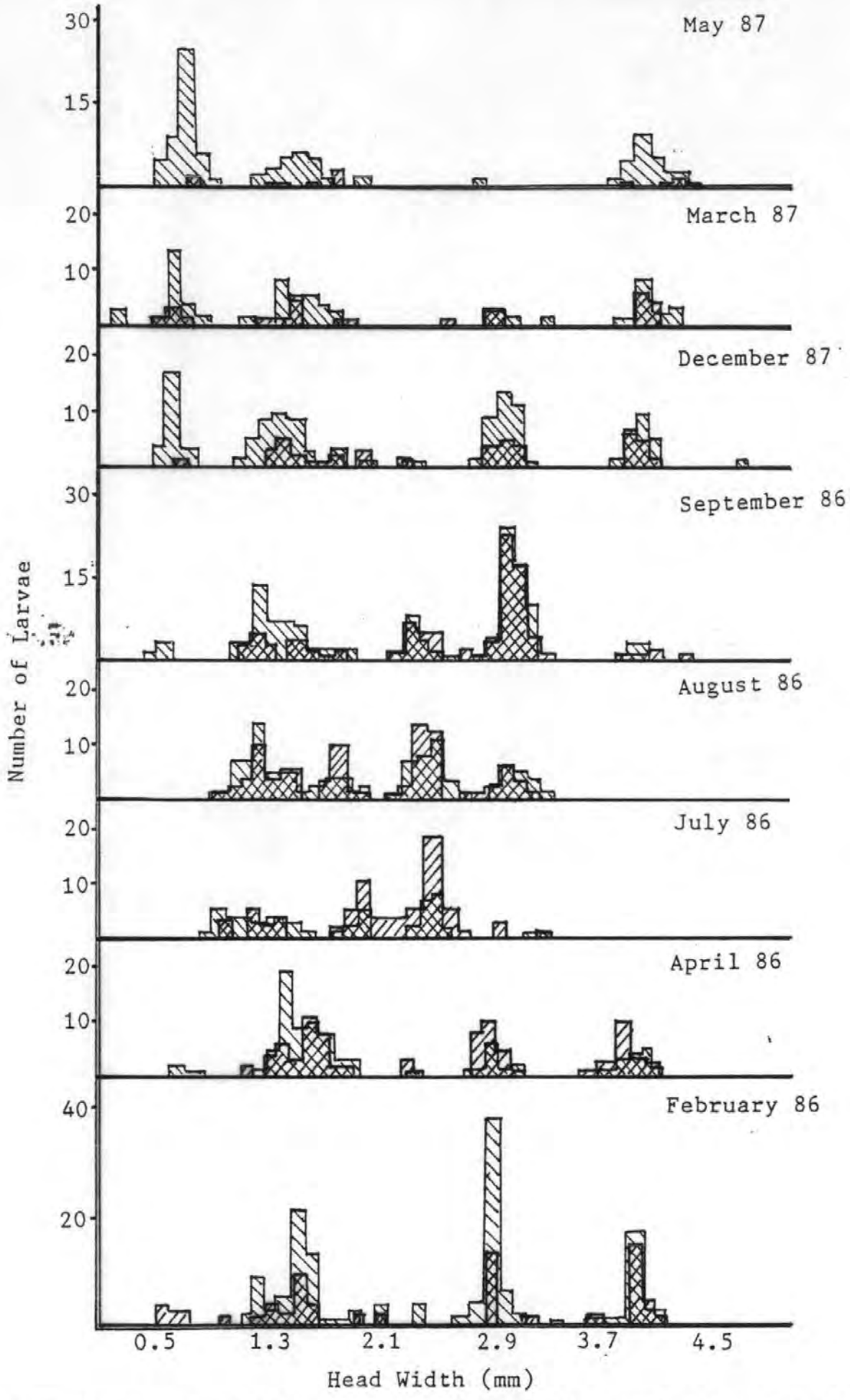


FIGURE 4.6b THE PATTERN OF GROWTH OF 1984 and 1985 YEAR CLASS LARVAE IN HIGH AND LOW DENSITY AREAS: HEAD WIDTH
High Density Area Low Density Area

	Density Area	n	Mean	SD	df	t	P
a) 1984 Year Class, Sampled February and April 1986							
Head Width (mm)	High (EF)	39	3.897	1.107	80	0.39	0.70
	Low (A-D)	46	3.888	0.105			
Body Length (mm)	High (EF)	38	21.066	0.931	81	1.09	0.28
	Low (A-D)	46	20.83	1.09			
b) 1985 Year Class, Sampled December 1986 and March 1987							
Head Width (mm)	High (EF)	36	3.996	0.0966	54	1.06	0.29
	Low (A-D)	23	3.972	0.0766			
Body Length (mm)	High (EF)	36	21.786	0.940	54	0.48	0.63
	Low (A-D)	23	21.891	0.738			

TABLE 4.7 t-TESTS COMPARING THE SIZE OF FINAL INSTAR LARVAE FROM HIGH AND LOW DENSITY AREAS.

	Density Area	n	S^2	F-ratio	P
1984 Year Class					
Head Width	High	39	0.011	1.00	ns
	Low	46	0.011		
Body Length	High	38	0.867	1.370	ns
	Low	46	1.189		
1985 Year Class					
Head Width	High	36	0.0093	1.632	ns
	Low	23	0.0057		
Body Length	High	36	0.8836	1.622	ns
	Low	23	0.545		

TABLE 4.8 A COMPARISON OF THE VARIANCE IN SIZE OF FINAL INSTAR LARVAE FROM HIGH AND LOW DENSITY AREAS.

	Density Area	n	Mean	SD	t	P
Head Width (mm)	High	36	3.000	0.0951	1.14	ns
	Low	14	2.976	0.0891		
Body Length (mm)	High	36	16.91	1.11	0.45	ns
	Low	14	17.036	0.771		

TABLE 4.9 THE SIZE OF LATER DEVELOPING, 1985 YEAR CLASS PENULTIMATE INSTAR LARVAE, IN HIGH AND LOW DENSITY AREAS.

Sample	Instar	Males		Females	
		n	%	n	%
Aug 86	L-2	21	43	28	57
	L-1	13	59	9	41
	Total:	34	48	37	52
Sep 86	L-1	48	48	52	52
	L	9	-	4	-
	Total:	57	50	56	50
Dec 86	L-1	25	54	21	46
	L	17	46	20	54
	Total:	42	51	41	49
May 87	L	15	54	13	46

TABLE 4.10 THE SEX RATIO OF 1985 YEAR CLASS LARVAE IN SUCCESSIVE INSTARS.

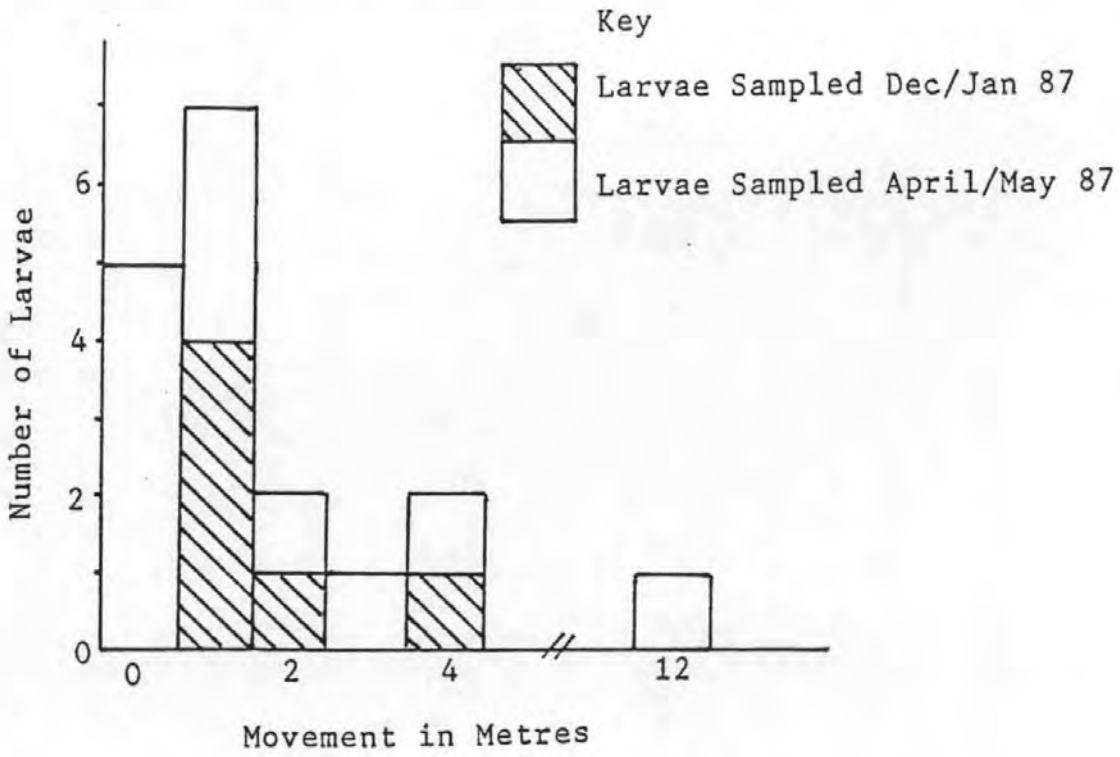


FIGURE 4.7 THE MOVEMENT OF MARKED 1985 YEAR CLASS FINAL INSTARS FROM THEIR INITIAL SAMPLE POSITION TO THEIR EMERGENCE POSITION. HISTOGRAMS REPRESENTING LARVAE FROM THE TWO SAMPLE DATES ARE SUPERIMPOSED.

4.4 DISCUSSION

4.4.1 Evidence for feeding competition between larvae.

Despite there being significant differences in density and body size within and between year classes, there was no firm evidence to suggest the two were related. The most reliable indications of density effects on body size would be those seen within year classes, where larvae in different density areas have experienced similar conditions (such as temperature) during development. Despite twofold differences in average densities in both year classes, and in local densities in the 1984 year class, there were no signs of an effect of density on growth and body size. In the 1985 year class a later developing sub-population was present in both high and low density areas, and was equally small in body size in each, which indicates that its origins were not due to feeding competition. In addition final instars within both year classes were the same size in high and low density areas. Since larvae in high density areas were significantly aggregated, a proportion will be developing at low density. Competition (whether or not size related) in high density areas is therefore likely to be apparent in increased variance in body size, but there was no difference in the variance in body size between high and low density areas.

Differences in prey density and temperature can markedly influence the growth of aquatic invertebrates (Sweeney 1986) including Odonata (Lawton et al 1980, Pickup and Thompson 1990). The lack of any indications of feeding related competition is unlikely to be due to these variables

confounding the effect of larval density. Stream temperature through development will be equal for all density areas within a year class. Although it was not possible to monitor prey density throughout development, a period of sampling indicated that prey densities were comparable between larval density areas.

The 1984 year class is likely to have developed at around double the average and local density of the 1985 year class, and 1984 year class larvae had smaller body sizes and lagged behind slightly in development time. There was no difference, however, in the variance in body size between the two year classes as might be expected if this was a density effect. Furthermore there was no difference in the average density of 1984 larvae in the low density area and 1985 larvae in the high density area, yet the 1984 year class larvae were still smaller. It seems unlikely therefore that the difference in the development of the two year classes can be attributed to the difference in their density. Nevertheless the two year classes have obviously experienced different growth conditions, and the way in which factors such as prey density and temperature could influence this are discussed in more detail in section 4.4.2.

The possibility of interaction between year classes has not been studied here, but the study of density effects within year classes will not be confounded by the density of the older year classes, since the pattern of their densities was similar. The larger body size and earlier development of the 1985 year class in the presence of the more numerous 1984

year class would suggest that the older year class had no significant ill effects on the younger one.

If larvae were highly mobile the effects of competition may be mitigated. The results presented here, however, suggest that larvae were very immobile: even the small amount of movement detected could be a consequence of removing and replacing larvae. The small proportion of recovered marks is unlikely to be a consequence of large numbers moving greater distances, because some of these would have been found. The low recovery rate is more likely to be due to the sampling process resulting in sedentary larvae not being detected, and the difficulty in finding exuviae. The marking took place in winter and spring, but the later instars continued to grow at this time, and the lack of movement is not likely to be due to diapause, although it may have been reduced by temperature. Larvae were also rarely found in the drift or on the Leat bed. These results agree with the direct observations of the behaviour of Calopteryx larvae in natural populations (Zahner 1959). The sex ratio of larvae in various instars did not deviate from a 1:1 ratio, giving no indication of differing development rates between the sexes as found for Ischnura verticalis (Baker et al 1992).

The lack of any indication of density effects on larval growth rate and body size strongly suggest that there is no interference or exploitation feeding competition occurring in this population in the 1984 and 1985 year classes. The densities of larvae studied were not particularly low compared to other populations of Odonata (Table 4.11), and a

four fold range in density was present. The lack of density effects cannot therefore be explained by atypical conditions. The results of this study add to the small, but growing body of evidence which suggests that feeding related larval competition is uncommon in natural populations of Odonata. Despite Baker's extensive laboratory studies indicating size related interference competition (see Chapter One), he has been unable to detect this in four separate studies of natural populations: these studies have concentrated on the immediate effects of larval density on size related wounding and dispersal (Baker and Dixon 1986, Baker 1987) and faecal pellet weight and larval 'condition' (Baker 1986, 1989), rather than longer term influences on growth patterns and body size

The possible longer term influences of density were studied by Banks and Thompson (1987a), who report finding evidence for feeding related competition. In natural populations of Coenagrion puella occurring in five ponds, larvae in high density populations tended to show greater asynchrony in growth and smaller body sizes than those in low density populations. The pattern was not unequivocal though, and as the authors acknowledge, their study between different ponds did not control for differences in prey density or temperature which are known to influence growth and body size. In addition Banks and Thompson identified later developing larvae in the five ponds, and selected two ponds to illustrate that these were only smaller in body size in high density populations- indicating a feeding competition effect. Data which the authors presented previously, however,

Species	Density (m^2) Mean	Range	Habitat	Source
Calopteryx virgo				
Small Larvae	14-112	0-400	Stream bank	Present Study
L-1 and L instars	11-64	0-272		
C. virgo				
Late instars	60-150		Stream bank	Zahner 1959 based on 30-75 per metre length of bank
Ischnura elegans				
Late instars	75-250		Pond	Banks and Thompson 1987a
Pyrrhosoma nymphula				
Small larvae	116-362		Pond	Lawton 1971
Late instars	2-93			
Tetragoneuria cynosura	16.2	0-45	Lake	Crowley et al 1987a

TABLE 4.11 EXAMPLES OF THE DENSITY OF ODONATA LARVAE IN NATURAL POPULATIONS.

showed that later developing larvae tended to be smaller in all populations regardless of density, and significantly so in one low density population, making it difficult to conclude that density dependent feeding competition was responsible.

Although uncommon, there is some evidence of feeding competition in natural populations. While unable to find signs of size related interference competition (see above), Baker (1986) did find weak evidence that the level of gut fullness of I.verticalis was related to larval density, indicating general interference or exploitation feeding competition. In addition Van Buskirk (1992) has found evidence for size related interference competition in a natural population of Aeshna juncea, and it is perhaps significant that the habitat where this occurred was very simple: small frequently disturbed rock pools with simple structure and fauna.

4.4.2 Factors other than feeding competition which may have influenced growth patterns and body size

This study clearly shows that differences in patterns of growth and body size can occur within and between year classes which are unrelated to density dependent feeding competition. Sub-populations of later developing larvae which are smaller in body size than early developing larvae can occur in high and low density areas, and development time and body size can differ between year classes. Alternative explanations for these trends must therefore be sought. The model of Crowley et al (1987b) predicts that asynchronous

larval development can be expected to occur in populations with a seasonal emergence 'window'. As a result a bimodal emergence peak occurs, with larvae emerging in early and late peaks having long and short larval durations respectively. Asynchronous development and variable voltinism within populations are widely reported (Baker and Clifford 1982, Banks and Thompson 1985, Wissinger 1988, Crowley et al 1987b), and the Crowley et al model shows feeding competition need not be a causal factor.

Two emergence peaks were found in this (see Chapter Five) and other studies of C.virgo (Corbet 1957), but the growth of larvae described here does not suggest that variable voltinism is the major cause. Although some 1985 year class larvae may have failed to emerge in 1987, most larvae appear to take two years to complete development. Larvae developing later in the season include late hatchers which 'catch up' with early hatchers to the extent of emerging in the same year. The large increase in the late hatching group in spring/early summer in both the 1985 and 1986 year classes strongly suggest that this group includes a large proportion of larvae which delayed hatching until this time. The large proportion of delayed hatchers in the 1986 year class, where poor weather delayed most oviposition until late summer, suggests that this phenomenon may be triggered by late oviposition. As in the model population the asynchronous growth appears to be caused by seasonal patterns of emergence and oviposition. A further similarity with the 'model' larvae is that the larvae developing and emerging

later in the season are those which have the shortest larval development time.

The Crowley et al model does not consider body size, and assumes that emergence will always occur at the same body size (development index), which seems unlikely in real populations of larvae with varying growth histories. Seasonal variations in prey density could account for a fall in body size as the season progresses, but this was not the case in a study of I.verticalis (Baker 1989). As in this study, Baker could find no relationship between density and the later emergence of smaller adults. Interestingly though, he noted that later developing larvae had reduced condition (dry weight:head width ratio) despite there being no change in prey density. He suggested that this could be due to larvae developing later in the season increasing their rate of development at the cost of body mass in order to bring emergence forward. This implies that larvae are able to modify their rate of development, and something similar appears to be happening in this study, where the later hatching group appears to develop very quickly over the summer to catch up with the early hatching group, at the cost of smaller body size. Where, as predicted by the Crowley et al model and as seen here, later emerging larvae have shorter larval periods, this is likely to be connected with the phenomenon of smaller body size.

A simpler explanation than facultative development rates may involve the temperature during development. Sweeney (1984) reviews the factors influencing life-history patterns

in aquatic insects, and notes that development rate (time taken to go through an instar) and growth rate (biomass accumulation) do not respond to temperature changes to the same extent. As a result body size varies depending on rearing temperature, and studies of multivoltine mayfly species consistently show that adults of winter-spring cohorts are significantly larger than those of summer cohorts (Sweeney 1984 and references therein). As temperature increases development rate therefore increases more than growth rate, resulting in reduced body size. It seems likely that the smaller body size of later emerging Odonata groups is due to the timing of their growth relative to seasonal increases in temperature. In the 1985 year class this difference in size was present in the penultimate instar, so that differing conditions must have been experienced before this instar. Larvae hatching at the normal time in August and September go through the more numerous early instars over the autumn, winter (if growth occurs) and early spring. Late or delayed hatching larvae spend little or no early development time (respectively) during the colder months, and therefore go through the numerous early instars in warmer temperatures. In addition it may be important that whereas the normal/early hatching larvae spend the cool winter in the final instar, late developing larvae will go through the final instar in the warm spring and summer months. Differences in the conditions experienced in the final instar alone can be sufficient to influence the size of emerging adults (Harvey and Corbet 1985), such that this difference in development temperature alone could influence adult body size. The widespread occurrence of smaller body size in later

developing sub-populations in Odonata (Banks and Thompson 1985, Koenig and Albano 1987, Tsubaki and Ono 1987, Van Buskirk 1987b, Fincke 1988, Michiels and Dhondt 1989, Gribbin and Thompson 1990, and Forbes and Baker 1991) and many other insects such as grasshoppers (Atkinson 1985), dungflies (Ward 1983), and fruitflies (Partridge and Farquhar 1983) strongly suggests that this phenomenon has a seasonal cause.

While high temperature may tend to reduce development time and reduce body size, Lawton et al (1980) have shown that high prey density tends to reduce development time and increase body size. Pickup and Thompson (1990) found that the interaction between prey density, temperature, growth rate and development rate is complex, and can result in varied body sizes and larval durations. Such phenomena are likely to have resulted in the variations in growth patterns and larval body size which were witnessed in the 1984 and 1985 year classes in this study.

CHAPTER FIVE

THE INFLUENCE OF LARVAL GROWTH ON THE TIMING OF EMERGENCE AND ADULT BODY SIZE

5.1 INTRODUCTION

In Chapter Four it was shown that differences in the pattern of larval growth and larval body size occurred within and between year classes. The aim of this Chapter is to examine how these differences in larval growth influence the timing of emergence and adult body size. General information on the diurnal pattern of emergence, emergence behaviour and sex ratios is also presented.

5.2 METHOD

In 1985 the onset of emergence only was noted, but in 1986 and 1987 emergence was monitored on a daily basis. In 1986 searches for emerging adults began on the 26th of May, and continued almost every day until emergence started. As soon as the first adults were seen all sections of the Leat were walked several times each morning, starting at one of five sequential start positions on successive days, namely sections A,C,E,G and I. Initially walks began at around 6.30am, but once the daily pattern of emergence was determined they began later. Emergence walks usually continued until most emerging adults were flying. By walking down the middle of the Leat itself it was possible to search the bank vegetation on either side for emerging adults. The exact position and stage of emergence of adults were noted.

Those that could be handled were carefully placed in a portable netting cage (a lampshade frame covered in netting with drawstring top and a shoulder strap) until the end of the appropriate 30m Leat section had been reached, when they were transferred to a netting wig-wam. Adults from both banks were collected, and those from the south facing bank were immediately marked with dot of white Pentel paint marker on the right hand femur. These marks lasted until the adults were measured in the field in mid or late afternoon, when they were fully expanded and their cuticles had hardened. Later in the day other newly emerged adults (as judged by body characteristics- see Chapter Six) which were flying were also caught and measured.

In 1987 the emergence of adults was monitored from section E and F only, in order to look more closely at the numbers emerging and to retrieve the exuviae of marked final instar larvae (see Chapter Four). A net was laid along the south facing bank of sections E3 and F1-3, as close to the water's edge as possible (Plate 5.1). The net was buried into the soil at the base and was a metre high. At the top it was attached to canes with clothes pegs, and each morning after emergence was over it was dropped to prevent it interfering with adult movement. Emerging adults were retrieved from the net and the vegetation at the water's edge before they could fly, and were transferred to the netting wig-wams to await measurement. Periodically the vegetation behind the net was also searched. All exuviae which were found were removed from the net and vegetation each day, and at the end of the day the net was raised again.

The body length of adults was measured from the foremost point of the head, the labrum, to the rear edge of the tenth abdominal segment. Head width was measured as the greatest distance across the eyes with a binocular microscope and eyepiece graticule while the damselflies were held gently by the base of the wings. Adults were released in the centre of the 30m section where they had been found by placing them in sunlight on top of the vegetation. Some flew off immediately after release, others rested five to ten minutes before doing so.

5.3 RESULTS

5.3.1 Emergence behaviour and sex ratio

In 1986 emerging adults were usually seen within thirty to forty centimetres of the water's edge, and were difficult to find since they remained low down in the vegetation until almost ready to fly. Larvae were found clinging to vertical stems, or hanging beneath overhanging leaves around fifteen centimetres above ground level. Newly emerged adults were not seen on the wing before 09.00h, and there were few exuviae on the net in F section in 1987 each morning which were not accompanied by an emerging adult, indicating that there was little or no overnight emergence. Figure 5.1 shows the proportion of adults at various stages of emergence through the morning on a typical day (sunny, with shade temperature 12-14^{0}C by 09.00h). It is not known when larvae began leaving the water, but at around 07.00-08.00h half of the emerging adults found had not begun ecdysis, and half were just emerging from the larval skin or in the 'rest' stage. When in

the 'rest' stage the emerging adults hung head downwards, attached to the exuviae by the tip of the abdomen only while their legs hardened. At around 08.00-09.00h half of those found were completely free of the exuviae, but none were fully expanded (Plate 5.2). Once free of the exuviae adults expanded their bodies rapidly and moved up the vegetation, and by 10.00-11.00h just over half were ready to fly, with deep although still dull colour. Very little mortality was observed in emerging adults, although most were first seen when they were at least half expanded and had moved up the vegetation. There was no sign of attack by invertebrate predators, and there was no sign of new wings on the ground to indicate wide-scale bird predation. The only mortality witnessed was uncommon, and caused by a failure to emerge properly from the larval skin, resulting in adults with severely twisted wings and abdomens. On three occasions exuviae were observed being rapidly eaten by Myrmica ants, with around half the exuviae eaten by 09.00h.

While most newly emerged adults flew between 11.00h and 12.00h on a typical morning, the whole emergence process was influenced by weather conditions. Seven individuals were observed emerging during rainy weather on 2/6/87. Five found before ecdysis failed to begin ecdysis that day but remained at their perches, and three of these were found in the same position early the following morning as almost fully expanded adults. Two found as half expanded adults were still with their exuviae the following morning, but looked ready to fly. On very cool but dry mornings (cloudy, with shade temperature only 10-11^{0}C by 09.00h), adults were delayed in their

a) NET RAISED READY TO COLLECT EMERGING ADULTS.

b) AFTER EMERGENCE THE NET IS DROPPED TO ALLOW FREE MOVEMENT OF ADULTS.

PLATE 5.1 THE MONITORING OF EMERGENCE IN SECTIONS E AND F IN 1987.

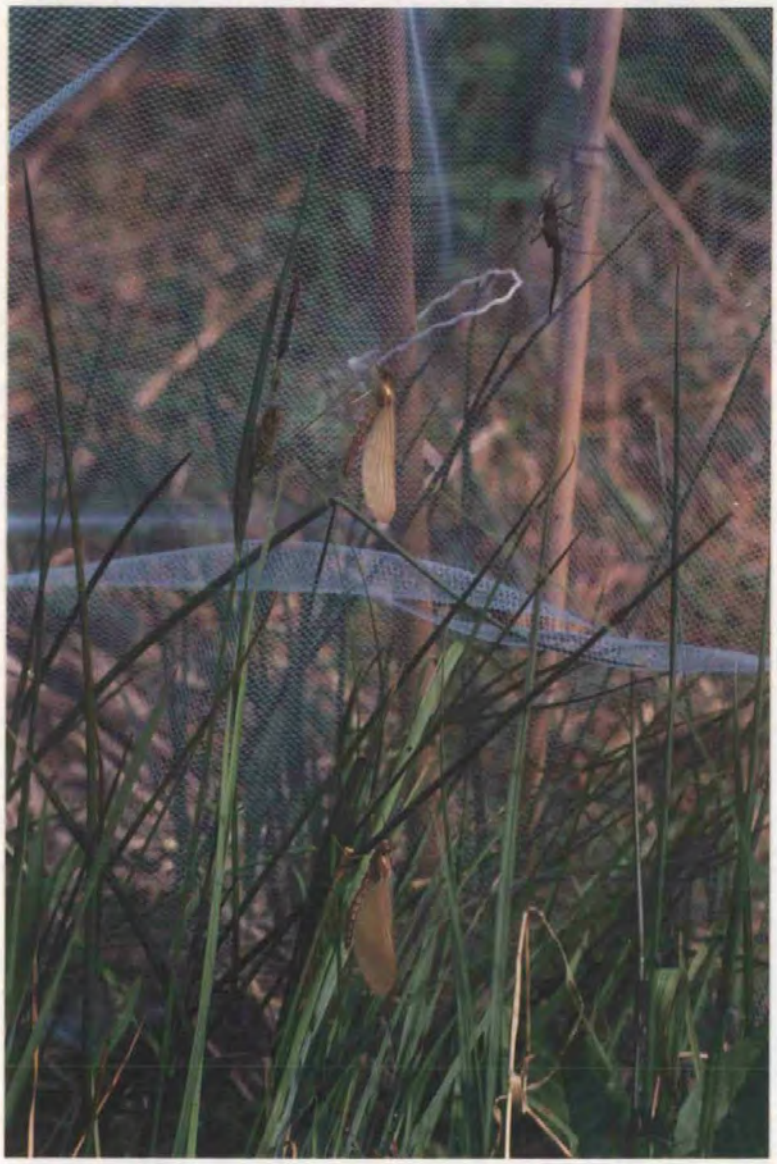


PLATE 5.2 ADULTS EMERGING INTO THE NETTING IN SECTIONS E AND F. THE STAGE REACHED HERE, WHERE ADULTS ARE FREE OF THEIR EXUVAE, WAS REACHED BETWEEN 8-9.00 am ON A TYPICAL MORNING.

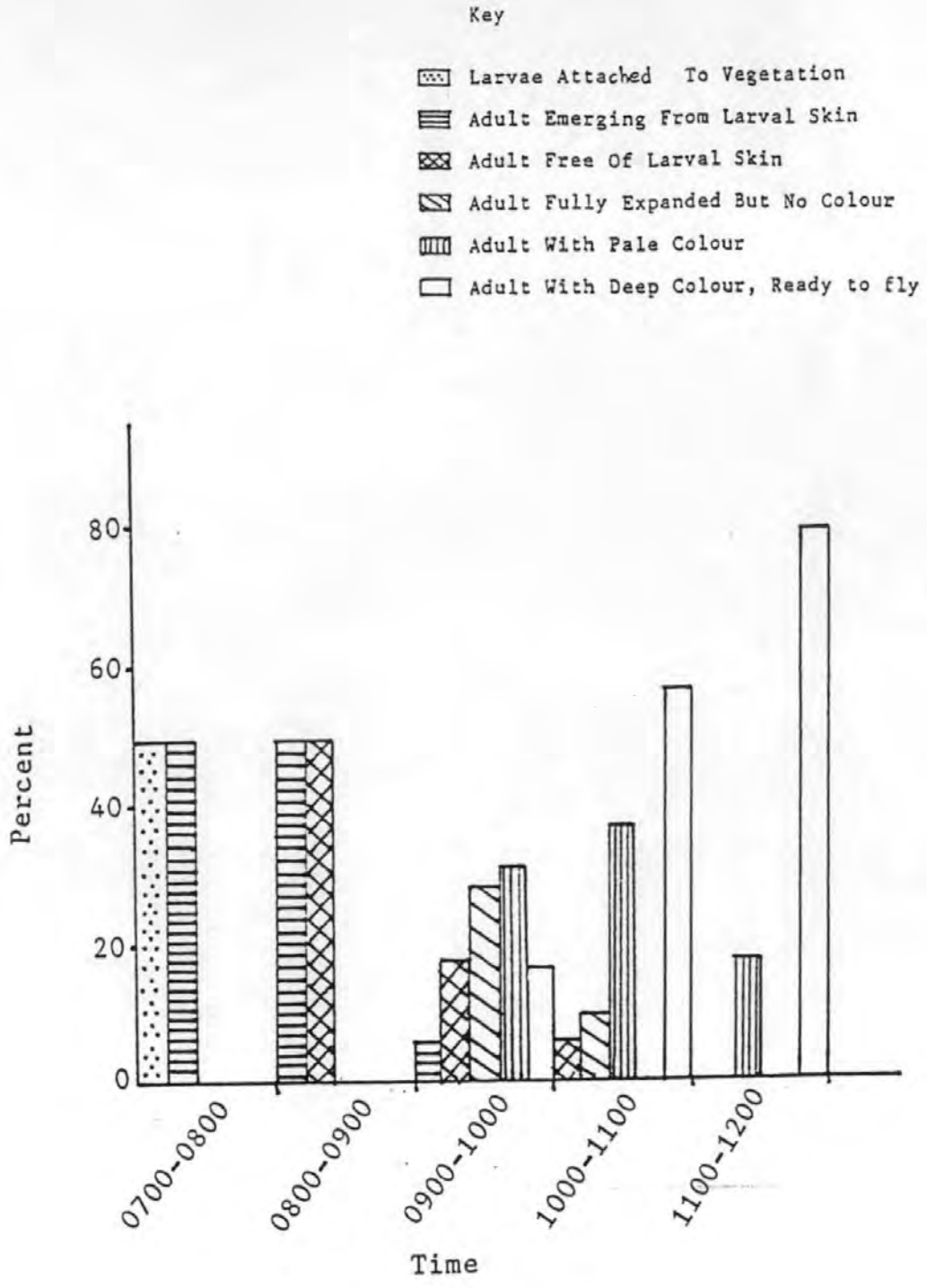


FIGURE 5.1 THE PROPORTION OF ADULTS SEEN AT VARIOUS STAGES OF EMERGENCE ON A TYPICAL MORNING. AIR TEMPERATURE IN THE SHADE 12-14°C at 0900h, n=85.

emergence stage, and of nine watched continuously during such weather, seven had not flown by 01.00h. Often on these cool days the first newly emerged adults were not seen flying until mid-afternoon. Conversely eighteen adults monitored on a hot morning (sunny, with air temperature 16^{0}C by 09.00h) had all flown between 09-10.00h. The maiden flight was often but not always a long one, and directed away from the sun and upwards to take the new adult up to the south facing side of the conifers on the south facing bank. New adults did not generally remain in the conifer tops, and many were seen feeding beside the Leat later in the day.

Table 5.1 shows that in both years a significant bias towards females in the sex ratio of emerging adults was recorded, largely because many more females than males were seen emerging later in the summer (see below).

5.3.2 The timing of emergence and adult body size

Emergence in 1985 and 1987 began at the end of May, but in 1986 it started nineteen days later on the 13th June. Figure 5.2 shows that in 1987 the emergence occurred in two distinct groups over forty days, but in 1986 there appeared to be three groups, although the overall time span of emergence was the same. The distribution of emergence along the Leat in 1986 reflected larval density (see Chapter Three), with the largest number of adults emerging from sections E,F and H (Figure 5.3). Most adults in 1986 emerged during the middle peak from the 25th June to the 3rd of July, while in 1987 slightly more adults emerged from section F during the early peak from the 27th May to the 6th June

(Figure 5.4). In total 140 adults were caught as they emerged from the 40m stretch in sections E and F in 1987, an average of 3.5 per metre length of bank, or approximately 14 per square metre of bank.

In 1986 there was a tendency for earlier emergence from the high density areas; in high density sections EF and H 35-37% of adults emerged in the first group, compared to 20-28% in AB and CD. Recently emerged males had a significantly larger body size than that of females (Table 5.2). The frequency distributions of body size of both sexes appeared normal, with no obvious skew, and across all groups the largest individuals had head widths 11% and body lengths 19% greater than the smallest individuals. The results of a t-test and F ratio, shown in Table 5.3 indicate that adults emerging in 1986 were significantly smaller than those emerging in 1987. While there was a trend that adults in 1986 were more variable in size than those in 1987, the differences were not significant. When the size of adults emerging in successive peaks from May to July in both year classes is examined, there is a consistent trend of decreasing body size with increasing date of emergence in both males and females (Figure 5.5 and 5.6). The differences between emergence groups in female size and male body length were significant in 1986 (female head width: $F=8.888$, $df=2, 147$, $P=0.000$, female body length: $F=5.07$, $df=2,191$, $P=0.007$, male body length $F=10.44$, $df=2,161$, $P=0.000$), but the differences in body size in 1987 were not significant.

Emergence Year	Sex	Emergence Group 1	2	3	Total	%	χ^2	df	P
1986	Females	77	82	49	208	60	8.4	1	0.01
	Males	52	88	13	153	40			
1987	Females	67	37	-	104	62	9.97	1	0.01
	Males	49	14	-	63	38			

TABLE 5.1 THE SEX RATIO OF ADULTS EMERGING IN 1986 AND 1987.

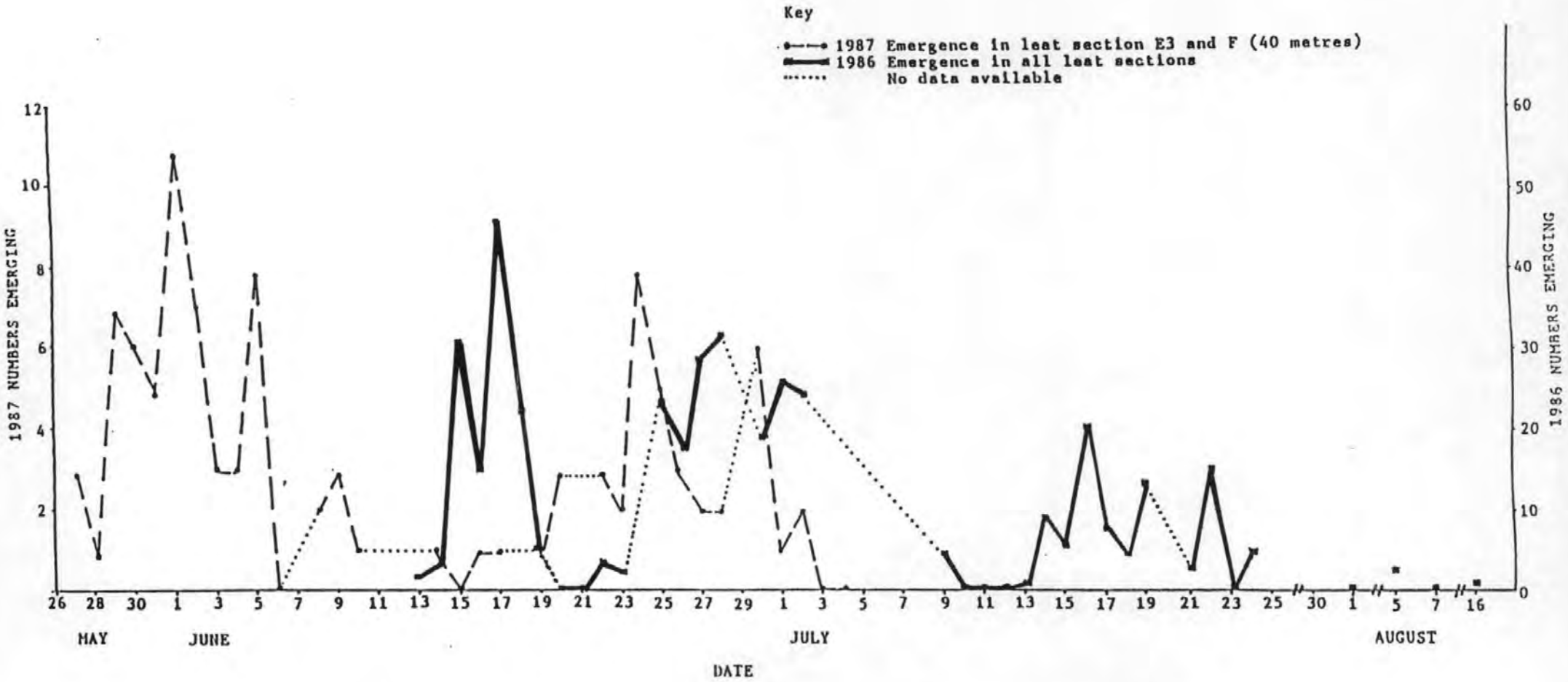


FIGURE 5.2 A COMPARISON OF THE PATTERNS OF EMERGENCE IN 1986 AND 1987. BREAKS IN RECORDING LARGELY DUE TO POOR WEATHER.

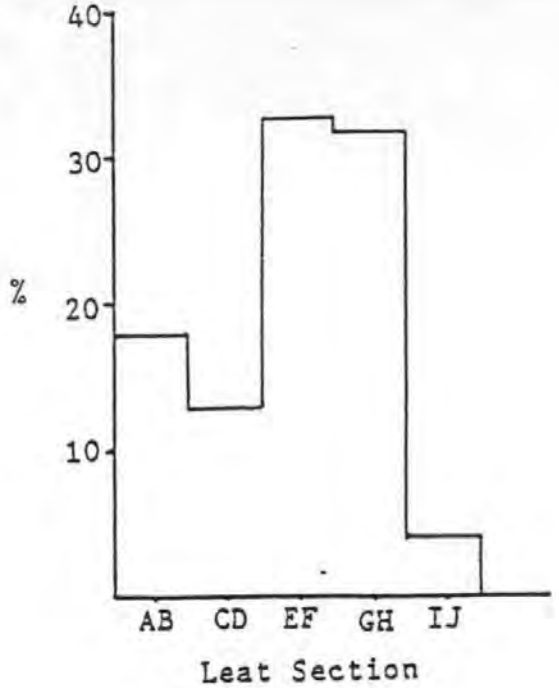


FIGURE 5.3 THE PROPORTION OF ADULTS EMERGING FROM DIFFERENT SECTIONS OF THE SOUTH-FACING BANK OF THE LEAT IN 1986

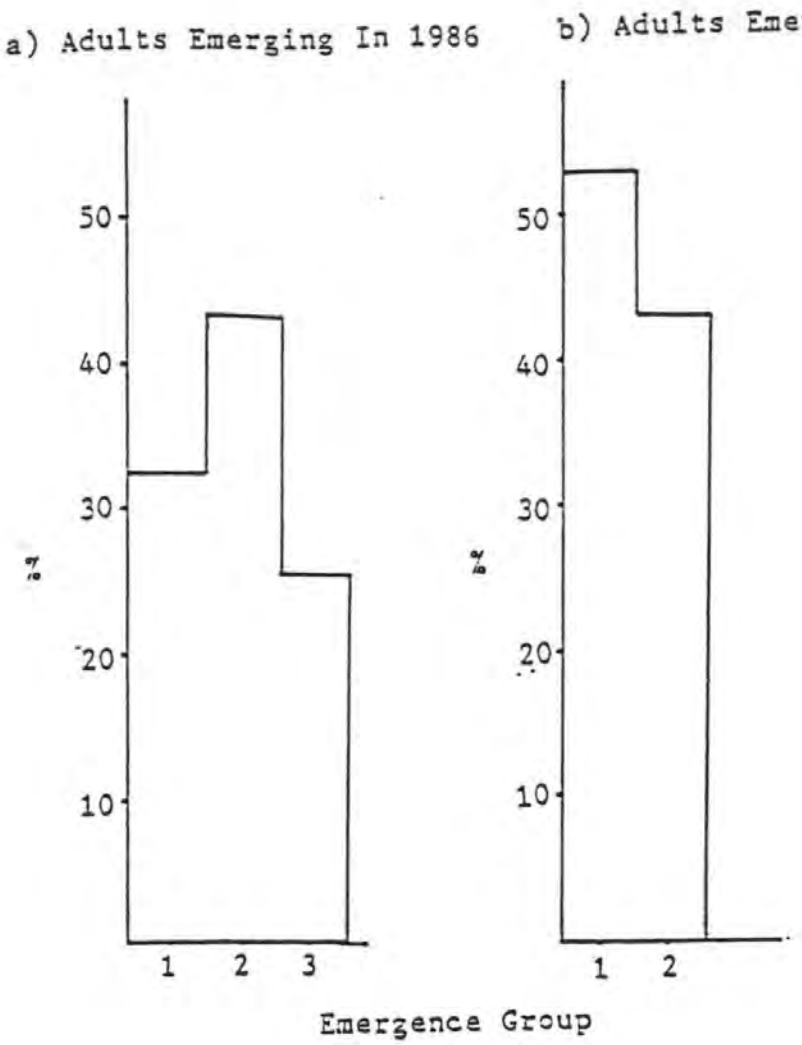


FIGURE 5.4 THE PROPORTION OF ADULTS EMERGING FROM THE SOUTH-FACING BANK IN DIFFERENT GROUPS IN 1986 AND 1987

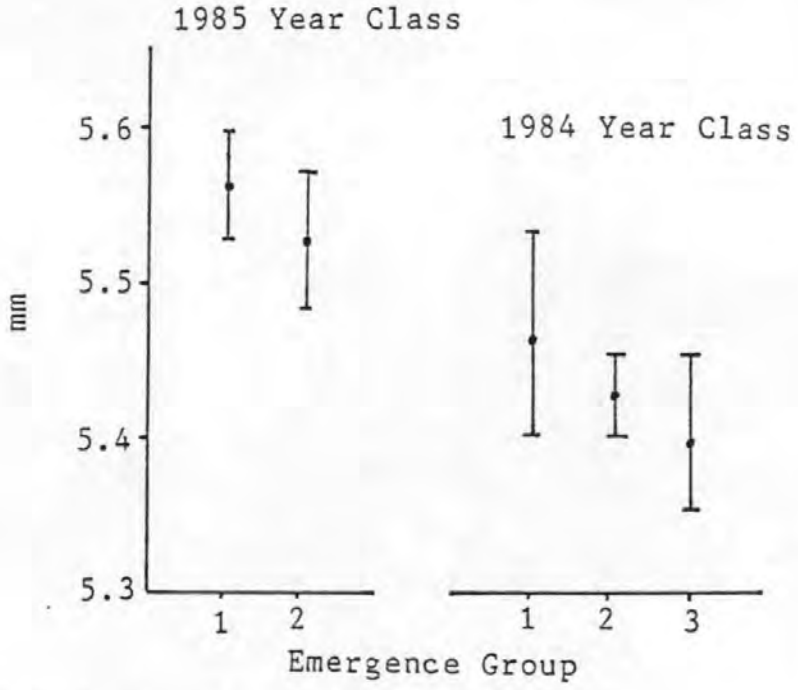
Year			n	mean	SD	df	t	P
1986	Head Width (mm)	Male	135	5.421	0.128	260	-4.71	0.0000
		Female	150	5.487	0.106			
	Body Length (mm)	Male	164	44.97	1.29	339	-2.7	0.0072
		Female	194	45.33	1.22			
1987	Head Width (mm)	Male	66	5.553	0.109	153	3.47	0.001
		Female	89	5.619	0.121			
	Body Length (mm)	Male	63	45.42	1.28	149	2.976	0.01
		Female	88	46.03	1.18			

TABLE 5.2 A t-TEST OF THE DIFFERENCES IN SIZE BETWEEN ADULT FEMALES AND MALES MEASURED 1-3 DAYS OF AGE.

	Year Class	n	Mean	SD	t	P	S^2	F	P
a) MALES									
Head Width (mm)	1984	135	5.421	0.128	7.58	0.0000	0.0164	1.378	ns
	1985	66	5.553	0.109			0.0119		
Body Length (mm)	1984	164	44.97	1.29	2.36	0.02	1.664	1.016	ns
	1985	63	45.42	1.28			1.638		
b) FEMALES									
Head Width (mm)	1984	150	5.487	0.106	8.57	0.0000	0.0112	0.767	ns
	1985	89	5.619	0.121			0.0146		
Body Length (mm)	1984	194	45.33	1.22	4.56	0.0000	1.488	1.069	ns
	1985	88	46.03	1.18			1.392		

TABLE 5.3 DIFFERENCES IN THE BODY SIZE, AND VARIANCE IN SIZE OF ADULTS FROM THE 1984 AND 1985 YEAR CLASS, WHICH EMERGED IN 1986 AND 1987 RESPECTIVELY

a) Head Width



b) Body Length

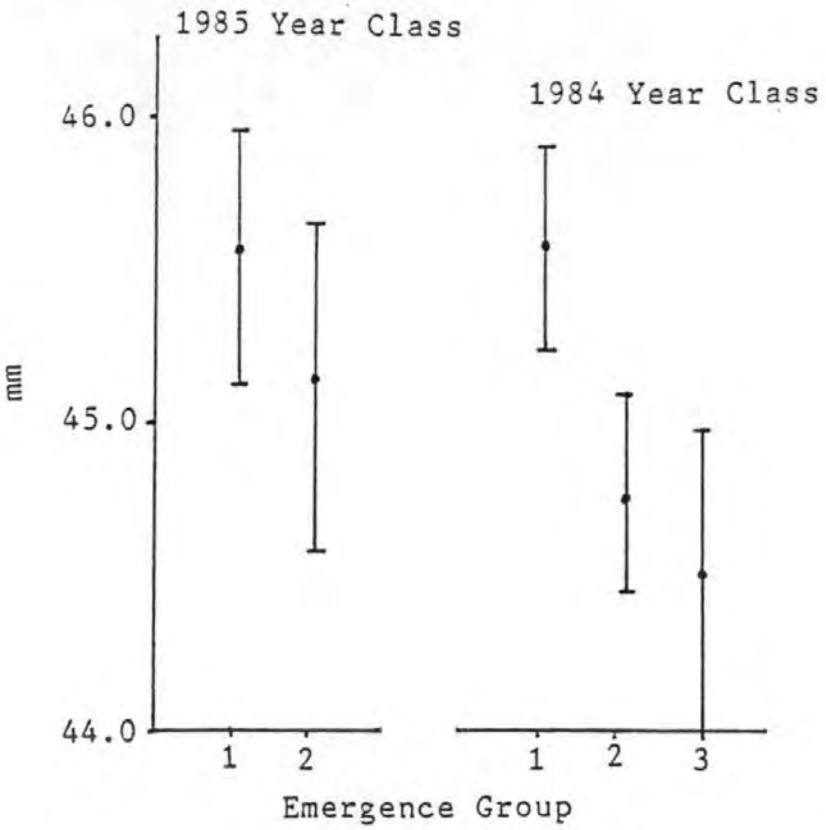


FIGURE 5.5 THE BODY SIZE OF 1984 AND 1985 YEAR CLASS ADULT MALES EMERGING IN SUCCESSIVE GROUPS IN 1986 AND 1987 RESPECTIVELY. MEANS ARE SHOWN +/- 95% C.L. DIFFERENCES IN THE BODY LENGTH OF THE 1984 YEAR CLASS WERE SIGNIFICANT (F=10.44, df=2,161, P=0.000)

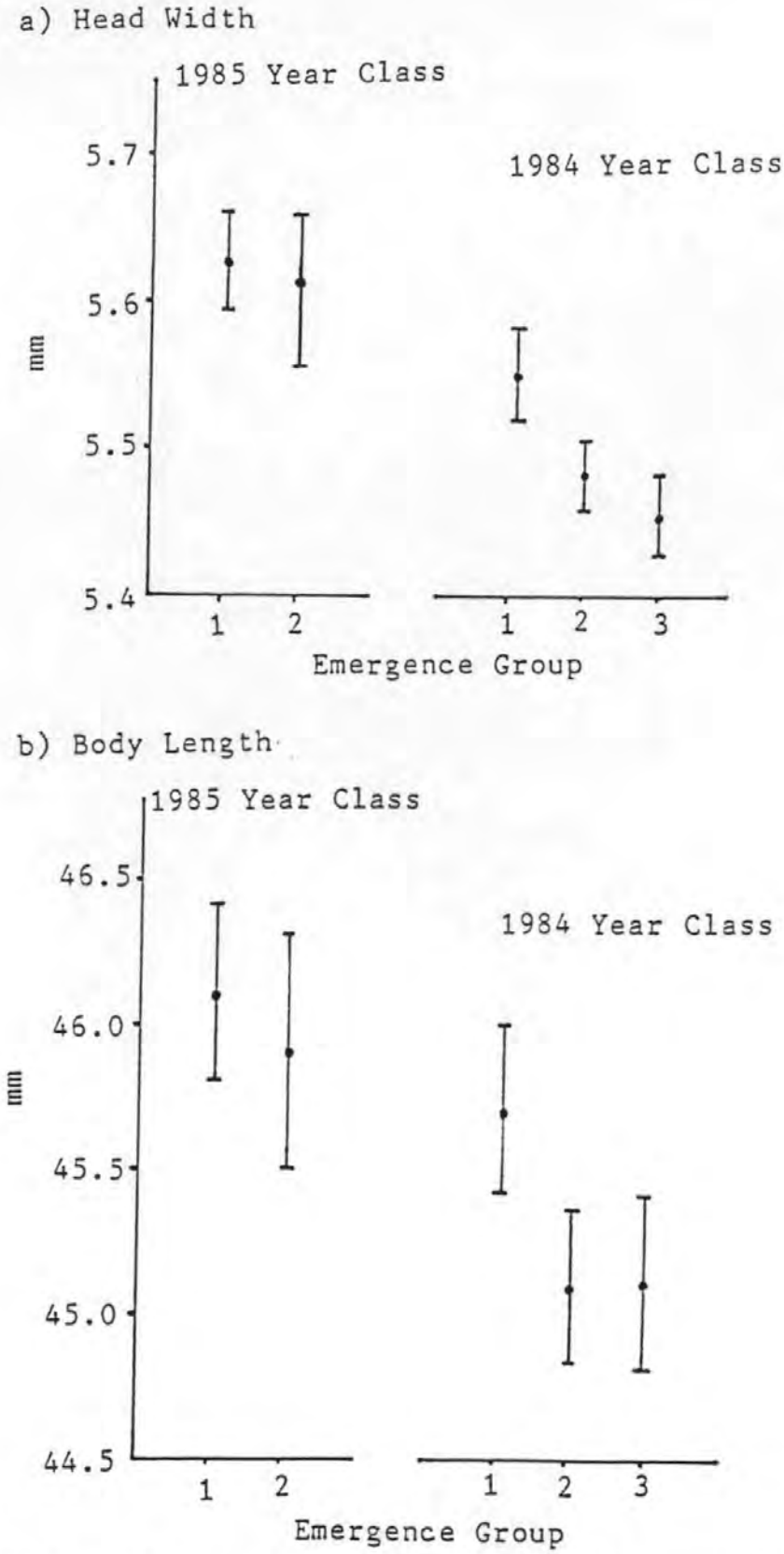


FIGURE 5.6 THE BODY SIZE OF 1984 AND 1985 YEAR CLASS ADULT FEMALES EMERGING IN SUCCESSIVE GROUPS IN 1986 AND 1987 RESPECTIVELY. MEANS SHOWN +/- 95% C.L. DIFFERENCES IN THE SIZE OF THE 1984 YEAR CLASS WERE SIGNIFICANT (HEAD WIDTH: $F=8.888$, $df=2,147$, $P=0.000$, BODY LENGTH: $F=5.07$, $df=2,191$, $P=0.007$)

The size of a smaller group of the 1984 year class, which were known to emerge from the high and low larval density areas on the south facing bank, was analysed using a two way analysis of variance to separate the effects of density and emergence group (Table 5.4). There was no overall effect of larval density area on head width or body length in either males or females. The influence of emergence group on male body length and female head width seen in the larger group described above was apparent, but the difference in female body length was not. In both measurements where there was no significant effect of emergence group, that is male head width and female body length, there was a large but insignificant interaction effect, indicating that the influence of emergence group was not the same in both density areas. When the average size of adults in different emergence groups in different density areas is examined, in both categories where there is strong interaction the later emerging groups are only smaller in the high density areas (Figure 5.7).

5.4 DISCUSSION

5.4.1 Emergence behaviour and sex ratio

The day-time emergence of this species is in line with most other Odonata in temperate climates (Corbet 1980). Although emergence during the day will increase the probability of bird predation, the adverse effects of poor weather on emergence support the contention that in cool climates nocturnal emergence is not possible for many

	Source	ss	df	ms	F	P
a) MALES						
Head Width	Emergence Group	0.0087	2	0.00435	0.311	ns
	Density Area	0.0125	1	0.0125	0.893	ns
	Interaction	0.0808	2	0.0404	2.89	ns
	Error	0.65	46	0.014		
	Total		51			
Body Length	Emergence Group	6.891	2	3.445	3.106	0.05
	Density Area	0.167	12	0.167	0.151	ns
	Interaction	0.737	2	0.368	0.332	ns
	Error	62.125	56	1.109		
	Total		61			
b) FEMALES						
Head Width	Emergence Group	0.06	2	0.03	3.968	0.05
	Density Area	0.01	1	0.01	1.323	ns
	Interaction	0.004	2	0.002	0.264	ns
	Error	0.295	39	0.0076		
	Total		44			
Body Length	Emergence	5.266	2	2.633	1.892	ns
	Density Area	1.258	1	1.258	0.904	ns
	Interaction	6.235	2	3.117	2.239	ns
	Error	79.34	57	1.392		
	Total		62			

TABLE 5.4 AN ANALYSIS OF VARIANCE OF THE INFLUENCE OF EMERGENCE TIME AND LARVAL DENSITY AREA ON ADULT BODY SIZE OF THE 1984 YEAR CLASS.

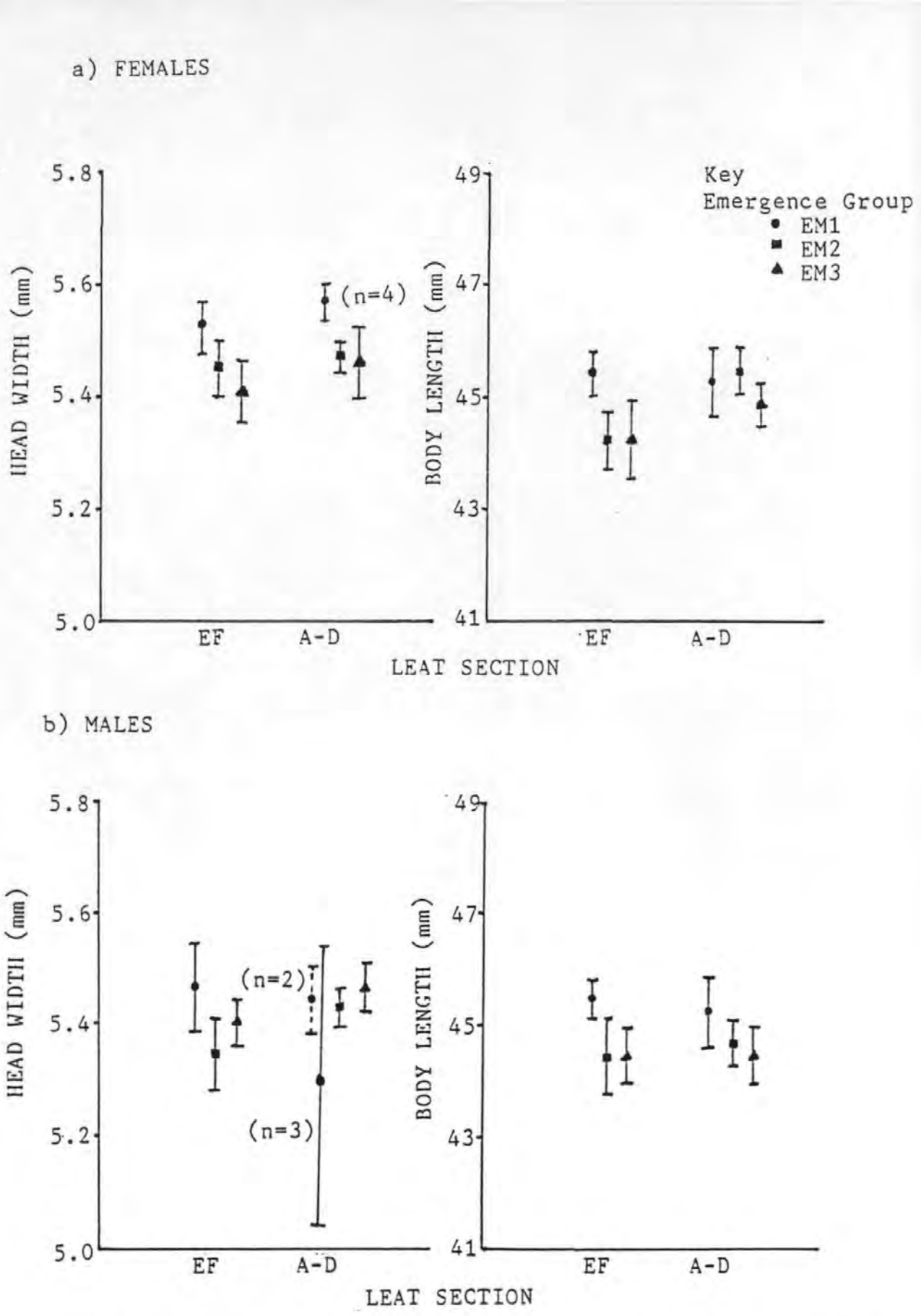


FIGURE 5.7 THE INFLUENCE OF EMERGENCE TIME AND LARVAL DENSITY AREA ON THE ADULT BODY SIZE OF THE 1984 YEAR CLASS. EF = HIGH DENSITY AREA, A-D = LOW DENSITY AREA. STRONG INTERACTION EFFECTS ARE PRESENT IN THE ANALYSIS OF VARIANCE OF FEMALE BODY LENGTH AND MALE HEAD WIDTH (SEE TABLE 5.4). MEANS ARE PRESENTED +/- SE, AND n IS GIVEN WHERE n<5

species. Although the low level of bird predation may be due in part to the presence of observers, the irregular distribution of emerging adults means that they are unlikely to have attracted high levels of predation under normal conditions. Mortality appeared to be low, and density dependent predation unlikely. The head downwards position this species adopts in the 'resting' stage of emergence is unusual for the Zygoptera (Corbet 1985), and presumably this is related to its larger body size.

The strong female bias seen in the sex ratio of emerging adults in both years is surprising, since there was no such bias amongst the larvae (see Chapter Four) or adults (see Chapter Six). It is puzzling that such a strong, erroneous effect could have been recorded in two separate years, and that in both cases most of the bias was due to the later emergence groups. Baker et al (1992) found that I. verticalis males in the antepenultimate instar were more mobile and wandered further than females, and suggest that this may increase male mortality and be responsible for female biased sex ratios at emergence (eg Pickup et al 1984, Michiels and Dhondt 1989). It is possible that in this study behavioural differences may have resulted in male larvae wandering further at emergence and not being detected in emergence counts. Females were significantly larger than males at emergence, but there was no difference in final instar measurements. The extra growth of females must therefore have been achieved during the final instar, and could explain why many females emerged later than males.

5.4.2 The timing of emergence and the size of emerging adults.

The differences in larval growth patterns and body size described the last Chapter were reflected in the emergence time and body size of adults. Adults emerging in 1986 were smaller and emerged later than those in 1987. In both year classes emergence was temporally divided, with later emerging adults being smaller in body size. The appearance of three emergence groups in 1986 does not represent a greater than usual variability in development time within this year class, since all the adults emerged over the same period of time as those in 1987.

While later emerging adults in 1987 were smaller than early emerging ones, the difference in size was no longer significant as it had been when individuals were in the penultimate instar. This suggests that later developing 1985 year class larvae had caught up in body size to some extent by the time of emergence, even in the high density area where emergence was monitored. In the more numerous 1984 year class the difference in body size of later emerging groups was significant, and there were trends, albeit insignificant ones, that the 1984 year class adults were more variable in size than the 1985 year class. Because of the influence of environmental variables on growth and body size it would be wrong to draw conclusions on density effects from comparisons between years. Closer examination of the data within the 1984 year class did, however, reveal a sign of a density effect, since male head width and female body length of later emerging groups were only smaller in the high density area.

In the other parameters of body size later emerging 1984 year class larvae were smaller in both high and low density areas, however, and the interaction between density area and emergence group was not significant. The density effect was therefore inconsistent and weak.

In 1986 and 1987 emergence began at roughly the same time in both larval density areas. In 1986 there was a trend for a higher proportion of adults emerging at an earlier time in the high density area, the opposite of what would be expected if larvae in the high density area were disadvantaged.

CHAPTER SIX

THE BEHAVIOUR AND SURVIVAL OF IMMATURE ADULTS

6.1 INTRODUCTION

In Chapter Six it was seen that later emerging groups of adults were smaller in head width and body length. Here the effects of these differences on the survival of immature adults is considered.

6.2 METHODS

In 1986 and 1987 as many damselflies as possible were caught at or near emergence, both during emergence samples (see Chapter Five) and in subsequent population samples. The head widths and body lengths of all adults caught were measured using the method described in Chapter Five, and they were individually marked. A white Pentel paint marker was used to write a number on the tip of each hind wing, and this was clearly visible from both sides of the insect at a distance of several metres when viewed with Carl Zeiss 8*30 binoculars. It was necessary to use a white pen because darker colours would become invisible when males matured and their wings darkened. To look for any effect of the white mark half the females in 1987 were marked with an inconspicuous blue permanent marker. Eighteen blue marked and nineteen white marked females had average mature lifespans of 4.316 and 4.778 days respectively, and these means are not significantly different (Mann-Whitney U = 157.5, P = 0.707).

Population samples were taken at regular intervals through the summer. Two observers walked down the centre of the Leat, the south facing bank and woodland ride noting the position, sex, identity and body colour of marked damselflies, and the position, sex and where possible body colour of those which were unmarked. Initially a wider area was searched, including the pasture to the south of the Leat but adults were rarely seen outside the area described above. The nomenclature of the 10m and 30m Leat sections were extended to apply to to the parallel areas of the bank and woodland ride (Figure 2.3, Chapter Two), and the 10m position of adults was recorded. The start point of the samples varied alternately between section A and F. These recording samples were followed by the catching samples, when, following the same route, as many unmarked damselflies as possible were caught. Captured damselflies were transported in portable netting cages until the end of each thirty metre section was reached, when they were transferred to a netting wig-wam to await marking and measuring.

Recording samples were usually taken from 10.00-12-00h, when most adults were feeding. Catching samples followed straight away while all the adults were immature, but once recording of territorial and oviposition behaviour began, catching samples were delayed until most oviposition had finished around mid to late afternoon. Samples were taken every other day in the early stage of emergence, and twice a week when emergence had ended. However, since adults were very scarce in poor weather in practice later samples were taken as often as the weather allowed.

On several occasions during 1986 and 1987 the neighbouring adult population centres upstream were also searched for marked adults.

6.3 RESULTS

In total 323 males and 386 females were marked and measured in 1986, and 186 males and 202 females in 1987.

6.3.1 Colour Changes During Maturation, and the Time Taken to Mature

As the damselflies matured there were changes in body, wing and eye colour. Figure 6.1 shows the change in body colour of males and females from the 1986 year class as they matured, and some of these changes are illustrated in Plates 6.1-3. Adults were referred to as nought days old on the same day that they emerged. In order to judge eye colour it was necessary to look at the damselflies head on, since the colour paled towards the back of the head. Wings continued to glisten up to 2 days after emergence, but in this time the eyes changed colour from cream to fawn. By 3 days of age the wings had usually stopped glistening, and the eyes had darkened to a light brown, the colour of milk chocolate. Males during this time had opaque but pale red-brown wings and bright metallic blue bodies. Females had paler red-brown, more transparent wings, with bright emerald green bodies. As males aged through 4 to 8 days old their eyes and wings darkened to the colour of plain chocolate and finally turned black. At 10 to 14 days old male's wings became black, and their bodies and particularly wings took on the deep blue-

COLOUR CATEGORY:

i) Cream eyes
Pale brown
glistening wings

ii) Fawn eyes
Pale brown
shining wings

iii) Light brown eyes
(milk chocolate colour)
Pale brown wings

iv) Dark brown eyes
(plain chocolate colour)
Light brown wings

v) Black eyes
Dark brown wings

vi) Black eyes
Blue/black wings

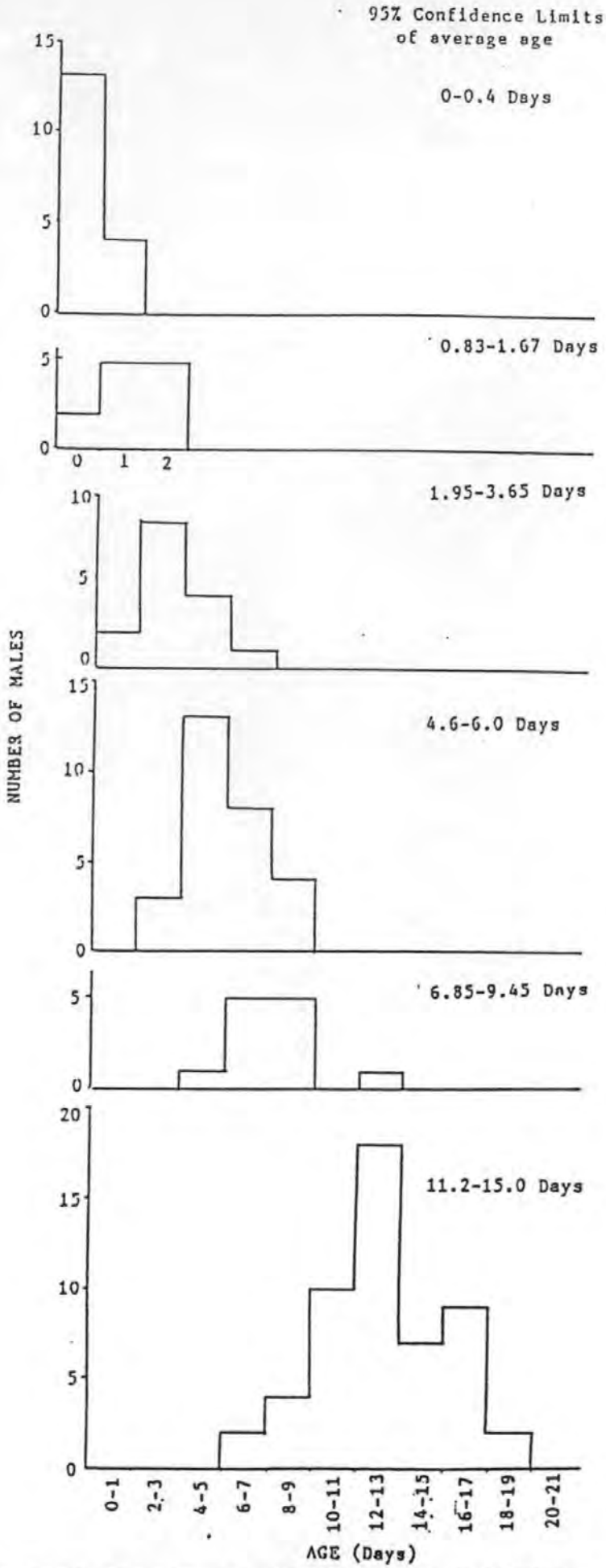


FIGURE 6.1a THE CHANGE IN BODY COLOUR OF MALES AS THEY MATURE. THE HISTOGRAMS REPRESENT THE AGE AT WHICH ADULTS WERE FIRST SEEN IN EACH COLOUR CATEGORY. THE FIRST TWO HISTOGRAMS INCLUDE ADULTS WHICH WERE FIRST CAUGHT AT EMERGENCE; LATER HISTOGRAMS INCLUDE ADULTS CAUGHT WITHIN 0-2 DAYS OF EMERGENCE

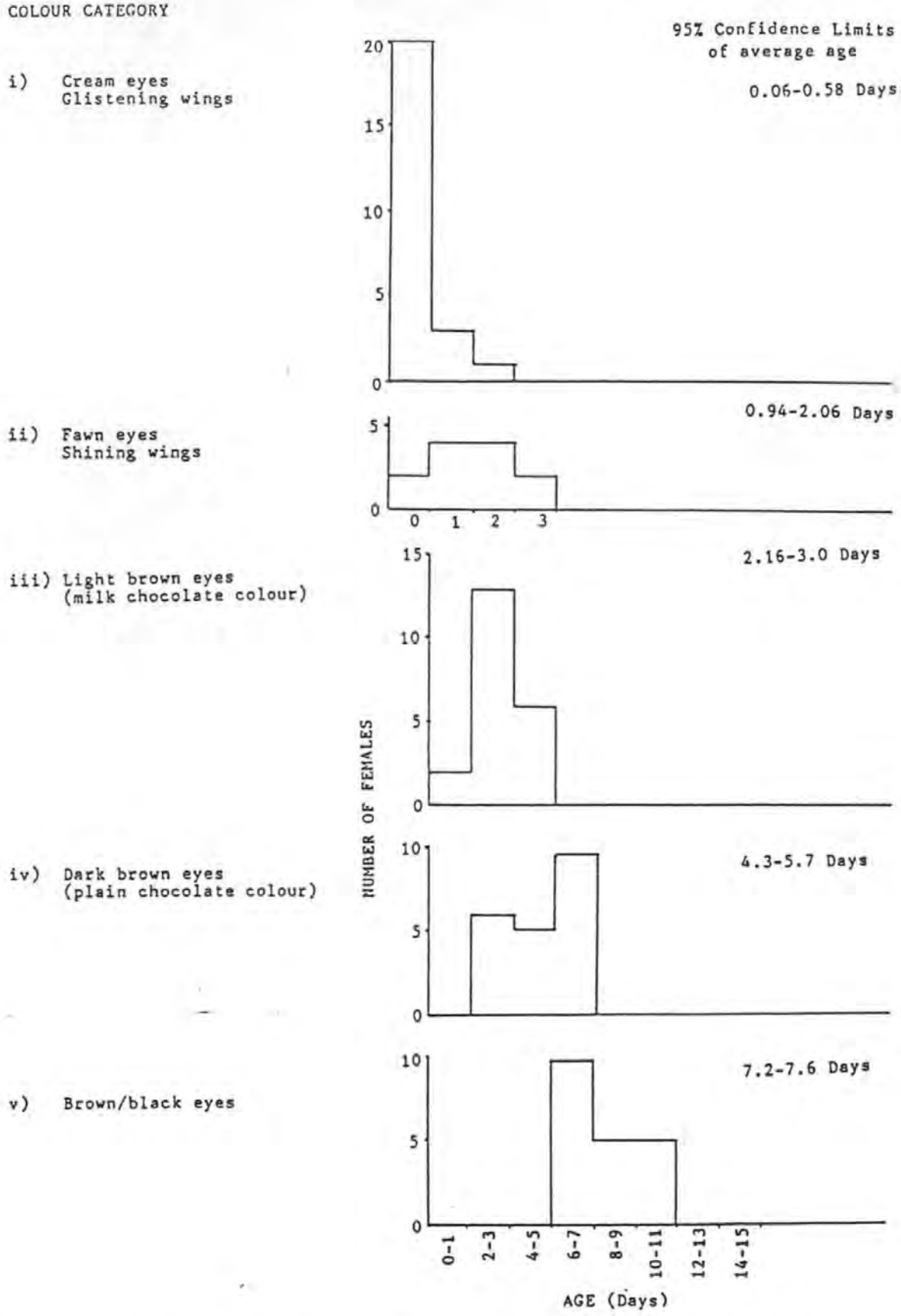


FIGURE 6.1b THE CHANGE IN BODY COLOUR OF FEMALES AS THEY MATURE. THE HISTOGRAMS REPRESENT THE AGE AT WHICH ADULTS WERE FIRST SEEN IN EACH COLOUR CATEGORY. THE FIRST TWO HISTOGRAMS INCLUDE ADULTS WHICH WERE FIRST CAUGHT AT EMERGENCE; LATER HISTOGRAMS INCLUDE ADULTS CAUGHT WITHIN 0-2 DAYS OF EMERGENCE

a) Cream eyes
Glistening wings
0-0.4 Days old

b) Fawn eyes
Glistening wings
0.83-1.67 Days old

c) Light brown
eyes (milk choc)
Pale brown wings
1.95-3.65 Days old

d) Mature colouration
10-13 Days old

PLATE 6.1 SOME COLOUR CHANGES IN MALES AS THEY MATURE

a) Light brown eyes
(milk chocolate)
Emerald green body
Fawn wings
2.16-3.0 Days old

b) Dark brown eyes
(plain chocolate)
Emerald green body
fawn wings
4.3-5.7 Days old

c) Brown/black eyes
Body and wings take
on bronze sheen
Wings become more
transparent
7.2-8.6 Days

PLATE 6.2 SOME COLOUR CHANGES AS FEMALES MATURE

a) Immature female

Dark brown eyes
(plain Chocolate)
Emerald green body
Opaque fawn wings

b) Mature females

Brown/black eyes
Bronze body
Wings darken and
become transparent

(note inconspicuous
blue mark)

PLATE 6.3 IMMATURE AND MATURE FEMALES

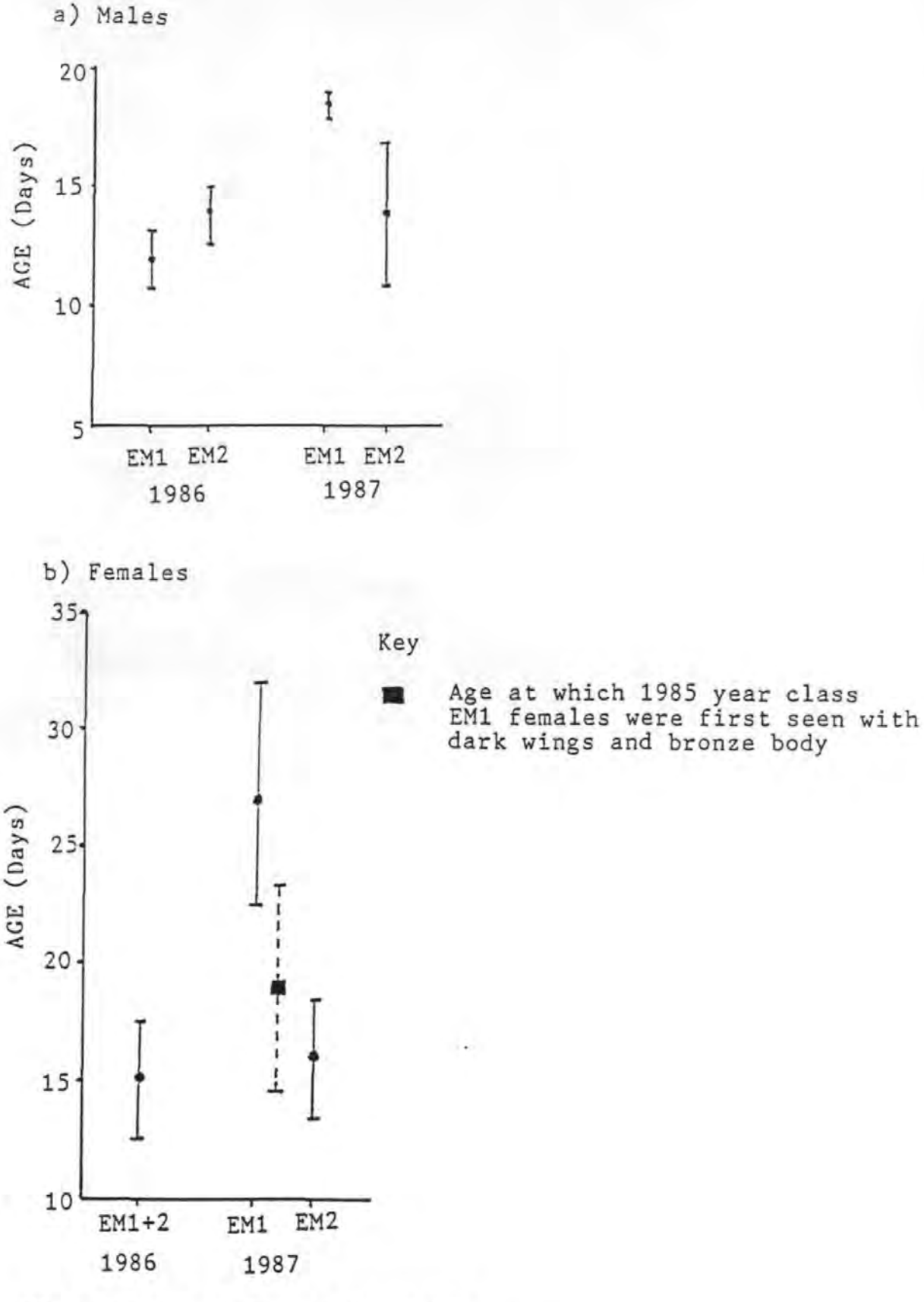


FIGURE 6.2 THE AGE AT WHICH MALES AND FEMALES MATURED IN 1986 AND 1987. EM1 AND EM2 REPRESENT ADULTS FROM THE FIRST AND SECOND EMERGENCE GROUPS RESPECTIVELY. DATA WAS TAKEN FROM ADULTS MARKED AT EMERGENCE. MATURITY IN MALES WAS JUDGED BY THE CHANGE IN WING COLOUR TO BLUE-BLACK, AND IN FEMALES BY FIRST OVIPOSITION. MEANS ARE SHOWN +/- 95% C.L.

green sheen of maturity. Females' eyes darkened to plain chocolate colour at around 5 to 6 days old, and finally to a brown-black colour at 7 to 8 days. The bodies of mature ovipositing females took on a yellow-bronze sheen, and the wings darkened while becoming more transparent. These changes in female wing and body colour seemed to gradually intensify with age, until very old females (over 30 days old) had almost completely transparent wings which looked grey.

The colour changes of adults were used to estimate the age of those marked after emergence. Maturation date in males was judged by the change in wing colour, but in females where the colour change was more subtle, it was judged by the first day of oviposition. Males in 1986 and the second emergence group in 1987 took an average of 12 to 14 days to mature (Figure 6.2a). The first emergence group in 1987 appeared to take substantially longer than this, and their maturation took place during June which was particularly cold and wet compared to the weather during the maturation period of the second emergence group, and the previous year class. Females were typically 15-16 days old on average when they produced their first clutch of eggs (Figure 6.2b), a day or so later than the males matured. First emergence group females of the 1985 year class were an average of 27 days old when they produced their first clutch, but had achieved mature body coloration by an average of 19 days. The slow arrival of females to oviposit once a period of fine weather was encountered in 1987 (see Figure 8.3, Chapter Eight) suggests that it was necessary for them to feed in good weather in order to mature a clutch of eggs, even though they were

likely to have reached physiological maturity some days earlier.

6.3.2 The Distribution and Behaviour of Feeding Adults

Sunny banks of sheltered vegetation were an obvious habitat requirement for feeding adults, and the population concentrated into areas along the leat with this feature (Figure 6.3, Table 6.1). Feeding behaviour was dependent upon the weather, and sunshine was more important than air temperature. With air temperature in the shade as low as $15^{0}C$ adults could feed, but with cloud cover at this temperature feeding stopped. Air temperature needed to be over $18^{0}C$ before feeding could take place under cloud. Immature and mature adults fed along the Leat, and the sex ratio there was usually close to unity (Figure 6.4).

6.3.3 Factors affecting the Survival of immature Adults

The pattern of numbers emerging, and feeding along the Leat and of mature males showing territorial behaviour in 1986 and 1987 is shown in Figures 6.5 and 6.6. Numbers of adults along the Leat rose steadily as the first and then the second group emerged, although the pattern is sometimes obscured by periods of poor weather. The peak in numbers of both year classes occurred after the second emergence, with the 1984 year class reaching 295, and the 1985 year class 168 adults in the population area. In both summers the decline in numbers after this peak appeared to be sudden and dramatic. However in 1986 and 1987 the fall in numbers occurred after breaks in population recording (five and eleven days respectively) due to poor weather, and the pattern of daily

mortality was examined to see whether this decline did represent a sudden increase in mortality.

In 1986 the average daily mortality (m) for all marked adults from one sample to another was calculated as:

$$m = 1 - e^{\ln(N_e/N_s)/T}$$

where N_s was the number of marked adults alive at the start of the interval, N_e the number still alive at the end, and T the duration of the interval in days.

Although this analysis is primarily concerned with the mortality of immature adults, the coincidence of both mature and immature adults as the different groups emerge and mature makes it impractical not to consider the two groups together. Figure 6.7 shows that in 1986 the pattern of daily mortality for males and females was very similar, with female mortality being slightly higher. Mortality peaked on three occasions. The first short-lived peak in mid June is of little importance since numbers at this time were very low, and mortality was generally low as the first group emerged. The second peak, from the 26th June to the 2nd July, represented a larger total mortality and occurred as the first group reached maturity and the second group emerged. Mortality then fell over seven days of cloud and rain before rising a third time.

Both the short-lived rises in mortality discussed above represent very small total mortality compared to that

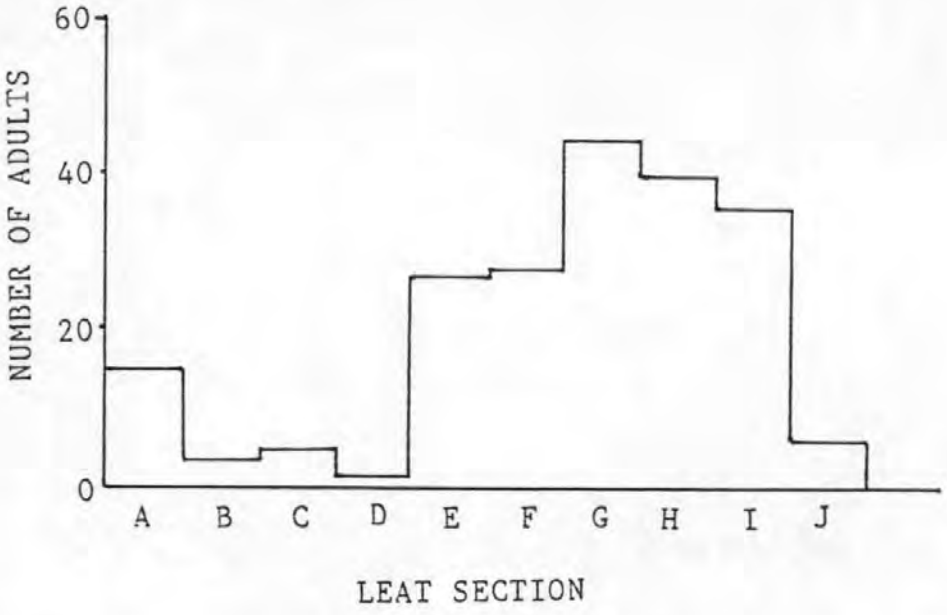


FIGURE 6.3 THE DISTRIBUTION OF FEEDING ADULTS ALONG THE LEAT ON 2.7.1986

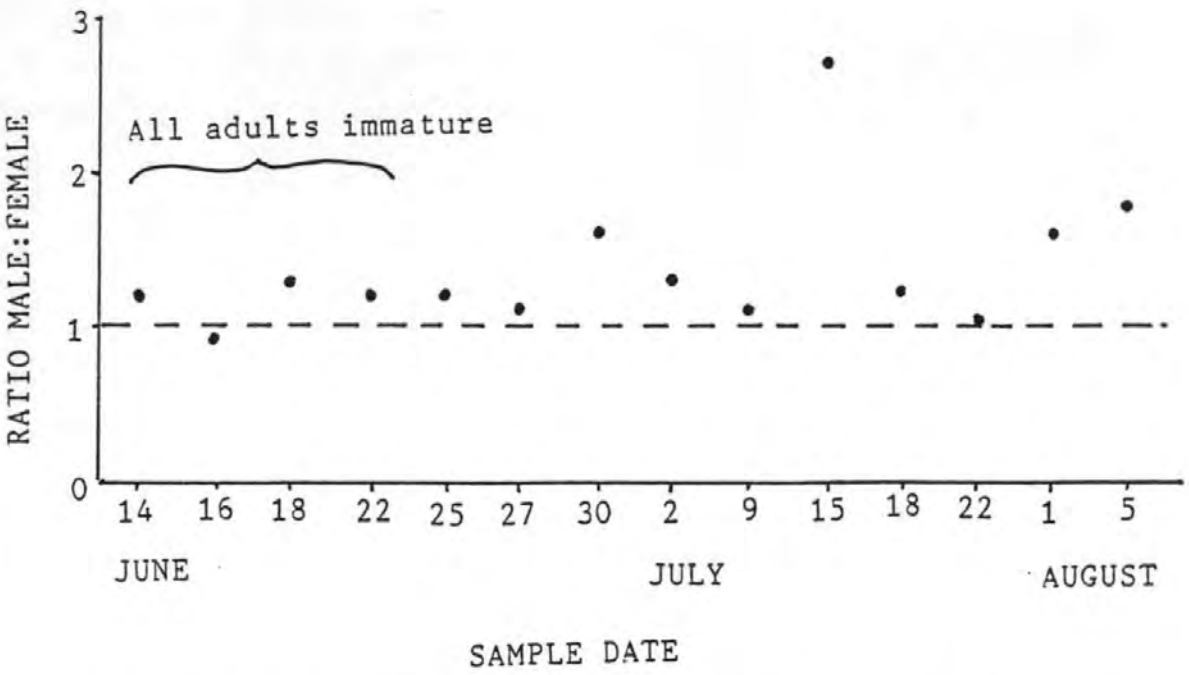


FIGURE 6.4 THE RATIO OF FEEDING MALES TO FEMALES ALONG THE LEAT IN 1986

		Adults Emerged In Leat Sections A-D and J		Adults Emerged In Leat Sections E-I	
		Staying Within These Areas	Moving To Population Centre	Staying Within Area	Moving To Low Density Areas
MALES	n	13	12	88	8
	%	52	48	92	8
FEMALES	n	20	13	88	5
	%	61	39	95	5

TABLE 6.1 THE MOVEMENT OF ADULTS BETWEEN THE POPULATION CENTRE AND EXTREMITIES IN 1986

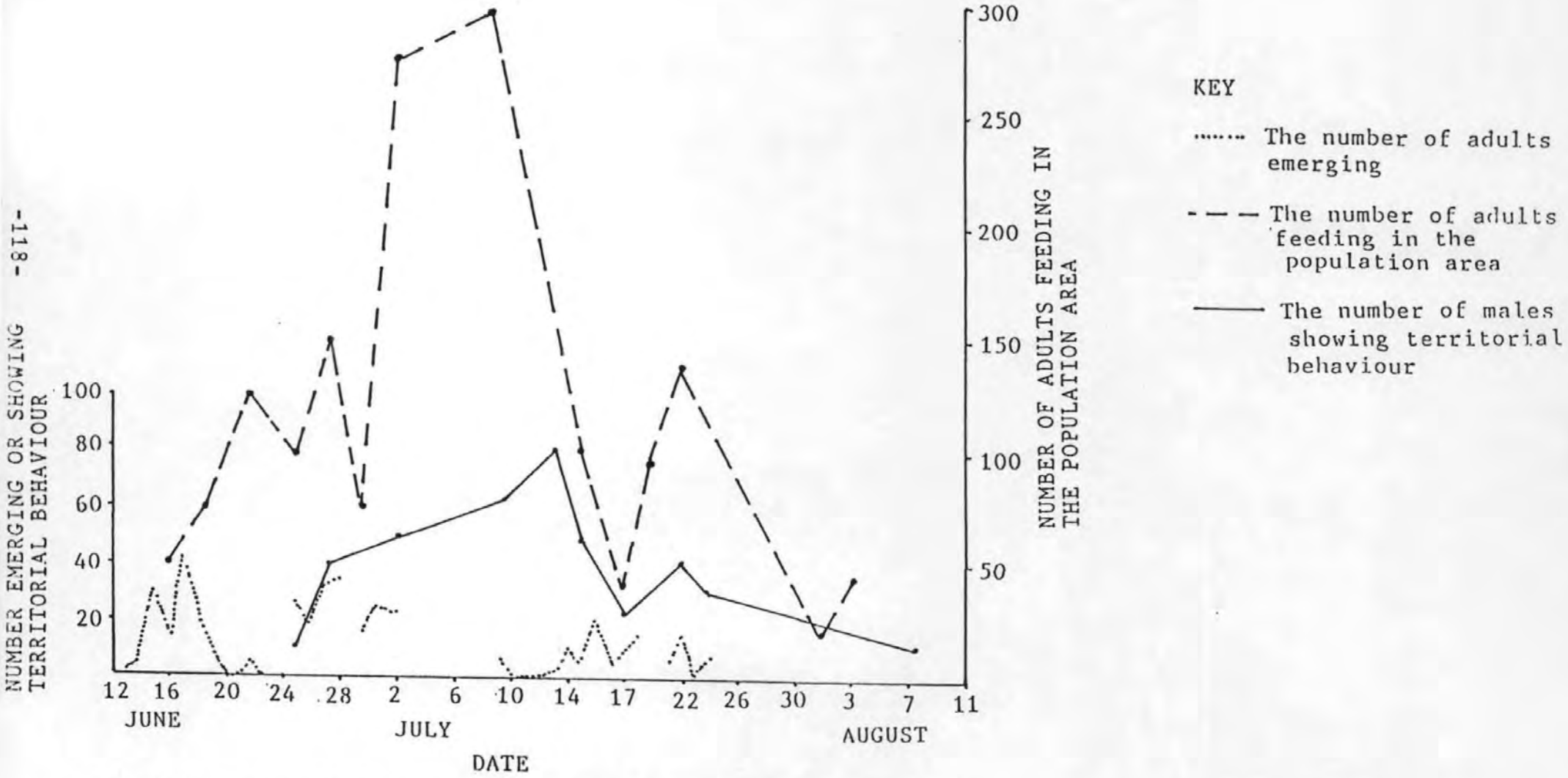


FIGURE 6.5 THE PATTERN OF NUMBERS OF ADULTS EMERGING, FEEDING AND SHOWING TERRITORIAL BEHAVIOUR IN 1986

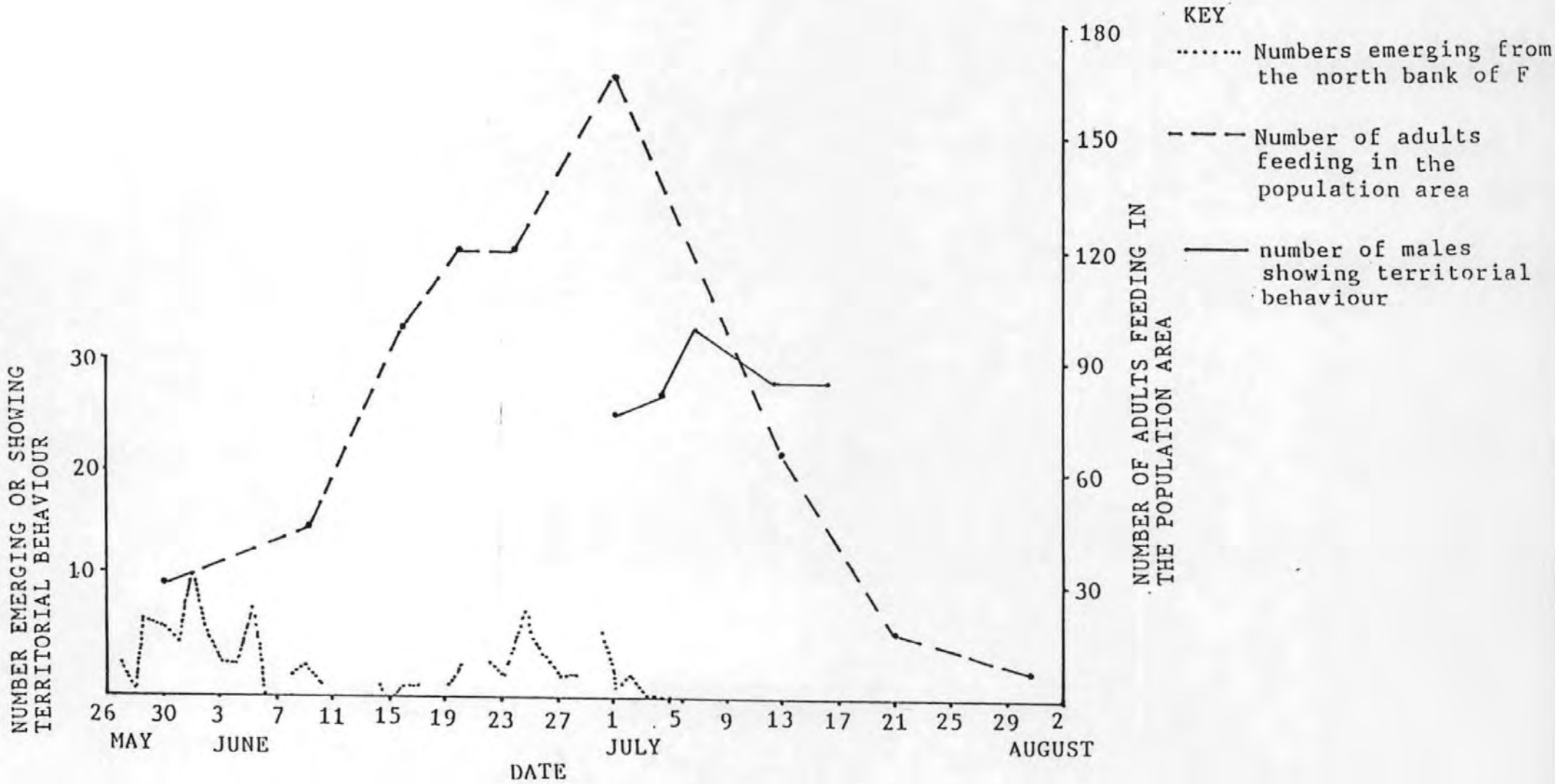


FIGURE 6.6 THE PATTERN OF NUMBER OF ADULTS EMERGING, FEEDING AND SHOWING TERRITORIAL BEHAVIOUR IN 1987

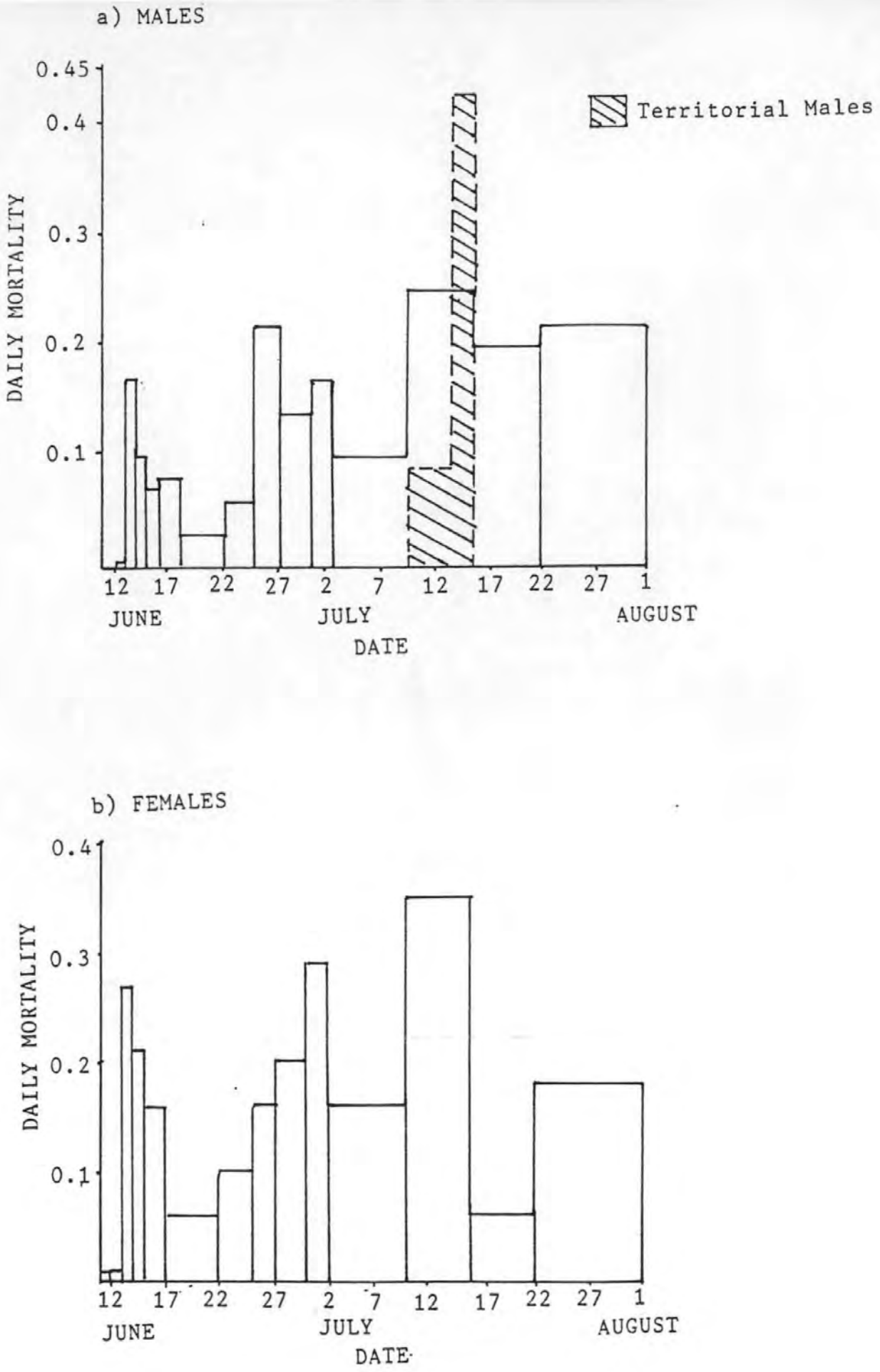


FIGURE 6.7 THE AVERAGE DAILY MORTALITY OF ADULTS IN 1986

represented by the high average mortality recorded over the long time span from the 9th to the 15th July, which resulted in the fall in numbers seen in Figure 6.5. This fall in numbers was so dramatic that it was immediately obvious to the observers, and 80% of marked males and 93% of marked females disappeared. Although poor weather caused the long interval between population samples, there was one sunny day on the 13th July when mature males were sampled for observations on breeding behaviour. There was no noticeablefall in overall numbers on the 13th, and the mortality of mature males, which can be broken down into smaller time spans, shows that the high average was mainly due to a short-lived but massive mortality which occurred from the 13th to the 15th of July. During this short time the daily average mortality was 0.43 and 67% of males disappeared. This massive mortality occurred as the second emergence group was reaching maturity and the numbers of breeding adults had increased significantly, and also as the third group was emerging.

A comparison of the mortality of different age groups from the 9th to the 15th of July showed that mature and immature adults were equally affected. During this time 84% of immature and 69% of mature males died, as did 93% of immature and 92% of mature females. Because the third group had only just started to emerge there were few newly emerged adults, and most of the mortality of immature adults occurred from the second emergence group just before they reached maturity.

In 1987 when work concentrated on breeding adults, detailed monitoring of the mortality of mature adults showed that the dramatic fall in overall numbers which occurred between population samples of the 1st and 12th of July was also due to a short lived episode of very high mortality (see Figure 8.4, Chapter Eight). Sixty six percent of males and 42% of females disappeared from the 7th to the 8th July. As in the summer of 1986 the dramatic mortality occurred just as the second emergence group matured, and numbers of breeding adults at the water's edge had increased rapidly. In 1987 however there were no newly emerging damselflies.

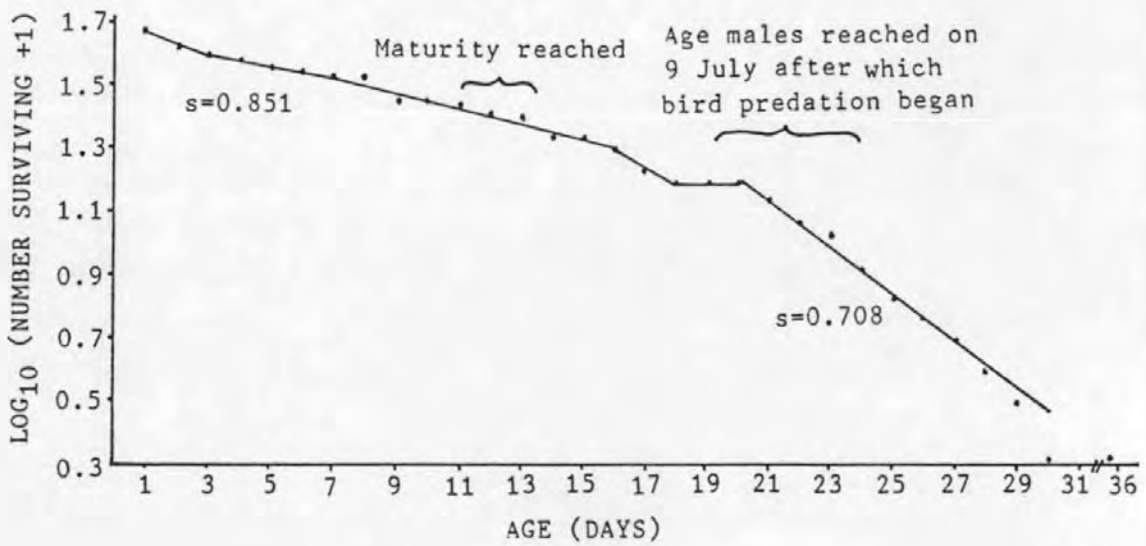
In both 1986 and 1987, in the days following the dramatic falls in overall numbers, a large number of severed wings was found in small clearings on the Leat banks, often in little piles. These were mostly the wings of mature males, but female wings, which were much harder to see, were also found. It seems likely, therefore, that a sudden increase in bird predation was responsible for the mortality. Severed wings were also found in the summer of 1985, indicating bird predation is a regular phenomenon. After the bird predation in 1986 mortality of males remained high, but fell in females, and in 1987 it fell in both sexes. There was a slight recovery in population numbers in 1986 following the emergence of the third group.

Patterns of daily mortality will not be directly evident in survivorship curves, since on each day adults will be a range of ages. Nevertheless changes in survivorship due to changes in daily mortality can be seen (Figures 6.8 and

6.9). First emergence group males experienced a decrease in survival due to bird predation some time after reaching maturity, but in females the decrease in survival began shortly after producing their first clutch of eggs, and possibly reflects the earlier high daily mortality experienced by this group from the 30th June to the 2nd July (Figure 6.7b). Both males and females from the second emergence group experienced lower survival during their immature life than the those from the first group, and the decrease in survival due to bird predation occurred just as both groups were reaching maturity. The survivorship curves show no sign of a continuous change with age, indicating that mortality was unrelated to age as an innate factor (Deevy 1947). It was not possible to obtain detailed records of the survival of the third group because the weather was very unsettled during the whole of August.

As a result of the timing of the episode of bird predation in 1986, almost twice as many adults from the first emergence group survived to maturity compared with the second group (Table 6.2). The higher recorded mortality of females was reflected in a lower survival to maturity compared to males. Although the timing of the bird predation in relation to the age of the emergence groups was similar in 1987, the long maturation time of the first emergence group seems to have taken its toll, and few reached maturity. The proportion of the second emergence group reaching maturity in 1987 was very similar to that in 1986.

a) FIRST EMERGENCE GROUP



b) SECOND EMERGENCE GROUP

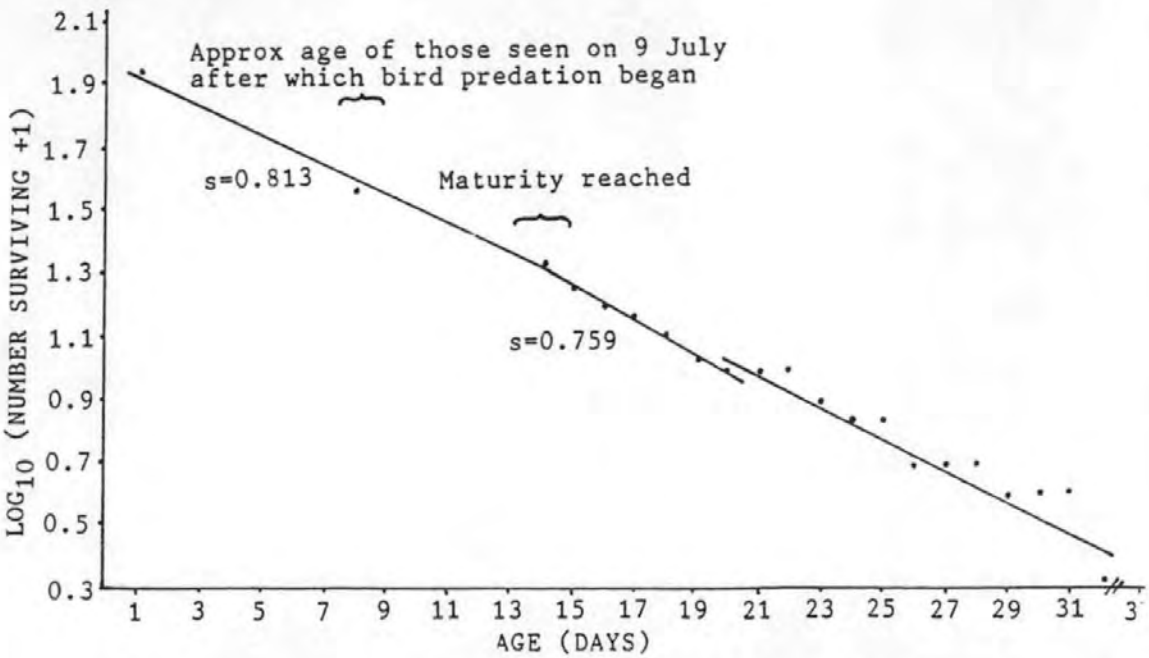
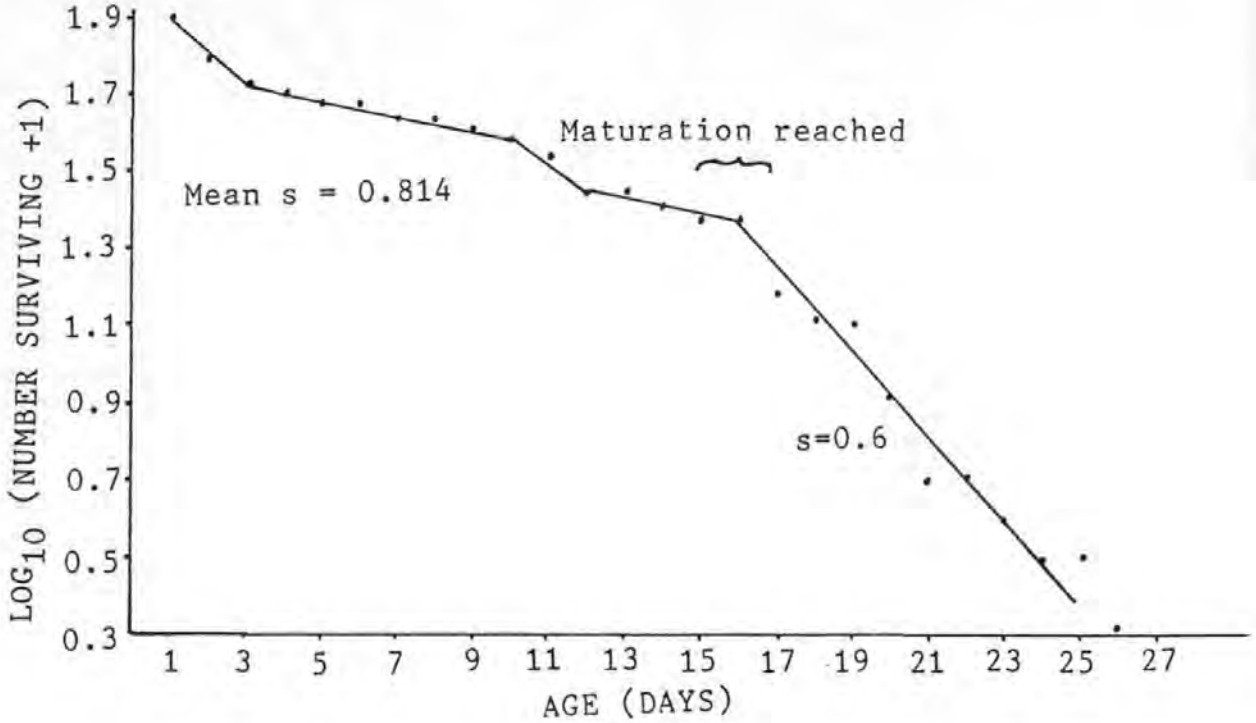


FIGURE 6.8 SURVIVORSHIP CURVES FOR MALES PRESENT IN 1986. MALES MARKED 0-1 DAY AFTER EMERGENCE. S = PROBABILITY OF SURVIVAL.

a) FIRST EMERGENCE GROUP



b) SECOND EMERGENCE GROUP

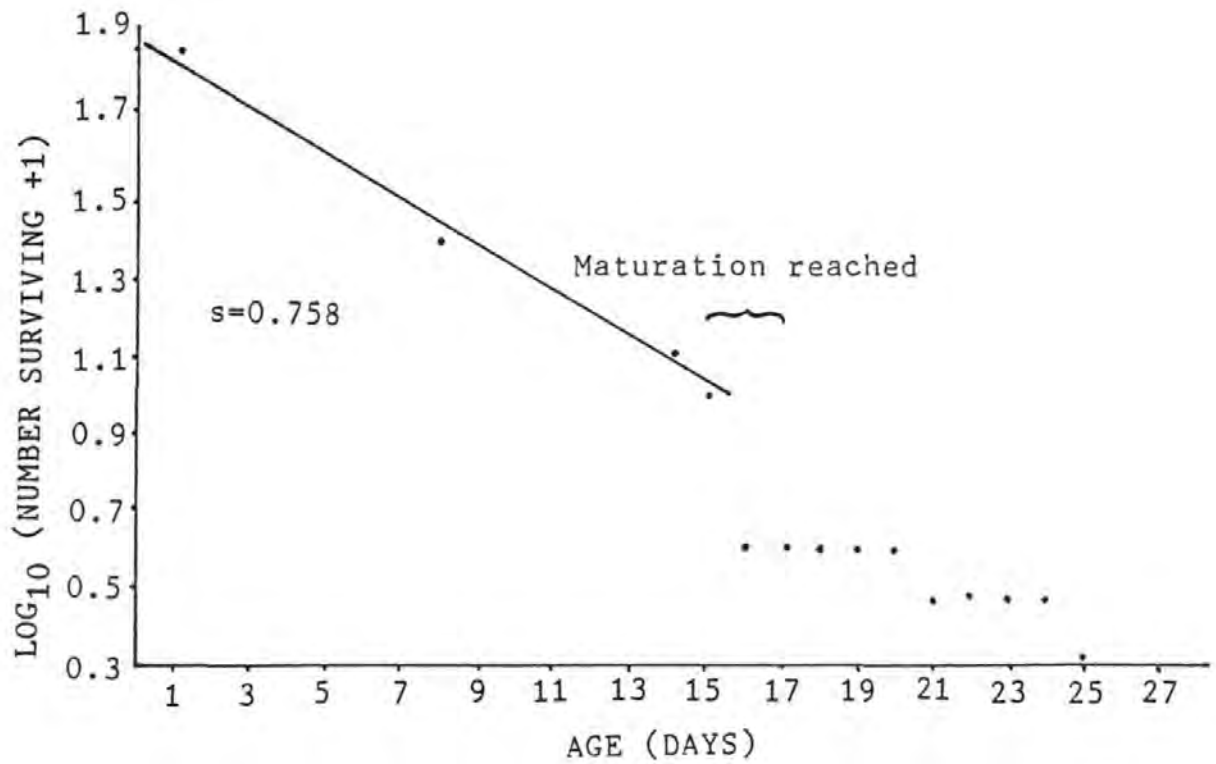


FIGURE 6.9 SURVIVORSHIP CURVES FOR FEMALES PRESENT IN 1986
FEMALES MARKED 0-1 DAYS AFTER EMERGENCE.
s = PROBABILITY OF SURVIVAL

Year		Emergence Group	Number Marked When 0-3 Days Old	% Surviving To Maturity
1986	Males	EM1	50	52
		EM2	82	24
		EM3	25	4
	Females	EM1	76	35
		EM2	80	15
		EM3	48	2
1987	Males	EM1	49	18
		EM2	34	24
	Females	EM1	72	8
		EM2	26	15

TABLE 6.2 THE PROPORTION OF ADULTS SURVIVING TO MATURITY IN 1986 AND 1987

The body size of adults measured 0-3 days after emergence in 1986 which survived to maturity were compared with those which did not (Table 6.3). Because the two emergence groups differed in both body size and the proportion which survived to maturity, it was necessary to look for size and survival effects within each group. For females there were only sufficient data to look at the first emergence group. There was no sign of an influence of size at emergence on survival in any of the groups examined, and there was no difference in the variance in size for all subsets except female head width. The head width of females which survived to maturity was significantly more variable than those which did not, but this result is hard to explain.

The size of adults measured at 0-3 days of age was compared with those measured at 6-26 days of age in order to see if body size changed with age (Table 6.4). There was a strong trend that males measured when older were larger in both head width and body length, but the differences were not significant. Amongst females there was no trend and no significant difference in the head width of the two age groups, but a strong significant difference in body length. The lack of a difference in variance between the age groups confirms that the size increases are due to growth rather than differential survival, and in females probably reflects the development of ovarioles.

Figure 6.10 shows that the greatest identifiable cause of mortality in adults that was seen over the three summers from 1985 to 1987 was bird predation. This was followed,

	Emergence Group		n		Mean	t	P	S^2	F	P
MALES	EM1	Head Width (mm)	16	s	5.494	1.37	0.19	0.019	2.00	>0.05
			11	x	5.400			0.038		
		Body Length (mm)	26	s	45.5	0.41	0.68	1.00	1.416	>0.05
			29	x	45.62			1.416		
	EM2	Head Width (mm)	16	s	5.419	0.22	0.83	0.0096	1.656	>0.05
			65	x	5.412			0.0159		
		Body Length (mm)	16	s	45.06	1.20	0.24	1.538	1.116	>0.05
			65	x	44.64			1.716		
FEMALES	EM1	Head Width (mm)	11	s	5.555	0.16	0.88	0.017	2.36	<0.05
			23	x	5.548			0.0072		
		Body Length (mm)	21	s	45.48	0.66	0.51	1.664	0.941	>0.05
			56	x	45.70			1.769		

TABLE 6.3 A COMPARISON OF THE SIZE AND VARIANCE IN SIZE OF ADULTS WHICH SURVIVED TO MATURITY AND THOSE WHICH DID NOT. ALL ADULTS MEASURED 0-3 DAYS AFTER EMERGENCE.

s=Survived to maturity
x=Did not survive to maturity

		Age (Days)	n	Mean	SE	t	P	S^2	F	P
MALES	Head Width (mm)	1-3	135	5.421	0.011	-1.86	0.064	0.016	1.067	>0.05
		6-26	169	5.448	0.0094			0.015		
	Body Length (mm)	1-3	164	44.97	0.10	-1.75	0.081	1.29	2.257	>0.05
		6-26	174	45.20	0.087			1.15		
FEMALES	Head Width (mm)	1-3	150	5.487	0.0086	0.10	0.92	0.011	1.375	>0.05
		6-26	86	5.485	0.013			0.015		
	Body Length (mm)	1-3	194	45.33	0.088	-2.64	0.0091	1.49	1.00	>0.05
		6.26	97	45.73	0.12			1.49		

TABLE 6.4 A t-TEST OF DIFFERENCES IN THE SIZE OF ADULTS MEASURED SHORTLY AFTER EMERGENCE (1-3 DAYS) AND JUST BEFORE AND AT MATURITY (6-7 DAYS) IN 1986, AND A COMPARISON OF THE VARIANCE IN SIZE OF THE TWO GROUPS.

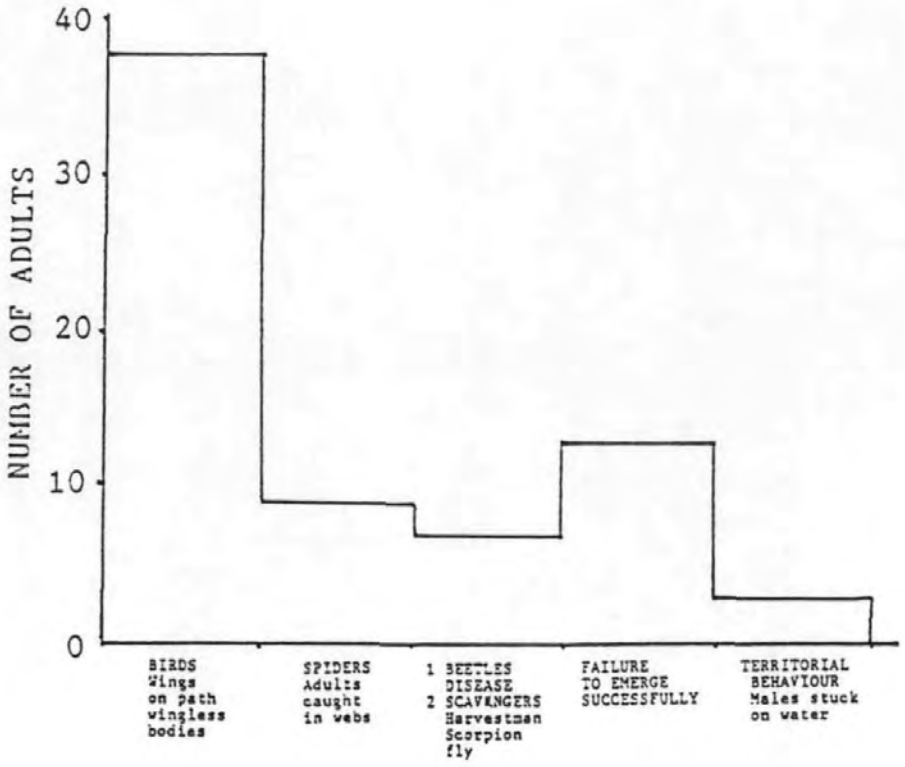


FIGURE 6.10 CAUSES OF ADULT MORTALITY SEEN FROM 1985-1987

much less importantly, by the failure of adults to emerge successfully. Other causes of mortality were spiders webs, unknown death followed by consumption by scavengers such as scorpion flies and harvestmen, and finally the death of territorial males following clashes with rivals .

6.4 DISCUSSION

6.4.1 Maturation time, Colour Change and Feeding Behaviour

Since the blue-black coloration of male wings extended from the base to the apex, the damselflies here do not represent the typical form of C.virgo where the fore wing apex is hyaline, but one of the subspecies (d'Aguilar et al 1986). The most likely one would seem to be the locally distributed schmidti (Conci), where in addition to the above differences in male colour, the females are described as having very 'smokey' wings compared to those of the typical form. Changes in body colour as Odonata mature have often been used to place these insects in progressive age categories (Corbet 1980 and references therein). Here changes in eye colour have been used in addition to general body colour, to enable more precise age categories to be determined. Eye colour was particularly helpful in aging females, where there was little body colour change between post-teneral and mature ages, and even the colour change at maturity was very subtle.

The typical average maturation time during this study (12-14 days for males, 15-16 days for females) is similar to that of Calopteryx maculata (11 days, Waage 1972) and

Calopteryx haemorrhoidalis (10 days, Heymer 1972). Other records of maturation time for Calopteryx are very much shorter, between 1-5 days (Buchholtz 1951, Conrad and Herman 1990), including a record for C.virgo of 1-3 days (Klotzli 1971). The shortest maturation time for males observed here was 6-7 days. Variations in observed maturation time may result from species differences and differences in the criteria used to recognise maturity. In addition it has been shown that temperature can affect the maturation rate (Buchholtz 1951), and it is clear from this study that poor weather, which dramatically reduces feeding ability, can result in a doubling of maturation time. It has often been recorded that, as found here, females take slightly longer to reach maturation than males (Corbet 1980 and references therein). Here maturation in females was judged by first oviposition, and it is possible that the extra time needed to reach maturation may be due to the time spent feeding to mature eggs after physiological maturity has been reached.

Unlike many species of Odonata, adults remained along the Leat throughout their maturation period. Similar behaviour has been observed in Calopteryx aequabilis (Conrad and Herman 1990) and in Ischnura elegans (Parr 1973). Most adults remained within central favoured feeding spots where there were banks of vegetation in full sunlight, and there was no sign of emigration to neighbouring population centres. This suggests that on the whole adults remain close to their emergence site (providing feeding sites are nearby), and similar results were found for C.virgo (Zahner 1960), and C.maculata (Waage 1972). The occasional sitings of marked

individuals several hundred metres from the population centre, however, indicates that some do wander further. The adjacent conifer plantation, with continuous shade, excluded feeding adults.

6.4.2 The Effect of Time of Emergence and Adult Body Size on Survival to Maturity.

The survival of immature adults in 1986 was largely independent of age per se. Sharp rises in daily mortality did, however, coincide with age related events. Both instances in 1986 coincided with the onset of a period of emergence and an increase in the number of breeding adults at the water's edge. The major mortality occurred so close to the start of the emergence of the third group that few newly emerged adults were present, and in 1987 the sudden increase in mortality coincided only with an increase in the number of breeding adults, showing that emergence was not the trigger. Although in 1986 and 1987 the number of adults along the Leat was high at the time of the main episodes of predation, numbers probably peaked before the mortality occurred. The close synchronisation each year with the arrival at the water of the newly mature adults from the second emergence group leads to the conclusion that it was this increase in breeding behaviour that triggered the sharp rise in bird predation. Wheras feeding adults spend very little time on the wing, mature males spend much time in flight during territorial disputes and defence. Even mature females are more mobile as they search up and down the Leat for oviposition sites and as they escape unwanted attention from males. Breeding behaviour therefore results in a frenzy of activity in a fairly

concentrated area at the water's edge. It is not surprising that a rapid build up in breeding adults would attract the attention of birds. Interestingly the mortality of immature adults was just as high as mature adults during the episodes of bird predation, and it seems that once breeding behaviour had brought the damselflies to the attention of the birds, even feeding adults became vulnerable.

In 1987 and in females in 1986 the high level of bird predation was very short lived, suggesting that once numbers of damselflies fell they were no longer worthwhile prey items, although male mortality remained high in 1986. The possible predators were blackbirds, chaffinches, great tits and wrens, all of which were seen amongst the fern. Chaffinches, which do take insects when feeding young in June and July, were by far the most common bird and were very numerous. A female chaffinch was seen taking a female C.virgo on the wing, and given the scale of the mortality (around 150 damselflies disappearing mainly over two days in 1986) it seems possible that the very numerous chaffinches were responsible. Crowley et al (1987b) note that while there is little information on the possibility of density dependent predation in adults, such predation may be expected at breeding sites where large numbers gather. Although the bird predation here was triggered by a rise in the numbers of breeding damselflies, the ensuing mortality did not appear to be density dependent since the proportion of damselflies eaten did not increase with the numbers present. In 1986 average male daily mortality (0.415) was lower than the daily

mortalities recorded in 1987 (0.48 and 0.67), yet numbers of breeding males in 1986 were around double the number in 1987.

The timing of the predation was disadvantageous to the second emergence group in 1986, with far fewer surviving to maturity than the first emergence group. Since the predation occurred in two consecutive years it is likely to be a feature of this population. The first emergence group may not always have a survival advantage however, as in 1987 when poor weather doubled the maturation time of the first emergence group, and consequently their survival to maturity was low.

In contrast to this study others have found that bird predation is most severe amongst tenerals (Parr and Parr 1972, Van Buskirk 1987b), with the consequence that mortality is highest at this time and then falls. Here the mortality of tenerals will have been under-estimated since marked individuals were retained in cages for several hours until their cuticle had hardened- possibly protecting them during a time when they were vulnerable to predation. Nevertheless no teneral wings were found; so it is unlikely that significant predation of tenerals was missed. Emerging C.virgo were highly dispersed along the bank, and were unlikely to attract birds. Other authors have reported an increase in mortality during reproduction; predation by other Odonates was greatest on breeding pairs of Crocothemis erythraea (Convey 1992), and predation by spiders was greatest in territorial males of C.haemorrhoidalis (Rehfeldt 1992).

It is perhaps not surprising that predation by birds resulted in survival to maturity being independent of body size, and similar results were found in a population of Sympetrum rubicundulum (Van Buskirk 1987b). The higher survival of larger, early emerging adults of Sympetrum danae reported by Michiels and Dhondt (1989) could simply reflect the likelihood that smaller individuals were less able to escape from spider's webs, a major cause of mortality in their study. Anholt (1991), however, proposes that body size may influence survival to maturity regardless of the cause of mortality, since smaller adults need to put on more weight between emergence and maturity than larger adults, and consequently have increased feeding activity. Similarly he suggests that females may have reduced survival compared to males because they put on more weight between emergence and maturity. Such phenomena are unlikely to be important in the present study, however, where the major cause of mortality was so shortlived, and observer bias is likely to account for the lower observed survival of females.

CHAPTER SEVEN

TERRITORIAL AND OVIPOSITION BEHAVIOUR ALONG THE LEAT IN 1985 AND 1986

7.1 INTRODUCTION

The aim of this chapter is to take a first look at breeding behaviour along the Leat, which is likely to depend on the weather and habitat features as well as differences between individual damselflies. The distribution of territorial males and ovipositing females along the Leat will give an insight into the factors which influence territory quality and reproductive success. This basic investigation forms the first stage of the more rigorous determination of reproductive success which was carried out in 1987.

7.2 METHODS

In 1985 the territories of individual males were monitored to become familiar with breeding behaviour, and to record the diurnal pattern of oviposition. Once the latter had been established, effort in 1985 and 1986 concentrated on sampling oviposition and territorial behaviour in each 30m Leat section during the peak of the oviposition period. It was intended to sample each 30m section twice a week, but in practice samples were taken as often as the weather would allow, since reproductive behaviour was strongly dependent on favourable conditions. Each sample unit consisted of one of the 10m stretches within a 30m section of the Leat. Samples were taken by walking down the centre of the 10m section

every five minutes for twenty minutes. During each walk the position on both banks, using the one metre markers, of territorial males and ovipositing females and the identity of marked adults was recorded. The different 10m sections were sampled consecutively within each 30m section, and at consecutive time slots through the peak oviposition period. In this way the total number of female oviposition minutes, (number of females*time present) per twenty minute sample, in a 10m stretch of Leat, could be determined.

In 1986 the position, and identity if marked, of all territorial and non-territorial males along the entire length of the Leat was also recorded on alternate days, as far as the weather allowed. The distribution of territories was then compared with the distribution of short and trailing vegetation and sunlight at the water's edge.

7.3 RESULTS

7.3.1 The distribution of territorial males and ovipositing females along the Leat

All territories were situated on the sunny, south-facing bank rather than the shady, north-facing one. As the sun moved round territorial males moved with it if their territory became shaded. The distribution of sunlight along the south-facing bank, at the water's edge, shows that sections F and H received most sunlight through the day (Figure 7.1). In particular these sections received most sunlight during the early afternoon when most oviposition occurred (see below). The distribution of the high numbers of

territorial and non-territorial males in 1986 reflects the distribution of sunlight, with most males in sections F and H (Figure 7.2a). In 1985 when numbers of males were very low (Figure 7.3) the pattern is not so evident, particularly because the few males that were present were often in sections A and E fighting over two very popular territories which are described below. Sections A, E, F and H had continuous stretches of sunshine, in contrast to sections B-D, G, I and J where shading from trees or the steepness of the bank resulted in very small patches of sunshine only. So few ovipositing females were seen in both 1985 and 1986 that the pattern of their distribution is also strongly influenced by small local variations (Figure 7.2b). In both 1985 and 1986 however, sections A, E, F or H, each with long sunny stretches, appear to be most popular with ovipositing females.

Vegetation trailing into the water was chosen as oviposition sites, and this was usually bracken and other ferns although grasses and roots were sometimes used (Plate 7.1). When the first bracken stem fell into the water early in 1985 in section A, the resulting localized abundance of fronds trailing in the water immediately attracted most of the ovipositing females in the section. Up to four females were ovipositing amongst its fronds at the peak time, and there were often five territorial males in almost continual aerial battle above it. Another very popular territory in 1985 was a patch of *Salix* roots just beneath the water surface in section E.

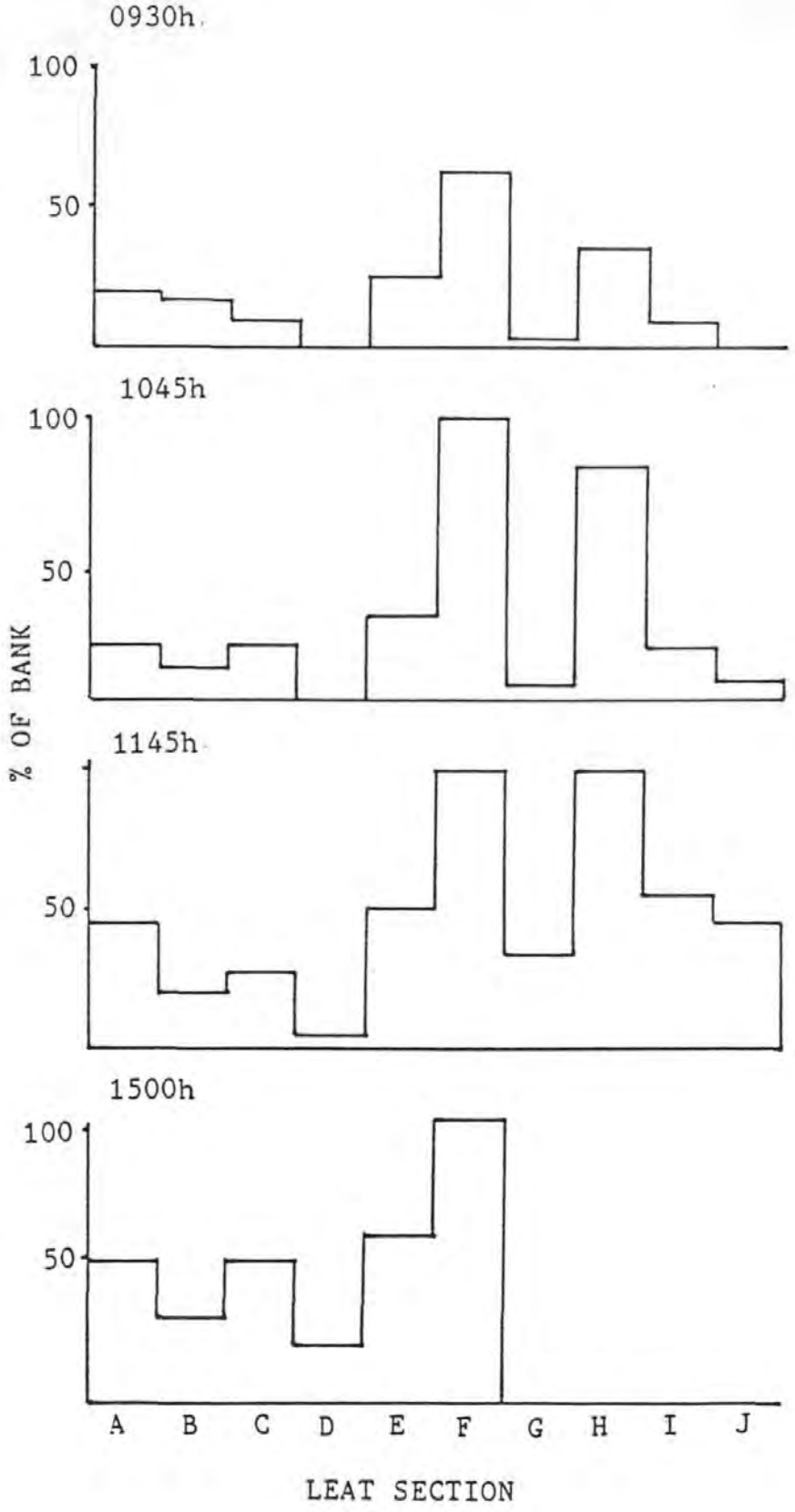


FIGURE 7.1 THE PROPORTION OF THE SOUTH FACING BANK IN SUNLIGHT AT THE WATERS EDGE AT VARIOUS TIMES THROUGH THE DAY IN 1986.

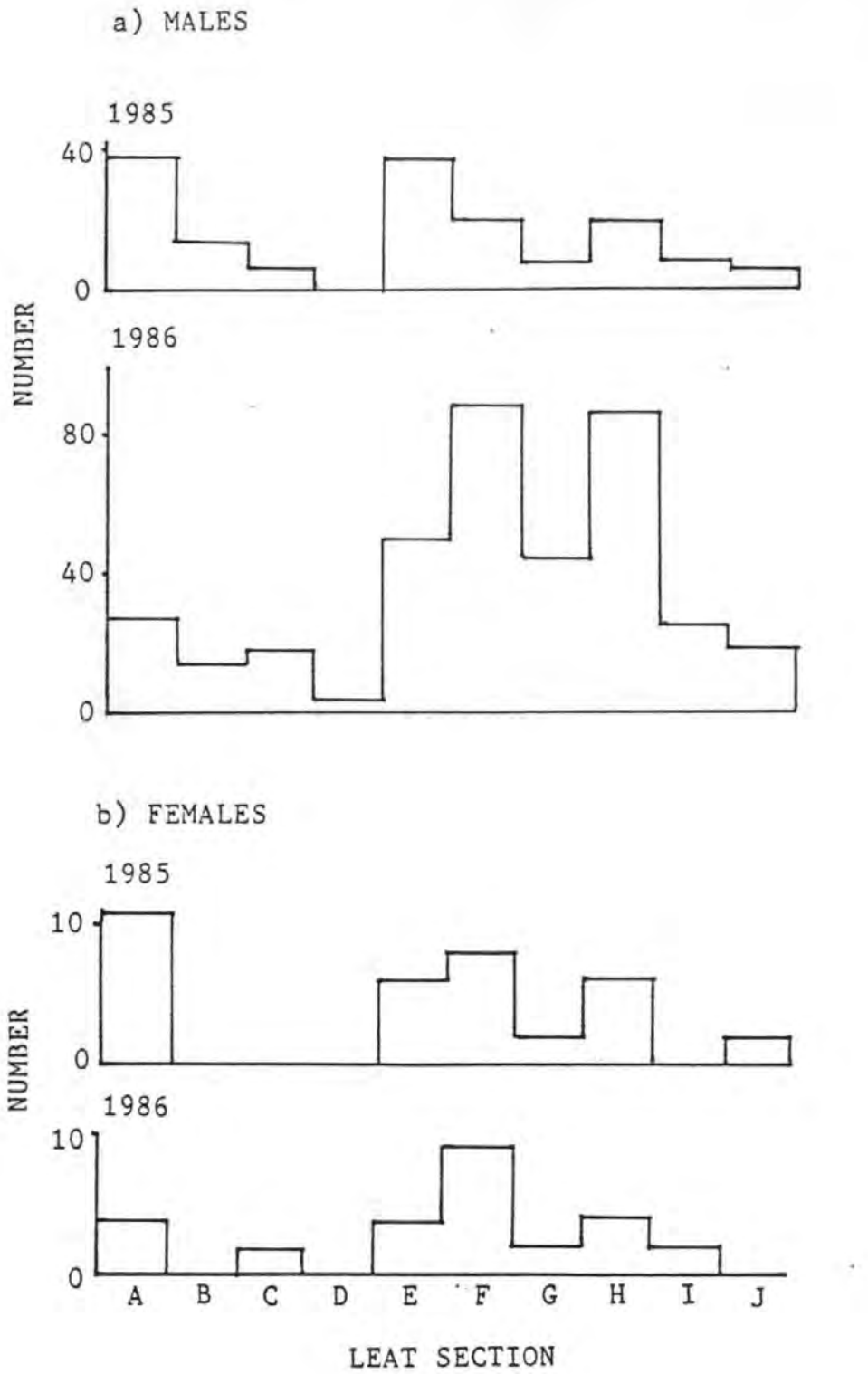


FIGURE 7.2 THE DISTRIBUTION OF TERRITORIAL AND NON-TERRITORIAL MALES AND OVIPOSITING FEMALES ALONG THE LEAT IN 1985 AND 1986. NUMBERS ARE POOLED FROM ALL OBSERVATION DAYS.

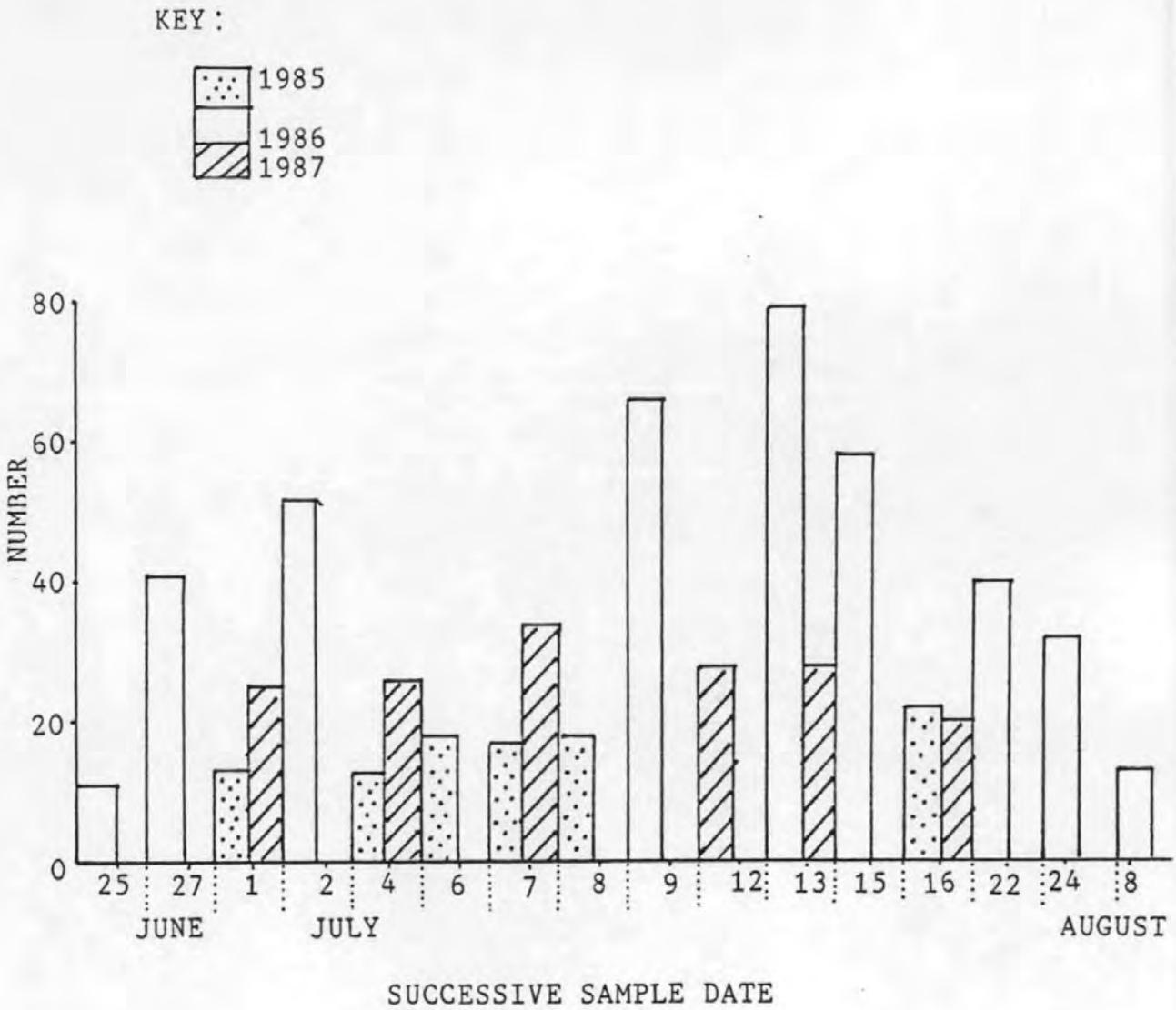


FIGURE 7.3 A COMPARISON OF THE NUMBER OF MATURE MALES IN THE POPULATION AREA IN 1985, 1986 AND 1987. WHERE SAMPLES FROM TWO YEARS FELL ON THE SAME DATE THEY ARE SHOWN SIDE BY SIDE.

PLATE 7.1 VEGETATION TRAILING INTO THE WATER WAS CHOSEN AS OVIPOSITION SITES. THIS WAS OFTEN FERNS; HERE A FEMALE TRIES, RATHER UNSUCCESSFULLY, TO OVIPOSIT INTO GRASS. NOTE MATURE BRONZE COLOURATION.

PLATE 7.2 FEMALES WERE CARRIED AWAY FROM THE TERRITORY TO BE MATED.

The proportion of bank with trailing vegetation rather than shorter grasses was also unevenly distributed along the Leat. In 1986 the low numbers of territorial and non-territorial males in sections A, G, I and J, where there was a large amount of trailing vegetation but little sunlight at the water's edge, shows that sunlight was the primary factor influencing the distribution of territory sites. As a result of the distribution of sunlight, most oviposition in 1985 and 1986 occurred along the south-facing bank in sections A, E, F and H.

7.3.2 Breeding behaviour and the Influence of Poor Weather

Breeding behaviour was completely dependent upon the weather, and the most important factor was sunlight rather than air temperature. With maximum air temperature in the shade as low as 15^{0}C oviposition could take place provided it was sunny. No oviposition was seen in cloudy weather, even when the temperature was as high as 18^{0}C and feeding could take place. The influence of sunshine was most obvious when behaviour was observed on days with sunny spells. Under complete cloud cover there would be no movement along the Leat, but within seconds of the sun coming out males were fighting over the water, females were searching for oviposition sites and others started feeding. With equal suddenness all activity stopped when the sun went in again. Mature males, particularly those with territories, were less influenced by the weather, and would sit in their territories and embark on occasional confrontations with other males when it was too cool for oviposition. The summers of 1985 and 1986

were both generally cold and wet, and opportunities for oviposition were few and far between.

On sunny days territorial males took up positions at the water's edge at around 10.00h, after feeding for an hour. Females did not arrive to oviposit until around midday, and numbers peaked at 13.00-13.30h before falling off sharply until the last females left the water at 16.00h (Figure 7.4). On hot, sunny days 70% of oviposition occurred during the peak period from 12.00-14.00h, but this pattern was disrupted by poor weather, and females would oviposit later in the afternoon if it was cloudy from 12.00-14.00h. The full courtship behaviour described in the literature (Pajunen 1966) was seen occasionally, but often females started ovipositing in a territory straight away, and were forcedly removed for mating by the territorial male (Plate 7.2). Casual records of oviposition duration were from 30-95 mins, and ovipositing females rarely submerged. Despite the fact that there were so few mature adults in 1985, and presumably an abundance of possible oviposition sites not within male territories, 98% of oviposition occurred within territories.

Territories were based on patches of oviposition sites (for example a few fronds of fern trailing into the water) with a nearby perch. Males holding small territories (a metre of bank or less) generally occupied one central perch, but in larger territories several perches would be used along the bank. Territorial males without ovipositing females frequently searched the bank on either side of their perch until another male was encountered, whereupon a brief fight

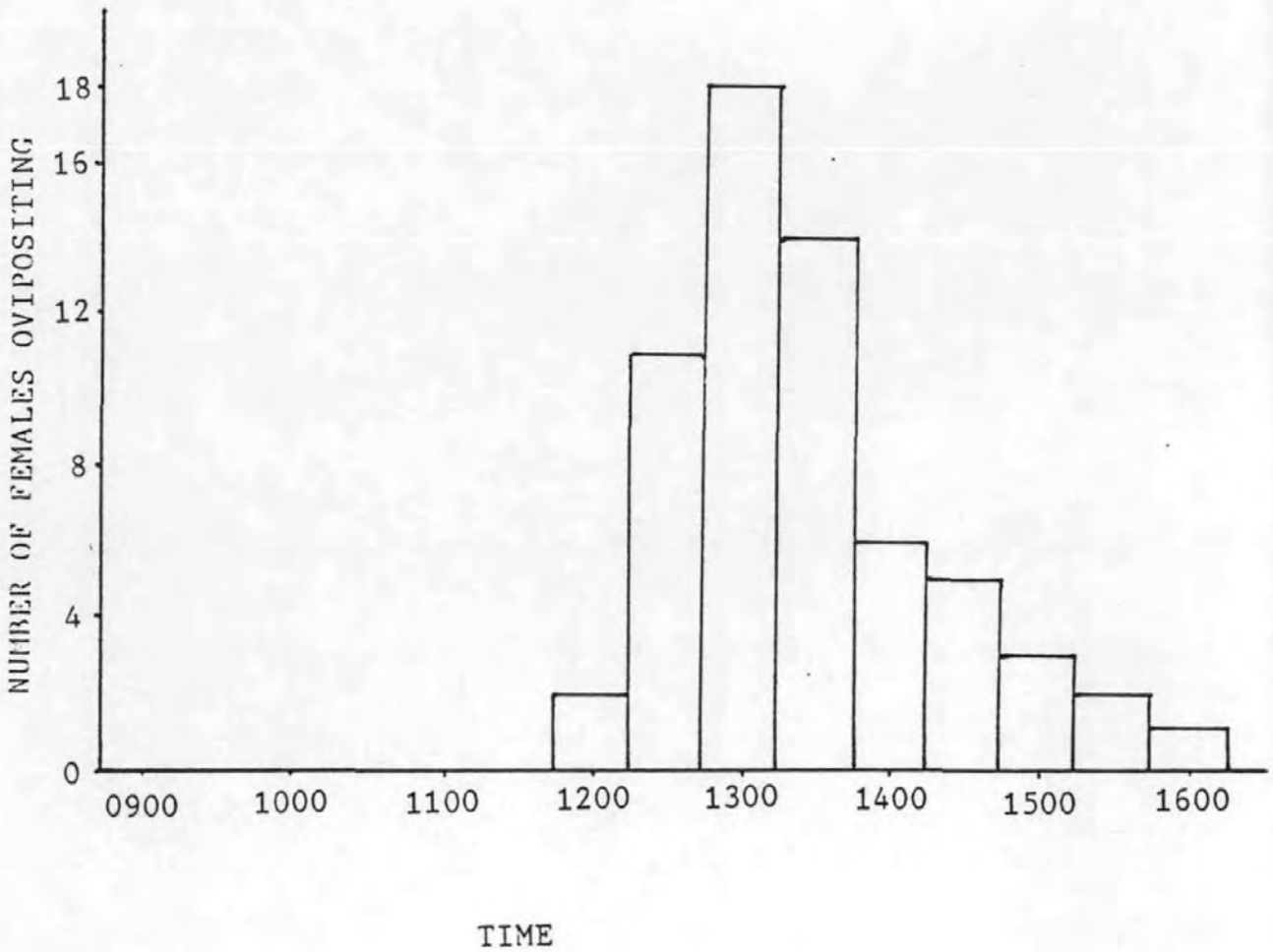


FIGURE 7.4 THE DISTRIBUTION OF OVIPOSITION THROUGH THE DAY. DATA POOLED FROM FOUR AREAS OF LEAT BANK IN SECTIONS A, E AND H DURING TWO CONTINUOUSLY HOT SUNNY DAYS IN 1985.

would ensue before the male returned to his perch. If ovipositing females were present in a territory males generally remained close by, but would fly out to challenge any other males who came too close. There appeared to be a great deal of variation in territory quality (judged by the number of females or competing males it attracted). Males in very popular territories seemed to spend so much time in aerial battles that ovipositing females often arrived unnoticed. Non-territorial males sat back from the water's edge, periodically flying down to challenge territorial males. Such males could be seen flying 100-200 metres along the water's edge, causing chaos amongst the territory owners along the way. Alternatively sometimes a non-territorial male would select one territorial male to challenge, and would sit close by, continually launching attempts to drive the owner away.

7.3.4 Oviposition samples, Territory Size and Body Size

Despite there being many more breeding adults in 1986, more oviposition was seen in 1985, and most of this during the long period of continuous hot weather at the beginning of July. In 1986 the first females started ovipositing at the end of June, but then only had three short spells of hot weather before the the episode of bird predation during which 93% of those from the first and second emergence groups disappeared (see Chapter Six). During these brief sunny periods very little oviposition was seen. The slow arrival of mature females to oviposit at the start of a long hot spell in 1987 (Figure 8.3, Chapter Eight) suggests that they must spend the first days of a fine spell feeding before

oviposition can start. Since the fine spells available to the first two emergence groups in 1986 were so short, it is possible that many mature females had to feed rather than oviposit during those times. Most oviposition in 1986 was seen in August when the third emergence group had matured, but this occurred in unpredictable sunny spells during unsettled weather, and recording had to be abandoned.

So few ovipositing females were seen during samples in 1986 that oviposition duration was not analysed. In 1985 the average total duration of oviposition per twenty minute sample in a 10m section ranged from 2.5- 31 mins (Figure 7.5). The variability in oviposition and small number of samples resulted in very large errors associated with each mean, and it was not worthwhile extrapolating these data to estimate total oviposition.

Because of the lack of data on females in 1986 analysis of breeding behaviour was restricted to territorial and non-territorial males. Territory size was measured as the length of bank occupied by each male. Boundaries between territories were judged to be half way between the nearest neighbouring perches, since this was approximately the point where neighbours would meet in confrontations. If there was no neighbour within 5m on one side of a territory, that half of the territory was assigned a size of five metres, the approximate distance an isolated male would search along the bank before returning to the central perch. The uppermost limit given to territory size was therefore 10m. In 1985 when there were few males, a Mann-Whitney U test showed that

territory sizes were significantly larger than in 1986, with means of 6 metres and 2.5 metres respectively (U=2606, P=0.007, Figure 7.6). In 1986 maximum numbers of territorial males per 30m section were 14 and 18, recorded in sections F and H respectively on the 13th July. The distribution of territory size in 1986 indicates that while most territories in the less popular Leat sections fall within the range of those in sections F and H, 28% were very large, and these represent isolated males in sections B to D where there was only dappled sunlight. If the 10m territories are excluded, a Mann-Whitney U test showed that there was no difference in the size of typical territories in popular and unpopular areas (U=1260, p=0.876).

In 1986 most territorial disputes recorded during the twenty minute samples were seen in sections E to H where most males were. Territorial males were categorised as those in possession of a territory for at least three out of the four five minute observations that made up one sample. Sometimes the difference between territorial and non-territorial males was clear, but at other times it was not, since twenty minute battles were not unusual. A comparison of the body size of males present from the 9th to the 24th of July shows that there is a suggestion that territorial males were larger than non-territorial males, and although this trend was stronger in head width neither difference was significant (Figure 7.7, head width: t=1.856, 34df, P=0.069, body length: t=0.906, 38df, P=0.626). When the size of males holding territories in the most popular areas for ovipositing females, sections E,F and H, was compared with those in other sections, mostly on

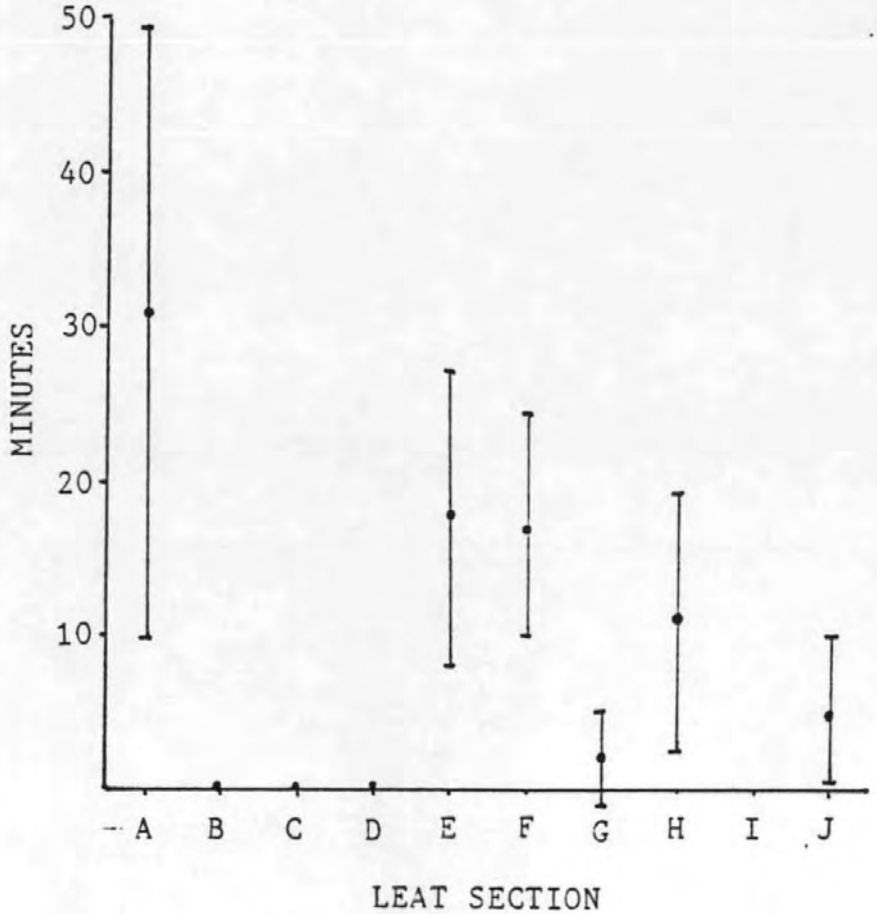


FIGURE 7.5 THE TOTAL NUMBER OF FEMALE OVIPOSITION MINUTES PER TWENTY MINUTE SAMPLES IN 1985. MEANS ARE PRESENTED +/- S.E., n=48. NO OVIPOSITION WAS RECORDED IN SECTIONS B,C,D AND I.

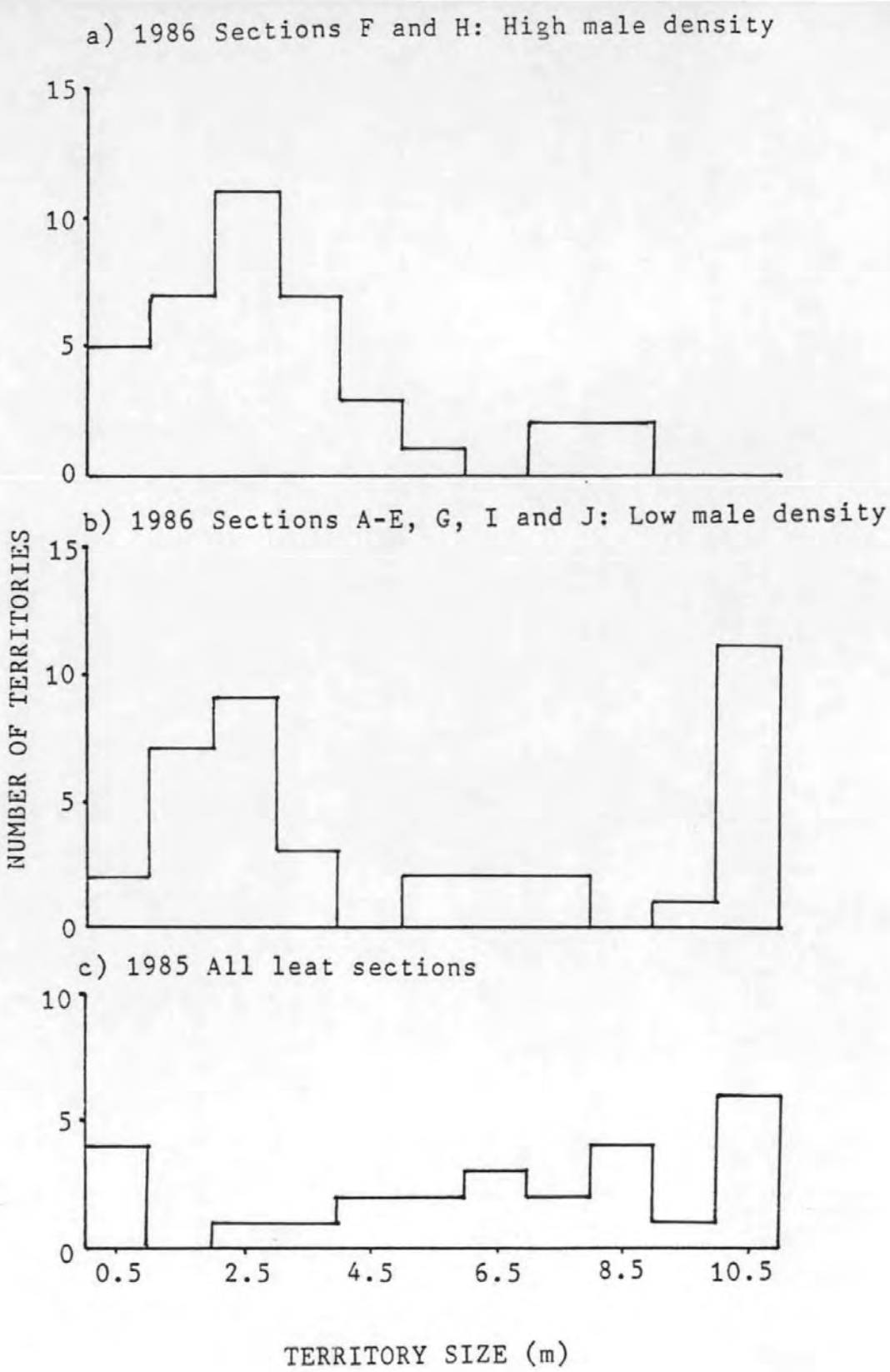


FIGURE 7.6 TERRITORY SIZES IN DIFFERENT LEAT SECTIONS IN 1985 AND 1986

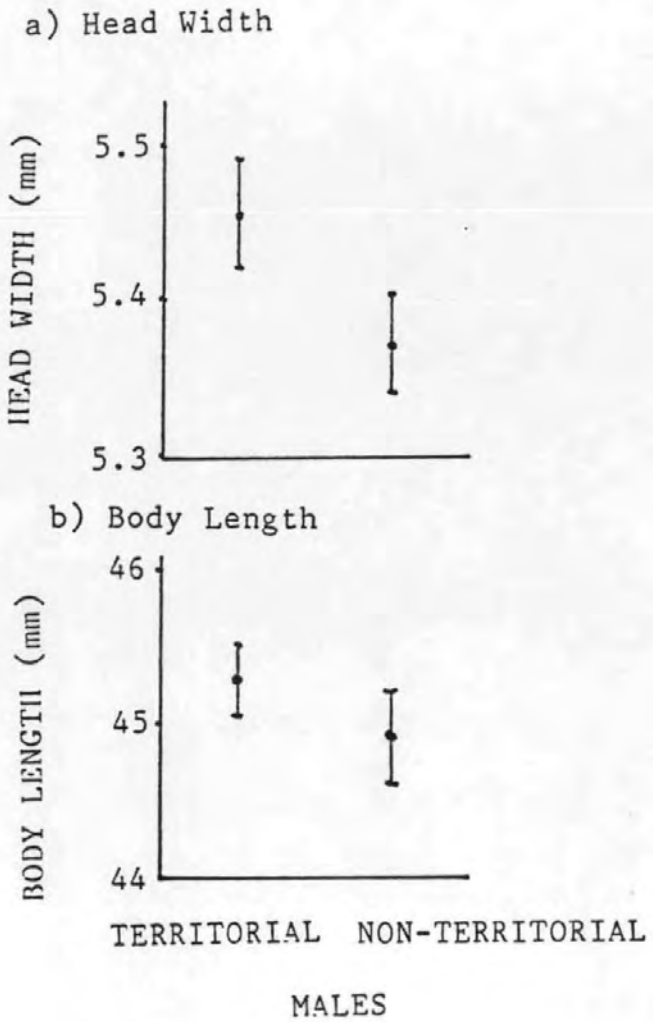


FIGURE 7.7 DIFFERENCES IN HEAD WIDTH AND BODY LENGTH BETWEEN TERRITORIAL (n=26) AND NON-TERRITORIAL (n=14) MALES IN E F G H ON THE 9th, 13th, 15th, 16th AND 24th JULY 1986. MEANS ARE SHOWN +/- S.E.

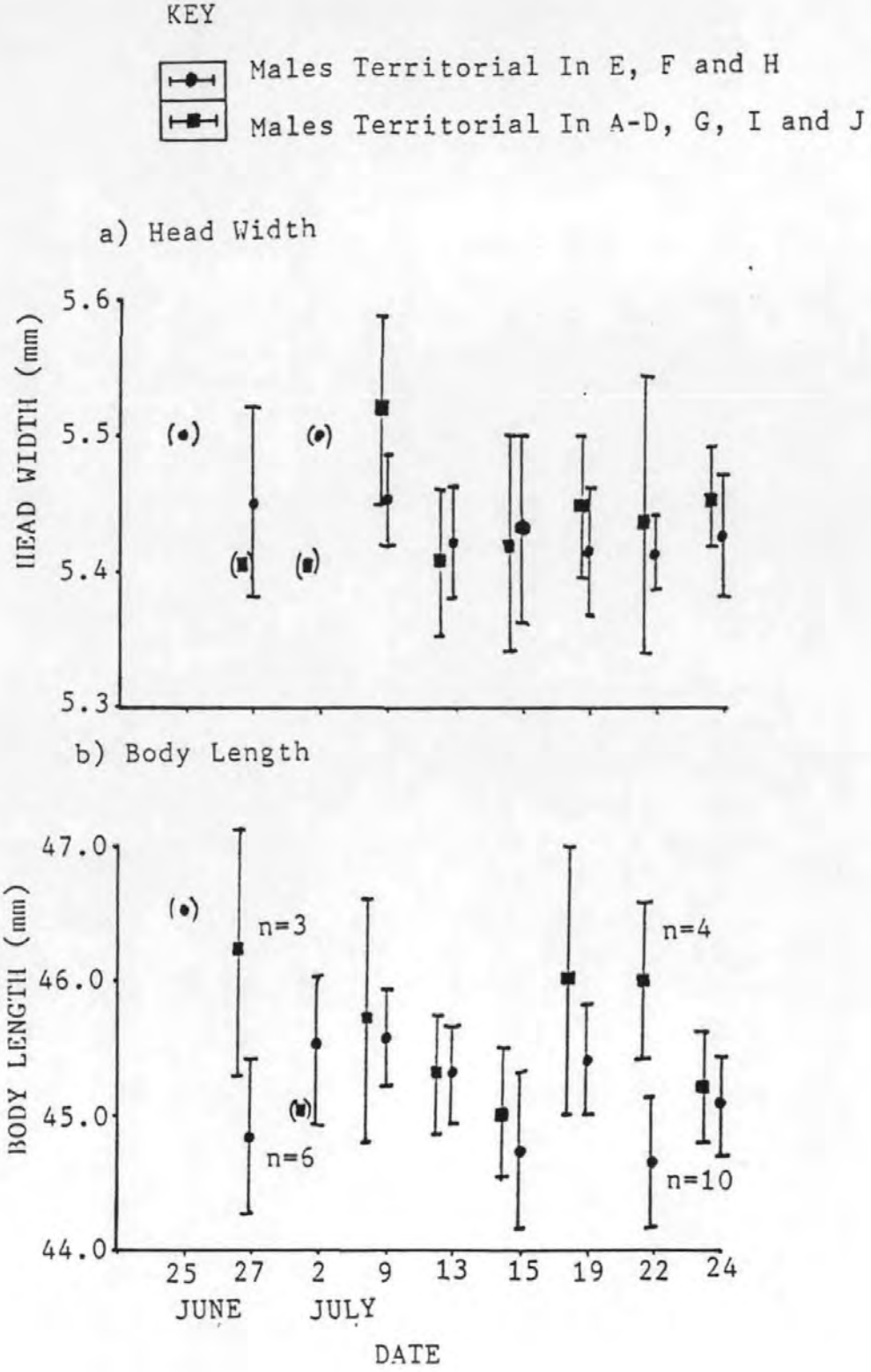


FIGURE 7.8 THE BODY SIZE OF MALES TERRITORIAL IN THE POPULATION CENTRE (LEAT SECTIONS E, F AND H) AND IN PERIPHERAL AREAS (A-D, G, I AND J) IN 1986. MEANS ARE SHOWN +/- 95% C.L.

the periphery of the population area, no difference was found (Figure 7.8). There was also no significant correlation between the body size and territory size of twenty males present on the 9th and 13th of July, when numbers of territorial males were at a peak (head width: Spearman rank correlation coefficient, r_s = 0.03, p=0.875, body length: r_s= 0.166, p=0.51)

7.4 DISCUSSION

Territorial males and ovipositing females were concentrated into sections of the Leat with long sunny stretches at the water's edge . Ovipositing females were occasionally seen to venture into the shade on very hot days, however, and Michiels and Dhondt (1990) found similar results with S.danae. Within sunny areas the distribution of territories and oviposition was influenced by the presence of bank vegetation trailing into the water, and certain areas with an abundance of vegetation, fallen fern for example, attracted a large number of females and males. The fact that nearly all oviposition in 1985 occurred in male territories, when low adult numbers must have resulted in an abundance of oviposition sites without males, indicates that either males can select the best sites where females naturally gather, or that females are attracted to sites by the presence of males.

It could be predicted, therefore, that for this population high quality territories would be those which received most sunlight through the day and had an abundance

of vegetation trailing into the water. In populations of Calopteryx splendens xanthostoma and C.haemorrhoidalis in southern France, territory quality increased with increasing water flow rate up to a point (Wingfield Gibbons and Pain 1992). Here, however, the flow rate at the Leat bank (0.15-0.3 metres per second) was generally fairly uniform, and within the limits which were found to be favourable in the French study.

Breeding behaviour was strongly influenced by the weather, and only took place during hot sunny days or sunny spells, as is commonly found in Odonata (Banks and Thompson 1985, Tsubaki and Ono 1987 and Michiels and Dhondt 1991). The period of peak oviposition in the middle of the day was short, but if this was disrupted by poor weather females appeared to be able to take advantage of sunny spells later in the day.

It was difficult to see which males were territorial in the short time allotted to samples, and the trend that territorial males were larger than non-territorial ones warrants further, more detailed investigation. Moreover, since so few ovipositing females were seen in 1986 it was not possible to compare the amount of oviposition occurring in individual territories. Consequently it is not clear how to interpret the lack of a relationship between male body size and territory size or position. Were males in the popular areas actually doing better than those with territories in other areas, or was there an equal distribution of ovipositing females between males? Would larger territories

have resulted in more ovipositing females, or were they the result of reduced male competition because they were in areas which did not attract many females? These questions are addressed in the next Chapter.

CHAPTER EIGHT

A FIELD EXPERIMENT TO LOOK AT THE IMPORTANCE OF ADULT BODY SIZE AND EMERGENCE TIME TO REPRODUCTIVE SUCCESS

8.1 INTRODUCTION

The aim of this Chapter is to look in detail at the importance of adult body size and time of emergence to the reproductive success of males and females. In the short term reproductive success can be measured as daily clutch size or daily eggs fertilized, but in the longer term lifetime reproductive success is dependent also upon survival. In the case of males the priority is to look at the influence of territorial behaviour on their daily reproductive success. Observations from the summer of 1986 have given rise to a number of questions:

1) How does the distribution of oviposition sites influence the distribution and behaviour of females- do areas of bank with a high number of oviposition sites attract more oviposition?

2) How do territorial males respond to variations in the distribution of ovipositing females? Do males which hold territories in areas with high levels of oviposition manage to achieve a higher daily reproductive success than those in other areas, or does the increased competition between males in popular areas result in all males doing equally well?

3) How does territory size interact with territory quality- do males which defend larger territories do better

than those in smaller territories, or is territory size a passive consequence of the number of competing males- with males in larger territories doing no better than others?

4) Are some males unable to obtain territories, and do these males manage to obtain matings and fertilize eggs?

To answer these questions experience from previous years was used to design a field experiment, where the distribution of oviposition sites was manipulated, and the distribution and behaviour of ovipositing females and mature males observed. The importance of territorial behaviour and daily reproductive success to the lifetime reproductive success of males can only be determined by monitoring breeding behaviour throughout their mature lifespan. Therefore, the experiment was also designed to concentrate oviposition, and hence all breeding behaviour, into a restricted area where individuals could be continually monitored. Emigration from the study area was not thought to be a problem since in previous years adults were rarely seen elsewhere, and were never seen at neighbouring breeding centres.

In females the priority is to look at the importance of body size and time of emergence to the number of eggs produced in their reproductive lifespan. By restricting oviposition to the experimental area all components of female lifetime reproductive success such as clutch size, rate of clutch production and survival can be measured. An estimate

of egg deposition rate can also be made, leading to an estimate of fecundity for this species.

It is a difficult analytical task to identify which components are important in influencing lifetime reproductive success, and although several methods are available each has its disadvantages. Here two methods will be employed. When the important components have been identified the extent to which they are influenced by body size and time of emergence can be examined.

8.2 GENERAL METHODS

8.2.1 The distribution of oviposition sites in the experimental area, and the concentration of breeding behaviour there

The south facing bank of Leat section F was chosen as the position for the experimental area, since it received maximum sunlight, and had been a popular breeding site in previous years. The north facing bank, which was in shade until late in the day was rarely used for territories or oviposition sites. Four patches of artificial oviposition sites were set up which differed in the density of oviposition sites available. The oviposition sites were provided by ferns, lodged in flower pots, and pinned to the leat bed close to the south facing bank. The ferns used were from those species found growing along the leat bank, whose fronds often trailed in the water and formed natural oviposition sites. Individual ferns used in the experiment grew well back from the leat edge and could not already

contain eggs. Prior to the establishment of the patches, natural vegetation at the water's edge was trimmed to a couple of centimetres in length.

Figure 8.1 shows the arrangement of the patches. Each patch was six metres long and separated from the adjacent patch by two metres of trimmed bank. The size of the patches was the result of a compromise between two requirements; they needed to be large enough to accommodate several territorial males, so that territory size within the different patches could be measured, but small enough to be monitored easily. In each patch twelve pots with ferns were pinned at half metre intervals, and differences in the density of oviposition sites were created by varying the amount of vegetation that was allowed to trail in the water. In two patches, HIGH 1 (H1) and HIGH 2 (H2), a high density of oviposition sites was provided by allowing three to five fronds per half metre to trail in the water. In the other two patches LOW 1 (L1), and LOW 2 (L2), no large fronds were allowed to trail in the water, and the only oviposition sites available were the stems of the ferns and 1-2 small leaflets per pot (Plate 8.1). In both H and L patches the remaining fronds were tied up in such a way as to provide perches close to the water's edge. As a result of pinning pots at half metre intervals the maximum distance between perches, occurring in the L patches, was half a metre. This distance was the closest that territorial males had been observed perching in previous years, and would ensure that the distribution of perches did not influence territory size. Care was taken to make the oviposition patches as homogenous

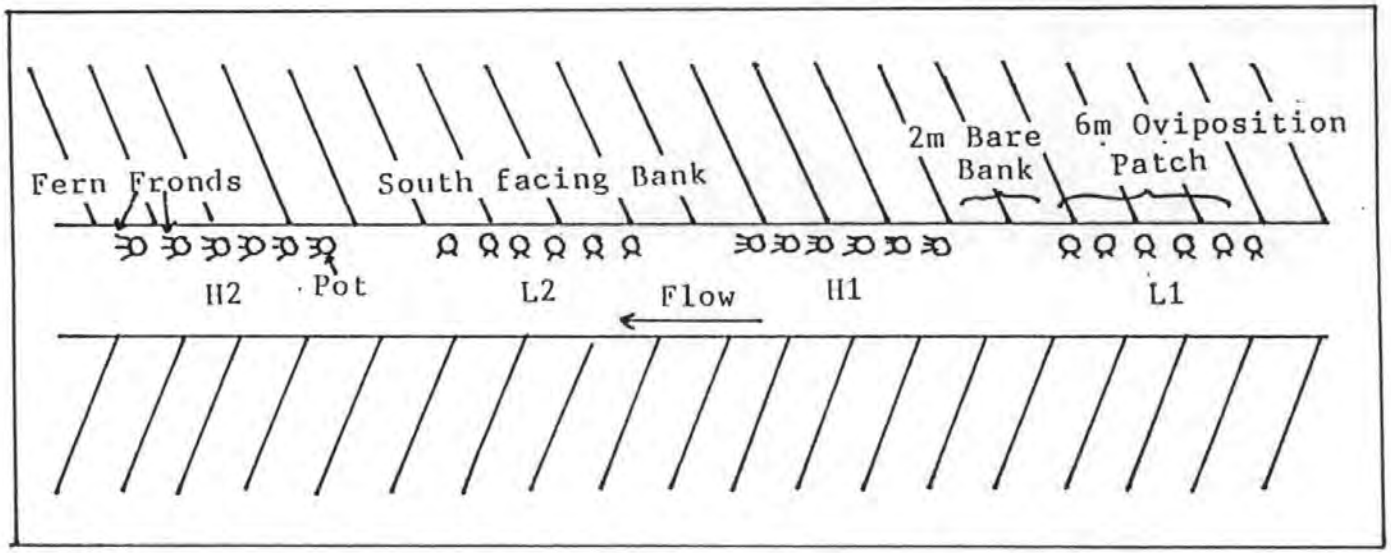


FIGURE 8.1 THE LAYOUT OF THE ARTIFICIAL OVIPOSITION PATCHES. H (1 & 2) AND L (1 & 2) REPRESENT PATCHES WITH A HIGH AND LOW DENSITY OF POTENTIAL OVIPOSITION SITES RESPECTIVELY.

a) H1 PATCH, WITH A HIGH DENSITY OF OVIPOSITION SITES

b) L1 PATCH, WITH A LOW DENSITY OF OVIPOSITION SITES

PLATE 8.1 THE ARTIFICIAL OVIPOSITION PATCHES.

as possible. H and L patches were arranged alternately along the bank, and each half metre position was marked.

Oviposition and territorial behaviour was concentrated in the experimental area by trimming the vegetation on the bank, and thus removing natural oviposition sites, at other sunny areas of the leat. This was repeated at regular intervals through the summer.

8.2.2 Marking, measuring and age determination

Adults caught during emergence samples and populations samples in the summer of 1987 were individually marked and measured (for a description of methods see Chapters Five and Six). The changes in eye and body colour described in Chapter Six were used to age individuals caught after emergence. The emergence of the 1985 year class has been described in Chapter Five, and the pattern of emergence assisted in assigning individuals to an emergence group. The female data used in the analysis of lifetime reproductive success came from females who were marked while immature, so that their first day of oviposition and hence mature lifespan could be monitored. While only a proportion of the mature females were marked, all previously unmarked males which reached maturity were marked. Marking of mature males took place every two days for males found outside the experimental area, and daily for those coming into it.

8.2.3 Recording breeding behaviour and survival in mature adults

Behaviour in the experimental area was recorded by two

observers. Observations were made by eye and using Carl Zeiss 8 * 30 binoculars, and recorded on prepared sheets. Each observer walked downstream in the Leat itself, along adjacent L and H patches, noting the position to the half metre and if marked the identity of ovipositing females. The return walk upstream to the start position was made up on the north facing bank, from where the position and identity of territorial and non-territorial males along the south-facing bank was noted. The difference between territorial and non-territorial males was usually clear at the time of recording, as a result of the lack of site attachment and site defence shown by non-territorial males. Care was taken that an equal time was spent in each patch. There was no sign that the behaviour of the damselflies was disturbed by the process of recording.

Waage (1978) recorded an average daily duration of oviposition for C.maculata of 33.6 mins + a standard error of 3.6 mins. Females in Waage's study were not restricted to the study area, and this estimate may therefore be conservative. Previous observations here suggested that the duration of oviposition in this population was longer, with incomplete records ranging from 30-95mins. In order to minimise the under-recording of short oviposition bouts the oviposition patches here were designed such that the periodicity of sampling was 15mins. On occasions during the oviposition period quick checks were made on other areas of the Leat to see if any ovipositing females were present.

Recording walks were repeated continuously, as far as possible, throughout the oviposition period. On hot sunny days this lasted from around 12.00-13.00h (see Chapter Seven), but cooler mornings and afternoon cloud occasionally shortened the duration of oviposition. The territorial males usually took up positions at the water's edge one to two hours before oviposition began, and while territorial disputes continued throughout the day it is likely that territory positions had stabilised to a large extent by the time recording had begun. Whenever a recorder was present at the start of mating the duration was timed to the nearest second from gonopore contact to release. Notes were also made of the identity of females feeding in section F, but these records were by no means complete.

The daily recording of marked adults enabled daily mortality to be estimated. Mortality was measured as the proportion of marked individuals disappearing from one day to the next and not seen later in another Leat section. The last time an individual was seen was considered to be the end of its reproductive lifespan.

8.3 THE PATTERN OF BREEDING BEHAVIOUR AND MORTALITY

In the summer of 1987 59% of adults emerged in the first emergence group, with a peak around the 1st of June, and 41% in the second group peaking on the 24th of June (see Chapter Five). The first males to mature from the early emergence group were seen on the 20th of June, and by the 24th of June 53% were mature. The first oviposition was seen

on the 26th of June (two females), but the weather was very unsettled from the 20th to the 30th of June with few, brief occasions when oviposition could take place. Suitable prolonged good weather for oviposition did not occur until the 1st of July, and lasted only until the 16th of July. The 16th of July was followed by 14 days of rain and cloud, with only scattered, brief, sunny spells. On the 20th of July, during a bright spell, the only adults seen in the population area were five males and eight females (compared to a peak of 168 adults), all in sections E and F, and on the 30th of July only eight adults in total were seen. During the sixteen day period of oviposition there were five days of poor weather when there was no breeding behaviour, and one day when recording could not take place.

The period of oviposition from the 1st to 16th of July can be divided into two periods according to the presence of adults from the two emergence groups. From the 1st to the 4th July, all the males present except one were from the first emergence group (Figure 8.2a). Most males from the first emergence group arrived within two days of the start of the good weather, although new individuals continued to arrive each day until the 6th of July (Figure 8.2b). Males from the second emergence group started to come in on the 4th of July, and there followed a very rapid change over to second emergence group males. On the 6th of July 53% of males are from the second emergence group, and by the 8th July there are no first emergence group males remaining. No new males arrived after the 13th of July.

Seventy percent of the first emergence group females were marked, but a lower unknown percent of second emergence group females. The relative proportion of the two emergence groups can be calculated by estimating the number of first emergence group females and obtaining the number of the second emergence group by subtraction. First emergence group females arrived more slowly than the males, and numbers rose to a peak on the 4th of July (Figure 8.3a). No new first emergence group females arrived after the 4th of July (Figure 8.3b), but unlike the males they continued to be present until the 16th. Second emergence group females arrived at the same time as the males, and numbers rose very rapidly from the 4th of July, peaking on the 13th. The large increase in numbers on the 13th may have been caused by the period of poor weather which preceded it, resulting in females which would have oviposited over a number of days arriving together.

The daily mortality of males and females is shown in Figure 8.4. Only three males and one female were later seen in other Leat sections after they had disappeared from section F, indicating that disappearance was usually due to mortality. During periods when there was no recording average daily mortality was calculated (see Chapter Six). The mortality of both males and females seemed fairly constant, with the exception of a sharp rise from the 6th-8th of July. Males generally suffered mortalities of 10-30%, but this rose to 48% from the 6th-7th of July, and 67% from the 7th-8th of July. On the 8th July only six males remained of the eighteen which were present on the 7th of July. Female

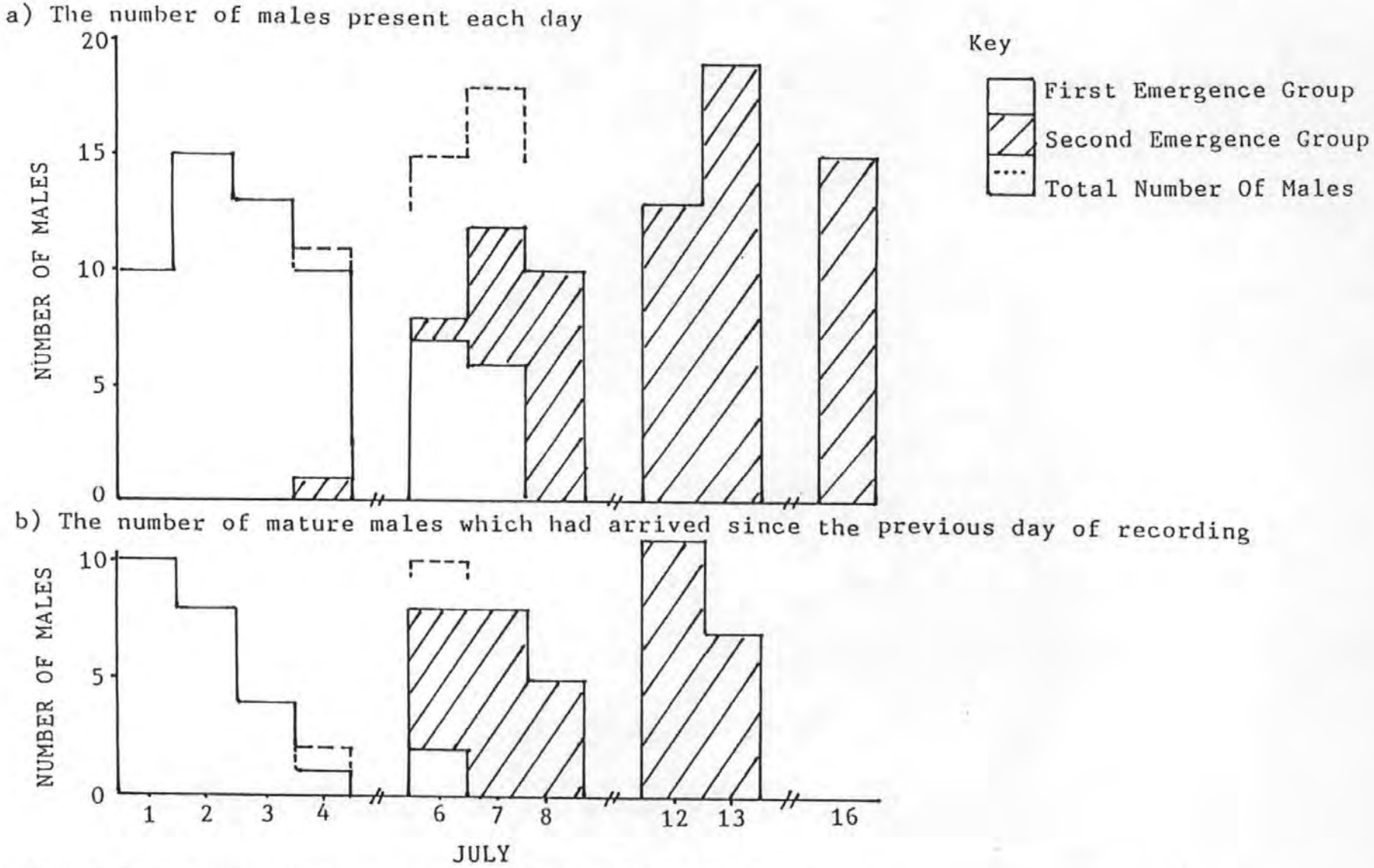


FIGURE 8.2 THE NUMBER OF MATURE MALES FROM EACH EMERGENCE GROUP IN THE EXPERIMENTAL AREA EACH DAY. HISTOGRAMS FOR THE TWO EMERGENCE GROUPS ARE SUPERIMPOSED.

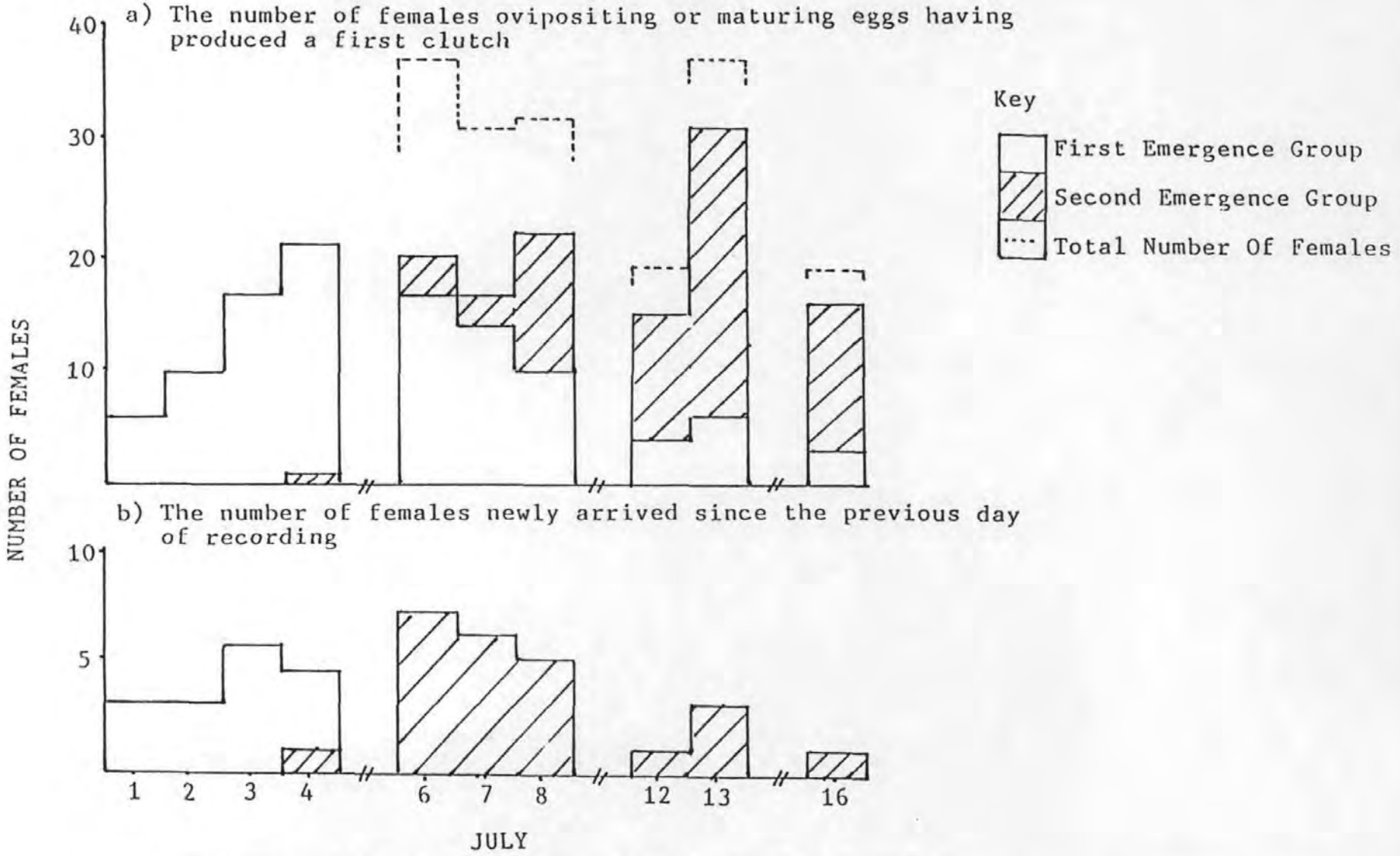


FIGURE 8.3 THE NUMBER OF MATURE FEMALES FROM EACH EMERGENCE GROUP IN THE EXPERIMENTAL AREA EACH DAY. HISTOGRAMS FOR THE TWO EMERGENCE GROUPS ARE SUPERIMPOSED.

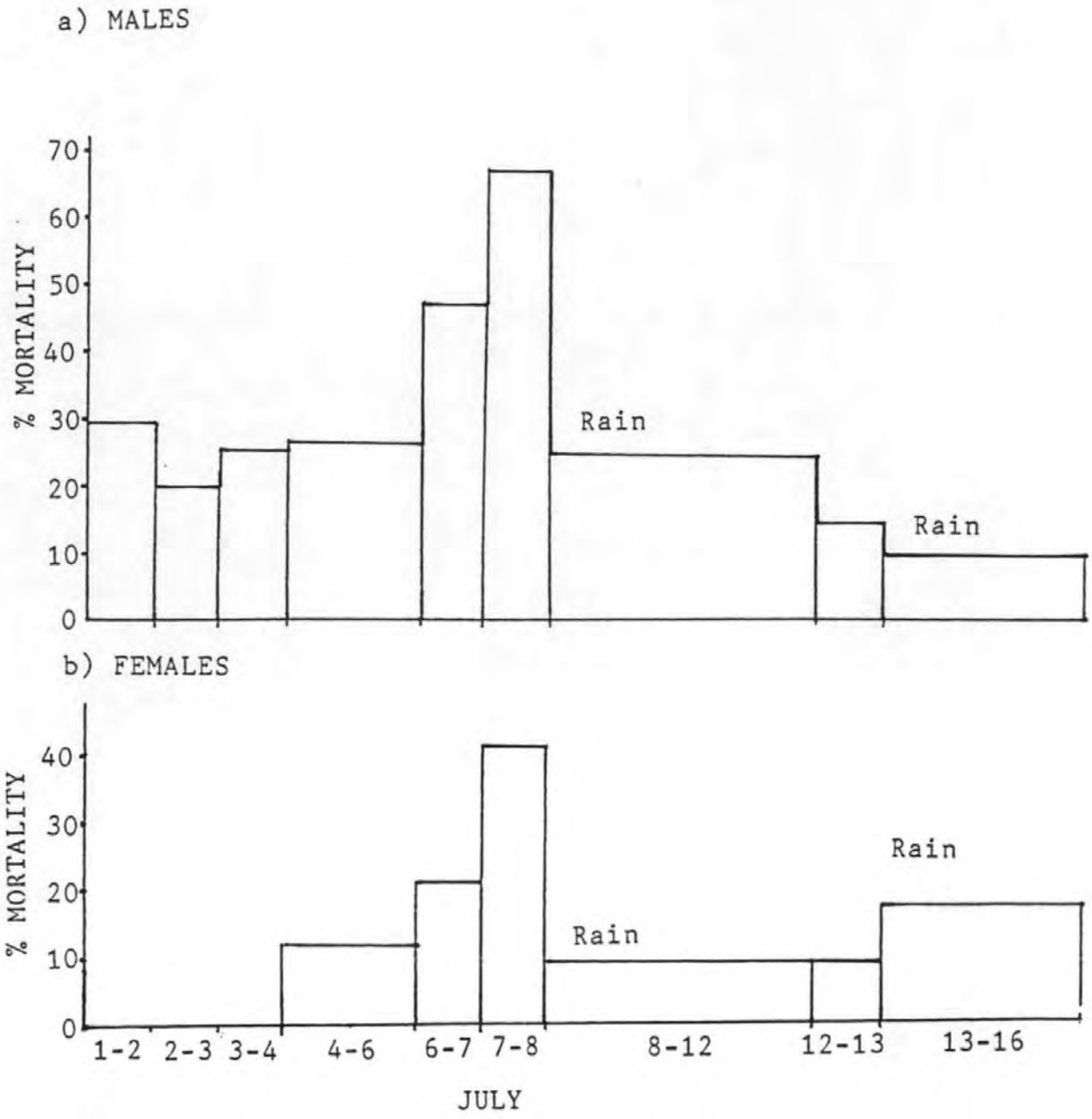


FIGURE 8.4 THE DAILY MORTALITY OF MATURE MALES AND FEMALES IN THE EXPERIMENTAL AREA

mortality was generally lower, between 0-19%, but this rose to 42% from the 7th-8th of July. On the morning of the 7th and 8th the wings of six territorial males were found on patches of bare earth on the bank, and wings of females were found later, suggesting that bird predation was responsible for the sudden rise in mortality.

8.3.1 Discussion

Adults had a very brief time to reproduce, when fine weather coincided with their mature lifespan. Most of the first emergence group males which were seen in the experimental area were mature on the 1st of July. It is likely that many first emergent group females were also mature before the 1st July, and their slow arrival at the oviposition sites indicates that it was necessary for them to feed in good weather in order to mature eggs. Adults from the second emergence group matured during good weather, and males and females arrived together. Many from the second group were still alive when oviposition was stopped by the onset of continuous poor weather on the 16th of July.

Female mortality was generally considerably lower than male mortality, probably because their less conspicuous colour and behaviour did not attract as much bird predation, and they did not suffer the adverse effects of territorial disputes. Mortality did not appear to drop during periods of poor weather, when most adults sheltered in trees or ground vegetation. Adults were seen being preyed upon by spiders and harvestmen, and are likely to have been susceptible to these when immobilised either at night or during poor weather. The

short-lived but large increase in bird predation as the second emergence group matures appears to be a regular phenomenon in this population, and is probably triggered by the increase in breeding behaviour (see Chapter Six). In 1987 it is clear that this contributed to the two emergence groups experiencing very different conditions during the oviposition period. The early emergence group enjoyed six days of continuous hot weather and relatively low mortality, with the sudden rise in mortality occurring at the end of this period. The later emergence group were subjected to high mortality as soon as they matured, and the remaining oviposition time was interrupted by spells of poor weather. The high mortality experienced by males from the 6th-8th of July resulted in the rapid change-over from first to second emergence group males, while some first emergence group females were able to escape this predation and continued to oviposit until the 16th of July.

8.4 ESTIMATING FEMALE EGG PRODUCTION

8.4.1 Method

On the 10th of August, each half metre of fern which had provided oviposition sites in H2 was carefully collected in a separate bucket. The fern was stored in a 15^0 C constant temperature room with a 15L:9D photoperiod regime, and kept aerated. Egg counts were made using a binocular microscope at *10-*35 magnification.

The total number of minutes of oviposition in each half metre of H2 was estimated by summing the times which each

female spent there from the 1st-16th of July. Each female was assigned an average value of oviposition duration based on the number of consecutive samples in which it was seen. For example where females were seen for two samples, and the periodicity of sampling was 15mins, the minimum possible oviposition time was 16mins and the maximum 44mins. In order to avoid consistently over-recording or under-recording oviposition each female was assigned an average value of 30mins, assuming that this reflects the average oviposition time for the group of females seen for two samples. Similarly when females moved from one site to another between samples, an average between maximum and minimum possible times in each site was recorded.

By counting the number of eggs laid in each half metre oviposition site, and dividing this by the total minutes of oviposition there, it is possible to obtain a rate of egg production. This can be used to estimate how many eggs females produced daily, and how many eggs territorial males potentially fertilized.

8.4.2 Results

The distribution of oviposition in H2 alternates between high and low levels in adjacent half metre sites (Figure 8.5). An initial examination of the fern from each half meter revealed that the alternating pattern was due to the species of fern which was present. Three species of fern were used, Broad Buckler Fern (*Dryopteris austriaca*), Scaly Male Fern (*Dryopteris pseudomas*) and Male Fern (*Dryopteris filix-mas*), and it was assumed that each species would be equally

suitable for oviposition. However the areas of low oviposition coincided with the presence of D.austriaca, and when the position of eggs in the three species was compared it was found that the few eggs in the D.austriaca were only placed close to the rachis, rather than all over the leaflets as in the other ferns. The distribution of eggs in the fronds suggests that the leaflets of D.austriaca were not thick enough to contain eggs, thus reducing the area available for oviposition. While almost half the area of H2 contained D.austriaca, only 13% of oviposition occurred there. The alternate arrangement of the fern species was accidental, and the result of pots being secured by two observers alternately selecting from two sources.

As a result of the difficulty in finding the few eggs in the D.austriaca, all effort was directed to counting eggs in the half metre sites with other fern. The eggs were approximately 1.3mm in length, and most were inserted into the leaflets of the fern where they were easily visible (Plate 8.2). Most eggs were at a late stage of development, and the structure of the larvae inside could easily be seen (Plate 8.3a). The eggs started hatching on the 15th of August, and by the 20th of August around 40% had hatched (Figure 8.6). The proportion hatching did not continue to increase, and the initial group to hatch possibly represented those laid by the first emergence group. The process of hatching did not interfere with the egg count, since hatched eggs were easy to see. A comparison of the time when approximately half the eggs had been laid (Figure 8.7) and half the eggs had hatched indicates that hatching took seven

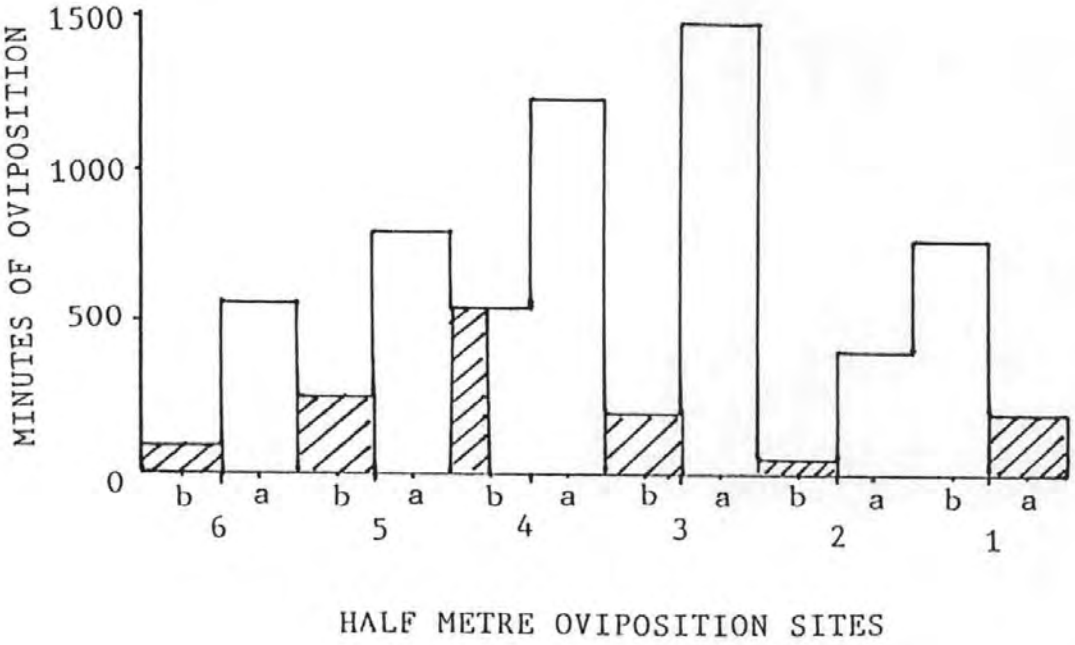
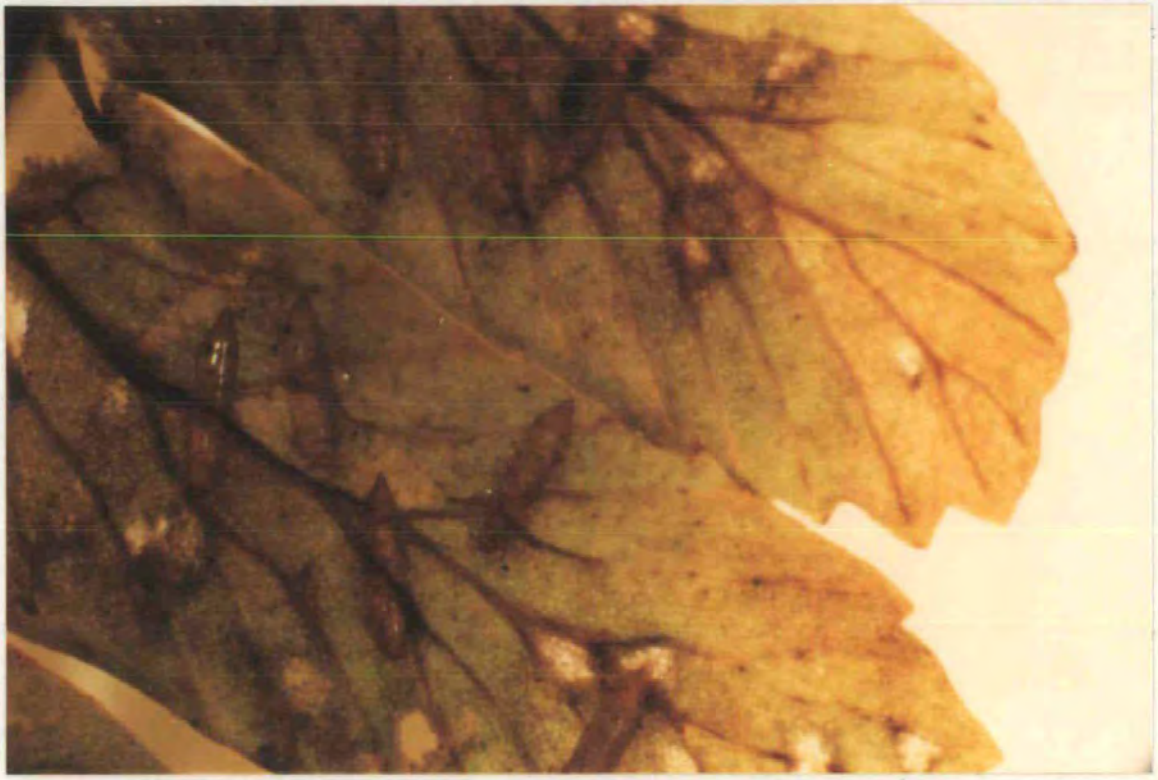


FIGURE 8.5 THE DISTRIBUTION OF OVIPOSITION IN H2. HATCHED AREAS INDICATE THE PRESENCE OF BROAD BUCKLER FERN (DRYOPTERIS AUSTRIACA)



a) Eggs were inserted into the spongy tissue in the middle of the fern pinnae (x21 magnification).

b) The anterior cap of each egg protrudes through the incision made by the ovipositor (x60 magnification)

PLATE 8.2 EGGS OF C.virgo IN FERN PINNAE

a) Healthy eggs with the well developed embryo clearly visible

b) An egg parisitised by a Hymenopteran wasp (Mymaridae)

PLATE 8.3 HEALTHY AND PARISITISED EGGS OF C. virgo

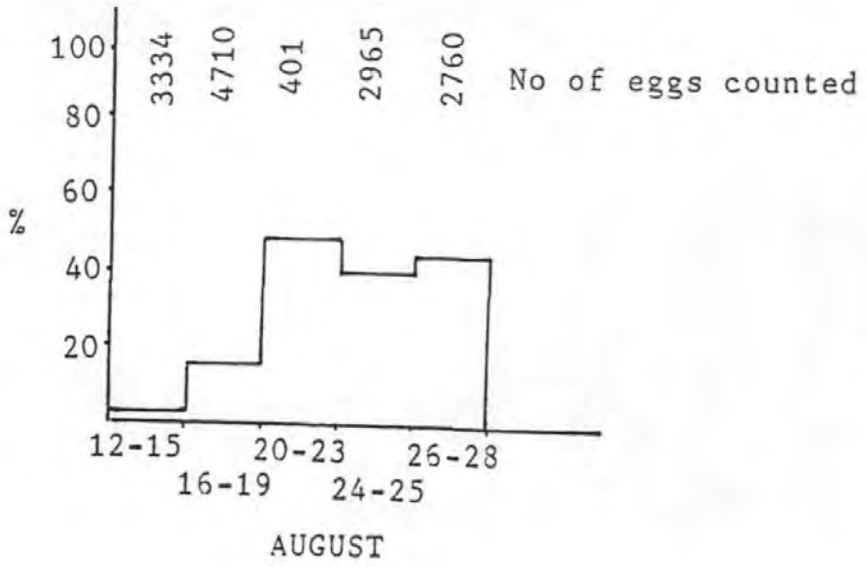


FIGURE 8.6 THE PROPORTION OF EGGS COUNTED WHICH HAD HATCHED

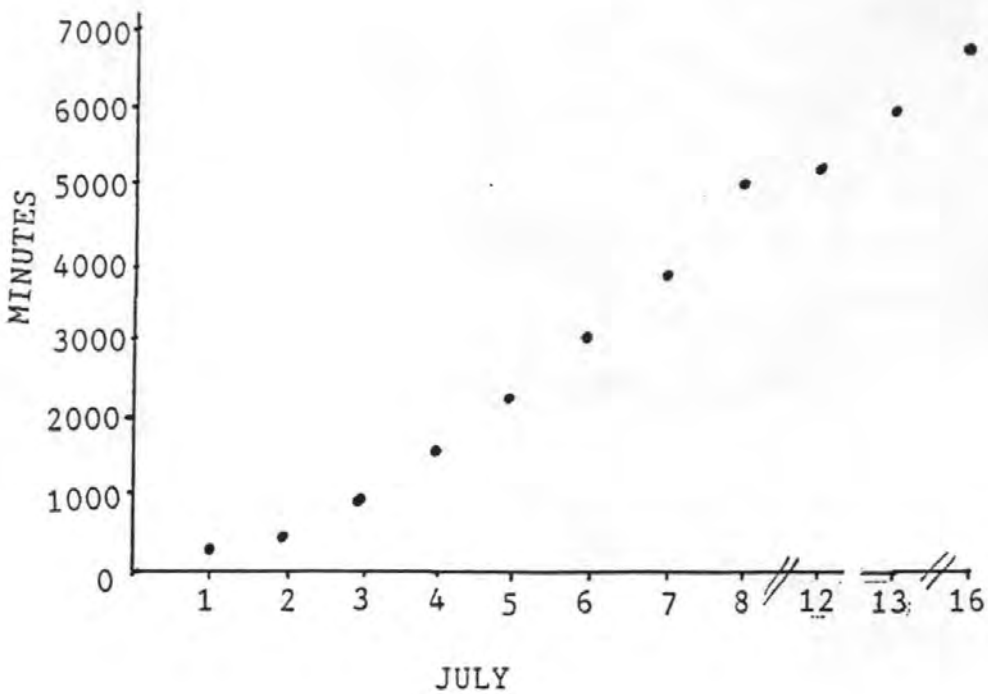


FIGURE 8.7 THE CUMULATIVE NUMBER OF OVIPOSITION MINUTES IN H2
BREAKS IN RECORDING OCCURRED DUE TO POOR WEATHER.

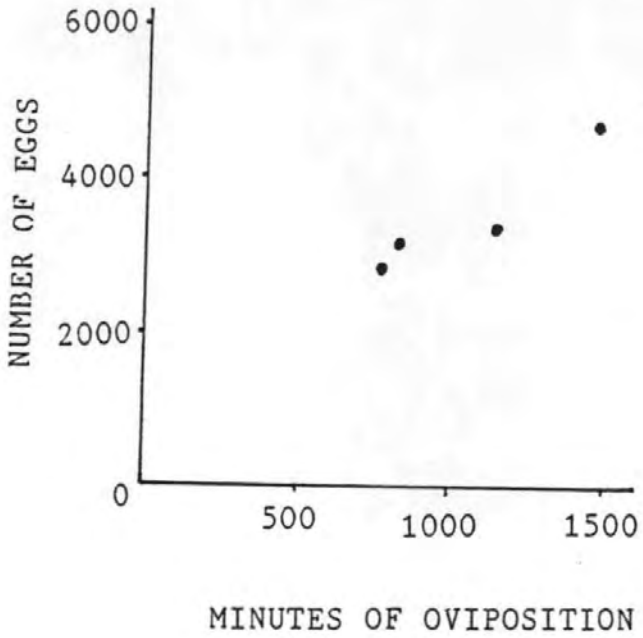


FIGURE 8.8 THE RELATIONSHIP BETWEEN THE NUMBER OF EGGS COUNTED AND THE MINUTES OF OVIPOSITION RECORDED IN FOUR HALF METRE SITES IN H2

to eight weeks. A small number of eggs did not contain obvious embryos, and in order to identify those which were viable, examples of suspect cases were removed for monitoring. In all cases where fungus or parasites were not immediately obvious, development was observed in the embryos.

14,170 eggs were eventually counted in four of the five popular sites. The number of non-viable eggs that were seen was extremely small. Twenty two eggs were infected with a white fungus, and two were parasitised by a tiny Hymenopteran (Mymaridae) (Plate 8.3b). The parasites were found among the 8,000 eggs counted from the 12th-19th of August when only 2-16% had hatched, indicating that few hatched parasites will have been counted as hatched damselflies, and that the incidence of parasitism was genuinely low. When egg counts were compared with the total number of oviposition minutes recorded, estimates of the number of eggs deposited per minute of oviposition range from 2.7 to 3.9 (Figure 8.8), with an average of 3.4 ± 0.84 (mean with 95% confidence limits)

8.4.3 Discussion

The accuracy of the estimate of the rate of egg production will depend largely on the accuracy of recording the oviposition in each site, since eggs were very easy to count. The number of oviposition bouts that are missed will depend on the relationship between the periodicity of sampling and the true range of oviposition duration, and an idea of this will be given by the number of samples in which females are seen. In an ideal situation all females will have been seen in more than one sample, indicating that the

periodicity of sampling was less than the shortest oviposition bout. As the periodicity of sampling increases relative to the true range of oviposition duration, the number of females seen for only one sample will increase and a significant proportion of shorter oviposition bouts will be missed. Only 29% of females in this study were seen for one sample, indicating that the periodicity of sampling was much less than the true average duration of oviposition, and that few oviposition bouts were missed. As a result the rate of egg production will not be greatly over-estimated.

Other estimates of average rates of egg deposition into plant material are considerably higher than that found here. Martens (1992) found average rates of 6.43-9.43 eggs per minute for Platycnemis pennipes, and Waage (1978) found average rates of 7-10 eggs per minute for C.maculata. The difference between these and the rate recorded here will be largely due to differences in the method of recording oviposition duration and egg number. In both Waage's and Martens's studies oviposition duration was measured accurately from the start of a bout of egg laying to the end, and eggs were counted when at a very early stage of development. In contrast the duration of oviposition recorded here also included mating times and movements of females from one site to another, and the eggs counted were mostly well developed and close to hatching. The number of eggs present at a late stage of development does not represent the number of eggs initially laid, since a proportion of these will have disappeared in the seven to eight week development period. Occasionally egg shaped scars were seen in the fern tissue,

where eggs may have been preyed upon, parasitised or decayed having failed to develop. Assuming that there would be little mortality in the late stages of development, the number of eggs counted in this study is equivalent to the number of first instars produced. The estimate of production obtained here is therefore best described as the number of first instars produced per minute of oviposition behaviour, and as such is not directly comparable to the estimates of egg deposition rate obtained for P.pennipes and C.maculata. A better comparison of the fecundity of the two Calopteryx species is given by the number of eggs/first instars produced per clutch, and this is very similar (see section 8.5), adding support to the estimates of oviposition duration and egg counts made in this study.

In the above studies rates of egg deposition were very variable, ranging from 3.85 to 8.68 eggs per minute for a single female of P.pennipes, and 3.4 to 17.3 eggs per minute for C.maculata. One of the reasons for this variation was differences in the suitability of plant species for oviposition. Both Martens and Waage report that in plants with a low rate eggs could only be placed in certain areas, usually in the stems or close by, indicating that thickness of the leaf is an important factor. Martens also reported that females tended to avoid plants with a low deposition rate, and the distribution of eggs in D.austriaca in this study and its avoidance by females strongly suggests that it was unsuitable as oviposition material. It is possible that all the plants used here were less suitable for oviposition compared to those used in other studies, and consequently may

have contributed to the lower average rates reported.

The estimate of hatching time obtained here is longer than the four weeks observed for a population of C.virgo in the New Forest (Corbet 1957), and the difference is likely to be due to differences in temperature (Pilon et al 1989). In this study the hatching time will have been influenced by the temperature at which samples were stored.

8.5 THE DISTRIBUTION AND BEHAVIOUR OF OVIPOSITING FEMALES

8.5.1 The distribution of oviposition in the Leat and experimental area

Observations of marked females indicated that most females were present in the experimental area during the oviposition period, either feeding or ovipositing, on each day they were known to be alive (Figure 8.9). Since only casual observations of feeding females were made, when females were not recorded for one day it is quite likely that they were missed when feeding. Only two females were missed on more than one day. Female 34 was not seen on three out of eight days, but she oviposited on each of the five days when she was seen and it is likely that at other times she was missed while feeding. Female 85 was not seen for six out of nine days, and since it is very unlikely that she would have been missed for so many days, a significant amount of her time was probably spent elsewhere. Ovipositing females were rarely seen during checks on nearby sunny areas of the Leat. There was also no sign that females were moving between the experimental area and other areas of the leat within each

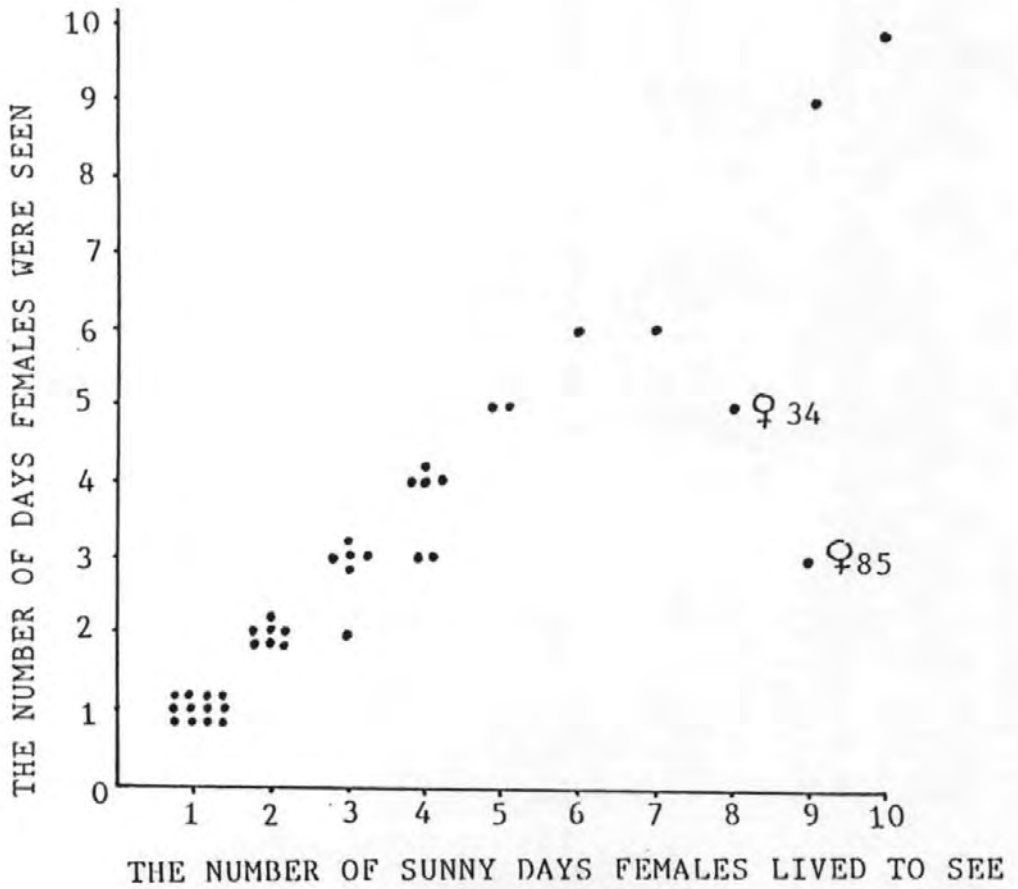


FIGURE 8.9 THE RELATIONSHIP BETWEEN THE NUMBER OF DAYS WHEN MARKED FEMALES WERE SEEN IN THE EXPERIMENTAL AREA, AND THE NUMBER OF SUNNY DAYS THEY LIVED TO SEE.

oviposition period, had movement been occurring breaks in oviposition would have been frequently recorded as females came and went, yet breaks were only observed in eight out of 104 records of daily oviposition, and these are easily attributable to recording error.

Within the experimental area oviposition was confined to the artificial oviposition patches; no oviposition was observed in the six metres of trimmed bank that existed between the patches; also females rarely crossed over to oviposit in the plentiful vegetation of the north facing bank, which was in the shade until well after the end of the typical oviposition period. Females made more visits to the H patches than L patches, but also visited H2 more frequently than H1 (Figure 8.10a). There was little difference in the time that each female spent in the H patches, but slightly less time was spent in the L patches (Figure 8.10b). Putting frequency and duration of visits together, the average daily total oviposition minutes in H2 was significantly greater than in H1, which in turn was significantly greater than in both L1 and L2 (Table 8.1). An examination of the distribution of oviposition within the H patches showed that it was significantly aggregated on a half metre scale in both H1 (mean to variance ratio=41.911,$p<0.001$), and H2 (mean to variance ratio=94.877, $P<0.001$).

8.5.2 Clutch size and the behaviour of individual females

Most females began ovipositing in territories immediately on arrival, and were forcedly removed for mating by the territorial male. After mating females returned to the

territory they had been taken from. Some females were able to arrive at oviposition sites unnoticed. These would not necessarily escape the attention of the male however, since on a number of occasions, when no new females had arrived for a while, males were seen to mate with females who were currently ovipositing. Observations of marked females showed that this would sometimes be a previous mate. Females were sometimes stolen from a territory by a neighbouring or non-territorial male, and successful matings followed. On release, however, females returned to the territory they were taken from, and if spotted by the owning male would be mated again before continuing with oviposition. Non-territorial males sometimes attempted to court feeding females, but no successful matings were seen. Females were involved in oviposition behaviour for an average of 58mins each day, with 95% confidence limits from 56.4 to 59.6mins (Figure 8.11). Assuming an average rate of first instar production of 3.4 per minute, females produced on average 192-203 first instars from each daily clutch of eggs. The variance between individual average oviposition duration was low (variance = 25.44, variance to mean ratio = 0.65), but there was a wide range in daily oviposition, with some females ovipositing for only 20mins but others up to 165mins, equivalent to the production of 561 first instars.

A large proportion of females, 58%, only visited one territory on each day of oviposition, although females were seen to visit up to four territories (Figure 8.12a). Since the size of territories differs, a more accurate picture of the number of different sites in which females oviposited is

given by the number and range of metre sites visited. 84% of females oviposited in just one or two different metre sites, 66% staying within a one to two metre range (Figure 8.12b and c). One third of females, however, covered greater distances each day, up to a maximum of twenty eight metres.

In order to see whether females tended to return to the same territory sites or areas to oviposit, the cumulative number of different territory and metre sites visited, and the total range covered, on successive days of oviposition was calculated. Figure 8.13 shows that the majority of females visit new sites and increase their range each day, although after day 5 the data are dominated by the behaviour of a few long lived females. By the 5th day females had visited on average to 4.7 territory sites involving six different metre sites over a range of 16-20m. There is a great deal of variation in female behaviour, some having visited 7 territory sites and covered the entire range of the experimental area by the 5th day whereas others repeatedly return to favoured sites.

There were frequent changes in the identity of males in control of territory sites. As a result the number of males which females oviposited with, and probably mated with, on successive days of oviposition was not always the same as the number of territory sites visited. Figure 8.14 shows that most females oviposit with new males each day. By the 5th day females had oviposited with 4-9 males. One female which repeatedly returned to three territory sites over nine days oviposited with eight different males.

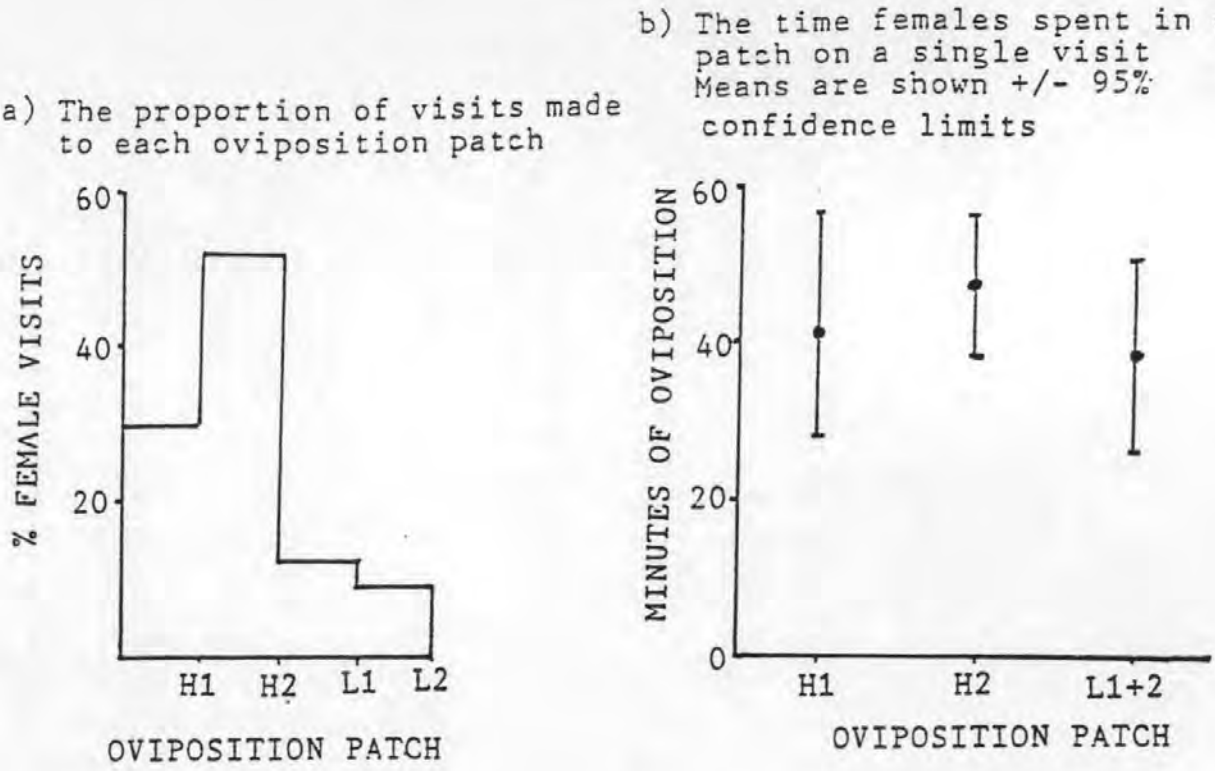


FIGURE 8.10 THE RESPONSE OF FEMALES TO THE ARTIFICIAL OVIPOSITION PATCHES

Oviposition Patch	n	Mean Daily Oviposition Minutes	U	P
H1	10	350	26	0.003
L1+2	10	60		
H2	10	660	16	0.032
H1	10	350		

TABLE 8.1 A MANN-WHITNEY U TEST OF THE DIFFERENCE IN TOTAL DAILY OVIPOSITION MINUTES BETWEEN THE OVIPOSITION PATCHES. H AND L REPRESENT HIGH AND LOW DENSITY OVIPOSITION PATCHES, n REPRESENTS NUMBER OF SAMPLE DAYS.

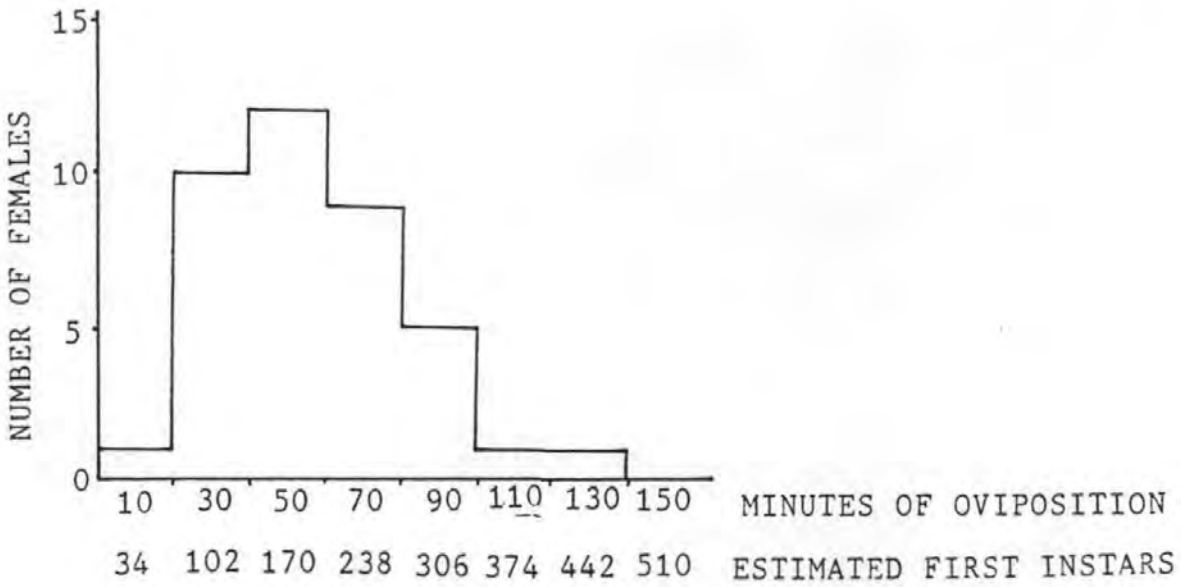


FIGURE 8.11 THE AVERAGE DAILY CLUTCH SIZE OF FEMALES, MEASURED IN TERMS OF OVIPOSITION MINUTES AND RESULTING FIRST INSTARS

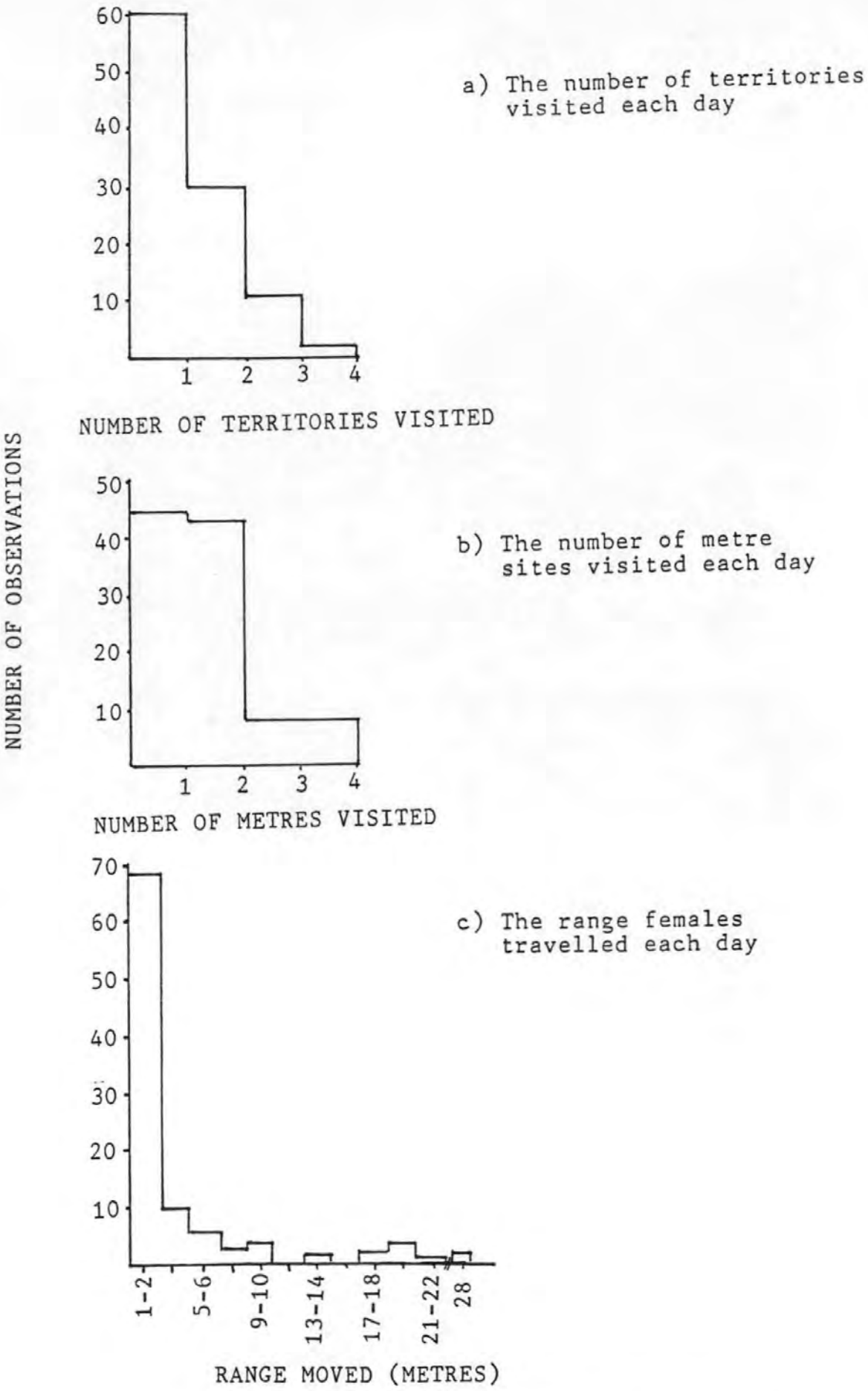


FIGURE 8.12 THE DAILY BEHAVIOUR OF INDIVIDUAL FEMALES

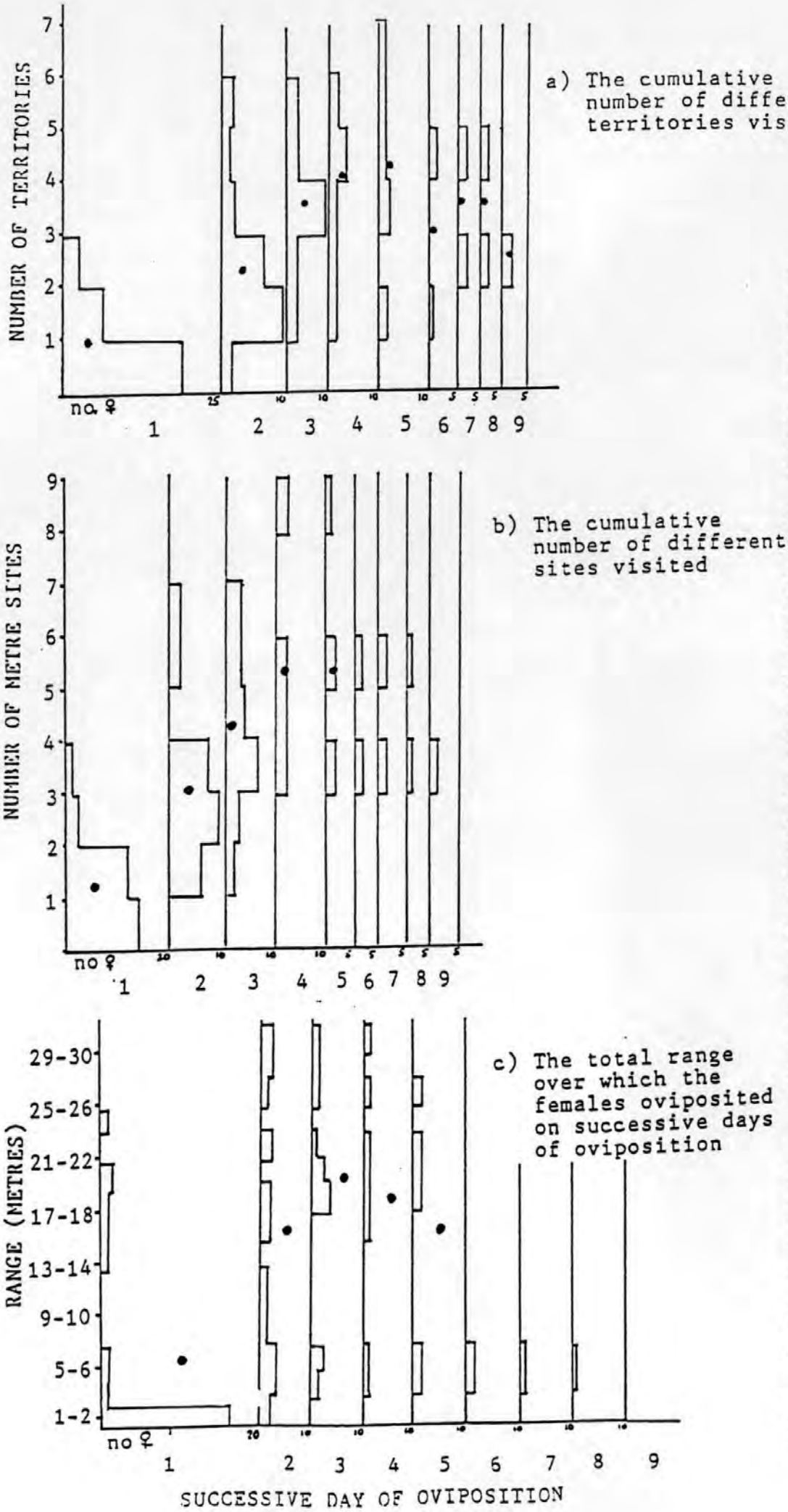


FIGURE 8.13 THE BEHAVIOUR OF FEMALES ON SUCCESSIVE DAYS OF OVIPOSITION. BLOCKS REPRESENT THE CUMULATIVE NUMBER OF TERRITORIES, METRE SITES AND RANGE VISITED, AND POINTS REPRESENT THE AVERAGE VALUE.

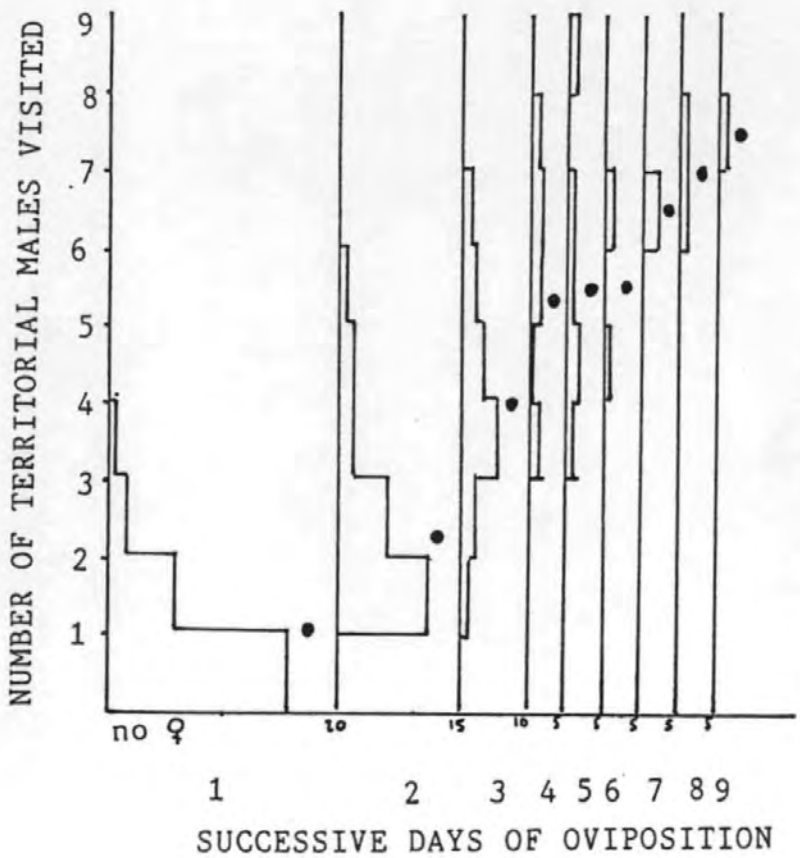


FIGURE 8.14 THE CUMULATIVE NUMBER OF DIFFERENT TERRITORIAL MALES WHICH FEMALES OVIPOSITED WITH ON SUCCESSIVE DAYS OF OVIPOSITION

8.5.3 Discussion

The experimental design was successful in concentrating oviposition in the experimental area. It was confirmed that females choose to oviposit into vegetation at the water's edge which is in full sunlight, indicating the importance of maintaining an optimum body temperature for oviposition. Egg deposition rates can be influenced by temperature (Fincke 1985), and it could be advantageous for females to produce their clutch as quickly as possible in order to resume feeding, since it has been shown that the time spent feeding between clutches can influence clutch size (Banks and Thompson 1987b).

Patches containing a high density of potential oviposition sites attracted significantly more oviposition each day than those with a low density of sites. Similar results have been found for other Calopteryx species, where a greater number of oviposition sites within territories attracted more oviposition in C.maculata (Alcock 1987), and larger oviposition patches attracted more oviposition in C.maculata, Calopteryx amata and C.aequabilis (Meek and Herman 1991). In contrast, Waage (1987) found that levels of oviposition were not significantly related to oviposition patch size in C.maculata, because individual females chose to oviposit with other females in preference to choosing a large patch, and other factors such as territory position also influenced female choice. Differences in the results between the above experiments will reflect differences in the distribution of oviposition sites offered (Meek and Herman

1991). Waage offered only subtle differences in oviposition patch size, whereas differences in the density of oviposition sites presented in this experiment were considerable, and reflected the variability in the distribution of natural oviposition sites along the Leat.

In addition to the difference in daily oviposition between high and low density patches in this study, there was also a significant difference in amount of oviposition occurring between the two patches with an equally high density of oviposition sites. It has been shown in section 8.4 that the distribution of oviposition within a patch is influenced by the fern species present in each half meter, with females avoiding D.austriaca. The H1 patch contained more D.austriaca than the H2 patch, and it seems likely that this resulted in the higher levels of oviposition in H2. These results show that when a natural range of oviposition material is present, the distribution of females will be influenced not only by the quantity of vegetation but also the suitability of the vegetation for oviposition.

Waage (1987) has clearly shown that ovipositing females are attracted to one another, and from the results of his experiments suggests that such aggregations may be largely random. He suggests that the primary selective advantage deriving from female aggregation is that it allows incoming females to benefit from the male mate-guarding of previous mates. Day to day aggregations were also casually observed in this study, but when data were pooled over the study period the aggregation was not random, but resulted in oviposition

being concentrated in the most suitable fern for oviposition. Females, although able to judge the quantity of vegetation in a territory visually, would be unable to judge its suitability for oviposition unless they actually tested it. Finding suitable vegetation could take a lot of time, and it seems likely that the aggregation behaviour enables females to locate suitable vegetation quickly. Such behaviour could be particulary important given the advantages to clutch size in producing previous clutches as quickly as possible (see above), and the unpredictability of suitable weather for oviposition.

The within-patch aggregation shown by females was on a smaller scale than the territory sizes, and occurred despite continual changes in territory ownership, confirming that the distribution of females was influenced primarily by oviposition sites, and not the identity of the males.

Females were surprisingly immobile each day, although this lack of movement may reflect the distribution of oviposition sites provided. The artificial oviposition patches mimic the natural situation where fern fronds fall into the water and oviposition sites are locally abundant, but stretches having few sites occur between them. Females searching for oviposition sites attract a lot of unwanted attention from both territorial and non-territorial males, and much time can be wasted escaping them. It is therefore likely to be advantageous for females to remain in one territory if enough oviposition sites are present. Studies of C.maculata indicate that unrestricted ovipositing females

Daily Clutch Size			
Species	Average	Maximum	Measure
Calopteryx virgo	192-203	561	First instars resulting from each clutch.
C. maculata (Waage 1978)	230-328	525-750	Eggs laid each day
C. maculata (Waage 1980)	250-295	598	Oocytes in ovariole before oviposition.
Coenagrion puella (Banks & Thompson 1987b)	100-400	-	Population range of mature eggs in ovariole before oviposition.
Enallagma hageni (Finke 1986)	377	-	Eggs laid each day.
E. ebrium (Forbes & Baker) (1991)	323	-	Mature eggs in ovariole.

TABLE 8.2 MEASURES OF DAILY CLUTCH SIZE FOR ZYGOPTERA WITH ENDOPHYTIC OVIPOSITION

were also relatively immobile, and did not move out of a 15 metre area each day (Waage 1978, 1980).

Despite the immobility of females forty two percent probably mated with more than one male each day, and from the number of times females changed territories it can be calculated that 36% of females entering a territory are likely to have mated with another male that day. Most females oviposited and potentially mated with new males on successive days of oviposition. Studies on the amount of sperm which females carry, suggest that on entering territories to begin oviposition each day, females still carry 65% of viable sperm from the previous mating and do not need to re-mate to continue oviposition (Waage 1980). It seems likely that, as suggested by Waage, females are obliged to re-mate in order to gain access to good oviposition sites, and this is supported by the observations here that most females were forcedly removed for mating.

On average 180-224 first instars resulted from each day of oviposition, and this is similar to the clutch sizes reported for other zygopterans with endophytic oviposition (see references in Table 8.2). The large variation in the day to day oviposition duration seen here seems to be typical of Calopteryx, since this has also been noted in C.maculata (Waage 1978).

8.6 THE DISTRIBUTION AND BEHAVIOUR OF MALES, AND THE POTENTIAL NUMBER OF EGGS FERTILIZED

8.6.1 Territorial behaviour and the distribution of males in the population area

Table 8.3 shows that territorial males were concentrated in the experimental area where the majority of oviposition took place. Territorial males were generally easy to distinguish from non-territorial males by their site attachment and site defence, which usually lasted at least one day. In a few cases, however, males showed territorial behaviour for only a very short period of time, such as one or two samples. Males were therefore arbitrarily defined as territorial if they were seen showing territorial behaviour in the same place for two or more consecutive samples. This rigid definition of territoriality could not be made for males outside the experimental area, and for these males territoriality was assigned more subjectively. A total of seventy nine mature males were seen, of which sixty one were seen in the experimental area. A third of the latter were first seen as mature males outside the experimental area, moving into it after one to two days. Only two males which had been territorial in the experimental area were later seen outside it. Non-territorial males in the experimental area were more mobile, however, and interchanged with the group of males outside the experimental area.

Much territorial fighting took place before oviposition and recording began, but territorial disputes continued throughout the oviposition period. Disputes with neighbours

		LEAT SECTION									
		Experimental Section									
		A	B	C	D	E	F	G	H	I	J
JULY	1					1	7	0	0	0	0
	2						8				
	3					4	11	0	4		
	4	2	1	0	0	6	10	1	2	0	0
	6					3	11	4			
	7	0	1	0	0	3	10	1	1	1	0
	8					4	10	2			
	12	0	0	0	0	1	11	0	0	0	0
	13					7	13	1	0		
	16					3	12	0	0	0	0

TABLE 8.3 THE NUMBER OF TERRITORIAL MALES IN EACH LEAT SECTION ON EACH SUNNY DAY FROM 1-16 JULY. AREAS WHICH WERE NOT SAMPLED HAVE BEEN LEFT BLANK.

were brief, but protracted fights with non-territorial males were common, and often continued intermittently for hours. These protracted fights sometimes resulted in the non-territorial male pushing out the resident male, or taking up a new territory in between existing ones. Actual physical contact between fighting males, rather than chasing and displaying, was rare. As described in the previous section, non-territorial males and neighbouring territorial males occasionally stole females from other territories.

8.6.2 Territory Size In The Experimental Area

Territory sizes were measured as described in Chapter Seven, and ranged in size from half a metre to six metres (Figure 8.15). Territories in H2, with a median size of 1.0 metre were significantly smaller than those in H1, where the median size was 2.5 metres (Mann Whitney U = 1098.5, P = 0.001). There was no difference between the median territory sizes of 3.0 metres and 3.5 metres in L1 and L2 respectively (Mann Whitney U = 162.5, P = 0.522), but territories in H1 were significantly smaller than those in both L patches (Mann Whitney U = 779.5, p = 0.009). As a result of the difference in territory sizes the H2 patch typically supported four to six territorial males, the H1 patch two to three territorial males and the L patches one to two territorial males. Figure 8.16 shows that there was a significant negative relationship between territory size within a patch and levels of oviposition in that patch (b=-1.41, F=24.62, P=0.000), demonstrating that territories were larger in patches with less oviposition.

Figure 8.17 shows that the number of territorial males in all patches remained very constant despite increases in the number of non-territorial males: there was no significant increase in the daily maximum number of territorial males as the total number of males seen each day increases ($b=0.303$, $F=3.16$, $P>0.05$), but there was a significant increase in the number of non-territorial males ($b=0.708$, $F=15.4$, $P<0.01$). The number of non-territorial males seen in each patch and the frequency with which they were seen, indicates that there was pressure from non-territorial males in all patches (Figure 8.18).

8.6.3 The Estimated Number Of Eggs Fertilised Each Day

The daily reproductive success of individual males was measured as the number of oviposition minutes occurring in each territory, and from this an estimate of the potential number of eggs fertilised can be made (the paternity of eggs laid in each territory is discussed in section 8.6.5). The daily reproductive success of non-territorial males will have been low, and in the absence of any measure is here considered to be zero. Figure 8.19 shows that daily reproductive success was very variable between males (variance = 140.4, variance to mean ratio = 1.25), with many males potentially fertilizing fewer than 200 eggs, but others potentially fertilizing up to 2,400 eggs.

The location of territories had a significant effect on the daily reproductive success of territorial males, as shown by the results of Mann-Whitney U test in Table 8.4. There was no difference between males territorial in the H patches,

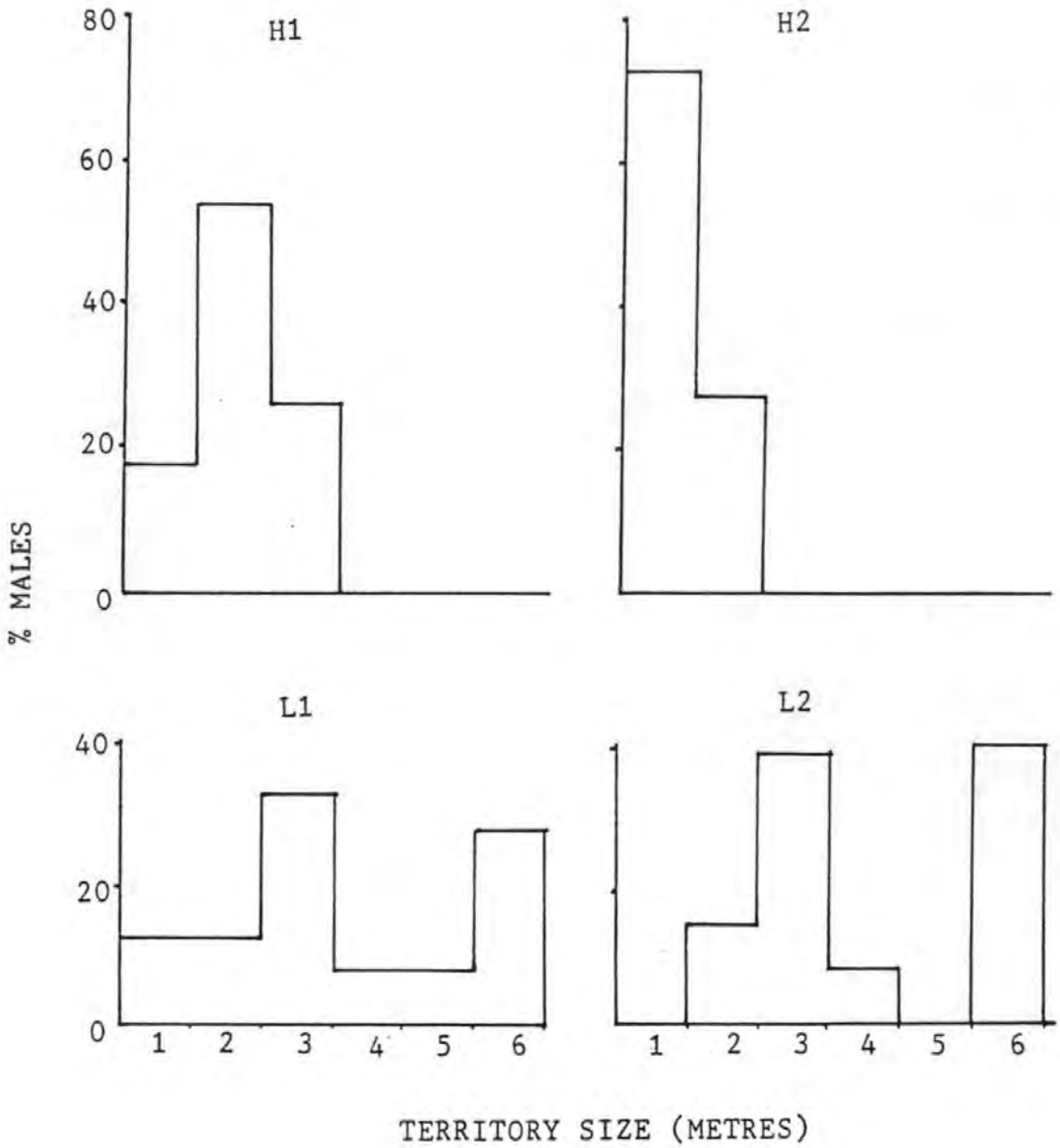


FIGURE 8.15 TERRITORY SIZES IN EACH OF THE ARTIFICIAL OVIPOSITION PATCHES

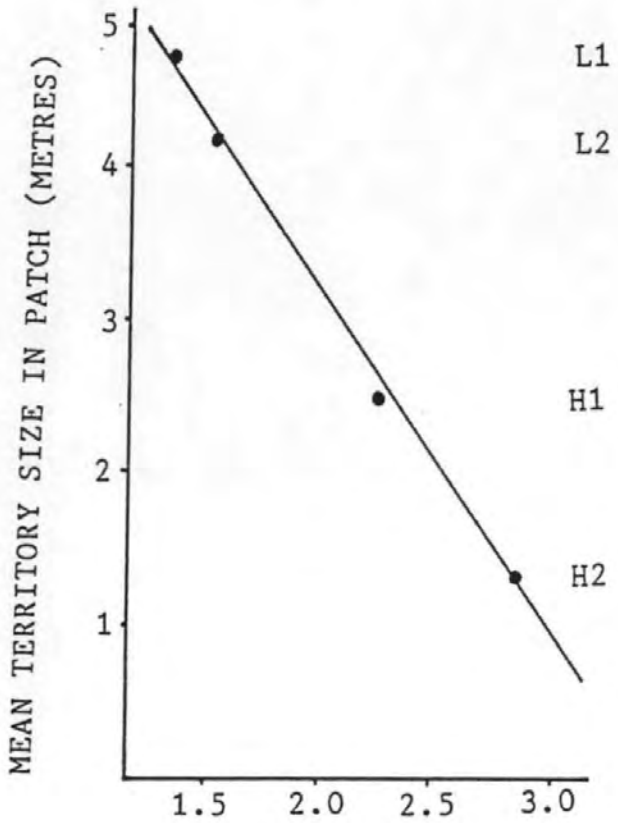


FIGURE 8.16 THE RELATIONSHIP BETWEEN TERRITORY SIZE AND THE AMOUNT OF OVIPOSITION OCCURRING IN EACH PATCH

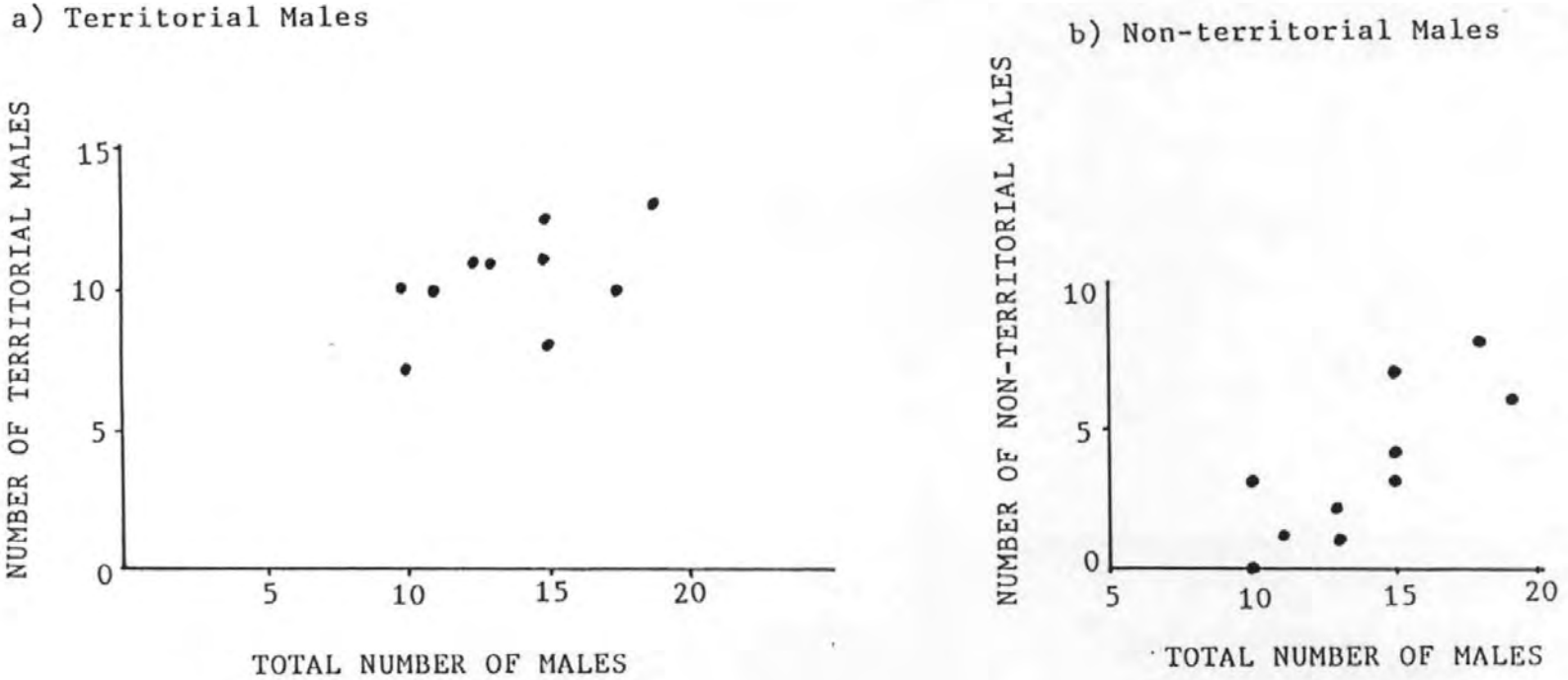


FIGURE 8.17 THE CHANGE IN THE NUMBER OF TERRITORIAL AND NON-TERRITORIAL MALES AS THE TOTAL NUMBER OF MALES INCREASED. DATA TAKEN AS THE MAXIMUM NUMBER OF MALES SEEN ON EACH DAY OF RECORDING.

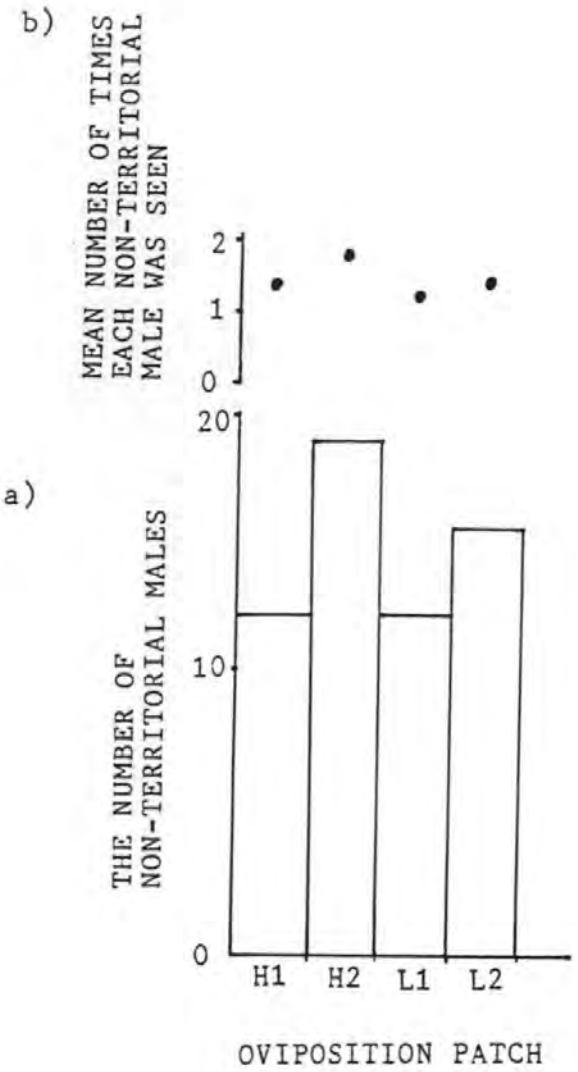


FIGURE 8.18 THE INTEREST THAT NON-TERRITORIAL MALES SHOWED IN EACH OVIPOSITION PATCH MEASURED IN TERMS OF a) THE NUMBER OF NON-TERRITORIAL MALES SEEN EACH DAY, SUMMED OVER THE OVIPOSITION PERIOD, b) THE AVERAGE NUMBER OF TIMES EACH WAS SEEN.

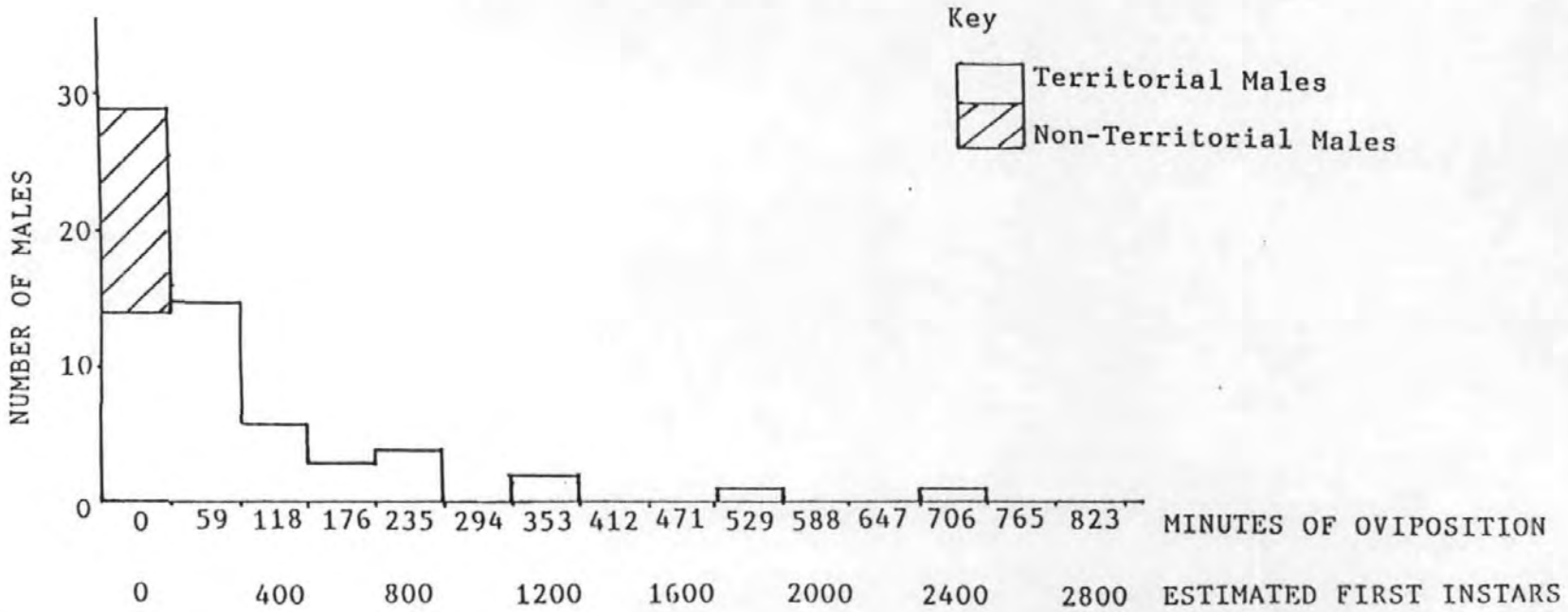


FIGURE 8.19 THE AVERAGE DAILY REPRODUCTIVE SUCCESS OF MALES MEASURED IN TERMS OF THE ESTIMATED NUMBER OF OVIPOSITION MINUTES OCCURRING IN EACH TERRITORY, AND THE POTENTIAL NUMBER OF EGGS FERTILISED.

Oviposition Patch	n	Daily Oviposition Minutes In Each Territory Median	(Mean)	U	P
H1	21	64.1	(132)	663.5	0.684
H2	44	70.6	(141)		
L1	13	25.0	(32)	158.5	0.397
L2	13	30.0	(44)		
H1+2	65	67.1		777.0	0.0002
L1+2	26	26.0			

TABLE 8.4 MANN-WHITNEY U TESTS OF THE DIFFERENCES IN MEDIAN DAILY REPRODUCTIVE SUCCESS OF MALES TERRITORIAL IN H AND L OVIPOSITION PATCHES.

with median values of oviposition minutes of 64-70, corresponding to 218-240 eggs potentially fertilised each day. Similarly there was no difference between males territorial in the L patches, with median values of oviposition minutes of 16-30, which corresponds to 85-102 eggs potentially fertilised each day. There was, however, a significant difference between the daily reproductive success typically experienced by males in the H and L patches.

8.6.4 The Duration Of Mating

Figure 8.20 shows that mating times varied widely between around 30 seconds and 5 minutes 30 seconds. Part of this variation is due to significant differences in mating duration between males territorial in different patches (Table 8.5). It was necessary to pool data from the two L patches because the number of recorded matings there was so low. Males from H2 where there was most oviposition mated for the shortest time, typically 60 seconds, while those from the L patches with least oviposition mated for the longest time, typically 120 seconds. On three occasions when males from the H2 patch stole females from neighbouring males the duration of mating was recorded, and averaged 195 seconds, much higher than that recorded for males mating with incoming females. These three records were not included in the H2 group in Table 8.5.

8.6.5 Discussion

Males were concentrated in the experimental area where competition for territories was often intense, occasionally resulting in the death of one of the combatants. Territory

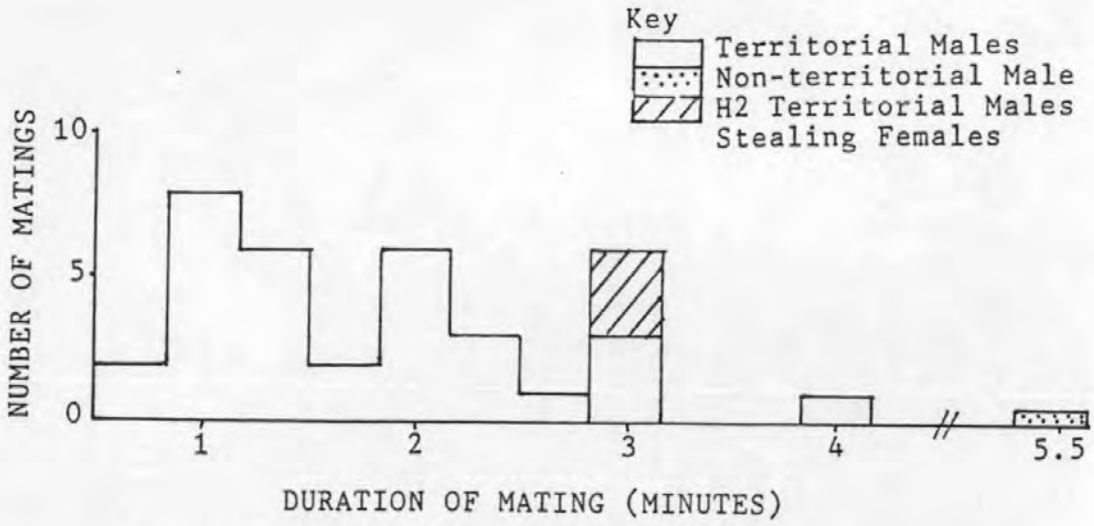


FIGURE 8.20 THE DURATION OF MATING

Oviposition Patch	n	Median (secs)	Average Rank	Z	H	p
H2	12	60.0	11.0	-2.41		
H1	14	92.5	17.5	0.83	7.633	<0.05
L1+L2	5	120.0	23.7	2.07		
Overall	31		16.0			

(H adjusted for ties)

TABLE 8.5 A KRUSKAL-WALLIS TEST OF THE DIFFERENCE IN MATING DURATION BETWEEN MALES TERRITORIAL IN H AND L OVIPOSITION PATCHES.

size reflected the distribution of females, with more males taking up smaller territories in patches with most oviposition, and this seems to be typical for this species and genus (Pajunen 1966, Alcock 1987, Meek and Herman 1991). Territory size was not, however, simply a passive consequence of the number of competing males. Territory sizes in all patches were usually almost constant despite fluctuating numbers of non-territorial males, with males holding larger territories in poorer patches actively defending these against non-territorial males. The degree of stability observed in territory sizes is likely to depend on the increase in male density which is witnessed. Both Buchholtz (1955) and Zahner (1960) report territory sizes in Calopteryx decreasing over time as male density increases. In the present study high numbers of mature males were present as soon as good weather and breeding behaviour began, and the observed stability in territory size is likely to be the consequence of a saturation point having been reached very early on in the breeding period.

There was a great deal of variation in the average daily reproductive success achieved by mature males, and this was significantly higher than the variation in the average clutch size of females ($F=5.157$, $df=45,38$, $P<0.01$). The high variability in male daily reproductive success was due to differences in territory quality, as well as to some males being unable to obtain territories.

The daily reproductive success of territorial males in each patch resulted from the interaction of territory size

and female distribution. Although the two H patches had different levels of oviposition, males which held territories in these two patches typically achieved the same high levels of daily reproductive success as a result of differences in territory size. Males from the L patches, despite defending very large territories, did significantly worse. In this study therefore some territorial males were achieving higher daily reproductive success than others. Meek and Herman (1991) presented Calopteryx males with oviposition patches which differed in size but not in the density of oviposition sites. Single males of C.maculata and C.amata were not able monopolise large patches, leading the authors propose that in Calopteryx the female 'resource' will be equally distributed between territorial males in an 'ideal free' system. The difference in the results of the two experiments is due to the differences in the distribution oviposition sites offered to males and females. While an 'ideal free' distribution of males and females was present to an extent in this study, the results here show that when there is sufficient variation in the distribution of oviposition sites and ovipositing females, some males do very badly.

Following a field experiment Waage (1987) has suggested that it would be difficult for Calopteryx territorial males to predict female distribution on any one day, since the distribution of oviposition sites was only one of several factors which may influence this, and because the tendency for ovipositing females to be attracted to one another introduces a random element. He therefore proposed that it is unlikely that territorial males can control their daily

reproductive success, and it follows that there would be little opportunity for some to compete more successfully than others. The consistent differences in the size and quality of territories between H and L patches clearly shows that males in this experiment could predict and profit from variations in female distribution. Again the difference in conclusions from the two experiments is likely to be due to differences in the distribution of oviposition sites offered, since Waage offered only subtle differences in oviposition patch size. The response of females to the oviposition sites in this study also suggests that short-term aggregations, although appearing random, may relate to vegetation suitability (see section 8.5.3). Although it seems unlikely that males would be able to predict the suitability of vegetation for oviposition, it seems likely that they could learn where females tend to aggregate either during initial spells as non-territorial males or by moving from unpopular sites. This learning ability is demonstrated by the greater interest which non-territorial males showed in the H2 patch which, although having the same density of oviposition sites as H1, was more popular with females.

The results of this and other experiments suggest that the ability of some territorial males to monopolise a disproportionate share of the eggs laid depends on the variability in the distribution of oviposition sites. Observations of breeding behaviour in 1986 strongly suggested that there was a great deal of natural variation in the distribution of oviposition sites of which competitive males could take advantage. Similarly Waage (1979b) reports that in

a natural population of C.maculata 32% of territorial males accounted for 79% of all matings, again indicating that some males were able to take advantage of a patchy distribution of ovipositing females.

Sperm removal mechanisms have been found in several species of Calopteryx, where, during mating, sperm from previous matings is removed (Waage 1979a, Adams and Herman 1991), and this is likely to occur in C.virgo. Waage (1980) has shown that most Calopteryx females arriving to oviposit each day still carry 65% of sperm from previous matings, indicating the advantage to males of sperm removal mechanisms. It has been shown in this study that in addition 34% of females arriving at a territory are likely to have mated with another male that day, further demonstrating the importance of sperm removal to male daily reproductive success. Matings by non-territorial males appeared to be uncommon in this population, although the incidence of these males stealing ovipositing females is likely to have been greater than that recorded. The benefits of such matings are hard to assess since females may be re-mated by territorial males on entering a territory to oviposit. Here, where 97% of oviposition occurred in territories (see Chapter Eight), the daily reproductive success of non-territorial males appears to be very low. Nomakuchi (1988) shows that this is not always the case in the Calopterygidae, however, since in Mnais pruinosa 20% of oviposition occurs outside territories, and a non-territorial colour form of male exists which does as well as the territorial form of male.

It seems unlikely that males in very high quality territories could fertilize all the eggs which are laid there, due to physiological constraints and females arriving unnoticed. Males in poorer territories and without territories increase their share of fertilised eggs by stealing females from males in very popular territories, and by their mates arriving to oviposit in popular territories unnoticed by the owner. Variation in the duration of mating results in variability in the amount of sperm from previous matings which is removed and replaced (Siva-Jothy and Tsubaki 1989a). By mating for longer, less successful males increase the probability that some of their sperm will remain to fertilize some eggs, even if their mate re-mates before ovipositing or before a full clutch has been laid. Unlike the results of this study, Siva-Jothy and Tsubaki (1989a and b) found that in M.pruinosa pruinosa mating time increased only when females were encountered away from the water. They proposed that the main influence on mating time was the likelihood that females would lay a clutch immediately after mating, but here mating time also appeared to be influenced by the likelihood that females would be re-mated by another male before producing all or part of the next clutch. The costs and benefits of investing time in mating, rather than territorial behaviour, are also likely to vary between males depending on their territorial status.

As a result of the above behavioural tactics the reproductive success of Calopteryx males is likely to be more uniform than suggested by the distribution of eggs laid (see also Waage 1979b). Nevertheless, the highly significant

difference in potential eggs fertilized by males in different territories, and the lack of matings by non-territorial males suggest that, despite uncertain paternity, some males were able to compete more successfully than others and hence monopolise a disproportionate share of the eggs laid.

8.7 IDENTIFYING THE IMPORTANT COMPONENTS OF LIFETIME REPRODUCTIVE SUCCESS

8.7.1 Methods

Lifetime reproductive success will be influenced by a number of components that relate to the daily reproductive output of individuals, such as clutch size and daily eggs fertilised, the proportion of adult life during which breeding can take place and the number of days individuals survive to breed. Several analytical methods have been used to quantify the importance of such components, and Brown (1988) notes that all have their disadvantages. Regression and multiple regression look at the proportion of variance in lifetime reproductive success attributable to the various components (for example Banks and Thompson 1987b and Tsubaki and Ono 1987), but do not generally allow the importance of covariance between components to be assessed. Arnold and Wade's (1984) method of partitioning the opportunity for selection through lifetime reproductive success into additive components does allow the separation of covariance and has been used extensively (for example Fincke 1986, Koenig and Albano 1987 and McVey 1988), but Brown notes that there are statistical arguments against its use in situations such as the one here. Brown describes a further method of

partitioning the variance in lifetime reproductive success which utilizes the exact relationship between the variance in lifetime reproductive success and the variances and covariances of its components. His method enables comparison of the proportion of variance in lifetime reproductive success which each component causes, and is one of the methods employed here.

Partitioning of variance is, however, liable to large errors if, as here, the distribution of any components departs markedly from normality (Brown 1988). Also, while the separation of the influence of covariance is possible, the calculation of these terms is complex and their interpretation difficult. In addition to Brown's method, therefore, a second method, which is based on regression analysis but has not previously been used in Odonata, will also be used. Path analysis (Sokal and Rholf 1981) looks at regression relationships between dependent and independent variables, and has the advantage of separating out the influence of covariance between components as simple correlation coefficients whose significance can be judged. Furthermore all relationships contributing to the analysis can be seen and assessed graphically, and the results can be presented in the form of a simple flow diagram.

Both path analysis and partitioning of variance require lifetime reproductive success to be described in terms of its component parts. In its simplest form, lifetime reproductive success will be equal to the product of the number of days on which individuals reproduce and how well they do on average

each day. For females who produce one clutch of eggs each day they return to oviposit this can be expressed as:

$$Et = Cs * Cn$$

where Et is the lifetime total number of eggs produced, Cs is average clutch size, and Cn is the number of clutches produced. Similarly for territorial males lifetime reproductive success can be expressed as:

$$Ft = Fd * Dt$$

where Ft is an estimate of the lifetime total number of eggs fertilised, based on the duration of oviposition in individual territories, Fd is an estimate of the average number of eggs fertilized each day, and Dt is the number of days on which males held territories. Males which died without holding a territory were assumed to have a reproductive success of zero (see section 8.6.5), and were not included in the analysis.

Cn and Dt can be divided into further multiplicative components. Since reproductive behaviour can only take place on sunny days, the number of sunny days adults survive to see is the critical time period in determining reproductive success. The number of clutches females produce will depend on the number of sunny days they survive to see and the rate of clutch production. The lifetime reproductive success of females can now be expressed as:

$$Et = Cs * SD * Rcp$$

where SD refers to the number of sunny days females survive to see and Rcp refers to the average rate of clutch production. Similarly, the number of days on which males hold territories will depend on the number of sunny days they survive to see and the proportion of these days on which they are able successfully to defend a territory. Thus the expression for males is:

$$Ft = Fd * SD * Tp$$

where SD refers to the number of sunny days males survive to see, and Tp refers to the proportion of that time when males successfully defended territories.

The number of sunny days which adults survive to see can be further divided into the number of days adults survived and the proportion of those days which were sunny. There are incomplete data on this for many adults, however, since detailed recording of adult lifespan could only take place during the spell of generally fine weather from the 1st to the 16th of July. Therefore, this further step is not included in the main analysis, but the components of sunny days seen will be considered further where the main analysis suggests that it is of importance.

The following analyses of the above components of lifetime reproductive success were applied:

a) Path Analysis (Sokal and Rholf 1981)

Regression analysis assumes that the sources of variation in the model to be analysed are additive, and in order to satisfy this criterion it is necessary for the data to undergo logarithmic transformation. The coefficient of determination (R^2) gives the proportion of variation in the dependent variable (eg lifetime reproductive success), explained by regression on an independent variable (eg one of the components of lifetime reproductive success). R^2 values of negative relationships are described here as negative proportions. In most natural situations there will be some degree of covariance between independent variables. The proportion of variation in the dependent variables which is explained by joint variation between components is included in the value of R^2 for each component. Where the covariance between components is positive, R^2 values will be enhanced such that sums of component R^2 values will be greater than 100%. If covariance between components is negative, R2 values will be reduced, and the sum of component R^2 values will be less than 100%.

Path analysis breaks down each R^2 value into the independent influence of components and the influence of covariance between components. The method is based on standardized partial regression coefficients derived from a multiple regression analysis. The standardized partial regression coefficient, or path coefficient, gives the average change in standard deviation units of the dependent variable caused by one standard deviation unit of the independent variable, when all other independent variables

are held constant at their means. The path coefficient therefore gives a measure of the importance of an independent variable while controlling for the effect of relationships with other independent variables. In path analysis the relationships between dependent and independent variables are described by path coefficients and the relationships between independent variables are described by correlation coefficients in a flow diagram. R^2 values of any independent variable can be derived directly from the paths connecting them to the dependent variable, enabling all the relationships contributing to it to be understood.

b) Partitioning of Variance (Brown 1988)

This method uses variables which have been standardised by division by their mean (X_s), and is based on the result given by Goodman (1962) that the variance of the product $X_{si}X_{sj}....X_{sn}$ is given by

$$H_i + \sum_{i<j} H_{ij} + \sum_{i<j<k} H_{ijk} + ... + H_{i..n}$$

where the H terms are defined as follows:

$$H_i = V(X_{si})$$
$$H_{ij} = V(X_{si}X_{sj}) - H_i - H_j$$
$$H_{ijk} = V(X_{si}X_{sj}X_{sk}) - H_i - H_j - H_k - H_{ij} - H_{ik} - H_{jk}$$

and $V(X_{si})$, $V(X_{si}X_{sj})$ and so forth represent the variances of the standardized variables, or product of standardized, variables within the brackets.

The variance in lifetime reproductive success can therefore be partitioned into a number of additive terms, each of which can then be expressed as percentages of the total, H'. Each single term (H'_i) represents the proportion of the total variance in lifetime reproductive success that would be achieved if that component alone was allowed to vary, all others being held constant at their means. The joint terms (H'_{ij}, H'_{ijk} and so forth) represent the proportion of variation in lifetime reproductive success that is due to joint variation between the components concerned. The joint terms are complex, involving simultaneous but independent variation (I), and covariance (J). If the components of lifetime reproductive success vary independently, with no covariance between them, then the joint components will simply result from joint independent variation. Joint independent variation can be shown to equal the product of each $V(X_s)$ for each component involved. For example

$$I_{ij} = V(X_{si}) * V(X_{sj})$$

Where there is covariance between the components the joint term will be greater, or in the case of negative covariance less than I. The proportion of the variation in lifetime reproductive success due to covariance between components can therefore be obtained by subtracting the proportion due to independent variation from the proportion due to the joint term as a whole.

$$J_{ij} = H_{ij} - I_{ij}$$

J terms involving three or more components are complex, involving the amplification of pairwise covariance by independent variation in other variables, as well as covariance involving all the variables.

Data from thirty eight females and forty six males were used in the analysis. Data from female 85, who was likely to have oviposited outside the experimental area, were not included. The analysis of males is restricted to those which were territorial in the experimental area at some time in their lives. Since there was little or no oviposition outside the experimental area, males which spent part of their time there were considered to be non-territorial during that time. The proportion of the total variation in male lifetime reproductive success which is due to males which were non-territorial throughout their mature life is examined at the end of section 8.7.2.

8.7.2 Results

a) Females

i)Path Analysis

The path analysis diagram in Figure 8.21 shows that the independent influence of clutch number on total eggs is greater than clutch size, and both these relationships will be slightly enhanced by the weak positive correlation between clutch number and size. The proportion of variation in the dependent variables explained by the components (R^2), is equal to the square of the sum of the product of path coefficients and correlation coefficients along all paths by

which they are connected; with the condition that pathways involving direct correlations (ie one correlation step) between independent variables must be used rather than those involving indirect correlations (ie two correlation steps). The proportion of variation in total eggs explained by clutch number can be described as:

$$R^2_{EtCn} = [0.739 + (0.258 * 0.509)]^2$$
$$= 0.76$$

thus 76% of the variation in total eggs is explained by clutch number, compared to 49% explained by clutch size, and these relationships are shown in Figure 8.22.

When the analysis is continued to look at the importance of the components of clutch number, it can be seen that the independent influence of sunny days seen is far greater than the rate of clutch production. Both relationships with clutch number will be modified by the significant negative correlation between the components. As a result of the weak independent influence of the rate of clutch production on clutch number, and its strong negative correlation with sunny days seen, the rate of clutch production has an overall small, negative influence, accounting for -5% of the variation; whereas the number of sunny days seen still exerts a strong, positive overall influence, accounting for 97% of the variation (Figure 8.23).

The significance of the negative correlation between the rate of clutch production and sunny days seen is enhanced by females who only survived long enough to produce their first clutch. These females must have a rate of clutch

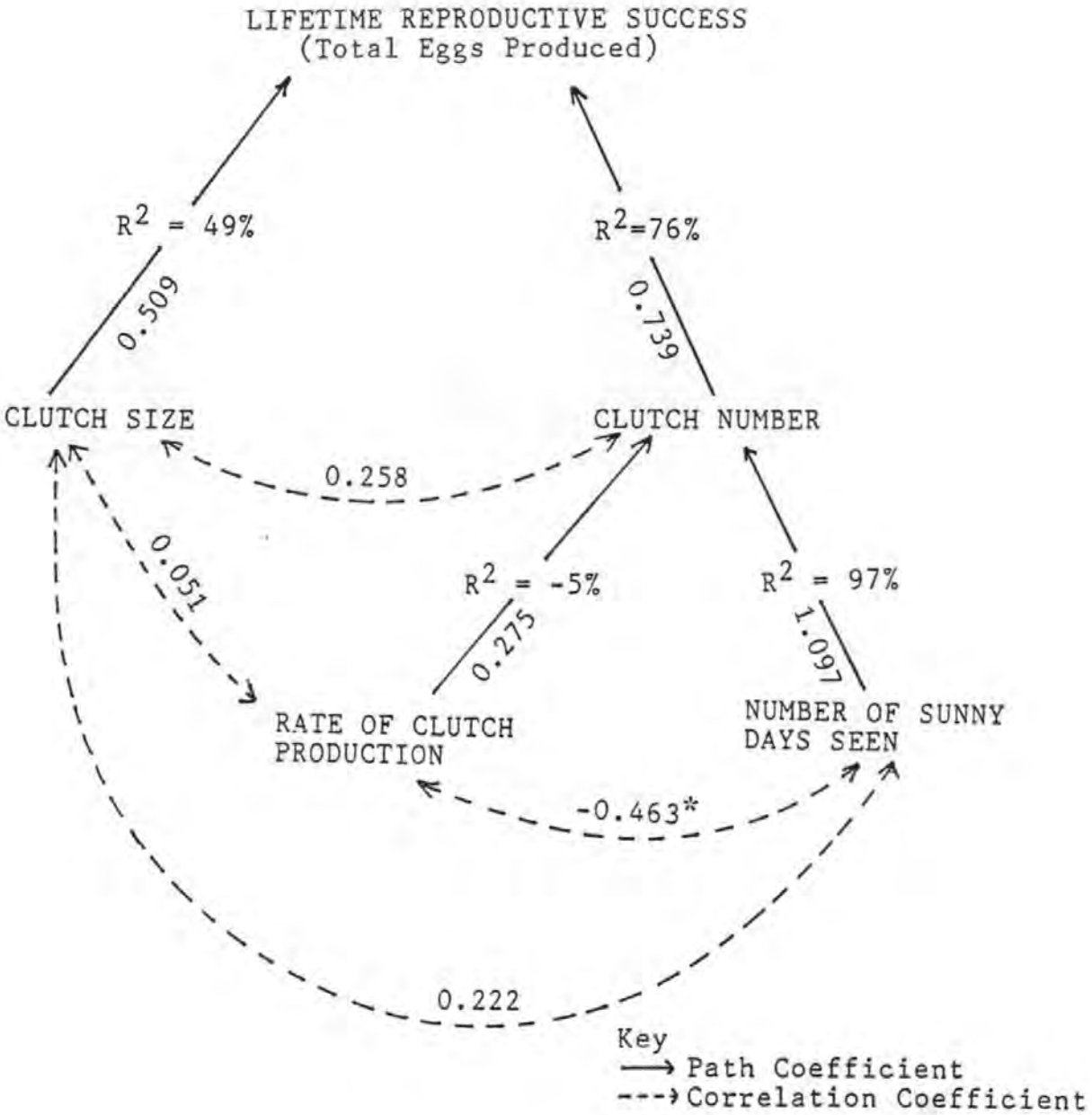


FIGURE 8.21 A PATH ANALYSIS OF THE CAUSAL RELATIONSHIPS IN THE LIFETIME REPRODUCTIVE SUCCESS OF FEMALES. PATH COEFFICIENTS SHOW THE INDEPENDENT INFLUENCE OF COMPONENTS, AND R^2 THE PROPORTION OF VARIANCE EXPLAINED BY EACH COMPONENT WHEN CORRELATION BETWEEN COMPONENTS IS INCLUDED. * DENOTES A CORRELATION COEFFICIENT WHICH IS SIGNIFICANT AT $P<0.05$.

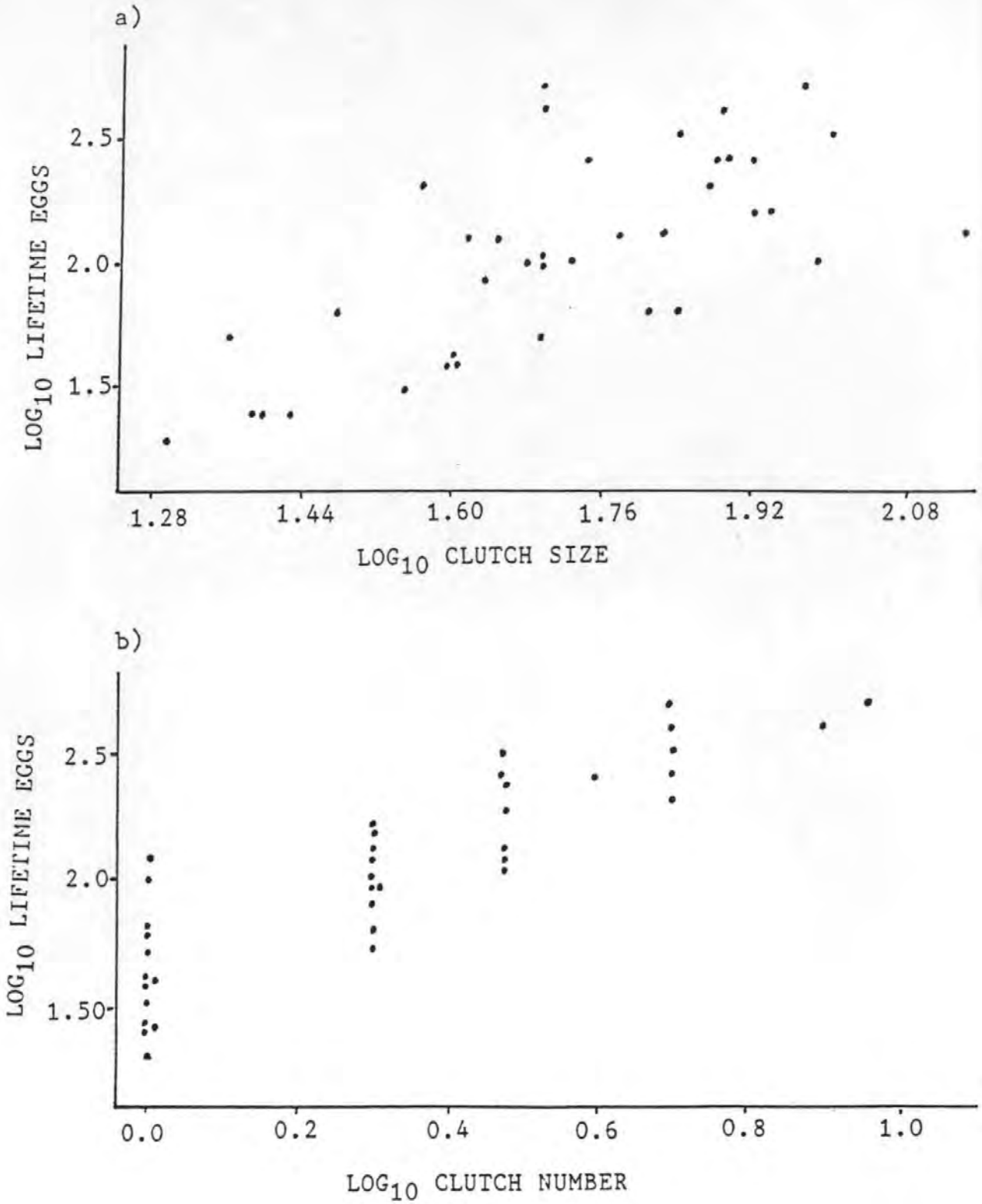


FIGURE 8.22 THE RELATIONSHIP BETWEEN a) LOG_{10} LIFETIME EGGS AND LOG_{10} CLUTCH SIZE AND b) LOG_{10} LIFETIME EGGS AND LOG_{10} CLUTCH NUMBER . LIFETIME EGGS AND CLUTCH SIZE WERE MEASURED AS MINUTES OF OVIPOSITION.

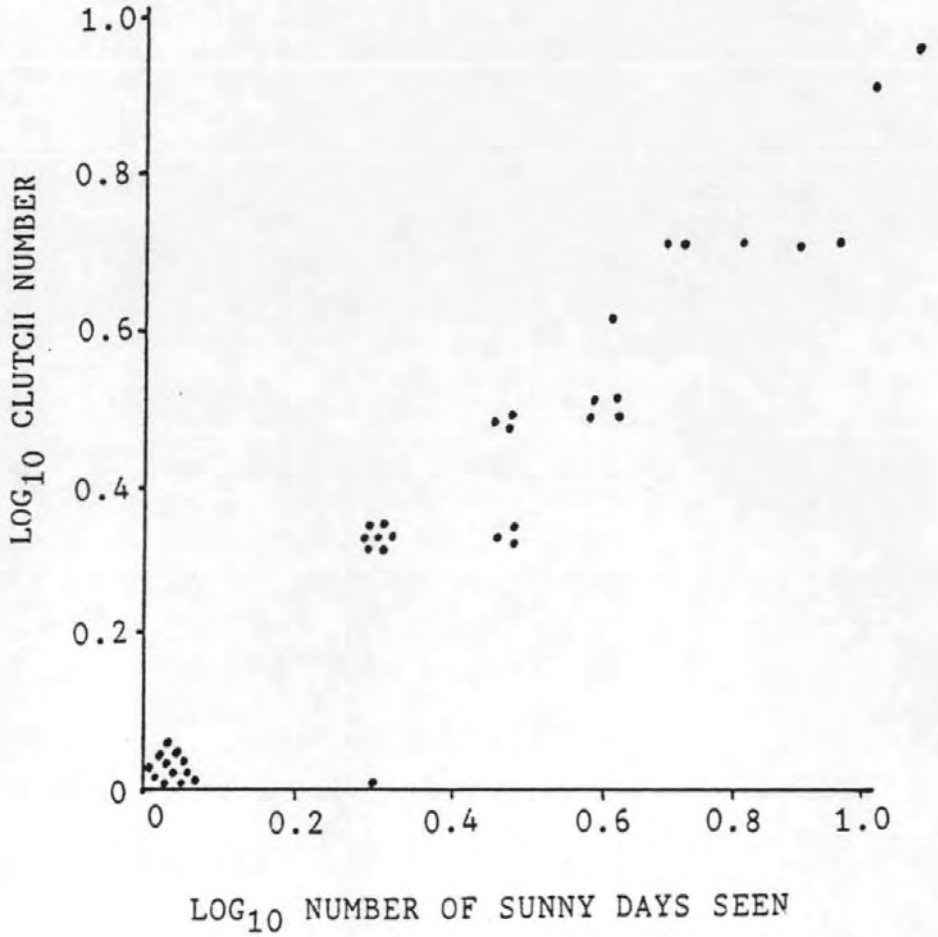


FIGURE 8.23 THE RELATIONSHIP BETWEEN LOG_{10} CLUTCH NUMBER AND LOG_{10} NUMBER OF SUNNY DAYS SEEN.

production of 1 per day, whereas others who survived to produce more than one clutch can have rates equal to or less than 1 per day. When one day females are excluded, the correlation between the independent variables is no longer significant ($r=-0.175$, $P>0.05$). The significant correlation between the independent variables is therefore somewhat spurious. Comparison between the path coefficients and R^2 values indicates that this problem does not alter the overall relative importance of the components.

When R^2 between components and total eggs are calculated, the number of sunny days females survive to see is the most important, accounting for 69% of the variation, followed by clutch size which accounts for 49%. The rate of clutch production is relatively unimportant, accounting for only -2%. There were no significant correlations between clutch size and either the rate of clutch production or the number of sunny days females survived to see.

ii) Partitioning of variance

An initial analysis of the data in terms of two components showed that clutch number accounted for 75% of the variation in total eggs, and clutch size 28%. However, a large negative covariance was indicated between clutch size and clutch number, even though the overall relationship showed a slight positive trend. This erroneous result was due to the presence of female 182, who had an exceptionally high clutch size recorded on only one day, and it was therefore necessary to excluded her from the analysis.

The results of the partitioning of variance are shown in Table 8.6, and mirror the results of the path analysis. The number of sunny days females survive to see again comes out as being the component with the most important independent influence, followed by clutch size, with the rate of clutch production being relatively unimportant. Small covariances are indicated between clutch size and the other components, and a larger, negative covariance between sunny days and the rate of clutch production. In order to see the overall effect of a component, all proportions of variance in which it is involved can be summed. This total gives the proportion by which the variance of lifetime reproductive success would be reduced if the component concerned was effectively removed by being held constant at its mean, while all other components were allowed to vary. Since this partition of the variance combines the independent and joint effects of a component it is this measure which is comparable to R^2 of the regression analysis. The importance of clutch size will be enhanced by overall positive variation with the other components, increasing its contribution to the variation in lifetime reproductive success to 31%. The influence of sunny days seen and the rate of clutch production will be reduced to 71% and -14% respectively by overall negative joint variation with other components, which is largely due to negative covariance between sunny days and the rate of clutch production. As previously discussed, the magnitude of this negative relationship will be enhanced spuriously by measurement problems, but despite this the relative importance of the components will not be greatly altered.

	Clutch Size	Sunny Days Seen	Rate Of Clutch Production
Clutch Size	23.0	-2.8	1.4
Sunny Days Seen	12.8	81.0	2.2
Rate Of Clutch Production	0.6	-18.5	4.0
Three Component Joint Term	-4.0		

TABLE 8.6 THE PARTITIONING OF VARIANCE OF FEMALE LIFETIME REPRODUCTIVE SUCCESS. THE VALUES ALONG THE DIAGONAL SHOW THE PROPORTION OF VARIANCE EXPLAINED BY THE INDEPENDENT INFLUENCE OF THE COMPONENTS; THE VALUES ABOVE SHOW CONTRIBUTIONS MADE BY COVARIANCE, AND BELOW BY SIMULTANEOUS BUT INDEPENDENT JOINT VARIATION. THE THREE COMPONENT JOINT TERM IS SHOWN AT THE BASE OF THE TABLE.

The number of sunny days females survive to see will result from their length of life and the proportion of their life which is sunny. Using logarithmic transformations, 88% of the variation in the number of sunny days seen was accounted for by regression on the length of life, with differences in weather conditions experienced by different females being relatively unimportant (R^2=-14%).

b) Males

i)Path Analysis

The results of a path analysis of the causes of variation in the lifetime reproductive success of territorial males (Figure 8.24), shows that the independent influence of average fertilizations per day on total fertilizations is much greater than the number of days males held territories. These relationships are little changed by the weak correlation between the independent variables, with the result that average fertilizations per day accounts for 91% of the variation in total fertilizations (Figure 8.25), compared to 21% due to the number of days that males held territories.

When the analysis is continued to look at the components of the number of days males held territories, the results show that the independent influence of sunny days seen was slightly greater than the proportion of time that males were territorial. These relationships are influenced by a significant negative correlation between the independent variables, resulting in sunny days seen accounting for 47% of the variation in days territorial compared to proportion of

time territorial accounting for 20%. If the correlation between the components of days territorial is examined when males who only survived to see one sunny day are excluded, it is found to be insignificant ($r=-0.130$, $P>0.05$). The significant correlation indicated in the path analysis diagram is therefore spurious, and due to the presence of one day males who must score 1 for the proportion of time that they defend territories. By comparing the independent influence of the components with their overall influence (R^2), the significant correlation results in the relative importance of the number of sunny days males see being slightly enhanced.

Another correlation which is marginally significant is indicated between average daily fertilizations and the number of sunny days males see. Again this is spurious, and due this time to six males who were only seen on 1-2 days and defended territories where no oviposition was seen. When the males with zero reproductive success are excluded, the correlation is no longer significant ($r=0.146$, $P>0.5$). The effect of the significant correlation is to enhance the direct influence of the number of sunny days males see on the total fertilizations. There was no significant correlation between average daily fertilizations and the proportion of time that males were able to defend territories.

When the direct relationship between the components and total eggs fertilized are examined, average daily fertilizations is by far the most important, accounting for

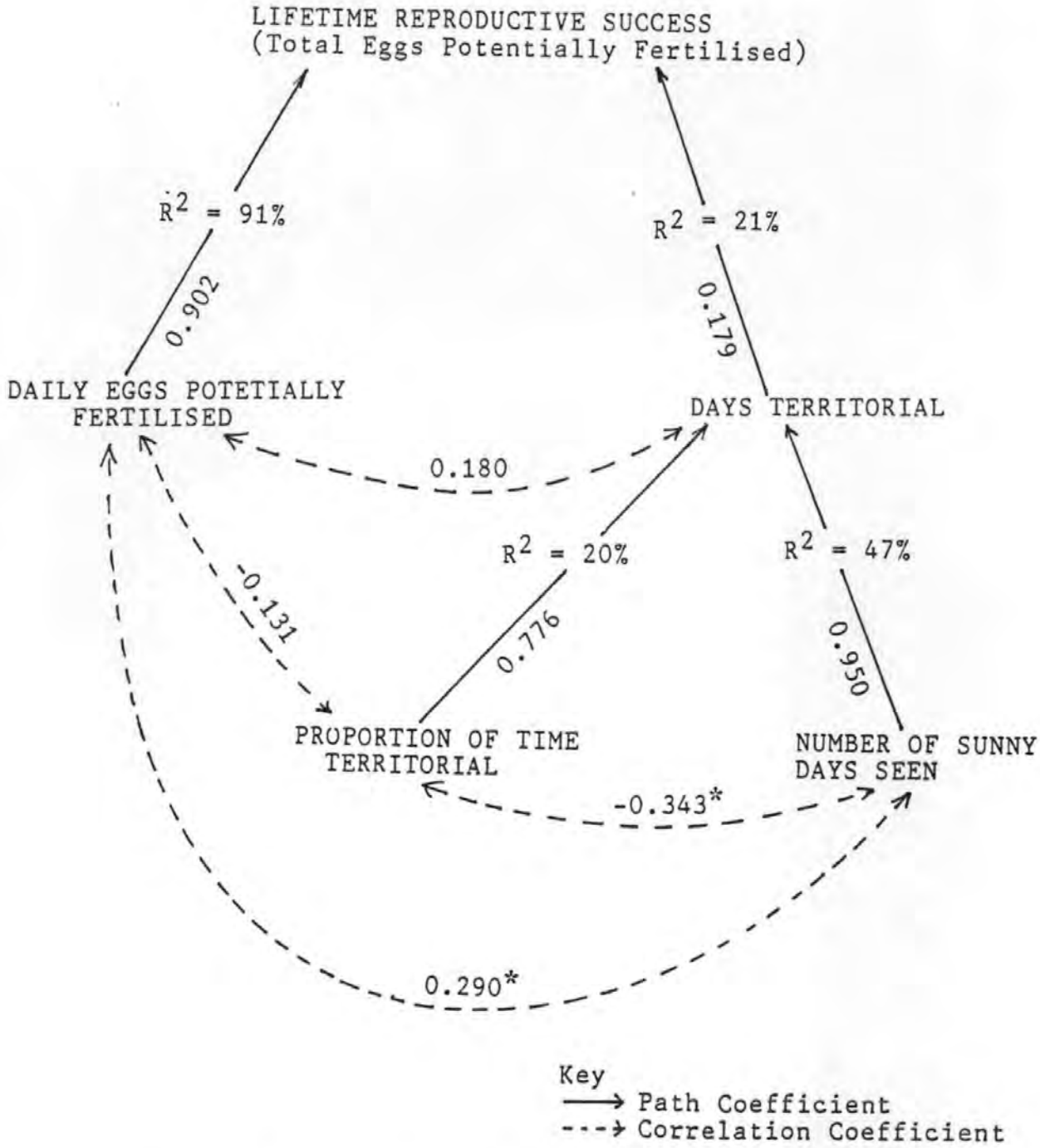


FIGURE 8.24 A PATH ANALYSIS OF THE CAUSAL RELATIONSHIPS IN THE LIFETIME REPRODUCTIVE SUCCESS OF MALES. PATH COEFFICIENTS SHOW THE INDEPENDENT INFLUENCE OF COMPONENTS, AND R^2 THE PROPORTION OF VARIANCE EXPLAINED BY EACH COMPONENT WHEN CORRELATION BETWEEN COMPONENTS IS INCLUDED. * DENOTES A CORRELATION COEFFICIENT WHICH IS SIGNIFICANT AT $P<0.05$.

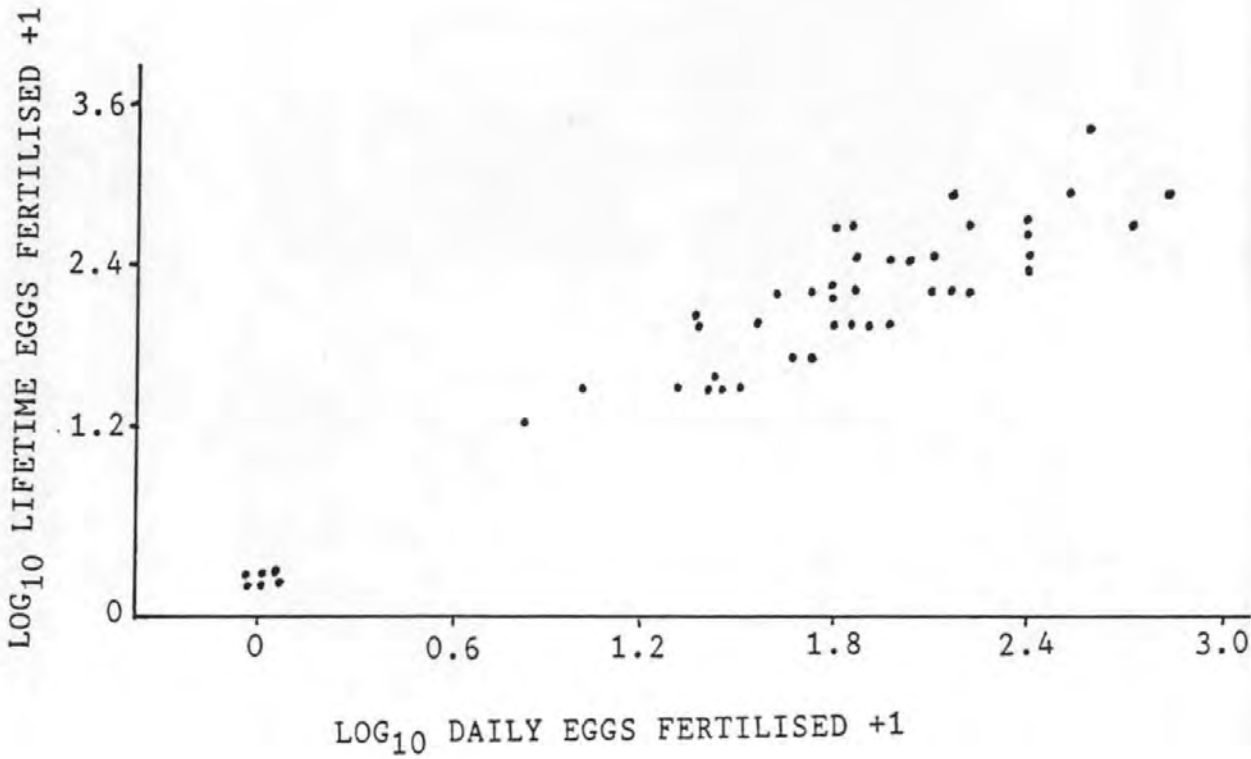


FIGURE 8.25 THE RELATIONSHIP BETWEEN MALE LIFETIME REPRODUCTIVE SUCCESS (LOG_{10} TOTAL EGGS FERTILISED +1) AND LOG_{10} DAILY EGGS FERTILISED +1. EGGS FERTILISED ARE MEASURED IN TERMS OF THE MINUTES OF OVIPOSITION OCCURING IN EACH MALES TERRITORY.

91% of the variation, with sunny days seen and proportion of time territorial accounting for 20% and 0.01% respectively.

ii) Partitioning of variance

An initial analysis of the data in terms of two components showed that the independent effect of average daily fertilizations accounted for 79% of the variation in total fertilizations, compared to 25% due to days territorial. Surprisingly a large, negative covariance was indicated between the components. Examination of the data revealed that the general relationship between the components was slightly positive, and that the negative covariance indicated in the analysis was due to the presence of male 115, who had a very high score for daily fertilizations and was only present on one day. This male was therefore removed from the data set. Experimental removal of other outlying individuals confirmed that the results were now stable for the group as a whole.

The results of a partitioning of variance analysis on the reduced data set are shown in Table 8.7. Average daily fertilisations still has by far the most important independent influence, followed by sunny days seen and then time territorial. A substantial covariance is indicated between daily fertilizations and sunny days seen, which, as previously discussed is not indicative of a general population effect. Surprisingly only a small negative covariance is indicated between time territorial and sunny days, despite the measurement problems discussed above, and a large covariance is indicated with daily fertilizations.

	Daily Eggs Fertilised	Number Of Sunny Days Seen	Proportion Of Time Territorial
Daily Eggs Fertilised	56.9	20.2	-16.6
Number Of Sunny Days Seen	19.4	15.5	-2.6
Proportion Of Time Territorial	7.4	2.0	5.8
Three Component Joint Term	-7.8		

TABLE 8.7 THE PARTITIONING OF VARIANCE OF MALE LIFETIME REPRODUCTIVE SUCCESS. THE VALUES ALONG THE DIAGONAL SHOW THE PROPORTION OF VARIANCE EXPLAINED BY THE INDEPENDENT INFLUENCE OF THE COMPONENTS: THE VALUES ABOVE SHOW THE CONTRIBUTION MADE BY COVARIANCE, AND BELOW BY SIMULTANEOUS BUT INDEPENDENT JOINT VARIATION. THE THREE COMPONENT JOINT TERM IS SHOWN AT THE BASE OF THE TABLE.

Examination of the relationship between time territorial and daily fertilizations did not suggest a general population effect, and a Kendall rank correlation coefficient was not significant (r_k=-0.05, P=0.589).

The inclusion of joint variation effects to give the overall influence of the components does not alter their order of importance, but the relative importance of sunny days is slightly increased. The average daily fertilizations is still the most important component, accounting for 87.3% of the variation overall, sunny days seen 54.5% and proportion of time territorial -4%.

Thirty three mature males in the population area, fifteen of which were seen fighting with territorial males in the experimental area during the oviposition period, did not hold territories in the experimental area during their lifetime. It is possible that the remaining eighteen males visited the experimental area and were pushed out before oviposition and recording began, and it seems unlikely that they were not part of the competitive scenario. Brown (1988) describes a method for calculating the contribution of individuals which did not have the opportunity to breed to the total variance in lifetime reproductive success. The total variance in lifetime reproductive success can be described as

$$pV(LRS) + p(1-p)LRS^2$$

where p represents the proportion of individuals who had the opportunity to breed, and V(LRS) and LRS represent the variance and mean of their lifetime reproductive success. The first term in the expression represents the variance in lifetime reproductive success due to individuals which had the opportunity to breed, and the second due to those which did not. If it is considered that all males which failed to get territories in the experimental area did not have the opportunity to breed, they would represent 42% of the total number. Using the above expression, despite representing a large proportion of the males, those which were 'non-territorial' would only account for 16% of the variation in total lifetime reproductive success for males as a whole.

8.7.3 Discussion

A comparison of the overall influence of components, given by R^2 values and sums of independent and joint proportions in the partitioning of variance, show that the two methods give broadly similar pictures of the relative importance of the components of lifetime reproductive success (Table 8.8). In both males and females a single component stands out as being of particular importance; in males this was average daily eggs fertilized whereas in females it was the number of sunny days seen. The greatest discrepancy between the results of the two methods is in the importance of the number of sunny days males saw, and since this was enhanced in the partitioning of variance by large covariances which do not appear to represent significant relationships, it seems fair to assume that this component was not of great importance. Clutch size was of secondary importance to

FEMALES

	Clutch Size	Sunny Days Seen	Rate Of Clutch Production
Path Analysis (R^2)	49%	69%	-2%
Partitioning Of Variance (Independent & Joint Effects)	31%	71%	-14%

MALES

	Daily Eggs Fertilised	Sunny Days Seen	Proportion Of Time Territorial
Path Analysis (R^2)	90%	20%	0%
Partitioning Of Variance (Independent & Joint Effects)	87%	54%	-4%

TABLE 8.8 A COMPARISON OF THE RESULTS OF A PATH ANALYSIS AND PARTITIONING OF VARIANCE OF LIFETIME REPRODUCTIVE SUCCESS.

females, being relatively more important in the path analysis results. The proportion of time that males were able to defend territories and the rate of clutch production were both relatively unimportant.

The interpretation of the results of both methods of analysis is not straightforward. Components in the form of rates or percentages, such as the rate of clutch production, led to spuriously enhanced negative correlations and covariances with the time periods over which they were measured. Such problems are inherent in this difficult type of analysis and must be dealt with in the best way possible (eg Fincke 1986). Here path analysis helped in the identification of significant correlations, and the contribution of spurious correlations could be easily seen and assessed. Further problems of spurious inter-relationships in the partitioning of variance were caused by the presence of outlying individuals, which were to an extent a feature, and therefore an important part, of these field data. In neither males nor females, however, did these problems confuse the overall picture of the relative importance of components because of the large differences in their independent influences. In addition, faith in the reliability of the results and their interpretation is strengthened by the concordance of the two methods.

The use of lifetime average values for clutch size, daily eggs fertilized and the rate of egg production ignores the fact that these components may change with age. Any significant changes with age would, however, have been

detected as increases or decreases in average values correlating with components relating to survival. It is noteworthy that no reliable significant relationships were found between the components of either male or female lifetime reproductive success.

Contrary to the results of this study, several authors have emphasised the importance of survival to male lifetime reproductive success (Koenig and Albano 1987, Michiels and Dhondt 1991). Often the proportion of variance due to survival is found to be the largest single contribution, but Table 8.9 shows that when the variance due to all components relating to male breeding breeding behaviour are considered together, the proportion of variance in lifetime reproductive success they account for is often little different to the proportion due to survival (eg Koenig and Albano 1987), and sometimes greater (eg Fincke 1988, McVey 1988). While Tsubaki and Ono (1987) report that most of the variation in lifetime reproductive success in male Nannophya pygmaea can be attributed to weather patterns and survival, number of sunny days in a top quality territory is one of the most important components, thus confounding breeding behaviour with survival and possibly hiding the importance of the former. The greatest bias towards the importance of survival in males is that found by Banks and Thompson (1985) in C. puella, where 78% of the variance in lifetime reproductive success is reported to be due to days spent at the breeding site compared to 22% due to mating success. The figure for the proportion of variance due to mating success is unlikely, however, to reflect its true value having been obtained by

SPECIES	TERRITORIAL	MALES Components Relating To BREEDING BEHAVIOUR		SURVIVAL	FEMALES Components Relating To BREEDING BEHAVIOUR		SURVIVAL	AUTHOR	METHOD OF ANALYSIS
Sympetrum danae	No	21.7% (mda)	(42%)	27% (sds)	23.2% (rcp)	(30.5%)	38.5% (sds)	Michiels and Dhondt 1991(1)	Partitioning of Variance (Brown 1988)
Enallagma hageni	No	65% (mdb+fm)		34% (sds+pm)	79% (cs)		69% (cn)	Finke 1988	Partitioning of Variance (Arnold & Wade 1984)
Coenagrion puella	No	22%(2) (mda)		78% (sds)	30%(2) (cs+rcp)		70% (sds)	Banks & Thompson 1985 & 1987b	Regression of Logged (male) and Unlogged (female) Data
Plathemis lydia	Yes	22% (mdb+fm+pm)	(52%)	27% (1)	24% (cs+rcp)	(28%)	48% (1)	Koenig & Albano 1987	Partitioning of Variance (Arnold & Wade 1984)
Nannophya pygmaea	Yes	95.2% (sds+sds in top ranked territory)						Tsubaki & Ono 1987	Multiple Regression of Unlogged Data
Erythemis simplicicollis	Yes	63% (mda+fm)		57% (1)	24% (cs+rcp)		68% (1)	McVey 1988	Partitioning of Variance (Arnold & Wade 1984)
Calopteryx virgo	Yes	62.7% / 91% (edm+pm)		15.5% / 20% (sds)	27% / 49% (cs+rcp) (cs)		81% / 76% (sds) (cn)	Present Study(3)	Partitioning of Variance (Brown 1988) / Path Analysis (Sokal & Rholf 1981)

TABLE 8.9 THE IMPORTANCE OF COMPONENTS RELATING TO BREEDING BEHAVIOUR AND SURVIVAL TO LIFETIME REPRODUCTIVE SUCCESS IN ODONATA. WHERE LARGE COVARIANCES OCCURRED THEY ARE SHOWN IN BRACKETS. l = LIFESPAN, sds = SUNNY DAYS SEEN, cs = CLUTCH SIZE, cn = CLUTCH NUMBER, rcp = RATE OF CLUTCH PRODUCTION, mda = MATES PER DAY ALIVE, mdb = MATES PER DAY BREEDING, pm = PROPORTION OF DAYS ALIVE ON WHICH BREEDING OCCURED, fm = EGGS FERTILISED PER MATING, edm = EGGS FERTILISED PER DAY MATING. SUBSCRIPTS: (1) = FIELD ENCLOSURE EXPERIMENT, (2) = VALUES OBTAINED BY SUBTRACTION OF % SDS FROM 100%, (3) = FIELD EXPERIMENT.

subtracting the value for survival (obtained by simple regression) from 100%. The significant correlation present between daily mating success and survival would result in a large degree of covariance. Had mating success itself been regressed against lifetime reproductive success it too could have a similar value to survival. In several studies large contributions due to covariance between breeding behaviour and survival are also found, making separation of the importance of these components even more difficult (eg Michiels and Dhondt 1991, Koenig and Albano 1987).

Studies of the lifetime reproductive success of territorial males do not indicate that breeding behaviour is more important than in non-territorial species (Koenig and Albano 1987, Mcvey 1988), as might be expected if competition between territorial males is more intense. Care needs to be taken in this assumption, however, since in some cases territories are abundant and there is little overt competition for them (eg P.nymphula, Gribbin and Thompson 1991, S.rubicundulum Van Buskirk 1987b). In the present study competition between territorial males was intense, possibly explaining the greater bias towards the importance of components relating to breeding behaviour. Despite the fact that 42% of males failed to obtain territories and were classified as non-breeders, they accounted for only 16% of the total variance in lifetime reproductive success. These figures emphasise the very large variation in lifetime reproductive success among males who were able to defend territories, due largely to variance in the breeding success of males.

Studies of female lifetime reproductive success generally indicate that, as found here, components relating to survival are more important than those relating to clutch size (Michiels and Dhondt 1991, Koenig and Albano 1987, McVey 1988). In the analysis of female data here a regression indicated that lifespan was much more important than weather patterns in influencing the most important component, the number of sunny days a female survived to see. Lifespans, however, were measured within the only prolonged period of generally fine weather from the 1st-16th of July, since most adults cannot be found in poor weather. The influence of weather patterns to female lifetime reproductive success will therefore have been underestimated, and is likely to be strong. Most other studies of lifetime reproductive success have suffered from similar problems, and many authors stress the probable importance of weather patterns (Tsubaki and Ono 1987, Banks and Thompson 1985, Michiels and Dhondt 1991). When the effects of random weather patterns on the lifetime reproductive success of a model population of C.puella were studied, Thompson (1990) found that they were often likely to be more important than survival.

8.8 THE IMPORTANCE OF BODY SIZE AND TIME OF EMERGENCE TO THE COMPONENTS OF LIFETIME REPRODUCTIVE SUCCESS

8.8.1 Females

The effect of body size and emergence time on lifetime reproductive success can most usefully be explored by assessing its effect on the critical components. The number of sunny days females survived to see was the most important

component of their lifetime reproductive success, through its influence on the number of clutches produced. The mature lifespan of the few females which were seen outside, as well as inside, the period of generally fine weather have been included in the survival data to give a more complete picture. The shortlived rise in daily mortality, due to bird predation (see section 8.3), is not directly translated into survival curves because individuals were of a range of ages when the mortality occurred (Figure 8.26). Nevertheless changes in the probability of survival as a result of the bird predation can be seen. The probability of survival of first emergence group females was generally 0.891, but this decreased to 0.741 when the predation occurred, at the time when most of these females had been mature for five to seven days. In contrast, the increased mortality occurred just as the second emergence group females were arriving to oviposit for the first time, and their survival from one to two days of age was very low. There is no continuous change in survival in either emergence group however, indicating that survival was independent of age as an innate factor. The majority of mature females lived for a very short time, one to six days, compared to the maximum recorded mature lifespan of twenty three days (Figure 8.27). For a number of females though, these data reflect the period of fine weather experienced rather than their full lifespan.

There was no relationship between length of mature life and head width ($r=0.124$, $P>0.05$). Because body length changed with age, females were divided into two groups according to the age at which they were measured. There was no correlation

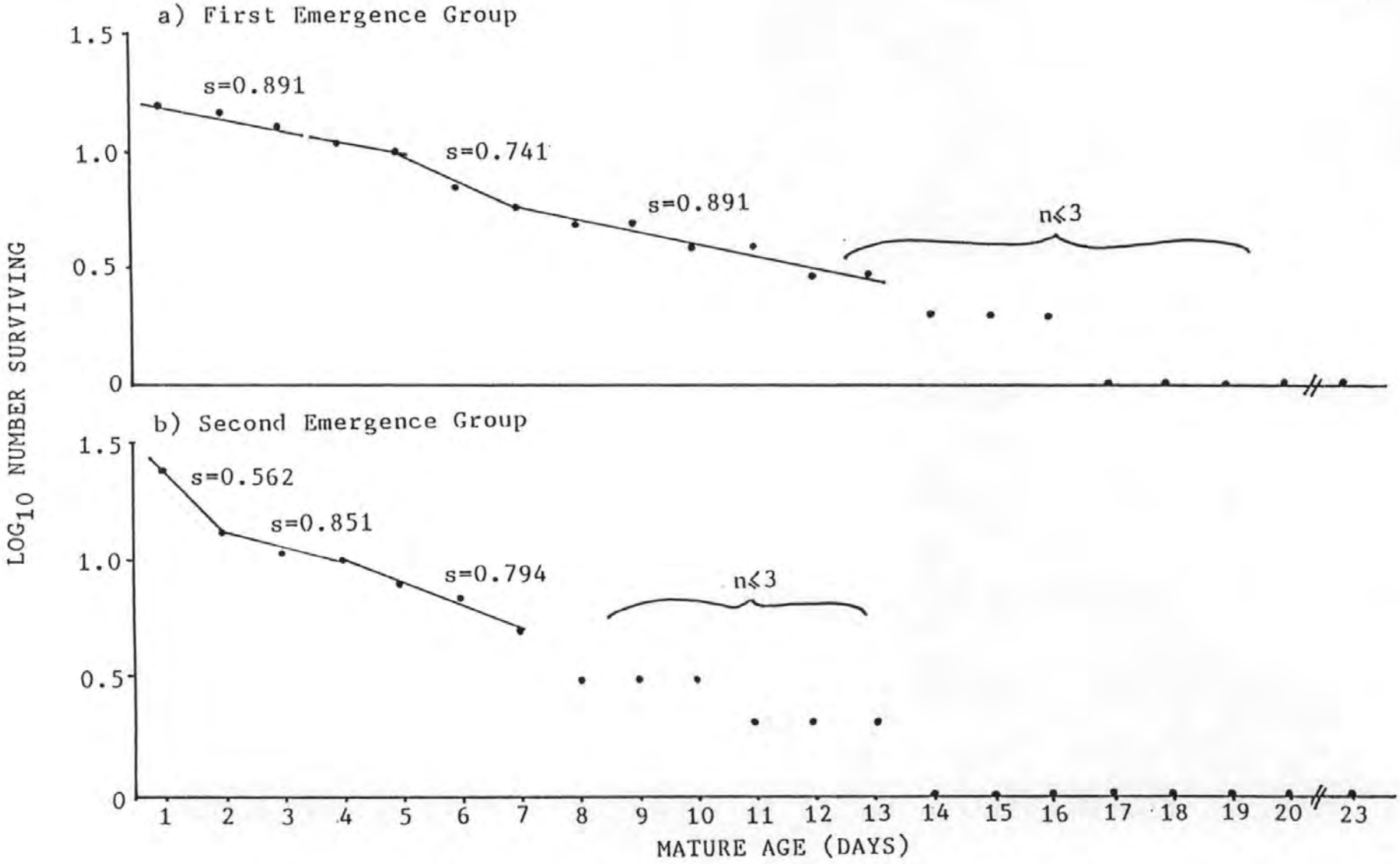


FIGURE 8.26 SURVIVORSHIP CURVES FOR MATURE FEMALES PRESENT IN 1987. s = PROBABILITY OF SURVIVAL.

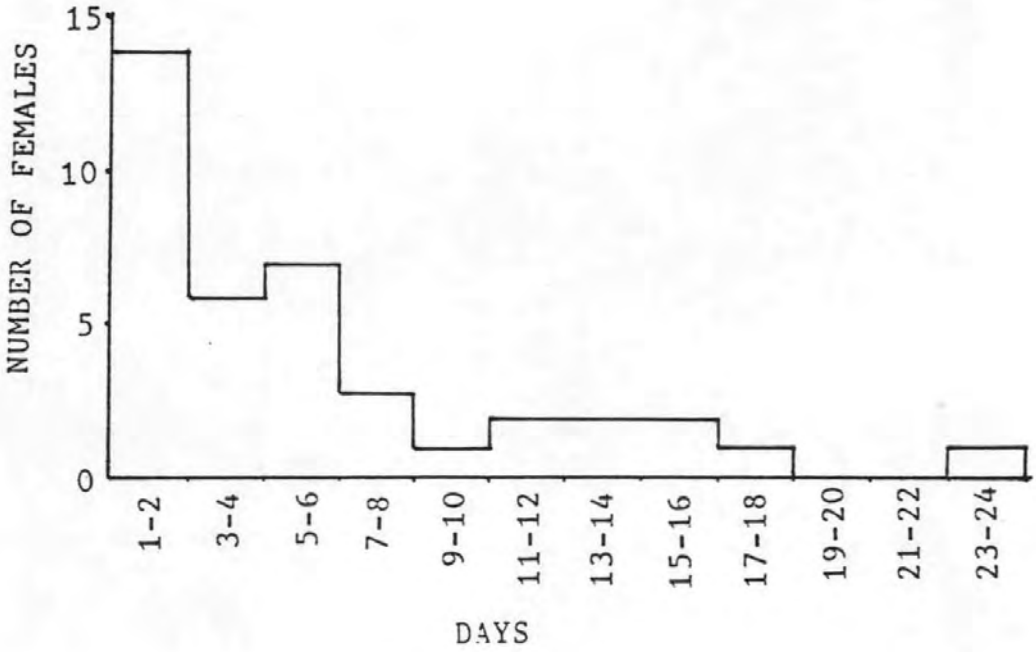


FIGURE 8.27 MATURE FEMALE LIFESPAN

between body length and mature lifespan among females measured within a few days of emergence (n=15, r=0.135, P=0.155), or those measured later (n=20, r=0.287, P=0.076). A spurious relationship between size and mature lifespan might have been expected since the second emergence group were smaller in body size and suffered higher mortality, but none was evident.

As a result of the pattern of weather from the 1st-16th July, the two emergence groups experienced different weather conditions. Those from the first group encountered eight days of continuous good weather before more unsettled weather set in, while the second group arrived as the unsettled weather started. Periods of good and poor weather could occur in any order during the females' mature lifespan, and this factor will act at random with respect to individuals. The influence of the pattern of mortality and poor weather on the number of sunny days the two emergence groups saw resulted in significant differences in the number of clutches they produced (Table 8.10). Females from the first emergence group produced a median of 3 clutches, with some females producing up to 9, while all except one from the second group produced only 1-3 clutches.

Clutch size, of secondary importance to lifetime reproductive success but still a significant factor, was related neither to head width (r=0.170, P>0.1), nor to body length of females measured within a few days of emergence (n=15, r=-0.337, P=0.272), or later (n=20, r=0.258, P=0.272). The clutch sizes of females from the two emergence groups

were compared to see if any innate differences between them were reflected there, but no difference was found (Table 8.10).

The rate of clutch production had little influence on clutch number because there was relatively little variation between females. The lack of variation in this component is in itself of interest, since females produced a clutch on almost every sunny day they survived to see (Figure 8.28); yet successive sunny days represent the only opportunity for females to feed as well as oviposit (see Chapter Six). The average rate of clutch production, measured over successive sunny days, was 0.85 per day. Two females were observed to produce clutches on four consecutive days, and seven females for three consecutive days. It is not known how long females could continue to produce consecutive clutches, since the onset of bad weather prevented longer runs. Of the females who lived to see more than two sunny days, 68% spent at least one sunny day feeding during the oviposition period, suggesting that females cannot produce clutches on consecutive sunny days indefinitely. The analysis of the relationships between the components of lifetime reproductive success showed that the rate of clutch production did not decline significantly with time (section 8.7.2). The number of sunny days spent feeding rather than ovipositing was therefore not related to the number of sunny days seen.

The distribution of lifetime reproductive success, shown in Figure 8.29, is skewed, with most females producing around 100-700 first instars, but some producing up to 1600.

	Median			
	First Emergence Group	Second Emergence Group	U	P
Clutch Size	59.1	56.6	160	0.500
Clutch Number	3	2	93	0.007
Lifetime Minutes Of Oviposition	207	103	99.5	0.015

TABLE 8.10 A MANN-WHITNEY U TEST OF DIFFERENCES IN MEASURES OF REPRODUCTIVE SUCCESS BETWEEN FEMALES FROM THE TWO EMERGENCE GROUPS IN 1987.

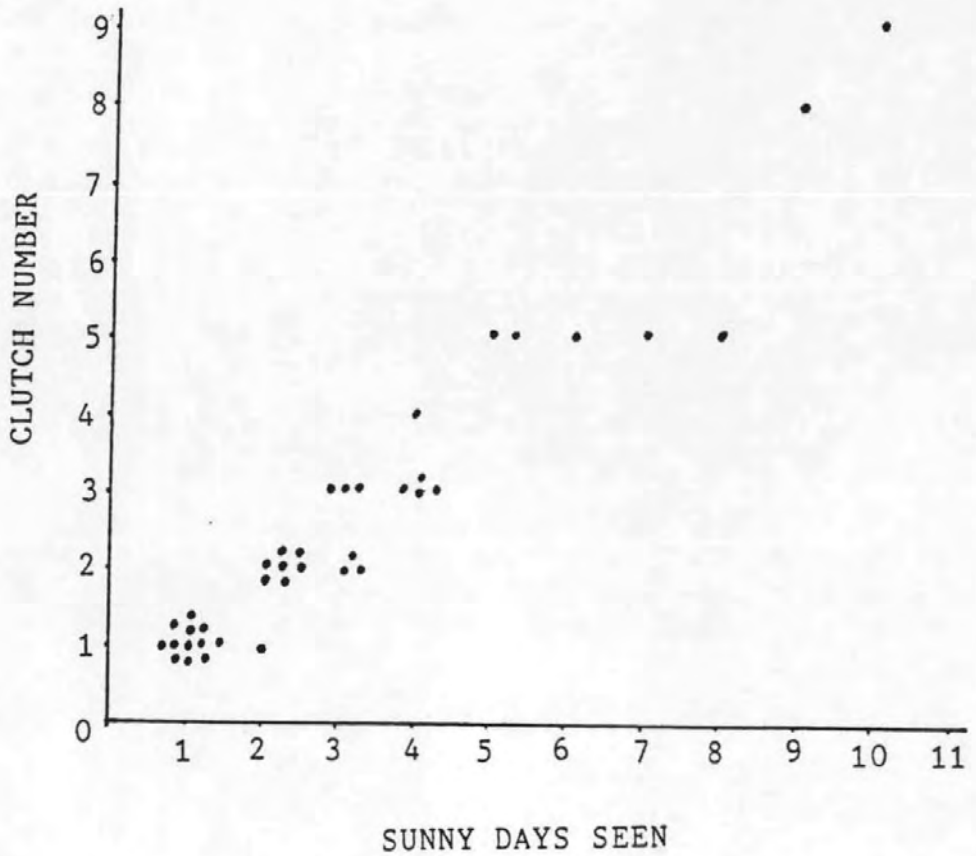


FIGURE 8.28 THE RELATIONSHIP BETWEEN CLUTCH NUMBER AND SUNNY DAYS SEEN

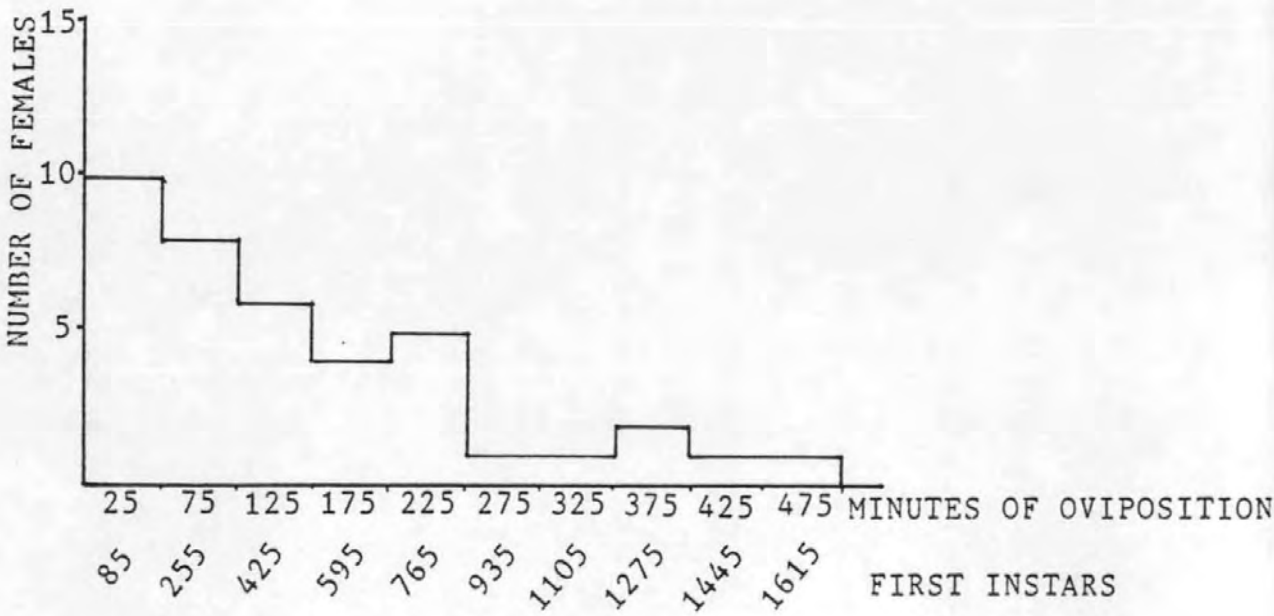


FIGURE 8.29 THE DISTRIBUTION OF FEMALE LIFETIME REPRODUCTIVE SUCCESS

Since the greatest influence on this variability is variation in clutch number, the differences in clutch number between the emergence groups described above results in significant differences in their lifetime reproductive success (Table 8.10).

8.8.2 Males

The most important component of the lifetime reproductive success of territorial males was average daily eggs fertilised. In section 8.7 it was found that territorial behaviour had a significant influence on daily reproductive success. Males who held territories in the H oviposition patches that attracted a high number of females, did better than those in the L patches that attracted a low number females. Males who were unable to obtain territories fared the worst, since they rarely had the opportunity to mate, and when they did their mate was likely to be re-mated by a territorial male before ovipositing. If body size or time of emergence influences the competitive ability of males, and in particular the ability of males to obtain high quality territories, then it could be an important influence on lifetime reproductive success.

The body size of territorial males fell as smaller males from the second emergence group arrived (Figure 8.30). In the analysis of male body size, all males which were unable to obtain a territory in the experimental area were considered to be non-territorial. When the sizes of non-territorial males and those which were territorial in the H and L patches are examined on a daily basis, a changing

picture is revealed (Figure 8.31). From the 1st to 4th of July when males from the first emergence group dominated, males from the H patches appeared to be larger than those from the L patches and males which were unable to obtain territories. After the 4th of July when the second emergence group males arrive and the average size of males falls, a fall in the size of all categories would be expected, maintaining the difference between them. Only the size of males in the H patches falls however, and from the 6th of July the size of males in the different categories are no longer segregated.

Each male from each emergence group was categorised as having held a territory in either H or L patch, or never having held a territory in the experimental area. Only two males changed territories, one finally became non-territorial on the day he moved territories, and was categorised as such that day; the second was only territorial for one day, and his final territory position was used. Among first emergence group males those in the good quality territories were larger in both head width and body length than those in poor quality territories, which in turn were larger than non-territorial males (Figure 8.32). The differences in body length among first emergence group males were significant, and there was a very strong trend of differences in head width (Table 8.11). An examination of the data suggests that the main difference lies between males in high quality territories and those which were unable to acquire territories, with males in low quality territories being intermediate in size. The results clearly indicate that body size influenced the ability of

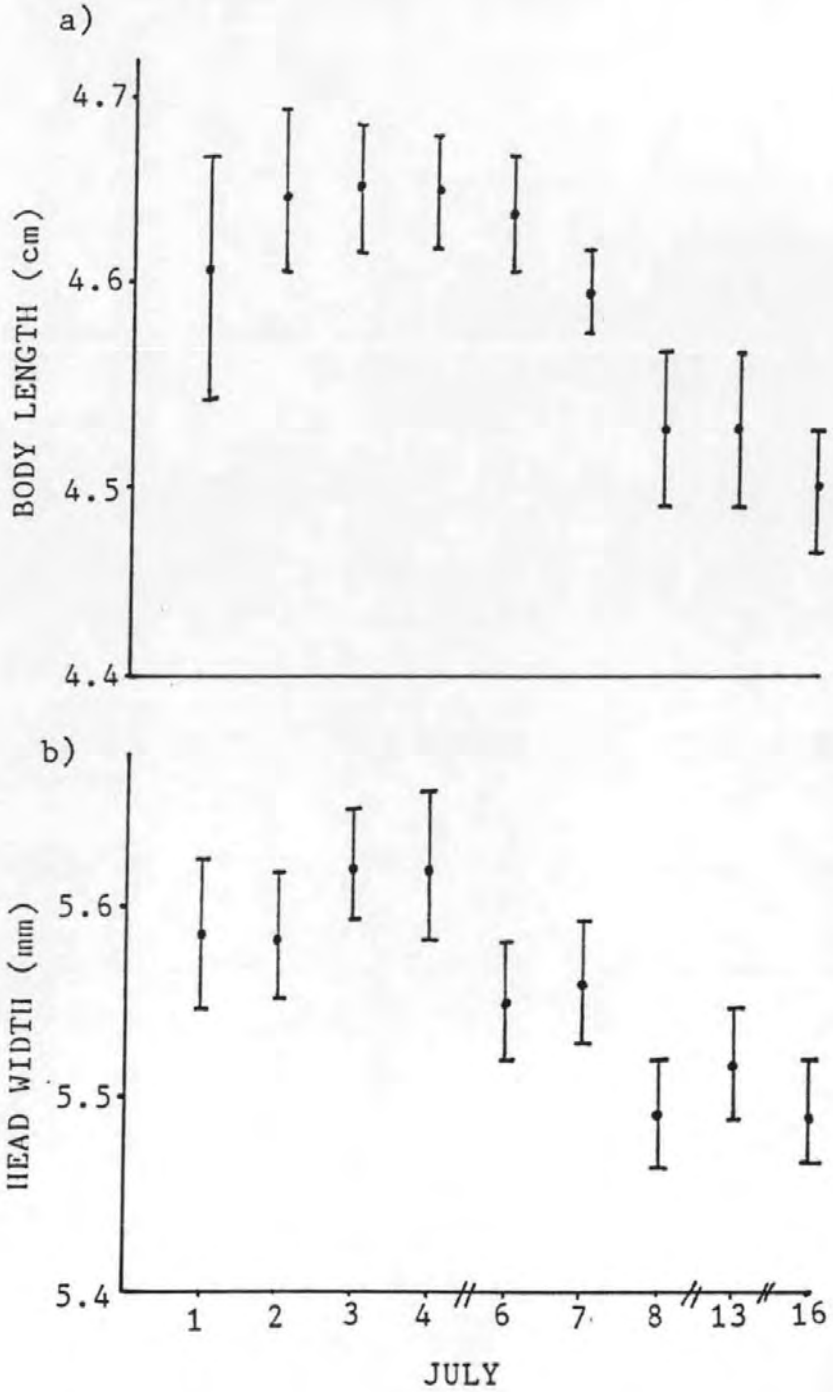


FIGURE 8.30 THE BODY SIZE OF MATURE MALES IN THE EXPERIMENTAL AREA FROM 1-16 JULY, a) BODY LENGTH, b) HEAD WIDTH. MEANS ARE PRESENTED +/- S.E. ALTHOUGH MALES WERE PRESENT ON THE 12th, MANY WERE NEWLY ARRIVED SINCE THE 8th, AND WERE NOT MEASURED UNTIL AFTER THE OVIPOSITION PERIOD.

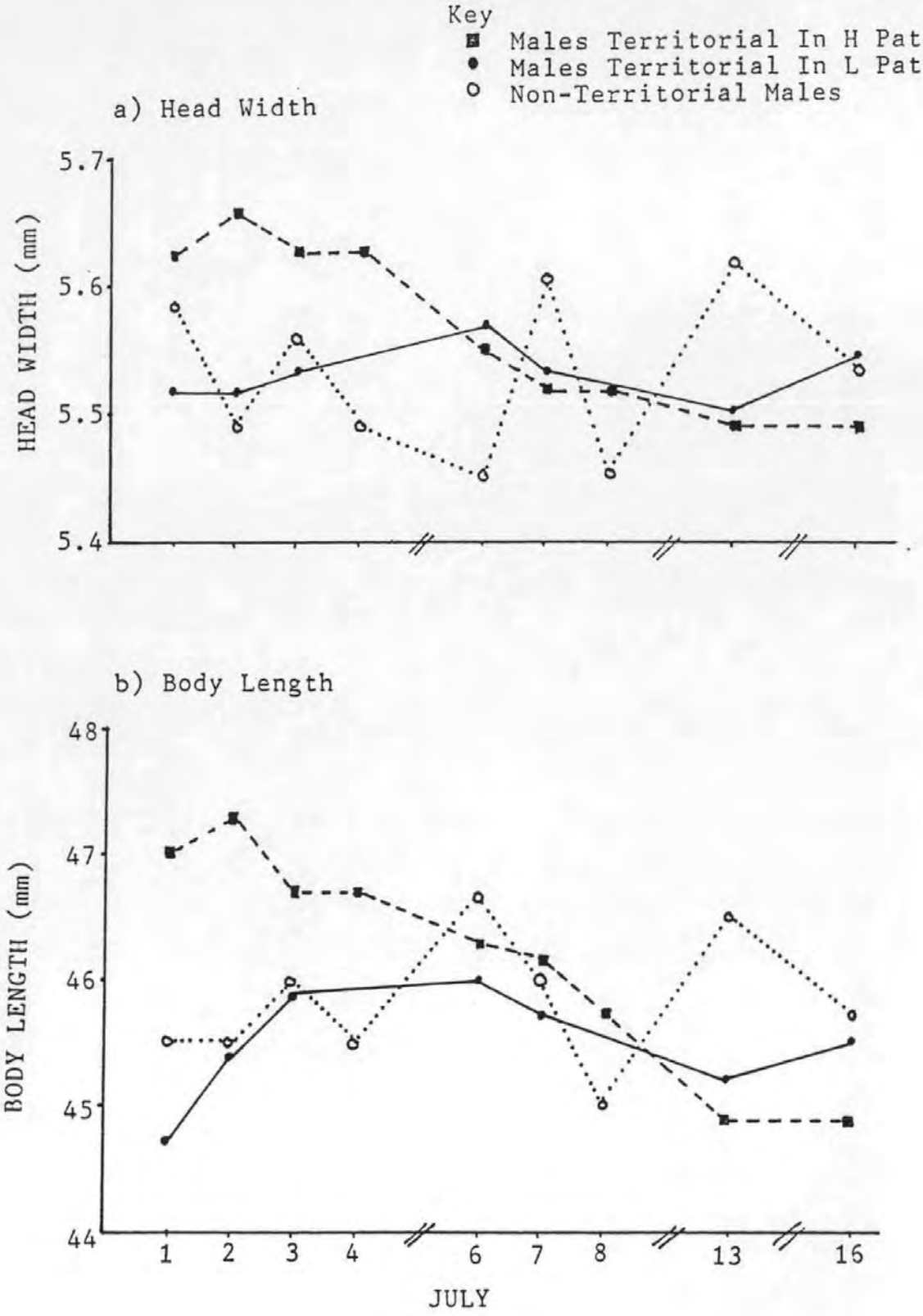


FIGURE 8.31 THE DAILY MEAN BODY SIZE OF TERRITORIAL AND NON-TERRITORIAL MALES

Source	SS	DF	ms	F	p
First Emergence Group Males					
Head Width	0.062	2	0.038	3.114	0.061
Residual	0.249	25	0.01		
Body Length	0.129	2	0.064	4.581	0.02
Residual	0.0351	25	0.014		
Second Emergence Group Males					
Head Width	0.023	2	0.012	0.69	0.512
Residual	0.745	44	0.017		
Body Length	0.039	2	0.019	1.000	0.377
Residual	0.899	46	0.019		

TABLE 8.11 ANALYSIS OF VARIANCE OF HEAD WIDTH AND BODY LENGTH OF MALES TERRITORIAL IN HIGH AND LOW QUALITY OVIPOSITION PATCHES, AND NON-TERRITORIAL MALES

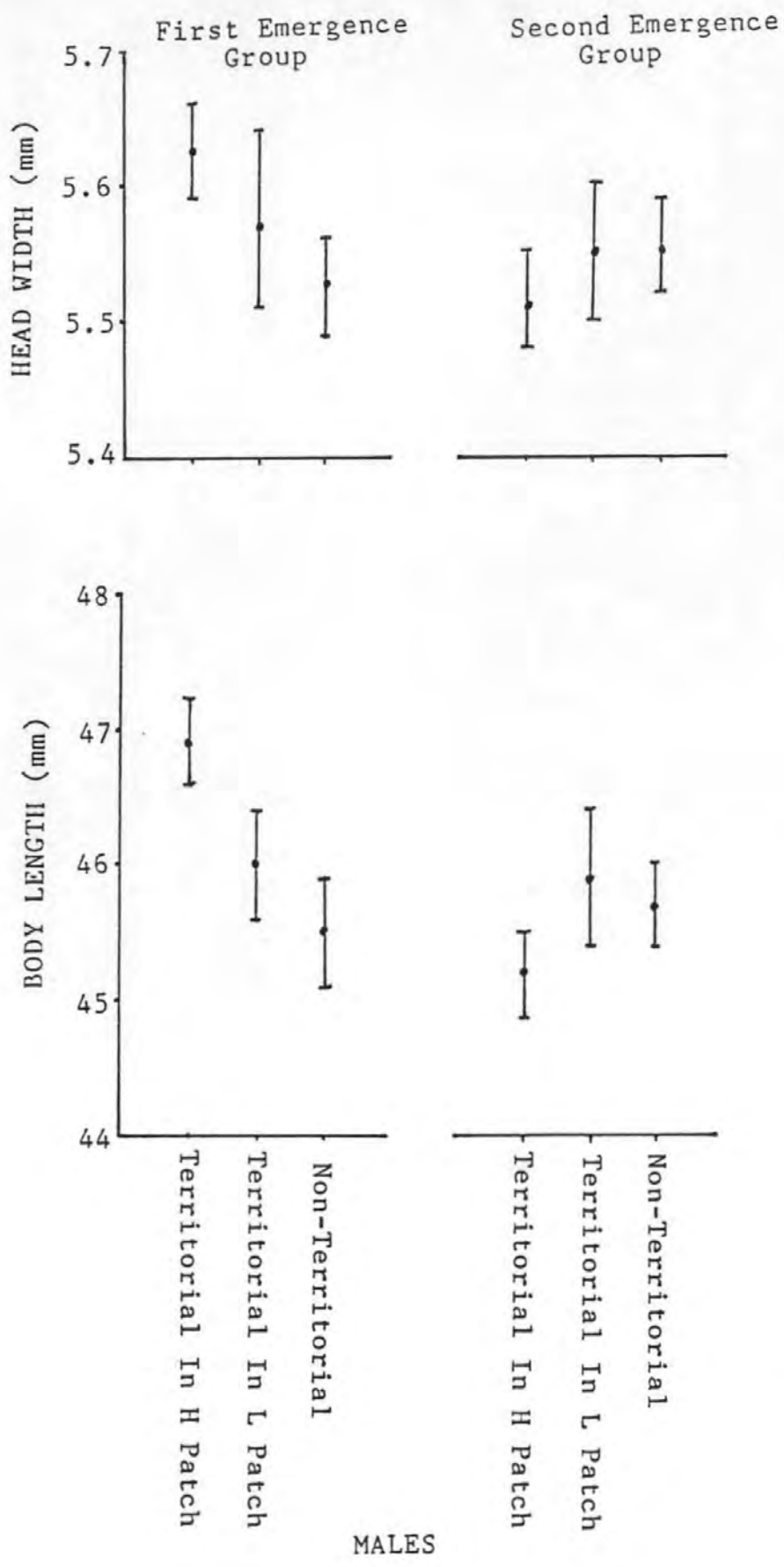


FIGURE 8.32 THE BODY SIZE OF MALES FROM THE TWO EMERGENCE GROUPS WHICH HELD TERRITORIES IN H AND L OVIPOSITION PATCHES AND WERE NON-TERRITORIAL MEANS ARE PRESENTED +/- 95% C.L.

first emergence group males to obtain territories, and is likely to influence territory quality also. In contrast there was no difference in the size of second emergence group males which held different quality territories or were non-territorial, indicating that body size did not influence their ability to obtain or defend territories. One possible explanation for the different influence of body size in the two emergence groups would be a reduction in the overall variability of body size amongst second emergence group males, but the variances in head width and body length of each emergence group were not significantly different (head width: $F = 1.408$, $P>0.5$, body length: $F = 1.04$, $P>0.05$).

Age was not an important factor in territory acquisition and defence. Most males arrived in the experimental area within one to two days of reaching maturity, after which some obtained territories straight away while others were initially non-territorial for a day. Five out of eight males who were observed losing their territories to non-territorial males had only held their territories for one day, and were young males.

The number of days males held territories was not an important component of lifetime reproductive success. The full mature lifespan of males seen mature outside as well as within the period of generally fine weather have been included in the survival data to give a more complete picture. Figure 8.33 shows that the probability of survival of the first emergence group was generally 0.794, but fell when most of these males had been mature for seven to eight

days due to the increase in bird predation. In contrast the bird predation occurred when second emergence group males had just started to arrive in the experimental area, and their probability of survival from one to three days of age was low. There was no continuous change in survival in either emergence group, and survival was therefore unrelated to age as an innate factor.

The mature lifespan of most males was only one to six days compared to the maximum recorded lifespan of twenty three days, and most saw only one to four sunny days (Figure 8.34). For several males the length of life will reflect the period of good weather seen rather than true lifespan. This is particularly true of first emergence group males, where 83% were mature on the 1st July, suggesting that many were mature before this. Twenty five percent of the second emergence group were still alive on the 16th July, and many will have lived longer than indicated. There was no correlation between length of life and either head width ($r=0.063$, $P=0.105$), or body length ($r=0.192$, $P=0.251$). As in the females there was no sign of a spurious correlation which could have resulted from smaller later emerging males experiencing higher bird predation.

While males from the first emergence group which survived to see the onset of good weather on the 1st of July experienced eight days of continuous good weather, those from the second emergence group arrived as more unsettled weather set in. The number of territorial males surviving from one sunny day to the next was therefore very low after the 8th of

July, and those that did survive experienced fewer sunny days in their life. Figure 8.35 shows that most males held territories for a very short time, only one to two days. As a result of the different effect of the pattern of mortality and weather on males from the two emergence groups, a Mann-Whitney U test indicates a strong trend of a difference in the number of days males from the two emergence groups were territorial. Those from the second group were territorial for on average only 1.6 days, compared to 2.7 days of those from the first group ($U=458.5$, $P=0.059$).

The difference in the number of days males from the two emergence groups held territories is reflected in the turnover of territorial males from one sunny day to the next (Figure 8.36). During the period of settled weather and average mortality, from the 1st to 4th of July, there was a much lower turnover of males than during the period of high mortality and unsettled weather. Differences in the conditions affecting the emergence groups are reflected in the ease with which males obtained territories. Fifty six percent of territorial males from the first emergence group were non-territorial in the experimental area before being able to obtain territories, and all the occasions when males were seen being ousted from territories by non-territorial males occurred among the first emergence group. In contrast most second emergence group males went straight into territories which were vacant due to mortality, with only 27% being non-territorial before being able to obtain a territory.

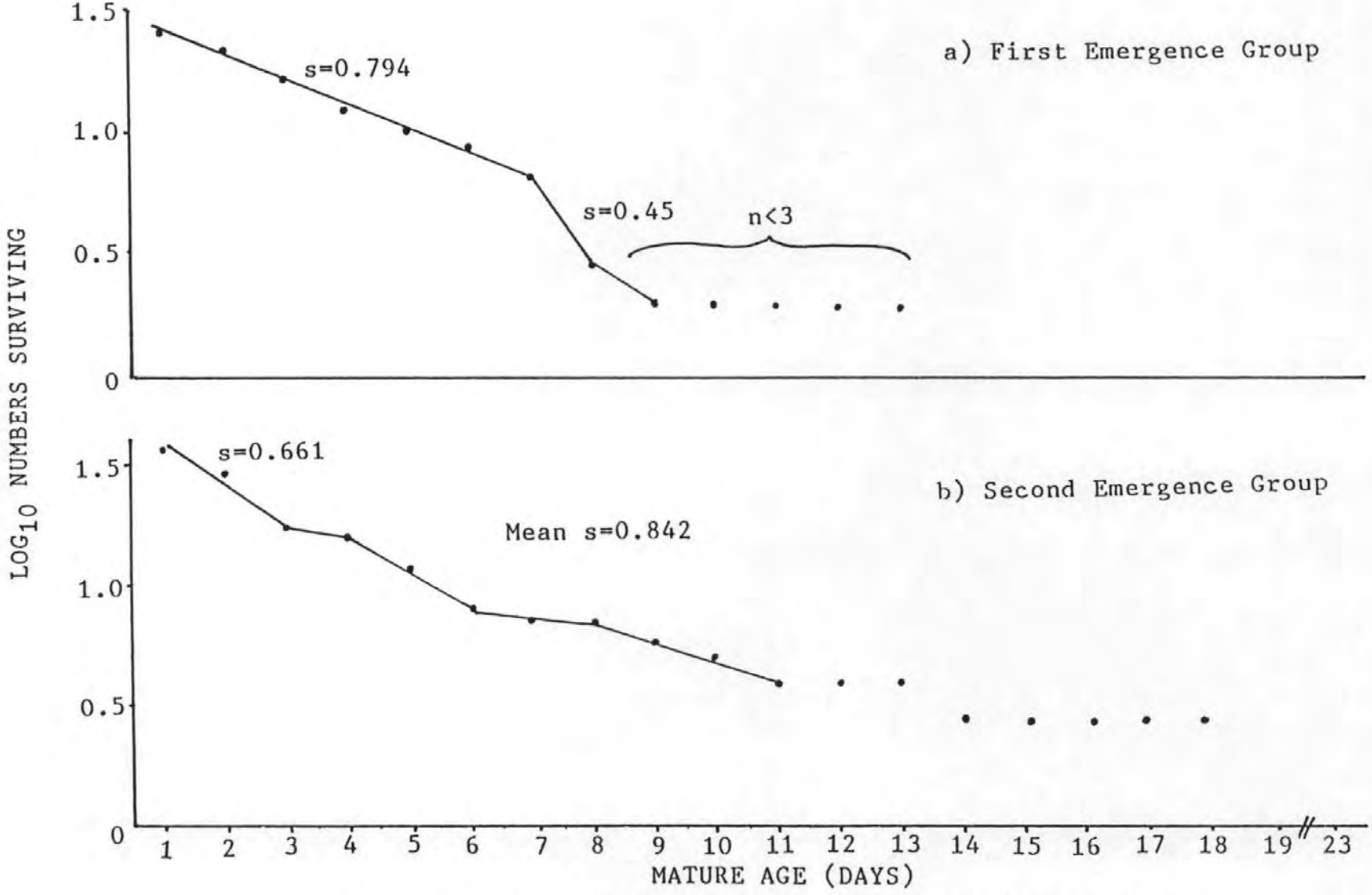


FIGURE 8.33 THE SURVIVORSHIP CURVES FOR MATURE MALES.
s = PROBABILITY OF SURVIVAL.

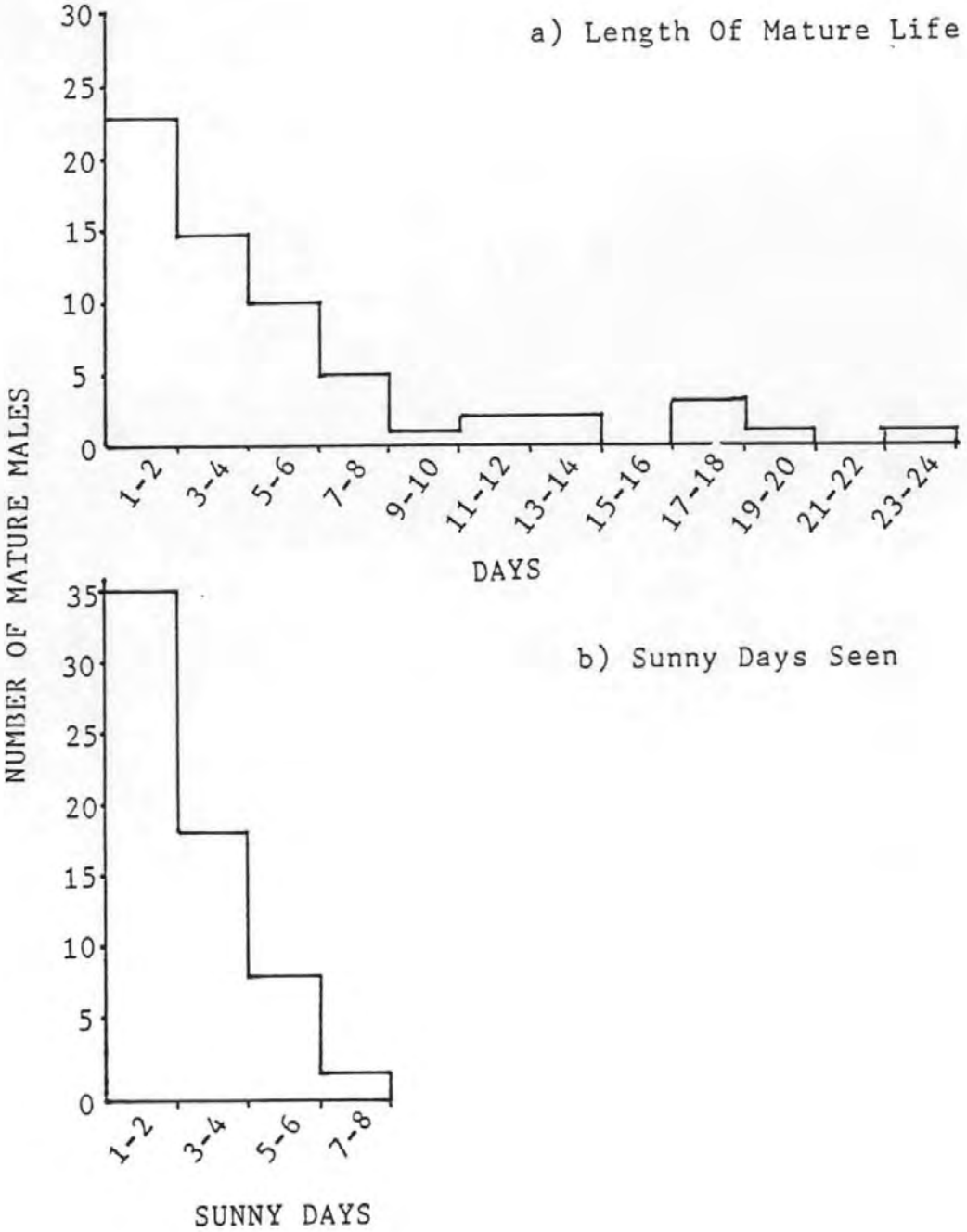
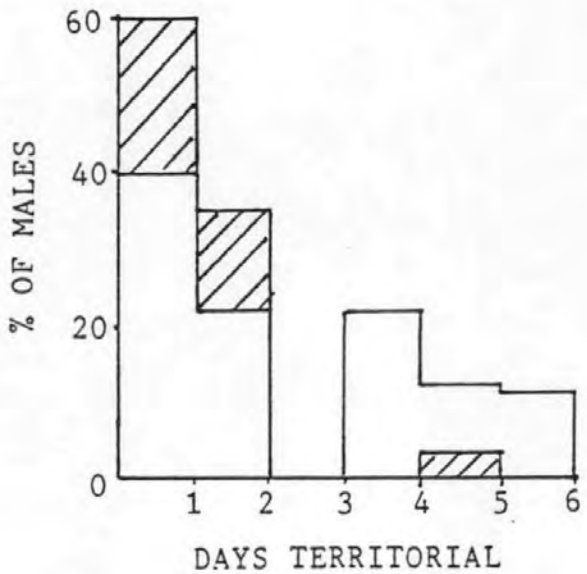
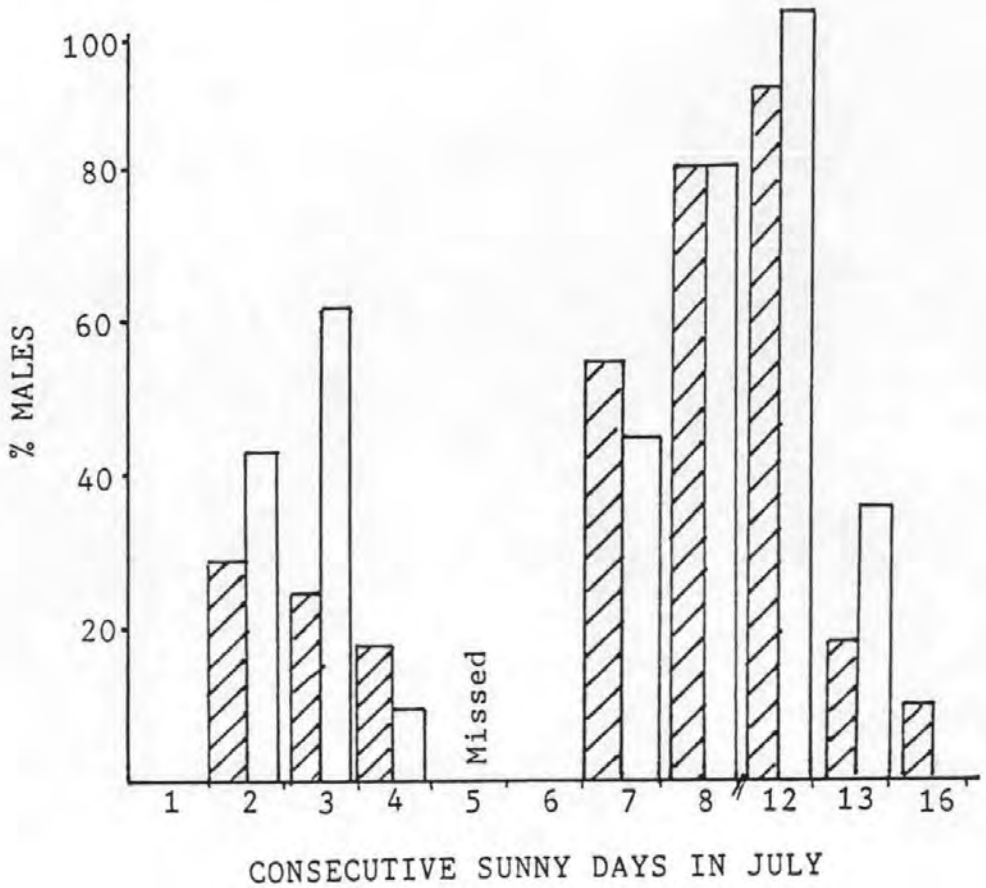


FIGURE 8.34 THE LENGTH OF LIFE AND NUMBER OF SUNNY DAYS SEEN BY MATURE MALES



Key
First Emergence Group Males
Second Emergence Group Males

FIGURE 8.35 THE NUMBER OF DAYS MALES FROM THE TWO EMERGENCE GROUPS WERE TERRITORIAL



Key
Males vacating Territories
Males Taking Up Territories

FIGURE 8.36 THE TURNOVER OF TERRITORIAL MALES FROM ONE SUNNY DAY TO THE NEXT, EXPRESSED AS A PERCENTAGE OF THE NUMBER OF TERRITORIAL MALES PRESENT ON THE PREVIOUS SUNNY DAY

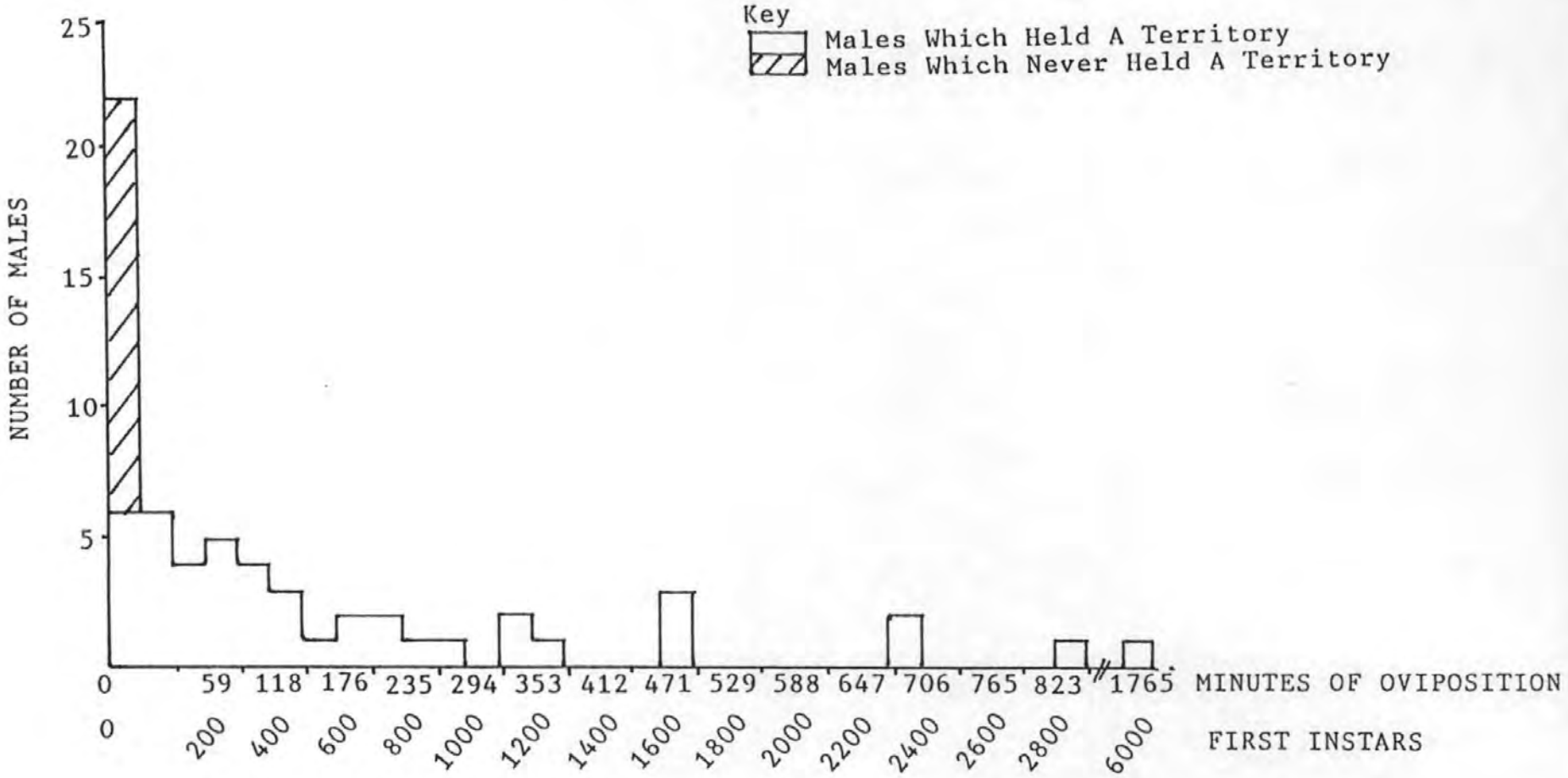


FIGURE 8.37 THE LIFETIME REPRODUCTIVE SUCCESS OF MATURE MALES

The variation in lifetime reproductive success, shown in Figure 8.37, reflects the variation in average daily eggs fertilised. While most males fertilised 0-500 eggs in a lifetime, a few potentially fertilised up to 2800 eggs. One exceptional male from the second emergence group presided over the laying of 6000 eggs. This male arrived on the 6th July and survived the episode of high bird predation which enabled him to control an unusually large, high quality territory on the 7th and particularly 8th of July, while numbers of other males were temporarily low.

8.8.3 Discussion

a) The importance of body size

i) Females

The mortality of mature females was random with respect to both age and body size, and can probably be largely attributed to bird predation (see Figure 6.11). The pattern of weather within females' lifespan was also the result of random weather patterns. Consequently the number of sunny days females survived to see, the most important determinant of lifetime reproductive success through its influence on clutch number, was influenced entirely by random factors. In most other species where the variance in female lifetime reproductive success has been analysed, survival is a significant, or more often the most important component and has been found to be unrelated to body size (S.danae, Michiels and Dhondt 1991, Enallagma hageni, Fincke 1986 and Plathemis lydia, Koenig and Albano 1987). In contrast to these studies Banks and Thompson (1987b) did find a weak

positive relationship between female size and survival in C.puella, resulting in a significant positive relationship between female size and clutch number, and hence lifetime reproductive success. Banks and Thompson study was confined to females whose lifespan fell within a period of continuously fine weather in order to control for the complicating variable of weather patterns. When the influence of random weather conditions on a model population of C.puella was examined, Thompson (1990) concluded that lifetime egg production would be largely determined by the number of sunny days they survived to see, which would be largely influenced by random weather patterns.

Clutch size, a secondary but still significant factor to lifetime reproductive success was not related to body size in this study. Although it has been found in the laboratory that larger females produce larger clutches (E.hageni, Fincke 1986, Ischnura graellsii, Cordero 1991), this has not yet been demonstrated in the field. There was no relationship between clutch size and body size in the field in S. danae (Michiels and Dhondt 1991), P.lydia (Koenig and Albano 1987) or P. nymphula (Gribbin and Thompson 1990). Unusually, in a field study of C. puella it was found that smaller females produced larger clutches where these were produced on consecutive days, but there was no relationship between body size and clutches produced after longer intervals (Banks and Thompson 1987b). For the longer interval clutches the time interval itself and temperature during the interval were the main influences on clutch size.

Most mature females lived a short time compared to the maximum mature lifespan, as is often found in other species of Zygoptera (Banks and Thompson 1987b, Fincke 1986). This, combined with the random nature of mortality probably explains the lack of any sign of trade-offs between the components of reproductive success, such as clutch size and clutch number. Even if females who produced smaller clutches had the ability to live longer, this would not be apparent in a population which survived for such a short time, and whose mortality was the result of random predation.

It is remarkable that females produced a clutch on almost every sunny day they survived to see, particularly because it is assumed here that females were not able to mature clutches on intervening poor weather days when they were usually not able to feed. Gribbin and Thompson (1990), however, observed that clutches which P.nymphula produced after spells of poor weather were larger than those produced on successive days, indicating that some species can mature clutches when not able to oviposit, possibly depending on the influence of temperature on feeding behaviour. Females of C.virgo were often observed to produce successive clutches on days when the weather allowed, indicating that the rate of clutch production is likely to be high even over successive days. Similarly high rates of clutch production have been found in Erythemis simplicicollis (McVey 1988) and P.lydia (Koenig and Albano 1987), although E.hageni takes on average 5.1 days to mature clutches. From clutch size data for C.puella, Banks and Thompson (1987b) show that females would maximize the number of eggs produced in their lifetime by

producing frequent small clutches rather than occasional larger clutches. The authors propose that frequent clutches would therefore be expected, provided that the probability of mortality during copulation and oviposition was not much higher than during feeding. The probability of mortality during copulation and oviposition in C.virgo is low, since copulation is very brief and oviposition is above water where females are hidden amongst vegetation. Although breeding behaviour can trigger higher bird predation, this increased mortality is felt by the whole population (see 7.4) and is not a cost associated only with ovipositing. The above theory may therefore explain the high rate of clutch production in C.virgo. In addition, given the importance of random weather patterns to reproductive success (see above), females would benefit from returning to oviposit as freqently as possible while good weather lasts, and more numerous clutches and mates would spread the risks of localised egg or larval mortality and the inheritance of poor genes.

ii) Males

Male body size was important to the lifetime reproductive success of first emergence group males, through its influence on territory acquisition and territory quality, but not to second emergence group males. This was not due to larger males from the first group arriving at the oviposition sites before smaller ones, taking up the best territories and then being able to hold onto them. In fact most males from the first group were mature before the 1st July, and arrived simultaneously to take up territories. There was also a turnover of territorial males in the high quality territories

from the 1st to the 4th of July, with thirteen males occupying six to eight sites at various times, and only three of the original six males remaining on the 4th of July. Large males from the first emergence group may have been relatively more competitive than large males from the on average, smaller sized second group, but it is difficult to see why this should be so.

The most probable explanation for the different influence of body size lies in the different conditions of predation and weather encountered by the two emergence groups, which led to the second group experiencing much higher mortality from one sunny day to the next than the first group. Males from the first group, who arrived almost simultaneously, had to fight to obtain territories as indicated by the high number seen initially as non-territorial and the number of disputes witnessed directly. In contrast males from the second group arrived over a number of days as they matured, and often went straight into territories which were vacant due to the higher mortality. Differences in mortality were also reflected in the lower turnover of territorial males from the first emergence group, and the strong trend that the early emerging males held territories for longer than later emerging ones. The differences in mortality from one sunny day to the next therefore led to differences in the levels of competition experienced by the two groups of males. Body size was important to first emergence group males because they experienced strong competition for territories and it influenced competitive ability. There was very low

competition for territories among second emergence group males, and as a result body size did not influence territory acquisition or defence.

Marden and Waage (1990) have recently explored the factors which influence the outcome of prolonged territorial disputes in C.maculata, and found that it was energy reserves rather than any aspects of body size which separated the winners from the losers. Although their study showed the importance of energy reserves it does not preclude the importance of body size, since the results are based on thirteen staged and eleven natural contests, and did not necessarily involve males with the full population range of body sizes. It is possible, for example, that the disputed territories were rather poor, or rather good in quality, and males competing for them were of similar size. This particularly could be the case if males only embark on protracted disputes with other males of similar size. Their study also does not compare the features of territorial males with those which were not able to obtain territories. It seems possible that energy reserves over the range of population sizes might correlate with body size, particularly if larger males are those which have fed better in a food limited population of larvae, and have an innate ability to feed well. The results of Marden and Waage's study therefore do not necessarily conflict with the findings here, that when the level of competition is high body size is important to success in acquiring good quality territories in Calopteryx.

In recent studies a large body size has been found to be an advantage to territorial males in Megaloprepus coerulatus, where larger males won more territorial disputes (Fincke 1992), in P.lydia where larger males experienced a higher daily mating rate and in N.pygmaea where larger males were more likely to control top ranked territories (Tsubaki and Ono 1987). Often a large body size is found to be of no advantage to territorial males, for example in S.rubicundulum (Van-Buskirk 1987b) and E.simplicicollis (McVey 1988), giving an inconsistent picture of the importance of a large body size to territorial males. It is possible that the reason for this inconsistency may be variation in the level of competition. The level of competition may vary with the distribution and abundance of territories, but as this study shows it can also vary as a consequence of the level of mortality experienced by territorial males from one sunny day to the next. Differences in the level of competition may also explain why two studies of P.nymphula gave different results of the importance of body size. Gribbin and Thompson (1991) found that intruders invariably lost encounters regardless of their relative size, but Harvey and Corbet (1985) found that territory owning males were larger than the general population.

There are very few studies which look at the importance of body size to lifetime reproductive success in species where body size is important to territorial behaviour. Koenig and Albano (1987) report stabilising selection in P.lydia, since, while larger males had a higher mating rate smaller males lived longer, and there was strong covariance between

the components of lifetime reproductive success. While body size was significantly positively correlated with lifetime reproductive success in N.pygmaea, it was the only insignificant variable in a multiple regression which also included the number of sunny days seen and sunny days in a top ranked territory (Tsubaki and Ono 1987). The importance of size relative to survival and weather in N.pygmaea is therefore hard to assess since survival, weather conditions and territory rank have been confounded. Body size obviously has the potential to be important to lifetime mating success in N.pygmaea though, and it seems inappropriate to dismiss it completely (eg Fincke 1992). In non-territorial species stabilising selection for body size is often reported (Fincke 1986 and Banks and Thompson 1985)

Body size was not related to survival in male C.virgo, and this is commonly found in other species (eg P.lydia, Koenig and Albano 1987, M.coerulatus, Fincke 1992 and S.rubicundulum, Van Buskirk 1987). A large body size has been related to survival in N.pygmaea, but Tsubaki and Ono (1987) note that this effect could be due to early emerging larger males experiencing better weather; and also in S.danae (Michiels and Dhondt 1991), but this result is based on a field enclosure experiment where natural predators may have been excluded.

The mortality of mature males was greater than that experienced by females, probably because males were more conspicuous to birds. As a result of high predation and the pattern of weather, males lived to see very few sunny days,

and were territorial for a very short time compared to their potential mature lifespan. The short time that males held territories explains the lack of any trade-offs between daily eggs fertilised and days territorial. Males suffered such high mortality in all territories that any potential relationship was not manifest.

b) The effect of date of emergence

The date of emergence influenced the reproductive success of males and females. There was a trend that males from the early emergence group held territories longer than those from the late group, and early emerging females produced more clutches. In females these differences led to early emerging females having significantly higher lifetime reproductive success than late emerging ones. Such differences however were the result of weather patterns, and the density triggered bird predation (see 7.4) which led to the early emerging group surviving to see more sunny days than the later group, and were not due to intrinsic differences between the emergence groups. Weather patterns are random and either group could experience better weather than the other. The density triggered bird predation, however, appeared to be a regular event, and it is likely that in this population early emerging adults which survive to maturity may subsequently have higher survival than later emerging ones. Mature females from the early emerging group may regularly have the potential for higher reproductive success than later females, but whether this can be realised will depend on weather conditions.

Where other studies have found an effect of emergence time on reproductive success it is often the early emerging adults who had the advantage. Higher lifetime reproductive success was experienced by early emerging females in E.hageni, and males in P.lydia since these lived longer than later emerging adults (Fincke 1986, Koenig and Albano 1987), and by early emerging females of P.lydia who had shorter inter-clutch intervals. Body size, which declined through the season, was not related to these differences, and the reason for them is not clear. Other studies have found that weather conditions, which are random through the season, are responsible for early emerging adults having an advantage through the number of sunny days adults survive to see (Tsubaki and Ono 1987), and also through the influence of weather patterns on clutch size (Gribbin and Thompson 1990). It seems likely that weather patterns may often explain such differences, and Anholt (1991) found that random weather patterns resulted in different emergence groups having the advantage in two consecutive years. The trend for early emerging adults having a survival advantage does however suggest that the cause is not entirely random, and density-triggered predation may also be involved.

8.9 COMPARING THE EXPERIMENTAL SITUATION IN 1987 WITH THE NATURAL CONDITIONS EXPERIENCED IN 1985 AND 1986

The results of the analysis of lifetime reproductive success were derived from an experimental rather than a natural field situation, and are based on one year's data. It is possible, however, to compare various parameters of

lifetime reproductive success between the experimental manipulation in 1987 and previous years. Such a comparison will allow an assessment to be made of the extent to which the results from the experimental year are representative of other years. The difference between a natural situation and the experimental situation lies in the distribution and number of potential oviposition sites. The extent to which the experimental distribution of oviposition sites mimics a natural situation depends on the time of year and the weather. During the early summer in settled weather usually small scattered amounts of vegetation trail in the water, with only occasional large patches. During these times oviposition sites tended to be more scattered than in the experimental set-up, but the patchy nature of their distribution led to obvious oviposition 'hot spots' over which many males fought. Later on, and/or after wind or rain vegetation tended to fall into the water in large patches, and the resulting distribution along the Leat was very similar to the experimental design, with males fighting to establish territories in large patches of fallen vegetation.

For females the influence of the experimental design on the results obtained is likely to be negligible. Any small differences in the distribution of oviposition sites between the experimental and natural situation are unlikely to affect significantly the population variation in clutch size or clutch number. How typical then were the results in view of general conditions such as levels of predation and weather patterns? The main source of variation in the lifetime reproductive success of females in 1987, the variation in

number of sunny days females survived to see, was influenced by survival and random weather patterns. The density triggered bird predation played a significant part in the amount of variation in survival between females in 1987. The fact that this predation also occurred in 1986 (and there was also evidence of bird predation in 1985), indicates that it is probably a regular event for this population, and possibly others in similar woodland situations. The mature lifespan of females in 1986 was similar to those in 1987, with most individuals living one to eight days, a much shorter time than the maximum observed time of twenty seven days (Figure 8.38a). As in 1987, the effect of the timing of the bird predation in 1986 resulted in mature females from the second emergence group having a significantly shorter lifespan and seeing significantly fewer sunny days than those from the first group (Table 8.12). As a result a two-tailed Kolmogorov-Smirnov test which is sensitive to centrality, skewness, and most importantly here, dispersion, showed that there was no significant difference in the distribution of the number of sunny days seen by mature females in the two years ($D=0.1039$, $P=0.956$). It seems fair to assume, therefore, that the number of sunny days seen by mature females was just as variable in 1986 as in 1987. Since it is unlikely that the variability in the rate of clutch production would have differed between years, it follows that clutch number is likely to have been as variable in 1986 as 1987. It is also unlikely that the variability in clutch size will have differed between years (especially since there was no difference in the variability in body size- see Chapter Five). Therefore the 1987 results that clutch number

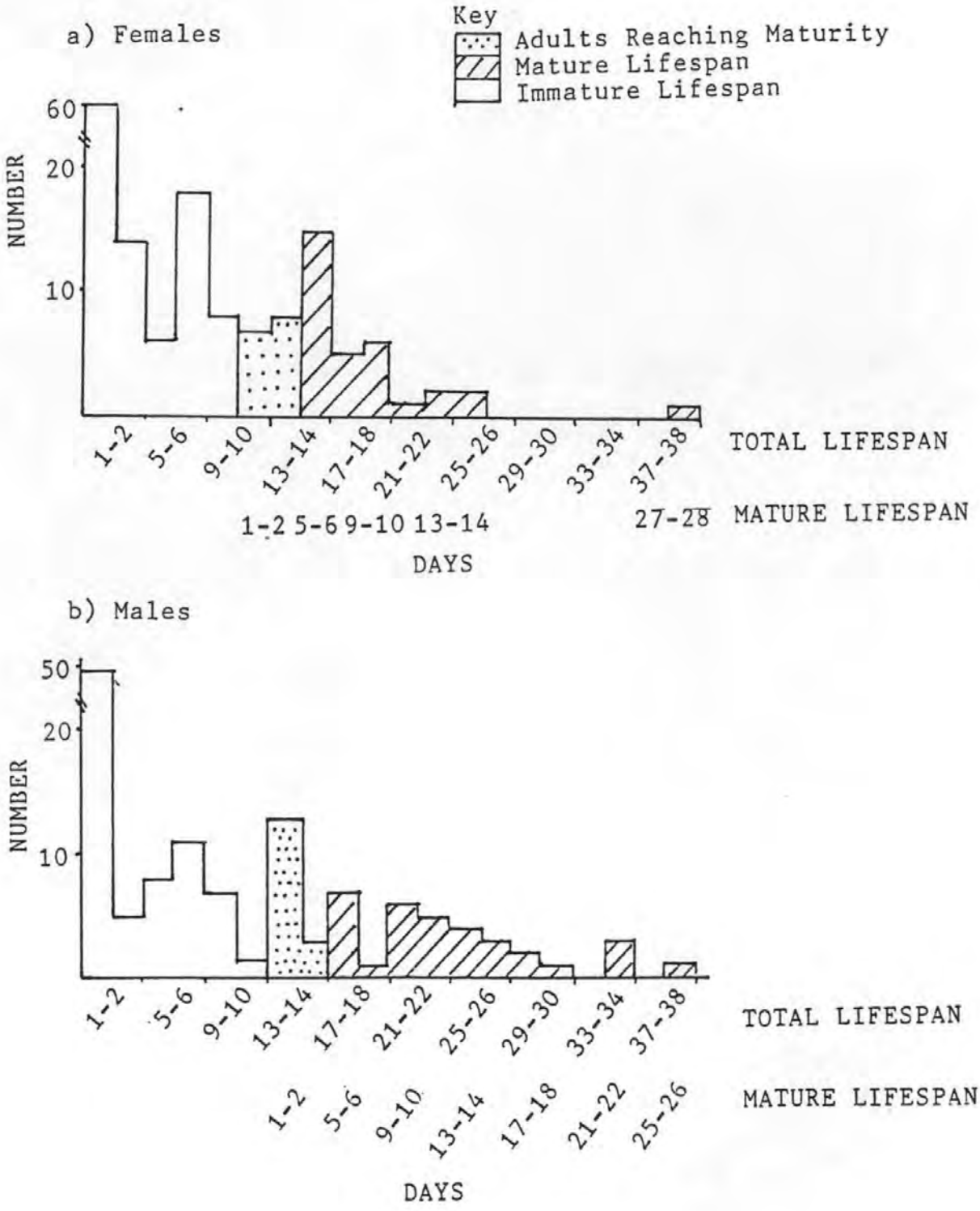


FIGURE 8.38 THE SURVIVORSHIP OF ADULTS PRESENT IN 1986

	Emergence Group	n	Mean	Median	U	P
Mature Length Of Life	EM1	23	4.48	4.00	421.5	0.0167
	EM2	8	2.75	1.00		
Days Suitable For Oviposition Seen	EM1	30	2.567	2.00	774.5	0.033
	EM2	15	2.067	1.00		

TABLE 8.12 A MANN-WHITNEY U TEST OF THE LENGTH OF MATURE LIFE AND DAYS SUITABLE FOR OVIPOSITION SEEN BY FEMALES FROM TWO OF THE EMERGENCE GROUPS IN 1986

influenced mainly by sunny days seen was the most important component of lifetime reproductive success is likely to be representative of females in 1986. There was no indication that body size influenced survival in either year class (see Chapter Six). Since it is unlikely that birds could distinguish between large and small damselflies among adults of this species, body size is unlikely to be important to female lifetime reproductive success if bird predation is the major cause of mortality.

In males the number of oviposition sites relative to the number of mature males will affect the general level of competition, and the distribution and quality of oviposition sites will be fundamental to the variation in territory quality and hence variation in daily reproductive success- the component found to have most influence on lifetime reproductive success in 1987. As discussed above, the experimental arrangement of oviposition sites often mimics that found naturally. Nevertheless it is important to try to compare the variation in male territory quality between 1987 and 1986 in order to see how well the experimental situation resembled a natural one. The proportion of males which were unable to obtain territories in their lifetime may give an indication of the general level of competition. In the experimental situation 42% of males never held territories (including males outside the experimental area). It was not possible to measure the proportion of non-territorial males in previous years, and although the figure in 1987 seems high it resembles other populations of Zygoptera. McVey (1988) reports that 44% of the territorial males of E.simplicicollis

were unable to obtain territories, and 41% of the non-territorial males of E.hageni did not have the opportunity to breed (Fincke 1988). Although in 1987 breeding behaviour was concentrated into one thirty metre section, this did not result in an unusually high density of mature males there. In 1986 there were usually around twice as many mature males along the Leat as in 1987 and many territorial males in 1986 concentrated naturally in sections F and H. From the 27th of June to the 13th of July 1986 14-19 (mean=17.5) territorial males were recorded along the south bank of section F, whereas in 1987 there were typically 10-11, with a maximum of 13. In addition maximum densities of six mature males per ten metres in section F in 1987 was much lower than other records for Calopteryx: 18 males/10 metres in C.maculata (Waage 1972), 30-60 males/10 metres in C.splendens (Zahner 1960) and 47 males/10 metres in C.virgo (Pajunen 1966). The experimental design did not therefore create unusually high levels of competition to obtain a territory.

The variation in territory quality is likely to depend on the degree of aggregation of ovipositing females along the bank. Where females are well dispersed territorial males are likely to be able to defend territories of equal quality. As oviposition becomes aggregated some males may be excluded from the good sites, as were the males in the L patches in 1987. So little oviposition was seen in previous years that it was not possible to look at the aggregation of females directly. However since territory size varied depending on the amount of oviposition along the bank, variation in territory size might give an indication of the potential

aggregation of females. Figure 8.39 and Table 8.13 show that average territory size was smaller in 1987 than in previous years, reflecting that a greater proportion of males were in areas of bank with high oviposition. Variance in territory size, judged by the mean to variance ratio, was slightly less in 1987 than other years, suggesting that the variance in daily reproductive success was less if any thing than in a natural situation. Although the number of adults was very low in 1985, the large variance in territory size, with some males aggregated in small territories, indicates that oviposition is aggregated even when there are few females. Variation in territory quality is likely to be high therefore in this and other (Waage 1979b) Calopteryx populations.

Mature males in 1986 were observed to live for one to eighteen days (Figure 8.38b), longer than most in 1987 who lived one to eight days. A Kolmogorov-Smirnov test showed that despite this there was no difference in the distribution, and hence variability, of sunny days seen by males from the two years ($D=0.190$, $p>0.1$). Given that there was unlikely to be a difference in the variation in the proportion of time that males were able to defend territories, the variation in the number of days males held territories is also likely to be similar in 1986 and 1987. It follows that the relative importance of the components of lifetime reproductive success of males in 1986 was likely to be similar to males in 1987, with variation in daily reproductive success being paramount.

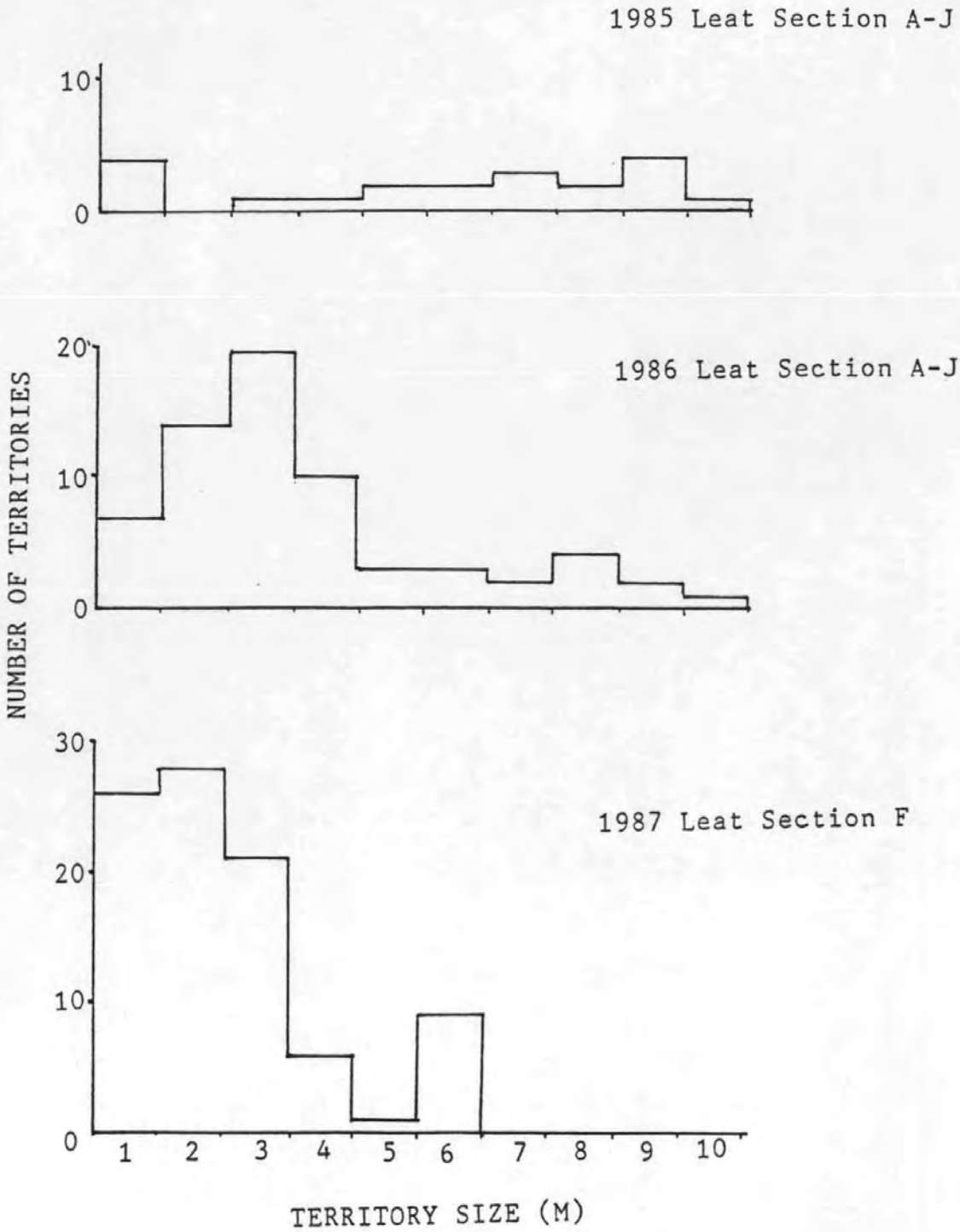


FIGURE 8.39 THE DISTRIBUTION OF TERRITORY SIZES 1985-1987

	n	Mean	S^2	I
1985	20	5.8	9.326	1.61
1986	66	3.667	4.841	1.32
1987	91	2.505	2.230	0.89

I = Index Of Dispersion

TABLE 8.13 A COMPARISON OF THE DISPERSION OF TERRITORY SIZES 1985-1987.

Despite the likelihood that many males would have been unable to obtain territories in 1986 and that there was significant variation in territory quality, there was only a weak effect of body size on territory acquisition and no sign that it affected territory quality (see Chapter Seven). The results in 1987 show that body size does influence the competitive ability of males, but this is not manifest in populations where the level of competition is reduced by high mortality from one sunny day to the next, and this may explain the lack of importance of body size in 1986. In 1987 the background average mortality from one sunny day to the next during which body size influenced territory quality was observed to be between 0.2-0.3. Before the increase in bird predation in 1986 there were only sufficient data to look at body size and territory quality on two days, the 9th and 13th of July. During this time daily mortality was lower than background levels in 1987, but the weather was much more unsettled, and the cumulative mortality between sunny days was 0.52 (from the 3rd to 9th July), and 0.38 (from the 9th to 13th July). After the 13th July in 1986 mortality increased due to bird predation, and the weather continued to be unsettled resulting in high mortality from one sunny day to the next. Body size therefore has the potential to be important to lifetime reproductive success in males, but whether this potential is realised depends on levels of predation and random weather patterns. In 1985 there was a prolonged spell of fine weather as in 1987, and it seems likely that the influence of body size on lifetime reproductive success will be very variable from year to year. It can be predicted that in populations which experience

stable fine weather and low mortality body size will be important.

CHAPTER NINE

GENERAL DISCUSSION

9.1 DIFFICULTIES IN DETECTING FEEDING COMPETITION, AND ITS IMPORTANCE AS A REGULATORY FACTOR IN NATURAL POPULATIONS OF LARVAE

Density dependent feeding competition in larvae may result in population regulation through increased mortality during an extended larval period, and this will be associated with decreased body size. Crowley et al (1987b) note that size at emergence will be correlated with larval stage duration and hence through stage survival, but care needs to be taken in accepting the assumption that later emergence and smaller body size will be an indication of a longer larval period due to feeding competition. The Leat population has shown that later emergence at a smaller body size can be unrelated to density, and may result from late or delayed hatching, and the coincidence of growth with higher seasonal temperatures resulting in faster larval development. As a result of the complex influence of temperature and prey density on growth patterns and body size, great care is needed in the interpretation of larval growth data from natural populations. In particular, comparisons between populations or year classes must be interpreted judiciously, since these may have experienced very different environmental conditions. It is tempting, for example, to conclude that the smaller body size and later development of the 1984 year class of the Leat population was due to its higher density, but detailed examination of the data found no evidence for

this conclusion. The degree of asynchrony in growth, and resulting emergence pattern, can also vary with prey density, temperature and the length of the emergence window (Crowley et al 1987b). As a result, populations can be expected to show a variety of growth patterns, and conclusions about density effects may be difficult to make when only a small number of populations is included (eg Banks and Thompson 1987a). The inclusion of a large number of populations in comparative studies is likely to be necessary when looking for trends which may be due to density (eg Baker 1989), and controls may be more easily made within populations. The fact that environmental variables can cause trends in the pattern of growth and body size similar to those expected from larval competition does not lessen the potential importance of the latter. Only changes in growth due to larval density will be density dependent and hence, where mortality is increased, potentially regulatory.

The lack of evidence for density dependent feeding competition in the larval data suggests that it is not a potential regulating factor in the Leat population, and similar results have been found in the majority of the small number of studies of natural populations so far conducted. Such results are contrary to evidence from laboratory and field experiments, which would lead us to expect larval competition to be commonplace. The effective density of larvae, that is the number of larvae per area of substrate (such as plant material) over which they interact, will be critical in influencing larval competition (Uttley 1980). It is likely that in natural environments habitat complexity is

greater than that achieved in field experiments such that effective densities are in fact often lower in natural populations. In addition, larvae in natural populations are able to move over greater distances in response to density, and high densities may be short-lived due to predation. The importance of habitat complexity is perhaps demonstrated by the fact that the only natural population where strong evidence for feeding competition was found occurred in a very simple environment (Van Buskirk 1992), and it is possible that it is in species existing in simple habitats, eg pioneering species such as Ischnura pumilio, that effective densities may reach levels where feeding competition will be important. If circumstances where interference behaviour is advantageous are uncommon in natural populations, it begs the question of why strong interference behaviour can be commonly seen in the laboratory. It is possible that the interference behaviour where larvae become distracted, reduce movement and compete to maintain perches (where they can remain immobile) could have evolved as anti-predator responses, and it is coincidental that this behaviour also reduces feeding rates at high larval densities.

Although uncommon, weak evidence for competition in natural populations in typical habitats has been found by Baker (1987), and a weak density effect was detected in the Leat population in the high density area of the high density year class. Since the strength of density dependent effects is likely to increase in a non-linear way with density (Sinclair 1988 and references therein), they are only likely to be detected at high densities. It is not surprising,

therefore, that so far evidence for feeding competition in natural populations of Odonata is uncommon when studies have been short term (Hassell et al 1989), and no attempt is made to conduct them when the population of small larvae is known to be, or likely to be, at high density. Although behaviour or growth are often compared at different densities, without long term knowledge of the dynamics of the population it is not possible to say whether the high densities monitored represent peaks in density fluctuations. Had this study been conducted when it was known that larval density was at a peak, it could have been predicted with confidence that larval competition is not important. In fact, detailed monitoring of larval growth was conducted when larval density was relatively low. The sign of a possible density effect at the highest density that was chanced upon indicates the need either for long term studies, or where short term for target studies on populations at peaks of density fluctuations. Comparisons between populations may be a way of picking up fluctuations in density in the short term, but environmental variables may make it difficult to attribute differences in larval growth to differences in density.

Crowley et al's model of damselfly population dynamics showed that strong density dependent predation results in the numbers of later instars varying little in response to variations in density independent factors, such as an influence of weather on female fecundity. Consequently numbers of later instars (and hence adults) remained low and very stable. Feeding competition is more likely to occur in later instars (Crowley et al 1987b), and the model suggests

it is unlikely in populations experiencing strong density dependent predation in early instars. This assertion is supported by the fact that circumstantial evidence for populations with multiple stable equilibria (where mortality balances production at several densities) shows that predation regulates populations at low density and competition at higher density (Sinclair 1988). Many populations in temperate climates do not show the stability in late instars or adults predicted by the model; a four-fold change in the number of territorial males was seen in the course of this study, Lawton (1971) noted a ten-fold increase in late instars and Parr and Parr (1972) a five fold increase in adults, suggesting that strong density dependent mortality in early instars is not always present. In fluctuating populations high densities of later instars and feeding competition are more likely to occur, and studies looking for feeding competition could usefully be targeted here. Constancy in the numbers of adults could, in the absence of strong predation, result from strong density dependence in feeding competition. Since starvation is uncommon in natural populations (Lawton et al 1980), and regulation through feeding competition is thought to occur by lengthening the larval period, it is likely that such competition will usually be a weaker density dependent effect than predation. The absence of predators from simple habitats may also explain why feeding competition is more likely to occur here.

Detection of a density dependent effect such as feeding competition may not mean that this is regulating the population, since it may be only one of a number of density

dependent factors which are present (Sinclair 1988). Looking for mechanisms of feeding competition in natural populations of Odonata is therefore only the start in assessing its importance as a regulatory mechanism. Density dependence has been found in most insect populations where there is sufficient data (Hassell et al 1989), and Sinclair (1988) observes that regulation appears to be caused by predation and competition in equal proportions (although Strong et al (1984) note that competition studies have been biased towards pest species). In Odonata, many more targeted, or long term studies of natural populations are needed before the importance of larval competition can be properly assessed.

9.2 THE IMPORTANCE OF A POPULATION REGULATION MECHANISM ACTING THROUGH ADULT FEMALE BODY SIZE

The results of this and other studies indicate that there is little opportunity for a population regulation mechanism acting through female body size; relationships between body size and clutch number are weak and unpredictable (Banks and Thompson 1987b, Thompson 1990), and expected relationships between body size and clutch size have not been found in the field (Koenig and Albano 1987 and Michiels and Dhondt 1991). Short term studies may again be hiding possible effects however (Hassell et al 1989). The opportunity for a relationship between clutch size and body size in the field will depend upon the variability in body size which is considered. To test the theory rigorously it is necessary to study populations when female body size is likely to be most variable due to high larval density, yet

studies are conducted at random with respect to population fluctuations. In addition the population regulation theory could equally apply where there is no change in the variance in body size between years, but body size may be significantly smaller overall in a high density year. While there may be no relationships between body size, clutch size and lifetime eggs in any one year, there may be significant relationships between years. To pick up a possible regulatory mechanism in the latter circumstance it would be necessary to relate body size to clutch size over several years.

9.3 THE IMPORTANCE OF ENVIRONMENTAL VARIABLES IN INFLUENCING THE OPPORTUNITY FOR SELECTION OF ADULT BODY SIZE AND TIME OF EMERGENCE.

The influence of body size and emergence time on adult survival to maturity and reproductive success was strongly influenced by environmental variables. The advantage of early emergence was due to density-triggered bird predation, rather than any characteristics of the adults themselves, but although the bird predation is likely to be a regular event in this population any advantage to the early emerging group could easily be lost through random weather patterns.

The importance of body size to mature males was determined by the level of competition. Conrad and Pritchard (1992) suggest that the 'resource control' mating system, where males are able to control most or all female oviposition sites would result in the highest levels of competition. The various experiments with Calopteryx have

shown, however, that even with resource control it is possible for there to be low competition between males. Only where females are sufficiently aggregated will some males be able to monopolize females to the exclusion of others, resulting in a high level of competition and an opportunity for body size to be important. Competition was always potentially high in the Leat population because females were highly aggregated in response to both vegetation quantity and quality (and this was probably assisted by ovipositing females being attracted to one another). Habitats can vary markedly in the distribution and abundance of suitable oviposition sites, both within and between populations, and the level of competition and hence importance of body size can be expected to vary accordingly. An example of the inluence of habitat differences on breeding behaviour within a species has been shown by a study of M.pruinosa, where the proportion of a non-territorial form of male in different populations varied depending on the distribution of oviposition sites (Nomakuchi 1992). While habitat differences within the typical range for the species may cause variations in the importance of body size to males in territorial systems, Nomakuchi has shown how populations outside typical habitats evolve different behavioural strategies. The level of competition between mature males was also influenced by the level of predation and the pattern of weather, such that high predation and unsettled weather resulted in high mortality from one sunny day to the next and low levels of competition. Differences in the level of competition between territorial males may explain why current studies give inconsistent results of the importance of body size, and an

understanding of the way in which environmental factors can influence the importance of body size will help to predict when it is likely to be important.

The distribution of oviposition sites, and hence the ability of some males to monopolise oviposition, will also influence the relative importance of breeding behaviour to lifetime reproductive success. Here, territorial behaviour, through its influence on daily eggs fertilised, was by far the most important influence on male lifetime reproductive success. Conversely other studies of territorial species have found survival to be the most important component, and differences in the distribution of oviposition sites may be partly responsible. In females, where survival was the most important component of reproductive success, there was no relationship with body size. Early emerging females had significantly higher reproductive success than later emerging ones, due to the density triggered predation reducing the survival of later females. Again, any advantage to the early females could be lost through random weather patterns.

If the importance of body size and the time of emergence to survival and reproductive success in the Leat population are influenced by environmental conditions which might vary from year to year, then it follows that the opportunity for selection based on these characteristics would also be variable. For example during a windy summer with an abundance of suitable oviposition sites blown into the water, and high mortality due to unsettled weather and prolonged bird predation there may be little selection of

male body size, but during a settled hot summer with few suitable oviposition sites and low mortality due to low bird predation, selection would be expected to be high. Such variability will result in weak selection in the short term, but in the long term it would exert a persistent pressure. An illustration of the importance of weak selection over the long term has perhaps been provided by Anholt et al (1991). Most studies of lifetime reproductive success in males, both territorial and non-territorial, have found that survival is the most important component (although components relating to individual fitness may be more important than authors recognise), leading authors to conclude that there is little opportunity for selection of attributes relating to breeding behaviour (Koenig and Albano 1987 and Michiels and Dhondt 1991). Despite this Anholt et al have found that in territorial species of Coenagrionidae males have much greater mass relative to females than in non-territorial species, suggesting that sexual selection for high mass has or is occurring. It is possible that the apparent discrepancy is due to the long term nature of selection, where even weak selection in the short term may influence populations over the long term. The importance of the daily reproductive success to lifetime reproductive success will give an indication of the strength of selection which may operate in any one year. If a relationship between phenotype and daily reproductive success has been identified, however, even a weak relationship with lifetime reproductive success may result in long term selection. This would be particularly true where random weather effects were the cause of low

opportunity for selection in any one year (eg Tsubaki and Ono 1987).

Extreme and unpredictable variability in summer weather, as a result of the oceanic climate, was responsible for much of the observed variability in the importance of emergence time and male body size. C.virgo is present across Europe, and in populations in similar latitudes but with more settled, continental summers, emergence time and body size may well be subject to stronger selection pressure. Conversely, high daily mortality of males, due to poor weather, in the extreme north of the species range will reduce the importance of body size.

9.4 THE INFLUENCE OF ADULT SELECTION ON LARVAL GROWTH

In the Leat population weak but long term selection in adults may exist for increased male body size and early emergence. For selection to influence larval growth the characteristics concerned must be heritable, and differences in the body size and time of emergence between sub-populations were strongly influenced by environmental variables. The advantage of large male body size was seen within an emergence group however, and the variability of size within this group could have been caused by heritable factors. In a population which is not food limited variance in size will reflect genetic variance only, but where there is food limitation variance in size will be increased due to differences in feeding ability. Finding heritable influences on emergence group is more difficult, since this is largely

perpetuated by the cycle of early and late oviposition. The tendency for females to emerge in later groups, however, suggests that the timing of emergence is influenced by factors other than the environment. While there may be no phenotypic control over the time eggs are laid, there may be phenotypic control over egg hatching time and adult emergence time.

Where size within emergence group and time of emergence are subject to phenotypic control what would be the consequence of the selective pressures identified? Population characteristics under genetic control will represent optimum states which meet different requirements. A large body size which gives males an advantage in territorial behaviour may have to be balanced against the needs of a small body size for feeding flight efficiency (Banks and Thompson 1985). The effect of continuing selective pressure in the males may be to shift the current genetic optimum towards increased body size. Where larvae are prevented from reaching optimum size by food limitation selection will favour behaviour which increases feeding rate or extends the period of growth. An increased feeding rate could be achieved through increasing activity or competitive behaviour. There may, however, be high risks of mortality associated with increased larval feeding rate (Heads 1985), and increasing the growth period, such that the benefits of increased body size would be balanced against the risk of not surviving to emergence. Under such conditions the increase in proportion of 'large' phenotypes due to increased reproductive success would have to outweigh the loss of the phenotype due to increased

feeding mortality for selection to operate. As a result of past selection females currently have a larger optimum size to achieve at emergence than males, and they do this by increasing the time spent feeding in the final instar and emerging later. Selective pressure on males also to increase body size may be seen in a closing of the body size gap between the sexes, and may be achieved by males also delaying emergence if this is less costly than increasing the feeding rate.

Later emergence to increase body size would, however, conflict with early emergence to increase the chances of survival to maturity. Later emergence in females would tend to indicate that for them achieving a large body size is more important than an inconsistent survival advantage in early emergence. Selection for early emergence could be achieved by late developing individuals delaying emergence until the following year, but again the benefits of this would need to be balanced against the costs of increased mortality. The outcome may be determined by the relative strengths of mortality during an extra period of larval life and an inconsistent advantage in avoiding density-triggered bird predation in adults. The influence of selection in adults on larval growth will therefore result from a balance of often opposing factors. Since selection in adults is inconsistent and weak, it may be unlikely to outweigh consistent, strong selection in larvae to reduce mortality.

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