A study of ground beetles (Carabidae, coleoptera) at adjacent woodland and grassland habitats in Durham, north-east England

Hatada, Yohko

Hatada, Yohko (1989) *A study of ground beetles (Carabidae, coleoptera) at adjacent woodland and grassland habitats in Durham, north-east England*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6493/

A Study of Ground Beetles (Carabidae, Coleoptera) at Adjacent Woodland and Grassland Habitats in Durham, North-East England

by

Yohko Hatada

**A Thesis submitted for the degree of
Master of Science (by Research)**

Biological Sciences

The University of Durham

1989

Abstract

Communities of Carabid beetles have been studied at adjacent woodland and grassland habitats in Durham, north-east England during the period 1988 May 12 to December 23.

From a total of 25 Carabid species identified, the data obtained on a subset of some 17 species were sufficient to permit a discussion of the biological seasons of adult individuals. Many measurements have been taken of the frequency of capture, the distance of movement, the length of the mandible tip, the ratio of the length of the abdomen to that of the elytra, the numbers and volumes of eggs, and the maturity of the reproductive organs of both sexes.

It is suggested that the results of the present work are compatible with those of previous studies of ground beetles at various habitats in north-west Europe, which have revealed a shift of the time of occurrence of the breeding and emergence seasons depending upon the harshness of the local environmental conditions.

The composition of the communities of Carabid species at the Durham woodland and grassland sites has also been investigated. The dominant species in the two habitats were found to be *Pterostichus madidus* and *Nebria brevicollis.*

To Vince and my parents

Contents

Appendix

Chapter I

Introduction

Species of Carabid beetles (family Carabidae within the order Coleoptera) may be grouped by differences in life cycle. A scheme for the sub-division of carabid beetles into several groups according to both breeding season and hibernation stage has evolved through the work of Larsson (1939), Lindroth (1945, 1949) and Thiele (1977).

Larsson (1939) employed museum samples from various parts of Scandinavia to classify Carabid species into three categories:

1. autumn breeders
2. spring breeders with autumn activity
3. spring breeders without autumn activity.

However, some species could not be classified uniquely into any one of these three groups.

Lindroth (1949) therefore suggested the use of the criteria of hibernation stages:

1. larval hibernators
2. adult hibernators.

However, the facts that females of several species reproduce more than twice in one year and that several species of autumn breeders survive after oviposition to reproduce during the following spring, have led to more detailed studies, including laboratory experiments on life cycles, with particular reference to dependence upon photoperiod and environmental temperature.

Thiele (1977) has proposed the following classification (see Table 1.1):

1. spring breeders which have summer larvae and hibernate as adults
2. species which have winter larvae and reproduce from summer to autumn but exhibit no adult dormancy
3. species with winter larvae, the adults of which emerge in spring and undergo aestivation dormancy prior to reproduction
4. species with flexible reproductive periods
5. species which require more than one year to develop.

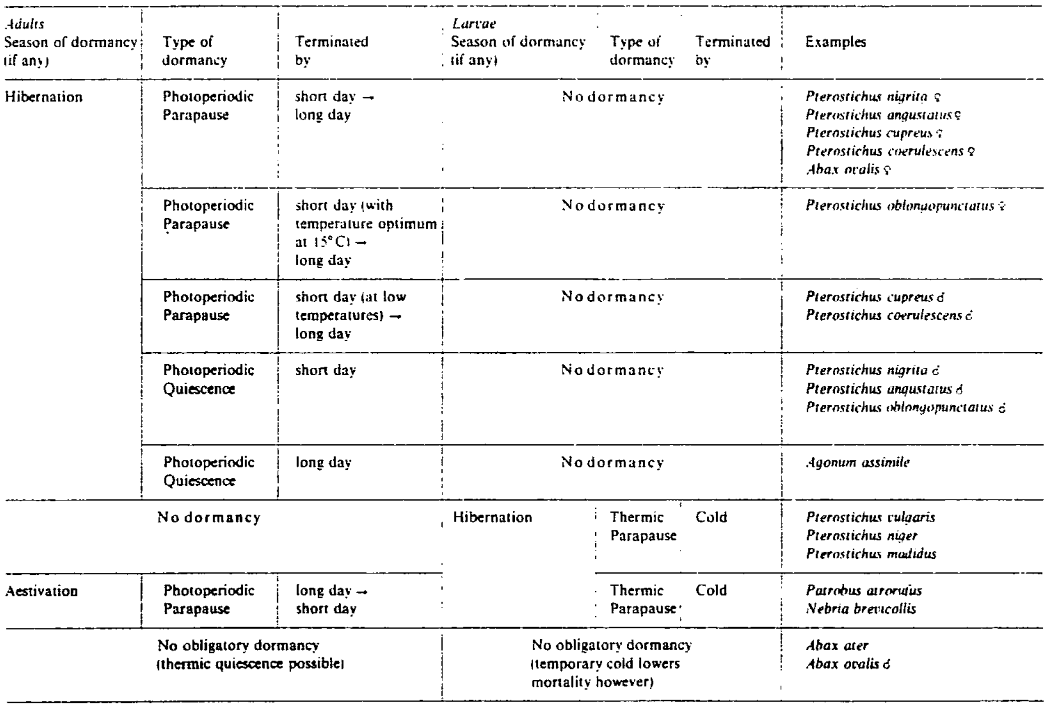
Recent studies have revealed that several carabid species display variations in life cycle with geographical location. Paarman (1979) suggested an evolutionary expansion by making a comparison of the life cycles observed from tropical to arctic zones. He divided species into 5 groups for the tropical and sub-tropical zones and 7 groups for the temperate zone. (See Table 1.2, Fig. 1.1.) In the climates of higher latitudes and altitudes, carabid beetles have a shorter period of summer activity. As a consequence they have a longer duration of development, including maturation. They are observed to have a two-year (semivoltine) life cycle in contrast to the one-year (univoltine) life cycle found at lower latitudes and/or lower altitudes. They also become more opportunist, e.g. they have a better low temperature survival rate than the lower latitude species and develop faster in optimum temperatures. On the other hand, the climates at lower latitudes and altitudes allow life cycles to be more flexible and more evenly distributed throughout the year. Further detailed studies on a larger number of species and on a wider geographical scale are important for the classification of the different types of life cycles of carabid beetles. These will assist the understanding of how Carabid beetles have spread so widely to many geographical areas .

The present study provides the results of an investigation of the life cycles of Carabidae at two adjacent habitats in Durham, northern England. The data are considered within the context of

1. life cycles of the species
2. morphological differences within a species
3. behavioural differences within a species
4. species composition.

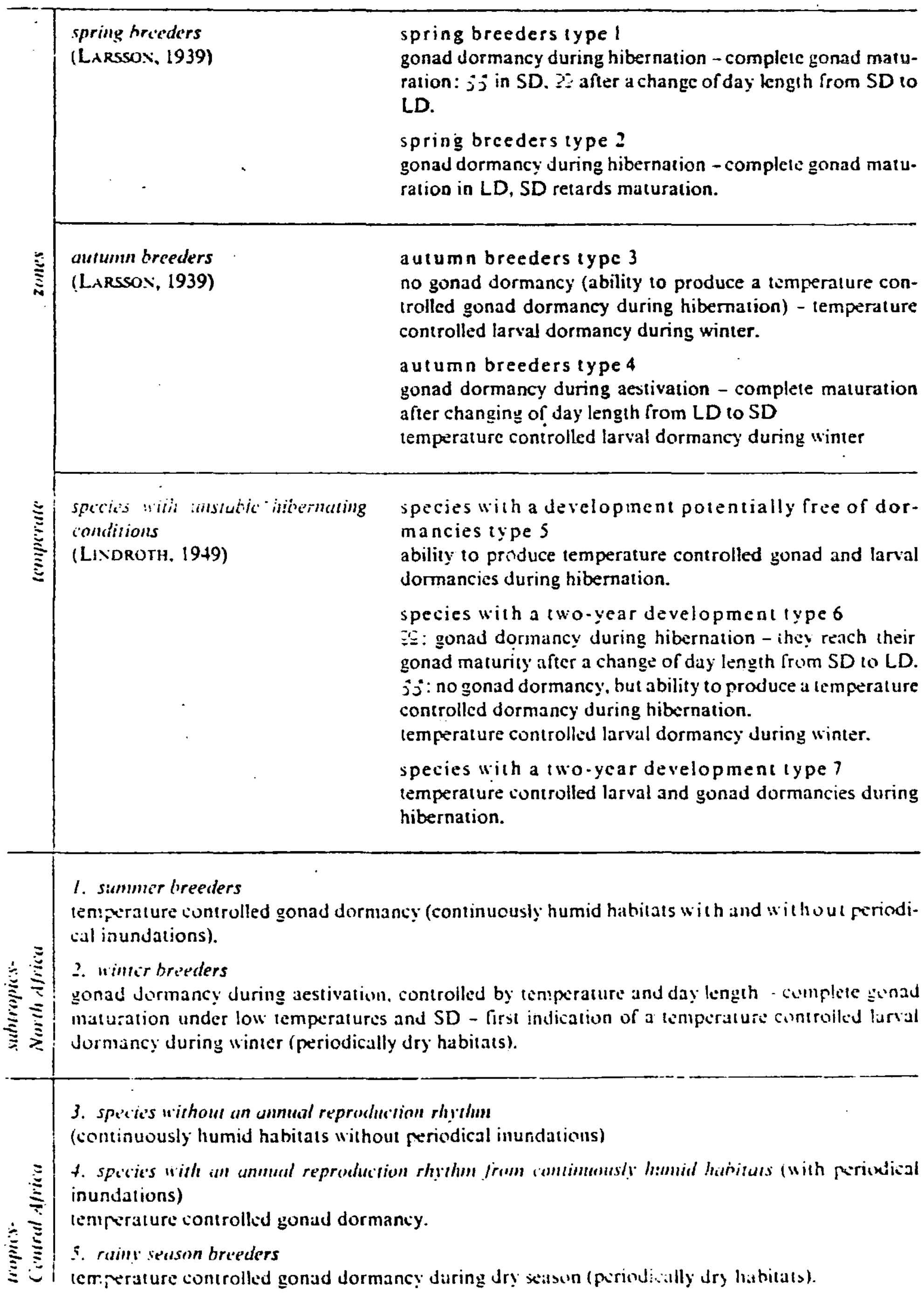
Finally, a comparison is made with the previous studies of the life cycles of Carabidae species.

<Table 1.1> Types of dormancy and dormancy control in carabids. From Thiele (1977).



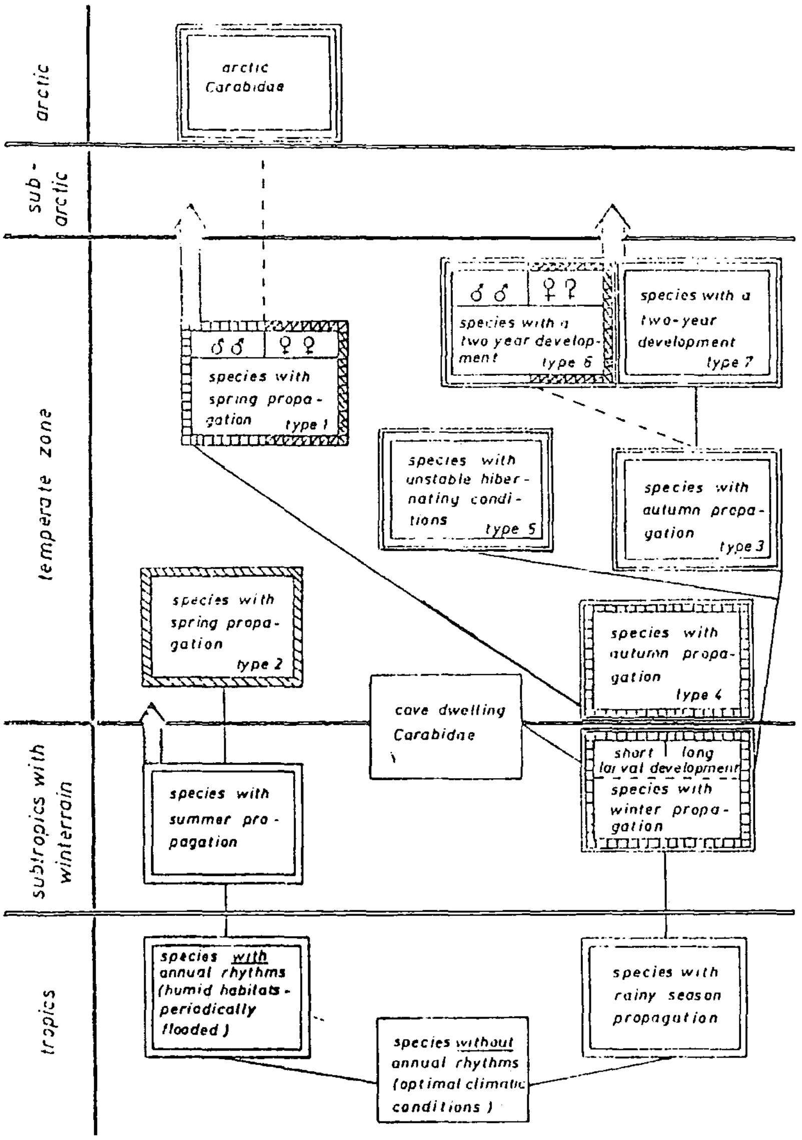
Adults Season of dormancy (if any)	Type of dormancy	Terminated by	*Larvae* Season of dormancy (if any)	Type of dormancy	Terminated by	Examples
Hibernation	Photoperiodic Parapause	short day → long day	No dormancy			*Pterostichus nigrita* ♀ *Pterostichus angustatus* ♀ *Pterostichus cupreus* ♀ *Pterostichus coerulescens* ♀ *Abax ovalis* ♀
	Photoperiodic Parapause	short day (with temperature optimum at 15° C) → long day	No dormancy			*Pterostichus oblongopunctatus* ♀
	Photoperiodic Parapause	short day (at low temperatures) → long day	No dormancy			*Pterostichus cupreus* ♂ *Pterostichus coerulescens* ♂
	Photoperiodic Quiescence	short day	No dormancy			*Pterostichus nigrita* ♂ *Pterostichus angustatus* ♂ *Pterostichus oblongopunctatus* ♂
	Photoperiodic Quiescence	long day	No dormancy			*Agonum assimile*
No dormancy			Hibernation	Thermic Parapause	Cold	*Pterostichus vulgaris* *Pterostichus niger* *Pterostichus madidus*
Aestivation	Photoperiodic Parapause	long day → short day		Thermic Parapause	Cold	*Patrobus atrorufus* *Nebria brevicollis*
No obligatory dormancy (thermic quiescence possible)			No obligatory dormancy (temporary cold lowers mortality however)			*Abax ater* *Abax ovalis* ♂

<Table 1.2> Types of annual reproduction rhythms, known from the tropics, subtropics and temperate zones (SD = short day: LD = long day). From Paarman (1979).



temperate zones	*spring breeders* (Larsson, 1939)	spring breeders type 1 gonad dormancy during hibernation – complete gonad maturation: ♂♂ in SD, ♀♀ after a change of day length from SD to LD.
		spring breeders type 2 gonad dormancy during hibernation – complete gonad maturation in LD, SD retards maturation.
	autumn breeders (Larsson, 1939)	autumn breeders type 3 no gonad dormancy (ability to produce a temperature controlled gonad dormancy during hibernation) - temperature controlled larval dormancy during winter.
		autumn breeders type 4 gonad dormancy during aestivation – complete maturation after changing of day length from LD to SD temperature controlled larval dormancy during winter
	species with 'unstable' hibernating conditions (Lindroth, 1949)	species with a development potentially free of dormancies type 5 ability to produce temperature controlled gonad and larval dormancies during hibernation.
		species with a two-year development type 6 ♀♀: gonad dormancy during hibernation – they reach their gonad maturity after a change of day length from SD to LD. ♂♂: no gonad dormancy, but ability to produce a temperature controlled dormancy during hibernation. temperature controlled larval dormancy during winter.
		species with a two-year development type 7 temperature controlled larval and gonad dormancies during hibernation.
subtropics-North Africa	*1. summer breeders* temperature controlled gonad dormancy (continuously humid habitats with and without periodical inundations).	
	2. winter breeders gonad dormancy during aestivation, controlled by temperature and day length - complete gonad maturation under low temperatures and SD – first indication of a temperature controlled larval dormancy during winter (periodically dry habitats).	
tropics-Central Africa	*3. species without an annual reproduction rhythm* (continuously humid habitats without periodical inundations)	
	4. species with an annual reproduction rhythm from continuously humid habitats (with periodical inundations) temperature controlled gonad dormancy.	
	5. rainy season breeders temperature controlled gonad dormancy during dry season (periodically dry habitats).	

<Fig.1.1> Evolutionary hypothesis of the expansion of Carabid beetles. From Paarman (1979).



The two 'lines of descent' in the annual reproduction rhythms of carabids from the different climatic zones. The different types are enclosed by differently formed frames:

—	(single)	– no dormancy
═	(double)	- gonad dormancy or the ability to produce a gonad dormancy
≡	(threefold)	– larval and gonad dormancies or the ability to produce these dormancies.

The kind of gonad dormancy is recognizable by the shape of the surrounding frame:

═	gonad dormancy only controlled by temperature or the ability to produce such a dormancy. This ability to produce a gonad dormancy controlled by temperature during hibernation is to be found in the species of the higher latitudes that are able to reach their sexual maturity potentially free of dormancies.	
▥	gonad dormancy controlled by photoperiods	- complete gonad development in SD (short day)
▨	gonad dormancy controlled by photoperiods	complete gonad development in LD (long day)
▥▨	gonad dormancy controlled by photoperiods	complete gonad development only after changing of day length from SD to LD.

The black arrows attached to some types of annual rhythm mean that members of the type also exist in the climatic zones to which the arrow points.

Chapter II

Study Area

The work was carried out from 1988 May 12 to December 23 at two adjacent habitats:

- A field station of the Department of Biological Sciencesat Hollinside Wood, Durham <Fig.2.1, Fig.2.2>.
- An adjoining grassland pasture, within which an electric fence was deployed to prevent the entrance of farm animals.

The geographical coordinates of the site are latitude 54.5°N, longitude 1.4°W and the altitude is 70–75m a.s.l.

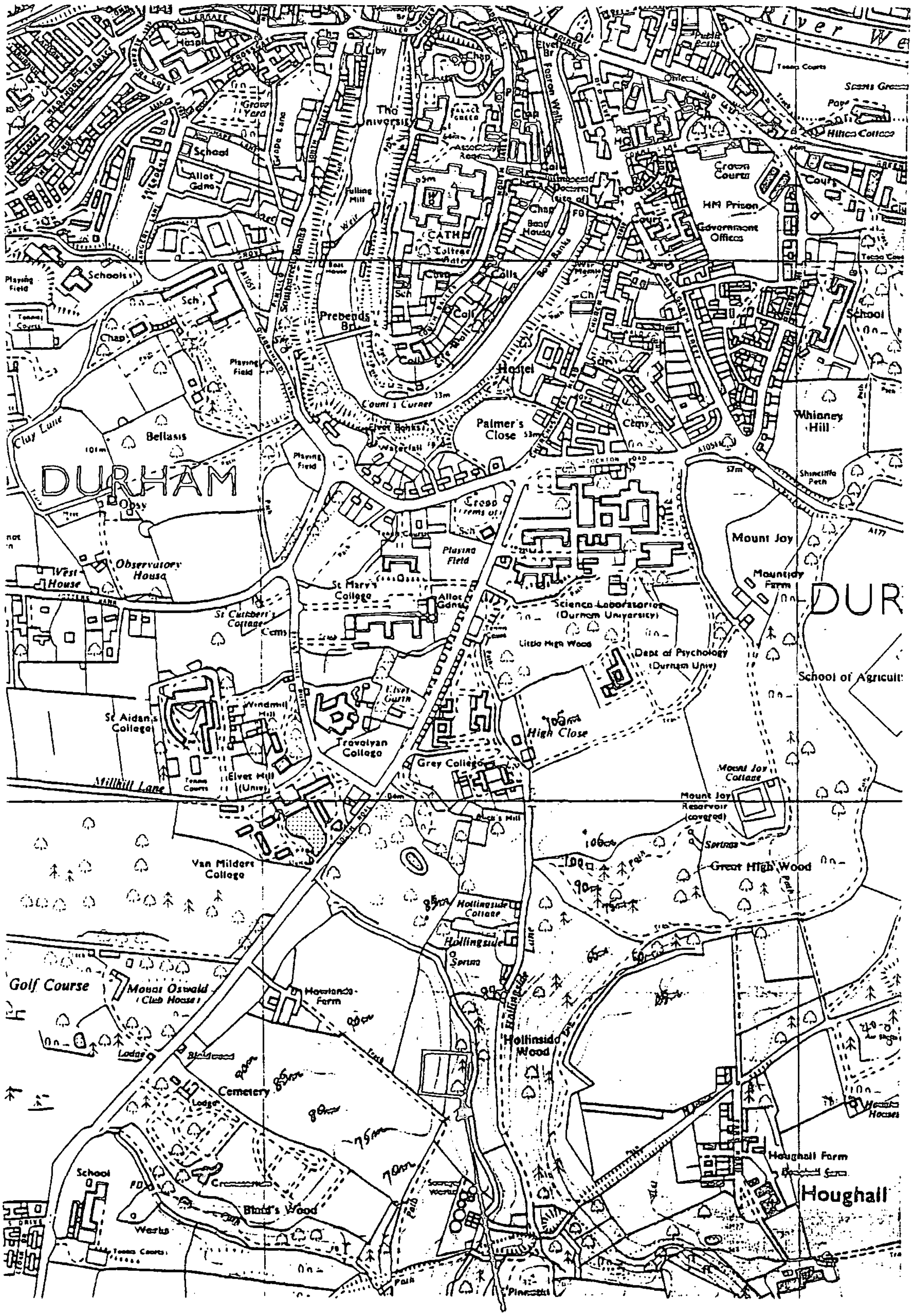
2.1 For Population and Activity Study

The woodland study area was 27m × 30m whilst the grassland area was 24m square <Fig.2.2>. The wood is about 20 years old.

2.2 For Anatomical Study

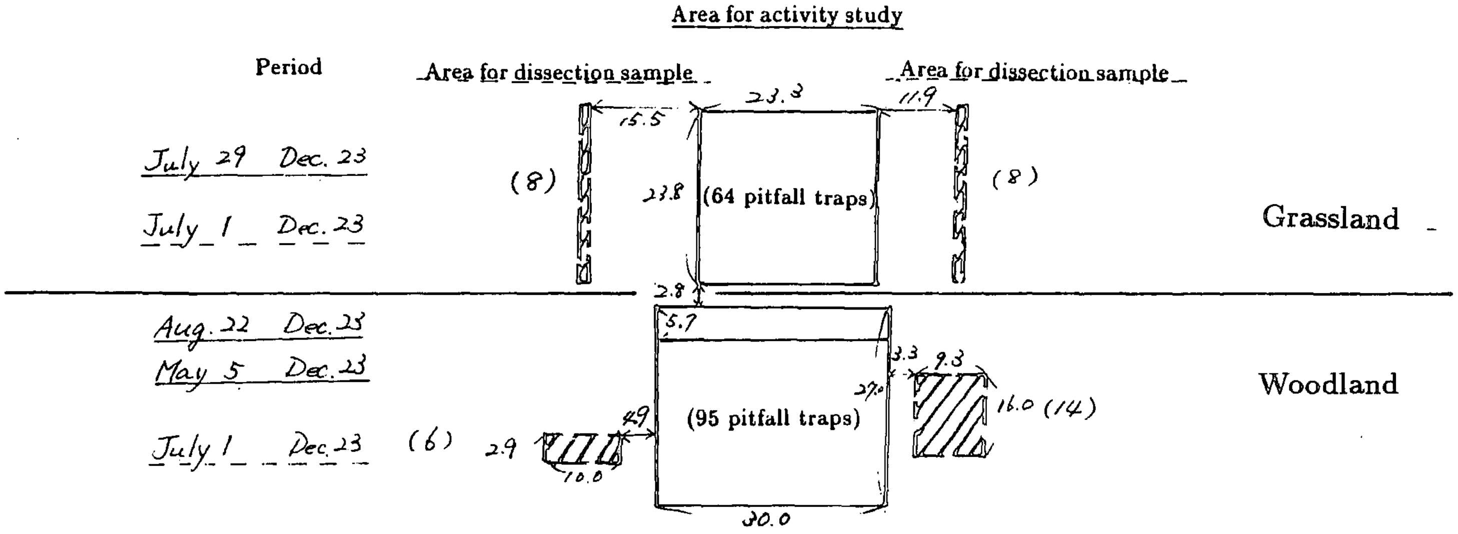
Samples for dissection were collected at both habitats outsides, but close to the study areas. <Fig.2.2>

<Fig.2.1> The location of the study area at Durham



the study area

<Fig.2.2> Field map



Unit of length : meter

Number in parentheses represent total pitfall numbers.

*The observations were made every 2days from 5th May to 18th September and every 7days from 20th October to 23rd December. There was no observation between 19th September and 19th October.

Chapter III

Methods

3.1 Pitfall Trapping

The pitfall trapping method was used to catch carabid beetles. Beetles were passively collected in glass jars (mouth diameter 6.2cm, depth 11.4cm) set with the mouth at soil level in woodland and in polystyrene cups (mouth diameter 6.7cm, depth 7.9cm) in grassland; the latter were used in order to avoid injury to farm animals. A small piece of soft tissue paper was put into each container, to prevent beetles from drowning in the standing water. Traps were checked and emptied after each observation. *

3.1.1 For Population and Activity Study

Some 64 woodland pitfalls were established on 11th May, with a further 31 from 22nd August. In grassland, a total of 64 pitfalls were established on 29th July. All pitfalls were monitored until 23rd December, with the exception of the period 18th September to 21st October. <Fig. 3.1, Fig.3.2>.

3.1.2 For Anatomical Study

Separate pitfalls were established in both areas for the trapping of dissection samples; they numbered 20 in woodland and 16 in grassland and were employed from 1988 July 1st to December 23rd <Fig.2.2>.

3.2 Mark-Recapture Method

Marks were made on individuals to enable unique identification. Most of the captured beetles were returned within 1m of the appropriate pitfalls after marking on the date of observation. Some individuals were kept for dissection.

3.2.1 Marking Method

I.D. numbers were made on the elytra and thorax of beetles by carefully positioning dot-marks. Various marking methods were tested as follows:

1. 12th May — 14th June; by painting with enamel: easily rubbed off. As a control, the painting marks were checked in an insectarium. The shortest duration for obvious fading was two weeks. Some of the painting marks, however, were not rubbed off for three months.
2. 10th June; by burning with a gas igniter: too harmful for specimens.
3. 16th June; by nicking with a stone tip: technically difficult to control.
4. 19th June — 23rd December; by nicking with a metal tip: the most successful of the methods tried, although it could not be used for callows.
5. Making a hole with a needle: for callows only.

The marking of small species by these methods was not possible.

3.3 Capture of specimens for Dissection

3.3.1 Preparation of Samples

The same capture methods were used for the activity study of dissection samples in each area. A small piece of tissue paper was put into each container in order to prevent beetles from drowning. Formalin was put into each capture container betwen 18th September and 20th October. After capture, specimens were suffocated by CO_2 in the field and retained in 70% alcohol. The majority of specimens were dissected from November to December 1988. However, some of the early specimens were dissected on the day of capture.

3.3.2 Mesurement and Observation

The following were recorded:

1. I.D. number
2. Elytra length
3. Capture site
4. Capture position within trapping grid
5. Mandible tip length: the measurements were made with ×80 binocular microscope
6. Maturity: the criteria are discussed in the next section (3.3.3, 3.3.4)
7. Previous capture position and date. Some of the dissection samples displayed capture I.D. marks.

3.3.3 Maturity of Male

The maturity was classified (1–4) by the criteria of Table 3–1.

Testes: The size and maturity were examined.

- Size: a check was made to determine whether the testes occupied less than half the length of the abdomen or more than half the length of the abdomen. (Houston 1981)

- Maturity: the quality of mature sperm was observed at three points (top, middle,bottom) of the testes. (Method by present author)

  The maturity criterion was considered only when the size of the testis was greater than half of the abdomen length. A check for the existence of mature sperm was made with a standard microscope and a phase-contrast microscope (up to ×1000 for both).

3.3.4 Maturity of Female

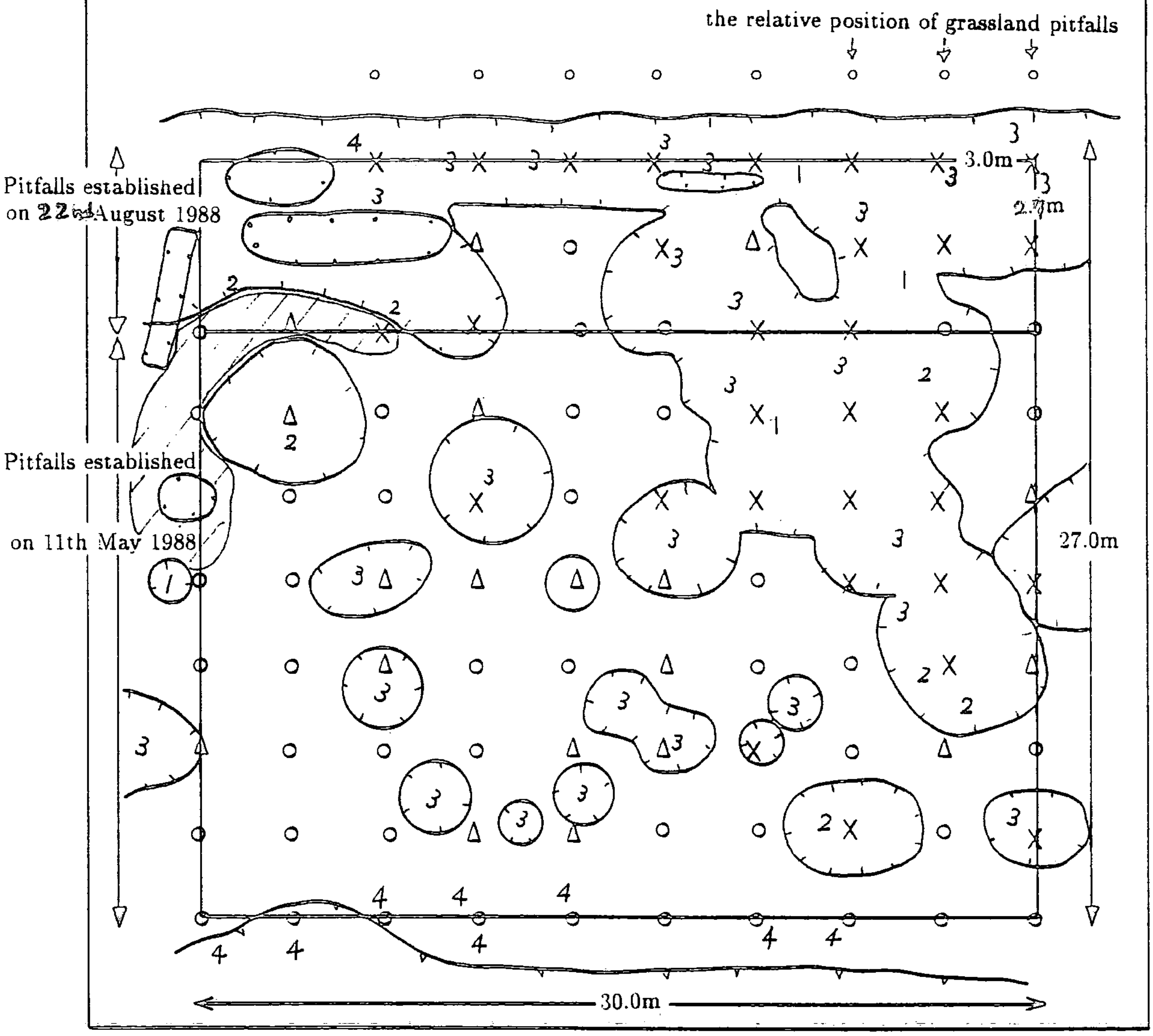
Maturity was classified (1–7) by the criteria of Table 3.2. (Houston 1981)

1. Egg:
    - number of eggs in one female: were counted only those eggs coloured from light yellow to brown
    - length and width of the largest egg in one female: measured with a dissection microscope (×20)
    - characteristics: colour, hardness, shape, texture

In addition, checks were made for the presence of

2. Corpora lutea
3. Sperm in the spermatheca

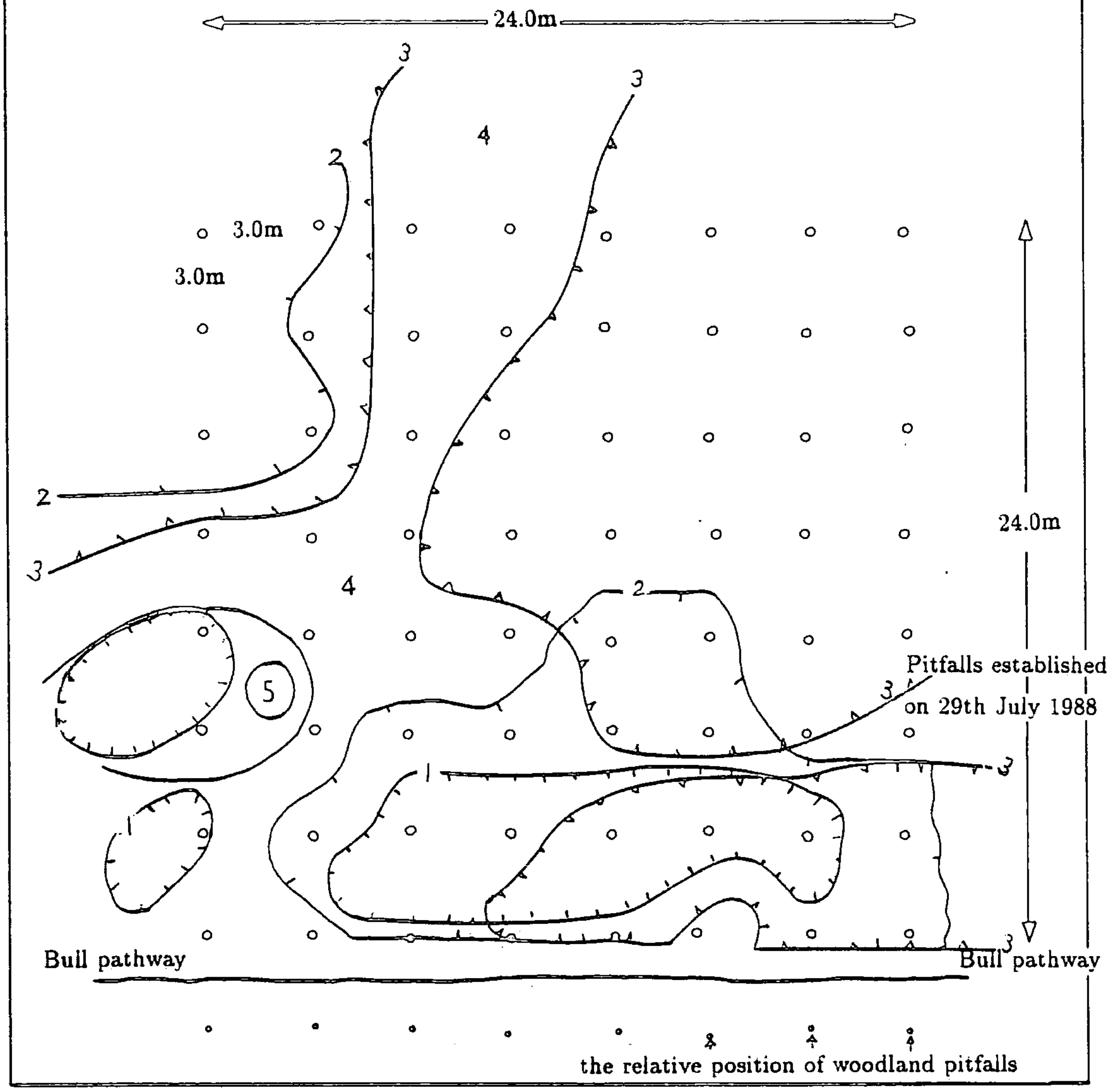
<Fig.3.1> The Durham woodland site (94 pitfalls)



Tree positions and identity	Pitfall position exposure to rain	Situation of groundsurface
1. Oak	○ Rain directly	Grass
2. Sitka spruce	△ Half rain	◯ Covered by fallen leaves and soil without grass
3.Scots pine		
4. Birch	× Dry	◯ Mud with grass
		⬭ Cut tree, dead tree
		▨ Humes

(Habitat data taken on 4th August, 1988.)

<Fig.3.2> The Durham grassland site (64 pitfalls)



Vegetation characteristic
1. Thistle
2. Thickest of thistle
3. Miscathus
4. Turf grass
5. Brier

(Habitat data taken on 4th August, 1988.)

<Table 3.1> Maturity criteria for males (Houston 1981, and present author)

Stage of maturity		1 Callow	2 Undeveloped	3 Developing	4 Mature
Mandible tip		Sharp	Not sharp		
Elytra		Soft	Hard		
Testes	Size	Thin	Less than half	More than half	
	Sperm			Mature sperm	
				Only present at the bottom of the testes	Present thrughout testes

<Table 3.2> Maturity criteria for females (Houston 1981)

Stage of maturity Check point		1 Callow	2 Undevel-oped	3 Re-gressed	4 Devel-oping	5 Redevel-oping	6 Mature	7 Spent
Mandible tip		Sharp	Not sharp					
Elytra		Soft	Hard					
Ovary		Very thin	Undeveloped small pointed ovary		Maturing not yet		fully developed	Small
Oocyte		Not visible	Opaque				Translucent	Opaque
			Soft Thin egg White		Glossy			
					Elastic eggs Small but complete egg shape Light yellow		Hard Fully developed Yellow-brown	Crumbly Sometimes developed Dark brown
Oviduct		Tight		Loose	Thight	Loose	In which eggs are sometimes observed	
Corpora lutea	1st repro-ductive period	Not present			Not present		Exist at the end of reproduction period Yellow-brown	Exist Dark colour
							Thin	
	2nd repro-duction period			Present Thin Dark coulour		Present Distinctive and large Dark colour		

Chapter IV

Results for Each Species

Results are given for 17 main species: for 14 species in the woodland from May to December, and for 10 main species in the grassland from August to December. Other species, for which only one individual was caught, are listed in Appendix A <Table A.1>. Two dominant species are presented at the beginning (*Pterostichus madidus, Nebria brevicollis*) and later species are presented in alphabetical order by genera and then species. The scheme for the classification of life cycles is taken mainly from Larsson (1939) and Thiele (1977).

Each subsection is composed of

- Previous Information
- Results
- Discussion
- Additional Information

Previous studies are considered after discussion of the present results.

Geographical and meteorological data are listed for the previous studies of carabid beetles in western and northern Europe:

- Table 4.0.1: authors of previous studies and their study areas, with habitat characteristics
- Figure 4.0.1: geographical locations

- Table 4.0.2: Annual average temperatures of the study areas, with minimum and maximum monthly average temperatures[1]; vegetation growth periods are also shown.

The vegetation growth period is defined by Bruum (1967) as the period when the daily mean temperature exceeds 6°C. However, the duration of the vegetation growth period is taken here to be the number of months in which the average monthly temperature exceeds 6°C.

- Figure 4.0.2: Average monthly temperature at study areas

---

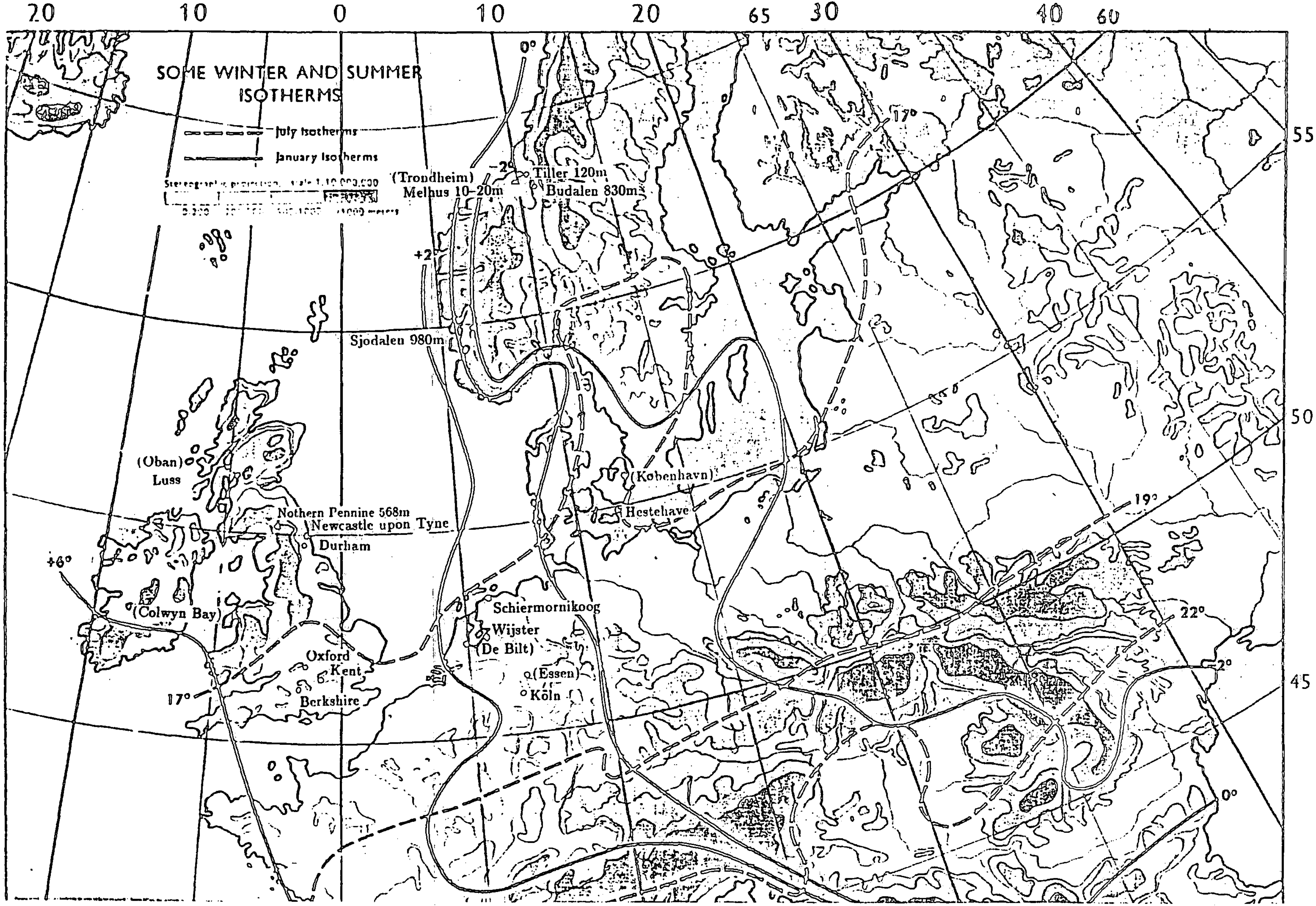
[1] Data from reference *Averages of temperature for the United Kingdom 1941–1970* (for U. K.); *Climatological normals for climat and climat ship stations for the period 1931–1961* (for European countries except U. K.).

<Table 4.0.1> List of references and study areas for the investigation of life cycle

Author	Year	Country	Main study area	Habitat
den Boer	1958	Netherlands	Meijendel (De Bilt)	Sea dunes
Briggs	1965	S. England	Kent	Weedy cultivated land, strawberry field
van Dijk	1972	Netherlands	Wijster (De Bilt)	High grass dune
	1973	Netherlands	Wijster (De Bilt)	Heathland
van Drift	1951	Netherlands	(De Bilt)	Beech forest
Gilbert	1956	N. Wales	(Colwyn Bay)	Gray-dune, marram grass
Greenslade	1965	S. England	Berkshire	Beech wood, bracken grass heath, arable land
van Heerdt	1976	Netherlands	(De Bilt)	Oak, birch wood
Houston	1970	N. England	Northern Pennine	High (465 549m) moorland, cowgreen (472m)
	1981	N. England	Northern Pennine	High (550m) blanket bog
Jorum	1980	Denmark	(Köbenhavn)	Beech wood
Krehan	1970	W. Germany	Köln (Essen)	Open country
Larsson	1939	Denmark	(Köbenhavn)	Museum samples
Loreau	1985	Belgium	Lembeek (Uccle)	Beech forest, pine-wood country
Löser	1970	W. Germany	Köln (Essen)	Oak woodlands (56, 186, 219, 340m)
	1972	W. Germany	Köln (Essen)	Oak woodlands (56, 186, 219, 340m)
Lauterbach	1964	W. Germany	Köln (Essen)	Young spruce plantation, spruce stand, Oak-hornbeam, oak-birch, beech forests
Lindroth	1945	Scandinavia		Museum samples
Luff	1973	N. England	Newcastle	Walled garden, cultivated land
Murdoch	1963	S. England	Oxford	Marsh streamside
	1967	S. England	Oxford	Marsh streamside
Penny	1969	S. Scotland	Luss (Oban)	Marsh streamside
Refseth	1980	C. Norway	10m Melhus	Alder (10m), spruce (120m), subalpine birch (830m) forests
	1984	C. Norway	120m Tiller (Trondheim)	Subalpine birch (830m) forest
	1986	C. Norway	160m Rognes, 330m Budalen	(20m), (120m), (160m), (830m), Alpine heather lands(980-1120m)
	1988	C., S. Norway	980-1120m Sjodalen	(20m), (830m), Alpine heather lands(980-1120m)
Szyszko	1977	Poland		Pine forest
Thiele	1969	W. Germany	Köln (Essen)	Moist forest (65m)
Vlijm	1968	Netherlands	Schiermornikoog (De Bilt)	Taller vegetation
Walker	1985	N. England	Durham	Pine-spruce-hemlock, oak, beech forests, stream side, pasture
de Zordo	1979	Austria		Mountain

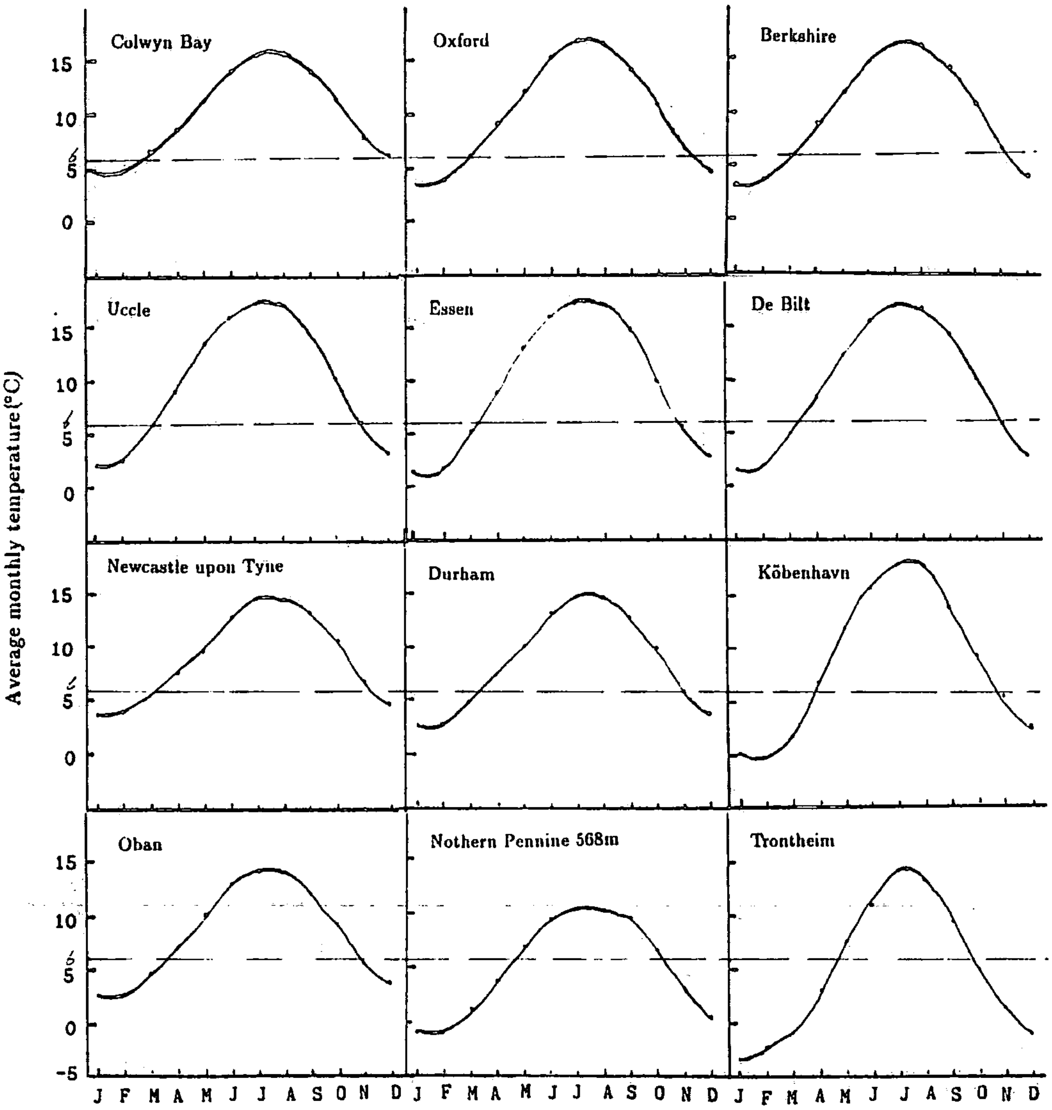
<Table 4.0.2> List of average temperatures of the study areas with minimum adn maximum monthly average temperatures, and number of months of vegetation growth periods with the durations.

Country	Study area or nearest meteorological station	Average temperature (min., max. temperature)	Number of vegetation growth periods and the duration
Belgium	Uccle	9.9(2.2, 17.5)°C	9 (Mar.—Nov.)
Denmark	Köbenhavn	8.5(−0.1, 17.8)°C	7 (Apr.—Oct.)
Netherlands	De Bilt	9.3(1.7, 17.0)°C	7 (Apr.—Oct.)
Norway	Budalen 830m	1.1°C	
	Melhus 10-20m	5.3(2.7, 14.9)°C	
	Rognes 160m	3.5°C	
	Sjodalen 980m	−0.1°C	
	Tiler (Trontheim) 120m	4.9(−3.4, 14.4)°C	5 (May.—Sep)
	Sjodalen 980m	−0.1°C	
United Kingdom	Berkshire	9.9(3.4, 16.5)°C	9 (Mar.—Nov.)
	Colwyn Bay	10.1(4.9, 15.7)°C	10 (Mar.—Dec.)
	Durham	8.5(2.7, 14.9)°C	7 (Apr.—Oct.)
	Kent	9.7(3.3, 16.5)°C	8 (Apr.—Nov.)
	Newcastle upon Tyne	9.1(3.9, 14.7)°C	8 (Apr.—Nov.)
	Nothern Pennine 568m	5.3(0.0, 11.3)°C	4 (Jun.—Sep.)
	Oban	8.3(2.7, 14.3)°C	7 (Apr.—Oct.)
	Oxford	10.1(3.5, 16.9)°C	9 (Mar.—Nov.)
West Germany	Essen	9.6(1.5, 17.5)°C	7 (Apr.—Oct.)



<Fig.4.0.1> Geographical locations of study area

<Fig.4.0.2> Average monthly temperature at study areas



4.1 Pterostichus madidus

PREVIOUS INFORMATION

Pterostichus madidus is most frequently found in grassland but may be found in woodland also (Greenslade 1965).

This species has been studied in northern England at low altitudes by Luff (1973) and at high altitudes (472m–893m) by Houston (1970). It has also been studied in southern England by Briggs (1965) and Greenslade (1965) < Fig.4.1.1 >.

Pterostichus madidus was classified as a member of the group "autumn breeders with a thermic hibernation parapause at the larval stage and no dormancy in the course of adult development" (Thiele 1977) . After autumn breeding, the larvae overwinter. The imagines emerge during the next spring. (Luff (1973) has suggested that the emergence might be stimulated by a photoperiodic signal). During maturation, the proportion of females to males amongst animals captured is higher than that observed at other biological seasons (Greenslade 1965, Luff 1973). Most females oviposit in autumn but some individuals overwinter and reproduce during the following spring (Luff 1973). At higher altitudes in England, a biennial life cycle is observed (Houston 1970): breeding occurs in May and June; larvae hibernate, adults emerge in the following summer–autumn (mid-August to mid-October) and maturation occurs during the following spring after hibernation. In southern England, mature females are observed in woodland from July to October (Briggs 1965).

RESULTS

4.1.1 Numbers Captured

The data displaying the frequency of capture of *Pterostichus madidus* in woodland <Fig.4.1.1a> show two peaks of abundance and/or activity in periods no.3 and 8 for the female and in periods no.4 and 8 for the male. This result becomes clearer by plotting the data on probability paper <Fig.4.1.2a, b>. It is seen that peaks occur in early June and in late August (periods no.3, 8) for the female and in late June and late August (periods no.4, 8) for the male.

Table 4.1.1 shows the proportion of females captured in each period of abundance (periods no.1–6 and 7–10) in the two habitats. In woodland, females formed a higher proportion of all captures in the first main period of abundance than in the second period ($\chi_1^2 = 4.17$, $0.025 < p < 0.05$). In grassland, the same comparison cannot be made, because sampling began only in July. During the second period of abundance, females formed a significantly higher proportion of all captures in woodland than in grassland ($\chi_1^2 = 22.00$, $p < 0.005$).

Some of these captures were of callows <Table 4.1.2>. The proportions of callows amongst the males and females captured in woodland were not significantly different ($\chi_1^2 = 1.29$, $0.20 < p < 0.30$). However, females formed a significantly lower proportion of all captures amongst non-callows than amongst callows ($\chi_1^2 = 4.20$, $0.025 < p < 0.05$). The ratio of females to males amongst the callows was close to 50% in both woodland and grassland.

The data summarised in Fig.4.1.3 show the average number of captures per pitfall in the two habitats in the second peak of abundance. In August, both males and females were significantly more abundant and/or active in grassland than woodland ($\chi_1^2 = 12.06$, $p < 0.005$).

The total numbers of *P. madidus* and other species captured (including recapture) are given in Table A.1. A comparison of the numbers captured in both habitats in periods no.7–17 shows that this species was observed more abundantly in grassland than in woodland. This result is in agreement with the previous studies (Williams 1959, Greenslade 1963, 1965).

4.1.2 Distance of Movement

The data summarized in Fig.4.1.4 and Table 4.1.3 suggest that in the second period of abundance, males moved significantly further than females in both habitats (in woodland $t_{45} = 2.91$, $p = 0.006$; in grassland $t_{125} = 4.95$, $p < 0.001$). In the first period of abundance, woodland males moved perhaps a little further, on average, than females, ($t_{29} = 1.62, p = 0.117$). However, although few recaptures were made in the third period (periods no.13–17) , woodland females moved significantly further than males ($t_5 = 2.69$, $p = 0.043$).

The comparisons amongst three sets of periods (periods no.1–6, 7–10, 13–17) in woodland for each sex show that females moved significantly further in the third period than others. (Between first and third period $t_{16} = 3.54$, $p = 0.003$; between second and third period $t_{32} = 3.81$, $p = 0.001$). However males did not show significant differences. (Between first and second period $t_{43} = 0.99$, $p = 0.326$; between second and third period $t_{31} = 0.97$, $p = 0.340$; and between first and third period $t_{18} = 0.64$, $p = 0.502$). In woodland the distances of movement by females in the first and second periods of abundance were identical ($t_{44} = 0.00$, $p = 0.999$).

The distances moved by females during the second main period of abundance were similar in both woodland and grassland; ($t_{58} = 0.0004$, $p > 0.9$); they may have differed for males, but the significance is low ($t_{37} = 0.42$, $p = 0.680$).

It is possible that the average distances moved, as recorded by recaptures, might increase with the time between mark and recapture. In Table 4.1.4, a comparison is made between distances moved in woodland by two groups of animals recaptured within periods no.7–10: namely, those that had been marked within periods no.1–6, and those that had been marked within periods no.7–10. These data suggest that each sex had a similar activity range in both habitats, regardless of season, in that animals recaptured soon after capture moved as far as those recaptured much later.

Fig.4.1.5a, b, c, d, e, f show the frequency of movement distances.

Table 4.1.5 shows the number of recaptures in each habitat. Females displayed a strong tendency to remain in their habitats (in grassland 30/30=100.0%; in woodland 42/44=95.5%). The grassland males showed a similar tendency (94/98=95.9%). However, a lower proportion of the males marked in woodland remained in the woodland habitat (43/60=71.7%). All movements between the two habitats were observed in the second period of abundance (periods no.7–10). None were found in the third period of abundance (periods no.13–17). A greater number of movements were observed from woodland to grassland than in the opposite direction: 2 females out of 2 and 17 males out of 21. This tendency supports the result of Table 4.1.1 in which the male ratio was seen to be significantly higher in grassland during the second period of abundance. Although the movements of the majority were small, a few males moved very large distances and departed the woodland, which might indicate competition in woodland for the preferred microhabitats.

4.1.3 Stage of Maturity

Fig.4.1.6a, b, c, d show the stages of maturity of animals grouped in 2-week periods.

In woodland, callows were observed from late July to early September (periods no.6–10) and a peak emergence occurred in late August (period no.8). In grassland, a peak emergence occurred from late July to late August (periods no. 6–8). The full period of emergence in grassland was not observed because, for this habitat, the collection of animals did not start until early July. However, the peak of oviposition seems to have occurred in early August. The start of emergence appears to have been earlier still, because an undeveloped female (maturity stage 2) was observed in period no.6. This individual must have emerged as a callow before period no.5 <Fig.4.1.6c>. It is concluded that the emergence in grassland may have occurred from mid-July to late August (periods no.5–8).

With the exception of males in woodland, mature or developing individuals (stage of maturity of male 3,4; of female 3–7) were observed both before and simultaneously with the main emergence season (period no.6). The individuals may therefore have been adults which had survived for two years or more.

The summary table <Table 4.1.6> indicates that the ratio of second-year females to newly emerged females was higher in grassland than in woodland. This is also implied by the results of the field observation <Fig.4.1.1>.

The corpora lutea is often indistinct; this caused difficulty in distinguishing between maturity stages 4 and 5. The data of maturity stage 4 may therefore occasionally include stage 5 also.

One woodland female was observed to be parasitized by Nematoda.

4.1.4 Elytra Length

The data summarised in Table 4.1.7 suggest that the elytra length of the female was significantly larger than that of the male in both habitats (in woodland $t_{420} = 5.59$, $p < 0.001$; in grassland $t_{416} = 6.85$, $p < 0.001$). Also, the difference between sexes was larger in grassland than in woodland. The elytra length of grassland individuals was significantly larger than that of woodland individuals of both sexes (female $t_{353} = 6.07$, $p < 0.001$; male $t_{483} = 6.17$, $p < 0.001$).

4.1.5 The Ratio of Abdomen to Elytra Length

During field work, some individuals with swollen abdomens were observed. The reasons for this were found during dissection to be the presence of developing or mature reproductive organs and/or a large fat body. The ratio of abdomen length to elytra length was measured in all individuals caught in order to provide information on the seasonal changes in maturity and to obtain fat body information.

The ratios of abdomen to elytra length of woodland individuals are summarised in Fig.4.1.7a. The ratios in females were large from early June to late July (in periods no.3–6). In period no.4, a mature female was found to hold 32 eggs <Table 4.1.10a> and a copulation was observed in the field. In period no.6 a spent female was collected <Fig.4.1.6a, b> which contained an egg whose size was the largest measured during the whole observation term in woodland <Table 4.1.9a>. The oviposition season in woodland therefore seems to have occurred in late June (period no.4). Also, a mature female was found with 14 eggs in late August (period no.8) <Table 4.1.10a> whereas only few females were observed in July (periods no.5,6). From these results, it is concluded that the oviposition season seems to have occurred at the Durham woodland site twice, mainly in June and secondly in August. In addition to larger egg volume and number, the greater ratios of abdomen/elytra length of females in the earlier oviposition season seem to indicate that most of the oviposition occurred during that season (periods no.5,6). Though the sample was small in late October and November (periods no.13–15), large ratios of abdomen/elytra length of both sexes were again observed and were possibly due to the storage of fat for overwintering. This may correlate with large distance movements of the few individuals in the third period <Fig.4.1.3a>.

The results of the shorter-term grassland study, illustrated by Fig.4.1.7b, show a pattern of change similar to that observed in woodland. The large ratio of abdomen/elytra length in July occurred at the time when the maximum egg size (of spent females) was observed <Table 4.1.9b>. The largest number of mature females was observed in early August <Fig.4.1.6c, d>. The largest mean number of eggs per mature female was also recorded in early August and after this time the number decreased <Table 4.1.10b>. Three copulations were witnessed in the field during August (periods no.7, 8). From these results, the oviposition season in grassland is taken to be continuous during July and August (periods no.5–8). Although the study in grassland started after July, earlier oviposition cannot be ruled out.

A comparison of the ratio of abdomen/elytra length for females in both habitats in periods no.7–10 reveals larger values in grassland than woodland for both sexes <Table 4.1.8>. The emergence season was probably earlier in grassland than in woodland so that the grassland individuals had more time to develop and to store nutrients. Living conditions in grassland may be more favorable than those found in woodland habitats in summer. For example, higher ground-surface temperatures were recorded in grassland than in woodland during summer and fewer natural enemies were observed in grassland. Fewer species of Carabidae and a higher proportion of *P. madidus* were observed in grassland, so competition may be less within the genus in grassland than woodland. (In grassland, 17 species, 72.5%; in woodland, 20 species, 53.6%: periods no.7–17) <Table 4.1.14>.

4.1.6 Mandible tip length

The mandible tip length of each individual in relation to its maturity stage is shown in Fig.4.1.8a, b, c, d.

Table 4.1.11 provides a comparison of mandible tip length of all individuals in each habitat for both sexes. It shows that the woodland individuals have a significantly larger mandible tip length for each sex than the grassland individuals (female $t_{53} = 2.40$, $p = 0.020$; male $t_{38} = 2.15$, $p = 0.038$). However, the difference between sexes in each habitat are not significant (woodland $t_{47} = 1.44$, $p = 0.158$; grassland $t_{40} = 0.32$, $p = 0.751$). The mandible tip lengths are independent of the elytra lengths observed in each habitat.

4.1.6.1 The Mandible Tip Length of Females

For newly emerged individuals (stages of maturity 1, 2), woodland females showed a relatively dense grouping of the maximum mandible tip lengths compared with those of grassland females <Fig.4.1.8a, b>. The mandible tip lengths of newly emerged females did not differ between the two habitats <Table 4.1.12> ($t_{28} = 0.65, p = 0.520$). The mandible tip lengths therefore appear to be independent of the elytra lengths observed in each habitat. In other words, the woodland female has a larger ratio of mandible tip to elytra length than the grassland female. The grassland females whose stages of maturity are 3–7 may be divided into two groups (by the differences of the mandible tip length) by plotting on probability paper <Fig.4.1.8b, Fig.4.1.9c, d>. It is therefore concluded that the grassland female group whose stages of maturity are 3–7 is probably composed of two generations, one of which is the second-year survivors whilst the other comprises the third year survivors. For the woodland females of the same maturity stage group, the same plot <Fig.4.1.9a, b> does not show clear subgroups. Therefore it might indicate that the woodland female group of maturity stages 3–7 is composed of one generation only.

4.1.6.2 The Mandible Tip Length of Males

Data plotted on probability paper show one group for woodland individuals <Fig.4.1.8c, Fig.4.1.9e> and two groups for grassland individuals <Fig.4.1.8d, Fig.4.1.9f>. Therefore the woodland male group seems to consist of one newly emerged generation and the grassland male group seems to be composed of two generations, one of which is a newly emerged generation and the other a second-year surviving imago generation. Almost all woodland males may have died after the spring oviposition at the latest, while some of the grassland males seem to have survived after that period.

The following suggestions are made using the data of Table 4.1.12, Fig.4.1.8a, b, c, d, Fig.4.1.9b, d, e, f:

1. Females in both habitats emerge with almost the same length of mandible tip despite the significant difference in elytra length (the elytra lengths of

grassland females were larger than those of woodland females). The reason for this might be that the food supply for *P. madidus* at the grassland site is better than that in the woodland. If so, the mandible tip length may not be influenced by food supply as easily as the elytra length, or the *difference* of food supply (qualitatively and/or quantitatively) may influence the mandible tip length.

2. The grassland groups of both sexes have one more adult generation than the woodland groups, i.e. the grassland female has three adult generations while two adult generations are found for the woodland female. Similarly, the grassland male has two adult generations while only one adult generation is found for the woodland male.

Possible reasons for this may be:

(i) a longer severe winter condition in grassland. Van Dijk (1972) and Luff (1973) suggest that, going from an Atlantic to a continental climate, the larval overwintering species reproduce more and more in the second year or even in a later year. The earlier in the year the seasonal conditions become unfavourable, the more beetles will reproduce only for a very short period and the more they may be expected to continue reproduction in the next year after overwintering;

(ii) in grassland, fewer natural enemies and lower competition within family allow longer survival;

(iii) previous studies (Williams 1959, Greenslade 1963, 1965) and the present study suggest that this species is found more in grassland habitats than in woodland habitats so that the living conditions may be more favourable in grassland than in woodland.

The suggestions 1. and 2. (previous page) assist the interpretation of the disproportionate results of Table 4.1.11 with Table 4.1.7, in which even though the elytra lengths of grassland individuals are significantly larger than those of woodland individuals, the mandible tip lengths of female callows of both habitats are not different.

Because of the different speed of maturation of the two sexes, the individuals whose maturity stage is 1 are selected here in order to see their original mandible tip length. The result of comparison between both sexes of woodland individuals is that the female callow is observed to have a significantly larger mandible tip length than the male callow <Table 4.1.13> ($t_{21} = 3.04$, $p = 0.006$). This result is consistent with the result of elytra lengths between sexes. Unfortunately, the same kind of comparison cannot be made for the grassland individuals, because of a lack of samples.

DISCUSSION

The numbers captured may be influenced by movement distances, since greater activity may lead to a higher chance of capture in pitfall traps. Therefore, the data in Fig.4.1.1a, b and Fig.4.1.4a, b should be considered together.

Before discussing the conclusions, the influence of distance of movement on the probability of capture must first be quantified. Fig.4.1.10 shows the capture possibility in relation to the distance from the point of release. This indicates that the results in Table 4.1.3 are underestimated more for smaller mean distances than larger distances, i.e. the mean distance moved by females is underestimated more than that of males so that the true significances of differences between two groups may in fact be greater than the derived results indicate.

In woodland, the ratio of females to males amongst non-callows is estimated to be higher than amongst callows. This is supported by previous results (Greenslade 1965, Luff 1973) which demonstrated that the female survival ratio is higher than that of the male. Because the sex ratios of non-callows in periods no.7–10 and in periods no.1–6 do not differ very much, the sex ratio might be stable in woodland.

In grassland, the number of female callows captured in periods 7–10 is estimated to be about the same as that of males. The male to female ratio amongst non-callows is much higher than that of callows. This is supported by the result that movement of males from woodland to grassland was more frequently observed than movement in the opposite direction. The reasons for this may be:

1. the movements in both directions occured at the same rate but, after moving, the lower survival of woodland males did not lead to as much transfer from grassland to woodland as in the opposite direction and/or
2. the movements themselves occurred at the rate shown in Table 4.1.5 because of the preference of individuals.

The observed significant difference of sex ratio provides evidence for quite different living conditions in the two adjacent habitats.

When Table 4.1.1 and Table 4.1.3 are considered together for the woodland individuals, the comparisons between the first and the second periods reveal certain features; Table 4.1.14 sumarizes these. It shows a changing recapture rate from the first period of abundance to the second period of abundance:

- from 0.239 to 0.299, i.e. an increase of 1.3 times for males and o from 0.116 to 0.256, i.e. an increase of 2.2 times for females.

If the proportion of females in woodland in 1987 had also been almost 50%, as in 1988, the results imply that more males had died before the spring than females and more females died during the first peak of abundance than males.

The present study of the *P. madidus* life cycle in Durham provides some results that differ from the life cycles observed during two previous studies: that of Luff (1973), who studied the seasonal life cycle of *P. madidus* in a cultivated field near Newcastle upon Tyne, and that of Houston (1970), who studied at a moorland habitat in the uplands in northern England.

At the Durham woodland site, oviposition seems to occur mainly in June and August. Larvae overwinter and emerge from the following mid-July to early September. The callows probably become mature in the following spring, because the oviposition season is overlapped with the emergence season. Probably some of the females which oviposit in the spring die and some of the remaining surviving females oviposit again in August and early September. Some of the spent and developing females were observed to have small immature eggs, irrespective of the oviposition seasons. Also, the total numbers of each peak of abundance were not significantly different even though the callows were added. Two oviposition seasons in one year are reported by Greenslade (1965) and Luff (1973).

At the Durham grassland site, oviposition seems to occur in July and August. After larval overwintering, imagines emerge. From observation, emergence seems to occur earlier in grassland than in woodland: from June to August in grassland and from late July to mid-September in woodland. In grassland, as shown in Fig.4.1.1b, the frequency of capture after late October decreases more rapidly than for the woodland individuals. The reason for this is thought to be that the living conditions in grassland become more severe than in woodland in winter because the ground is more directly exposed. Therefore grassland *P. madidus* seems to have a shorter favourable period and to become inactive for longer than the woodland individuals.

Luff (1973) studied annual activity and suggested four periods of change in sex ratio:

1. early summer activity of overwintered, mostly female beetles;
2. mid-summer activity of newly emerged beetles of both sexes;
3. late summer activity of mature, mostly male beetles;
4. autumn activity of mature and spent, mainly female beetles.

Oviposition was observed from the middle of section 3. to the middle of section 4. Greenslade (1965) also reported on section 3..

The present study of annual activity patterns produced results similar to those of Houston (1970) for an upland site in northern England. Houston's study shows a gap of captures between two abundance peaks in July and early August while the present work shows a gap in July. The reason why the abundance gap was found at the Durham woodland site is implied by the result of Fig.4.1.8c (mandible tip length). Second year surviving males, detected by the measurements of mandible tip lengths, were not observed in woodland so perhaps, after the spring oviposition, almost all males died. Similarly, the results of Table 4.1.6 imply a low ratio of female survivors to new generation individuals, so that a number of females may also have died after the spring oviposition. In addition, female survivors became quite inactive, in contrast with the male survivors <Fig.4.1.5a, c>. This inactivity is also displayed by Houston's results.

The present study offers support for the first two of the four sections of change in sex ratio suggested by Luff (1973). With reference to the above list of the four sections:

1. Overwintered Durham woodland females appeared earlier than the overwintered males.
2. When the callows are isolated, both sexes appeared with almost the same ratio in both Durham habitats.
3. This section was not observed, perhaps because of both the different life cycle in woodland and the high male ratio in grassland.
4. This section fits the result in grassland; only a few females were observed in October and November. However, in woodland this is not clear and after mid-September both sexes appeared with almost the same ratio, again probably in part because of the different life cycle.

When the comparisons are made between the study of the Durham woodland site, Luff's lowland study, and Houston's upland study, an order of progressively less favourable habitats may be inferred for the *P. madidus* life cycle:

(i) lowland at Newcastle upon Tyne

(ii) the woodland at Durham

(iii) upland in the Pennines.

The reasons for this order are:

1. emergence occurred later in the order presented because severe and longer winter conditions may delay larval development and metamorphosis.

2. habitats (i) and (ii) have two separate oviposition seasons but habitat (iii) has one oviposition season in one year, because of the relatively shorter duration of favourable conditions for (iii).
3. a transfer can be found from mainly autumn breeding of (i) to mainly spring breeding of (ii) and then to only spring breeding of (iii) because of the variation of the duration of favourable conditions for maturation after emergence.

The following conclusion is drawn from these comparisons. For emergence, a rising temperature is necessary in addition to or instead of a photoperiodic signal. This fits the result that, in Durham, the grassland callows seem to emerge earlier than woodland callows. Because grassland is an open environment, a rise in temperature at the onset of summer would be expected to occur earlier than in woodland.

From a comparison of the previous and present studies, *Pterostichus madidus* in Great Britain is found to be, depending upon the severity of the environment,

1. a univoltine summer-autumn breeder;
2. a mixture of a univoltine summer breeder and a semivoltine spring breeder;
3. a semivoltine spring breeder.

At the same time, it is concluded that the emergence season shifts from late spring–early summer to autumn, and the breeding season from summer–autumn to spring.

<Table 4-1.1> The number of males and females of *Pterostichus madius* caught in the two main periods of abundance (periods no.1-5 and 7-10) at the two habitats

P. madidus	Woodland		Grassland
Period no.	1-5	7-10	7-10
Female	129	121	148
Male	67	97	266
(Total)	196	218	414

<Table 4.1.2> The number of callows and non-callows of *Pterostichus madius* caught at the two habitats in periods no.7-10

P. madidus	Woodland		Grassland	
Period no.	Callow	Non-callow	Callow	Non-callow
Female	35	86	19	129
Male	36	61	17	249
(Total)	71	147	36	378
Female ratio	50.7%		52.3%	

<Table 4.1.3> Distances moved by both sexes of *Pterostichus madidus* in the two habitats. Recaptures during periods no.7-10 are separated from those during periods no.1-6

Periods no.	1-6		7-10	
Sex	Female	Male	Female	Male
Wood- land	5.3547 15 5.2706 1.3609	8.2864 16 4.8329 1.2082	5.3522 31 4.9999 0.8980	10.5390 29 8.2961 1.5405
Grass- land	0	0	5.5266 29 5.5428 1.0293	9.8525 98 5.8907 0.5951

in each cell
mean (m) sample number st. deviation st. error

<Table 4.1.4> Distances moved by both sexes of *Pterostichus madidus* in woodland in periods no.7-10, separating the captures made in periods no.1-6 from those made in periods no.7-10

Periods no.	7-10	
Sex	Female	Male
Data whose capture were in periods no.1-6	5.7250 6 7.1668 2.9259	11.1209 2 9.7282 6.8788
Data whose capture were in periods no.7-10	5.2627 25 4.9275 0.9857	10.4963 27 8.1054 1.5599

in each cell
mean (m) sample number st. deviation st. error

<Table 4.1.5> Number of recaptures of *Pterostichus madidus* in the two habitats (periods no.7-17)

Habitat	Woodland	Grassland	(Sex total)
Female	44 42 2	30 30 0	74 72 2
Male	60 43 17	98 94 4	158 137 21
(total)	104 85 19	128 124 4	232 209 23

in each cell
total number of recaptures number of recaptures in the same habitat number of recaptures in the alternative habitat

<Table 4.1.6> Comparison of the number of emerged and survival females of *Pterostichus madidus* stage of maturity 1 and 2 as emerged individual, 6 and 7 as survival individual (periods no.6-10 in woodland and periods no.6-8 in grassland)

See also Fig.4.1.7a,b.

Habitat	Woodland	Grassland
Emerged female	28	9
Survived female	6	8

<Table 4.1.7> Elytra length of both sexes of *Pterostichus madidus* in the two habitats

Habitat	Woodland	Grassland	(Sex total)
Female	8.458	8.712	8.568
	201	154	355
	0.388	0.395	0.410
	0.027	0.032	0.022
Male	8.249	8.455	8.361
	221	264	485
	0.379	0.355	0.380
	0.025	0.022	0.017
(Habitat total)	8.349	8.550	8.449
	422	418	840
	0.397	0.390	0.406
	0.019	0.019	0.014

in each cell
mean (mm)
sample number
st. deviation
st. error

<Table 4.1.8> The ratio of abdomen to elytra length of *Pterostichus madidus* in periods no.7-10 in the two habitats

Habitat	Woodland	Grassland	(Sex total)
Female	1.0116	1.0269	1.0191
	155	147	302
	0.0272	0.0508	0.0411
	0.0022	0.0042	0.0024
Male	1.0104	1.0128	1.0119
	161	264	425
	0.0306	0.0318	0.0313
	0.0024	0.0020	0.0015
(Habitat total)	1.0110	1.0179	1.0149
	316	411	727
	0.0289	0.0402	0.0359
	0.0016	0.0020	0.0013

in each cell
mean
sample number
st. deviation
st. error

<Table 4.1.9> Mean egg volume of *Pterostichus madidus* in relation to stage of maturity (in 2-week periods) (a) in woodland (b) in grassland

(a)

Maturity level Period no.	4 Developing	6 Mature	7 Spent	(Period total)
2	1081 1			1081 1
6			3221 1	3221 1
8		1342 1	1932 1	1637 2
10			1862 1	1862 1
(Maturity stage total)	1081 1	1342 1	2338 3	1888 5

(b)

Maturity level Period no.	4 Developing	6 Mature	7 Spent	(Period total)
6	1466 1	2075 1	3361 1	2301 3
7		1470 4		1470 4
8	1309 1	2601 1		1955 2
9			1309 1	1309 1
(Maturity stage total)	1388 2	1759 6	2355 2	1800 10

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.1.10> Mean number of eggs carried by female *Pterostichus madidus* in relation to stage of maturity in 2-week periods (a) in woodland (b) in grassland

in each cell
mean number
sample number

(a)

Stage of maturity Period no.	1 Callow	2 Undeveloped	3 Regressed	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period otal)
2				10 1				10 1
4						32 1		32 1
6	0 2							1.33 3
7	0 4							0 4
8	0 7	0 5	0 1			14 1	5 1	1.27 15
9	0 5	0 5	0 2					0 12
10							2.67 3	2.67 3
(Stage of maturity total)	0 18	0 10	0 3	10 1	0	23 2	3.04 5	1.87 39

(b)

Stage of maturity Period no.	1 Callow	2 Undeveloped	3 Regressed	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period total)
5			0 3					0 3
6	0 3	0 1		19 1		13.50 2	1 1	5.88 8
7	0 3		0 2			15.25 4		6.78 9
8	0 1	0 1	0 1	5.50 2		5 1		2.67 6
9		0 2					6 1	2.00 3
11			0 2					0 2
(Stage of maturity total)	0 7	0 4	0 8	10.00 3	0	13.29 7	3.50 2	4.19 31

<Table 4.1.11> Mandible tip length of both sexes of *Pterostichus madidus* in the two habitats

Habitat	Woodland	Grassland	(Sex total)
Female	2.2139	1.9105	2.1091
	36	19	55
	0.4199	0.4930	0.4653
	0.0700	0.1131	0.0627
Male	2.0794	1.8696	1.9587
	17	23	40
	0.2570	0.3355	0.3188
	0.0623	0.0700	0.0504
(Habitat total)	2.1708	1.8881	2.0458
	53	42	95
	0.3782	0.4093	0.4148
	0.0519	0.0632	0.0426

in each cell
mean (mm)
sample number
st. deviation
st. error

<Table 4.1.12> Mandible tip length of female *Pterostichus madidus* whose maturity stages are 1 and 2 in the two habitats

Habitat		Woodland	Grassland	(Total)
Mandible Tip length	mean (mm)	2.4663	2.4143	2.4542
	sample number	23	7	30
	st. deviation	0.1799	0.2015	0.1829
	st. error	0.0573	0.0762	0.0334

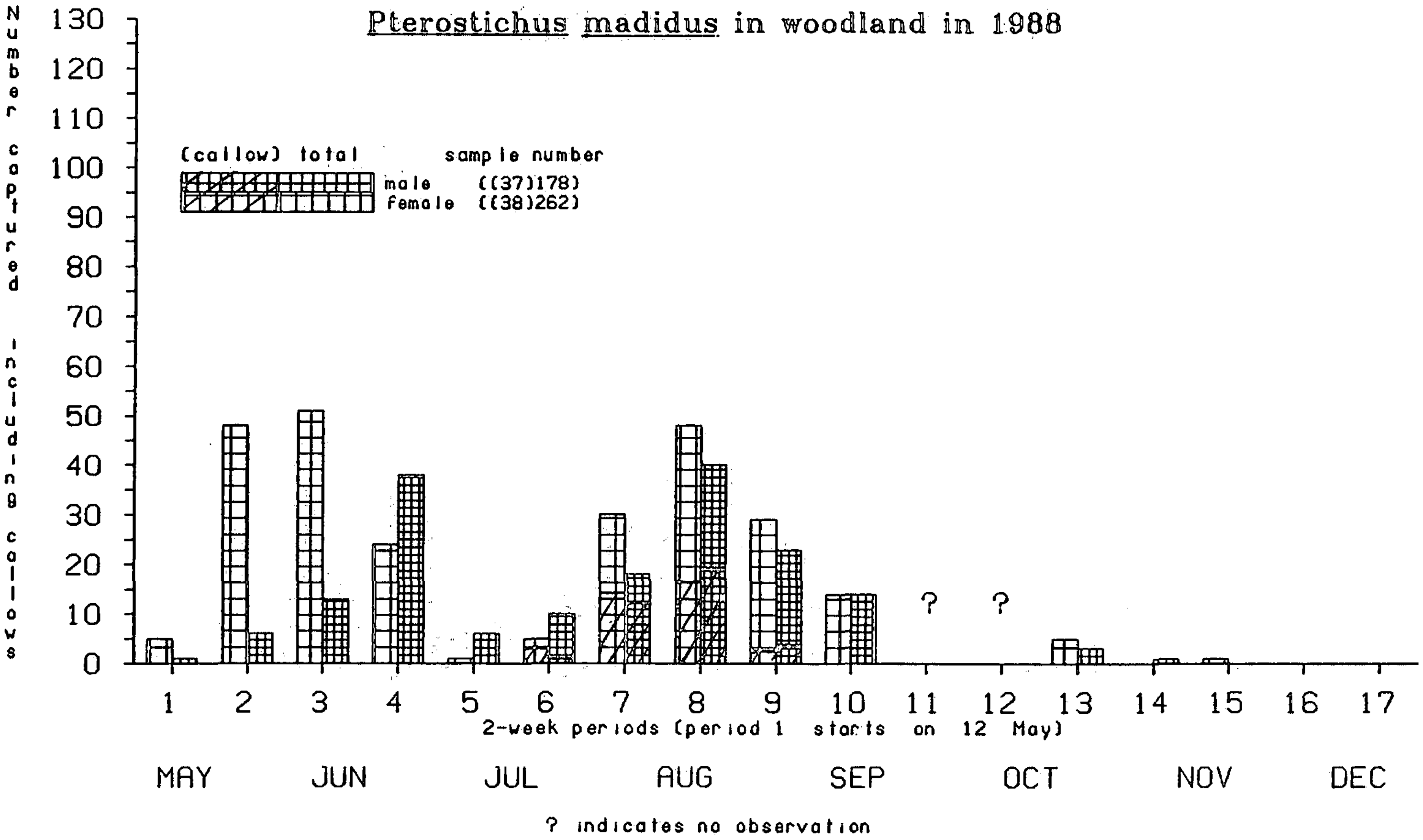
<Table 4.1.13> Mandible tip length of both sexes of *Pterostichus madidus* whose maturity stage is 1 (callow) in woodland

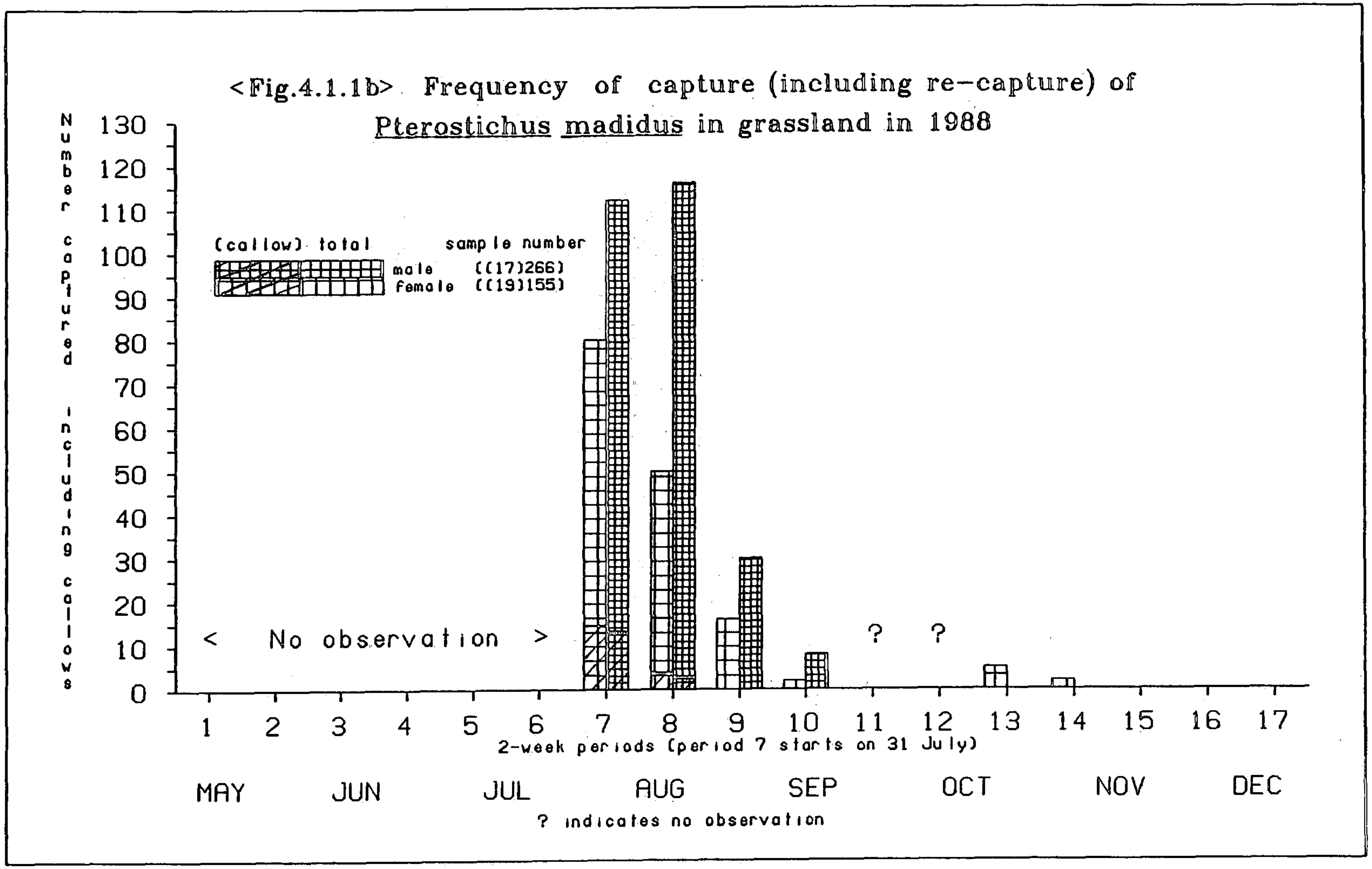
Sex		Female	Male	(Total)
Mandible Tip length	mean (mm)	2.4911	2.4083	2.3804
	sample number	14	9	23
	st. deviation	0.1783	0.2695	0.2552
	st. error	0.0477	0.0898	0.0532

<Table 4.1.14> The recapture ratio and the changing ratio of woodland *Pterostichus madidus* for the first period and the second period of abundance

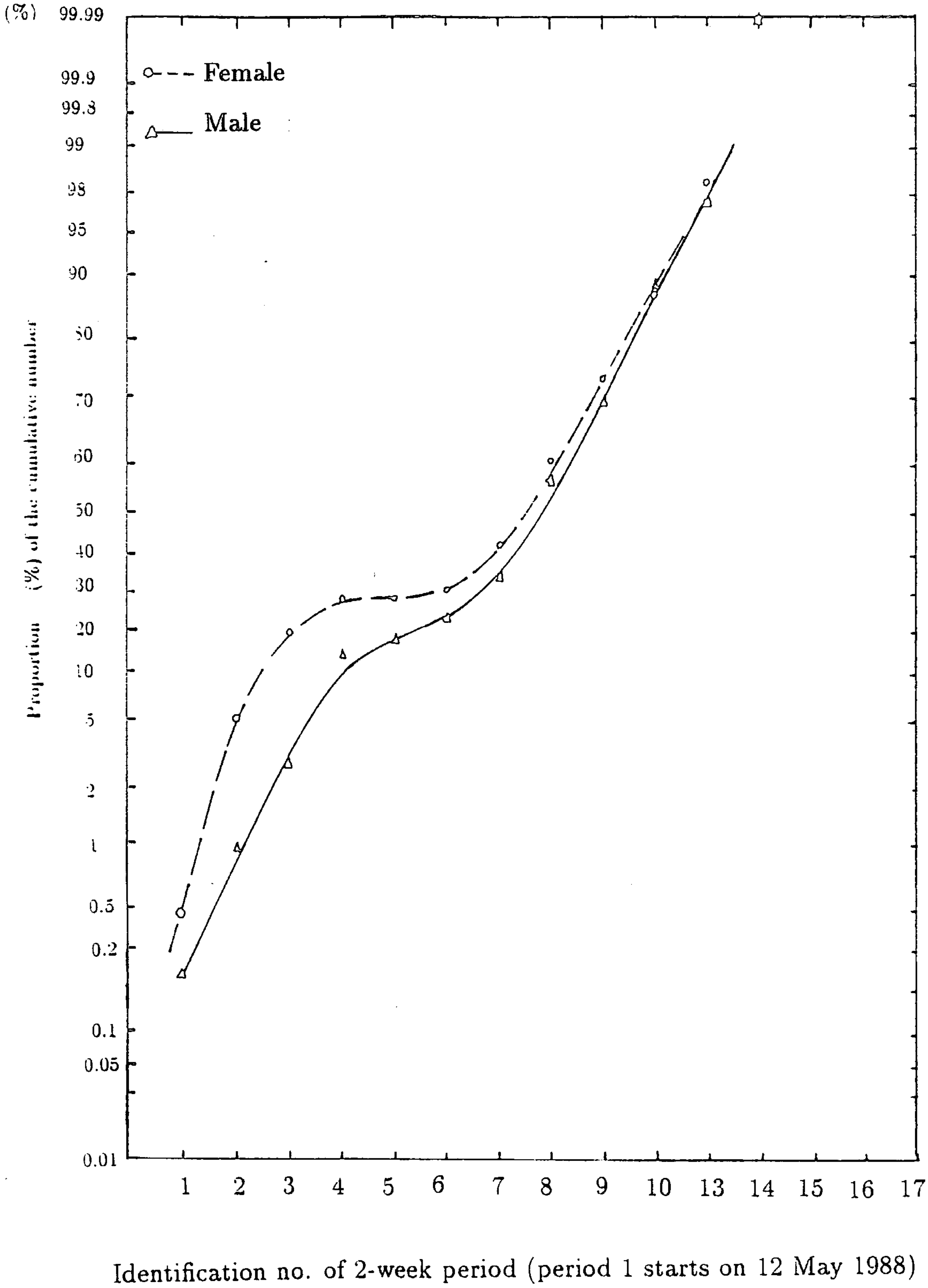
Sex		Male		Female	
Period no. of abundance		I	II	I	II
Capture	(Callow)		(36)		(35)
	Total	67	97	129	121
Recapture		16	29	15	31
Recapture ratio		0.239	0.299	0.116	0.256
Increasing ratio of recapture from period no. of abundnce I to II		1.251		2.207	

<Fig.4.1.1a> Frequency of capture (including re-capture) of *Pterostichus madidus* in woodland in 1988

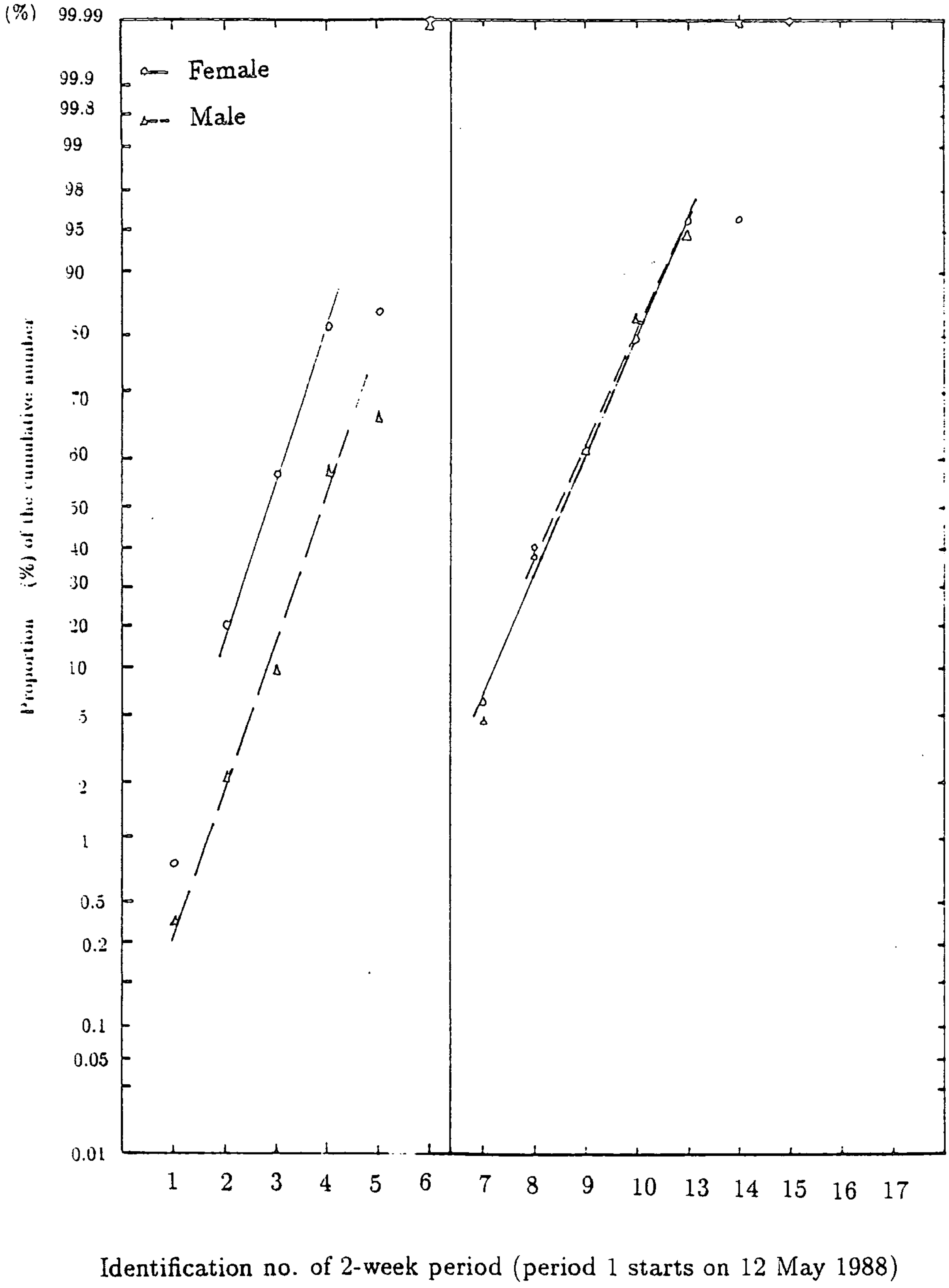



<Fig.4.1.1b> Frequency of capture (including re-capture) of *Pterostichus madidus* in grassland in 1988

<Fig.4.1.2a> Proportion (%) of the cumulative number of *Pterostichus madidus* in woodland by 2-week period

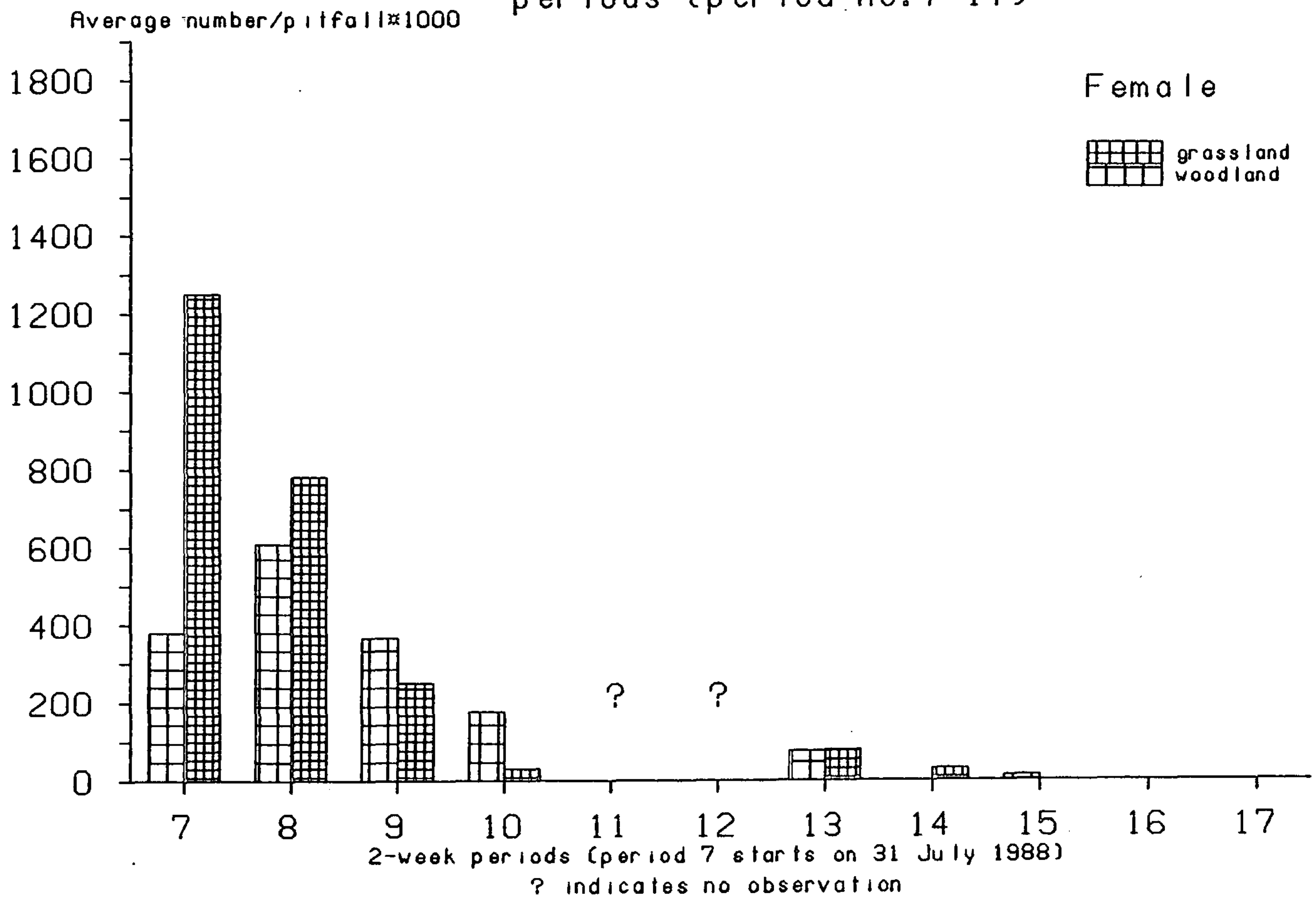


<Fig.4.1.2b> Proportion (%) of the cumulative number of *Pterostichus madidus* in woodland in periods no. 1 — 6 and 7 — 17



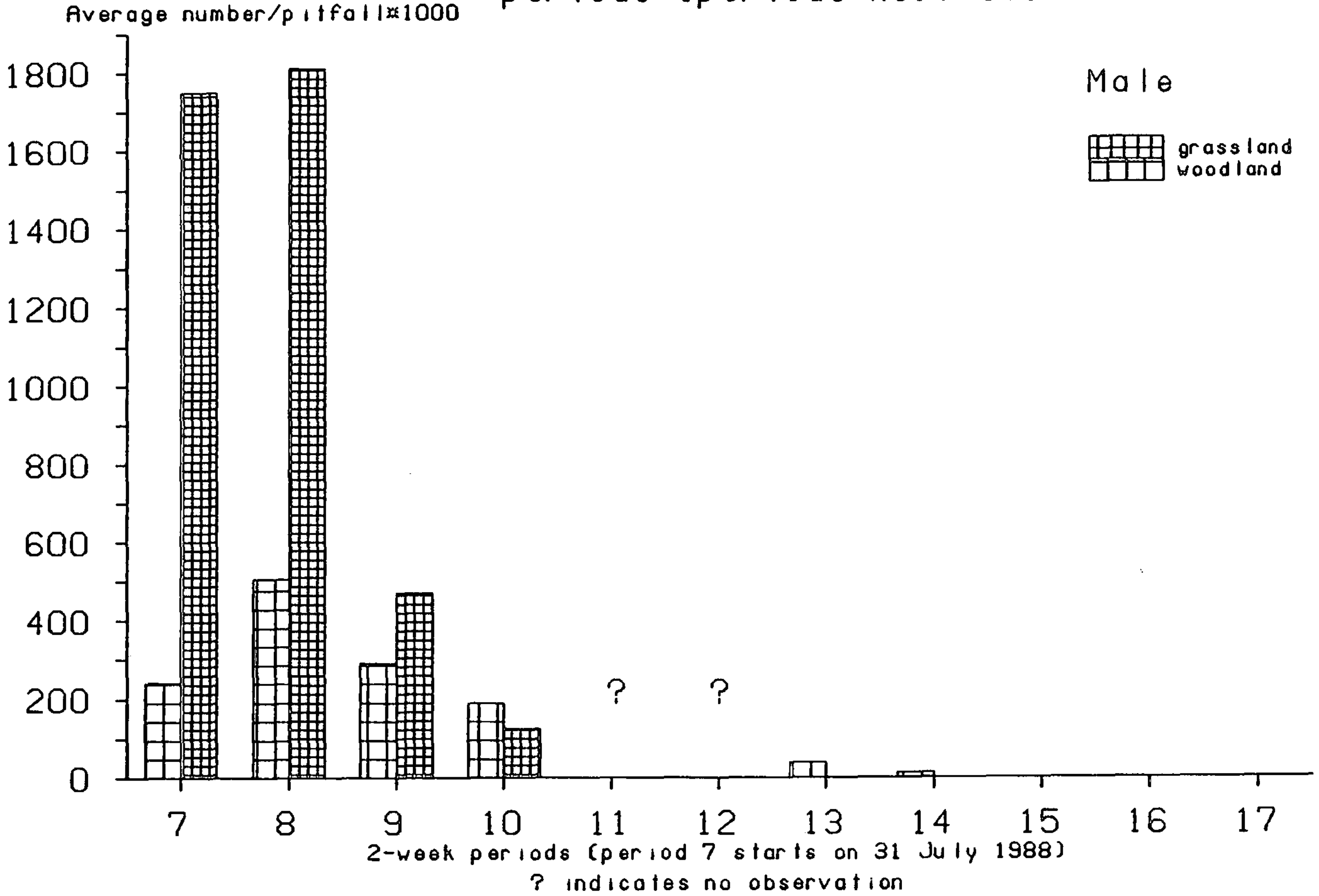
<Fig.4.1.3a>

Number of *Pterostichus madidus* per pitfall in 2-week periods (period no.7-17)

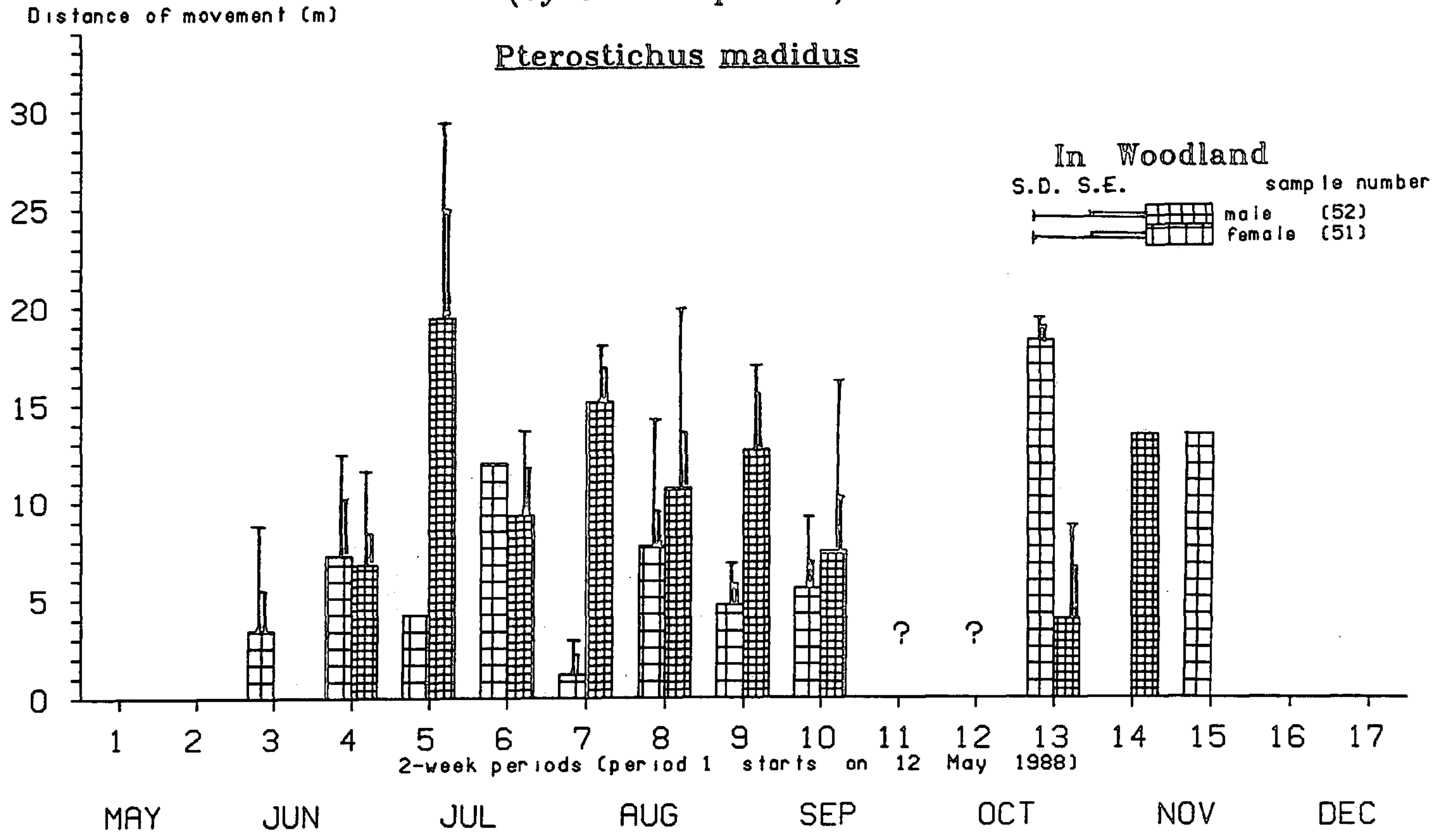


<Fig.4.1.3b>

Number of *Pterostichus madidus* per pitfall in 2-week periods (periods no.7-17)



<Fig.4.1.4a> Distance between capture and re-capture points (by 2-week periods)

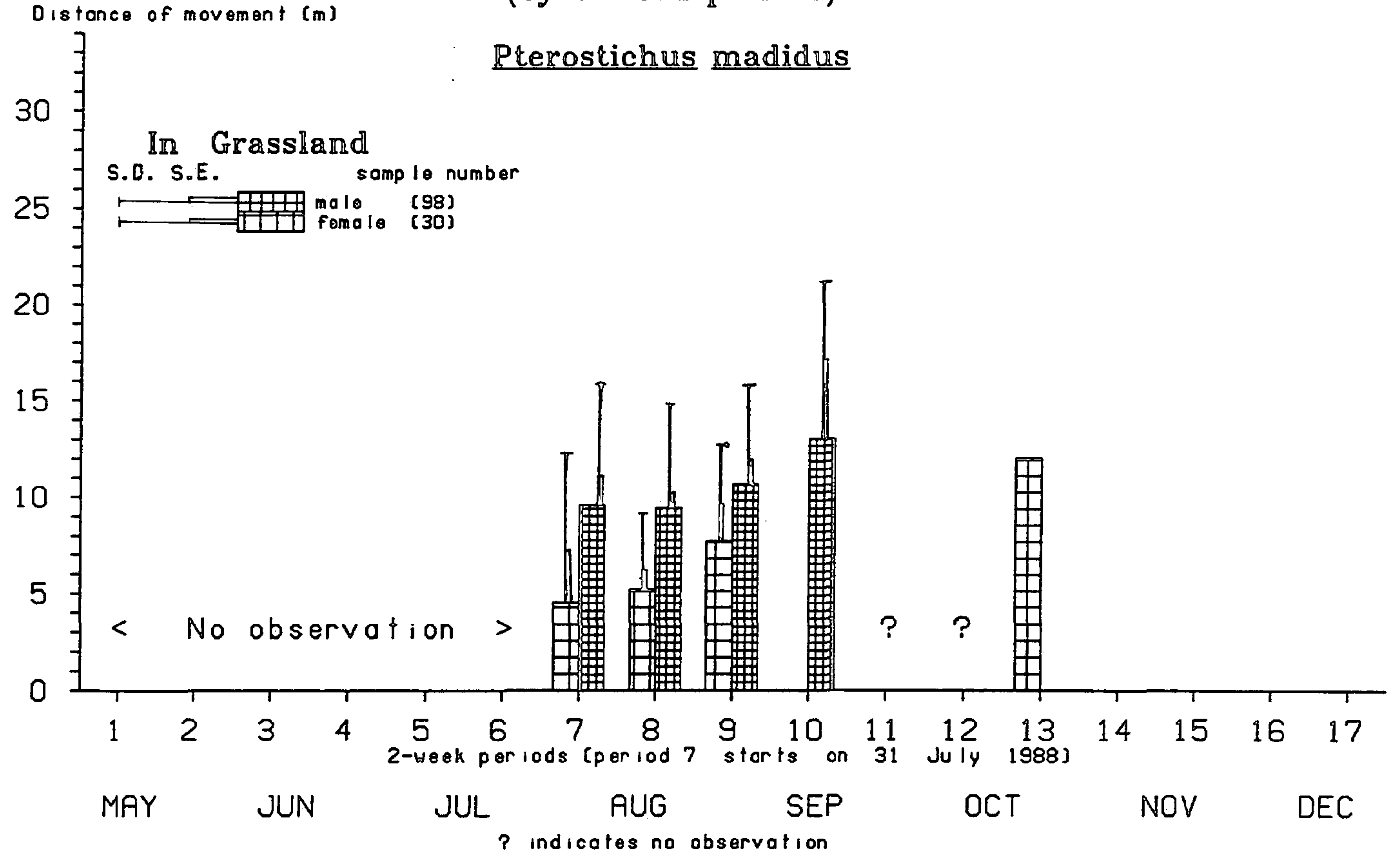


Pterostichus madidus

In Woodland

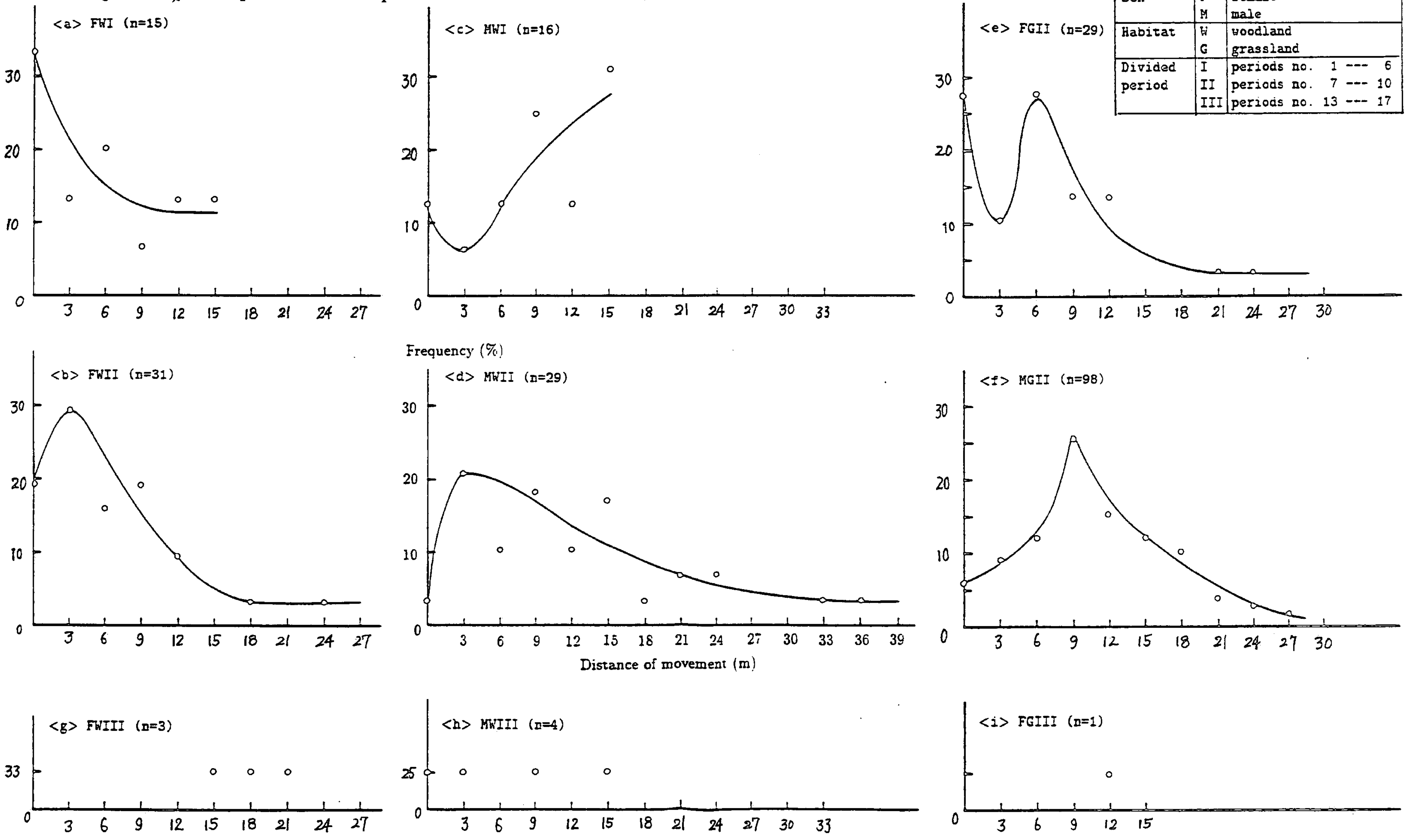
? indicates no observation

<Fig.4.1.4b> Distance between capture and re-capture points (by 2-week periods)



<Fig.4.1.5> The distribution of frequency for the distance of movement of each sex of *Pterostichus madidus* in the two habitats (in three divided periods). If capture and recapture habitats are different, the datum is put into the capture habitat.

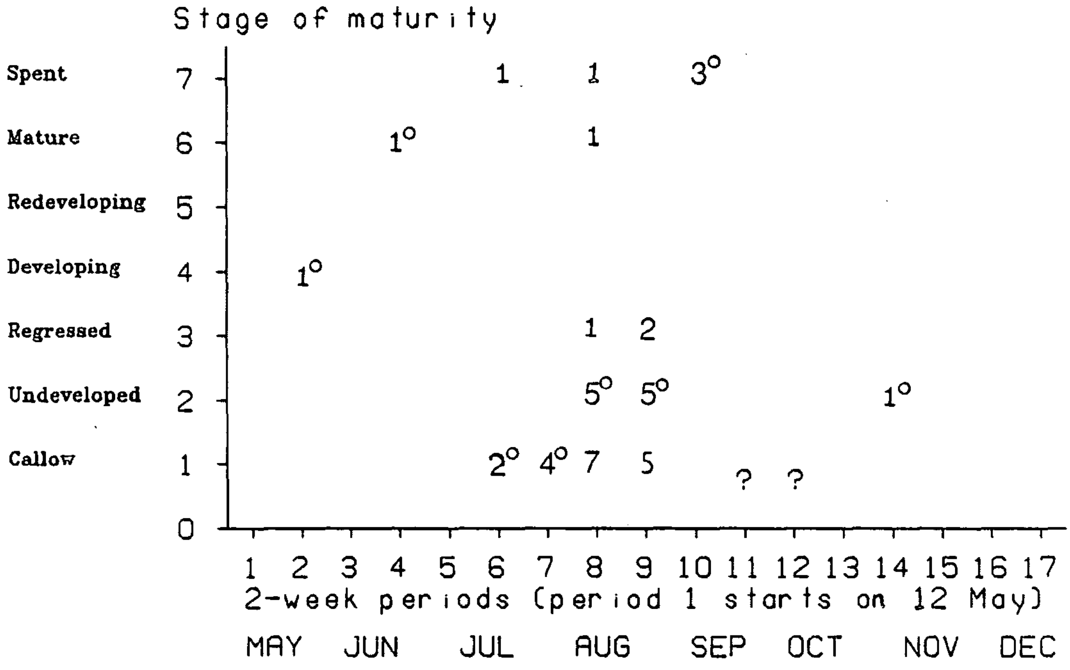
Sex	F M	female male
Habitat	W G	woodland grassland
Divided period	I II III	periods no. 1 --- 6 periods no. 7 --- 10 periods no. 13 --- 17



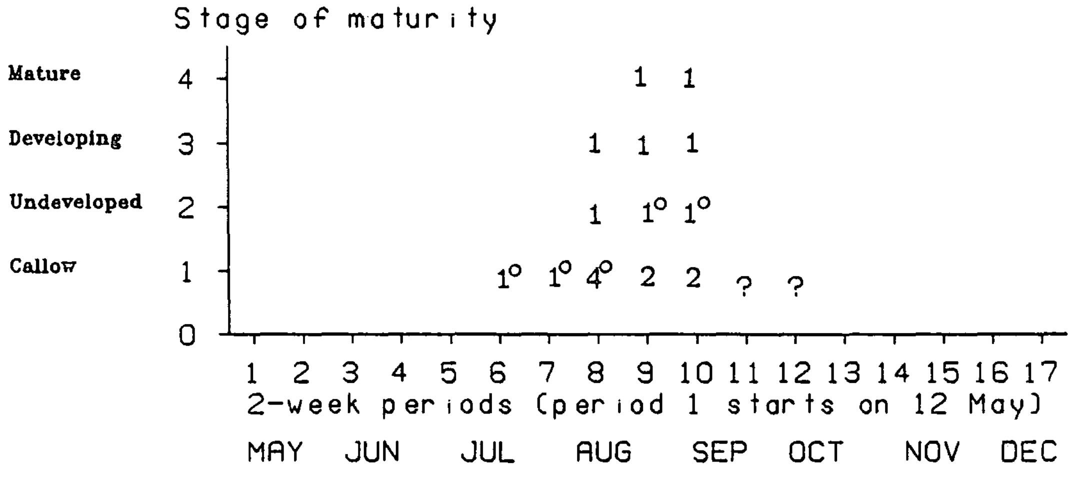
<Fig.4.1.6> Stages of maturity of <u>Pterostichus</u> <u>madidus</u> caught in successive 2-week periods in woodland

Frequencies are plotted
O indicates median value in each period
? indicates no observation

<a> Female (40)



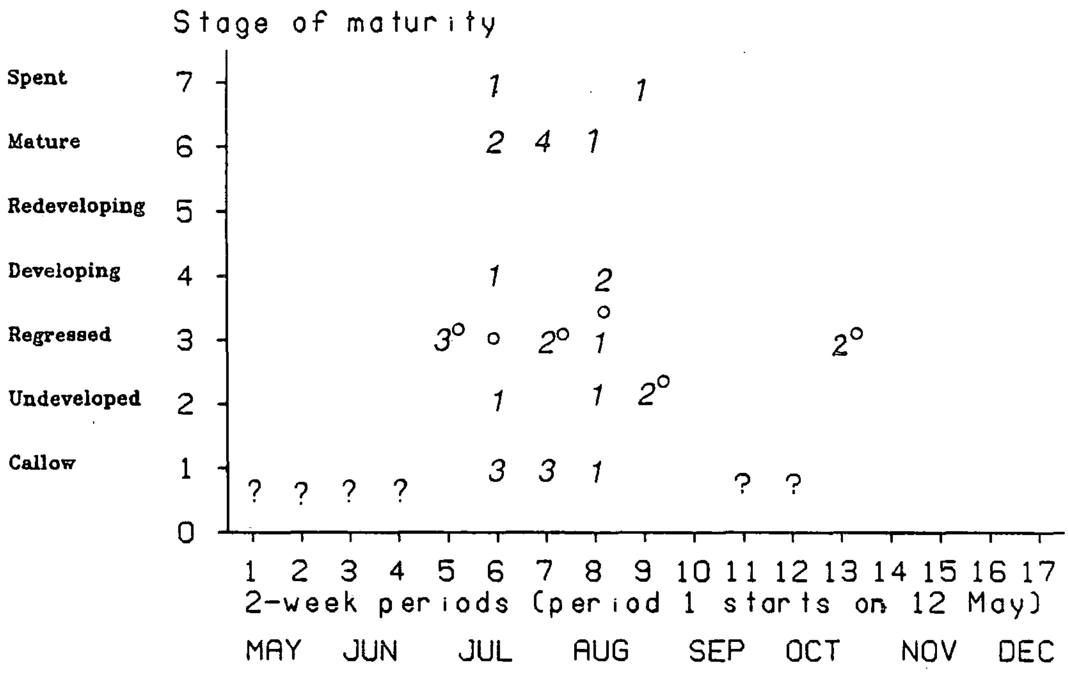
<b> Male (18)



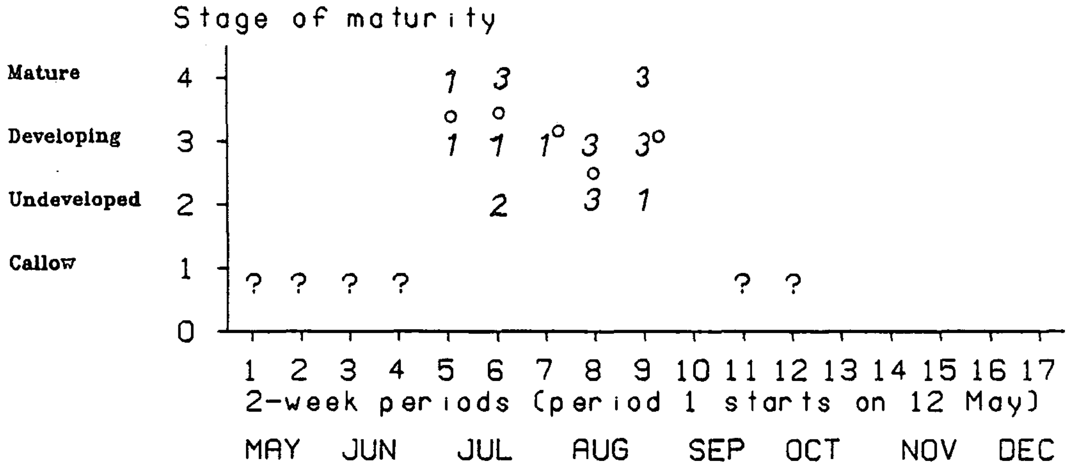
<Fig.4.1.6> Stages of maturity of <u>Pterostichus</u> <u>madidus</u> caught in successive 2–week periods in grassland

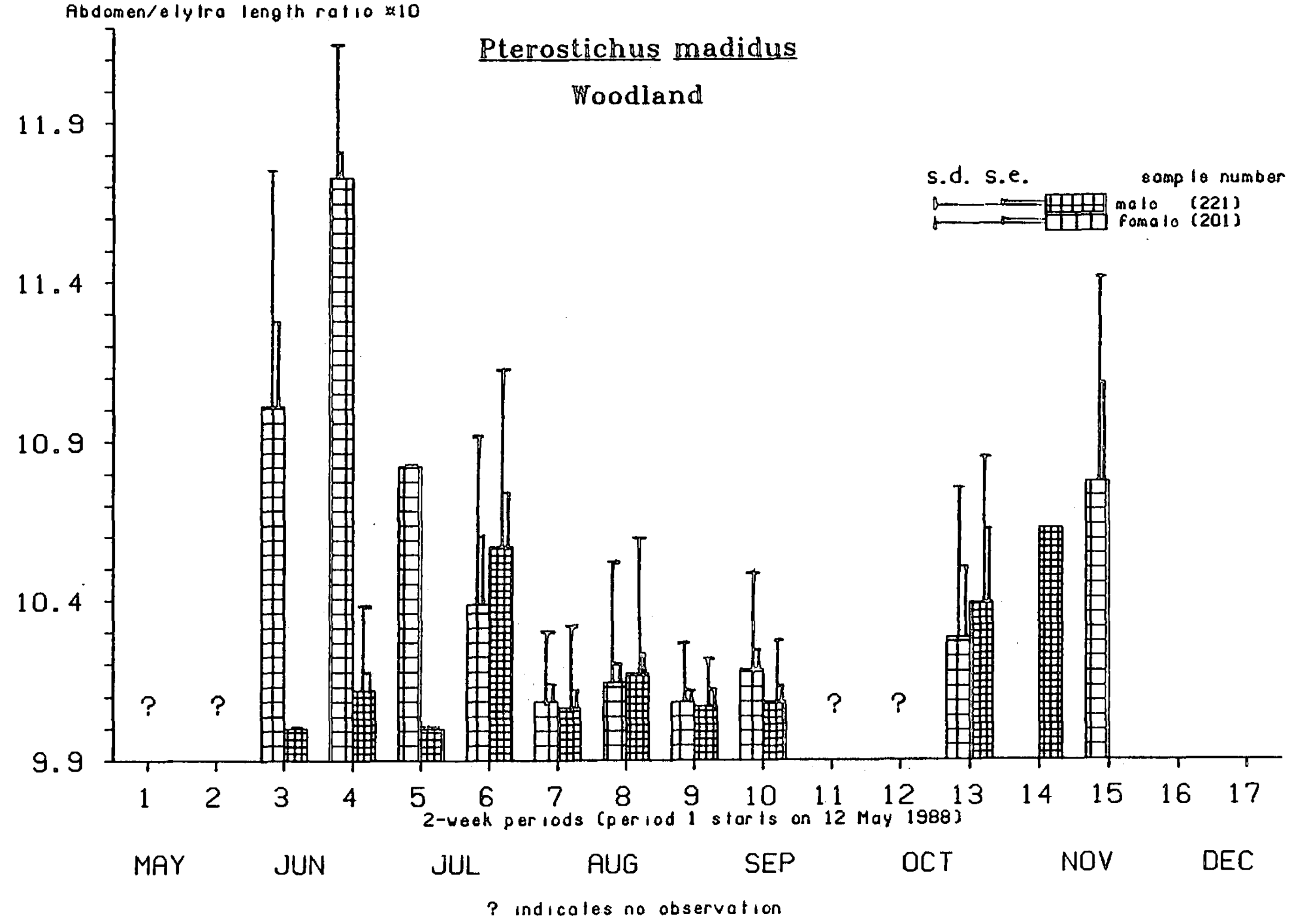
Frequencies are plotted
o indicates median value in each period
? indicates no observation

<c> Female (31)



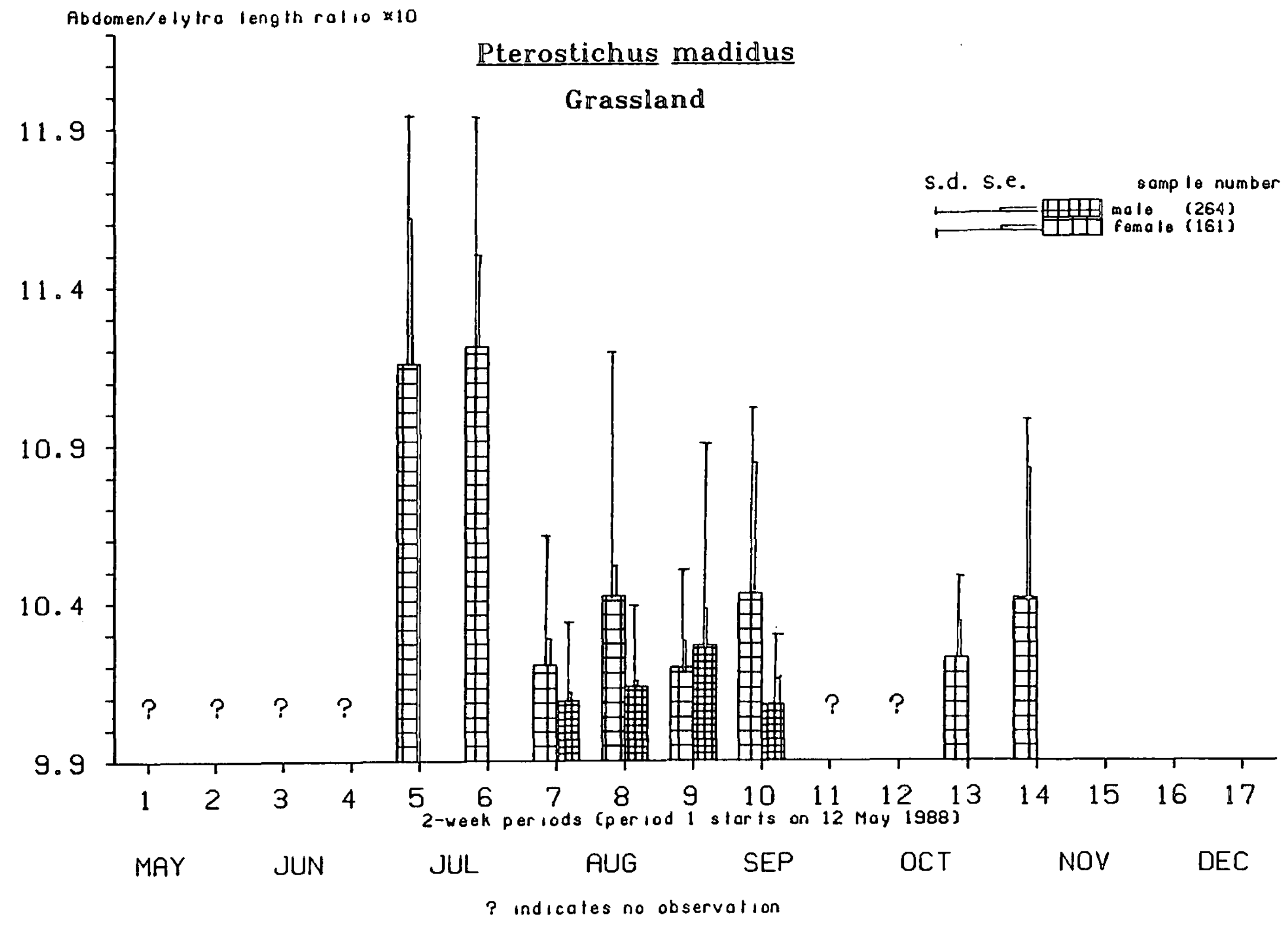
<d> Male (22)





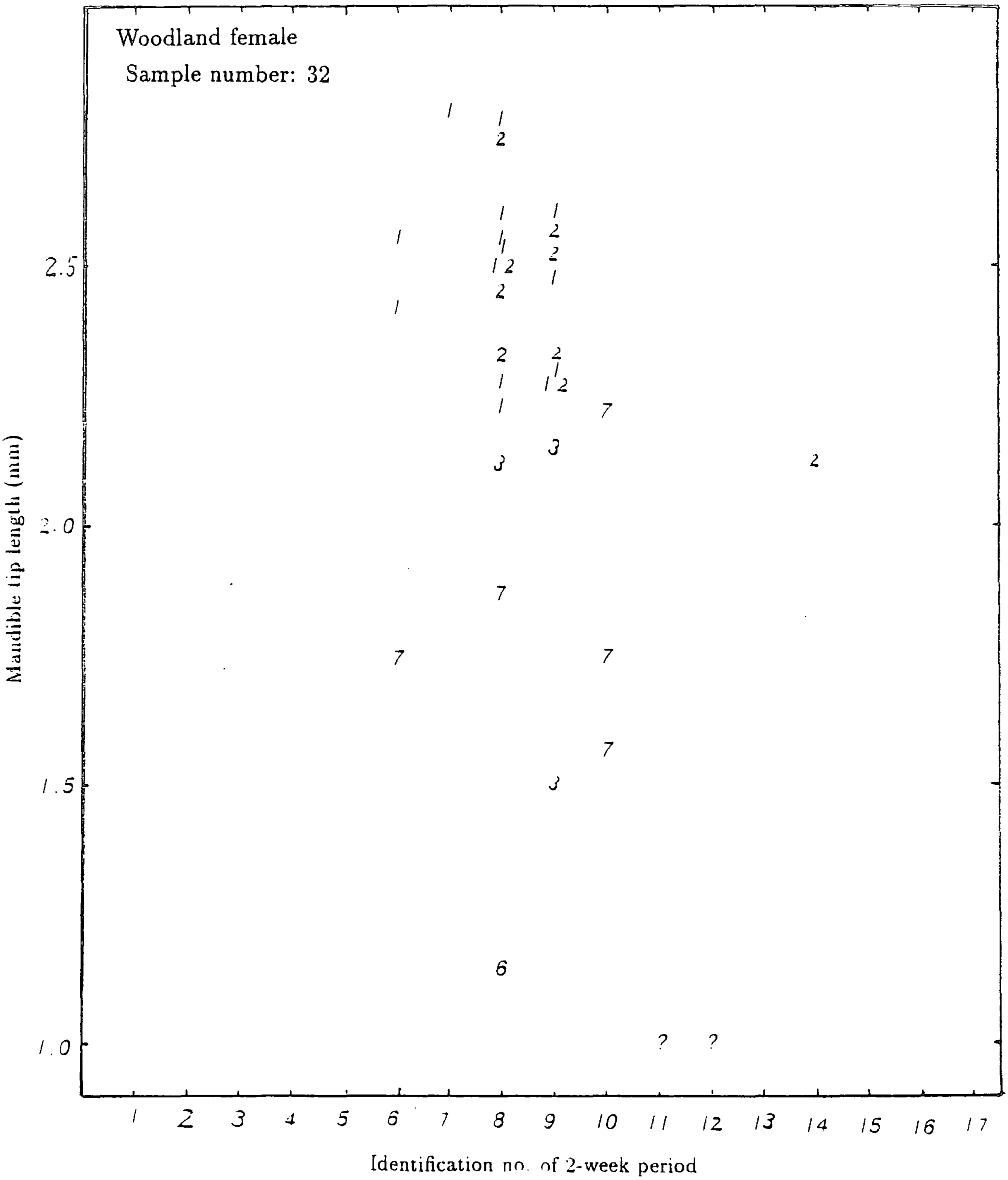
<Fig.4.1.7a> Abdomen/elytra length ratio in 2-week periods

<Fig.4.1.7b> Abdomen/elytra length ratio in 2-week periods



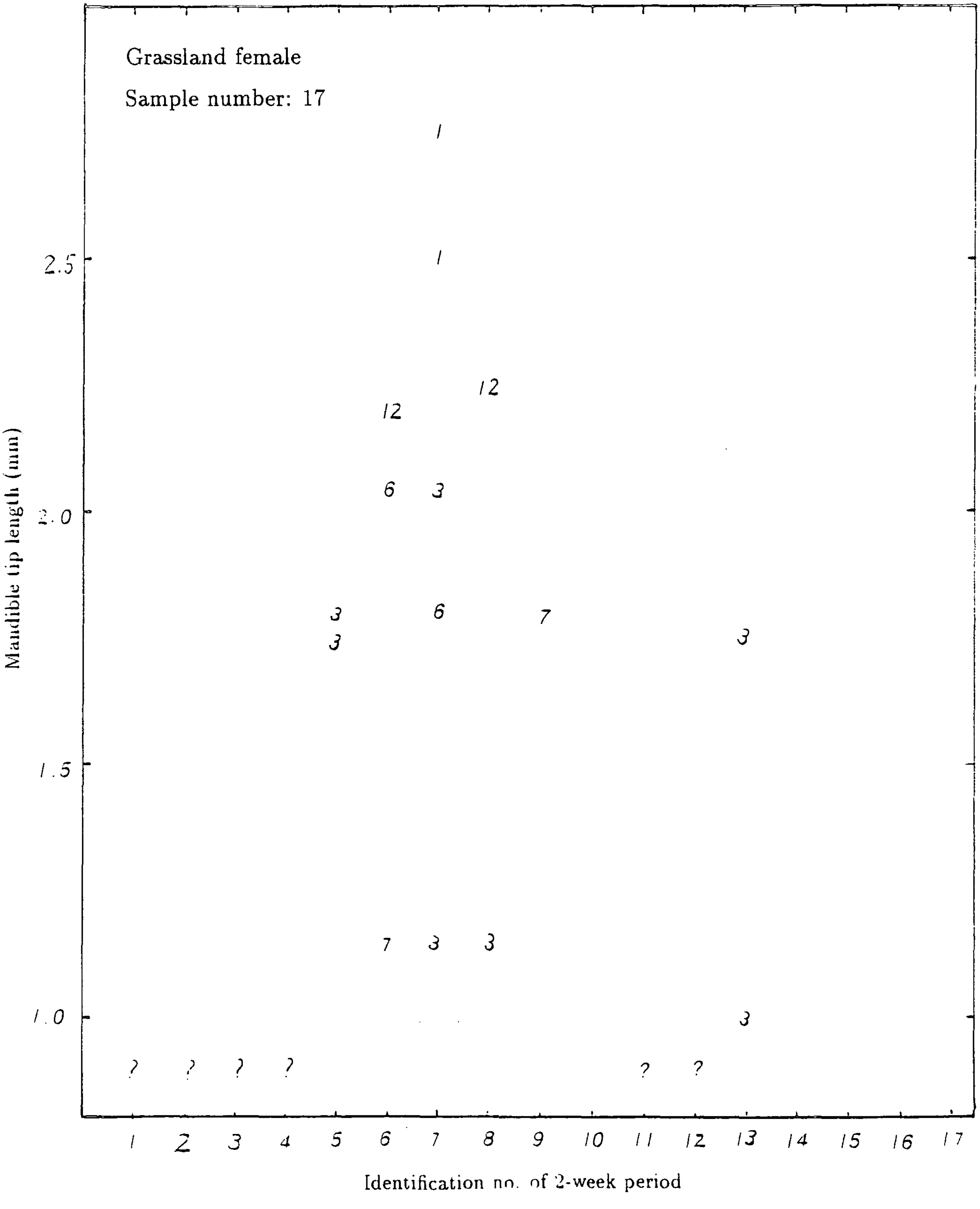
<Fig.4.1.8a> Mandible tip length of *Pterostichus madidus* by 2-week periods, with maturity stage

(Maturity stages are plotted)



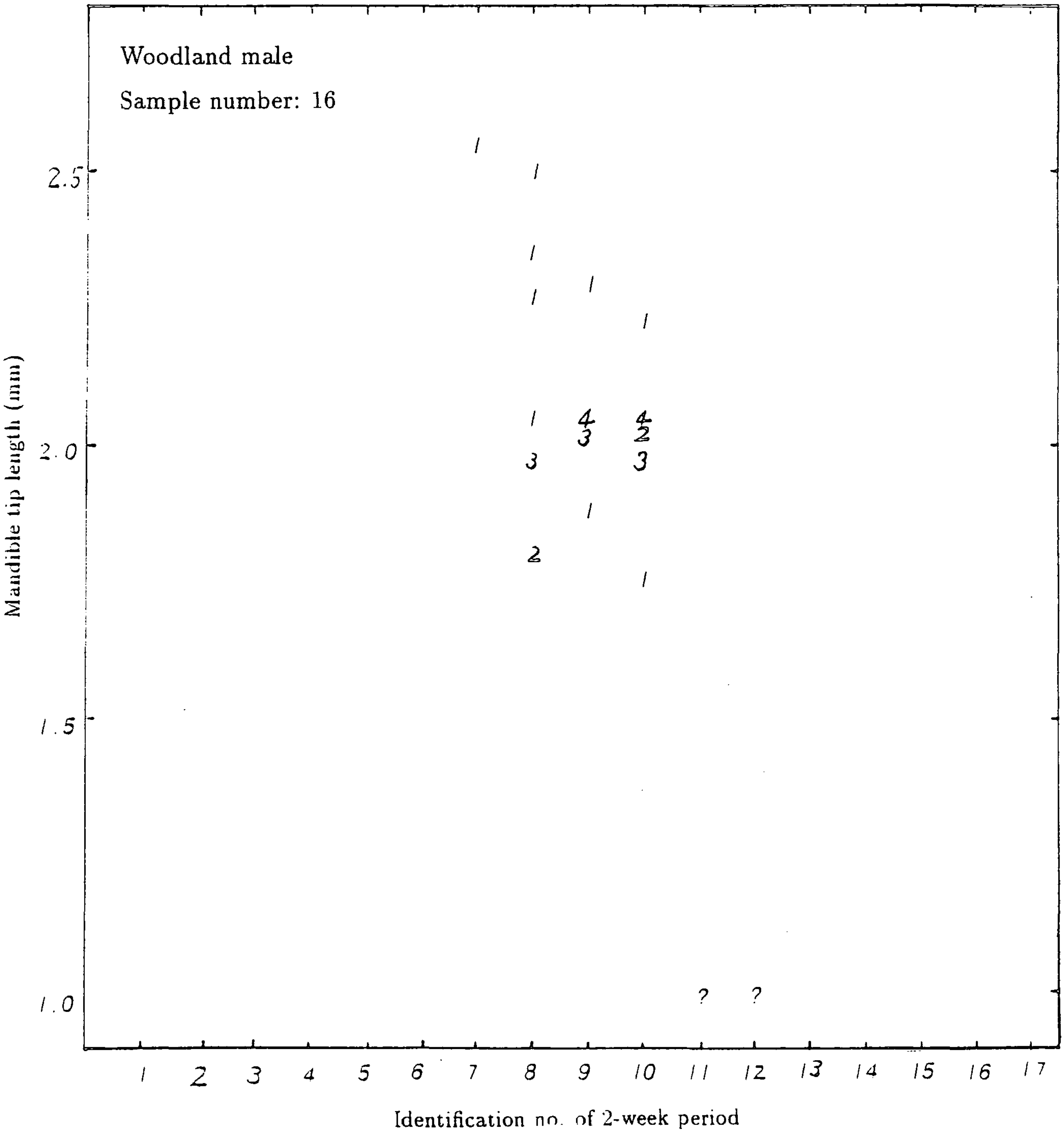
<**Fig.4.1.8b**> Mandible tip length of *Pterostichus madidus* by 2-week periods, with maturity stage

(Maturity stages are plotted)



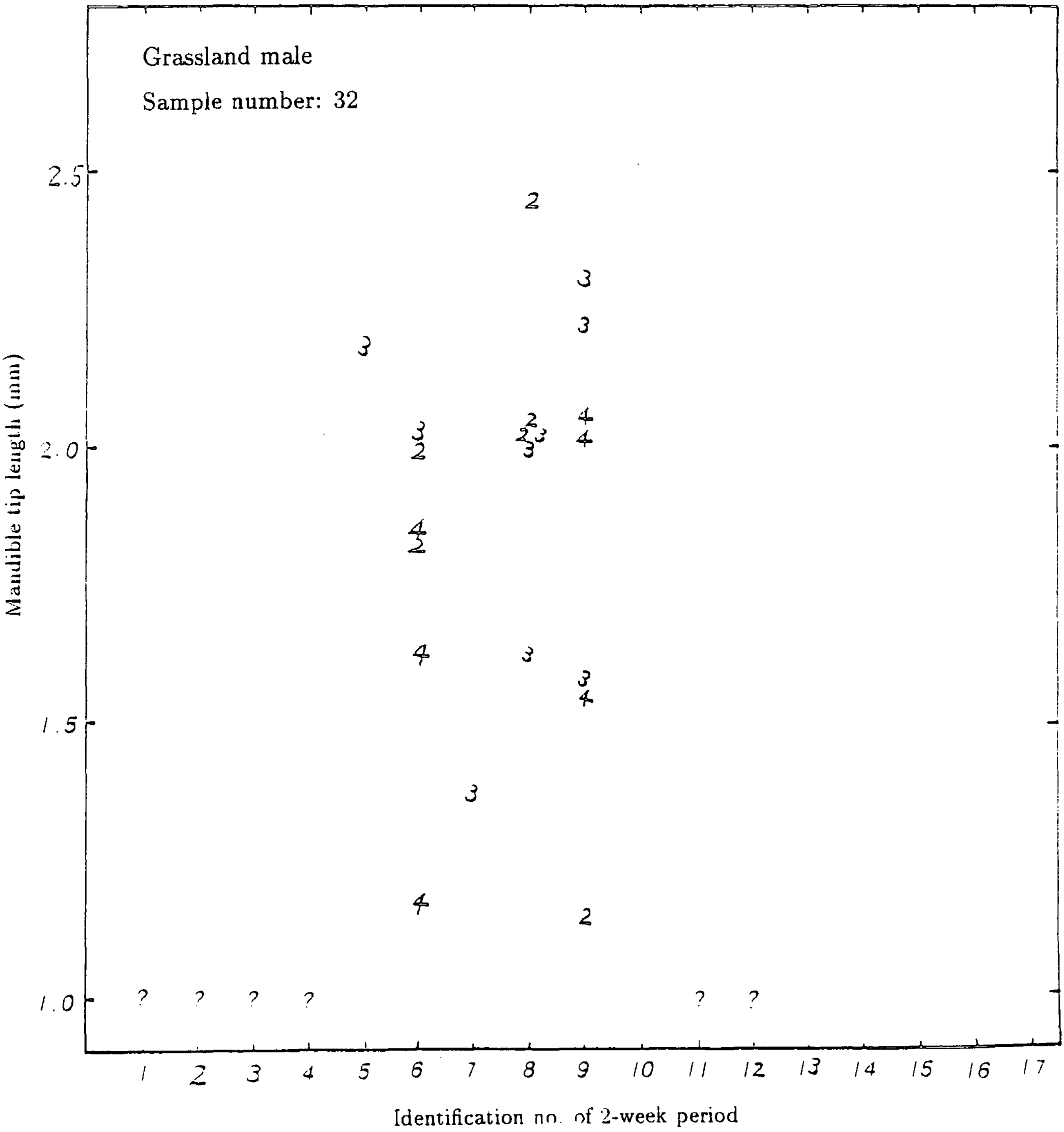
<**Fig.4.1.8c**> Mandible tip length of *Pterostichus madidus* by 2-week periods, with maturity stage

(Maturity stages are plotted)

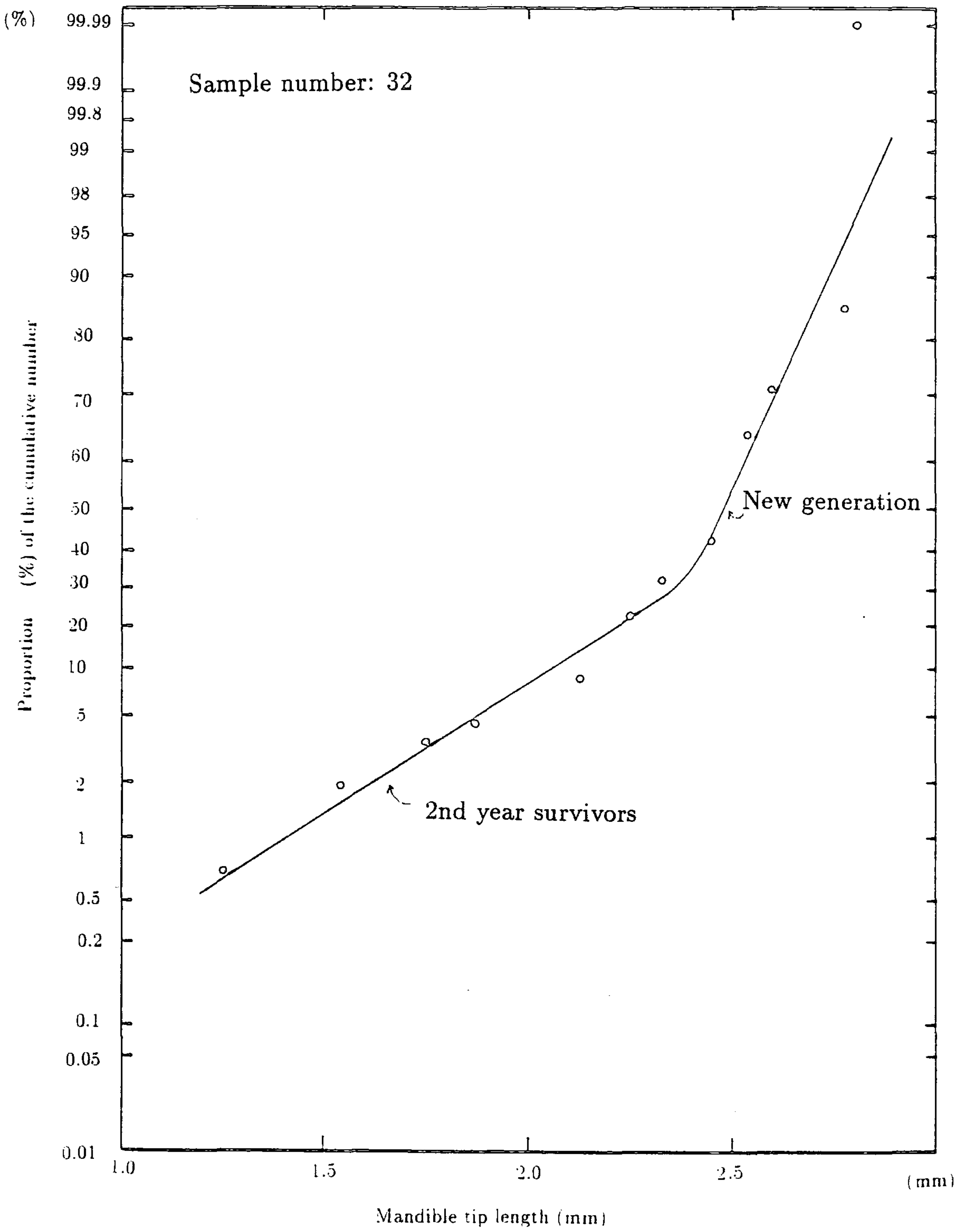


<Fig.4.1.8d> Mandible tip length of *Pterostichus madidus* by 2-week periods, with maturity stage

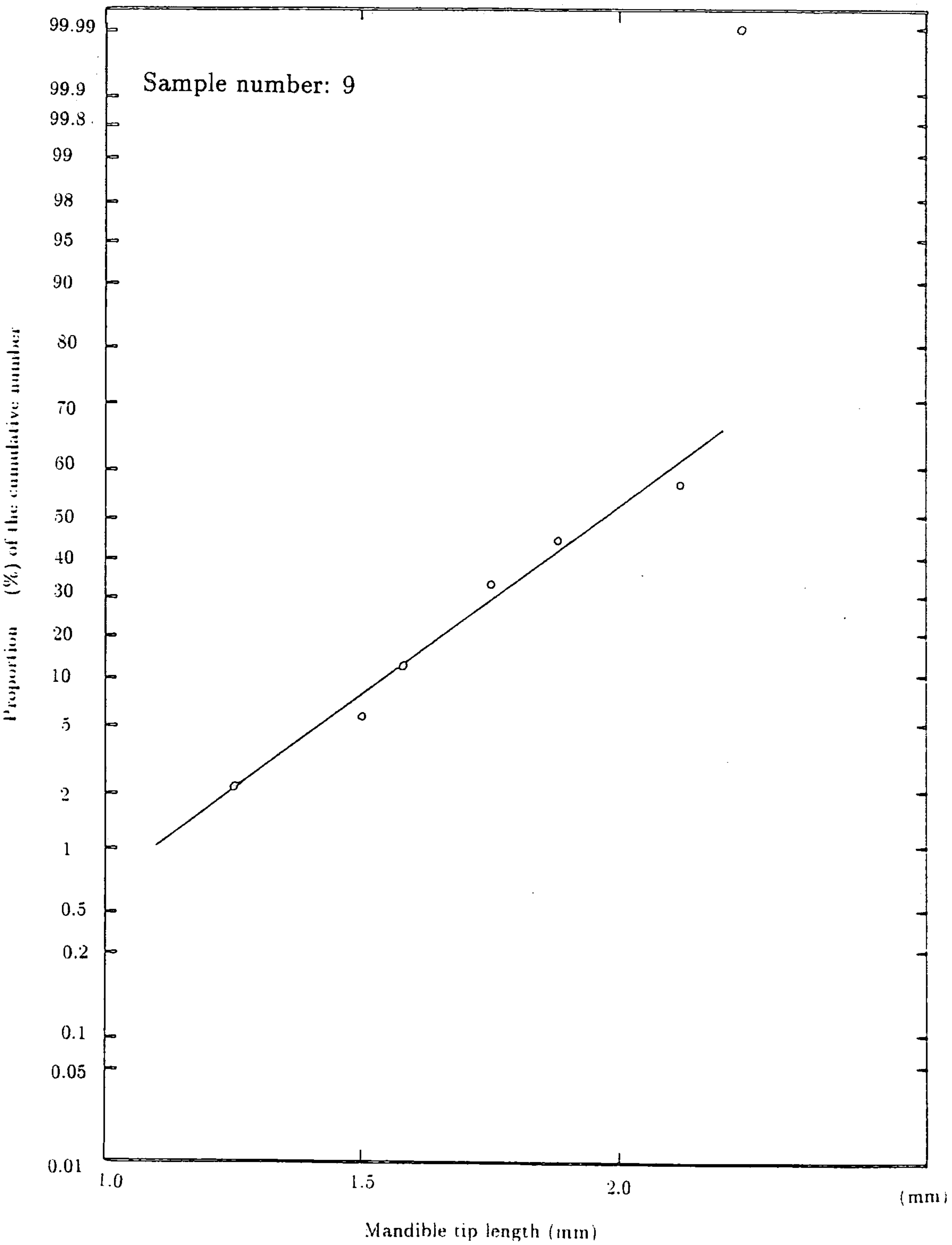
(Maturity stages are plotted)



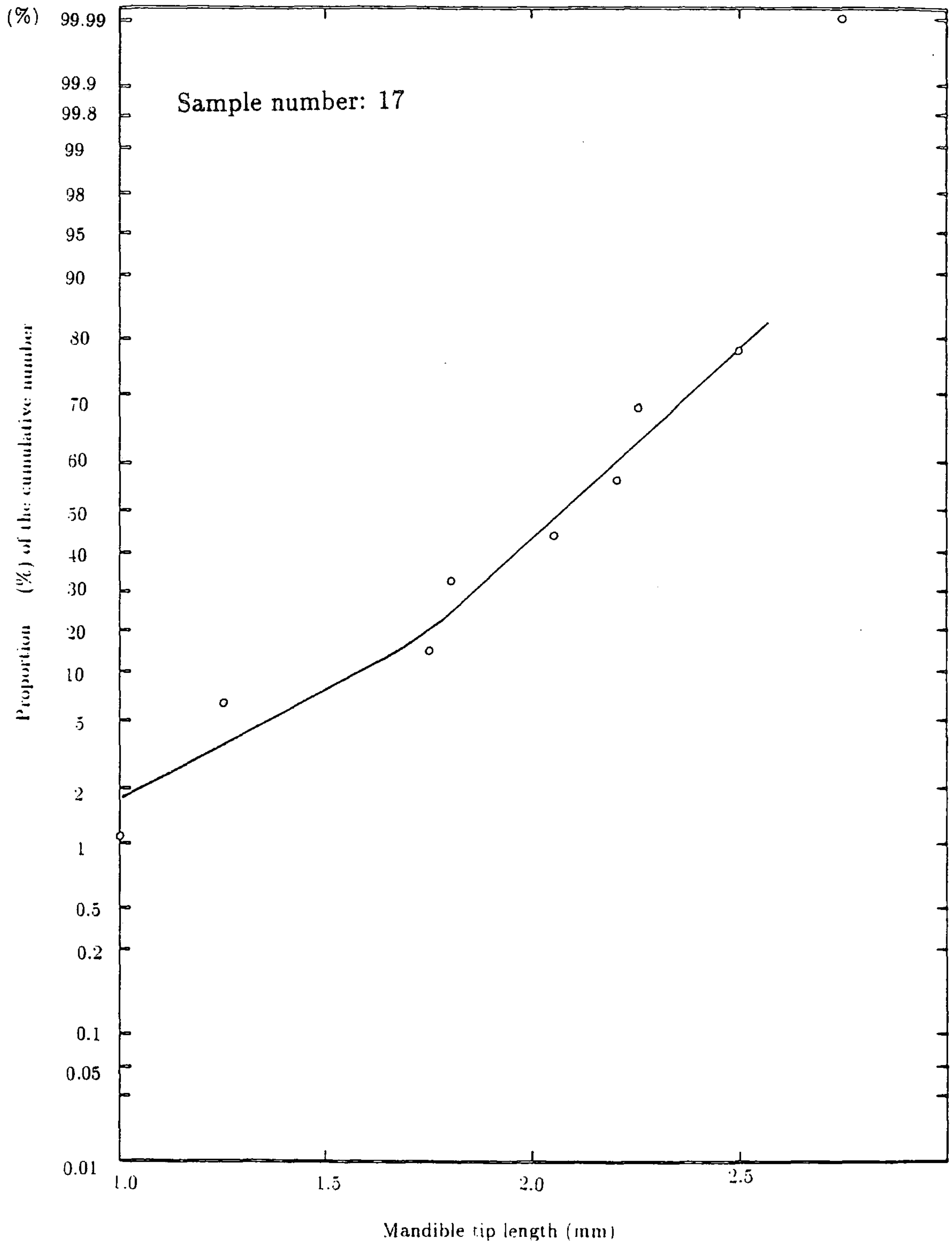
<Fig.4.1.9a> Proportion (%) of the cumulative number of woodland females of *Pterostichus madidus* by the differences of the mandible tip length



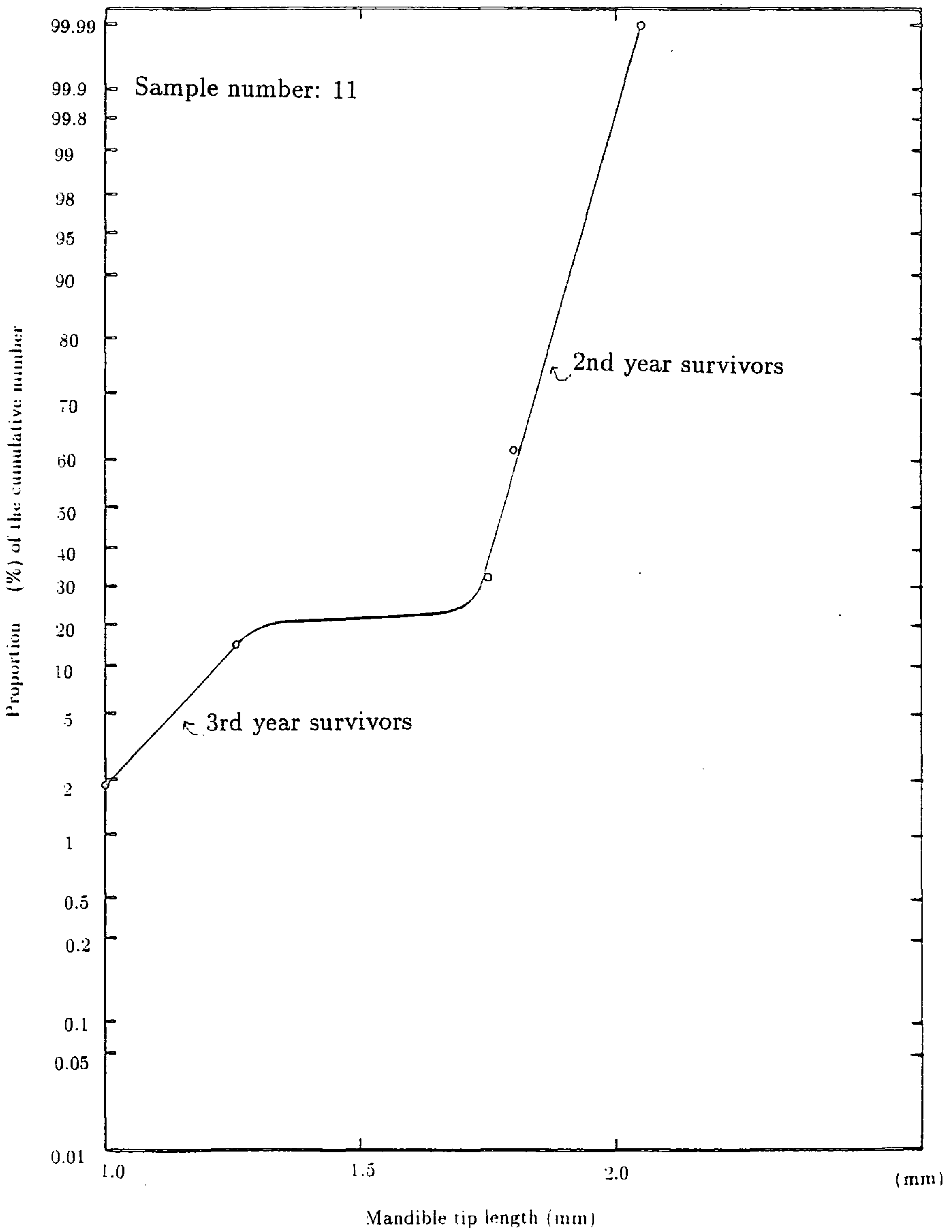
<Fig.4.1.9b> Proportion (%) of the cumulative number of woodland females of the maturity stages: 3 — 7 of *Pterostichus madidus* by the differences of the mandible tip length



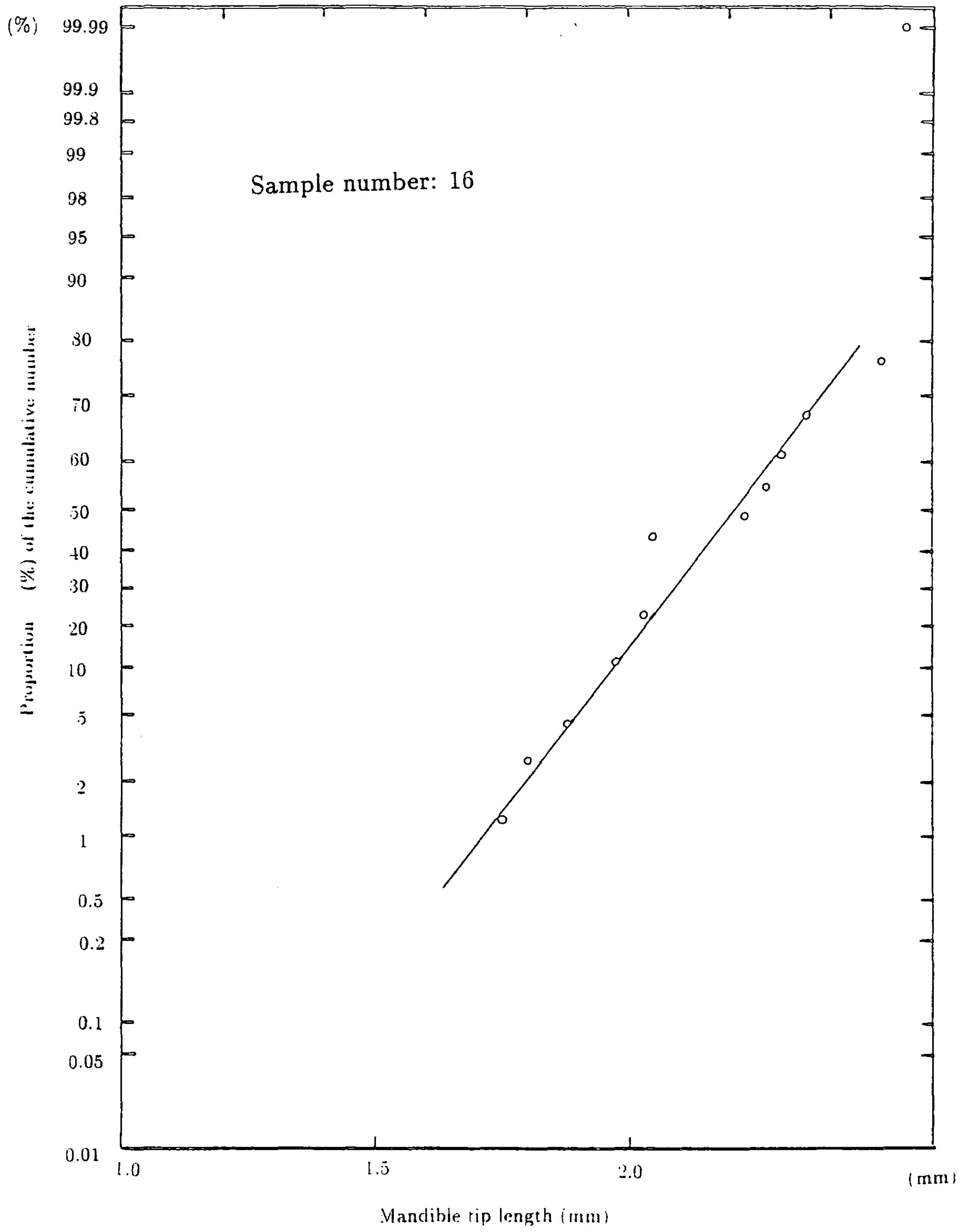
<Fig.4.1.9c> Proportion (%) of the cumulative number of grassland females of *Pterrostichus madidus* by the differences of the mandible tip length



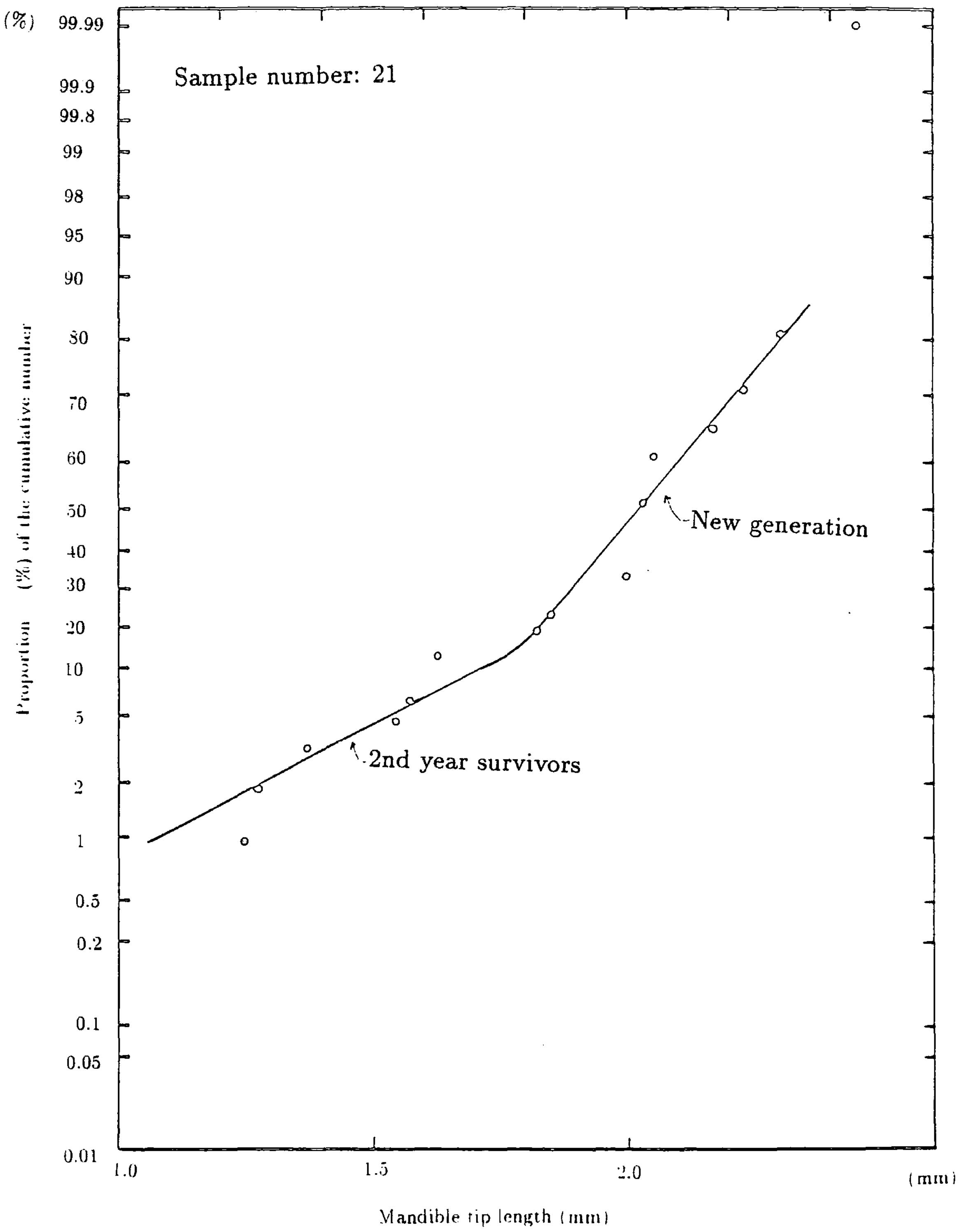
<**Fig.4.1.9d**> Proportion (%) of the cumulative number of grassland females of the maturity stages: 3 — 7 of *Pterrostichus madidus* by the differences of the mandible tip length



<Fig.4.1.9e> Proportion (%) of the cumulative number of woodland males of *Pterrostichus madidus* by the differences of the mandible tip length



<Fig.4.1.9f> Proportion (%) of the cumulative number of grassland males of *Pterrostichus madidus* by the differences of the mandible tip length

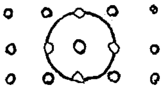


<Fig.4.1.10> The probability of capture as a function of movement distance

(Average pitfall diameter ≈ 6.5cm)

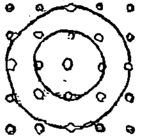
e.g. A 3m annulus including 4 pitfalls

$$\frac{4 \times 6.5^2\pi}{3^2 \times 10^4\pi}$$

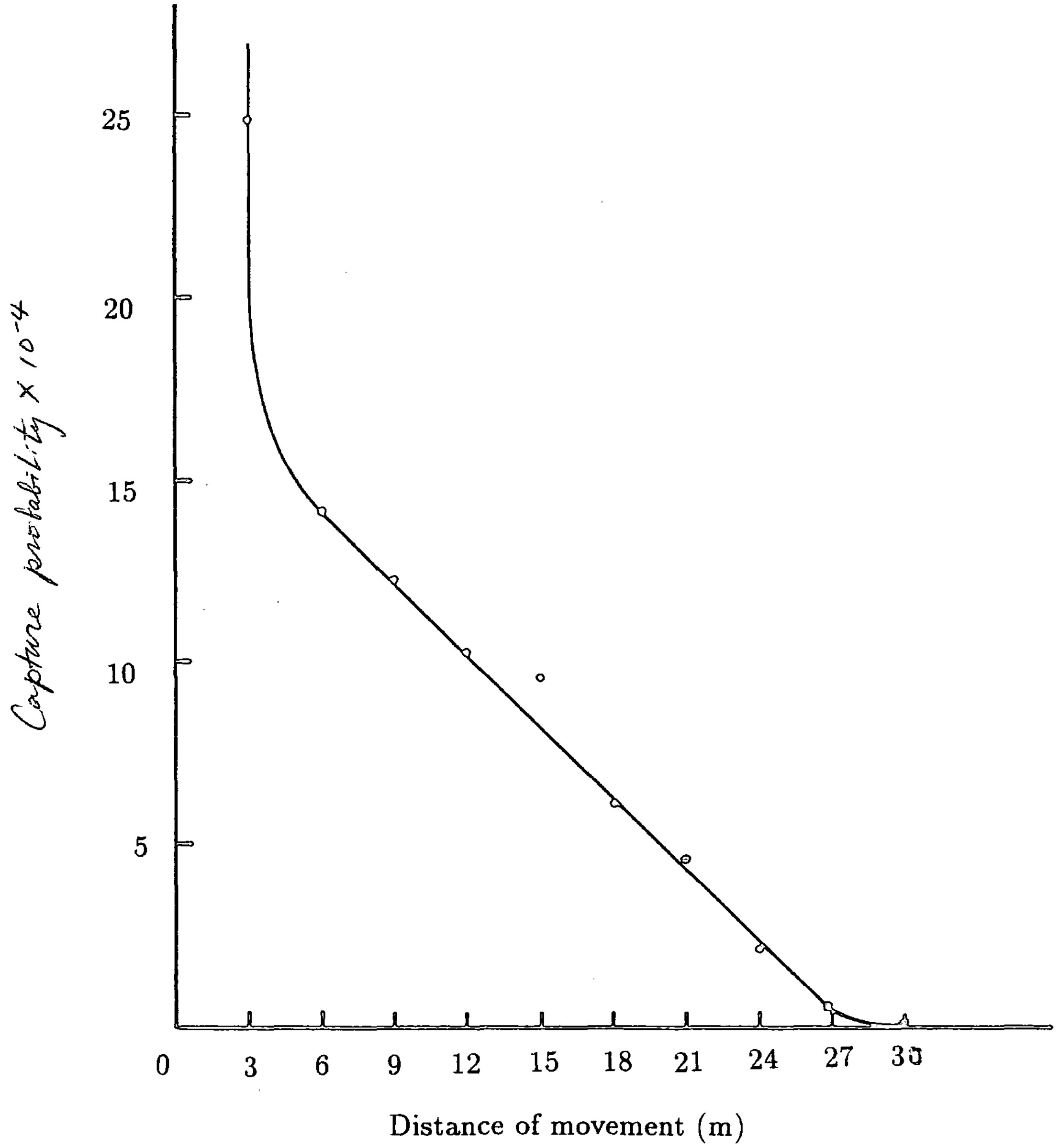


e.g. An annulus of radius $3 < r \leq 6$m includes 8 pitfalls

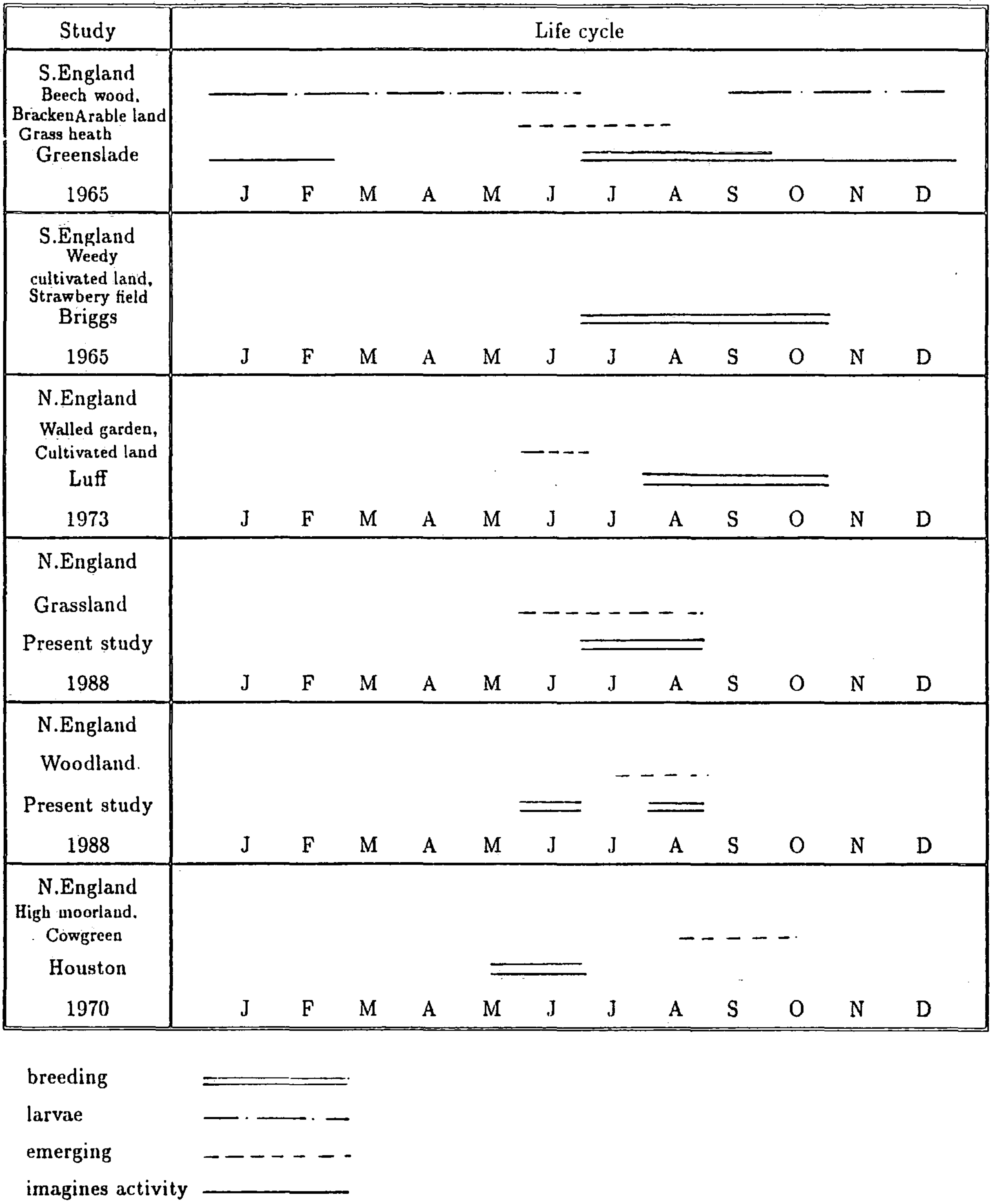
$$\frac{8 \times 6.5^2\pi}{(6^2 - 3^2) \times 10^4\pi}$$



ture probability=Ratio of areas= $\frac{\text{The pitfall apertures}}{\text{Area of an annulus}}$



<Fig.4.1.11> The results of previous and present study of life cycle of *Pterostichus madidus*



4.2 Nebria brevicollis

PREVIOUS INFORMATION

Nebria brevicollis is found mainly in woodland litter (Greenslade 1964), although the species is very eurytopic (Lindroth 1974).

Detailed laboratory studies of the development of this species were made by Thiele (1969, 1971).

Field studies were performed as follows:

- Gilbert (1958) studied at a gray-dune and marram grass lowland site in northern Wales .
- Greenslade (1964) studied at beech wood, bracken, arable land and grassland sites in Berkshire. Penny (1969) reported results from lowland woodland in southern Scotland.
- Thiele (1969, 1971) and Krehan (1970) studied at forest sites at 65m above sea level in Köln in West Germany.

Museum data were analysed by

- Larsson (1939) in Denmark
- Lindroth (1945, 1949) in Scandinavia.

Nebria brevicollis is "an autumn breeder with a thermic hibernation parapause in the larva and a photoperiodic aestivation parapause in the adult" (Thiele 1977). The larva hatches later in the year, then hibernates. (Cold is obligatory for hibernation from the 1st to the 3rd larval stages). Next spring, the adult emerges. (High temperature is needed for larval transformation). Changeover to a short-day photoperiod provides the signal for egg-ripening; 16–17h light per day was found to be the critical photoperiod in the experiments by Thiele (1969, 1971), i.e. the beginning of July onwards. Maturation in short-day proceeds much better at 15°C than at 20°C (Thiele 1971). During the summer interruption in ovarian development, the females of *Nebria brevicollis* become inactive following fat storage (Thiele 1969, 1971), whereas starved *N. brevicollis* remain active (Penny 1969). Females begin to reproduce 2.5 months after the summer solstice. Maturation of the male is more or less independent of photoperiod (Thiele 1969, 1971).

Consider the results of field studies of the development of the imago. (See Fig.4.2.7, and Appendex E for meteorological data.)

- In southern England (Greenslade 1964), emergence has been reported to occur at the end of April–early June (mainly in May), and a maximum activity related to oviposition has been observed in October. Mature females have been observed in autumn and winter, and larvae from November until early spring.
- In northern Wales (Gilbert 1956) emergence occurred in May–June and breeding in September–November.
- In uplands in northern England (Houston 1970), breeding was found in August–September.
- In southern Scotland (Penny 1966), emergence was observed in mid May–mid June and breeding in September–February (mainly in September–October).

For other European countries;

- In Köln, West Germany (Thiele 1969); emergence was reported in May–June, with complete aestivation for five weeks and then breeding in September–October.
- In Denmark (Larsson 1939); emergence occurred in June and breeding in mid August–September.
- In Scandinanvia (Lindroth 1945, 1949); maximum activity was observed in June and a small peak of activity in August.

RESULTS

4.2.1 Numbers Captured

The data on the frequency of capture of *Nebria brevicollis* in the Durham woodland <Fig.4.2.1a> show two peaks of abundance and/or activity in periods no.3 and 10 for females and in periods no.5 and 10 for males. This is confirmed by plotting the data on probability paper <Fig.4.2.2a, b>; the result shows peaks in mid-June and mid-September (periods no.3 and 10) for females and in early July and mid-September (periods no.5 and 10) for males. Table 4.2.1 shows the proportion of females captured in the two halves of the study period (periods no.1–7 and 9–17) in the two habitats. In woodland, the proportion of males may have been lower in the second half than the first, though the significance of the difference was low ($\chi^2_1 = 1.96$, $p > 0.05$). The same comparison cannot be made in grassland because of the late starting of the sampling. During the second half of the study, the proportion of females captured was significantly larger in grassland than in woodland ($\chi^2_1 = 10.03$, $0.001 < p < 0.01$). A few of the captures in woodland in the first half of the study were of callows in June (periods no.3 and 4): See Fig.4.2.1a.

The data in Fig.4.2.3a, b show the captures per pitfall in the two habitats after period no.7. Although the timings of the peaks of abundance and/or activity could not be identified accurately, the start of the second peak of abundance appeared to be earlier in woodland than in grassland. Females remained more abundant and/or active later in grassland than in woodland.

4.2.2 Distance of Movement

The data summarized in Table 4.2.2 indicate that both sexes of *N. brevicollis* may tend to move further in woodland than in grassland, though the differences are small (female: $U = 12.5$, $p > 0.10$; male: $U = 23.0$, $p > 0.10$). Differences in movement distance between sexes are also not significant (in woodland: $t_{24} = 0.48$, $p = 0.637$; in grassland: $U = 6.5$, $p \gg 0.10$). Unfortunately the comparison of movement distances between the two halves of the study period in woodland cannot be shown because of a lack of appropriate data. The summarized data of Table 4.2.3, comparing the movements of both sexes in the two habitats in the second half of the study (periods no.9–17), show results similar to those above (male: $U = 13.0$, $p > 0.10$; female: $U = 31.5$, $p > 0.10$; woodland: $U = 44.5$, $p > 0.10$).

One female was found to move from woodland to grassland within 18 females recaptured <Table 4.2.4>. One male moved from grassland to woodland within 25 males recaptured. Movement of females from grassland to woodland and that of males from woodland to grassland were not observed. The populations of this species therefore seem to be quite closed in each habitat.

4.2.3 Stage of Maturity

In woodland, the stages of maturity of dissected animals <Fig.4.2.4a, b> show that female callows emerged in early June (period no.3), and male callows earlier than late June (period no.4) by the field observation <Fig.4.2.1a>. Mature females were observed from mid-September to late November (periods no. 10–15) and males from mid-September to late October (periods no.10–13). In grassland, mature females were observed in late October and early November (periods no.13–14) but callows were not caught because of the late starting date for data collection in grassland <Fig.4.2.4c>.

In early December (period no.16), two males did not have mature sperm. The following causes are suggested:

1. They had matured once and resorbed sperm; or
2. They failed to become mature or were maturing very slowly.

4.2.4 Elytra Length

The data summarized in Table 4.2.5 suggest that the elytra lengths of females were significantly larger than those of males in both habitats (in woodland $t_{100} = 6.05, p < 0.001$; in grassland $t_{35} = 3.15, p = 0.003$). For females, elytra lengths in woodland were significantly larger than those in grassland ($t_{70} = 3.52, p = 0.001$). For males, the elytra lengths of the woodland individuals tend to be larger than those of grassland individuals, though not significantly so ($t_{65} = 1.28, p = 0.206$).

4.2.5 The Ratio of Abdomen to Elytra Length

The ratios of abdomen/elytra length are shown in Fig.4.2.5a,b. The ratios for woodland females were large during the second peak of abundance from early

September to late November (periods no.9–14); in grassland, the ratios were large from mid-September to early December (periods no.10–16). For males, the largest ratios were observed in late October (period no.13). Indeed, the largest ratio of abdomen/elytra length occurred in late October (period no.13) for both sexes in the two habitats.

4.2.6 Mandible Tip Length

The mandible tip length of woodland individuals of *Nebria brevicollis* showed the presence of two subgroups for both sexes when plotted on probability paper <Fig.4.2.6>. The first group displayed mandible tip lengths which were both approximately equal for the two sexes and greater than the lengths observed in the second group. However, the second group showed female mandible tip lengths that were larger than those of the males. From these results, the following conclusions are drawn.

1. The woodland individuals of both sexes are composed of two generations in which one is a new generation and another is a 2nd year surviving generation.
2. The new generations of both sexes have almost the same mandible tip length despite a significant difference of elytra length (the female elytra length is larger than that of the male).
3. The mandible tip of the male survivors is worn out more than that of the female survivors so that the males may use their mandibles more strenuously than the females.
4. The difference between the male mandible tip length in the two subgroups is larger than that for the females. The males may take food for a greater fraction of the year than the females, especially during the first half of the

study. <Fig.4.2.1a>.

Although the data on the mandible tip length of grassland females are few, the following points are observed. For the grassland females:

1. smaller mandible tip lengths were observed than those of the woodland females;
2. the rate at which the mandible tip is worn out may be greater than that of the woodland females.

The reason for 1. may be a difference of original mandible tip length between the females of the two habitats, because the elytra length of the woodland female was significantly larger than that of the grassland female <Table 4.2.5> and both populations of females were quite restricted to each habitat (See the results section of 4.2.2). The reasons for 2. may be

(i) the grassland individuals consume different foods to those taken by woodland individuals, food which makes the mandibles wear away more quickly and/or

(ii) the grassland individuals eat more than the woodland individuals.

DISCUSSION

When the data on the capture frequencies <Table 4.2.1> and movement distances <Table 4.2.3> are considered together for the second half of the study (periods no.9–17), the sex ratio of woodland individuals is seen to be approximately 1:1. The reason for this is that movement distances of both sexes do not indicate significant differences of their activities; the numbers captured of both sexes were approximately equal. From the results of movement distances, the woodland individuals were observed to move futher than those in grassland for both sexes. (See the results section for movement distance <Table 4.2.3, Table 4.2.4>.)

In the woodland, emergence was observed in June (periods no.3 and 4) <Fig.4.2.1a, Fig.4.2.4a, b>. This agrees with the results of studies by Gilbert (1958), Greenslade (1964) and Penny (1969), in which *Nebria brevicollis* was found to emerge in spring. After emergence at Durham in June, few females were observed in woodland in July and August. This result also agrees with previous reports that females become inactive 2–3 months after emergence (Gilbert 1958, Greenslade 1964). The peaks of the oviposition season seem to have occurred in both Durham habitats in late October (period no.13). The evidence for this is that the two sexes were observed to have both the largest ratio of abdomen/elytra length <Fig.4.2.5a,b> and the largest number of individuals during the latter half of the month <Fig.4.2.1a,b>. Oviposition in woodland seems to have occurred between early September and early November (periods no.9–15). The evidence for this is:

1. large mean ratios of abdomen/elytra length for females were found during the second peak from early September to early November (periods no.9–14) <Fig.4.2.5a>;
2. the data on maturity revealed the presence of mature females from mid-September to late November (periods no. 10–15) <Fig.4.2.4a>;
3. after the inactive period, many individuals of both sexes were found, from early September to mid-October (periods no.9–13) <Fig.4.2.1a>.

In grassland, oviposition seems to have occurred mainly from mid-September (or perhaps earlier) to November (periods no.10–14); some of the females may perhaps have continued to lay eggs during winter. The evidence for this is threefold:

1. high mean ratios of abdomen/elytra length were observed from mid-September to early November (periods no.10–14) <Fig.4.2.5b> and in early December (period no.16);
2. mature females were observed from late October to early November (periods no.13 and 14) <Fig.4.2.4a>;
3. high proportions of the total numbers of both sexes captured were found in late October and early November (periods no.13 and 14) <Fig.4.2.1b>.

These conclusions concerning the oviposition season in the two habitats are in general agreement with previous studies (Gilbert 1958, Greenslade 1964, Penny 1966), in which *N. brevicollis* was found to start to breed in autumn, 2–3 months after the summer solstice. The reasons why some of the females were expected to oviposit during winter are:

1. in woodland, after the numbers captured fell (after period no.14), the egg volumes did not decrease <Table 4.2.6>,
2. the numbers of eggs carried by a given female did not decrease in late November (period no.15) <Table 4.2.7a>.

The conclusion that some of the females continued to oviposit is supported by the previous studies of Penny (1966), who found that females laid eggs until February; the 1st instar larvae appeared until April and the 2nd and 3rd instar until May. Tipton (1960) and Greenslade (1964) have also suggested the continuation of ovipoposition during winter.

The oviposition season seems to occur earlier in the Durham woodland than in the grassland. (See the results from Fig.4.2.3a, b) This supports the results of the study by Thiele (1971), in which female maturation proceeded much faster under lower temperatures (15°C was much more favourable than 20°C in the laboratory). The ground surface temperature in woodland is lower in summer than in the exposed grassland.

The mean elytra lengths of the woodland individuals were larger for both sexes than those found in grassland <Table 4.2.5>. This might be because of better developmental conditions in woodland. Evidence in support of this is:

1. a higher proportion of the total number captured is observed in woodland than in grassland in periods no.7–17 (13.6% in woodland; 6.4% in grassland);
2. a balanced sex ratio is found (female percentages are close to 50%) amongst animals caught in woodland but significantly more females were found in grassland in the second half of the study;
3. the late appearance of grassland individuals just before overwintering might indicate a lack of stored nutrients.

A comparison of all the results of previous and present studies at he various geographical areas shows

1. a shift of emergence (from May to June), and
2. a shift of breeding (from autumn–winter to late summer–autumn), i.e. as the environmental conditions become more severe, the duration of aestivation becomes shorter. See Fig.4.2.7.

1. is in agreement with the suggestion of Thiele (1969, 1971), that a high

temperature is necessary for larval transformation. The comparison of monthly average temperatures suggests that emergence may be initiated at temperatures more than 10°C <Fig.4.0.2>.

2. is also in agreement with the suggestion by Thiele (1969, 1971) that the breeding seasons are controlled by both temperature and photoperiodical signal, which inhibit the ovarian maturation.

<Table 4.2.1> The number of males and females of *Nebria brevicollis* caught during the two halves of the study (periods no.1-7 and 9-17) at the two habitats

N. brevicollis	Woodland		Grassland
Period no.	1-7	9-17	9-17
Female	15	30	24
Male	28	29	7
(Total)	43	59	31

<Table 4.2.2> Distances moved by each sex of *Nebria brevicollis* at the two habitats

N. brevicollis	Woodland	Grassland
Female	9.7551 9 8.4078 2.8026	5.7838 6 8.1276 3.3181
Male	8.4096 17 5.8776 1.4255	3.3540 2 4.7434 3.3541

in each cell
mean (m) sample number st. deviation st. error

<Table 4.2.3> Distances moved by each sex of *Nebria brevicollis* during the second half of the study (periods no.9-17)

N. brevicollis	Woodland	Grassland	(Sex total)
Female	10.3363 8 12.2666 4.3369	6.9403 5 8.5170 3.8089	9.0302 13 10.7197 2.9731
Male	9.3417 9 6.9335 2.3117	3.3541 2 4.7434 3.3541	8.2531 11 6.8246 2.0577
(Habitat total)	9.8098 17 9.4936 2.3025	5.9157 7 7.4278 2.8074	8.6740 24 8.9644 1.8299

in each cell
mean (m) sample number st. deviation st. error

<Table 4.2.4> Number of recaptures of *Nebria brevicollis* at the two habitats (periods no.9-17)

Habitat	Woodland	Grassland	(Sex total)
Female	12	6	18
	11	6	17
	1	0	1
Male	23	2	25
	22	2	24
	1	0	1
(total)	35	8	43
	33	8	41
	2	0	2

in each cell
total number of recaptures
number of recaptures in the same habitat
number of recaptures in the alternative habitat

<Table 4.2.5> Elytra length of both sexes of *Nebria brevicollis* in the two habitats

N. brevicollis	Woodland	Grassland	(Sex total)
Female	7.827	7.526	7.714
	45	27	72
	0.364	0.325	0.378
	0.054	0.063	0.045
Male	7.302	7.090	7.270
	57	10	67
	0.483	0.486	0.486
	0.064	0.154	0.059
(Habitat total)	7.533	7.408	7.500
	102	37	139
	0.506	0.417	0.486
	0.050	0.069	0.041

in each cell
mean (mm)
sample number
st. deviation
st. error

<Table 4.2.6> Mean egg volume of *Nebria brevicollis* in relation to stage of maturity in (2-week periods)
(a) in woodland (b) in grassland

(a)

Stage of maturity Period no.	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period total)
9		622 1			622 1
10		812 2	531 1		718 3
13	596 1	626 8	684 5	1087 1	674 15
15			898 2		899 2
(Stage of maturity total)	596 1	659 11	719 8	1087 1	699 21

(b)

Stage of maturity Period no.	5 Redeveloping	6 Mature	(Period total)
13	653 3	872 1	708 4
14		729 1	729 1
(Stage of maturity total)	653 3	800 2	712 5

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.2.7> Mean number of eggs carried by female *Nebria brevicollis* in relation to stage of maturity (in 2-week periods)
(a) in woodland (b) in grassland

(a)

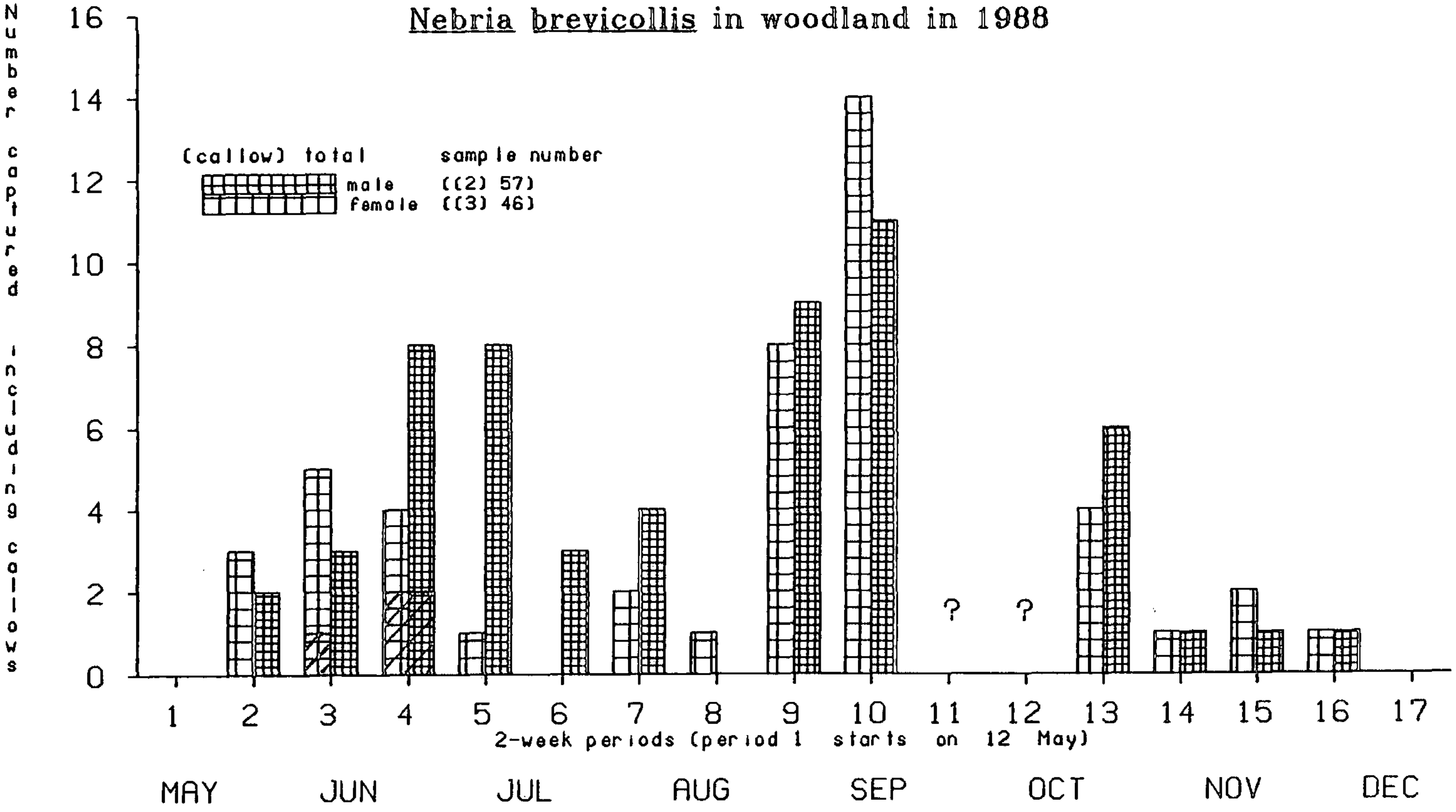
Stage of maturity Period no.	1 Gallow	2 Undeveloped	3 Regressed	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period total)
3	0 1	0 1						0 2
5		0 1						0 1
9					15 1			15 1
10					23.0 2	11 1		19.0 3
13				8 1	14.9 8	9.6 5	4 1	11.9 15
15						10.0 2		10.0 2
(Stage of maturity total)	0 1	0 2	 0	8 1	16.4 11	9.9 8	4 1	11.3 24

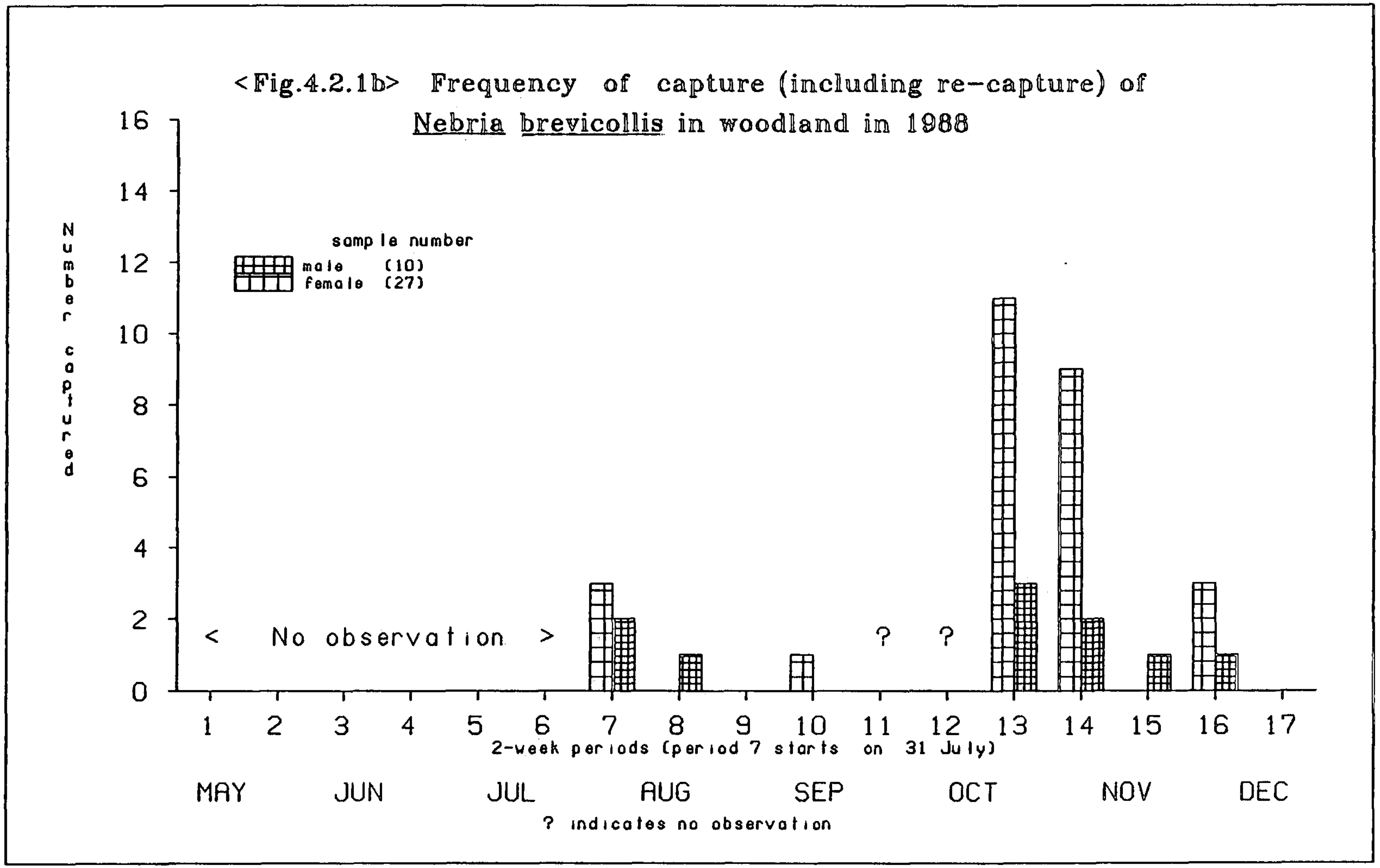
(b)

Stage of maturity Period no.	5 Redeveloping	6 Mature	(Period total)
13	11.3 3	11 1	11.25 4
14		20 1	20 1
(Stage of maturity total)	11.3 3	15.5 2	13.0 5

in each cell
mean number sample number

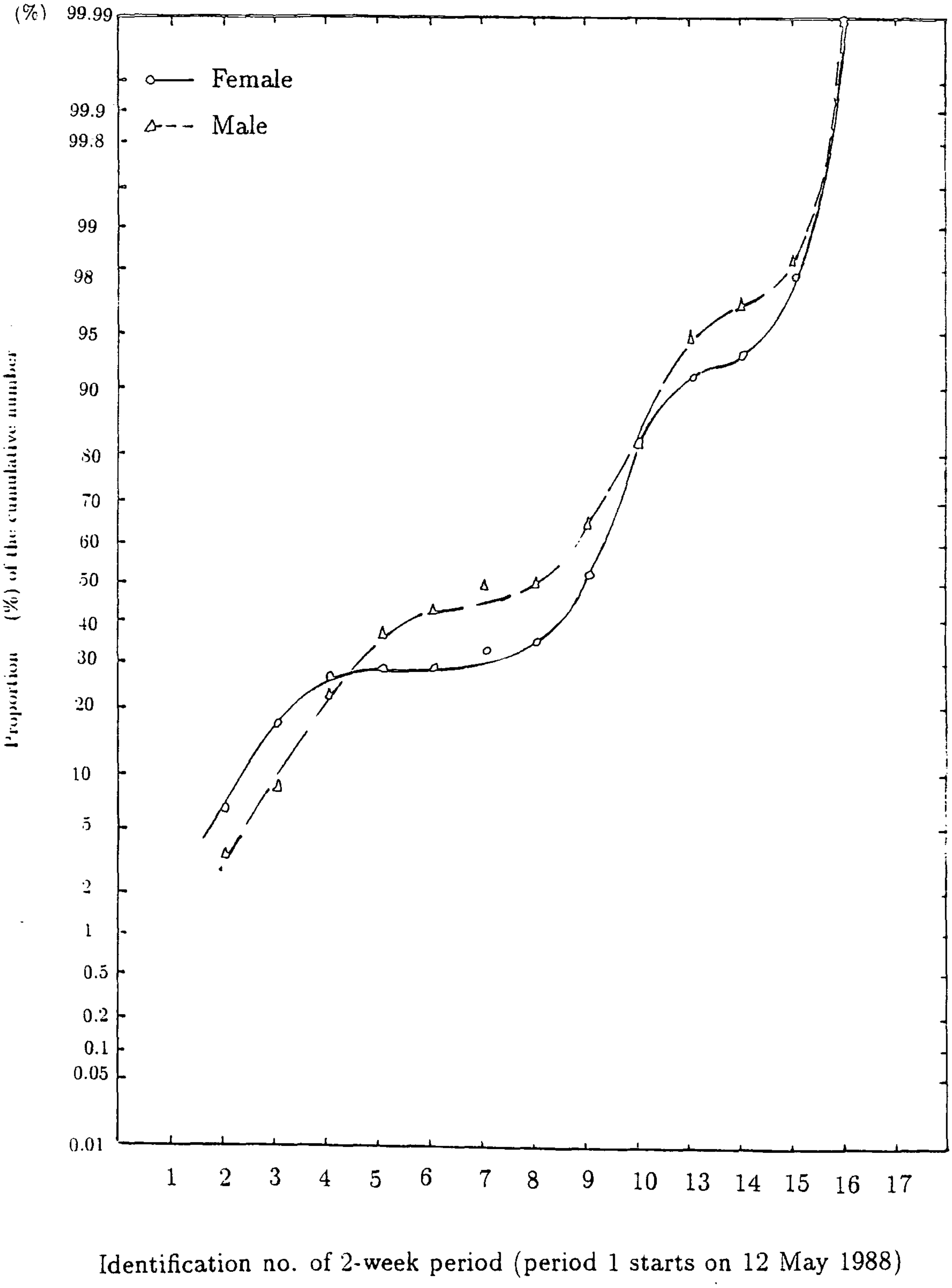
<Fig.4.2.1a> Frequency of capture (including re-capture) of <u>Nebria</u> <u>brevicollis</u> in woodland in 1988



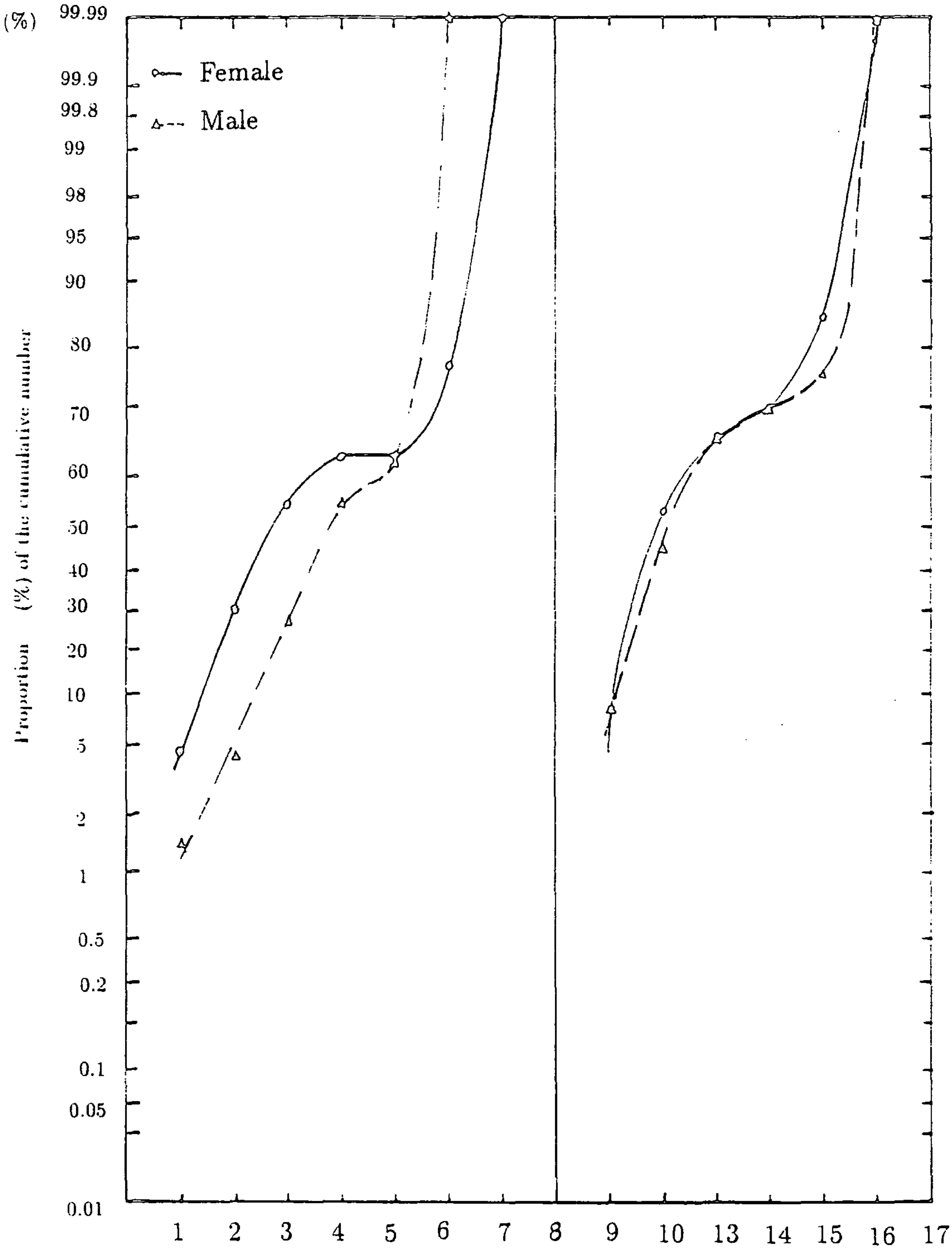


<Fig.4.2.1b> Frequency of capture (including re-capture) of <u>Nebria brevicollis</u> in woodland in 1988

<Fig.4.2.2a> Proportion (%) of the cumulative number of *Nebria brevicollis* in woodland by 2-week period



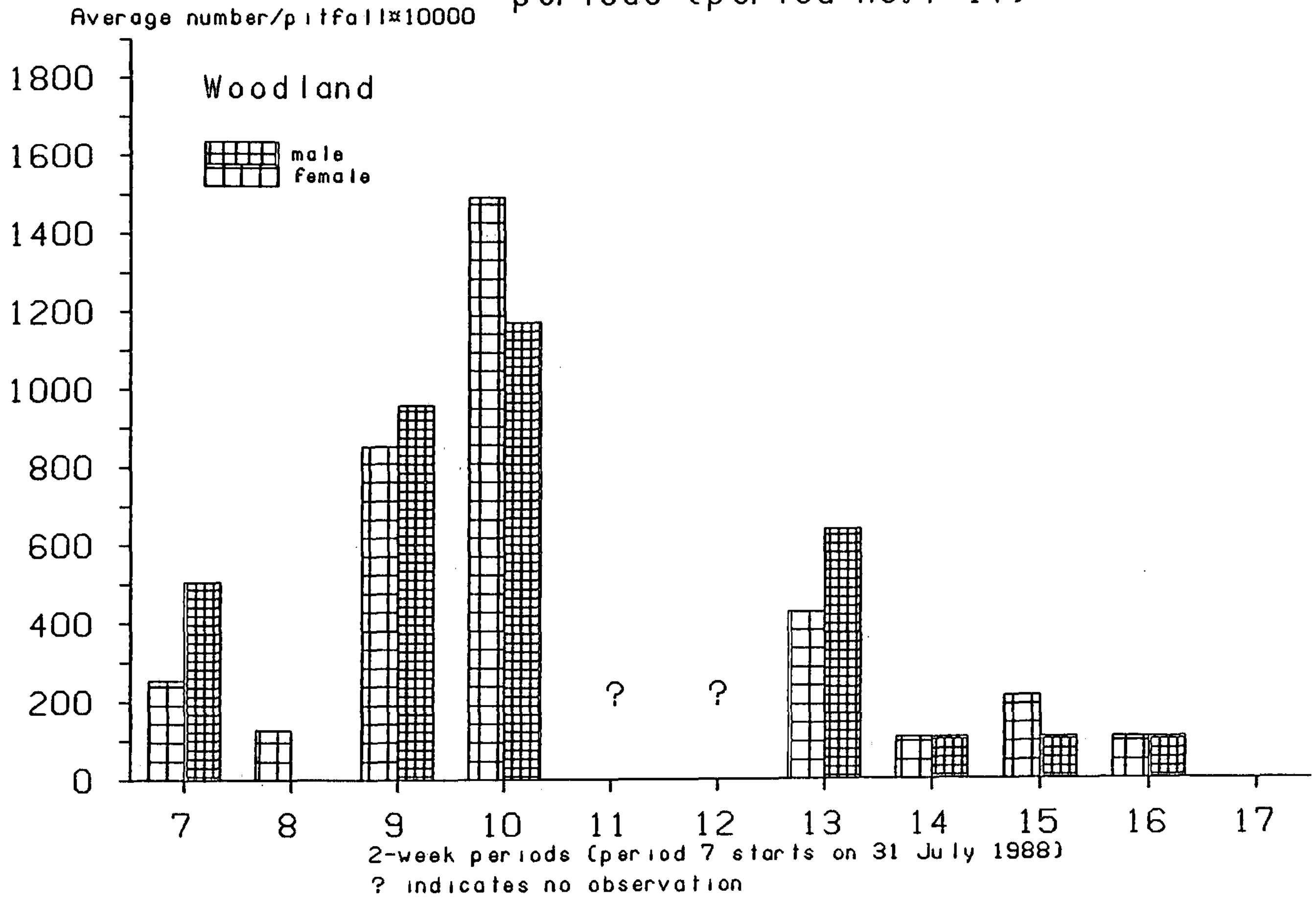
<**Fig.4.2.2b**> Proportion (%) of the cumulative number of *Nebria brevicollis* in woodland in periods no. 1 — 7 and 8 — 17



Identification no. of 2-week period (period 1 starts on 12 May 1988)

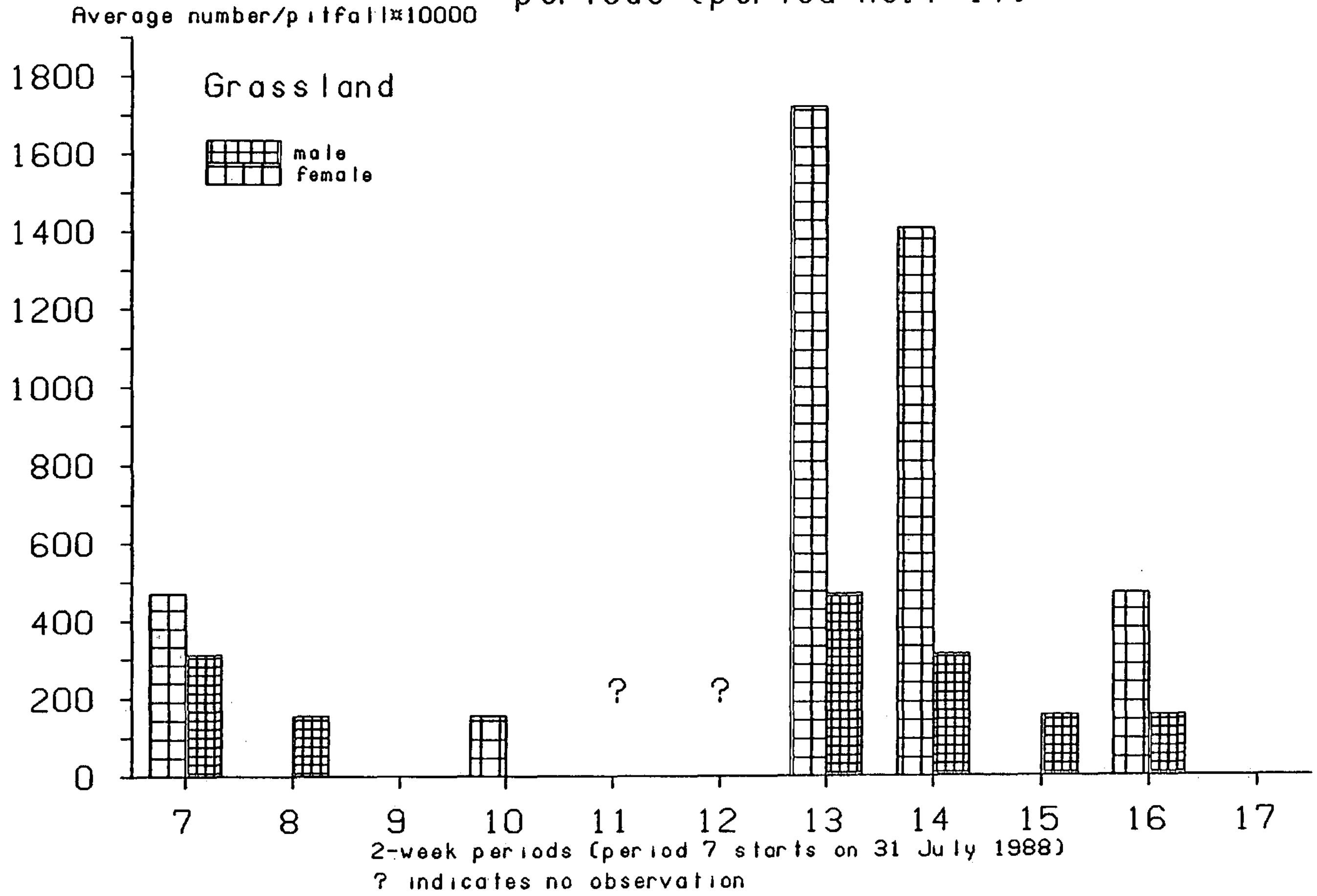
<Fig.4.2.3a>

Number of *Nebria brevicollis* per pitfall in 2-week periods (period no.7-17)



<Fig.4.2.3b>

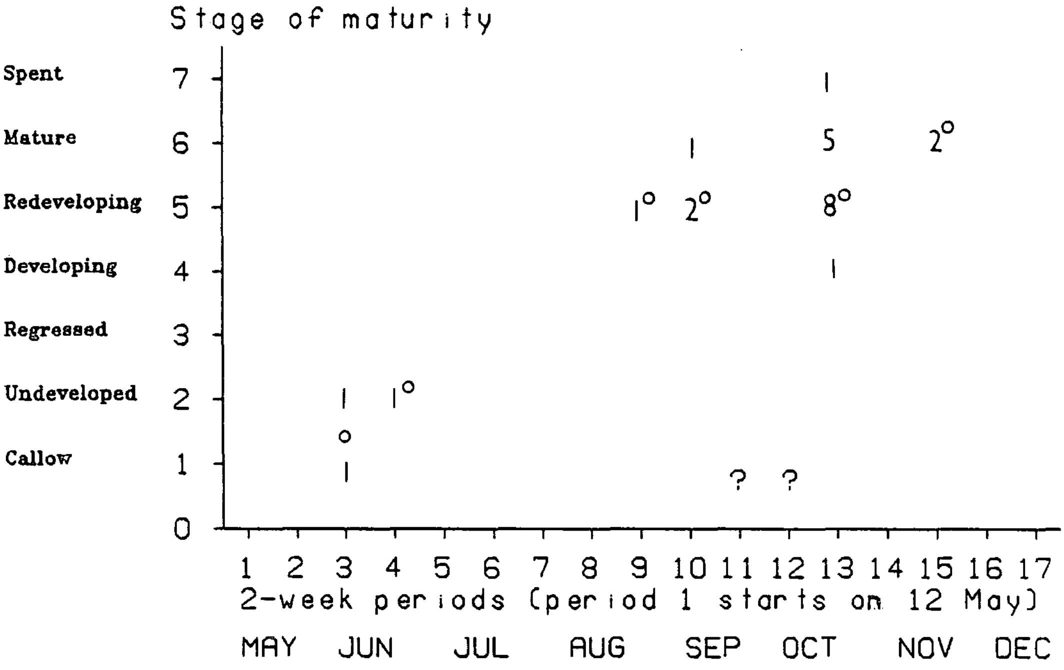
Number of *Nebria brevicollis* per pitfall in 2-week periods (period no.7-17)



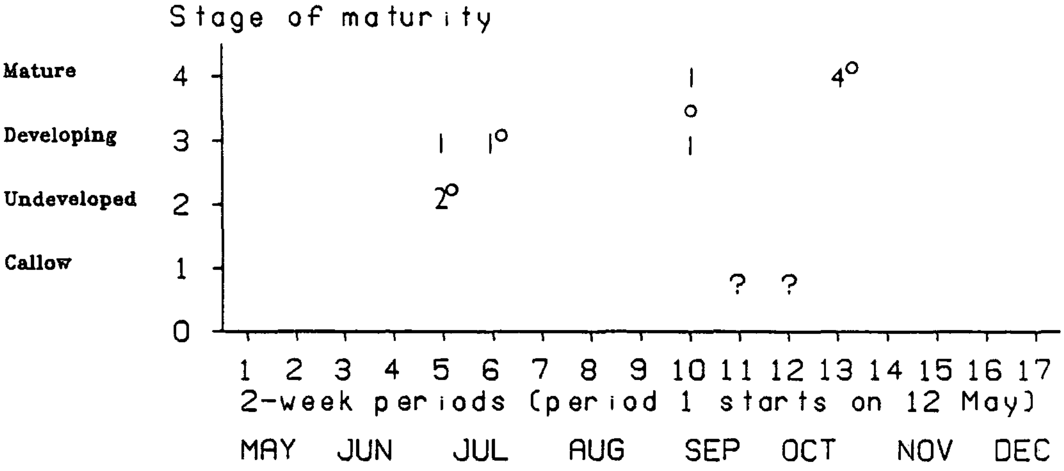
<Fig.4.2.4> Stages of maturity of Nebria brevicollis caught in successive 2-week periods in woodland

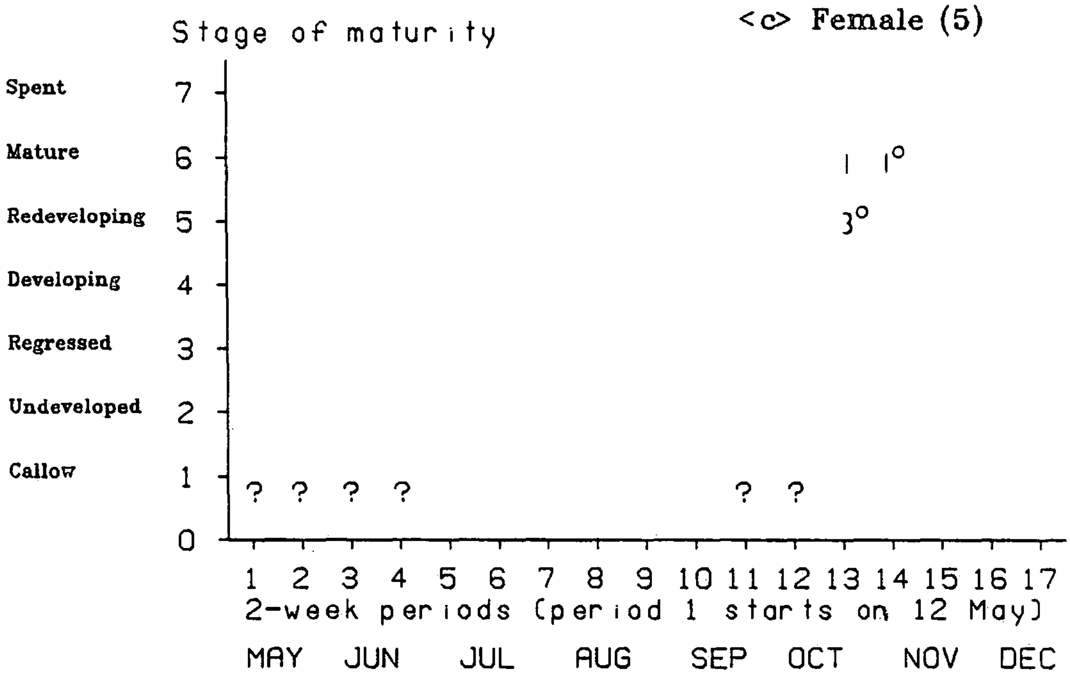
Frequencies are plotted
o indicates median value in each period
? indicates no observation

<a> Female (24)



<b> Male (10)

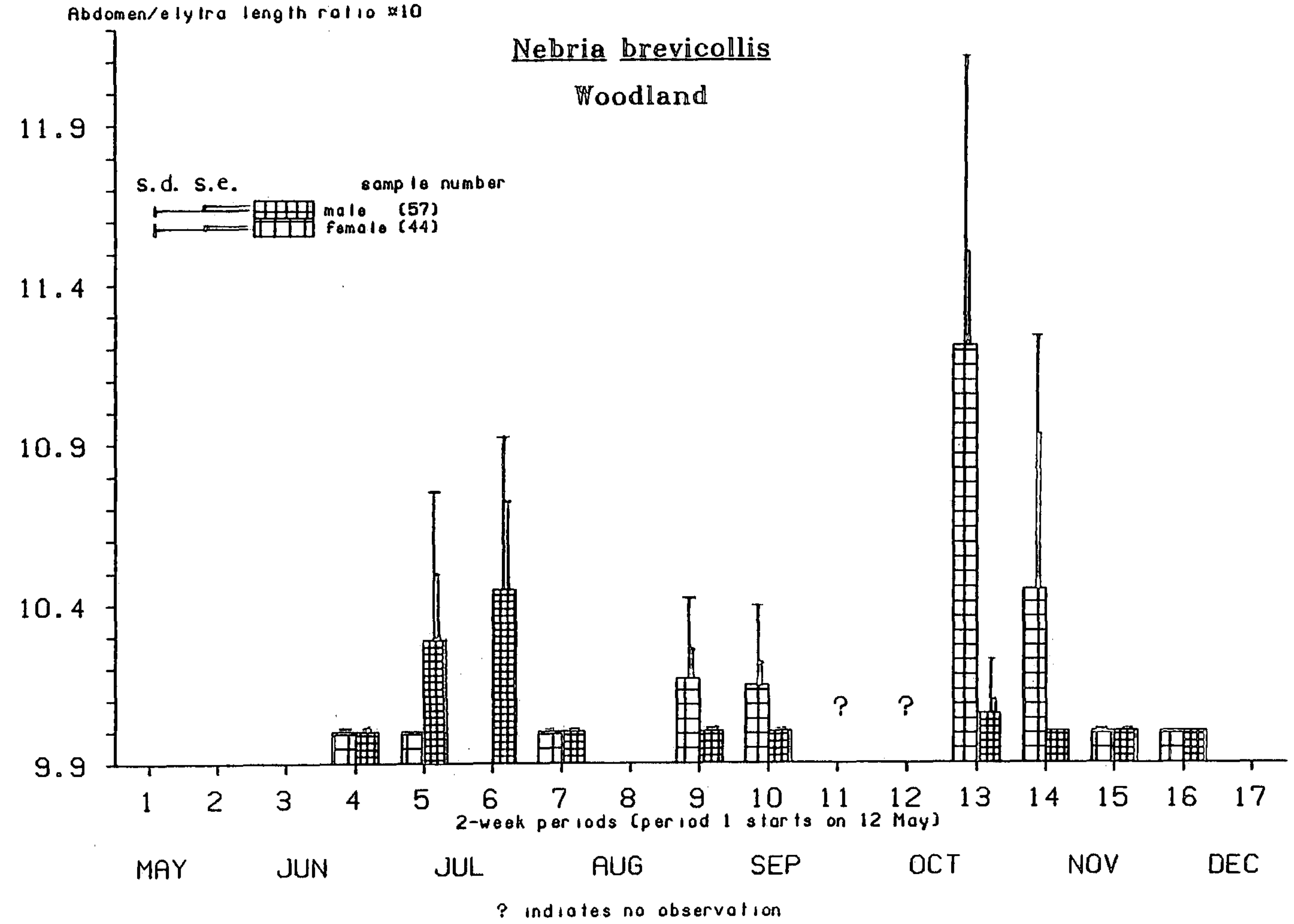




<Fig.4.2.4> Stages of maturity of Nebria brevicollis caught in successive 2-week periods in grassland

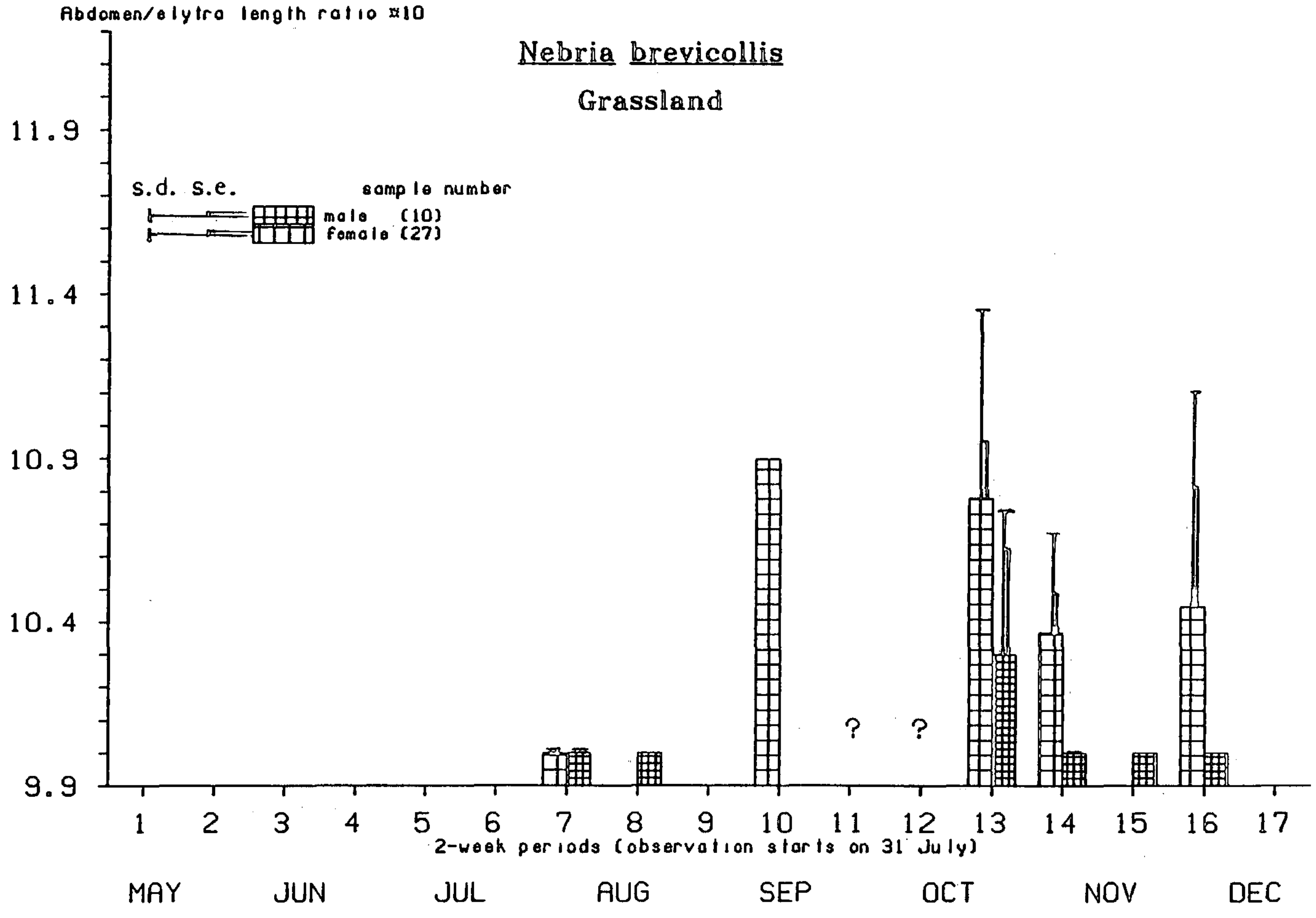
Frequencies are plotted
o indicates median value in each period
? indicates no observation

<Fig.4.2.5a> Abdomen/elytra length ratio in 2-week periods



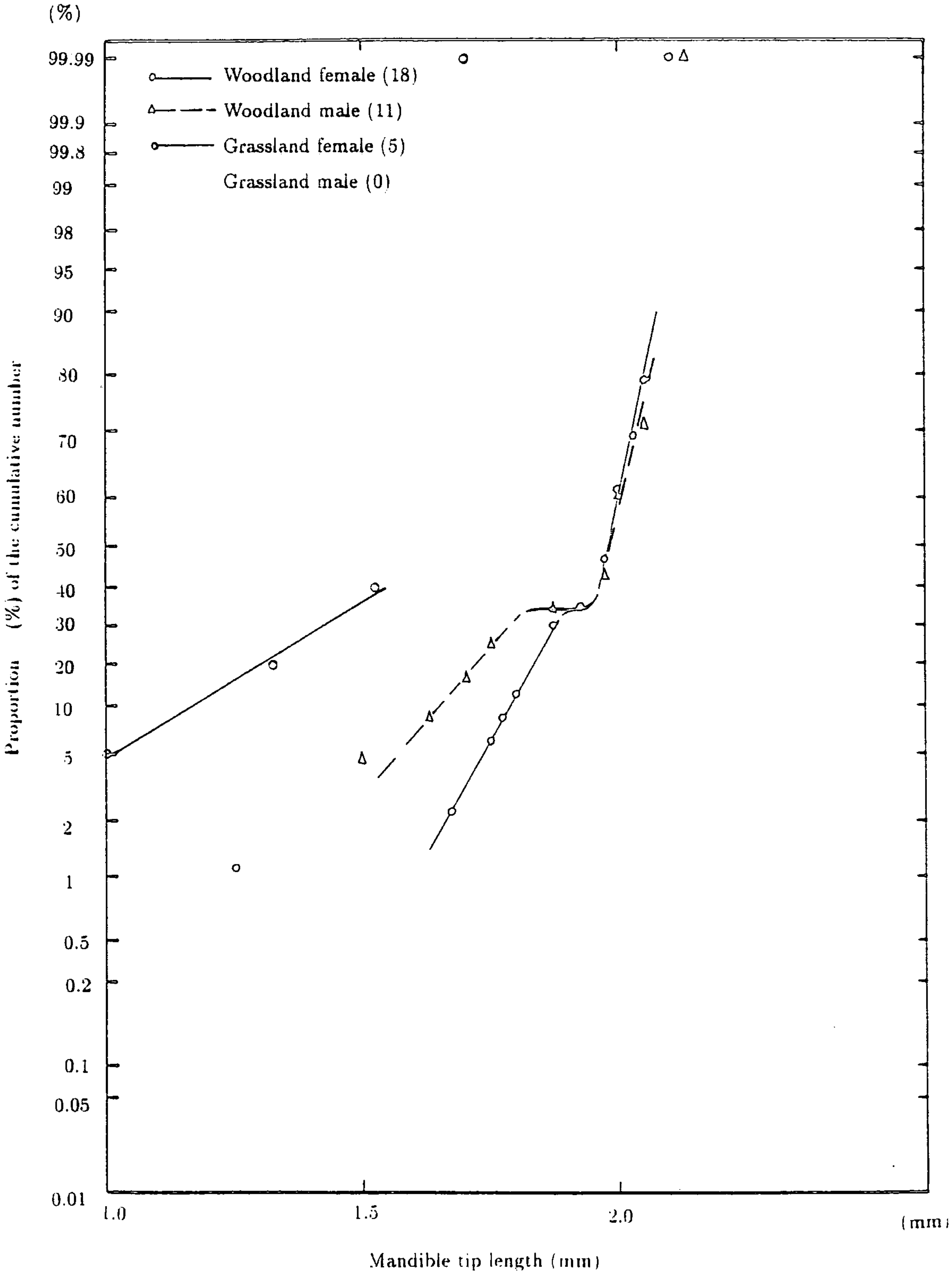
? indiates no observation

<Fig.4.2.5b> Abdomen/elytra length ratio in 2-week periods

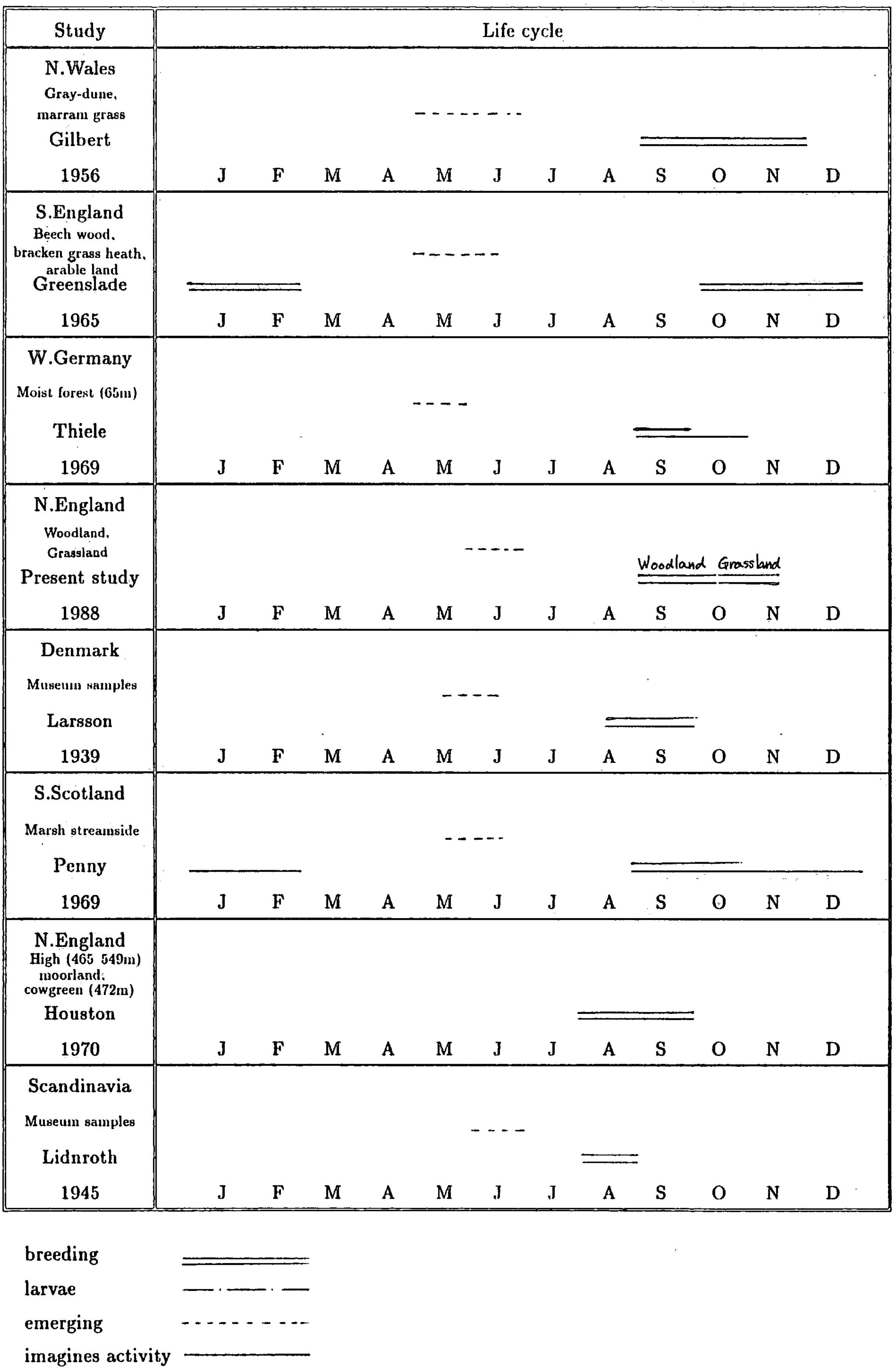


? indiates no observation

<Fig.4.2.6> Proportion (%) of the cumulative number of *Nebria brevicollis* by the differences of the mandible tip length



<Fig. 4.2.7> The results of previous and present study of life cycle of *Nebria brevicollis*



4.3 Abax parallelepipedus Piller & Mitterpacher

PREVIOUS INFORMATION

Abax parallelepipedus is a woodland species (Greenslade 1965).

This species has been well-studied experimentally in the laboratory (Löser 1972). Field studies were carried out

- in southern England: in beechwood, grassland and bracken and arable land by Greenslade (1965), in marsh and riverside areas by Murdoch (1967),
- in northern England: high moorlands by Houston (1970);
- in the Netherlands: in beech forest by van Drift (1951);
- in Belgium: in pine wood and beech forest by Loreau (1985);
- in West Germany: in hill forests by Lauterbach (1964) and at various altitudes (56m–340m) in oak woodland by Löser (1972).

The species is classified in the group: "species with unstable condition of hibernation and potentially lacking dormancy" (Thiele 1977). *Abax parallelepipedus* is thermally quiescent: low temperatures cause a slowing down of development. Photoperiod has no influence on development (Löser 1970).

Fig.4.3.5 shows the results of previous field studies of the life cycle of this species. In lowlands or warm years, *A. parallelepipedus* emerges in spring and in autumn. Those beetles which emerge in spring reproduce in summer. Autumn-emerged beetles reproduce in the following spring shortly after hibernation, and then reproduce in summer again. Two peaks of activity may therefore be observed, in spring and in summer. In higher regions or cold years, *Abax paral-*

lelepipedus emerges only in spring and becomes mature in summer. One peak of activity can be seen in summer. The two types of activity patterns as described above are not separated entirely and a shift from two peaks to one peak of activity has been observed in this species, depending on the temperature conditions of the microclimate in forest plant communities (Lauterbach 1964). In West Germany (Löser 1970, 1972), a similar kind of shift has been reported: from two breeding seasons in spring and autumn by two generations of autumn breeders in warmer environmental conditions (e.g. low regions, slopes with southern exposure, warmer years), to one breeding season in summer by spring breeders. In the Netherlands (van Drift 1951), autumn emergence occurred; young females bred in summer and autumn and old females bred in spring and summer. Mature females have been observed from spring to autumn continuously in southern England (Murdoch 1967), the Netherlands (van Drift 1951) and Belgium (Loreau 1985). In the uplands of northern England, spring emergence and summer breeding have been observed (Houston 1970).

This species is reported to employ brood care (Löser 1972). Females scrape off particles of moist clay, using circular movements, and form a chamber of specific shape in which eggs are laid. This probably serves to prevent dessication and fungal attack. The females lay the eggs in the clay cocoons, but there is no further brood care afterwards, in contrast to some other species in the *Abax* genus.

RESULTS AND DISCUSSION

More captures were made in woodland than in grassland <Fig.4.3.1>. Animals were active at least from May to early September (and perhaps earlier).

During this period they moved large distances <Fig.4.3.2a>.

In woodland, a male callow was observed in June <Fig.4.3.1a>; undeveloped females were also observed in July <Fig.4.3.3a>. In grassland, a female callow was observed in September <Fig.4.3.3b> Therefore, in the two habitats emergence may have occurred twice: once in spring and once in autumn. The occurrence of two oviposition seasons in one year is in agreement with results obtained in warmer environmental conditions in West Germany (Löser 1972).

In woodland, mature females were observed in June–September <Fig.4.3.3a>; the egg volumes and egg numbers per female are listed in Table 4.3.1 and Table 4.3.2, respectively. Large mean ratios of abdomen/elytra length for woodland females were found in July and August <Fig.4.3.4a>. After October no captures were made in either habitat. To summarize, *Abax parallelepipedus* seems to oviposit between June and September.

Two mature females in June in woodland possessed many small eggs at the previtellogenesis stage in addition to mature eggs. Therefore it may be that those females were able to reproduce again in the same year after early summer oviposition. This possibility of two ovipositions by one female in one year is supported by previous studies in continental countries: the Netherlands (van Drift 1951) and West Germany (Lauterbach 1964) <Fig.4.3.5>. However, the data are not sufficient to decide whether this species in Durham had two peaks of oviposition or one continuous oviposition season.

In grassland, one female with a large ratio of abdomen/elytra length was recorded in September <Fig.4.3.4b>. This may indicate that the oviposition season in grassland also included September.

ADDITIONAL INFORMATION

Two male *A. parallelepipedus* that secreted pheromone were observed in woodland in July: the timing suggsts that this may be a sex pheromone.

During the field work, two mud-coated females were found in both habitats in late August. This might be accounted for by brood-care (Löser 1972).

Elytra lengths of both sexes in the two habitats are shown in Table 4.3.3. No differences in elytra lengths between sexes in each of the two habitats were observed (in woodland $t_{27} = 1.07$, $p = 0.294$; in grassland $t_5 = 0.49$, $p = 0.648$). The elytra lengths of each sex is similar in the two habitats for both sexes (female $t_{34} = 0.35$, $p = 0.728$; male $t_{19} = 0.07$, $p = 0.943$).

<Table 4.3.1> Mean egg volume of *Abax parallelepipedus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	4 Developing	6 Mature	(Period total)
6		3672 1	3672 1
7	2251 1	5678 2	4536 3
8		4985 2	4985 2
9		5389 1	5389 1
(Stage of maturity total)	2251 1	5064 6	4662 7

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.3.2> Mean number of eggs carried by female *Abax parallelepipedus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	2 Undeveloped	4 Developing	6 Mature	(Period total)
6			17 1	17 1
7	0 1	8 1	5.5 2	4.75 4
8			9 2	9 2
9			4 1	4 1
(Stage of maturity total)	0 1	8 1	8.33 6	7.25 8

in each cell
mean number sample number

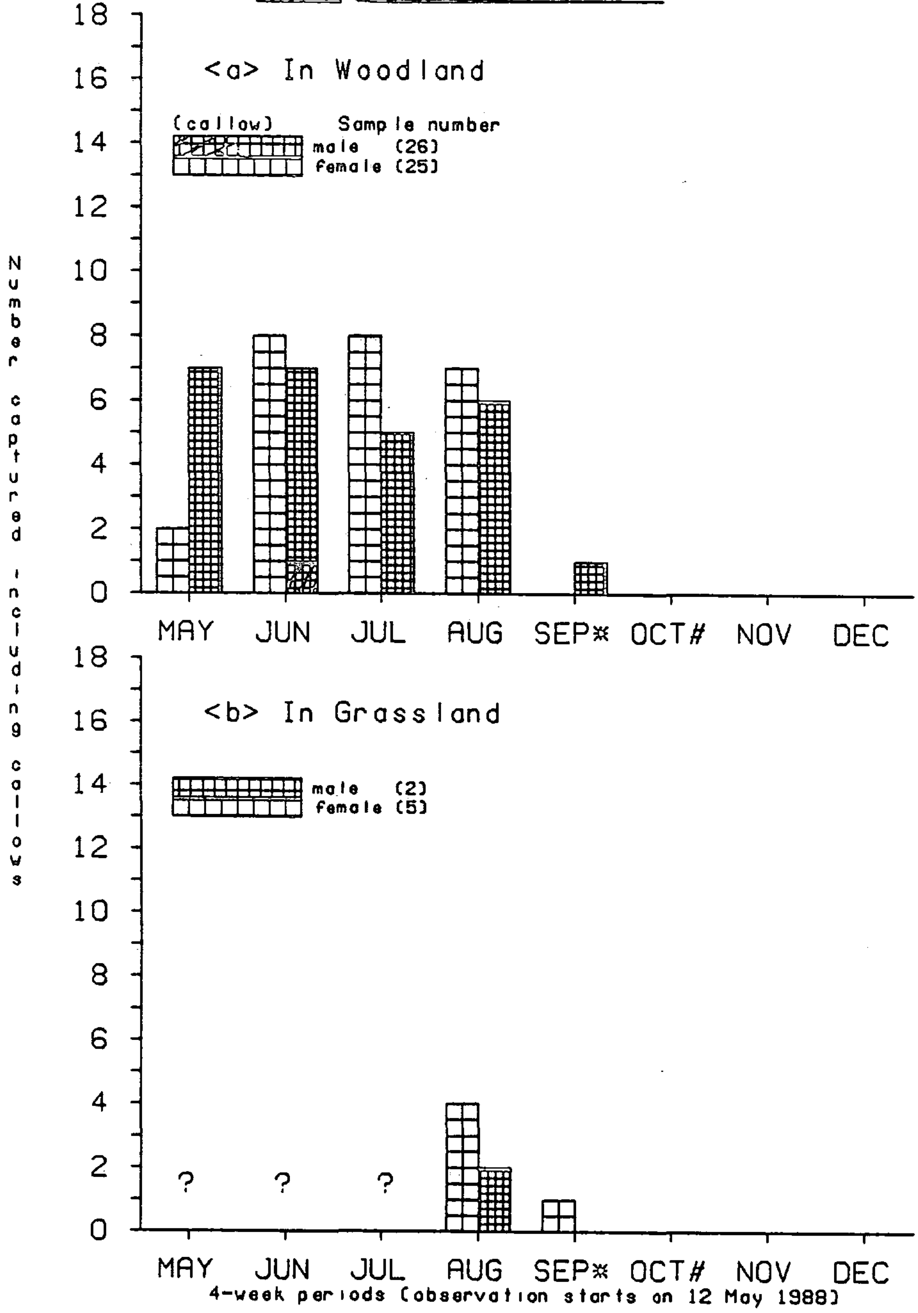
<Table 4.3.3> Elytra length of both sexes of *Abax parallelepipedus* in the two habitats

	Woodland	Grassland	(Sex total)
Female	10.877 31 0.616 0.111	10.980 5 0.536 0.240	10.892 36 0.599 0.100
Male	11.147 19 0.987 0.226	11.200 2 0.566 0.400	1.152 21 0.945 0.206
(Habitat total)	10.980 50 0.780 0.110	11.043 7 0.506 0.191	10.988 57 0.748 0.099

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.3.1> Frequency of capture (including re-capture) in 4-week periods

<u>Abax paralellepipedus</u>

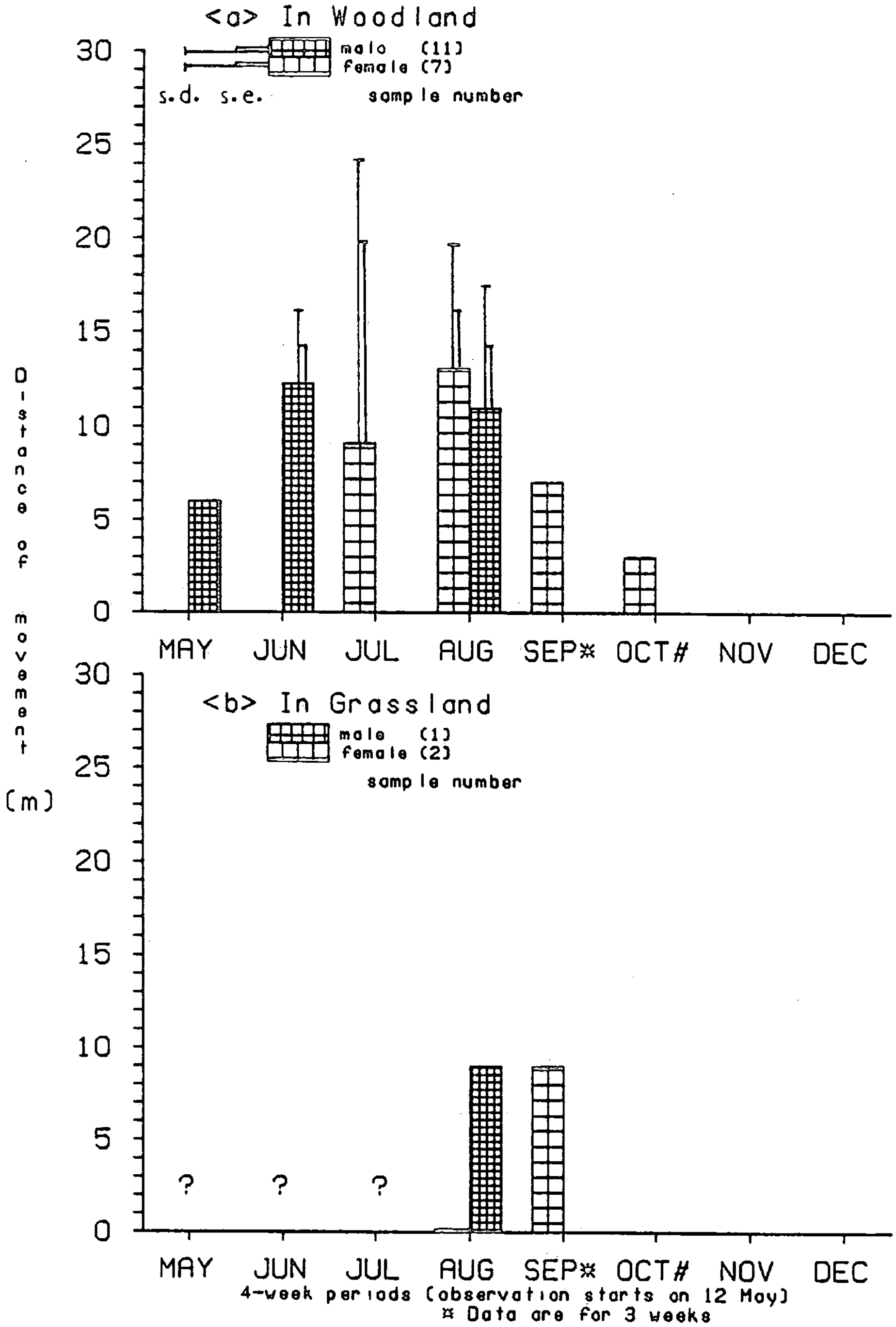


※ Data are for 3 weeks

\# Data are for 1 week

? indicates no observation

<Fig.4.3.2> Distance between capture and recapture points
Abax paralellepipedus



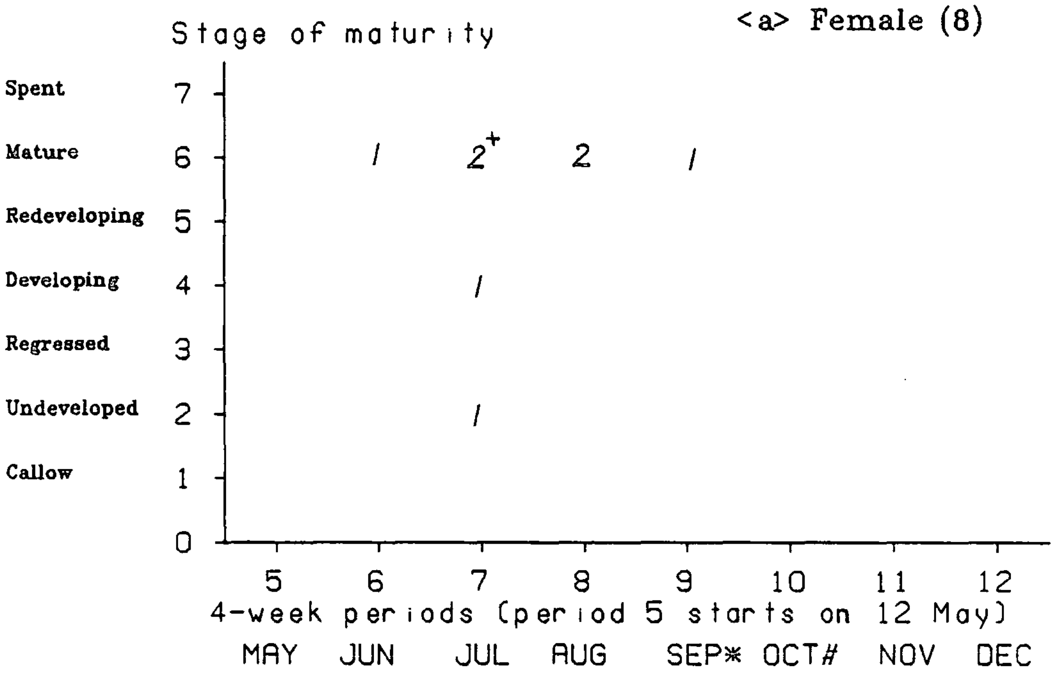
※ Data are for 3 weeks
Data are for 1 week

<Fig.4.3.3> Stages of maturity of <u>Abax</u> <u>parallelepipedus</u> caught in successive 4-week periods in woodland

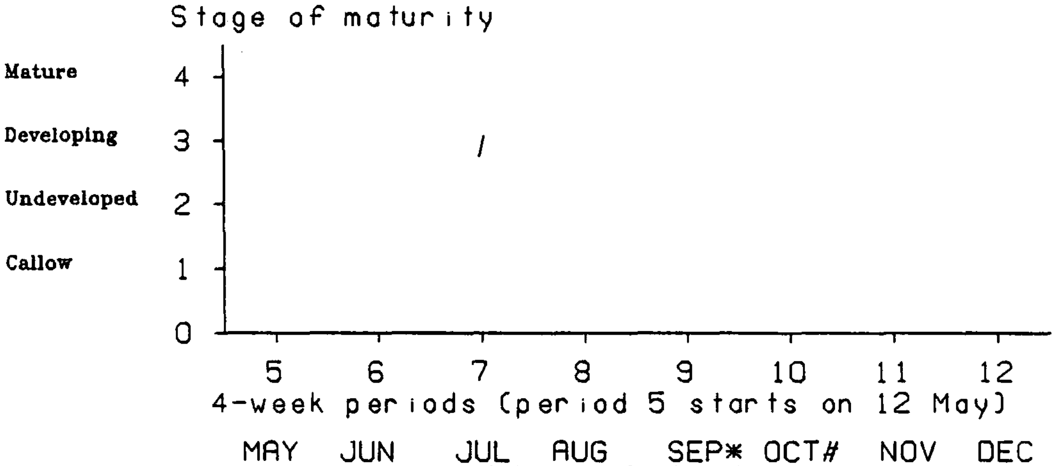
Frequencies are plotted

? indicates no observation
+ indicates developing small immature eggs at the same time in addition to mature eggs

<a> Female (8)



<b> Male (1)



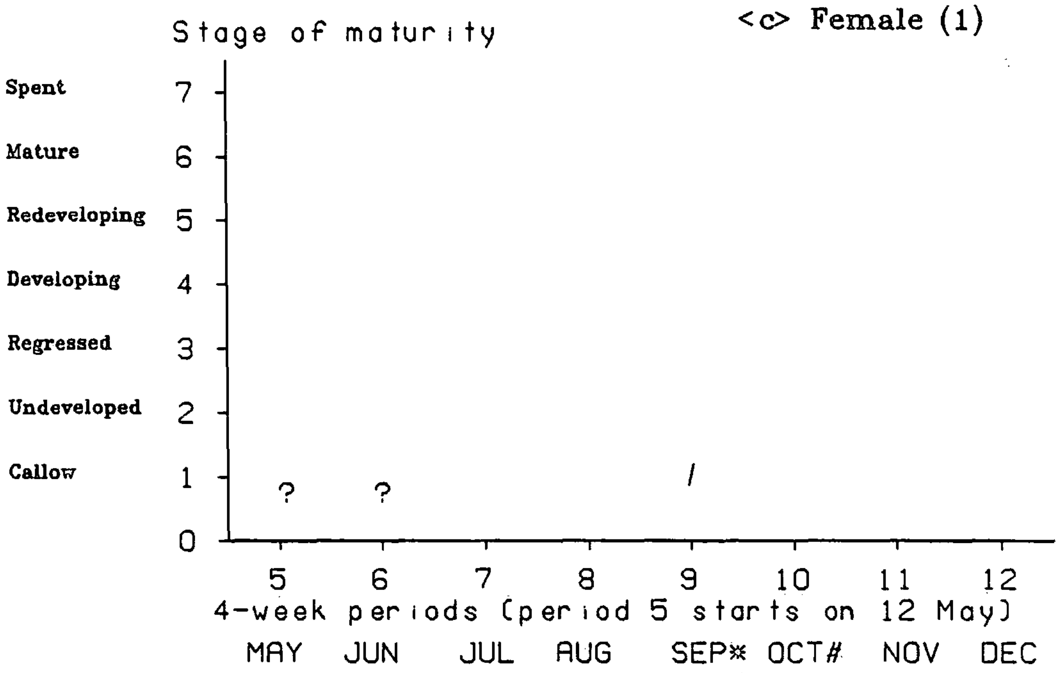
data are for 1 week
* data are for 3 weeks

<Fig.4.3.3> Stages of maturity of <u>Abax parallelepipedus</u> caught in successive 4-week periods in grassland

Frequencies are plotted

? indicates no observation

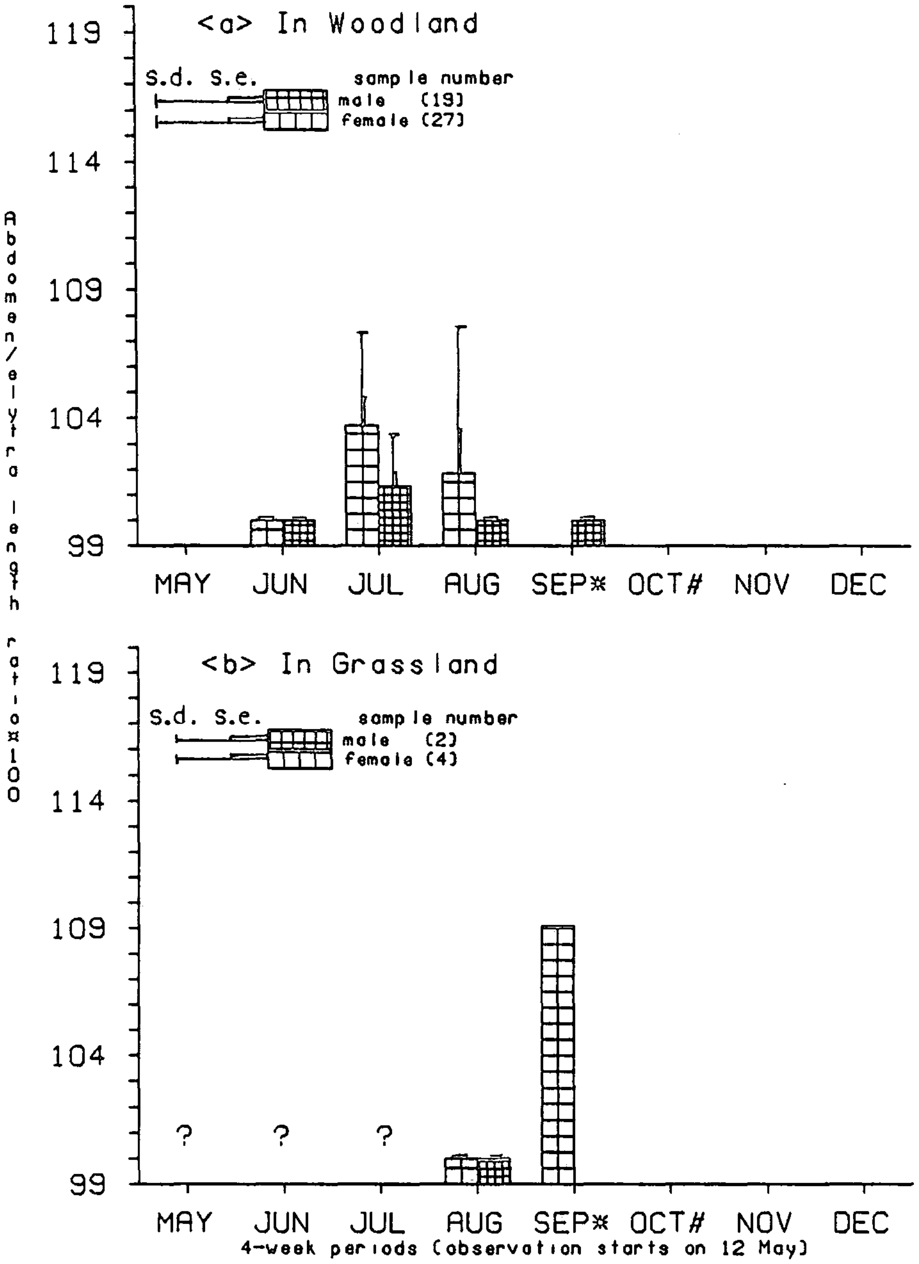
<c> Female (1)



data are for 1 week

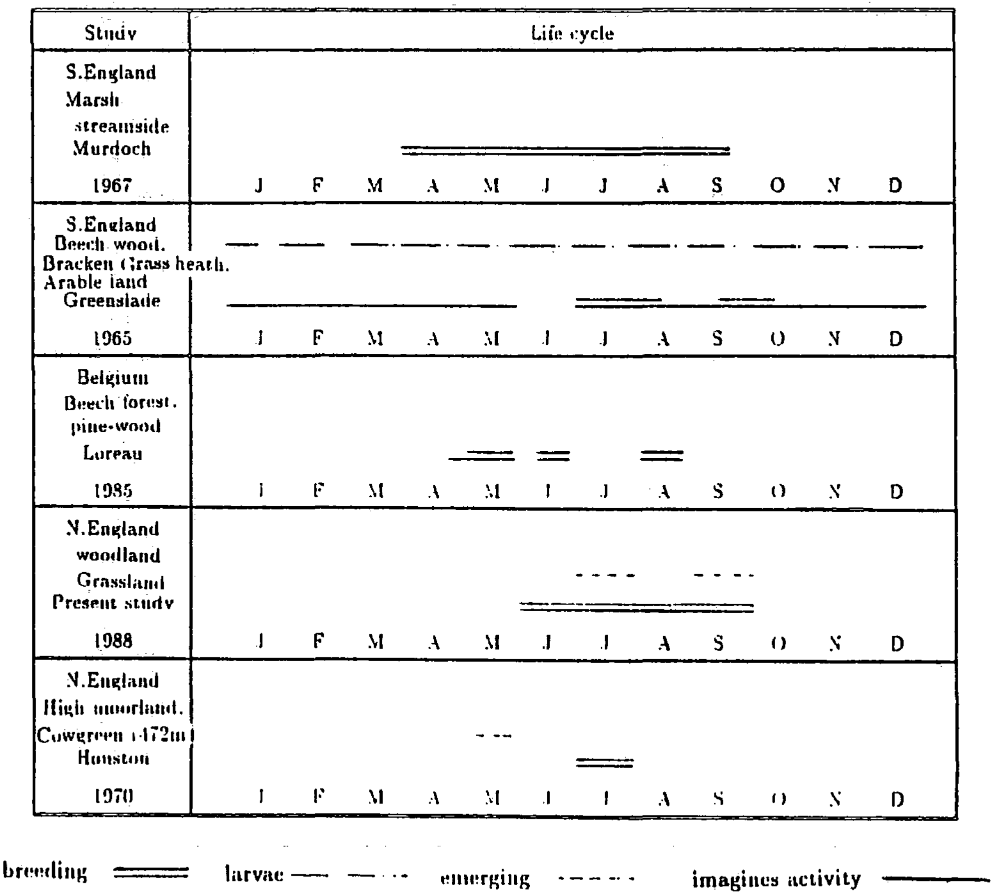
¤ data are for 3 weeks

<Fig.4.3.4> Abdomen/elytra length ratio in 4-week periods
Abax paralellepipedus



¤ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig. 4.3.5> The results of previous and present study of life cycle of *Abax parallelepipedus*



4.4 Calathus melanocephalus Linnaeus

PREVIOUS INFORMATION

Calathus melanocephalus is principally a grassland species although it occurs in a variety of habitats from sand dunes to environments which are almost mountainous (Greenslade 1965).

This species was classified as a member of the "group of autumn breeders with a hibernation at the larval stage and no dormancy in the course of adult development" (Thiele 1977). *Calathus melanocephalus* has been studied widely in a geographical sense. Fig.4.4.4 shows the results of previous field studies of the life cycle of this species. After reproduction, some individuals hibernate and reproduce again in the following year (Gilbert 1956 and Greenslade 1965 in southern England; Vlijm *et al.* 1968 and van Dijk 1972, 1973, 1979, in the Netherlands). In southern England (Gilbert 1956 and Greenslade 1965), this species is found to have a univoltine life cycle: it reproduces from July to December with a peak in September and October, emerges in the next spring after larval hibernation and breeds in the summer without dormancy. However, in the Netherlands (van Dijk 1972), *C. melanocephalus* is partly semivoltine. Survivors reproduce from June to July: larvae hibernate, new imagines emerge in the next July and a fraction of them reproduce in July and August (slightly later than old imagines). In alder forests (20m a.s.l.) in central Norway, this species has also been found to be a semivoltine which breeds in August with a peak of activity just before breeding (Refseth 1988). After larval hibernation, a new imago emerges at the end of August. The immature imago hibernates and breeds in the next summer. However, at 830m of subalpine birch forests, emergence has occurred in late August–early September and breeding in late June–early August. Similar semivoltine life cycles are observed in northern Finland (Forsskåhl 1972) and in the Austrian mountains (De Zordo 1979 by mention of Refseth 1988).

RESULTS AND DISCUSSION

In the present study, more individuals were found in the Durham grassland than in the woodland, in agreement with the findings of Greenslade (1965) in southern England. No callows were caught in either habitat. Mature females were observed in the two habitats in August although the ratios of abdomen/elytra lengths were not large <Fig.4.4.1, Fig.4.4.2, Fig.4.4.3, Table 4.4.1, Table 4.4.2>. From the distinctiveness of the corpora lutea, one of the four mature grassland females captured was found to be in its second oviposition season. These results therefore indicate that oviposition occurred in August and that the Durham grassland population has involved second year survivors. Two conclusions are drawn from a comparison of the previous and present studies <Fig.4.4.4>. As studies are made of progressively more severe environments,

1. the life cycles observed vary from univoltine autumn breeding to a mixture of univoltine and semivoltine breeding to, finally, semivoltine summer breeding;
2. the time of emergence shifts from spring to autumn.

ADDITIONAL INFORMATION

The mean elytra lengths of grassland individuals are shown in Table 4.4.3.

<Table 4.4.1> Mean egg volume of *Calathus melanocephalus* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	6 Mature
8	176 1

<b>

Stage of maturity Period no.	4 Developing	6 Mature	(Period total)
8	164 1	149 3	153 4

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.4.2> Mean number of eggs carried by female *Calathus melanocephalus* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	6 Mature
8	10 1

<b>

Stage of maturity Period no.	4 Developing	6 Mature	(Period total)
8	26 1	15 3	17.5 4

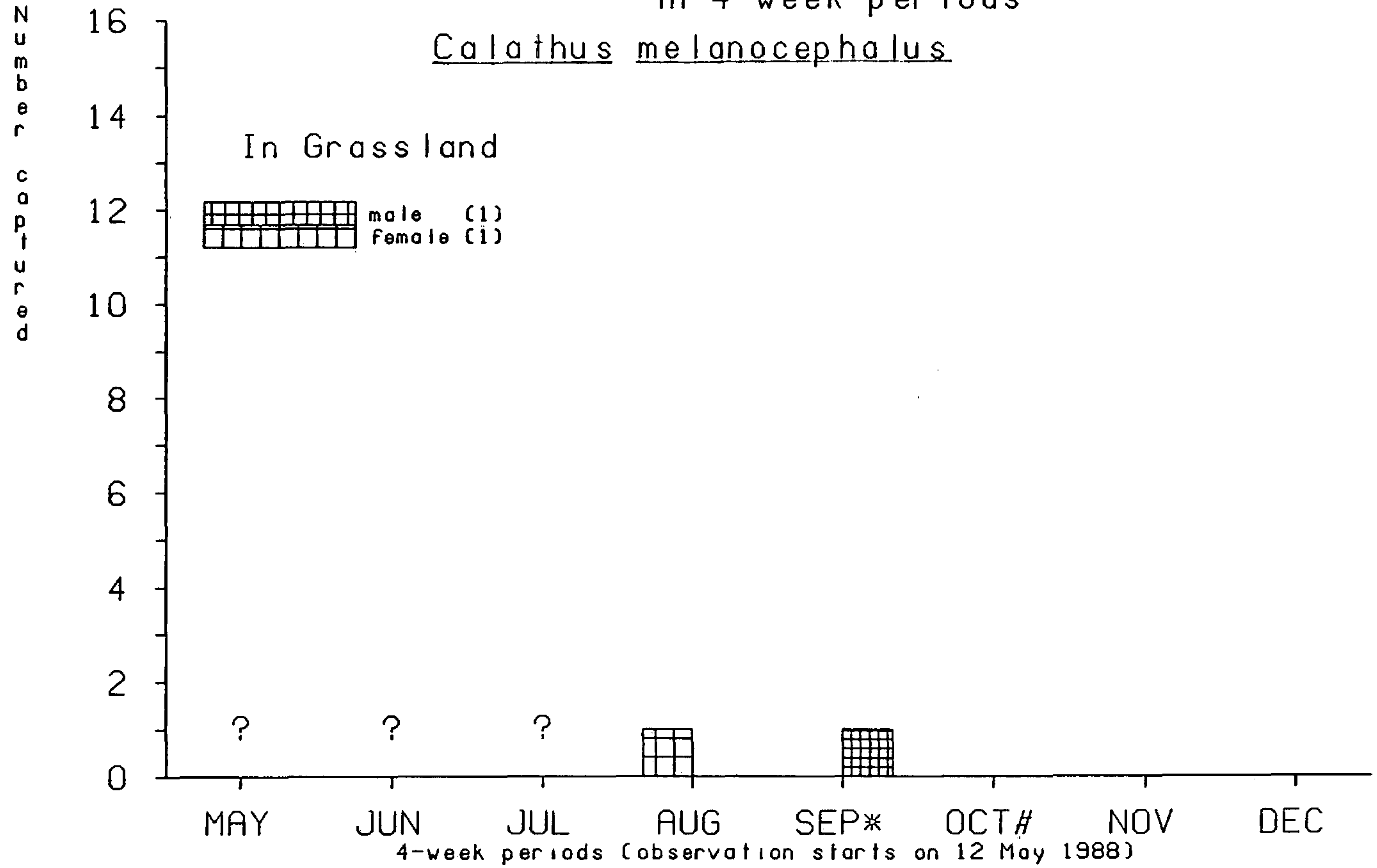
in each cell
mean number sample number

<Table 4.4.3> Elytra length of both sexes of *Calathus melanocephalus* in grassland

	Grassland
Female	4.700 2 0.283 0.200
Male	4.500 1 – –
(Habitat total)	4.633 3 0.231 0.133

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.4.1> Frequency of capture (including re-capture) in 4-week periods



※ Data are for 3 weeks

Data are for 1 week

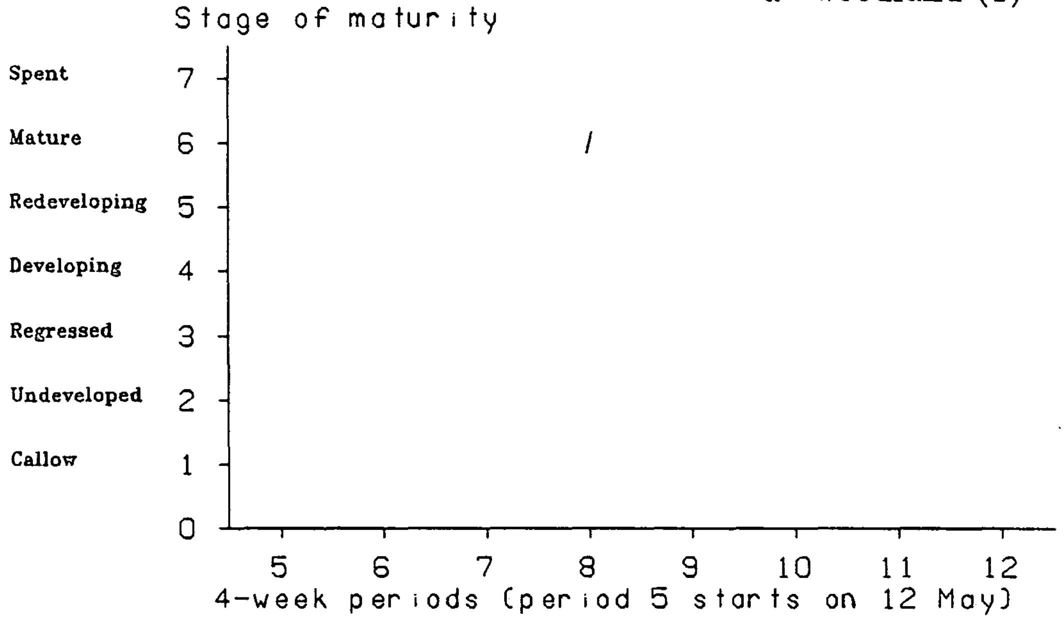
? indicates no observation

<Fig.4.4.2> Stages of maturity of female
<u>Calathus</u> <u>melanocephalus</u> caught in successive 4-week periods

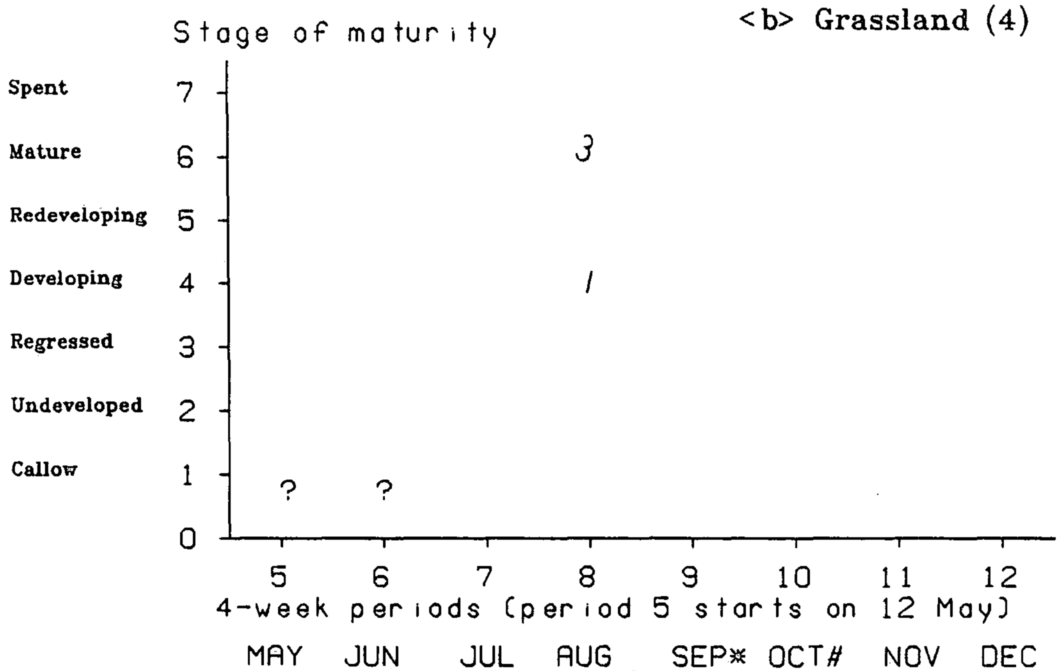
Frequencies are plotted

? indicates no observation

<a> Woodland (1)

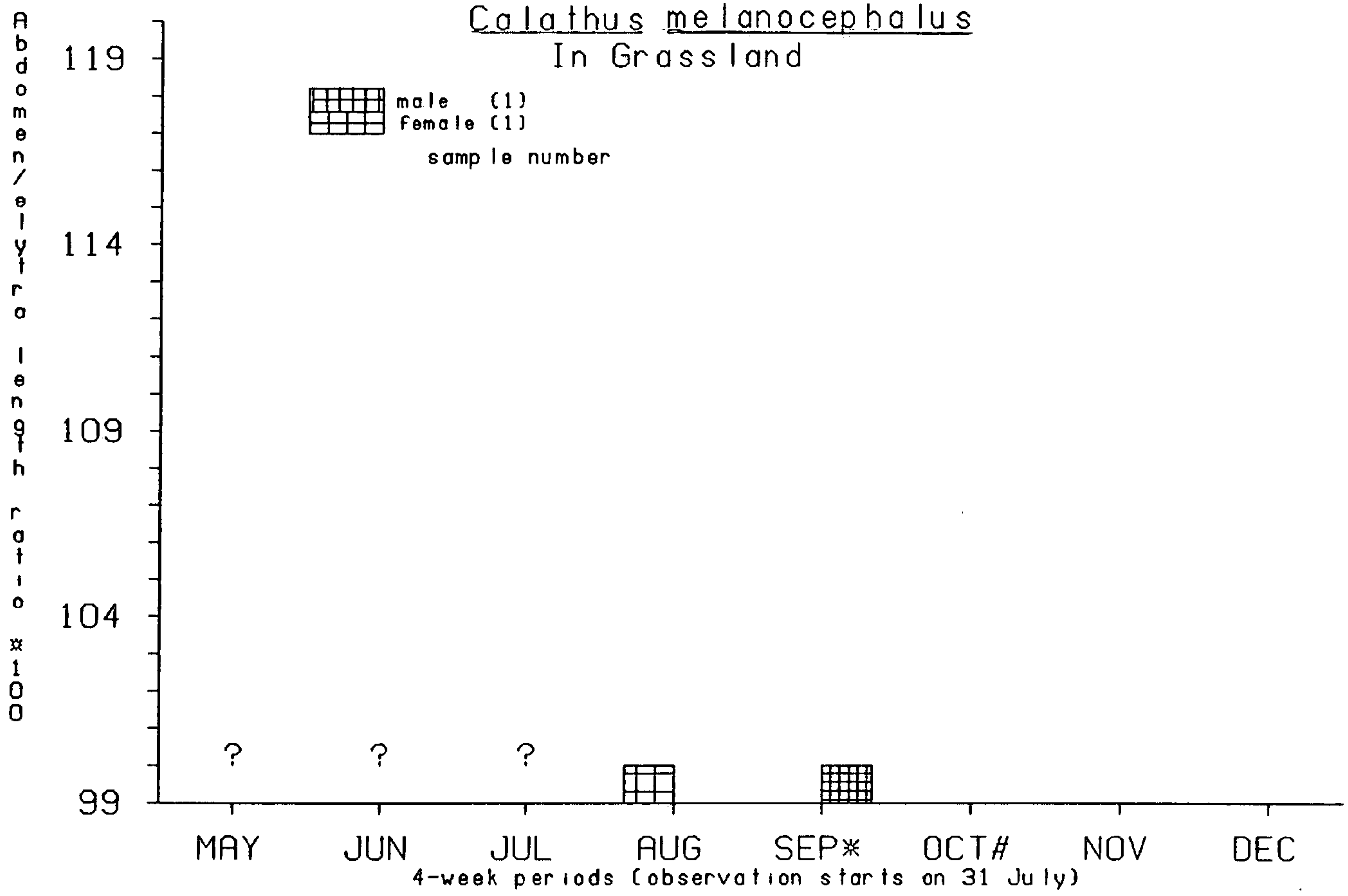


<b> Grassland (4)



data are for 1 week
¤ data are for 3 weeks

<Fig.4.4.3> Abdomen/elytra length ratio in 4-week periods

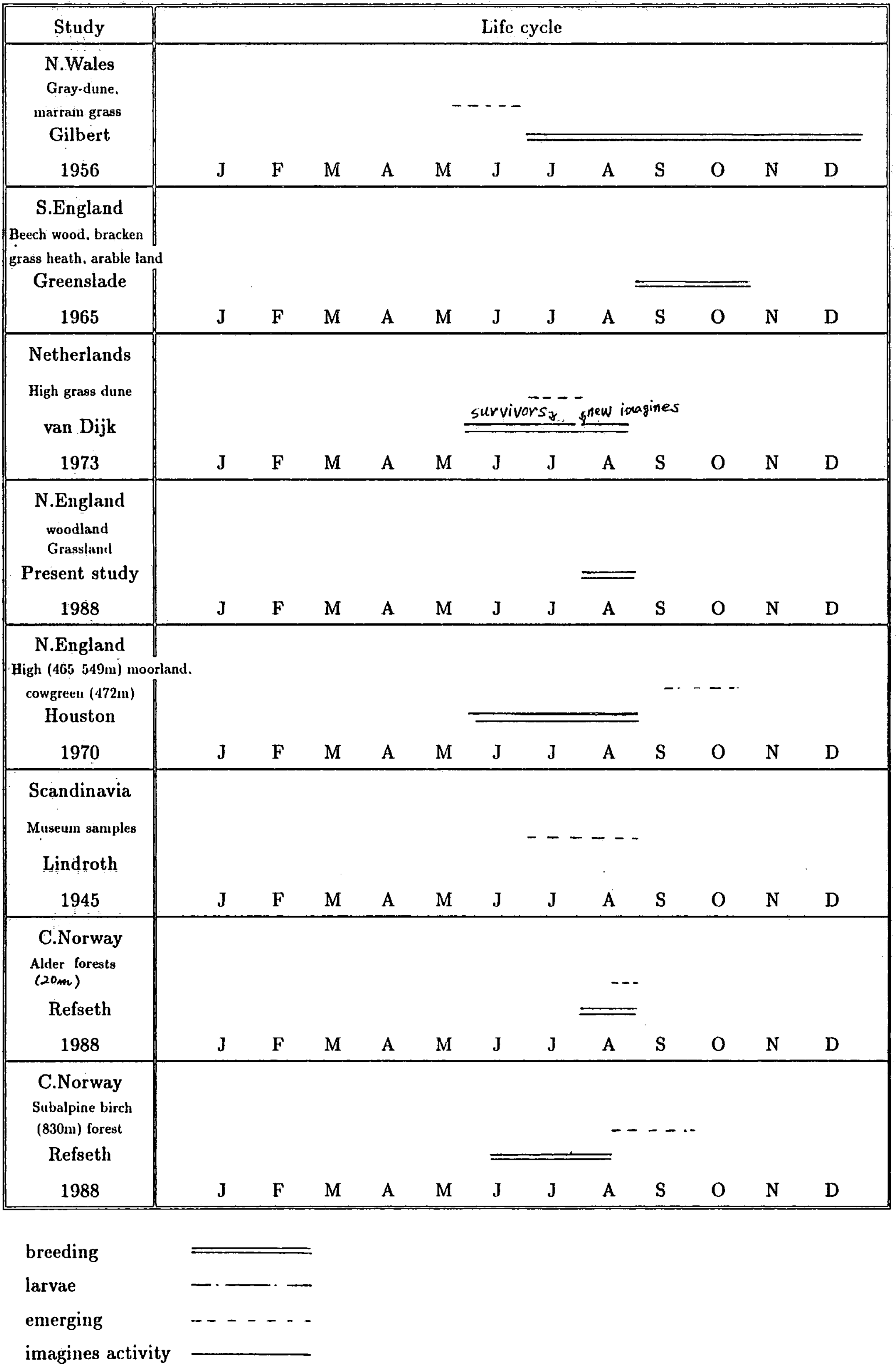


※ Data are for 3 weeks

Data are for 1 week

? indicates no observation

<Fig. 4.4.4> The results of previous and present study of life cycle of *Calathus melanocephalus*



4.5 Calathus piceus Marsham

PREVIOUS INFORMATION

The habitat of *Calathus piceus* is woodland litter (Greenslade 1965).

Only a small number of studies have been made of this species. *Calathus piceus* is an autumn breeder with larval hibernation and emergence in the next summer (Larsson 1939). Imagines were caught from April to December with maximum activity from May to August in southern England (Greenslade 1965). In Denmark (Larsson 1939), maximum activity has been found in August, with breeding in August and September.

RESULTS AND DISCUSSION

In this study, individuals of the species were captured mainly in woodland, with three callows in late June and July <Fig.4.5.1>.

Fig.4.5.3 shows the results of previous field studies of the life cycle of this species. Eight mature females were observed in the Durham woodland in July and four in September; a spent female was observed in October <Fig.4.5.1>. Egg volumes and numbers are shown in Table 4.5.1 and Table 4.5.2. Large mean ratios of female abdomen/elytra length were observed in June and July, with a peak in July <Fig.4.5.2>. It is concluded that the oviposition season occurred between July and September and mainly in July, with emergence from late June to July. This indicates that a main part of the population may have a biennial life cycle. Two out of eight mature females captured in July were found to possess small eggs at the previtellogenesis stage, in addition to mature eggs. These females may therefore be able to reproduce twice in one year.

From these results, it is concluded for the Durham woodland population of *C. piceus*:

1. emergence occurred in early summer (late June to July)
2. a part of the new imago generation was univoltine whilst the majority was semivoltine
3. a univoltine group may have bred in the autumn, with some surviving to reproduce again in the following summer
4. a semivoltine group may have oviposited in the summer, after which some may have bred again in the autumn.

In grassland, one mature female was observed (with six eggs). The oviposition season in grassland may possibly be later than in woodland.

ADDITIONAL INFORMATION

The elytra lengths of females were significantly larger than those of males in woodland <Table 4.5.3> ($t_{26} = 3.63$, $p = 0.001$).

<Table 4.5.1> Mean egg volume of *Calathus piceus* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period total)
7			608 8		608 8
8	494 2	570 2			532 4
9			638 4		638 4
10				891 1	890 1
(Stage of maturity total)	494 2	570 2	618 12	890 1	614 17

<b>

Stage of maturity Period no.	6 Mature
10	487 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.5.2> Mean number of eggs carried by female *Calathus piceus* in relation to stage of maturity in 4-week periods
<a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	1 Callow	4 Developing	5 Redeveloping	6 Mature	7 Spent	(Period total)
6	0 1					0 1
7	0 1			25.6 8		22.8 9
8		11.5 2	13.5 2			12.0 4
9				15.0 4		15.0 4
10					1 1	1 1
(Stage of maturity total)	0 2	11.5 2	12.5 2	22.1 12	1 1	16.5 19

<b>

Stage of maturity Period no.	6 Mature
10	6 1

in each cell
mean number
sample number

<Table 4.5.3> Elytra length of both sexes of *Calathus piceus* in the two habitats

	Woodland	Grassland	(Sex total)
Female	5.804 25 1.141 0.228	5.700 1 – –	5.800 26 1.118 0.219
Male	4.900 4 0.200 0.100		4.900 4 0.200 0.100
(Habitat total)	5.679 29 1.105 0.205	5.700 1 – –	5.680 30 1.085 0.198

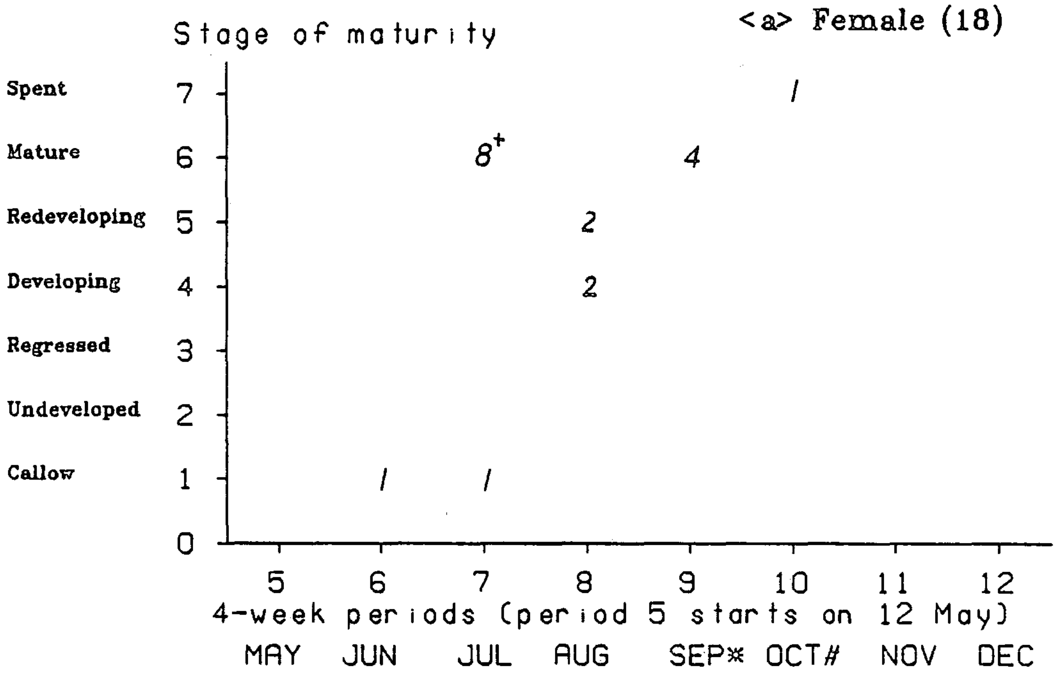
in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.5.1> Stages of maturity of <u>Calathus piceus</u> caught in successive 4-week periods in woodland

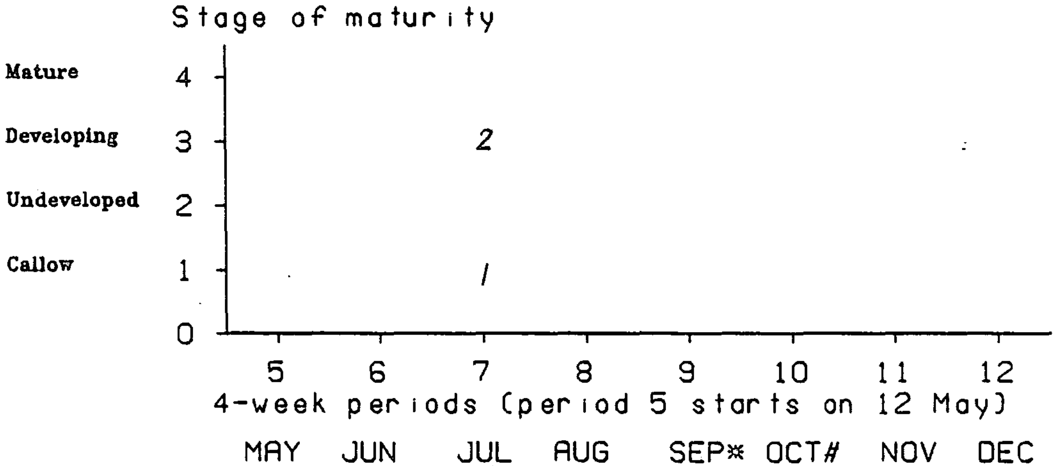
Frequencies are plotted

+ indicates developing small immature eggs at the same time in addition to mature eggs

<a> Female (18)



<b> Male (3)

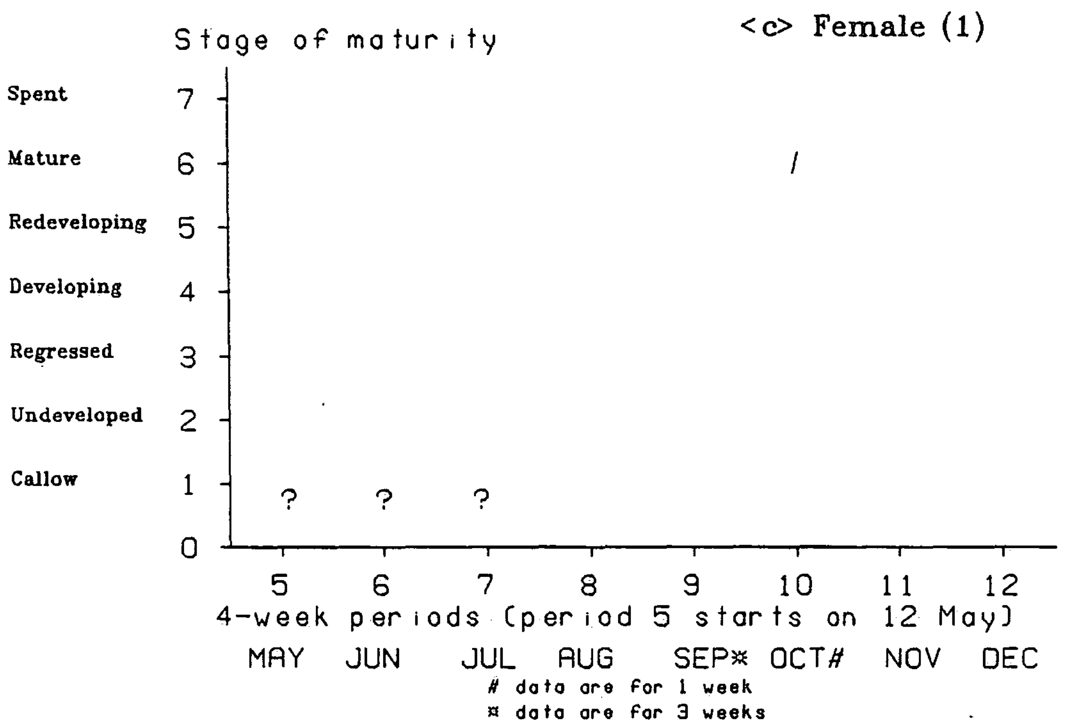


data are for 1 week
¤ data are for 3 weeks

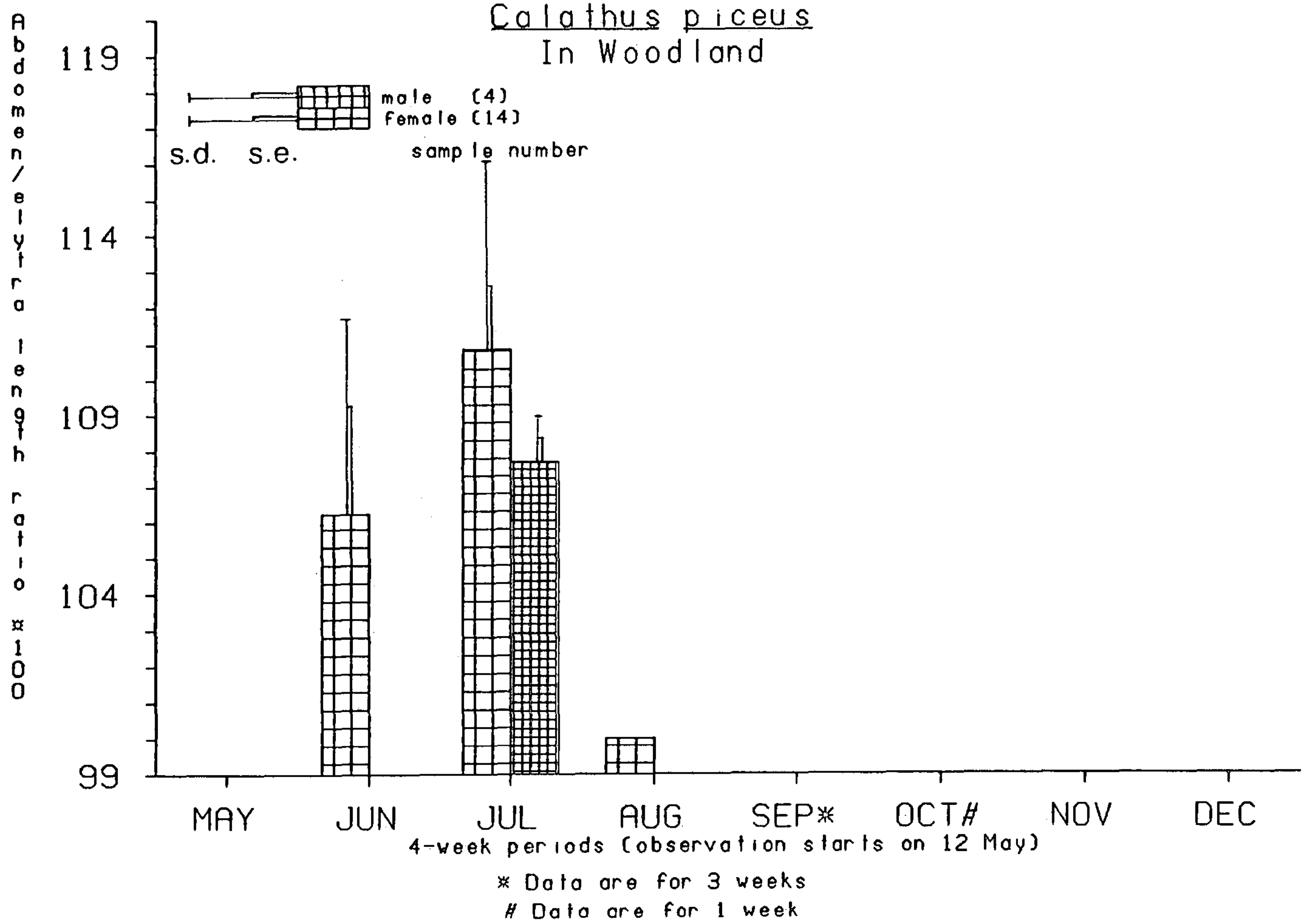
<Fig.4.5.1> Stages of maturity of <u>Calathus</u> <u>piceus</u> caught in successive 4-week periods in grassland

Frequencies are plotted

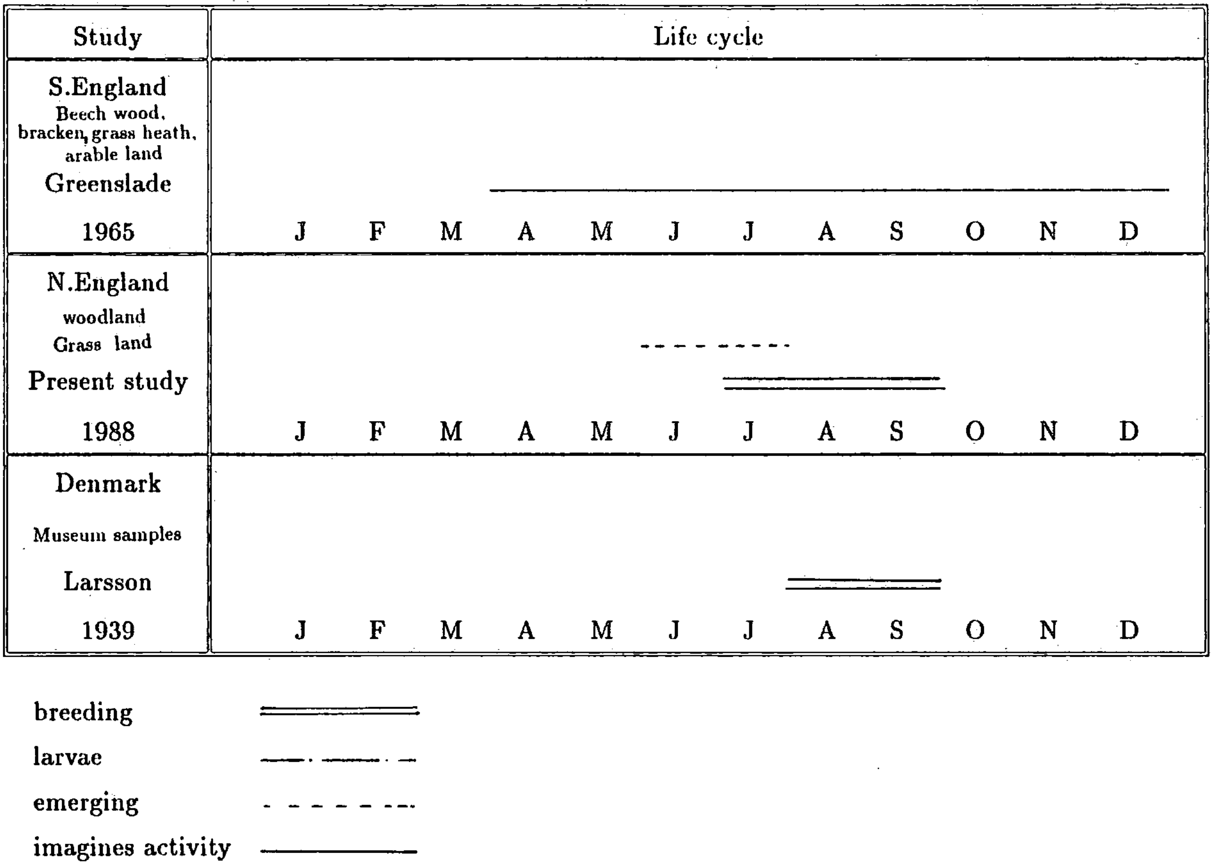
? indicates no observation



<Fig.4.5.2> Abdomen/elytra length ratio in 4-week periods



<Table 4.5.3> The results of previous and present study of life cycle of *Calathus piceus*



4.6 Carabus violaceus Linnaeus

PREVIOUS INFORMATION

Habitats of *C. violaceus* are woodland, arable land and grassland heath (Greenslade 1965).

Fig.4.6.5 shows the results of previous field studies of the life cycle of this species. The following three studies in southern England, the Netherlands and Denmark seem to indicate univoltine life cycles.

- In beech wood, bracken, grass heath and arable land in southern England (Greenslade 1965), imago activity has been observed from May to September (with a maximum in July) and larval activity in September and October.
- In beech forest in the Netherlands (van Drift 1951), emergence has been observed in late summer and breeding in autumn, followed by larval overwintering.
- In Denmark (Larsson 1939), emergence has been recorded in April and June, with breeding in July and August.

On the other hand, the results of studies in the uplands of northern England and central Norway show a semivoltine life cycle.

- In moorland in northern England (Houston 1970), emergence occurred in late July–August and breeding has occurred in June–July.
- In subalpine birch forest at 830m a.s.l. in central Norway (Refseth 1984), emergence occurred in late August and breeding in June–July.

RESULTS AND DISCUSSION

Carabus violaceus was observed mainly in the Durham woodland; few individuals were seen in grassland. Only woodland individuals are discussed here. Males were captured in July, August and September and females mostly in September <Fig.4.6.1a>. Males moved further in August and September than in earlier months <Fig.4.6.2>.

One male was observed emerging in late July <Fig.4.6.3b>.

In June, a large abdomen/elytra length ratio was found for one female <Fig.4.6.4a>. In July, a redeveloping female (maturity stage 5) was observed <Fig.4.6.3a>. Mature females were observed in August and October <Fig.4.6.3a>; the largest egg was found in a mature female in October <Table 4.6.1> whilst the largest mean number of eggs per female was found in developing females in August <Table 4.6.2>. From these results, it appears that univoltine females bred in the previous autumn. Although some oviposited in the early summer of the study year before emergence of the next generation of imagos, the main oviposition season seems to have occurred between August and October.

The present study of *C. violaceus* at the Durham woodland site suggests

1. a univoltine life cycle: breeding occurred in autumn following emergence in July. Some may have survived as spent imagines into a second year to breed in the summer again;
2. a fraction of the population may perhaps follow a semivoltine life cycle and contribute to early summer breeding. (See Fig.4.6.5)

From a comparison of previous and present studies, this species seems to have a shift of life cycle from that of an annual autumn breeder to a biennial summer breeder, in parallel with a geographical shift from warmer to cooler conditions.

ADDITIONAL INFORMATION

When certain individuals of both sexes were marked with a drill for identification, a defence mechanism was observed which consisted of the emission of a stimulative liquid from the apex of the abdomen which gave the present author a strong sensation of pain. Thiele (1977) also reported a similar observation.

One female and two males were observed to secrete pheromone in late July. The role of this may be related to maturation because it was seen during emergence and just before the breeding season.

Table 4.6.3 shows that the female elytra lengths were perhaps larger than those of the male, though not significantly so ($t_{16} = 1.74$, $p = 0.100$).

<Table 4.6.1> Mean egg volume of *Carabus violaceus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	4 Developing	5 Redeveloping	6 Mature	(Period total)
7		10680 1		10680 1
8	11739 2		9415 3	10345 5
10			14556 1	14556 1
(Stage of maturity total)	11739 2	10679 1	11986 2	11626 5

in each cell
mean (mm^3)
sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.6.2> Mean number of eggs carried by female *Carabus violaceus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	4 Developing	5 Redeveloping	6 Mature	(Period total)
7		2 1		2 1
8	12 2		4 1	9.3 3
10			2 1	2 1
(Stage of maturity total)	12 2	2 1	3 2	6.4 5

in each cell
mean number
sample number

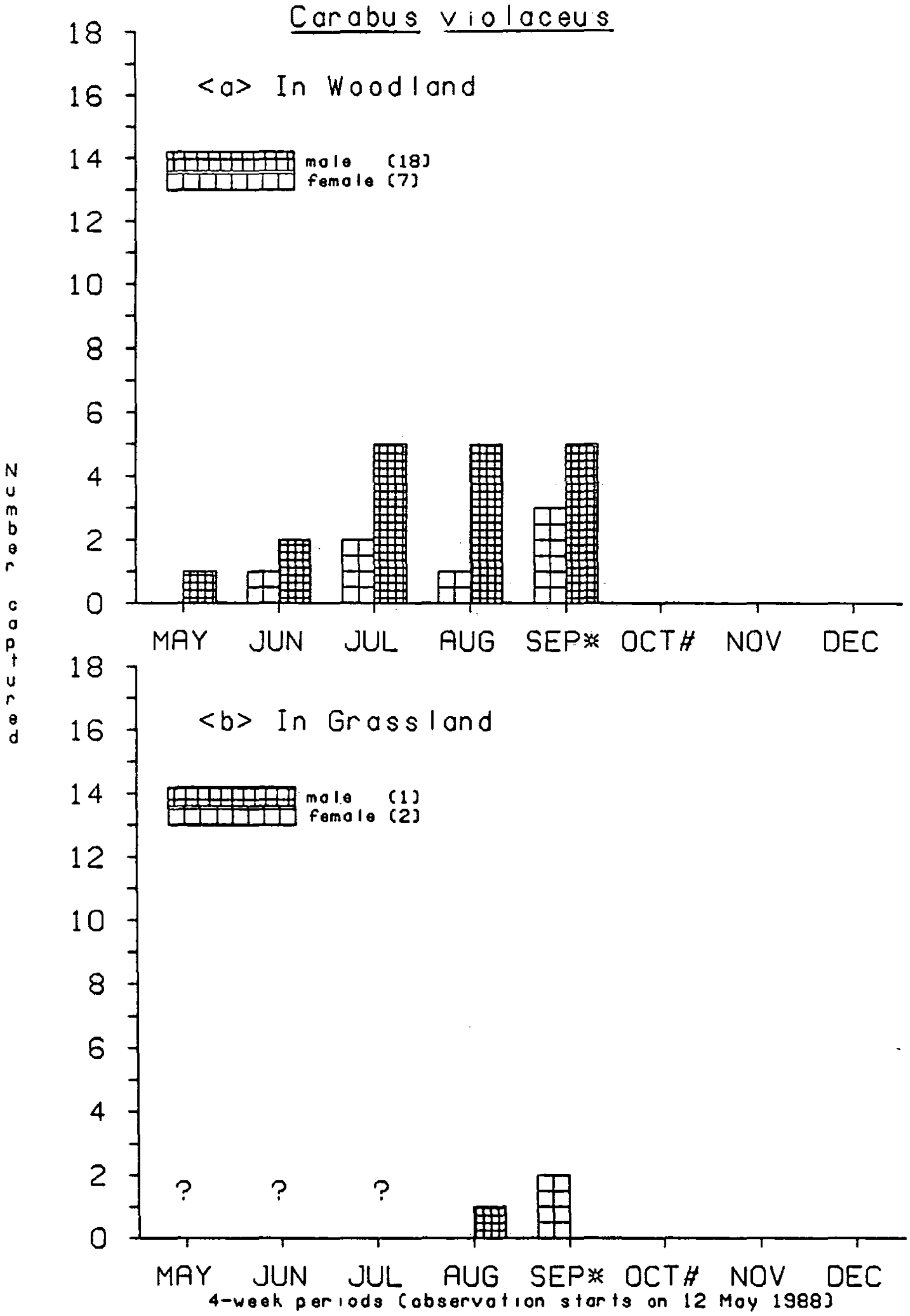
<Table 4.6.3> Elytra length of both sexes of *Carabus violaceus* in the two habitats

	Woodland	Grassland	(Sex total)
Female	15.662 13 1.677 0.465	15.650 2 0.495 0.350	15.660 15 1.558 0.402
Male	14.783 18 0.828 0.195	15.800 1 – –	14.837 19 0.837 0.192
(Habitat total)	15.152 31 1.306 0.235	15.700 3 0.361 0.208	15.200 34 1.259 0.216

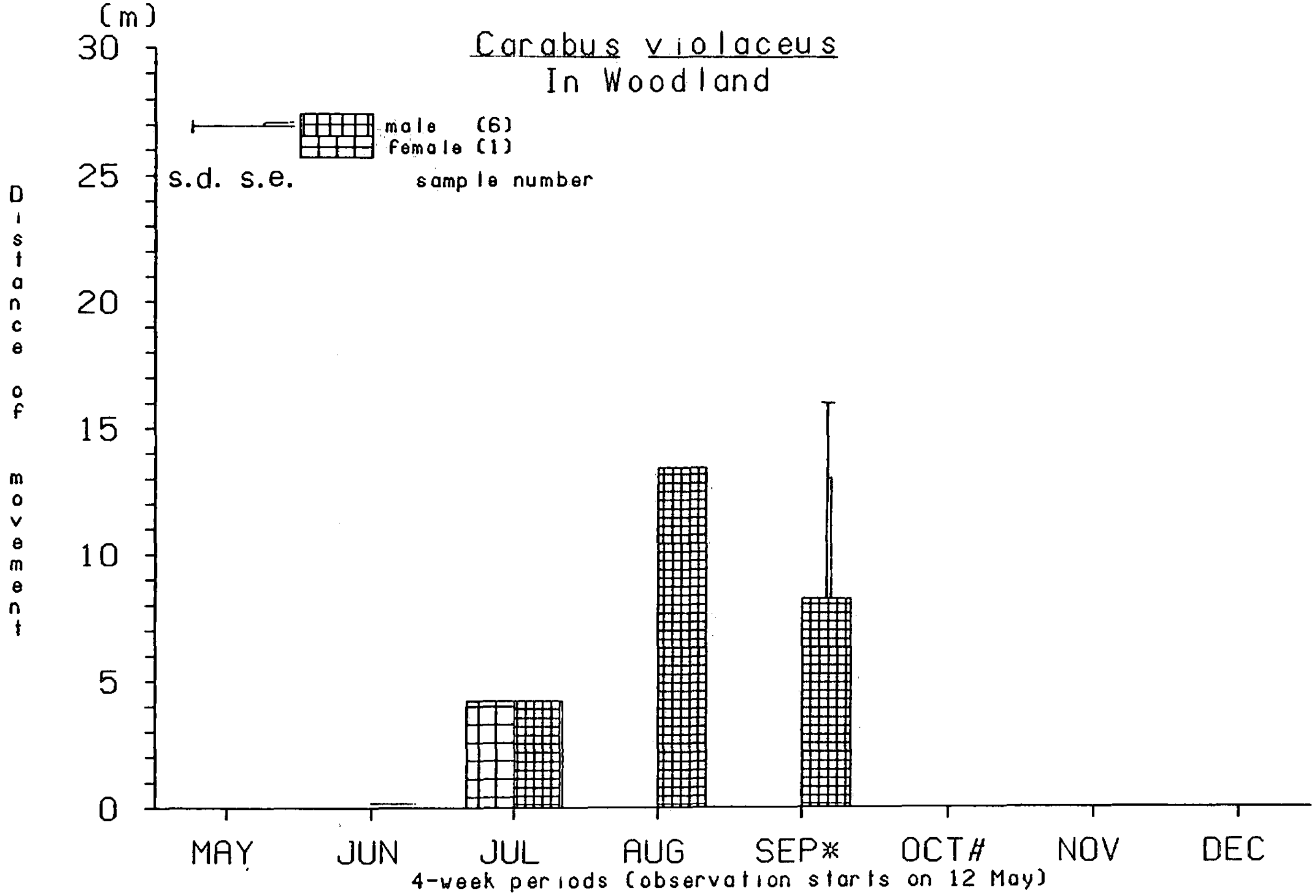
in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.6.1> Frequency of capture (including re-capture) in 4-week periods

Carabus violaceus



※ Data are for 3 weeks
\# Data are for 1 week
? indicates no observation



<Fig.4.6.2> Distance between capture and recapture points

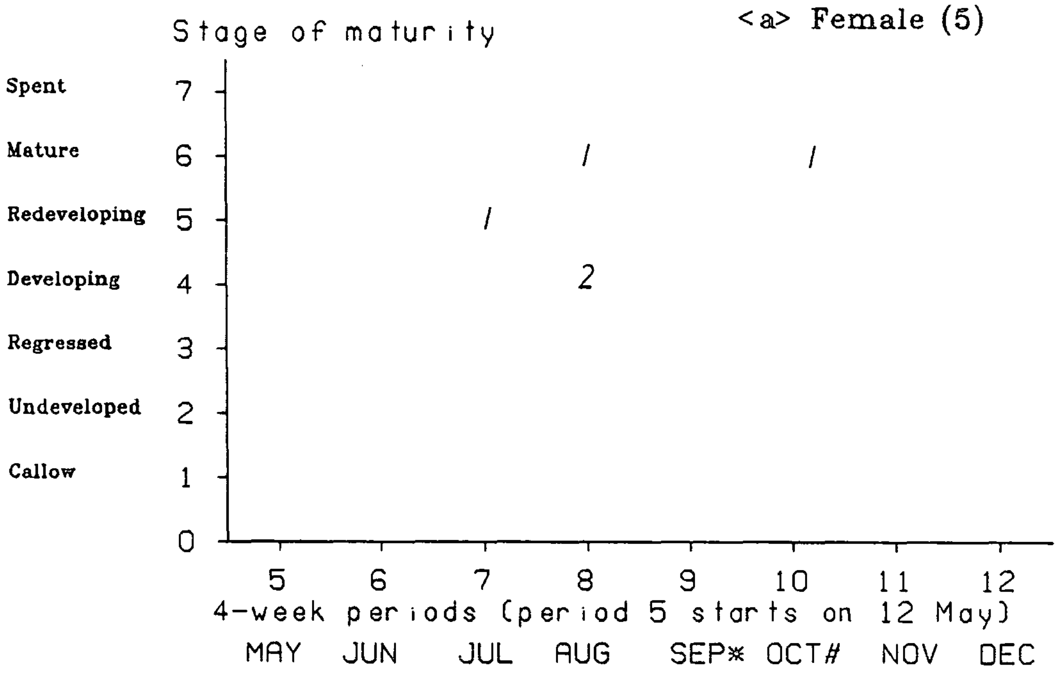
※ Data are for 3 weeks

Data are for 1 week

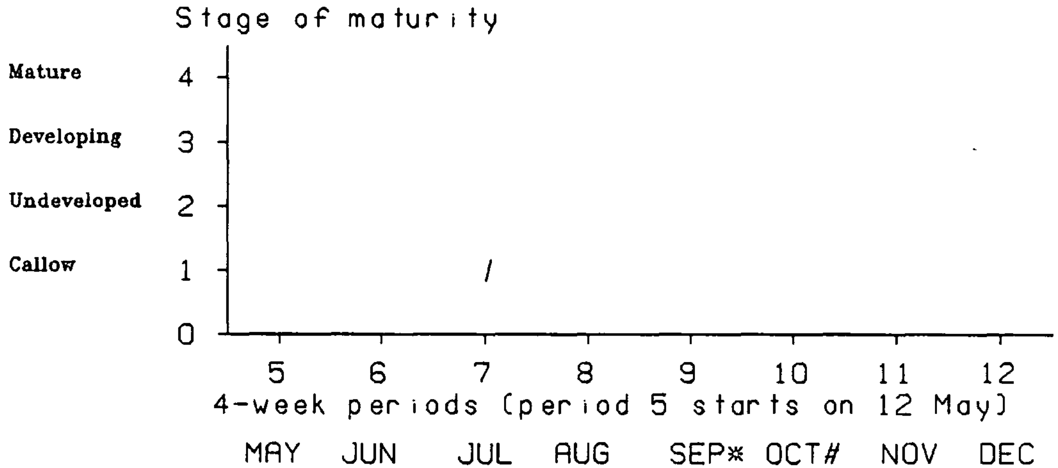
<Fig.4.6.3> Stages of maturity of *Carabus violaceus* caught in successive 4-week periods in woodland

Frequencies are plotted

<a> Female (5)

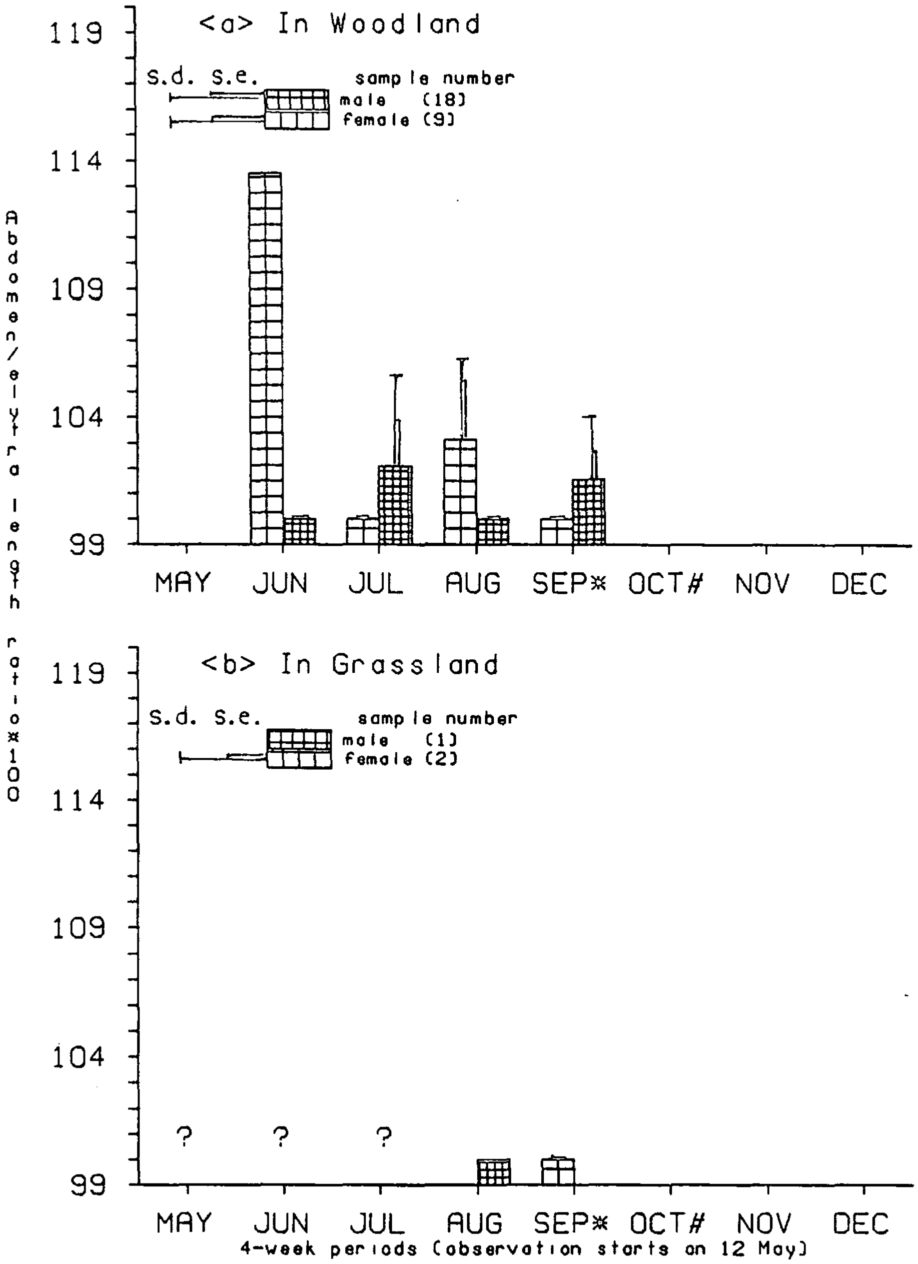


<b> Male (1)



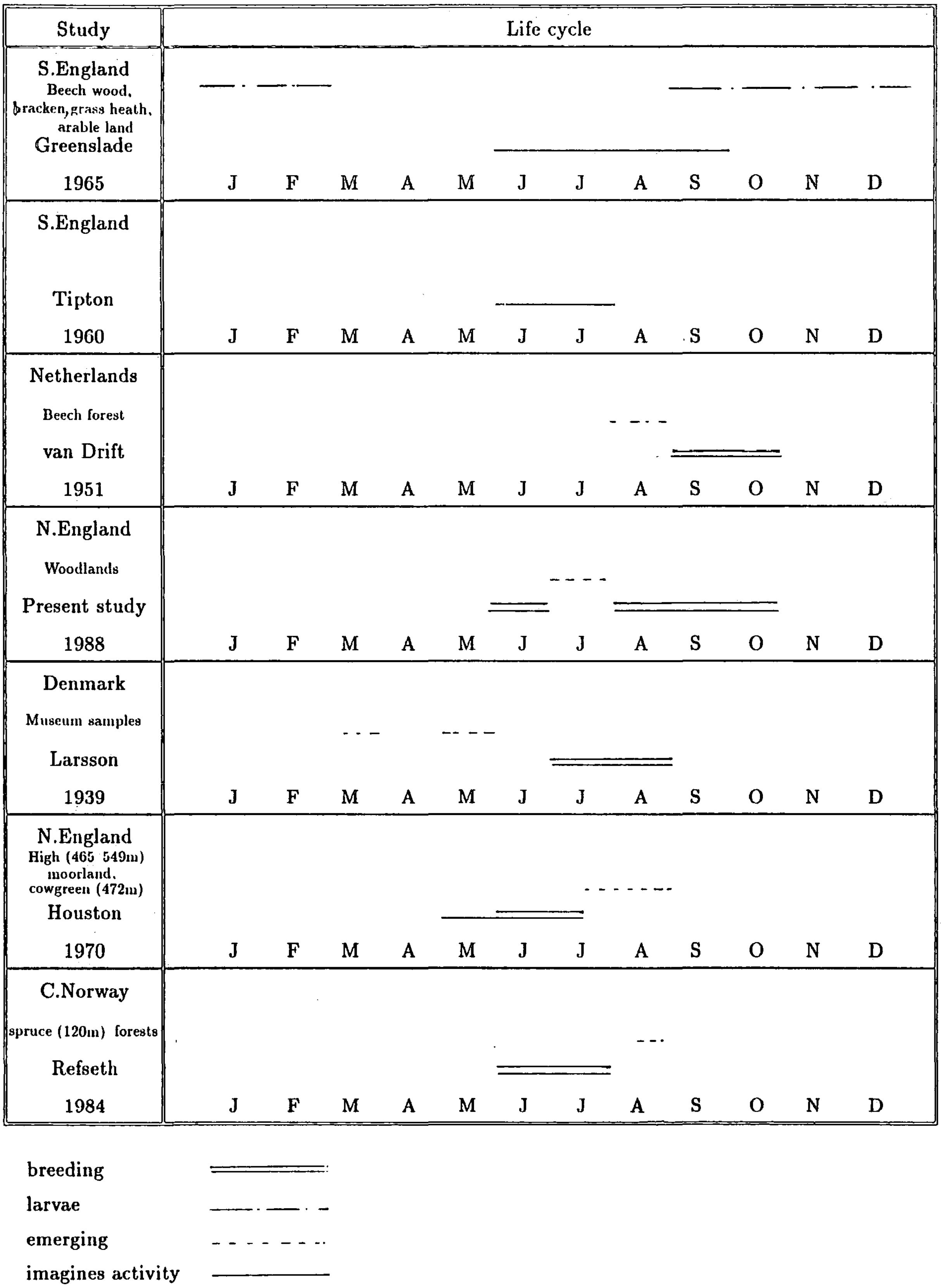
data are for 1 week
¤ data are for 3 weeks

<Fig.4.6.4> Abdomen/elytra length ratio in 4-week periods
Carabus violaceus



¤ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig. 4.6.5> The results of previous and present study of life cycle of *Carabus violaceus*



4.7 Cychrus caraboides Linnaeus

PREVIOUS INFORMATION

Cychrus caraboides is a woodland species (Greenslade 1965). It is found in shady, rather moist places (Lindroth 1974).

Fig.4.7.5 shows the results of previous field studies of the life cycle of this species.

- In southern England (Tipton 1960; Greenslade 1965: beech wood, bracken, grass heath and arable land), a peak of activity has been observed from June to August, which involves emergence and breeding; a breeding season in August–October at a marsh and streamside has been observed by Murdoch (1967).
- In central Denmark (Larsson 1939), larvae were trapped in late August–November and in April; pupa and callows were caught in late May–early June and the majority of imagines were caught in July. Breeding occurred in August–September.
- In high moorland in northern England, breeding has been observed in late July–August (Houston 1970) .
- In central Norway (Refseth 1988: subalpine birch forest at 830m a.s.l.), an active season was found from June to early July, which coincides with maturation; breeding was found in July and emergence occurred in July and August.

Similar life cycles have been observed in Scandinavia (Lindroth 1945) and in the Austrian mountains (De Zordo 1979).

RESULTS AND DISCUSSION

Cychrus caraboides was observed only in the Durham woodland. This is consistent with the work of Greenslade (1965) and Lindroth (1974).

Captures were made from June to September <Fig.4.7.1>. These involved one female callow in mid-June, i.e. at the beginning of the capture period for this species. A copulation was observed in woodland in early September. Following dissection, a mature female in August was found to have 15 eggs; also, undeveloped females were observed in September <Fig.4.7.3a>. In August, females had the largest mean abdomen/elytra length ratio <Fig.4.7.4>. It is suggested:

1. *Cychrus caraboides* emerged in June to breed in August and September;
2. a part of the *C. caraboides* population may have a biennial life cycle; this is a result that is also reported by De Zordo (1979) and Refseth (1988) <Fig.4.7.5>.

It is therefore concluded that a mixture of univoltine and semivoltine life cyles may co-exist in the Durham woodland.

From the comparison of present and previous studies <Fig.4.7.5>, this species seems to have a shift of life cycle geographically from a univoltine late-summer breeder to a semivoltine mid-summer breeder, as environments become more severe.

ADDITIONAL INFORMATION

When caught with the fingers, individuals of this species were observed to make sounds by a squeezing of the expanded abdomen. Such behaviour may form a defence mechanism, and is similar to an observation by Thiele (1977).

Elytra lengths did not differ between sexes ($t_{27} = 0.38$, $p = 0.706$) (See Table 4.7.1).

<Table 4.7.1> Mean egg volume of *Cychrus caraboides* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
8	2345 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.7.2> Mean number of eggs carried by female *Cychrus caraboides* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	2 Undeveloped	6 Mature
8		15 1
9	0 2	

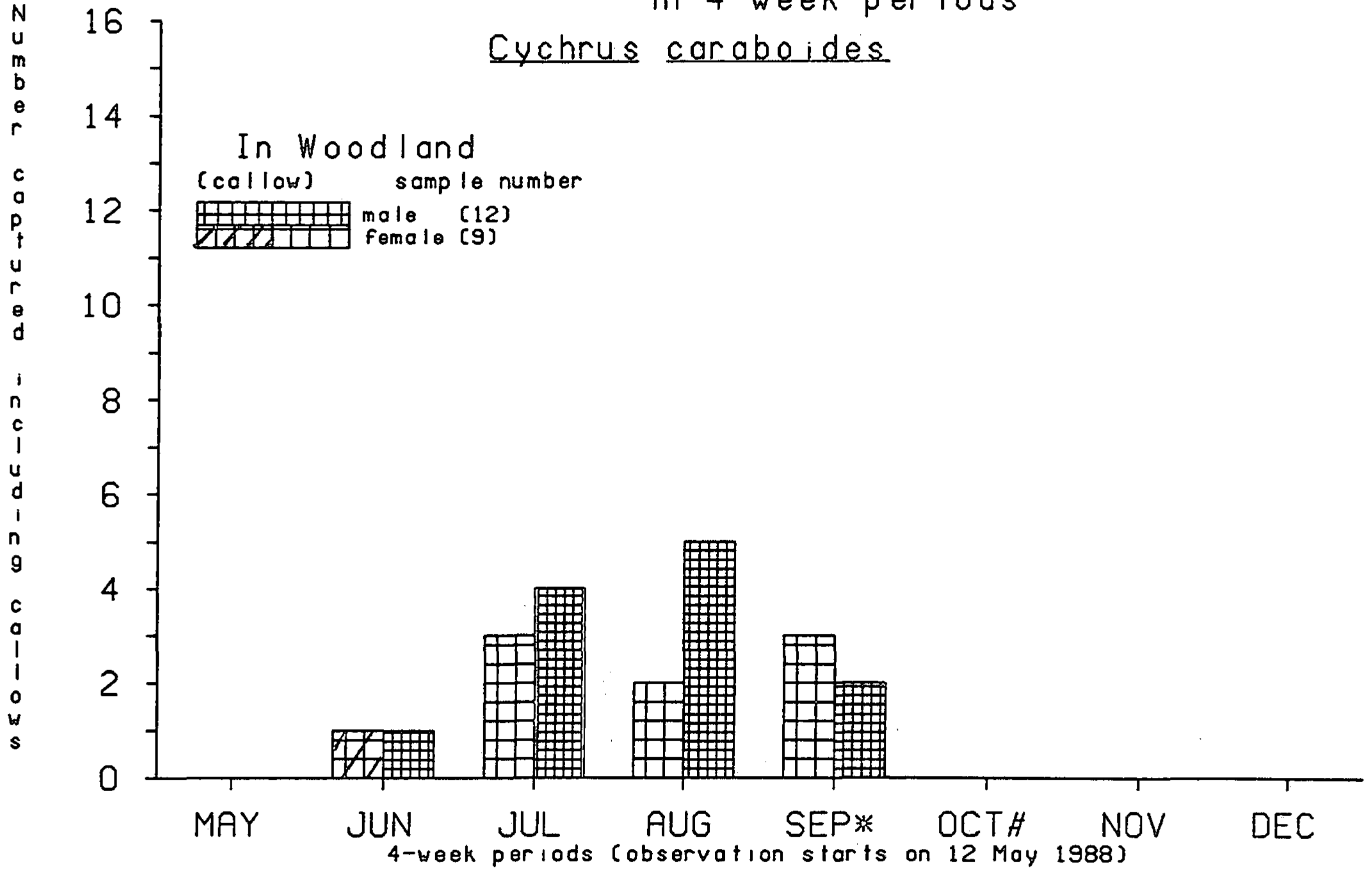
in each cell
mean number sample number

<Table 4.7.3> Elytra length of both sexes of *Cychrus caraboides* in the woodland

	Woodland
Female	10.217 12 1.214 0.350
Male	10.359 17 0.796 0.193
(Habitat total)	10.300 29 0.973 0.310

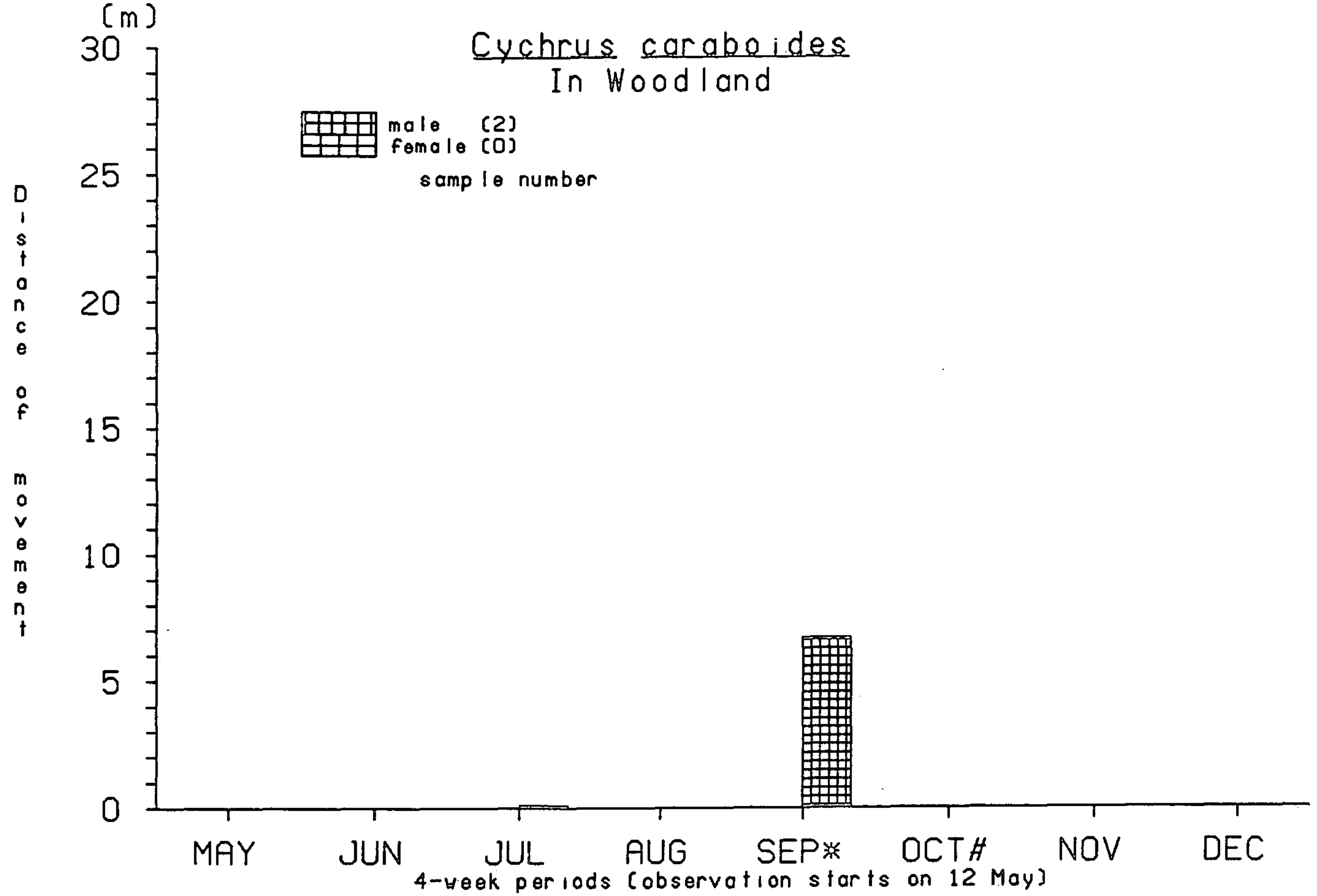
in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.7.1> Frequency of capture (including re-capture) in 4-week periods



※ Data are for 3 weeks
Data are for 1 week

<Fig.4.7.2> Distance between capture and recapture points



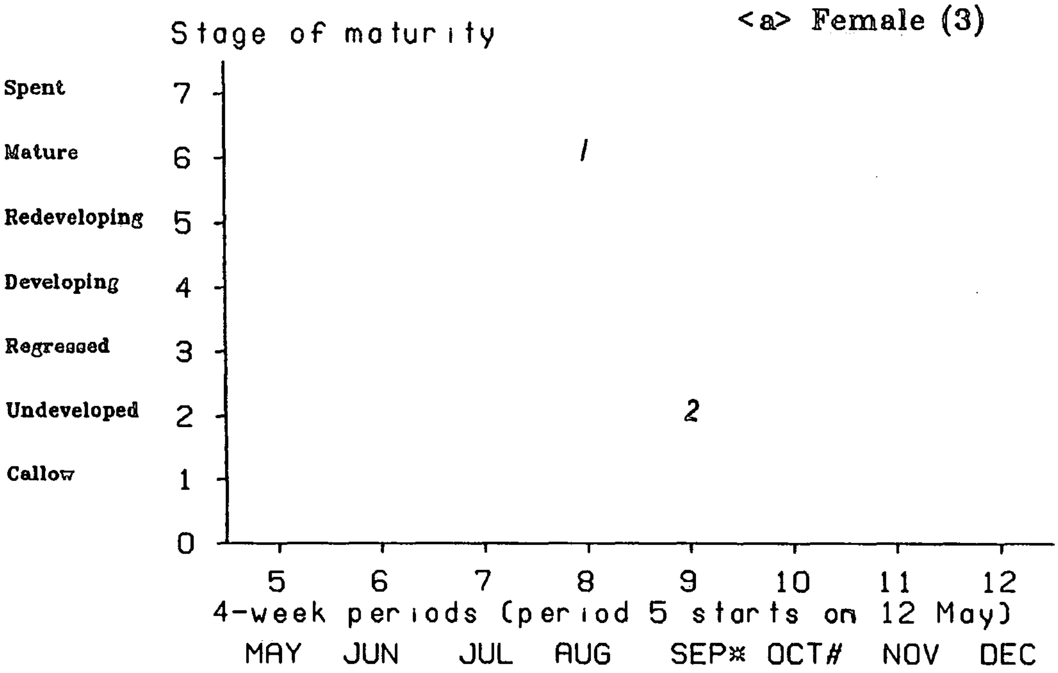
※ Data are for 3 weeks

Data are for 1 week

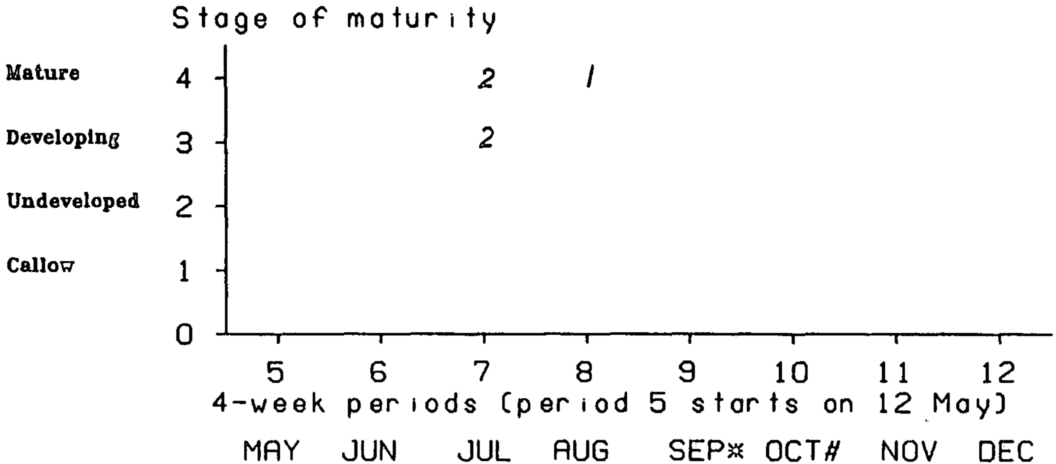
<Fig.4.7.3> Stages of maturity of *Cychrus caraboides* caught in successive 4-week periods in woodland

Frequencies are plotted

<a> Female (3)



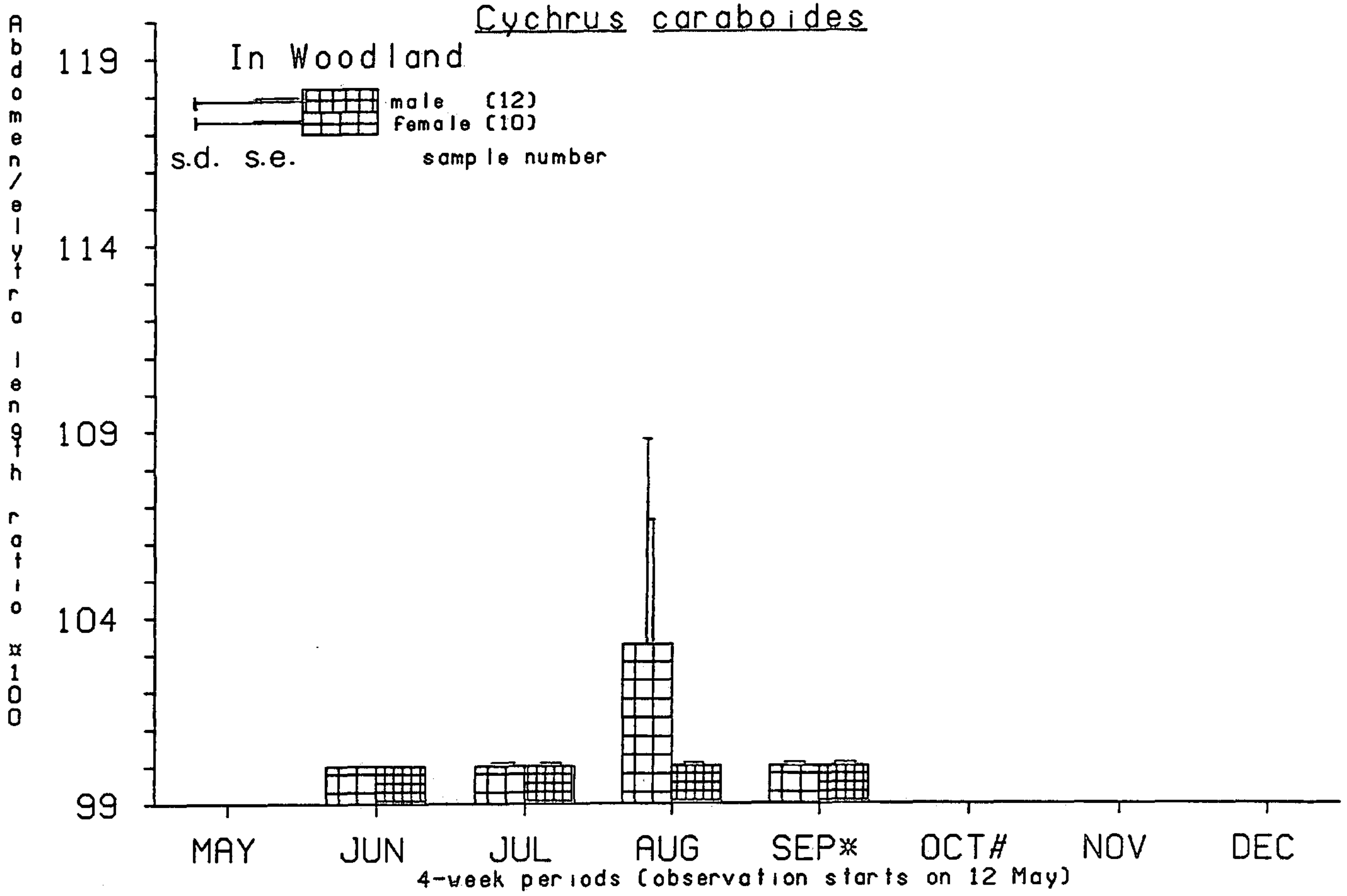
<b> Male (5)



data are for 1 week
¤ data are for 3 weeks

<Fig.4.7.4> Abdomen/elytra length ratio in 4-week periods

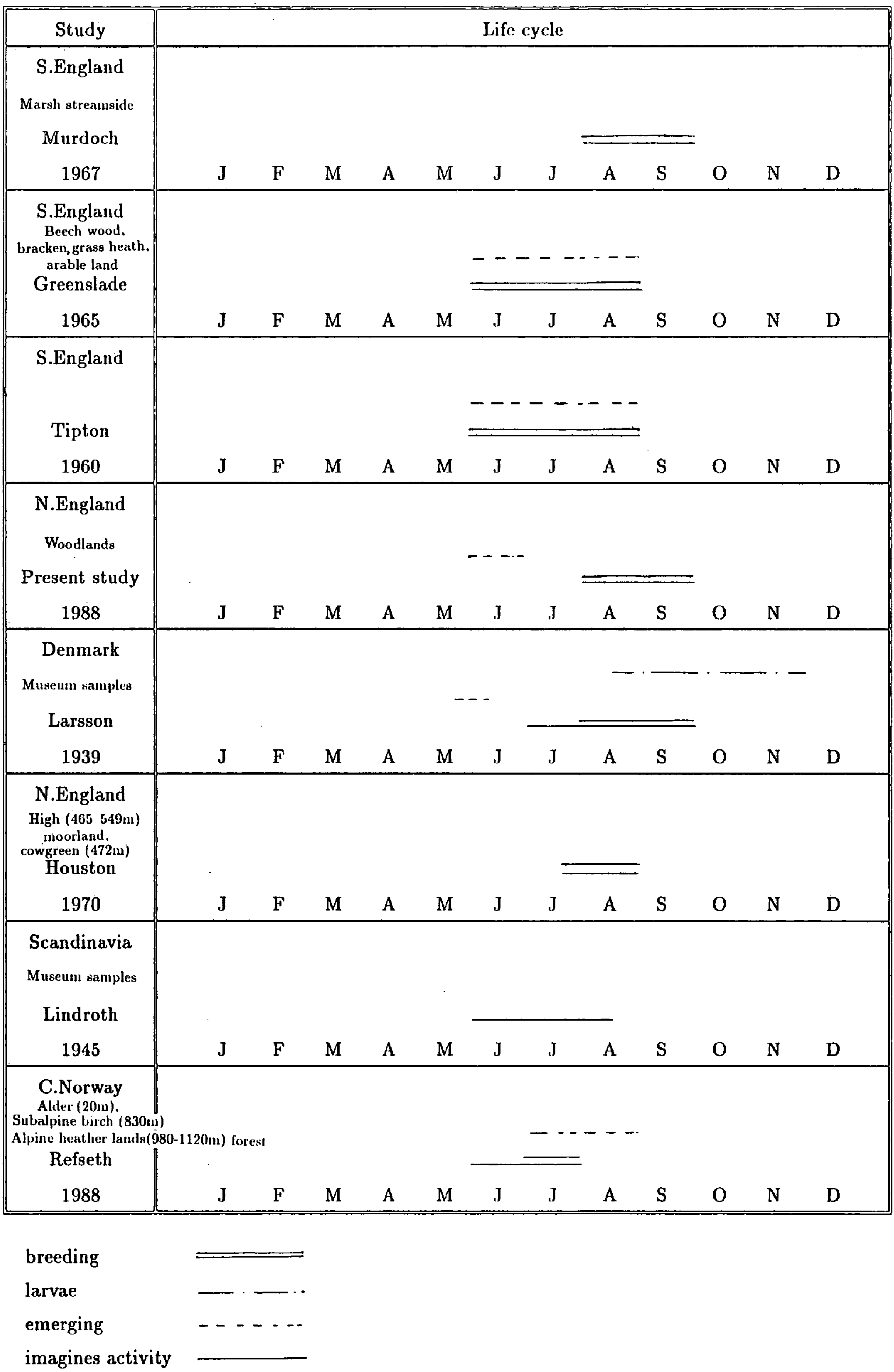
Cychrus caraboides



¤ Data are for 3 weeks

Data are for 1 week

<Fig.4.7.5> The results of previous and present study of life cycle of *Cychrus caraboides*



4.8 Leistus ferrugineus Linnaeus

PREVIOUS INFORMATION

Leistus ferrugineus lives on the edge of canopied areas or in open woodland, rather than litter (Greenslade 1965).

This species is in a group with winter larvae, the adults of which emerge in spring and undergo aestivation dormancy prior to autumn reproduction.

Fig.4.8.4 shows the results of previous field studies of the life cycle of this species.

- In southern England (Greenslade 1965) *L. ferrugineus* shows two peaks of activity in breeding (August–October) and perhaps in emergence (May–June).
- Similarly, two peaks of activity were found in the Netherlands (emergence in July and breeding in October: den Boer 1958) and in Denmark (June emergence and September–October breeding: Larsson 1939).
- A single peak of activity has been observed in June in Scandinavia (Lindroth 1945).

RESULTS AND DISCUSSION

In the Durham study, this species was found only in woodland and mostly in October and November <Fig.4.8.1>, when mature individuals were observed <Fig.4.8.2>. The egg volumes and numbers per female are shown in Table 4.8.1 and Table 4.8.2. From these results it is concluded that the oviposition season occurred in autumn and early winter (at least in October and November). This is supported by the previous studies of Larsson (1939), Den Boer (1958) and Greenslade (1965), in which breeding has been observed until October <Fig.4.8.4>.

ADDITIONAL INFORMATION

The elytra lengths of the females are significantly larger than those of the males <Fig.4.8.3> ($t_{10} = 2.70$, $p = 0.022$).

<Table 4.8.1> Mean egg volume of *Leistus ferrugineus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
10	237 3

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.8.2> Mean number of eggs carried by female *Leistus ferrugineus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
10	9 3

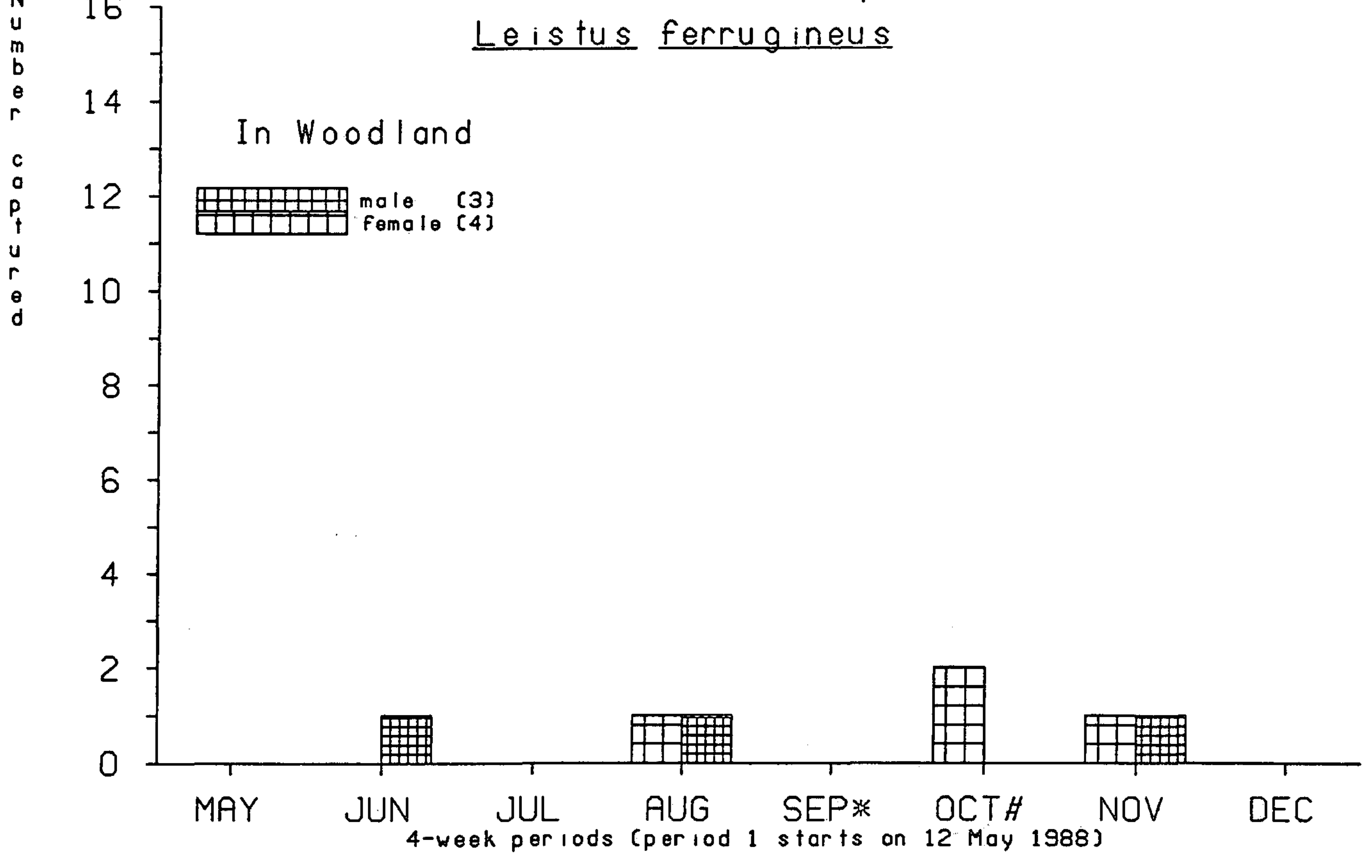
in each cell
mean number sample number

<Table 4.8.3> Elytra length of both sexes of *Leistus ferrugineus* in the woodland

	Woodland
Female	4.457 7 0.127 0.048
Male	4.280 5 0.84 0.038
(Habitat total)	4.383 12 0.140 0.040

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.8.1> Frequency of capture (including re-capture) in 4-week periods



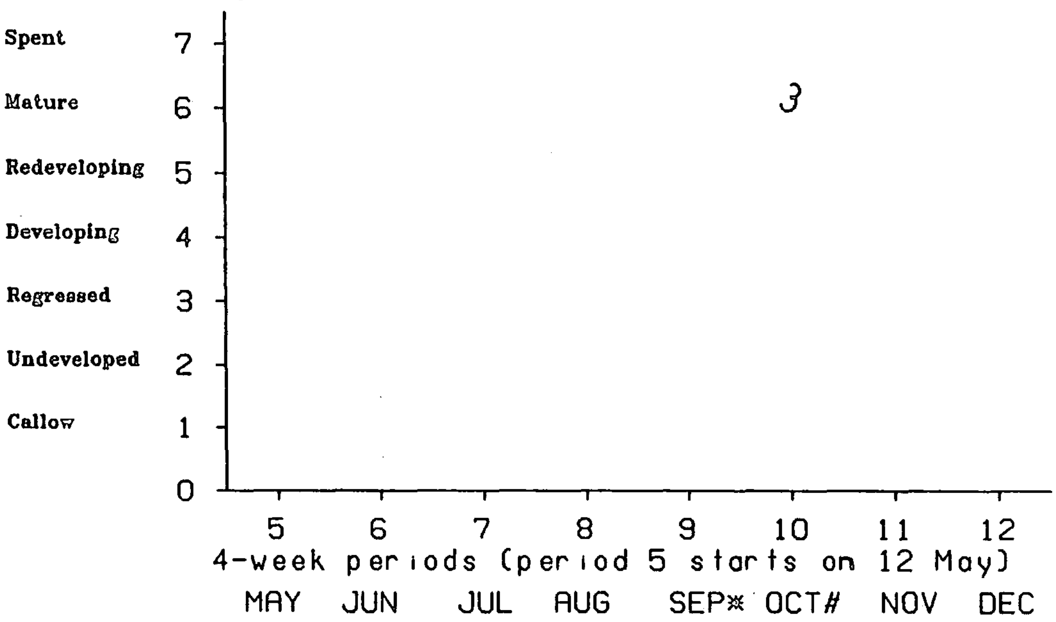
¤ Data are for 3 weeks

Data are for 1 week

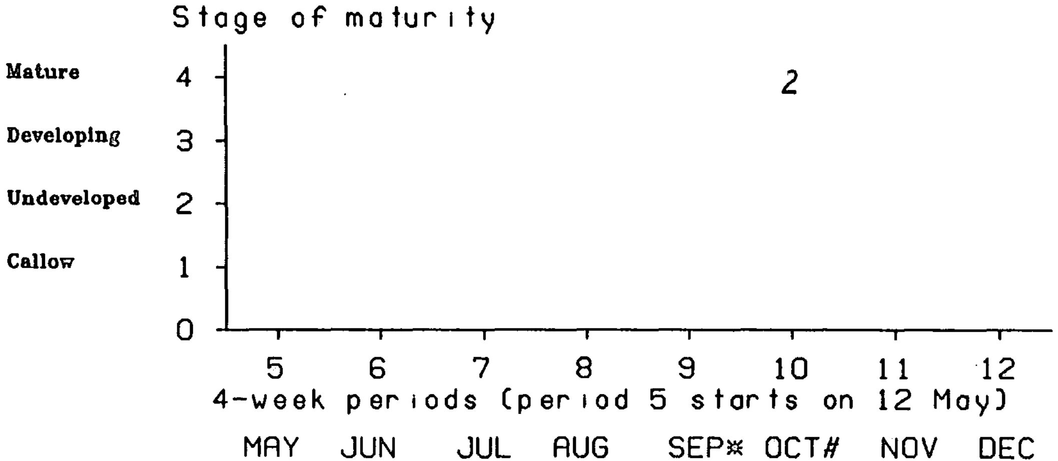
<Fig.4.8.2> Stages of maturity of <u>Leistus</u> <u>ferrugineus</u> caught in successive 4-week periods in woodland

Frequencies are plotted

<a> Female (3)

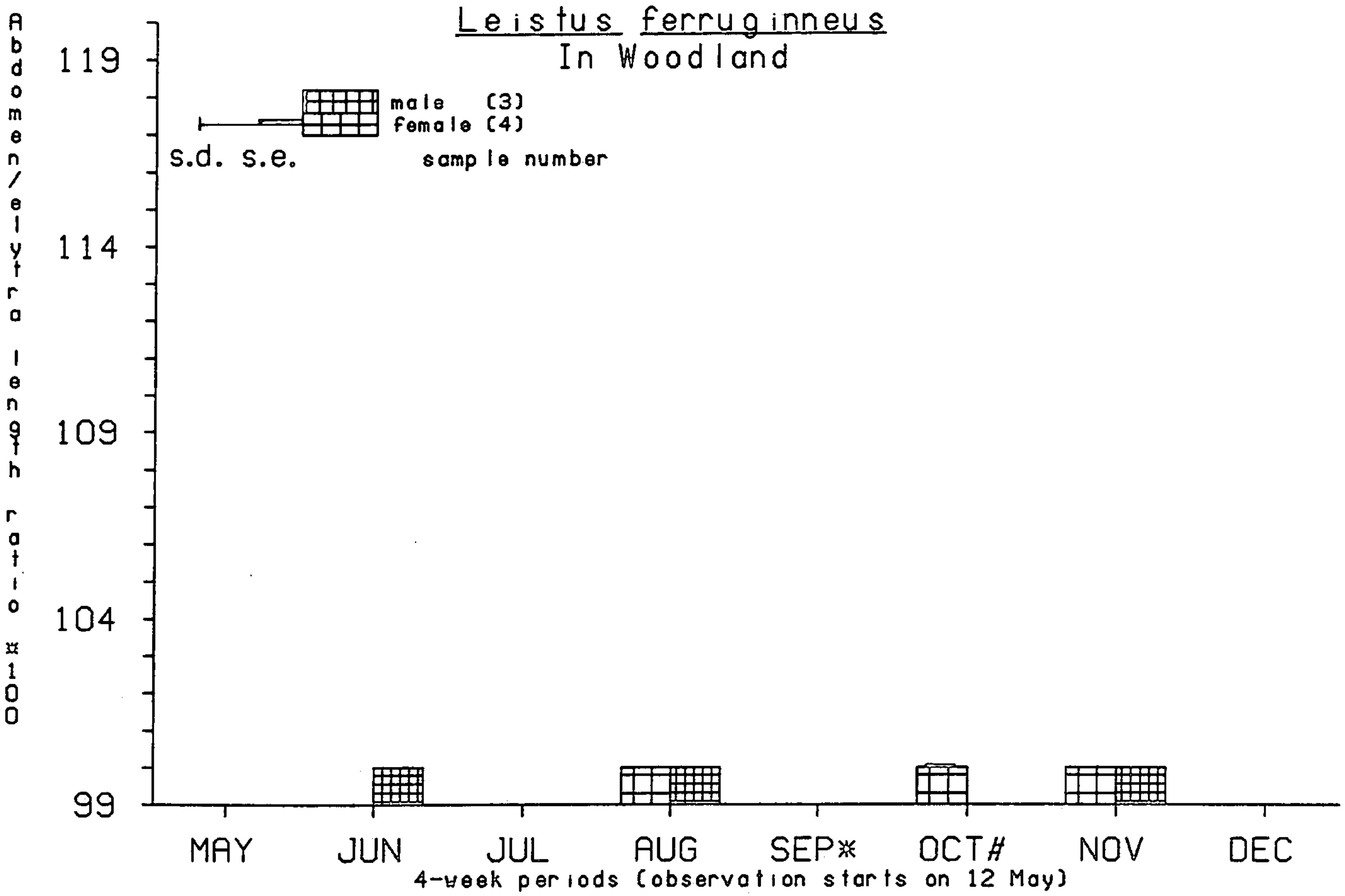


<b> Male (2)



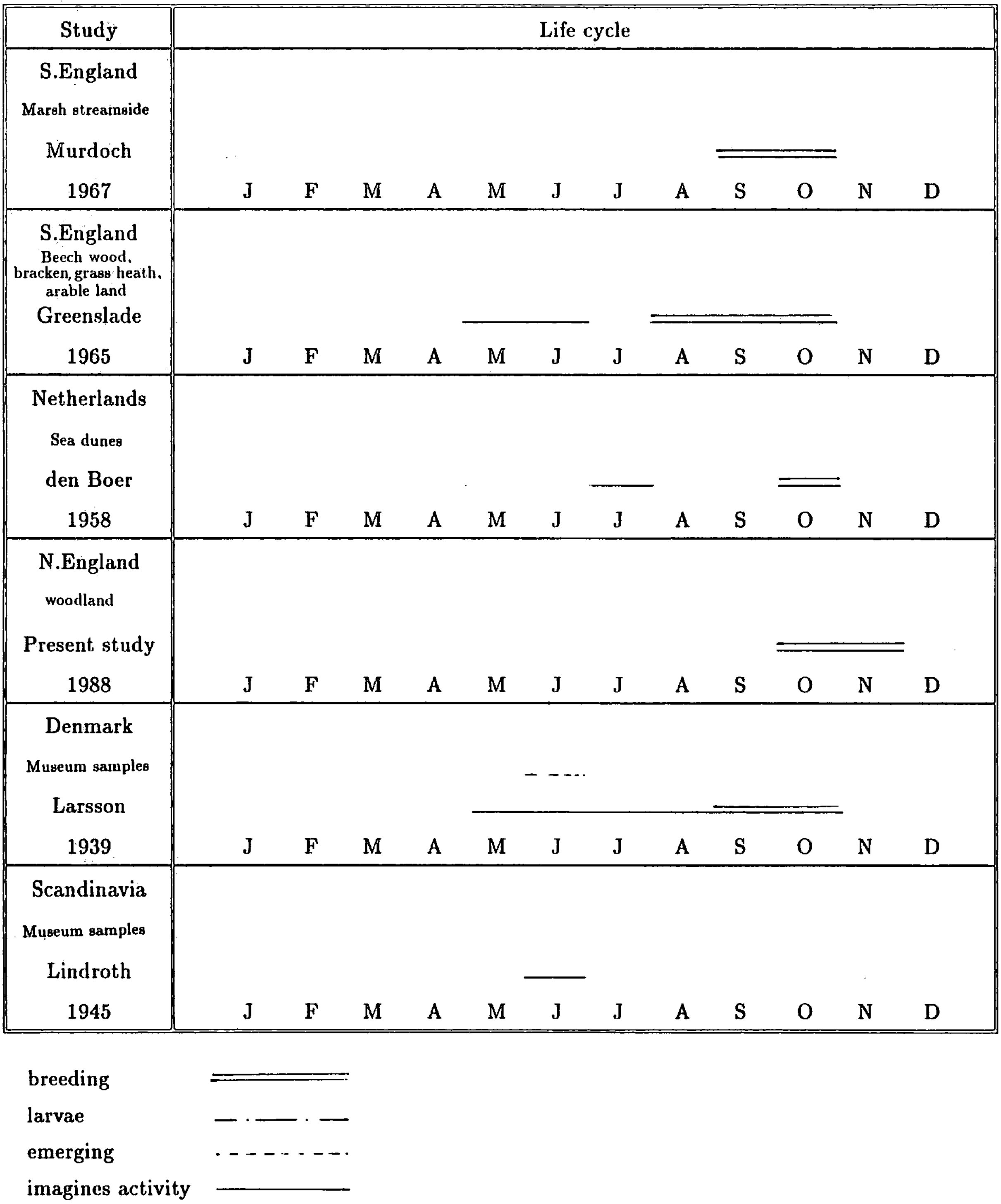
data are for 1 week
¤ data are for 3 weeks

<Fig.4.8.3> Abdomen/elytra length ratio in 4-week periods



※ Data are for 3 weeks
Data are for 1 week

<Fig.4.8.4> The results of previous and present study of life cycle of *Leistus ferrugineus*



4.9 Leistus rufescens Fabricius

PREVIOUS INFORMATION

Leistus rufescens is the most hygrophilous of the carabid species and lives in moist shady places amoung wet leaves, often under alders (Lindroth 1974).

This species has been studied at only a few geographical areas <Fig.4.9.4>.

- In southern England (Murdoch 1967), mature females have been found from June to September and emergence in May has occurred after larval overwintering.
- In the uplands of northern England, the results of Houston (1970) show mature females in July-October, larval overwintering and emergence in June-July.
- In Denmark, the results of Larsson (1939) indicate similarities to Houston's (1970) study, with an earlier occurrence of breeding and emergence: breeding in July-August and possibly September, and emergence in late June–early July.

RESULTS AND DISCUSSION

In the present study, captures were made in woodland from June to Sepember <Fig.4.9.1> with one mature female found in August <Fig.4.9.2> <Table 4.9.1> <Table 4.9.2>. The abdomen/elytra length ratios did not show high values. Therefore a breeding season perhaps occurred around August, in agreement with the previous studies. When the results of previous and present studies are considered together they show that, as environmental conditions become colder, there is a shift of the time of emergence from spring (May) to summer (late June–early July) <Fig.4.9.4>. The breeding seasons do not show such a marked difference (June–September). It is therefore suggested:

1. Emergence seems to be dependent upon temperature, i.e. lower temperatures inhibit the larval development of *L. rufescens.*
2. The breeding season has been observed to start one month after the beginning of emergence, irrespective of geographical area; temperature therefore has a lesser influence on maturation than on larval development.
3. *Leistus rufescens* may be a univoltine summer–autumn breeder, with larval overwintering and emergence during the beginning of the next summer.

ADDITIONAL INFORMATION

The elytra lengths did not differ between sexes <Table 4.9.3> ($t_{10} = 0.36$, $p = 0.724$).

<Table 4.9.1> Mean egg volume of *Leistus rufescens* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
8	411 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.9.2> Mean number of eggs carried by female *Leistus rufescens* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
8	14 1

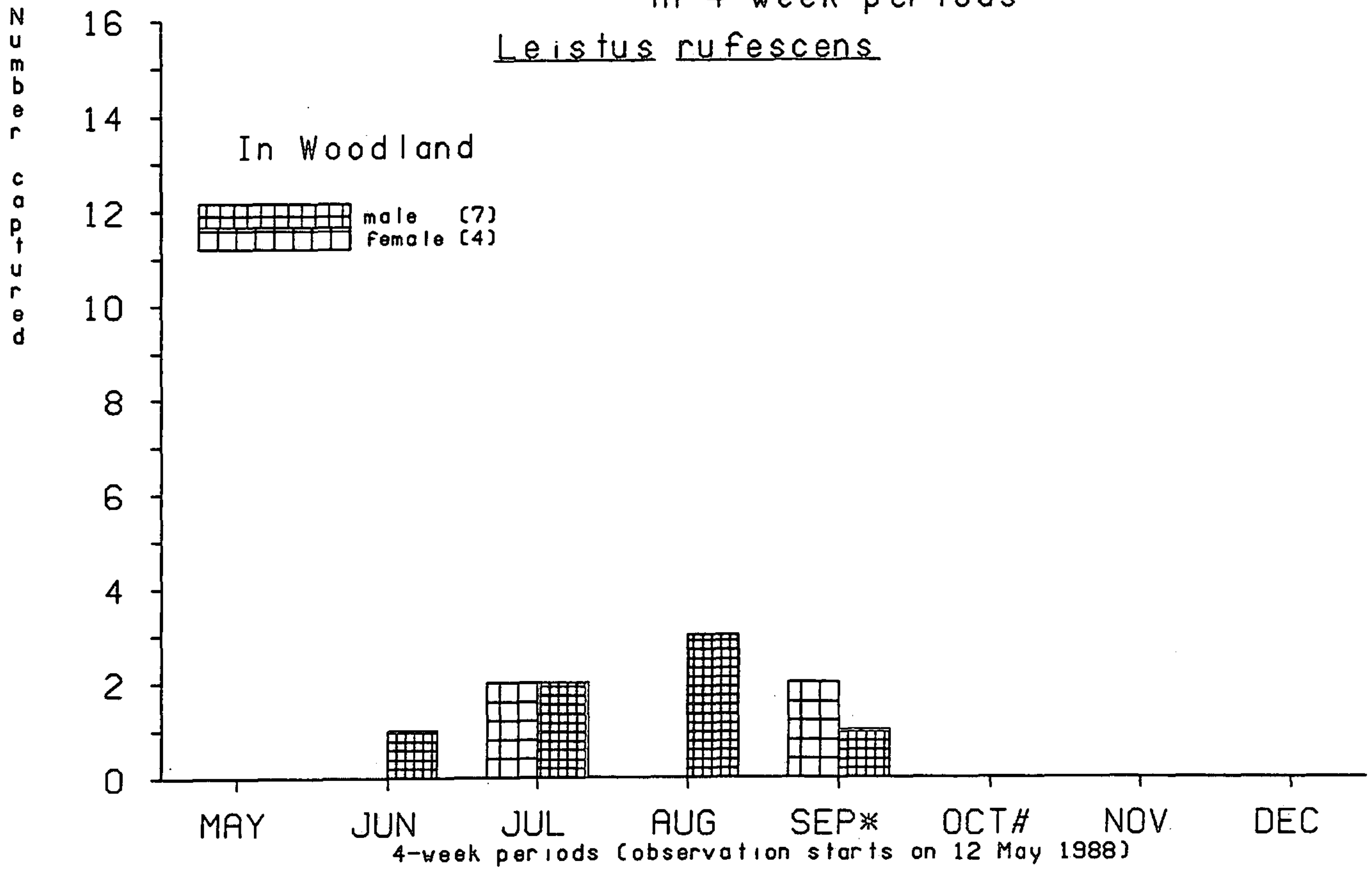
in each cell
mean number sample number

<Table 4.9.3> Elytra length of both sexes of *Leistus rufescens* in the woodland

	Woodland
Female	4.220 5 0.295 0.132
Male	4.171 7 0.170 0.064
(Habitat total)	4.192 12 0.219 0.063

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.9.1> Frequency of capture (including re-capture) in 4-week periods

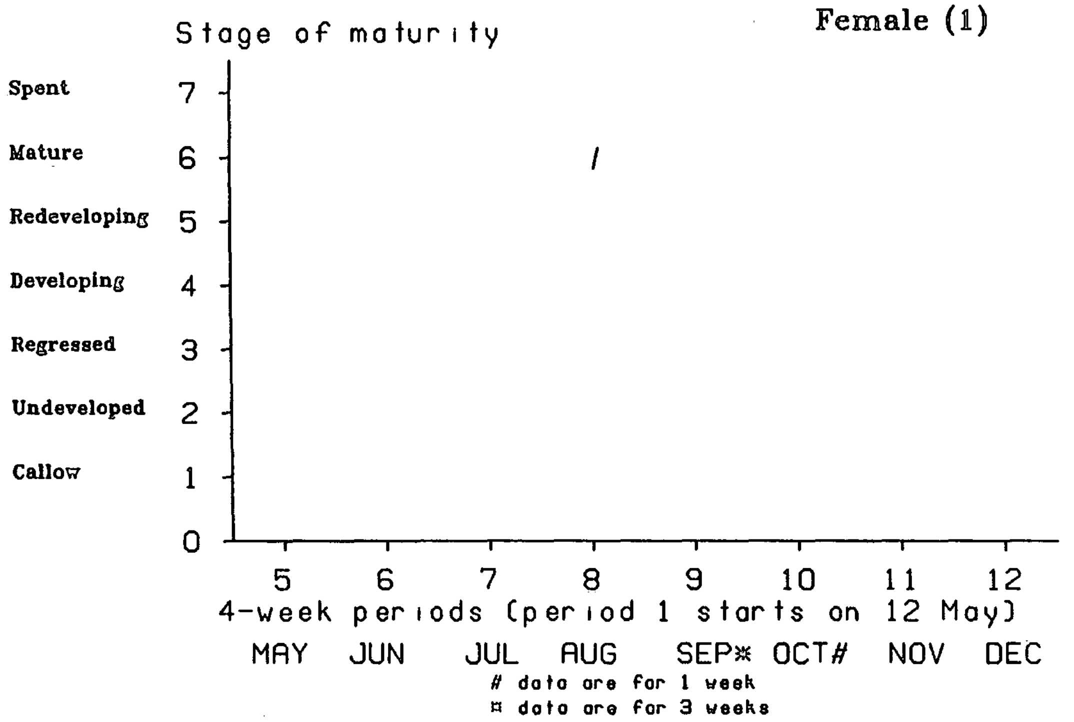


※ Data are for 3 weeks

Data are for 1 week

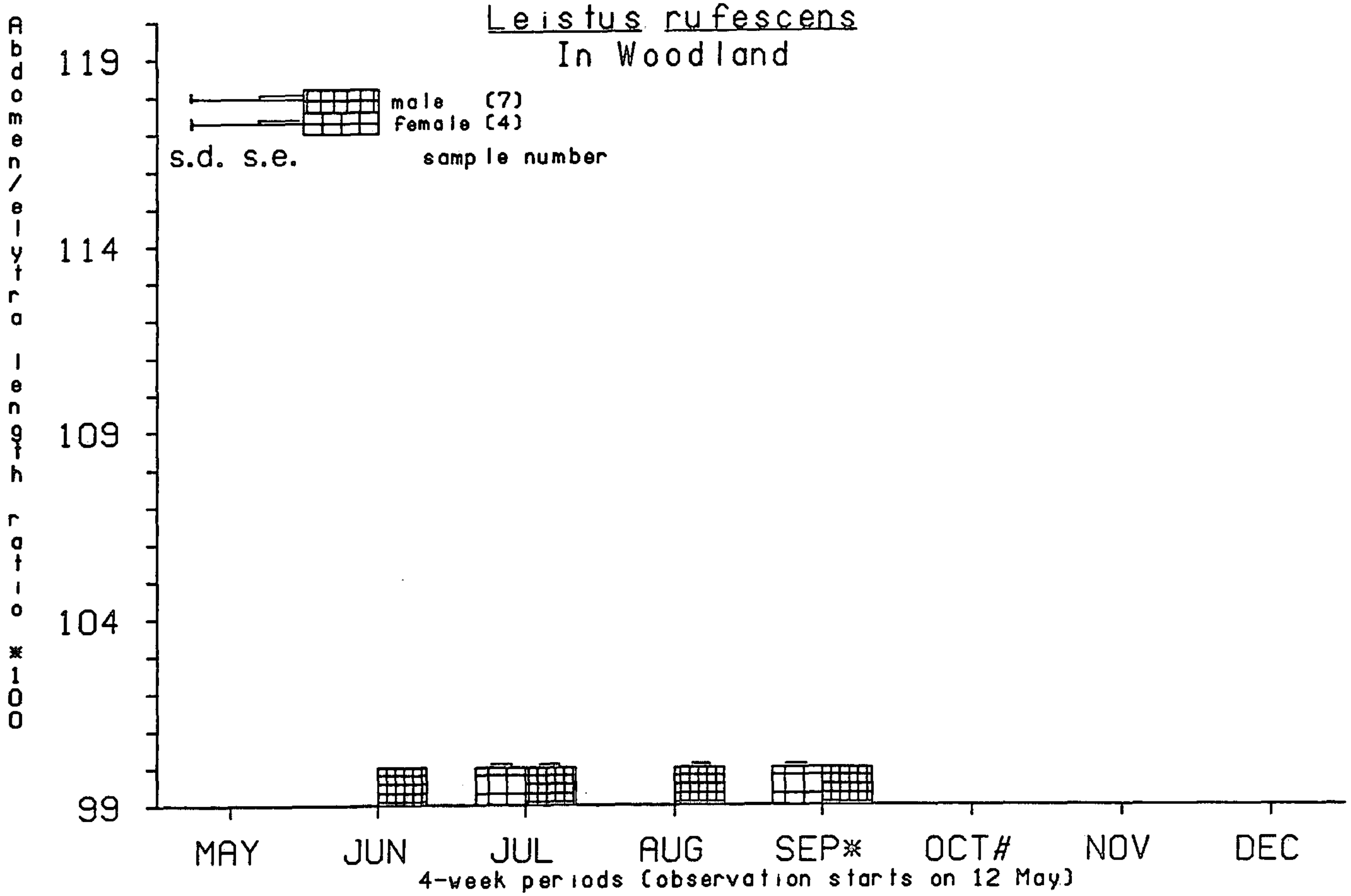
<Fig.4.9.2> Stages of maturity of <u>Leistus</u> <u>rufescens</u> caught in successive 4–week periods in woodland

Frequencies are plotted



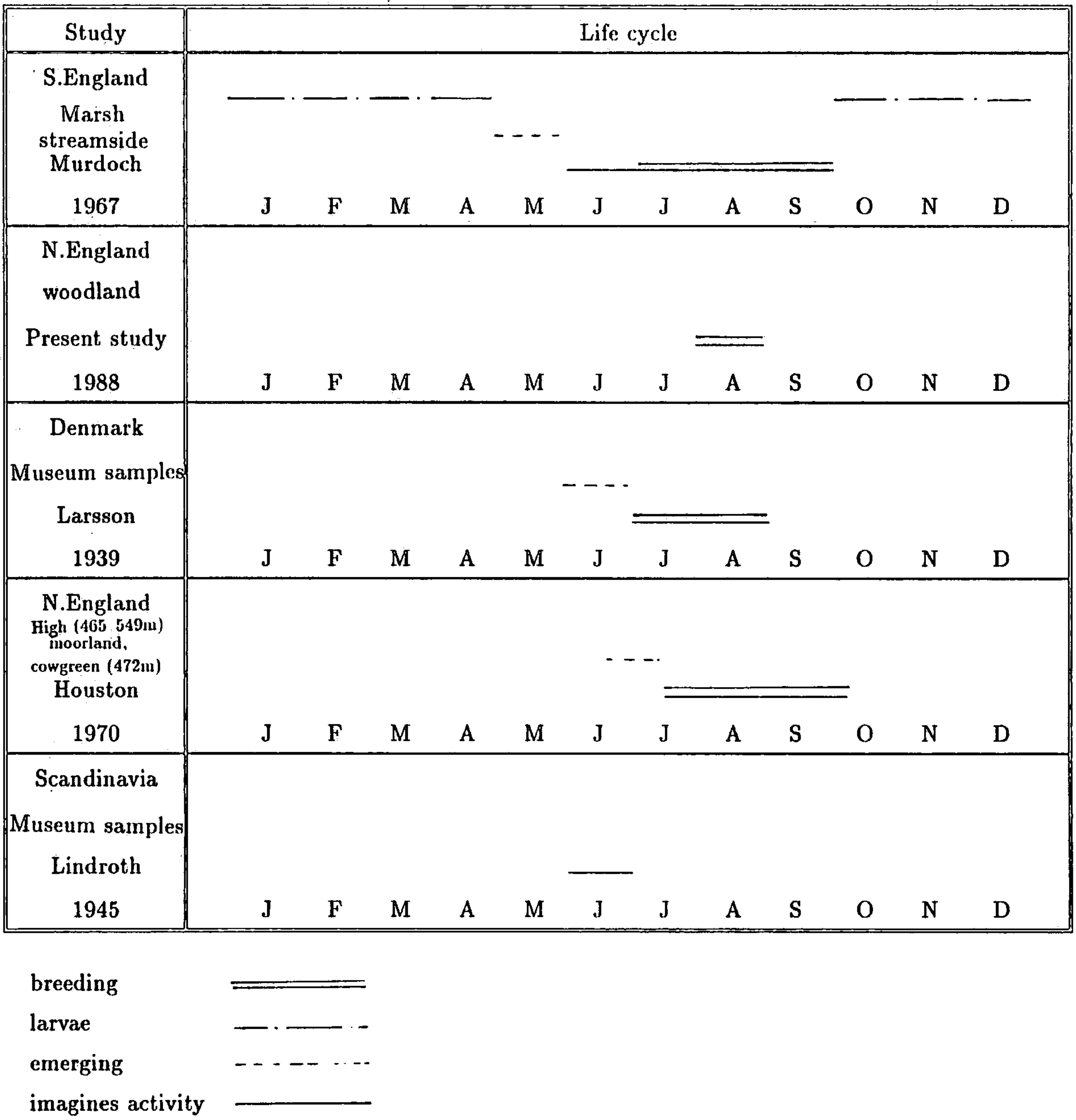
data are for 1 week
¤ data are for 3 weeks

<Fig.4.9.3> Abdomen/elytra length ratio in 4-week periods



* Data are for 3 weeks
# Data are for 1 week

<Fig.4.9.4> The results of previous and present study of life cycle of *Leistus rufescens*



4.10 Leistus rufomarginatus Duftschmid

PREVIOUS INFORMATION

Leistus rufomarginatus is found at the base of deciduous trees in dark forests (Lindroth 1974).

This species seems to have a life cycle which is similar to that of *Leistus rufescens*, but shows a longer appearance at the adult stage in Denmark (Larsson 1939) <Fig.4.10.4>. At marshland and streamside in southern England (Murdoch 1967), emergence has been observed in April–May and mature females in June–October. A maximum imago activity was observed in June–July in Belgium (Loreau 1985: in pine-wood), in August-September in Denmark (Larsson 1939) and in July in Scandinavia (Lindroth 1945). The results of Loreau (1985) for beech forests in Belgium show two peaks of activities of imagines in summer and winter; the summer peak involves emergence and the winter one involves oviposition.

RESULTS AND DISCUSSION

In the present study, the captures were made in the Durham woodland from May to November <Fig.4.10.1>. No callows were observed. These results are consistent with a result of Larsson (1939) which found a longer appearance period than for *Leistus rufescens*. A clear peak of captures was not observed, perhaps because of an insufficient number of captures. One mature female was found in October <Table 4.10.1, Table 4.10.2> and a large ratio of female abdomen/elytra length was observed in July <Fig.4.10.3>. These results may indicate two oviposition seasons, in summer and autumn during the same year at the Durham woodland site. Two suggestions are made:

1. The two oviposition seasons may have included two generations, of which one is a new imago generation bred in autumn. The other may have been a surviving generation bred in spring following oviposition in the previous autumn and adult overwintering; or
2. a part of the population may have been semivoltine and have bred as a first oviposition in the spring following the year of study.

Such life cycle shifts have been reported in other autumn breeder species of Carabidae by van Dijk (1972) for *Calathus melanocephalus* and Luff (1973) for *Pterostichus madidus* <Fig.4.10.4>. Since the present results are quite different from previous studies, more data are essential before further discussion.

ADDITIONAL INFORMATION

The elytra lengths of females tend to be larger than those of males, but not significantly so ($t_{12} = 1.77$, $p = 0.101$) <Table 4.10.3>.

<Table 4.10.1> Mean egg volume of *Leistus rufomarginatus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
10	411 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.10.2> Mean number of eggs carried by female *Leistus rufomarginatus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
8	6 1

in each cell
mean number sample number

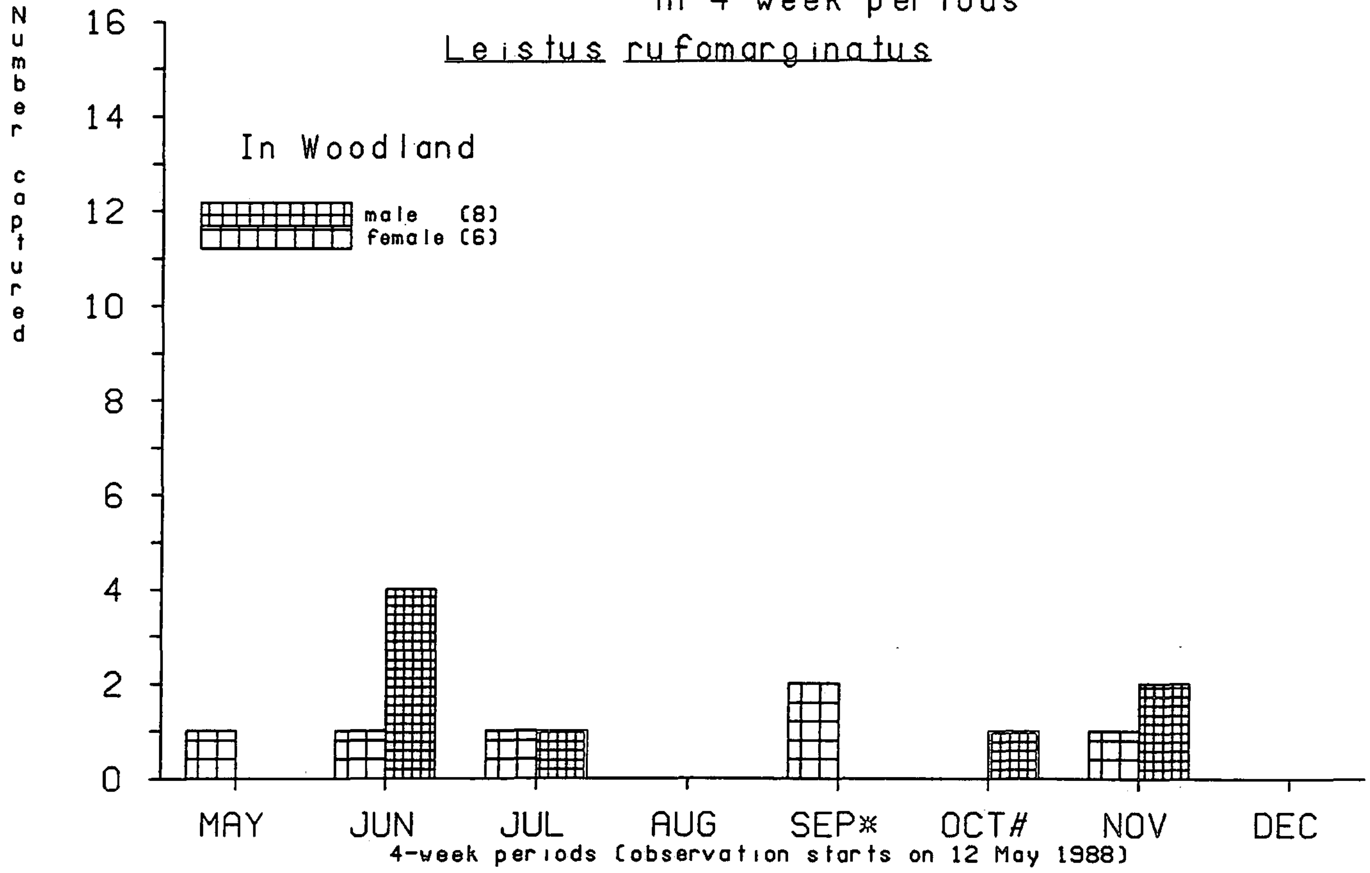
<Table 4.10.3> Elytra length of both sexes of *Leistus rufomarginatus* in the woodland

	Woodland
Female	4.767 6 0.266 0.119
Male	4.550 8 0.193 0.068
(Habitat total)	4.643 14 0.244 0.065

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.10.1> Frequency of capture (including re-capture) in 4-week periods

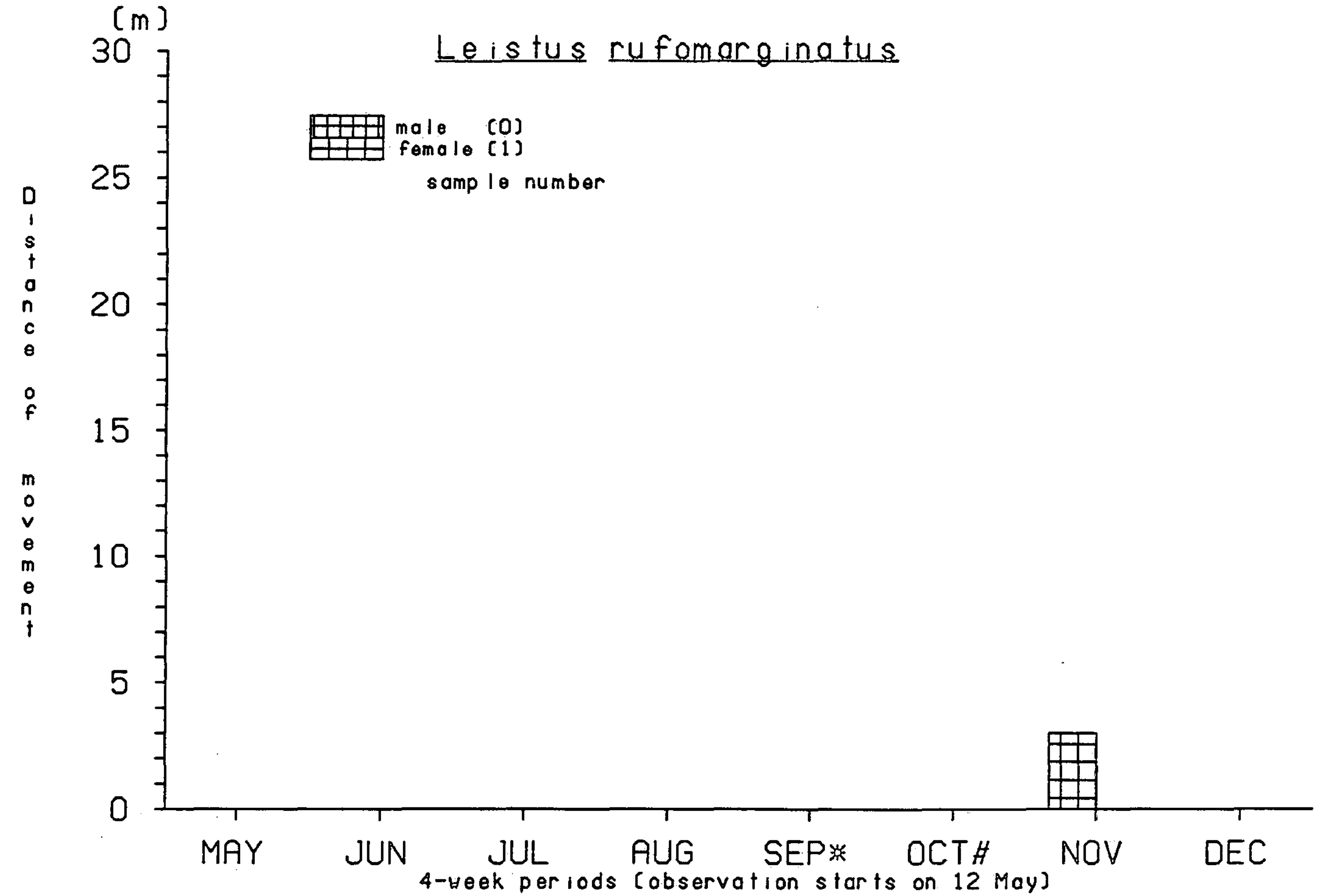
Leistus rufomarginatus



※ Data are for 3 weeks

Data are for 1 week

<Fig.4.10.2> Distance between capture and recapture points

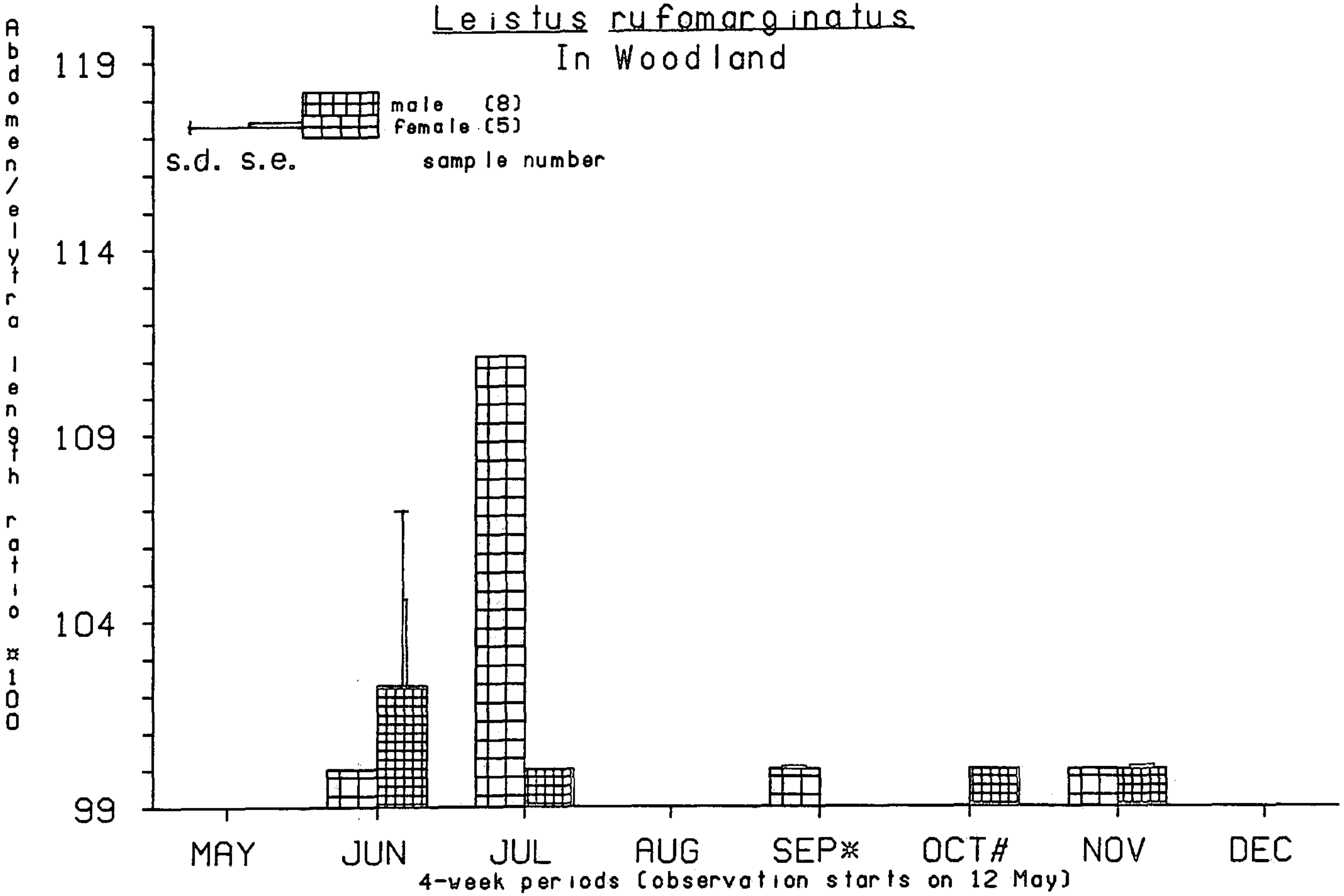


※ Data are for 3 weeks
Data are for 1 week

<Fig.4.10.3> Abdomen/elytra length ratio in 4-week periods

Leistus rufomarginatus

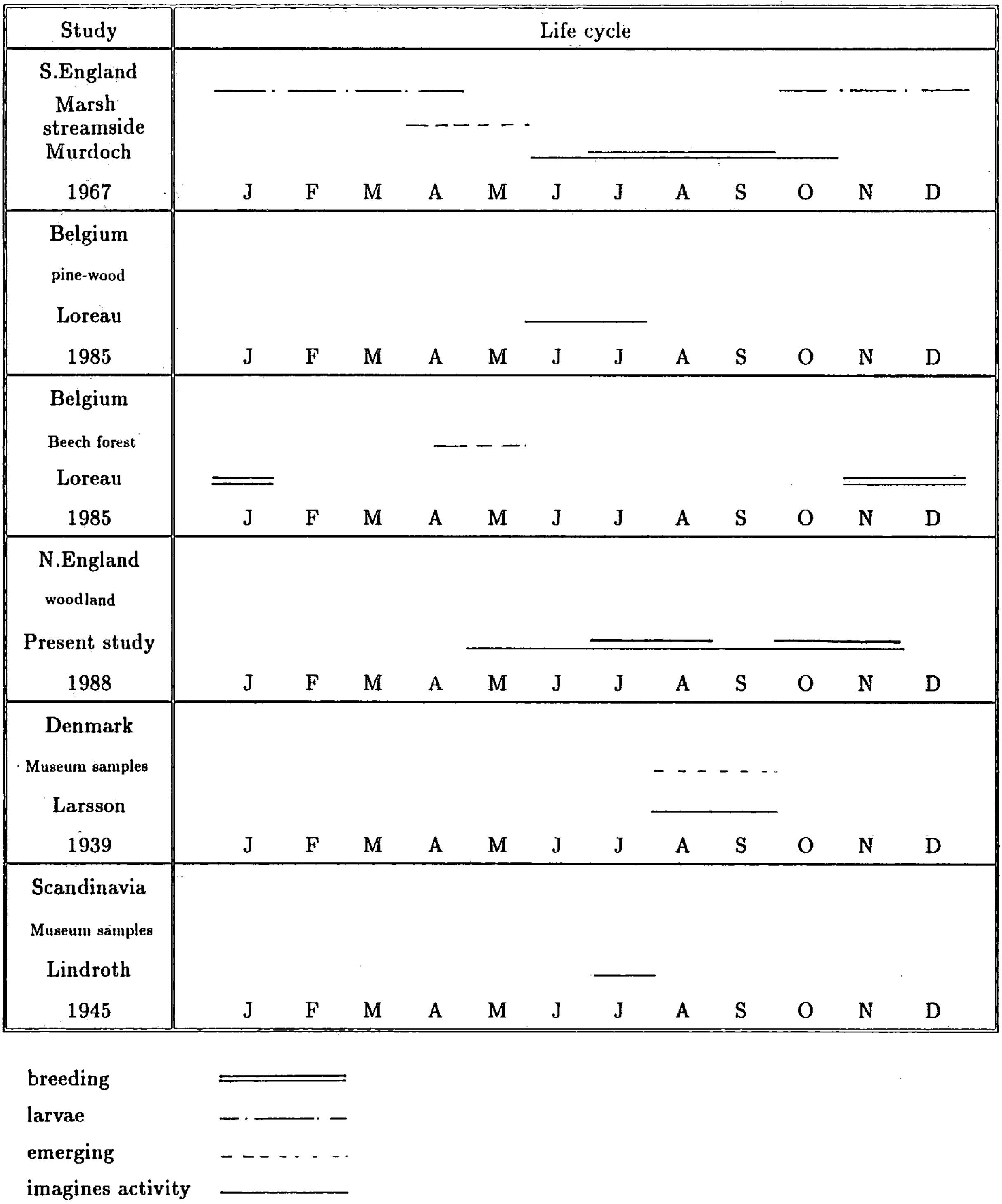
In Woodland



※ Data are for 3 weeks

Data are for 1 week

<Fig.4.10.4> The results of previous and present study of life cycle of *Leistus rufomarginatus*



4.11 Loricera pilicornis Fabricius

PREVIOUS INFORMATION

Loricera pilicornis is reported to occur in a wide range of habitats in beech woodland and arable land (Greenslade 1965).

This species is a spring breeder. In summer the larvae develop and imagines emerge in autumn to hibernate and breed in the next spring (Larsson 1939, Lindroth 1949, Greenslade 1965, Refseth 1988) <Fig.4.11.5>. This species has been studied in various geographical areas. In beechwood, grassland , bracken and arable land in southern England, adult activities have been observed from March to August, with a maximum in April-May and larvae have been recorded in May–July (Greenslade 1965); a maximum of adult activity has been recorded in April, with a decline in mid-summer and a slight increase in autumn (Tipton 1960: from reference by Greenslade 1965). In Denmark, two peaks have been observed in April-May and July-August (Larsson 1939). Detailed studies by Loreau (1985) have shown that in pine wood and beech forests in Belgium two breeding seasons occur. The main breeding season was found to be principally in April-May with a less important one in July-August. Refseth (1988) reported that in alder forests in central Norway, breeding occurred in May-June, with a callow emergence in August–September. Loreau (1985) suggested that there were two generations in the population in Belgian , the largest of which was made up of spring breeders and the other of autumn breeders. However, in central Germany, a single peak has been observed in May-July (Geiler 1960).

RESULTS AND DISCUSSION

Loricera pilicornis was found in both Durham habitats, in agreement with the results of Greenslade (1965).

Captures were made in the Durham woodland from May to October <Fig.4.11.1, Fig.4.11.3>. For females, a main peak was observed from June to August, and for males the main peaks were found in June and August. Captures were made in grassland until November.

Male callows were observed in both habitats in August <Fig.4.11.1>. Emergence therefore seems to have occurred in summer (July and August). Undeveloped females were observed in July, August and October in woodland, and in August in grassland <Fig.4.11.3>. Maturation may therefore have followed in the next year.

Mature females of *Loricera pilicornis* were observed in July in woodland and a spent female was observed at the beginning of August in grassland <Fig.4.11.3>. Egg sizes and numbers per female are listed in Table 4.11.1 and Table 4.11.2, respectively. A copulation was witnessed in woodland in early June. It is concluded from these results that an oviposition season occurred in June and July in both habitats. In grassland, a spent female was found to possess many small eggs at the previtellogenesis stage in addition to a mature egg in early August. Moreover, captures were made in October and November after a break during September. This seems to indicate that two reproductive seasons have occurred in the year. The main oviposition was in June–July and the less important one perhaps in October–November. The possibility of two oviposition seasons in one year is supported by the results of Tipton (1960) and Loreau (1985), although the timing of seasons is later than indicated by the Belgian results. If this conclusion that *Loricera pilicornis* at the Durham grassland site had two generations can be applied to *L. pilicornis* in the woodland also, then this helps to explain why an undeveloped female was observed in the woodland in July during the oviposition season <Fig.4.11.3>. This is because the life cycle of autumn breeders must have been delayed relative to that of the main summer breeders. The shift of the breeding season when compared with the result from Belgium (Loreau 1985: late April–May and June–July) may be due to the prevalence of colder environmental conditions in Durham. (Average temperature 8.5°C at Durham, 9.9°C at Uccle, in Belgium; vegetation growth period 7 months at Durham, 9 months at Uccle)

The results of a study in central Germany (Geiler 1960; reference from Greenslade 1965) in which only a single peak of activity occurred in May-July, might indicate that imagines mature one year after emergence so that the emergence and breeding seasons overlap in May–July: this may be due to a colder winter and a shorter favourable season for maturation.

When the Durham results are combined with those of the previous studies, it may be suggested that <Fig.4.11.5>:

1. *Loricera pilicornis* is a member of the group classified by Thiele (1977) as "spring breeders with no larval dormancy but obligatory dormancy in the adults (parapause) mainly governed by photoperiod"

2. a greater spread of activity and two breeding seasons are observed in lower latitude areas and oceanic climates;

3. restricted and single-peak activity and only one breeding season are found in higher latitude areas and continental climates.

In parallel to this oviposition season suggested by the results of the present studies, cases of females which secreted pheromone were observed in late June and July; this might be related to maturation or oviposition.

ADDITIONAL INFORMATION

The elytra lengths of woodland females were significantly larger than those of grassland females ($t_{20} = 2.53$, $p = 0.020$). A difference in the elytra lengths of the males was not found between the two habitats ($t_6 = 0.92$, $p = 0.395$). The elytra length between sexes also did not differ in both habitats (in woodland: $t_{30} = 0.22$, $p = 0.828$; in grassland: $t_8 = 1.61$, $p = 0.281$) <Table 4.11.1>.

<Table 4.11.1> Mean egg volume of *Loricera pilicornis* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	6 Mature
7	226 2

<b>

Stage of maturity Period no.	7 Spent
7	109 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.11.2> Mean number of eggs carried by female Loricera pilicornis in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	2 Undeveloped	3 Regressed	6 Mature	(Period total)
7	0 1		14 2	9 3
8		0 1		0 1
10	0 1			0 1
(Stage of maturity total)	0 2	0 1	14 2	5 5

<b>

Stage of maturity Period no.	3 Regressed	7 Spent	(Period total)
8	0 1	1 1	0.5 2

in each cell
mean number sample number

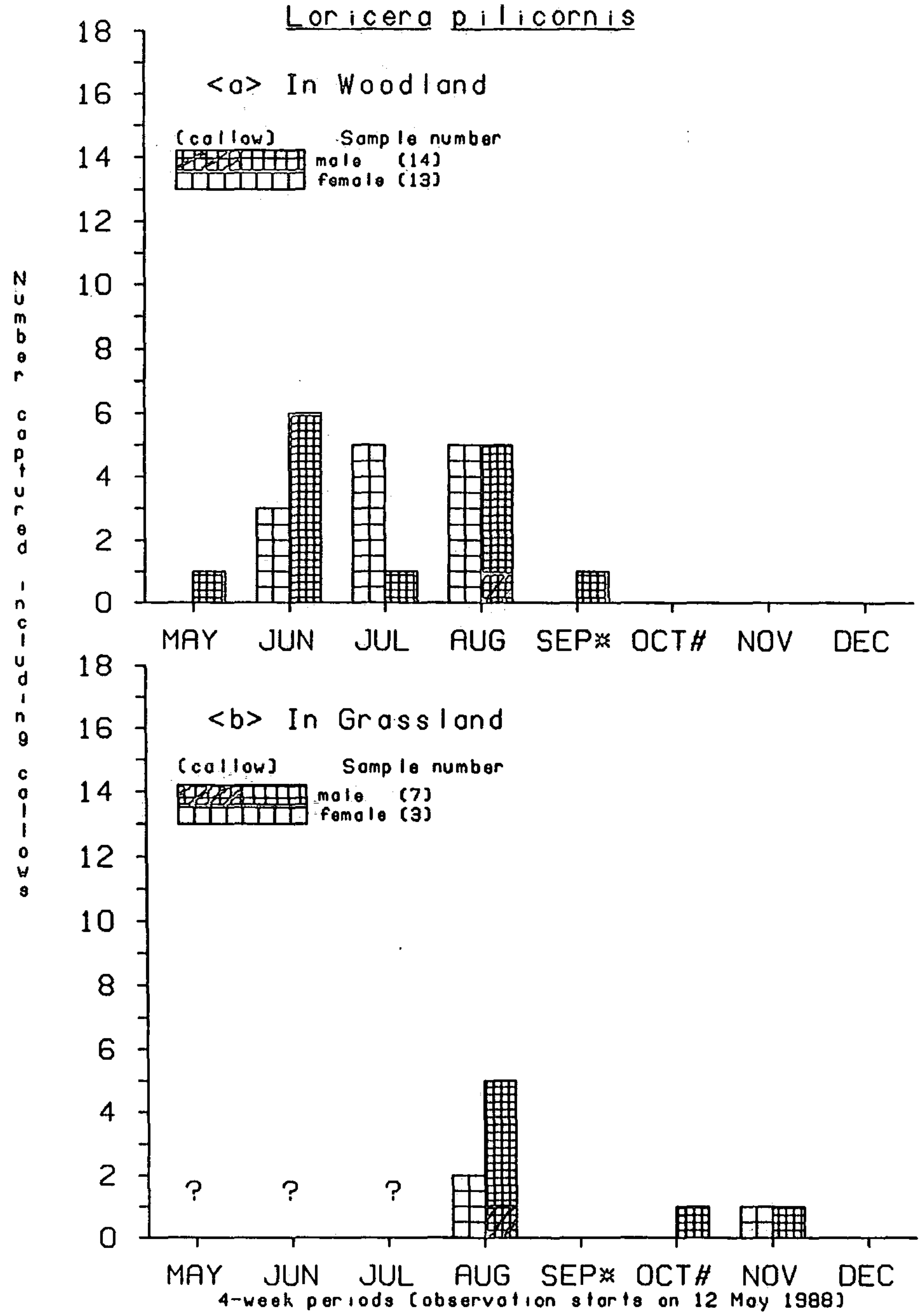
<Table 4.11.3> Elytra length of both sexes of *Loricera pilicornis* in the two habitats

	Woodland	Grassland	(Sex total)
Female	4.728 18 0.202 0.048	4.450 4 0.173 0.087	4.677 22 0.222 0.047
Male	4.714 14 0.123 0.033	4.617 6 0.248 0.101	4.685 20 0.169 0.038
(Habitat total)	4.722 32 0.170 0.030	4.550 10 0.227 0.072	4.681 42 0.197 0.030

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.11.1> Frequency of capture (including re-capture) in 4-week periods

Loricera pilicornis

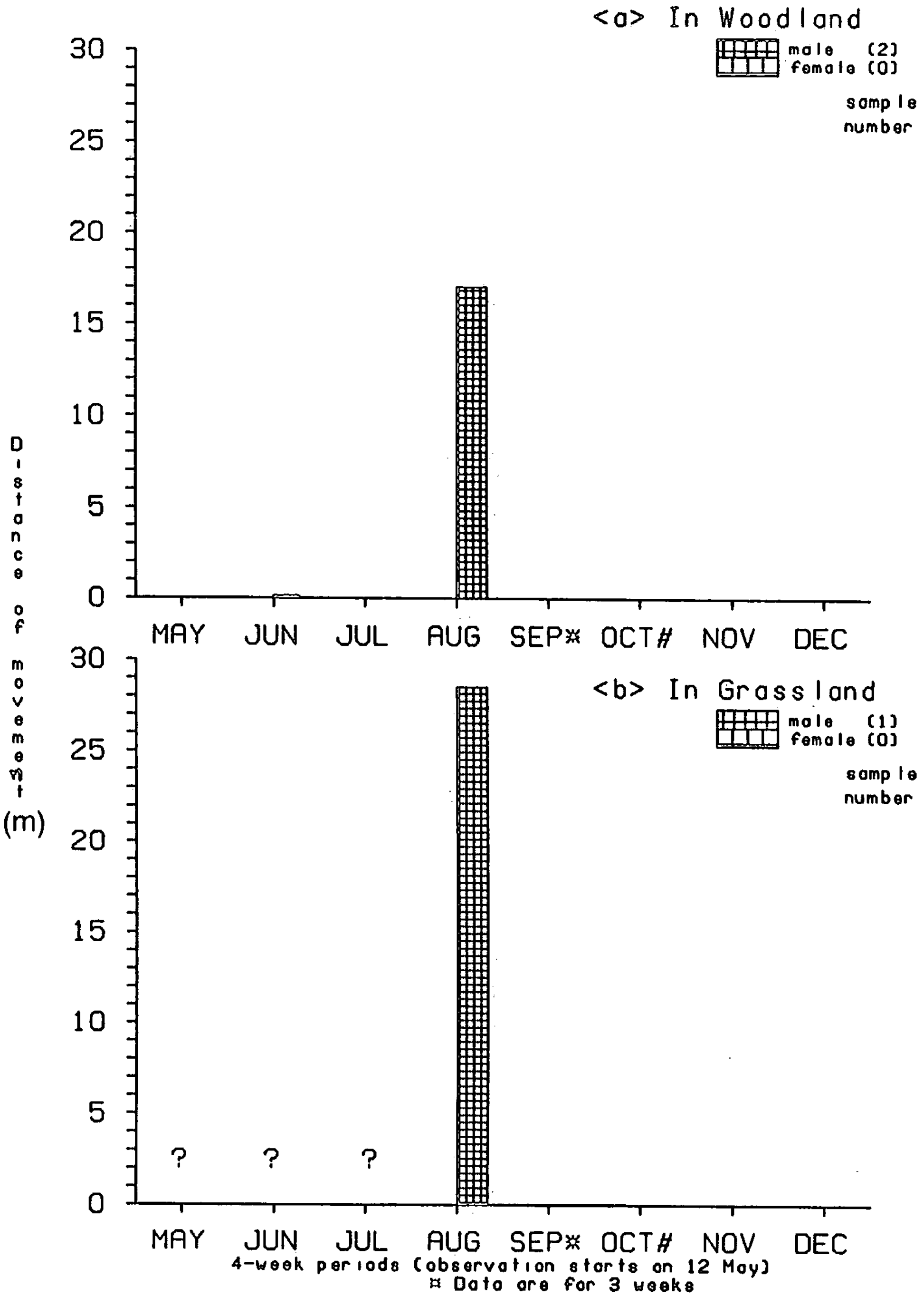


¤ Data are for 3 weeks

Data are for 1 week

? indicates no observation

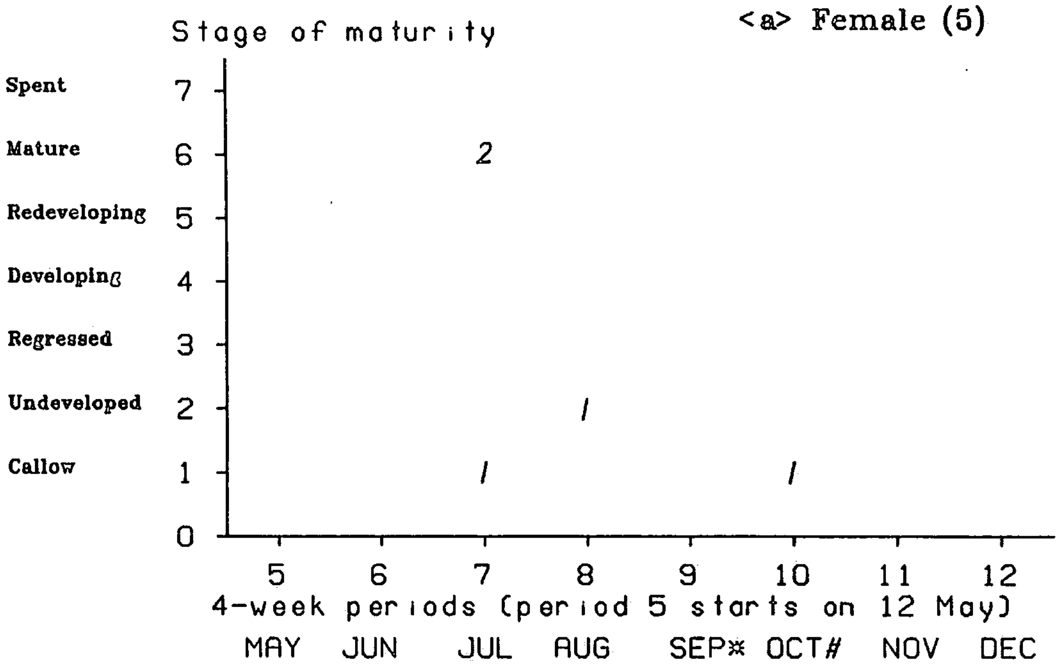
<Fig.4.11.2> Distance between capture and recapture points
Loricerara pilicornis



¤ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig.4.11.3> Stages of maturity of Loricera pilicornis caught in successive 4-week periods in woodland

Frequencies are plotted

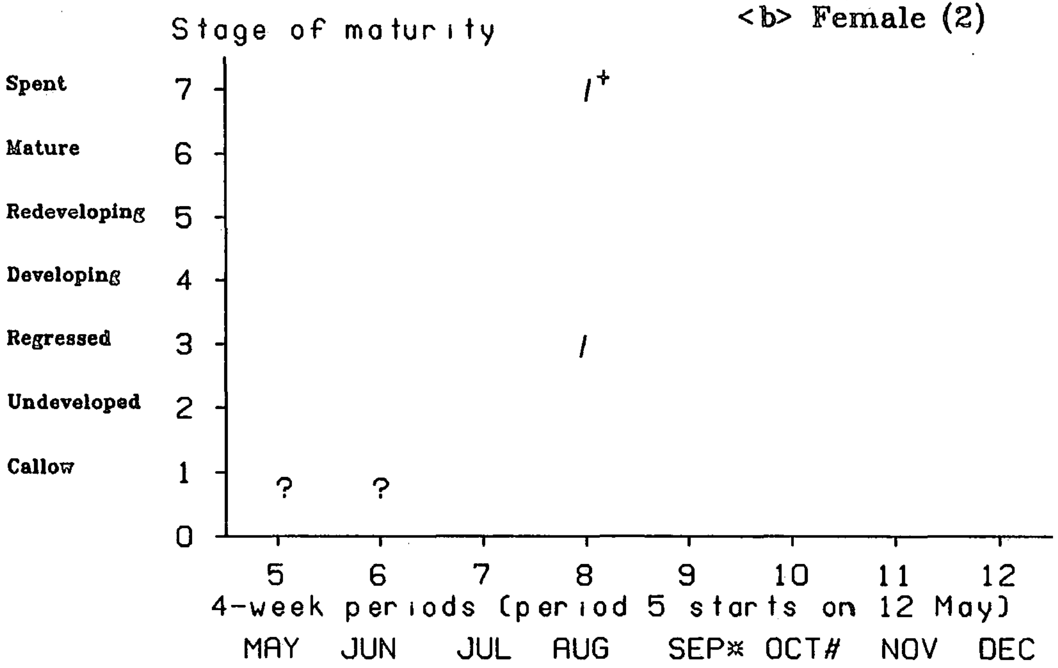


data are for 1 week
※ data are for 3 weeks

<Fig.4.11.3> Stages of maturity of <u>Loricera pilicornis</u> caught in successive 4-week periods in grassland

Frequencies are plotted

? indicates no observation
+ indicates developing small immature eggs at the same time in addition to mature eggs

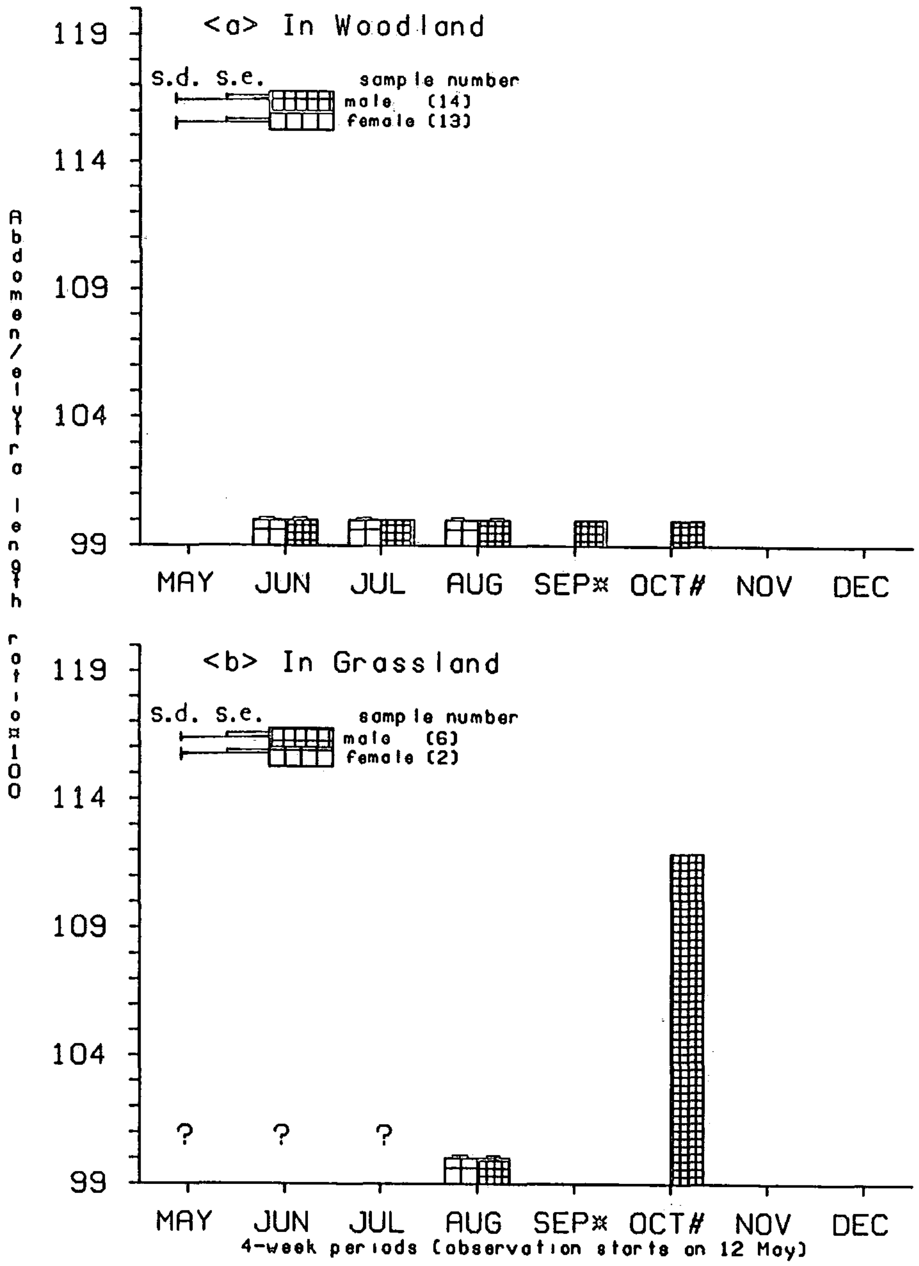


<b> Female (2)

data are for 1 week
※ data are for 3 weeks

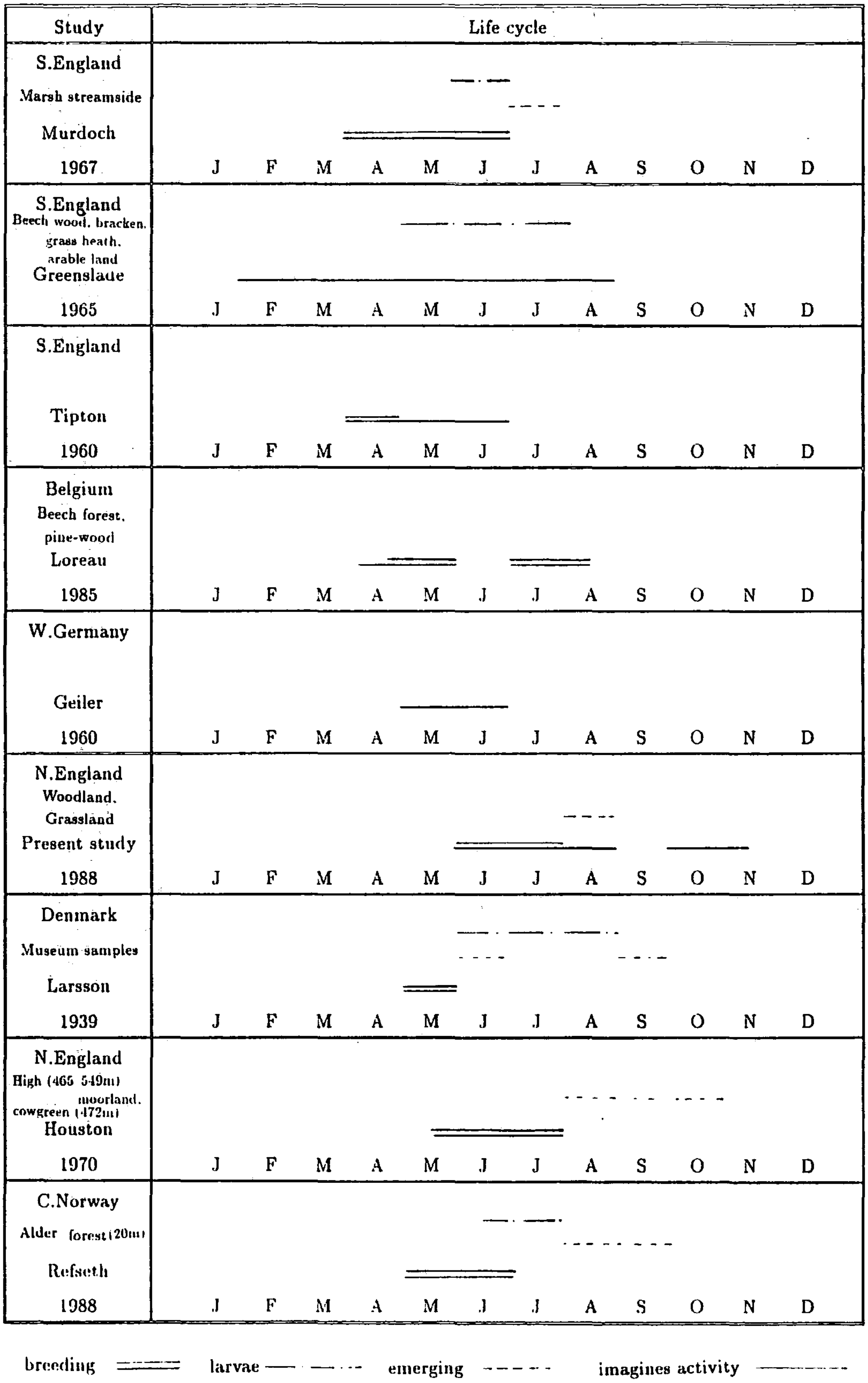
<Fig.4.11.4> Abdomen/elytra length ratio in 4-week periods

Loricera pilicornis



¤ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig. 4.11.5> The results of previous and present study of life cycle of *Loricera pilicornis*



4.12 Notiophilus biguttatus Fabricius

PREVIOUS INFORMATION

Notiophilus biguttatus is found in woodland litter (Greenslade 1965), in shady but dry places (Lindroth 1974).

This species has been classified as a spring breeder with facultative autumn activity by Larsson (1939) in Denmark <Fig.4.12.4>. This classification has been supported by Lindroth (1945) in Scandinavia, by Greenslade (1965) in beech wood, bracken, grass heath and arable land in southern England, and by Houston (1970) in high moorland in northern England.

- In southern England, imagines have been found to be active in April–early August and January–February, with a peak in May–June with larvae observation May–September.
- In Denmark, larvae and adults have been observed in summer, with emergence in late September–early October.
- In Scandinavia, imago activity has been reported mainly in May–September (with a peak in June) with larvae in July–September and imago overwintering.
- In highland in northern England, mature females have been recorded intermittently: late April-early May, early June, early August, and September–October; two emergence seasons have been observed in July and in September–October.

However, Loreau (1985) reported a study of the species in beech forest and pine wood in Belgium in which *N. biguttatus* matured soon after autumn emergence in September and had a late autumn breeding season in October and November. This continued to the next spring. The results of van der Drift (1951) from beech forest in the Netherlands support the suggestion by Loreau that *N. biguttatus* bore ripe eggs throughout the year. It must be concluded that a part of the Belgian population of *N. biguttatus* had two generations during the same year (Loreau 1985).

RESULTS AND DISCUSSION

N. biguttatus was observed in the present study only in the Durham woodland. From field observations, there appear to have been two peaks of capture abundance from May to July and from October to December, although the data were relatively few.

One mature female was found to possess two eggs in July <Fig.4.12.2, Table 4.12.1, Table 4.12.2>. This fact, together with the large mean ratio of abdomen/elytra length for females in July <Fig.4.12.3>, indicates that an oviposition season occurred during that month.

The present study shows agreement with the previous works, in which *N. biguttatus* was found to breed in May and June (Larsson 1939, Lindroth 1945, Greenslade 1965, Houston 1970). However, although they report that the adult emerges in autumn before hibernation and breeds in the following spring, the occurrence of an undeveloped female in July in the Durham woodland is inconsistent with this <Fig.4.12.2a>. A possible conclusion for the Durham site is that a spring emergence has occurred; this is supported by the results of van Drift (1951), who found that *N. biguttatus* bore ripe eggs throughout the year; and by the results of Houston (1970) who reported that *N. biguttatus* emerged in two seasons in July and September.

The elytra length of the female was significantly larger than that of the male

<Table 4.12.3> ($t_{27} = 2.98$, $p = 0.006$).

Notiophilus biguttatus does not fit clearly into any one of the four types of spring or autumn breeders defined by Thiele (1977). (See Table 1.1). Examples of previous studies of *Notiophilus biguttatus* which illustrate this are:

- for the two types of spring breeders which are:
    1. controlled by firstly short-day photoperiod and then by long-day photoperiod. Loreau (1985) found autumn breeding shortly after emergence;
    2. controlled by short-day photoperiodical quiescence. Van Drift (1952) found mature females throughout the year.
- for autumn breeding types with winter larvae: all previous studies show summer larvae

It is therefore suggested that *Notiophilus biguttatus* may be in the group classified by Thiele (1977) as having "unstable conditions of hibernation and potentially lacking dormancy". This classification offers a possible explanation for the result of Houston (1970), in which two emergence seasons and several intermittent breeding seasons were observed in one year. Loreau (1985) suggested that after autumn emergence they can start to reproduce before winter and continue breeding, with a winter quiescence induced by low temperatures.

The life cycle of this species may therefore be more heavily dependent on biotopic conditions than on photoperiodic and temperature conditions, depending on the geographical location.

<Table 4.12.1> Mean egg volume of *Notiophilus biguttatus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	6 Mature
7	84 1

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.12.2> Mean number of eggs carried by female *Notiophilus biguttatus* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	2 Undeveloped	6 Mature	(Period total)
8	0 1	2 1	1 2

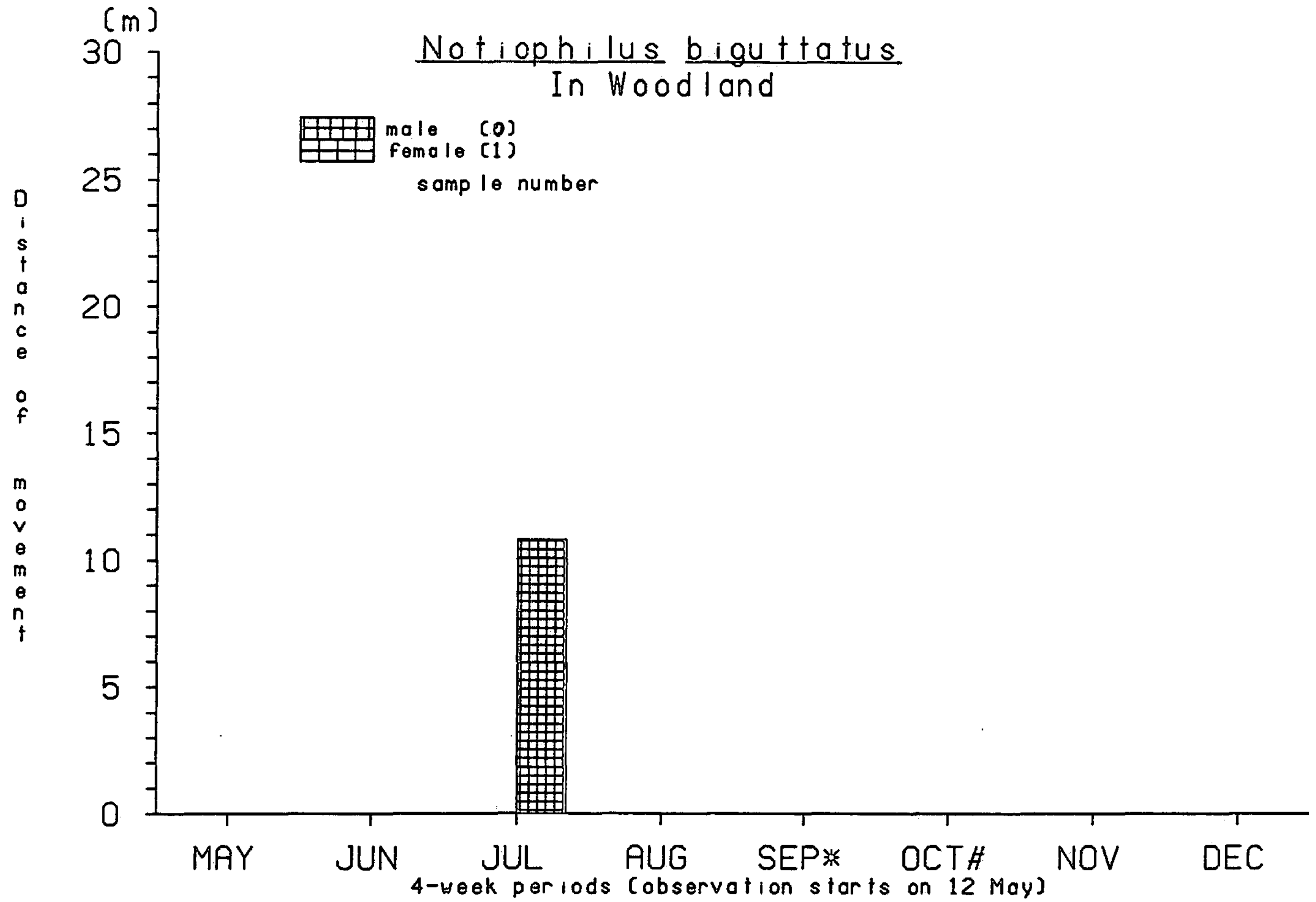
in each cell
mean number sample number

<Table 4.12.3> Elytra length of both sexes of *Notiophilus biguttatus* in the woodland

	Woodland
Female	3.615 26 0.882 0.173
Male	3.086 7 0.107 0.040
(Habitat total)	3.503 33 0.811 0.141

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.12.1> Distance between capture and recapture points



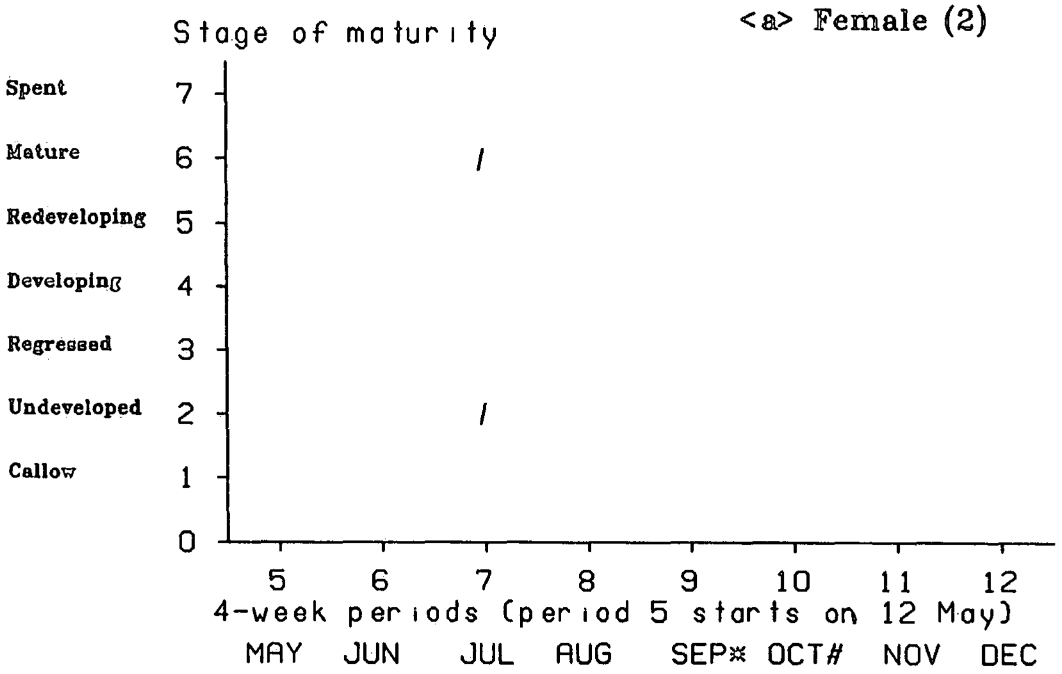
※ Data are for 3 weeks

Data are for 1 week

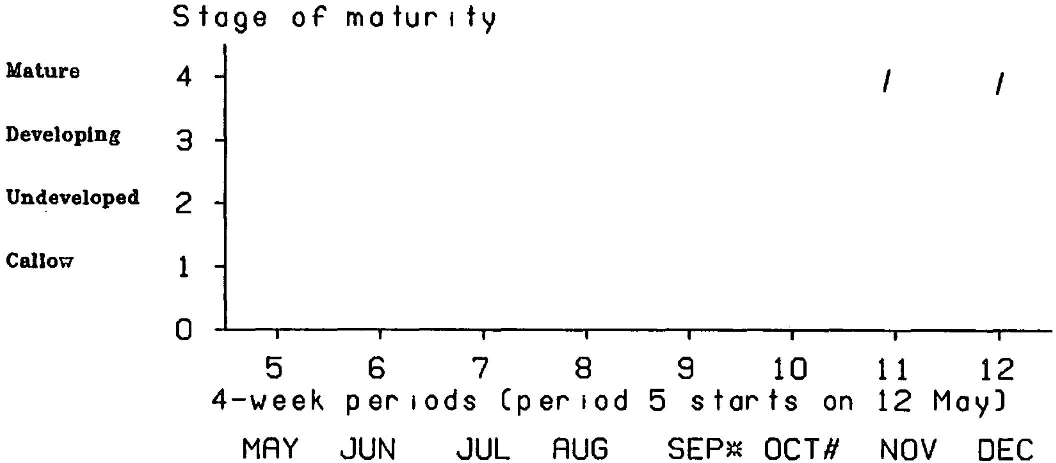
<Fig.4.12.2> Stages of maturity of *Notiophilus biguttatus* caught in successive 4-week periods in woodland

Frequencies are plotted

<a> Female (2)

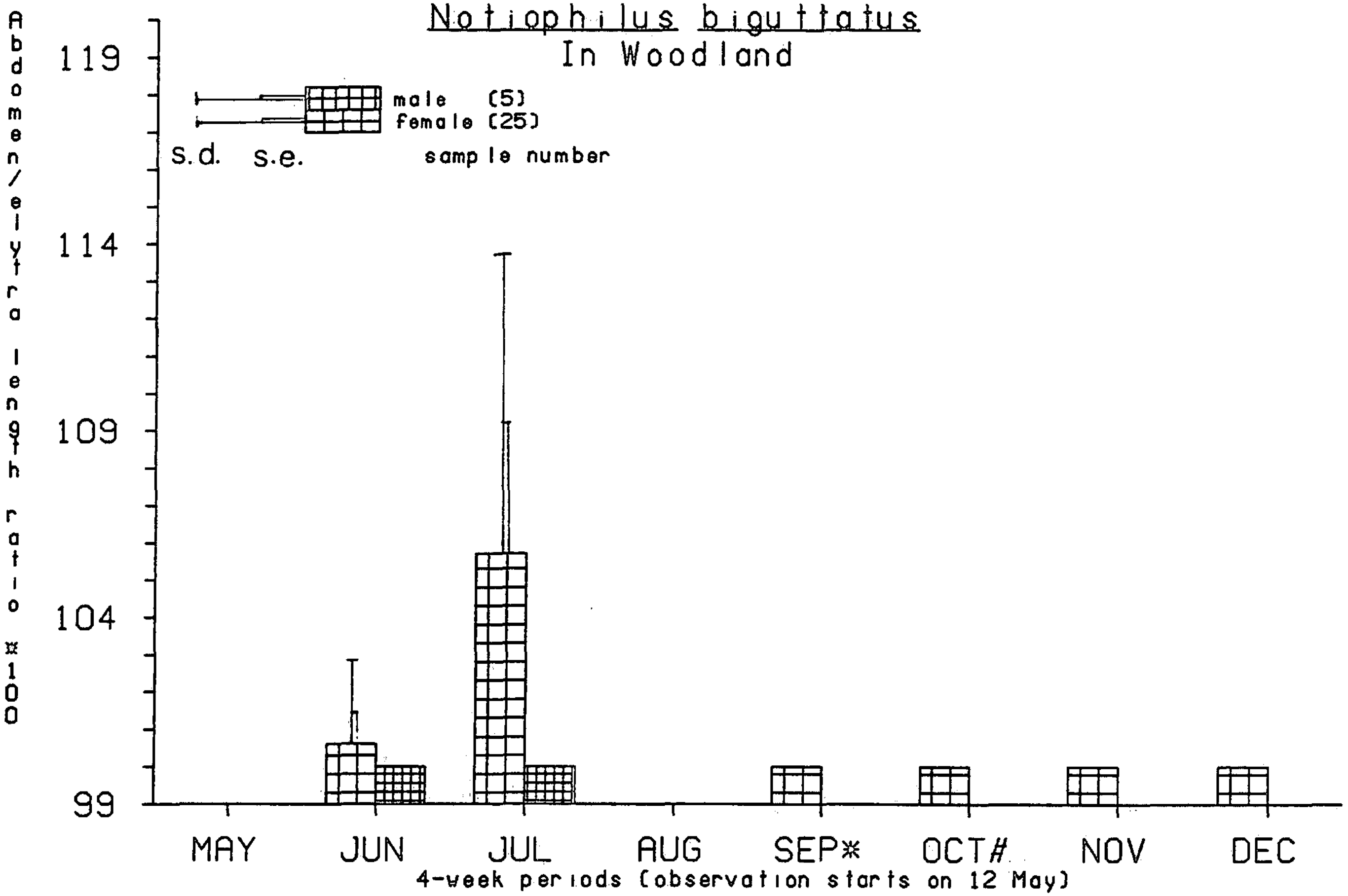


<b> Male (2)



data are for 1 week
¤ data are for 3 weeks

<Fig.4.12.3> Abdomen/elytra length ratio in 4-week periods



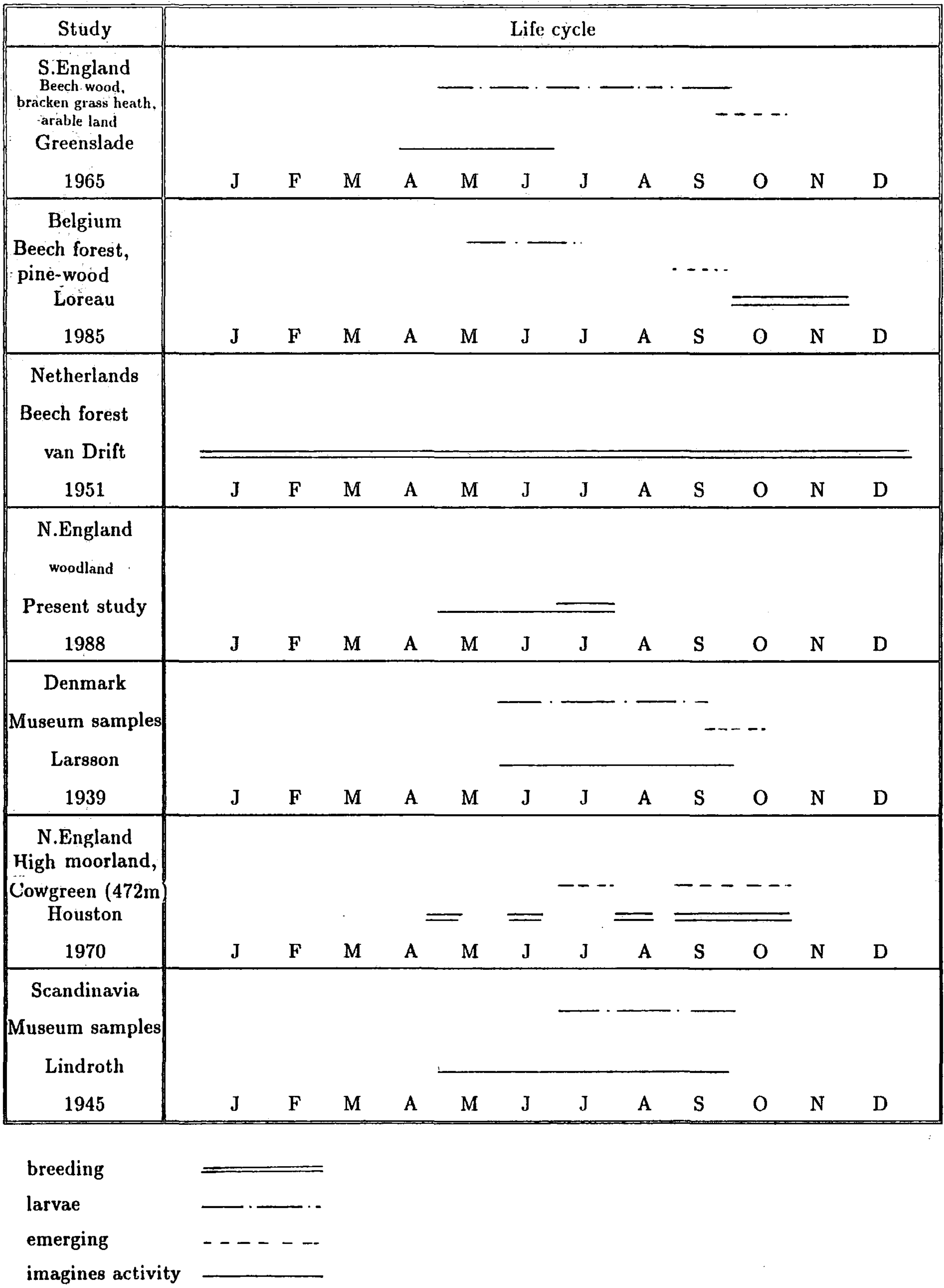
Notiophilus biguttatus

In Woodland

※ Data are for 3 weeks

Data are for 1 week

<Fig.4.12.4> The results of previous and present study of life cycle of *Notiophilus biguttatus*



4.13 Patrobus atrorufus Ström

PREVIOUS INFORMATION

Patrobus atrorufus lives in damp deciduous forests (Lindroth 1974).

Patrobus atrorufus has been classified as a member of "autumn breeders with a thermic hibernation parapause in the larva and a photoperiodic aestivation parapause in the adult" (Thiele 1977). This species breeds from late summer to autumn and hibernates after exposure to cold at the 3rd larval stage. The adult emerges in the following spring after a high temperature 'signal'. Ovarian development starts with the changeover to short-day photoperiods (the critical photoperiod is 16-17h light/day); this means that, as experienced in the field by *P. atrorufus*, short-day conditions already prevail from the beginning of July onwards at Köln in West Germany. Females of *P. atrorufus* matured and started to reproduce about one month after the summer solstice, in agreement with the experimental results. Maturation of the male appears to be independent of photoperiod (Thiele 1969, 1971).

Fig.4.13.5 shows the results of previous field studies of the life cycle of this species. At marsh and streamside habitats in southern England, emergence has been observed in May and June, and mature adults were observed from July to October (Murdoch 1967). This is the same life cycle as that found in Denmark (Larsson 1939) and in moist forest in West Germany (Thiele 1969). On high moorland in northern England, a biennial life cycle was observed (Houston 1970). Mature females appeared mainly from July to August. After larval overwintering, callows appeared from mid-June to September. Biennial life cycles have also been found in central Norway (Refseth 1980, 1986), with emergence during the summer (August–September) after larval overwintering. This is followed by hibernation at an immature imago stage and maturation during the next spring from late May. Breeding then occurs in the summer. At progressively higher latitudes, breeding seasons have been observed to shift earlier from August to June.

RESULTS

Patrobus atrorufus was observed mainly from June to September in the Durham woodland, with three male callows captured from late June to early July <Fig.4.13.1>. An undeveloped male was observed in June <Fig.4.13.3c>. The emergence season is therefore considered to have occurred during June to July.

Mature females in woodland were observed in July–September <Fig.4.13.3a>. Large mean ratios of abdomen/elytra length for females were measured in July and August <Fig.4.13.4a>. During July to September, two females and three males were recaptured: the distances moved by the females were significantly larger than those of the males <Fig.4.13.2, Table 4.13.1> ($t_3 = 8.374, p = 0.004$). The oviposition season in woodland may therefore have occurred during July, August and September.

In grassland, mature females were observed in September–October <Fig.4.13.3b> and one female with a large ratio of abdomen/elytra length was observed in September <Fig.4.13.4b>. It is suggested that the oviposition season in grassland occurred later or continued until later than in woodland.

Although the sample sizes were small, the egg volumes of woodland females were perhaps larger than those of grassland females for the same stage of maturity <Table 4.13.2> ($t_3 = 3.01, p = 0.057$).

The elytra lengths of woodland females also seemed to be larger than those found in grassland, although not significantly so <Table 4.13.4> ($t_2 = 2.28$, $p = 0.144$). The possibility that the woodland females have a larger body size and produce larger eggs suggests that the woodland may offer more favourable conditions for development than the grassland site. This is consistent with the earlier reports that *P. atrorufus* prefers damp deciduous forests (Lindroth 1974).

The elytra lengths of the woodland female tended to be larger than those of the woodland male but not significantly so ($t_{20} = 1.75$, $p = 0.095$) <Table 4.13.4>.

The egg numbers per female in both habitats are listed in Table 4.13.3.

DISCUSSION

The present study shows that no captures of females were made in woodland during a period of three weeks from late June to early July. This is thought to be due to aestivation, a conclusion that is supported by the experimental work of Thiele (1967, 1969) in which aestivation was observed for approximately one month.

Combining the present results for the emergence season with those of the previous studies, it is concluded that emergence occurs later in more severe environmental conditions <Fig.4.13.5>.

e.g.

- May–June: southern England and Denmark;
- June–July: Durham;
- July–August: central Norway;
- June–September: upland of northern England

The reason for this shift of emergence to later periods may be thermal quiescence in the larvae induced by low temperatures, while the reason for this length of the emergence season may be that the ambient temperature is often not high enough for metamorphosis; the surrounding microhabitats therefore have a great influence on the emergence of each individual.

The oviposition season seems to have occurred from July to September in both Durham habitats and may possibly have continued until a little later. The conclusion drawn from the present and previous studies is that the length of the breeding season is restricted by increasingly severe conditions:

e.g.

- July–October: southern England and Denmark;
- July–September: Durham;
- July–August: upland in northern England.

Also a shift of breeding season from autumn to spring has been observed without aestivation in extremely severe conditions in central Norway (Refseth 1986):

- August–September: 10m a.s.l.;
- July: 830m a.s.l.;
- June: 980–1120m a.s.l..

Therefore, the inhibition of maturation of the female in long-day conditions, as found in the experiment by Thiele (1969), is not applicable to the observation of *P. atrorufus* by Refseth (1986). The restriction of the duration of breeding may be related to the length of the warm season. Refseth (1986) also suggested that the shift of the breeding season in central Norway may be connected with the displacement of the final date of the vegetation growth period (See Fig.4.18.1). Generally, *P. atrorufus* is a univoltine autumn breeder, a biennial autumn breeder and a biennial spring breeder, respectively, from warm to cold environments. From these geographical comparisons, imagines are seen to mature faster after emergence in higher latitudes than in lower latitudes. The oviposition season is earlier or shorter in woodland than in grassland. The results of the present and previous studies of the oviposition season seem to indicate that, as for *Nebria brevicollis* (which experiences a similar life cycle), *Patrobus atrorufus* also matures faster in lower temperatures (Thiele 1969, 1971 for *N. brevicollis*).

Some of the Durham woodland females may have emerged after the aestivation period because one male callow was caught in early July. If so, those females which did not undergo aestivation soon after emergence cannot have bred during the year. A fraction of the individuals may therefore have followed a biennial life cycle.

ADDITIONAL INFORMATION

After aestivation, one woodland female was observed to secrete pheromone in early July. Because of the timing, this may be related to maturation.

When caught with the fingers in early August, two woodland females of this species were observed to secrete pheromone, an action which is possibly related to a defence mechanism.

<Table 4.13.1> Mean egg volume of *Patrobus atrorufus* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	6 Mature
7	203 1
9	229 2
(Stage of maturity total)	220 3

<b>

Stage of maturity Period no.	6 Mature
9	115 1
10	159 1
(Stage of maturity total)	137 2

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.13.2> Mean number of eggs carried by female *Patrobus atrorufus* in relation to stage of maturity in 4-week periods
<a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	6 Mature
7	8 1
9	7 2
(Stage of maturity total)	7 3

<b>

Stage of maturity Period no.	6 Mature
9	15 1
10	11 1
(Stage of maturity total)	13 2

in each cell
mean number sample number

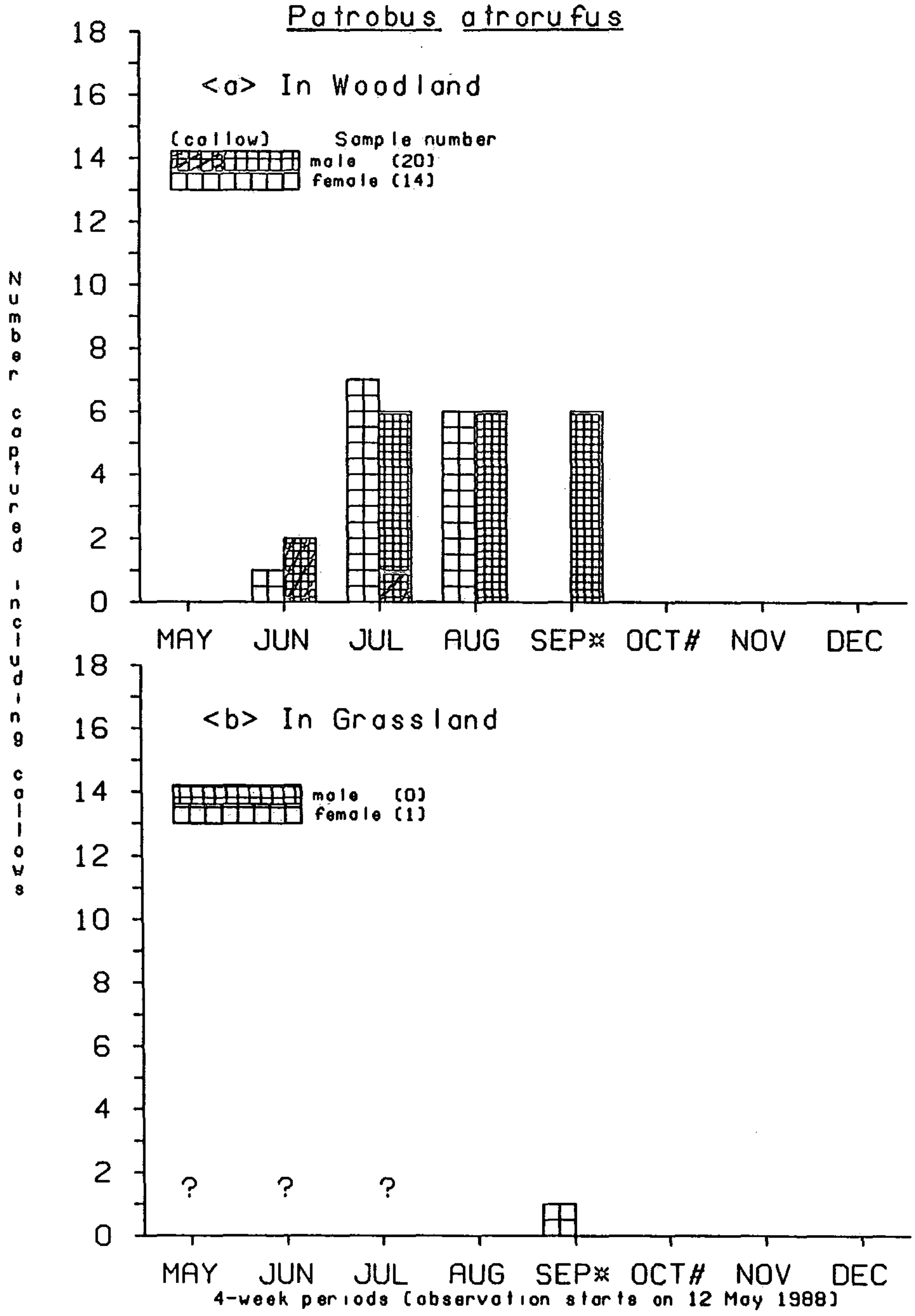
<Table 4.13.3> Elytra length of both sexes of *Patrobus atrorufus* in the two habitats

	Woodland	Grassland	(Sex total)
Female	4.982	4.367	4.890
	17	3	20
	0.170	0.462	0.313
	0.041	0.267	0.070
Male	4.684		4.684
	19	0	19
	0.719		0.719
	0.165		0.165
(Habitat total)	4.825	4.367	4.790
	36	3	39
	0.549	0.462	0.552
	0.092	0.267	0.088

in each cell
mean (mm)
sample number
st. deviation
st. error

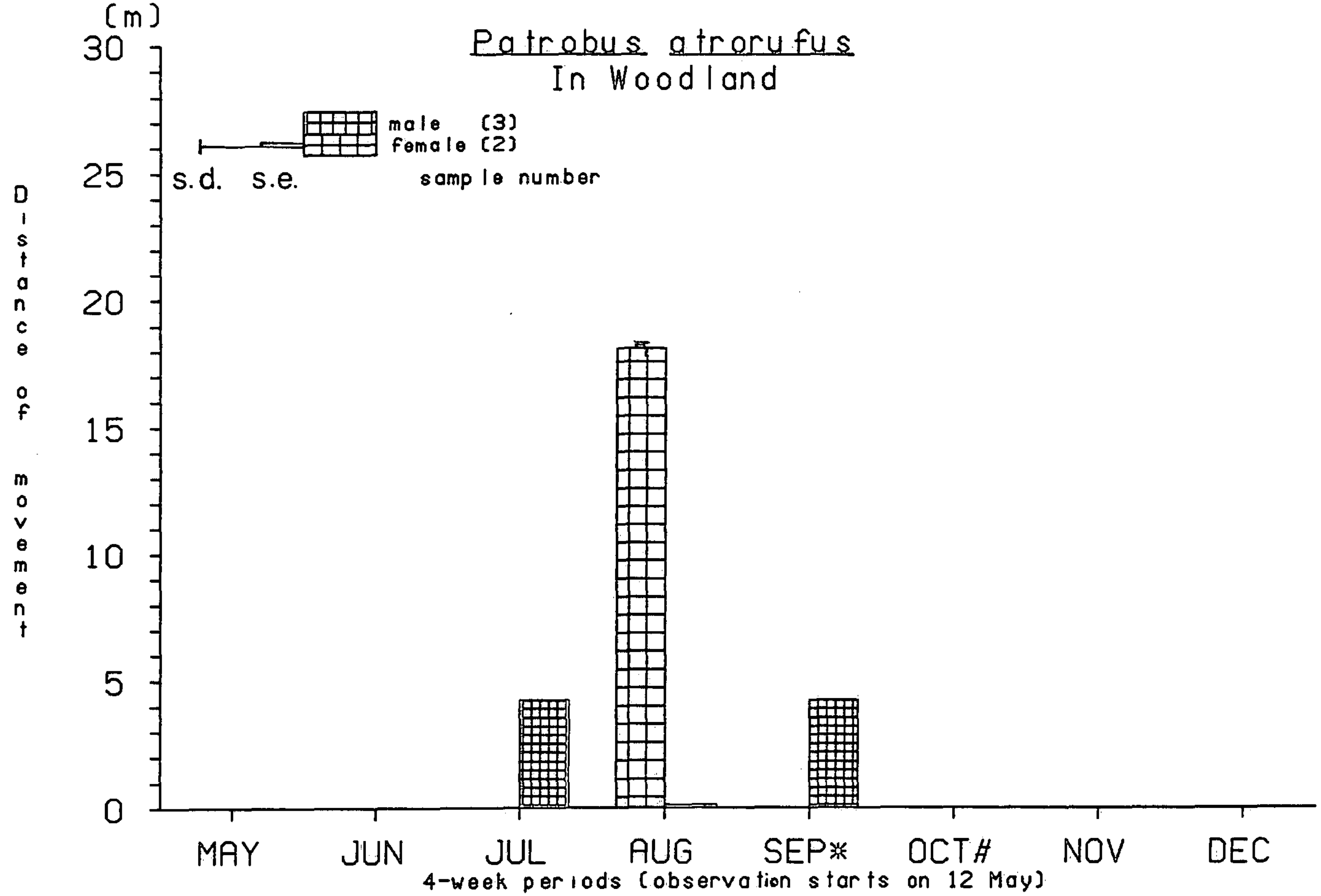
<Fig.4.13.1> Frequency of capture (including re-capture) in 4-week periods

Patrobus atrorufus



¤ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig.4.13.2> Distance between capture and recapture points

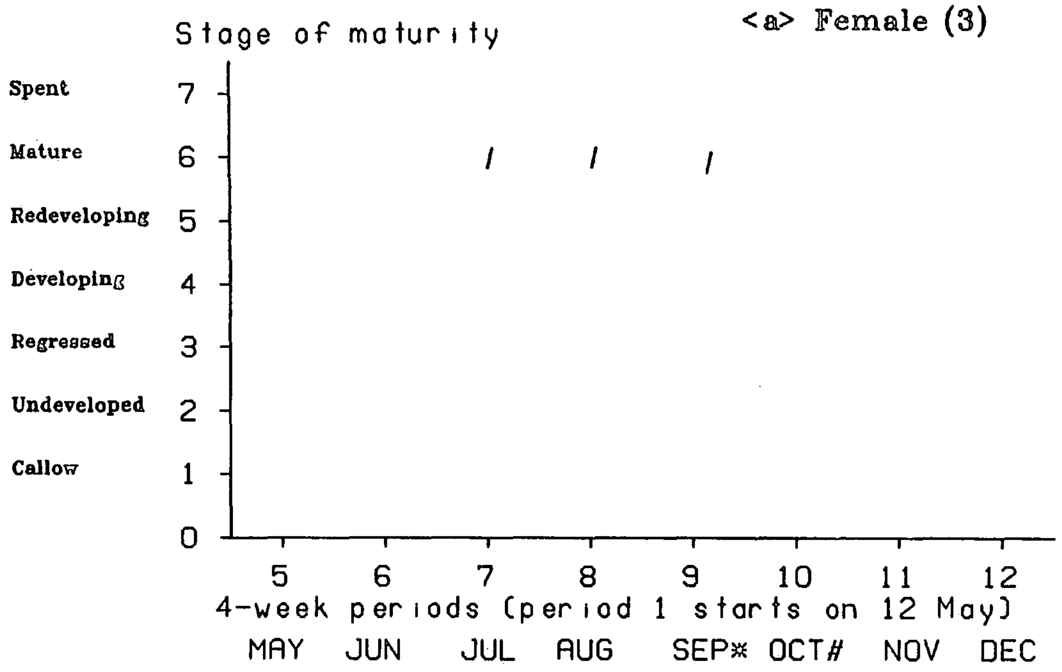


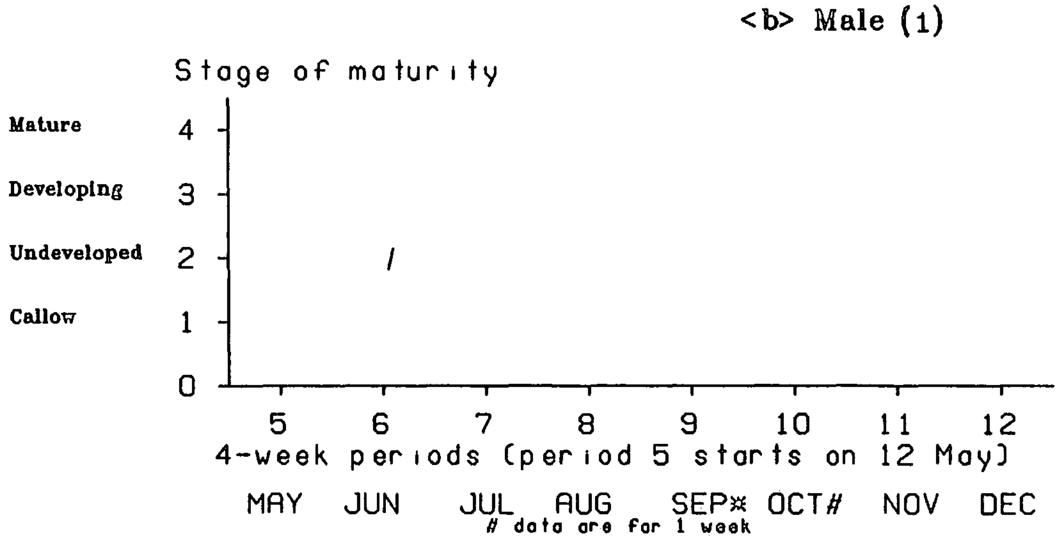
※ Data are for 3 weeks

Data are for 1 week

<Fig.4.13.3> Stages of maturity of <u>Patrobus</u> <u>atrorufus</u> caught in successive 4-week periods in woodland

Frequencies are plotted

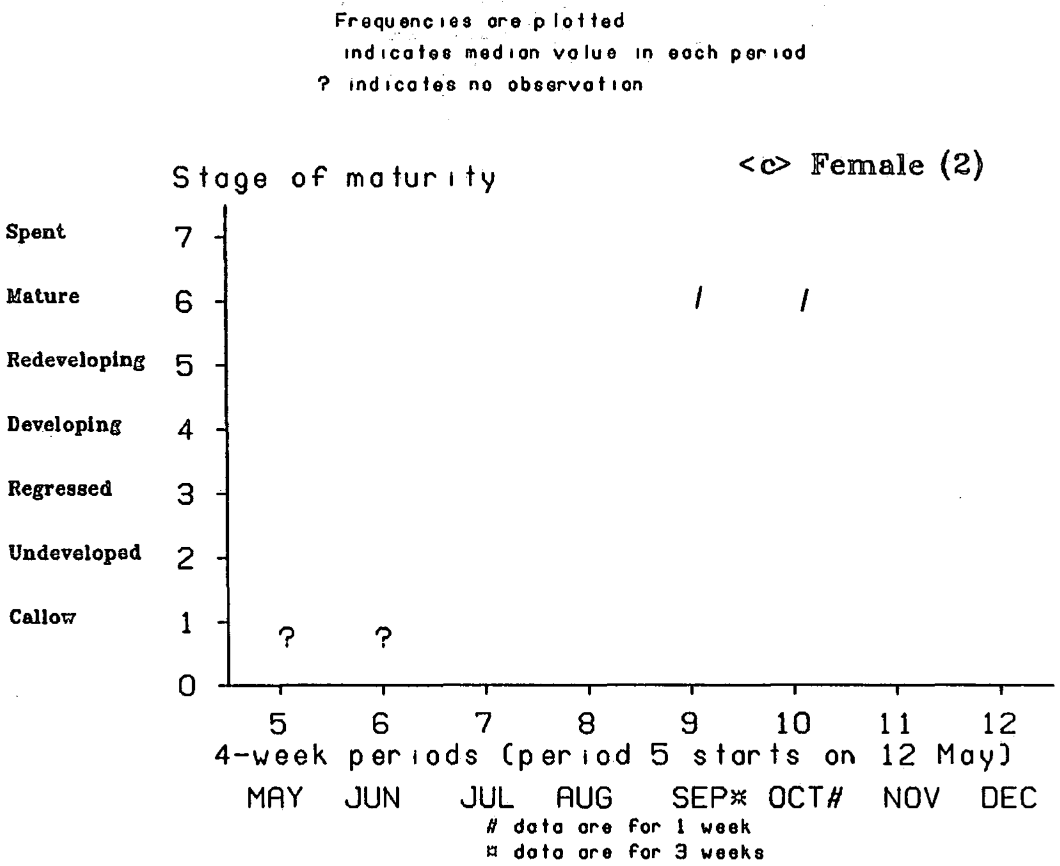




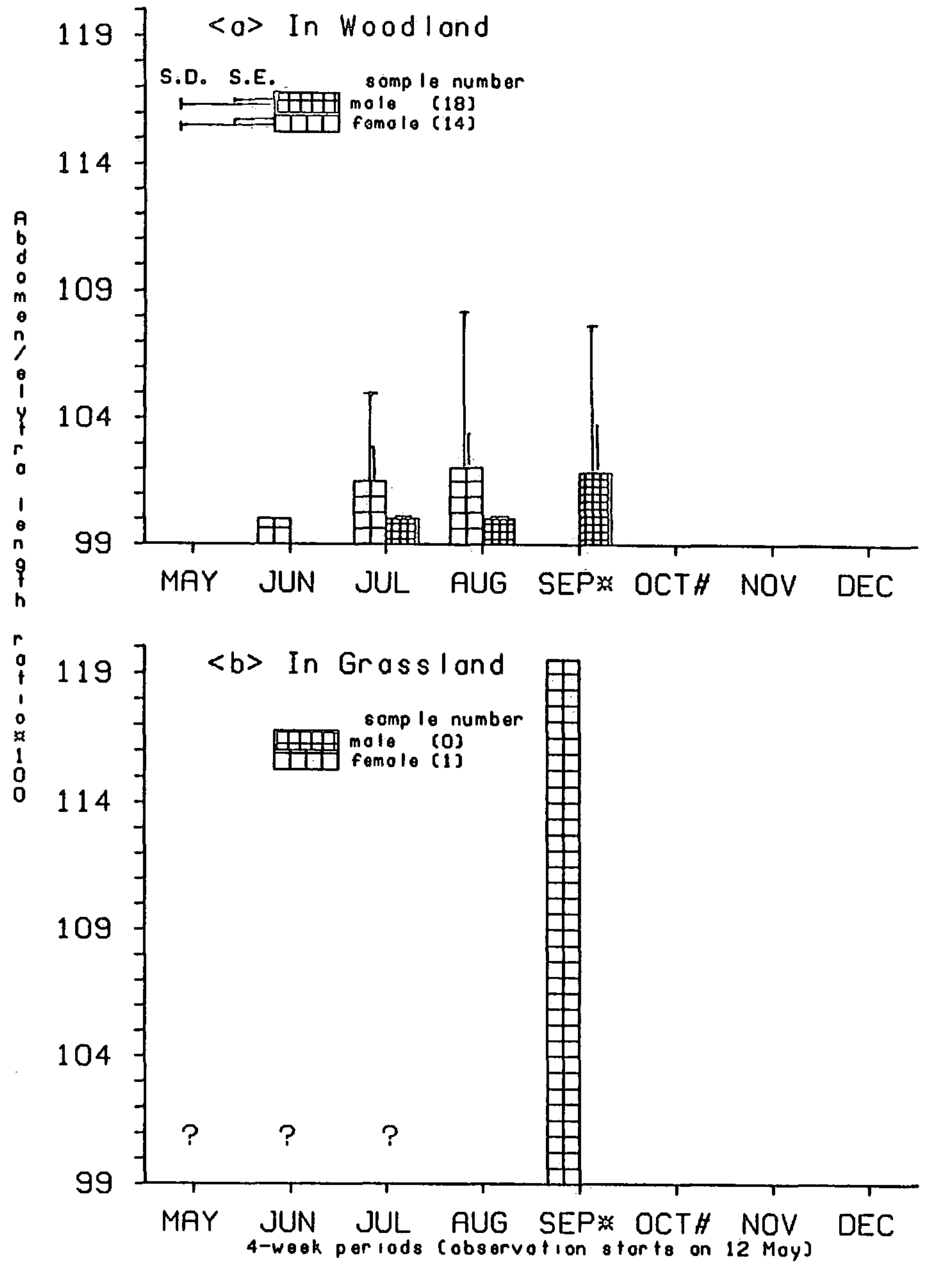
data are for 1 week

¤ data are for 3 weeks

<Fig.4.13.3> Stages of maturity of Patrobus atrorufus caught in successive 4-week periods in grassland



<Fig.4.13.4> Abdomen/elytra length ratio in 4-week periods *Patrobus atrorufus*

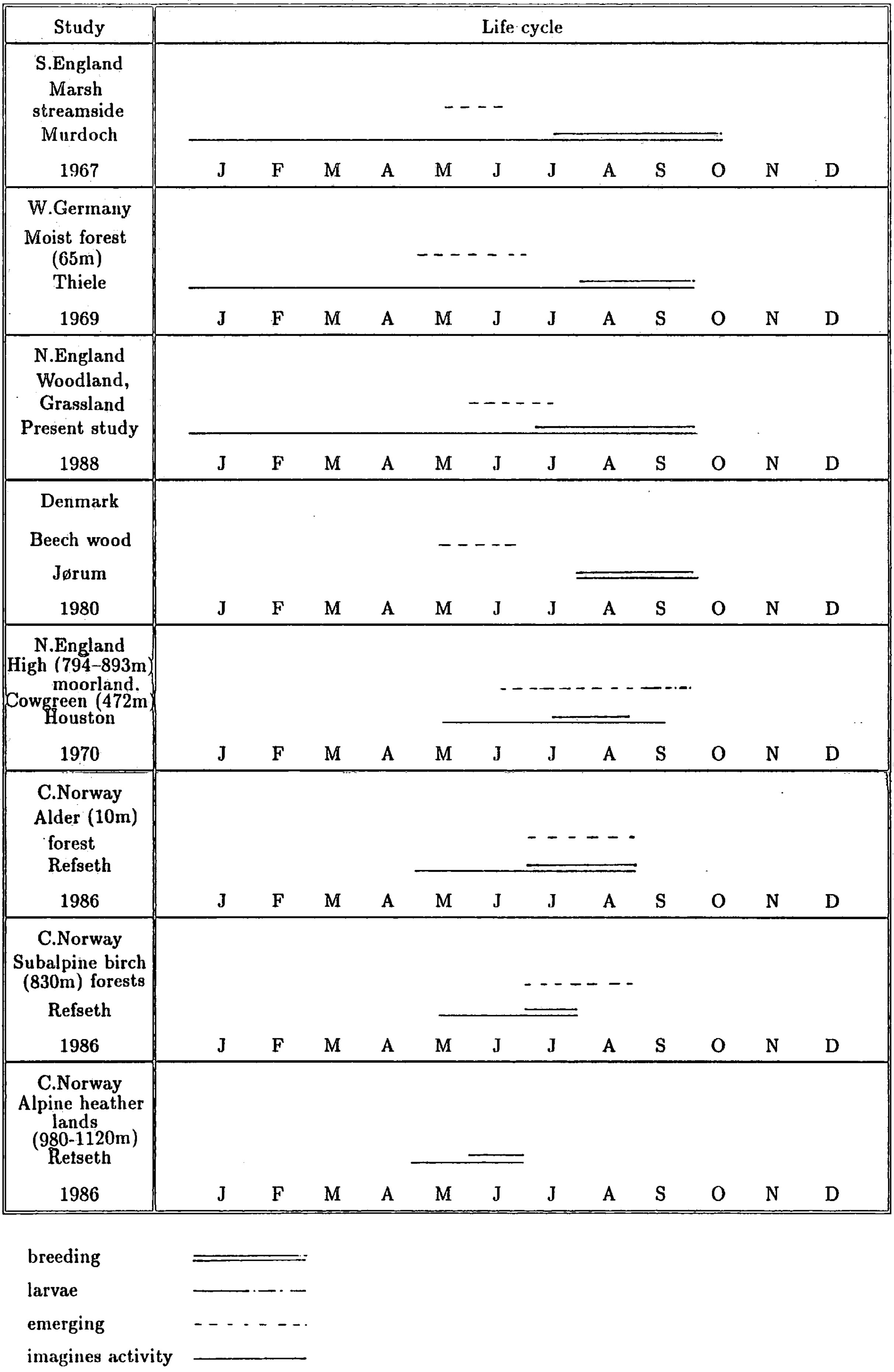


¤ Data are for 3 weeks

Data are for 1 week

? indicates no observation

<Fig. 4.13.5> The results of previous and present study of life cycle of *Patrobus atrorufus*



4.14 Pterostichus melanarius Illiger (vulgaris Linnaeus)

PREVIOUS INFORMATION

Pterostichus melanarius is found in grasslands and arable fields (Greenslade 1965), and generally in areas that are not too dry (Lindroth 1974).

The development of this species was investigated experimentally by Thiele and Krehan (1969), Thiele (1970), Krehan (1970, 1971), Hůrka (1975) and Witzke (1976). See Table 4.18.1. Field studies in southern England were carried out in weedy cultivated land and strawberry fields by Briggs (1957, 1967), and in marsh and streamside areas by Murdoch (1967). Studies were also made in open country in West Germany by Krehan (1970) and beech forest in Denmark by Jørum (1980).

This species is classified as "an autumn breeder with a thermic hibernator parapause at the larval stage and no dormancy in the course of adult development" (Thiele 1977). Coldness is essential at the end of the second instar of larval development and a long period of low temperature is required for normal development of the third instar. This is followed by a need for a rising temperature in order to achieve metamorphosis (Thiele and Krehan 1969 , Hůrka 1975). After emergence in the following spring, individuals become mature without dormancy in southern England (Briggs 1957, 1967, Murdoch 1967) and Denmark (Larsson 1939). In the laboratory (Thiele 1969, Krehan 1970) it was found that, after emergence, both sexes become mature in about 3 weeks at 20°C. Emergence may take longer in fields (Hůrka 1975), irrespective of photoperiod and without the occurrence of dormancy. During maturation, thermal quiescence can occur at low temperature (Thiele 1969, Krehan 1970). Some of the females which have already reproduced in the year prior to hibernation are found to reproduce again

(Briggs 1967, Krehan 1970, Jørum 1980). Biennial life cycles have been observed in most parts of the distributional range in Scandinavia (Lindroth 1949), in West Germany (Krehan 1970) and in Denmark (Jørum 1976, 1980). Fig.4.14.5 shows the results of previous field studies of the life cycle of this species.

RESULTS AND DISCUSSION

More samples of this species were captured in the Durham grassland than in the woodland <Fig.4.14.1>. This follows previous observations that *P. melanarius* is mainly associated with grasslands and arable lands (Lindroth 1945, Thiele 1964, Greenslade 1965). Grassland individuals will be discussed here.

A mature female in July and a spent female in August were observed. Also, large ratios of abdomen/elytra length for females were found in August (See Fig. 4.14.4b). The data for egg volumes and egg numbers per female are shown in Table 4.14.1 and Table 4.14.2, respectively. These results suggest a summer breeding season, perhaps in July and August. Although no callow was captured, both undeveloped and developing females were observed in July and August <Fig.4.14.3b>. To account for the simultaneous appearance of an undeveloped female and a spent female in August, it is suggested that at least a part of the population at Durham may have a biennial life cycle. *P. melanarius* matures quickly, as reported by Hůrka (1975), so that a part of the population which emerged earlier in the emergence season may be univoltine: e.g. a developing female in July. A mature female had small eggs at the previtellogenesis stage at the same time in grassland in July <Fig.4.14.3b>. Therefore, some of the females may reproduce later in the year and reproduce more than once in one year.

These results for the life cycle of *P. melanarius* at the Durham grassland site indicate the simultaneous occurrence of a univoltine life cycle and a semivoltine life cyle. Activity did not continue after August, in contrast with the reports from southern England (Murdoch 1967) and Köln (Krehan 1970) in which activity continued until October. It is concluded that the life cycle of this species may alter geographically as the environment becomes more severe <Fig.4.14.5>:

1. univoltine summer-autumn breeding with spring emergence in southern England (Briggs 1965, Murdoch 1967) to
2. a mixture of univoltine summer–autumn breeding and semivoltine spring breeding in northern England (present study), West Germany (Krehan 1970) and Denmark (Larsson 1939) to
3. semivoltine spring breeding with summer emergence in Denmark (Jørum 1976, 1980). Jørum has suggested that the biennial life cycle may be a consequence of longer winters and cooler springs causing a delay in metamorphosis.

ADDITIONAL INFORMATION

The elytra lengths of grassland females were significantly larger than those of the males ($t_{21} = 3.98$, $p = 0.001$) <Table 4.14.3> .

<Table 4.14.1> Mean egg volume of *Pterostichus melanarius* in relation to stage of maturity in 4-week periods <a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	4 Developing
8	771 1

<b>

Stage of maturity Period no.	4 Developing	6 Mature	7 Spent	(Period total)
7	1145 1			1145 1
8	1309 1	2251 1	1932 1	1831 3
(Stage of maturity total)	1227 2	2251 1	1932 1	1659 4

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.14.2> Mean number of eggs carried by female *Pterostichus melanarius* in relation to stage of maturity in 4-week periods
<a>in woodland <b>in grassland

<a>

Stage of maturity Period no.	4 Developing
8	12 1

<b>

Stage of maturity Period no.	2 Undeve	4 Developing	6 Mature	7 Spent	(Period total)
7		19 1			19 1
8	0 2	5 1	28 1	1 1	6.8 5
(Stage of maturity total)	0 2	12 2	28 1	1 1	8.8 6

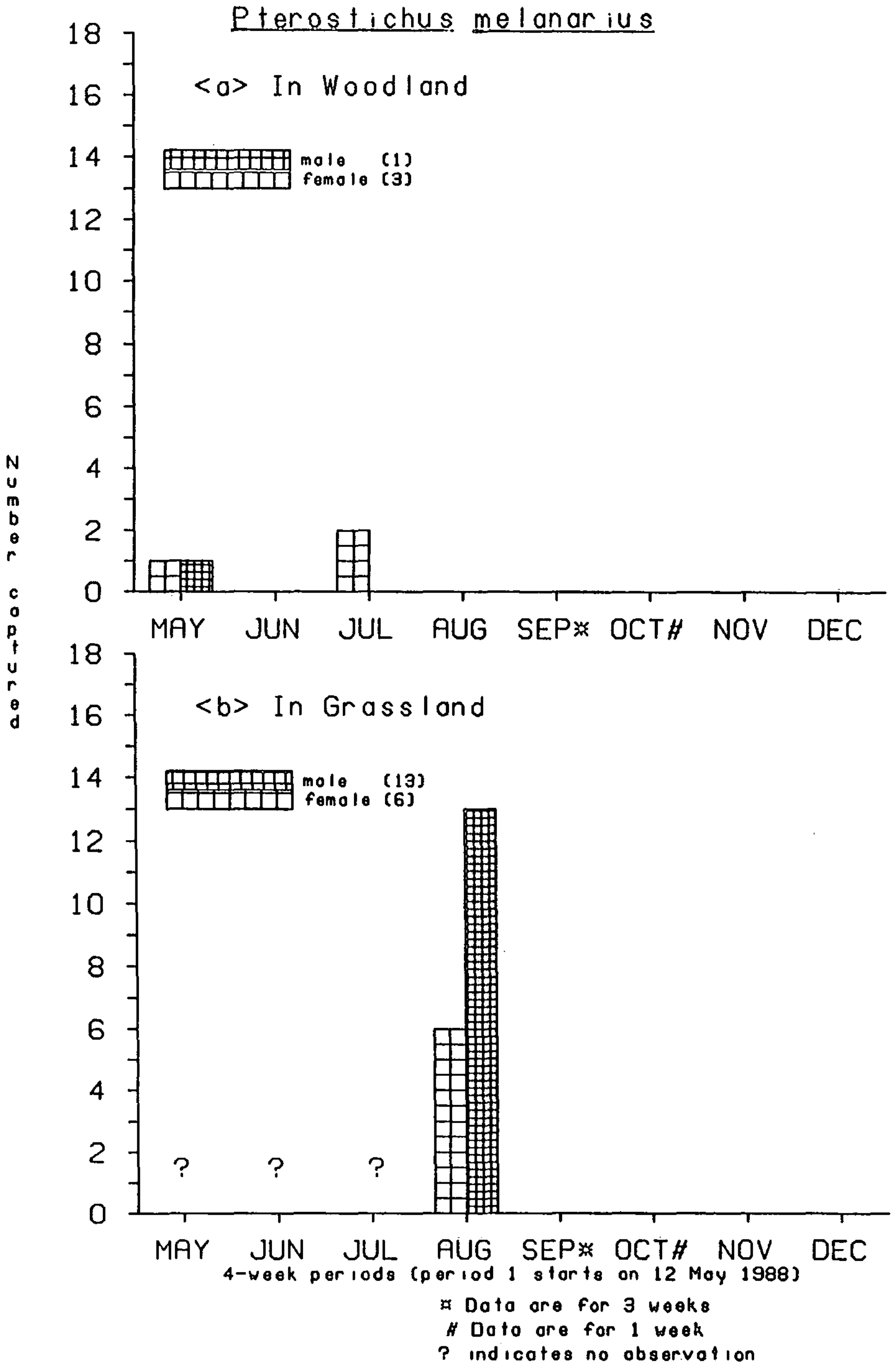
in each cell
mean number sample number

<Table 4.14.3> Elytra length of botth sexes of *Pterostichus melanarius* in the grassland

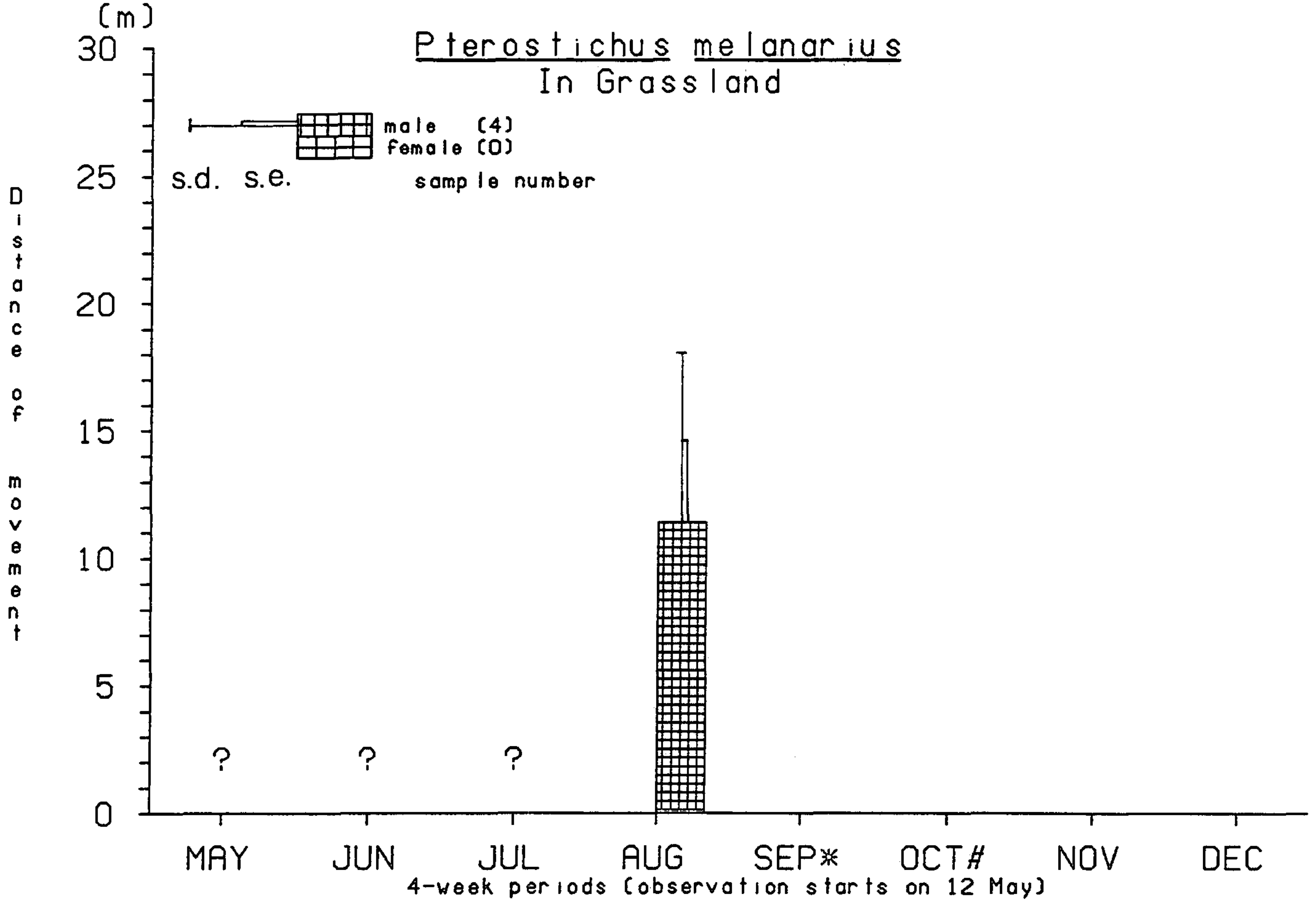
	Grassland
Female	9.460 10 0.502 0.159
Male	8.577 13 0.546 0.151
(Habitat total)	8.961 23 0.683 0.142

in each cell
mean (mm) sample number st. deviation st. error

<Fig.4.14.1> Frequency of capture (including re-capture] in 4-week periods



<Fig.4.14.2> Distance between capture and recapture points

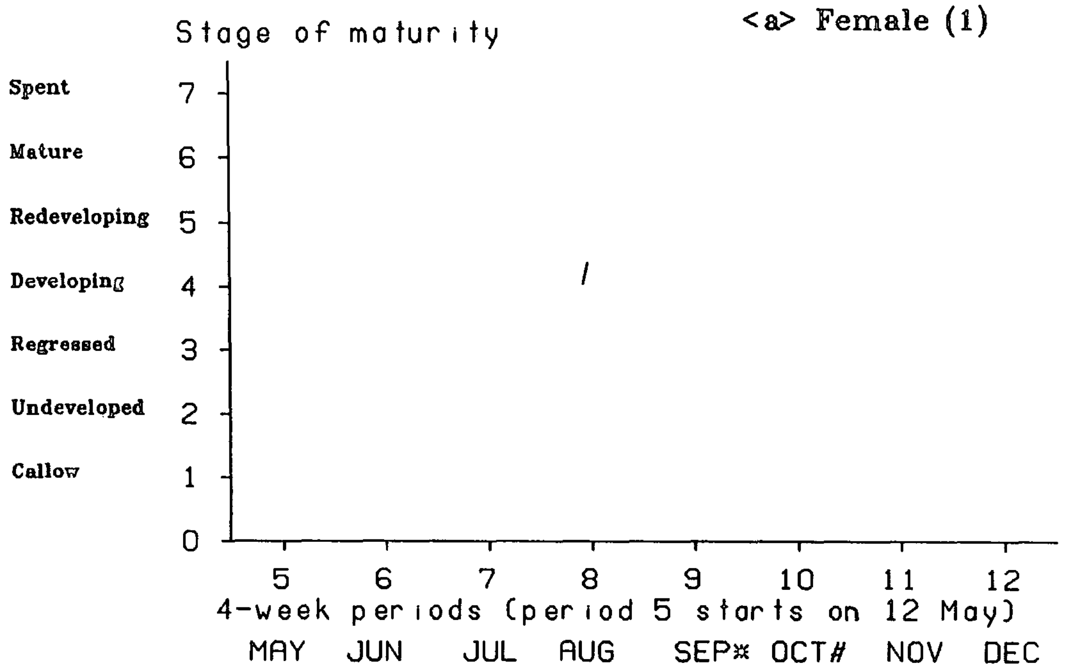


Pterostichus melanarius
In Grassland

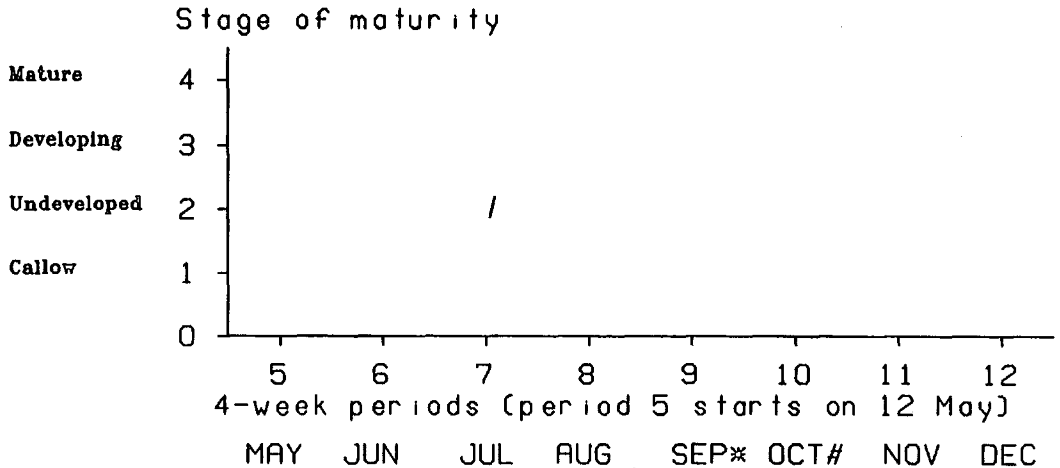
※ Data are for 3 weeks
Data are for 1 week

<Fig.4.14.3> Stages of maturity of <u>Pterostichus</u> <u>melanarius</u> caught in successive 4-week periods in woodland

Frequencies are plotted

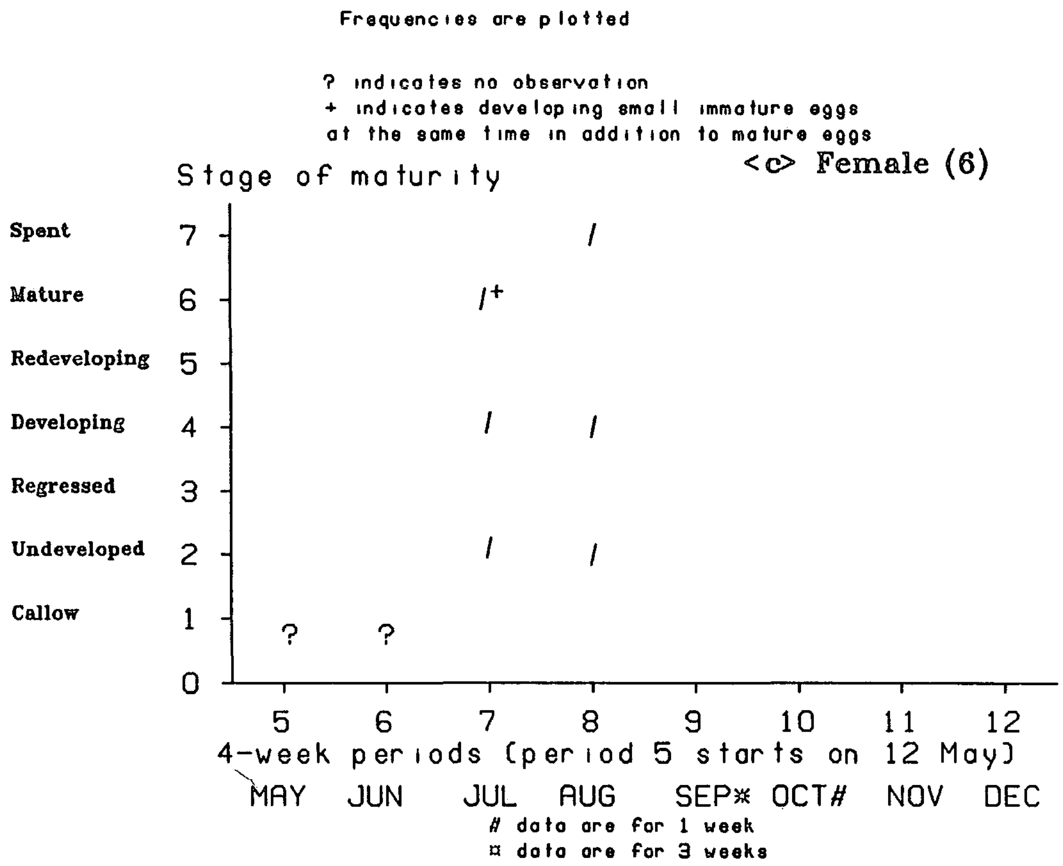

<a> Female (1)

<b> Male (1)



data are for 1 week
※ data are for 3 weeks

<Fig.4.14.3> Stages of maturity of *Pterostichius melanarius* caught in successive 4-week periods in grassland

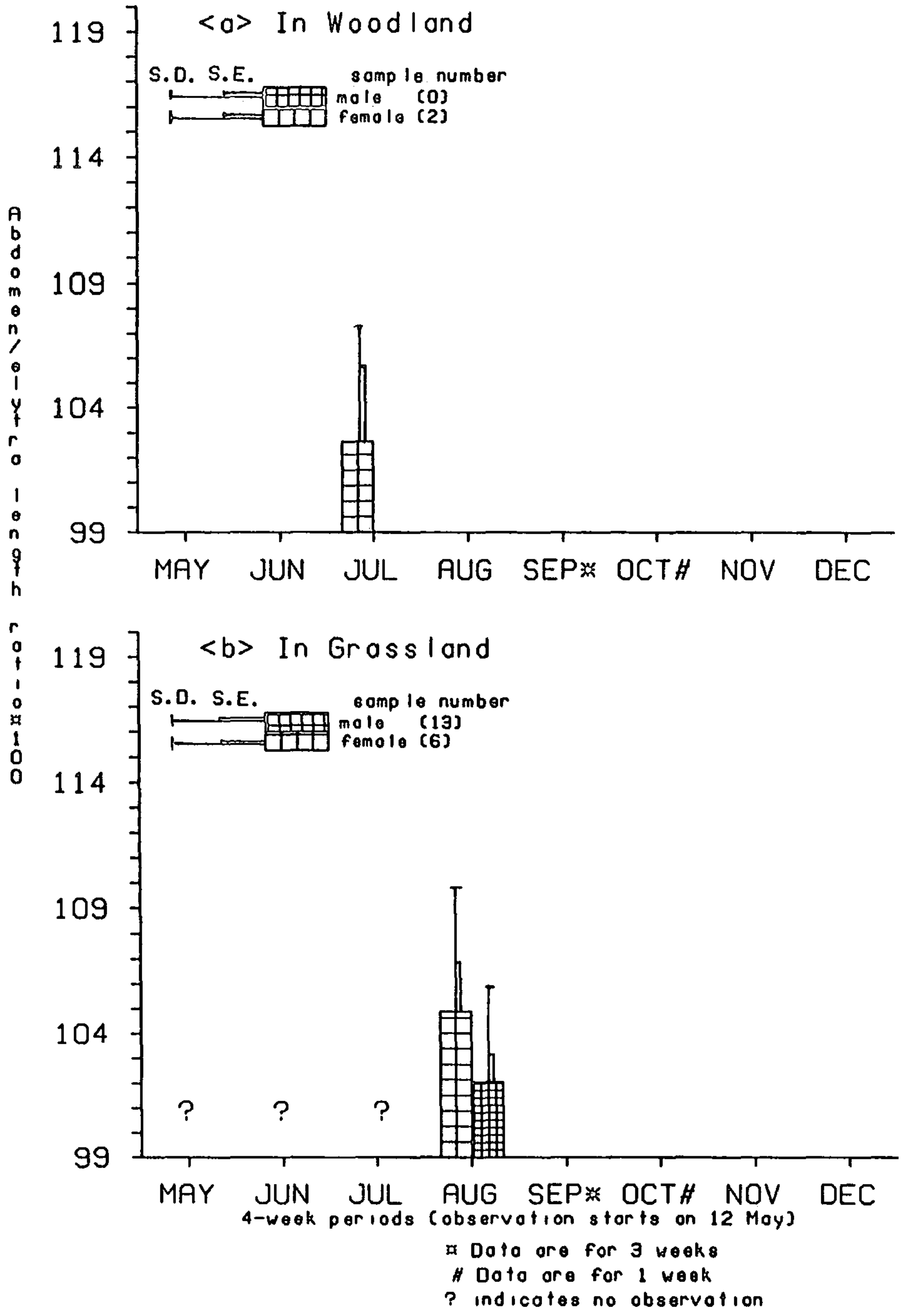

Frequencies are plotted

? indicates no observation
+ indicates developing small immature eggs
at the same time in addition to mature eggs

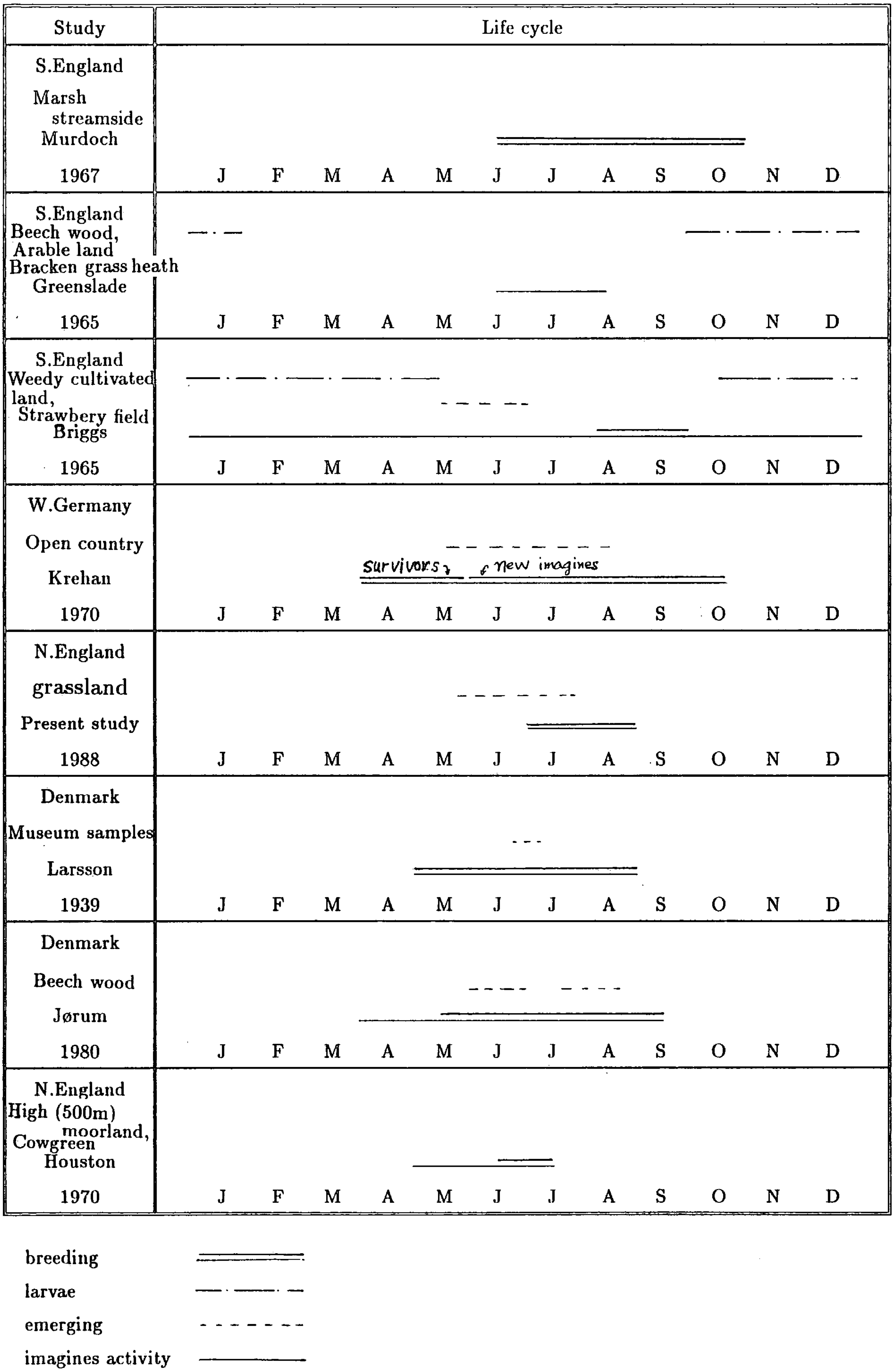
<c> Female (6)

data are for 1 week
¤ data are for 3 weeks

<Fig.4.14.4> Abdomen/elytra length ratio in 4-week periods *Pterostichus melanarius*



<Fig. 4.14.5> The results of previous and present study of life cycle of *Pterostichus melanarius*



4.15 Pterostichus niger Schaller

PREVIOUS INFORMATION

Pterostichus niger lives in woodlands and grasslands and, less frequently, in arable lands (Greenslade 1965) and soils which are not too dry (Lindroth 1974).

This species has been studied in southern England in beech wood, bracken, grassheath and arable land by Greenslade (1965); also in Denmark by Larsson (1939) and in beech forest by Jørum (1976, 1980); in West Germany by Witzke (1976); in central Norway by Lindroth (1945) and in alder forest by Refseth (1988).

Pterostichus niger has been classified in the group of "autumn breeders with a thermic hibernation parapause at the larval stage and no dormancy in the course of adult development" (Thiele 1977). Witzke (1976) found that larval development requires a period of cold, followed by a rising temperature, a result which confirmed the classification of Thiele. Fig.4.15.5 shows the results of previous field studies of the life cycle of this species.

In West Germany (Witzke 1976), an annual life cycle has been found: breeding was from August to mid-September and the third instar larva hibernated. Emergence occurred in the next year from May to July, followed by breeding in the summer. Some individuals survived and reproduced again in the next year.

However, both annual life cycles and biennial life cycles have been observed simultaneously in southern England (Greenslade 1965) and Denmark (Larsson 1939, Jørum 1976, 1980). In Denmark (Jørum 1976, 1980), a biennial life cycle has been suggested: the breeding season is from June to September (mainly July), followed by larval overwintering and emergence in the following July-August.

Jørum found a small number of spent females which were about to start a new breeding period in August and September. He agreed with Greenslade (1960) that *P. niger* may either breed in two seasons or those individuals emerging late in one season will not breed until the next year. The work of Greenslade (1965) in southern England revealed autumn breeding with overwintering larvae, with emergence perhaps in summer and adult hibernation as well. Larsson (1939) has reported a similar life cycle in Denmark following observations that larvae were present at all times of the year.

Biennial life cycles have been observed in central Norway (Refseth 1988): breeding occurs in July and August, with emergence in August and September of the next year after larval hibernation and adult hibernation. This is then completed by breeding in the following summer.

RESULTS

Fig.4.15.1 shows that individuals of *P. niger* were trapped mainly in the Durham woodland; relatively few were caught in grassland.

Most of the woodland individuals were caught from June to August, including callows during late July and August. No callows were caught in grassland.

Table 4.15.1 summarizes the data obtained during the main period of captures (June to August). This is also displayed in Fig.4.15.1a and Fig.4.15.2a. The data represent the ratio of females to males in woodland. The numbers of male and female callows captured were similar but a higher proportion of females was observed among non-callows. It may therefore be that the survival rate of females is higher than that of males.

The distances of movement for woodland beetles are shown in Fig.4.15.2a.

Measurements were made for the peak periods of capture. Females may have tended to move further than males but not significantly so ($t_{18} = 1.77, p = 0.094$) <Table 4.15.2> .

From the results in Fig.4.15.3a, it is seen that the summer population may involve more than two adult generations, because in July and August both callow (or undeveloped) and mature females were observed at the same period. The same phenomenon was witnessed in the sample of woodland males <Fig.4.15.3b>, although male maturation is usually faster than that of the female so that the strength of this suggestion is reduced.

For woodland females the abdomen/elytra length ratio was large in June and July, coinciding with the oviposition season <Fig.4.15.4>. Although for grassland females large ratios were observed in August and September, the sample numbers were too small to permit the identification of peak periods of oviposition.

One undeveloped female was observed in December <Fig.4.15.3a>. This had a large fat body and showed a large ratio of abdomen/elytra length <Fig.4.15.4>.

During June and August, both egg volumes and egg numbers increased <Table 4.15.3, Table 4.15.4>

The low egg numbers imply low fecundity for this species. This is in contrast to the Durham results for *P. madidus*, a species which is closely related and of similar body size (*P. madidus* 13-17mm, *P. niger* 15-20.5mm). See Table 4.1.10.

DISCUSSION

The grassland sample is too small to allow consideration of the life cycle. Only woodland individuals will be discussed here.

Pterostichus niger seems to have an oviposition season between June and August (or perhaps a little later) because

1. mature females were observed in August <Fig.4.15.3a>;
2. large ratios of abdomen/elytra length were recorded in June and July <Fig.4.15.4a>;
3. many captures were made between June and August <Fig.4.15.1a>;
4. individuals moved large distances in July and August <Fig.4.15.2a>.

The field observations <Fig.4.15.1a> and the dissection results <Fig.4.15.3a> suggest that emergence in woodland occurred in late July and August.

A biennial life cycle is inferred because

1. mature females and callows were observed at the same time in July and August;
2. in December, an undeveloped female was observed.

The Durham population of *P. niger* showed a similar life cycle to that found in the studies of a Danish population (Jørum 1976, 1980), which revealed animals with a univoltine and a semivoltine life cycle.

From a comparison of the previous and present studies, the effect of moving to increasingly severe environments, i.e. from low latitude and oceanic climate areas to high latitude and continental climate areas for this species <Fig.4.15.5> is as follows:

1. there is a shift of life cycle from a univoltine autumn breeder to a mixture of a univoltine and a semivoltine summer breeder to, finally, a semivoltine summer breeder,
2. the time of emergence undergoes a shift from spring–early summer to late

summer–autumn, as the environmental conditions become more severe.

ADDITIONAL INFORMATION

Two females were observed to secrete pheromone in woodland in July; because of the timing, it may have been related to oviposition.

Elytra lengths were significantly larger for male grassland individuals than for woodland individuals ($t_{39} = 2.42$, $p = 0.021$), but not significantly so for females ($t_1 = 1.19$, $p = 0.444$) <Table 4.15.5>. Elytra lengths did not differ between sexes in each habitat. (In woodland, $t_{45} = 0.33$, $p = 0.746$; in grassland, $t_4 = 0.09$, $p = 0.934$).

<Table 4.15.1> The estimation of population ratio of female/male of *Pterostichus niger* in woodland in periods no.6 — 8

Sex		Female	Male	% of female
Capture number	Total	42	34	55.3
	Non-callow	37	27	57.8
	Callow	5	7	41.7

<Table 4.15.2> The distance of movement of both sexes of *Pterostichus niger* in woodland

Sex		Female	Male
Movement Distance	Mean (m)	8.929	4.390
	Sumple number	13	7
	st. deviation	6.295	3.243
	st. error	1.746	1.226

<Table 4.15.3> Mean egg volume of *Pterostichus niger* in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	4 Developing	6 Mature	(Period total)
72	1466 1		14662 1
8	2488 1	2246 3	2306 4
(Stage of maturity total)	1977 2	2246 3	2138 5

in each cell
mean (mm^3) sample number

(The egg volume used here is that of the largest egg of a given female)

<Table 4.15.4> Mean number of eggs carried by female Pterostichus niger in relation to stage of maturity in 4-week periods in woodland

Stage of maturity Period no.	1 Callow	2 Undeveloped	4 Developing	6 Mature	(Period total)
7	0 1		4 1		2 2
8		0 1	7 1	9.3 3	7 5
12		0 1			0 1
(Stage of maturity total)	0 1	0 2		9.3 3	4.9 8

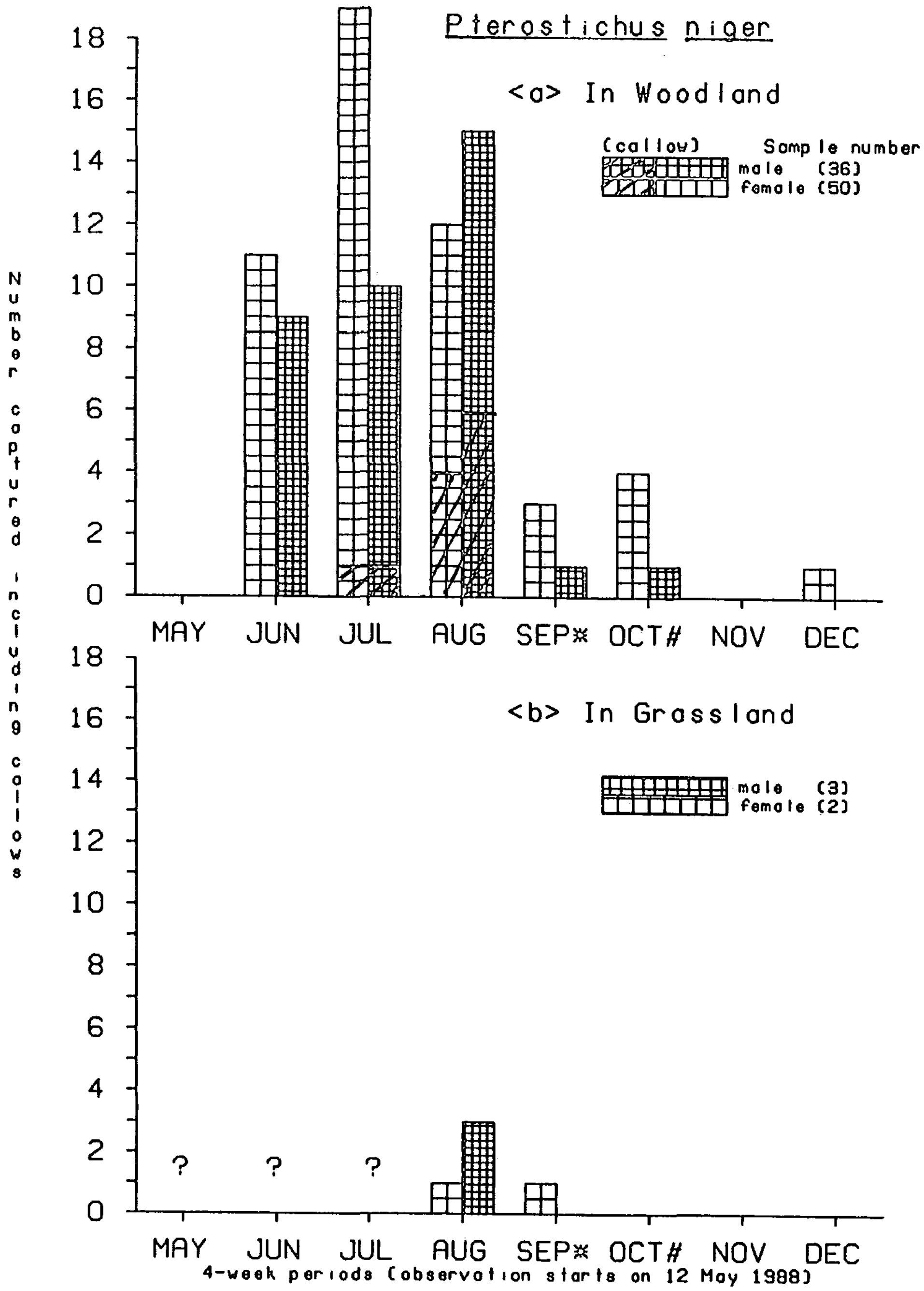
in each cell
mean number sample number

<Table 4.15.5> Elytra length of both sexes of *Pterostichus niger* in the two habitats

	Woodland	Grassland	(Sex total)
Female	8.761	10.250	8.812
	57	2	59
	0.524	1.768	0.626
	0.069	1.250	0.081
Male	8.830	10.350	8.978
	37	4	41
	1.203	1.103	1.266
	0.198	0.552	0.176
(Habitat total)	8.788	10.317	8.880
	94	6	100
	0.853	1.165	0.940
	0.088	0.476	0.094

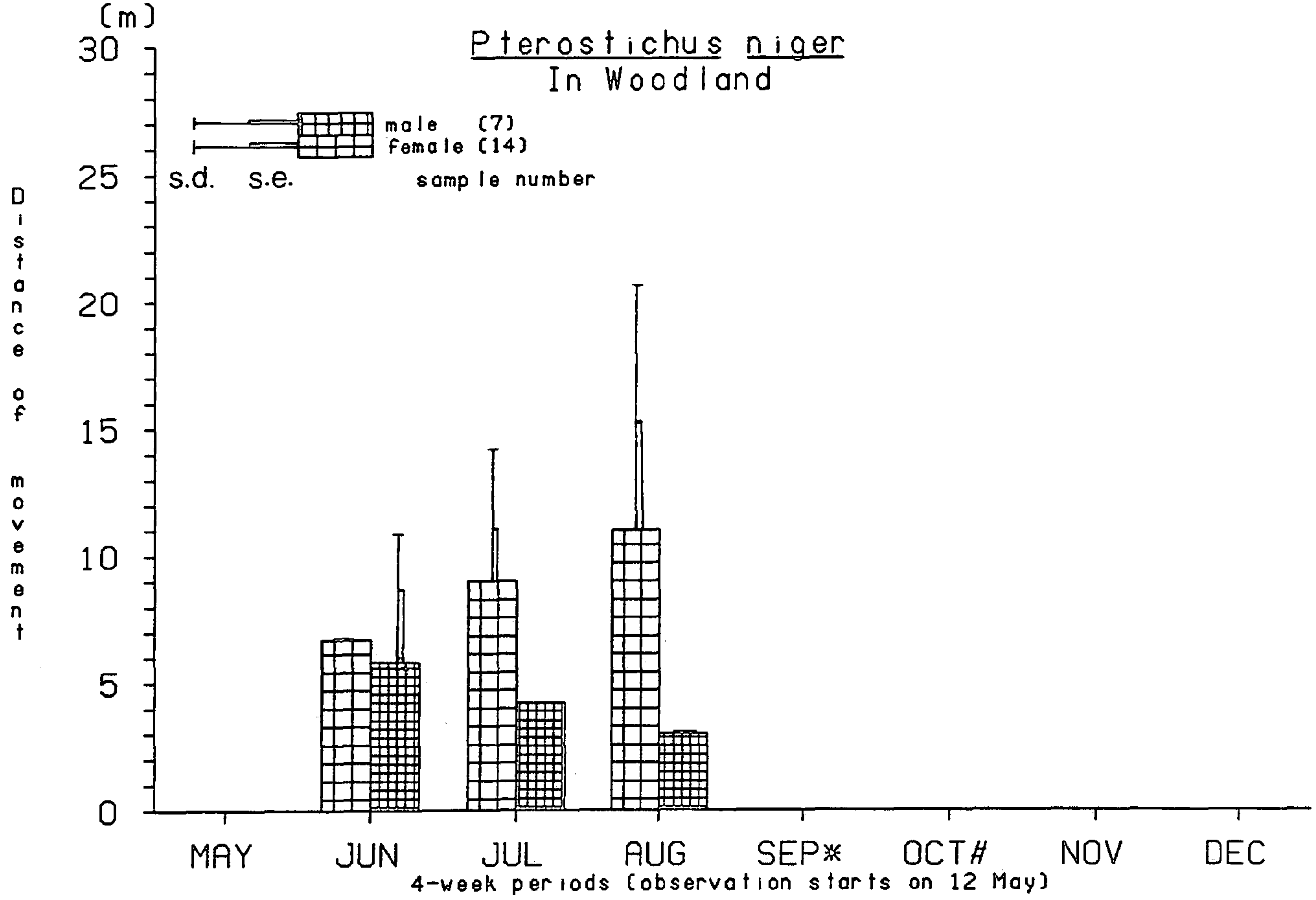
in each cell
mean (mm)
sample number
st. deviation
st. error

<Fig.4.15.1> Frequency of capture (including re-capture) in 4-week periods



※ Data are for 3 weeks
Data are for 1 week
? indicates no observation

<Fig.4.15.2> Distance between capture and recapture points



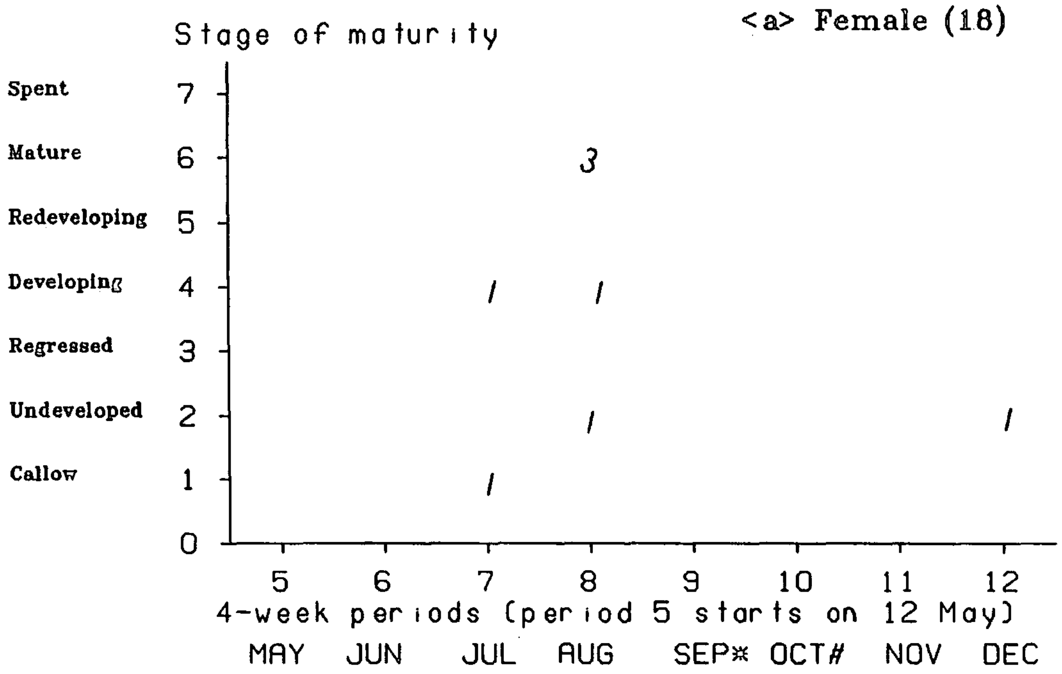
※ Data are for 3 weeks

Data are for 1 week

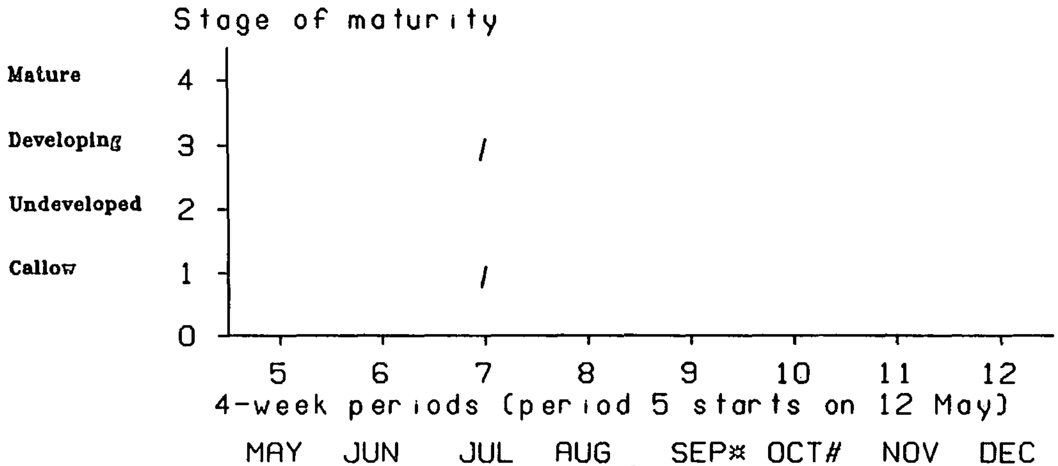
<Fig.4.15.3> Stages of maturity of *Pterostichus* *niger* caught in successive 4-week periods in woodland

Frequencies are plotted

<a> Female (18)

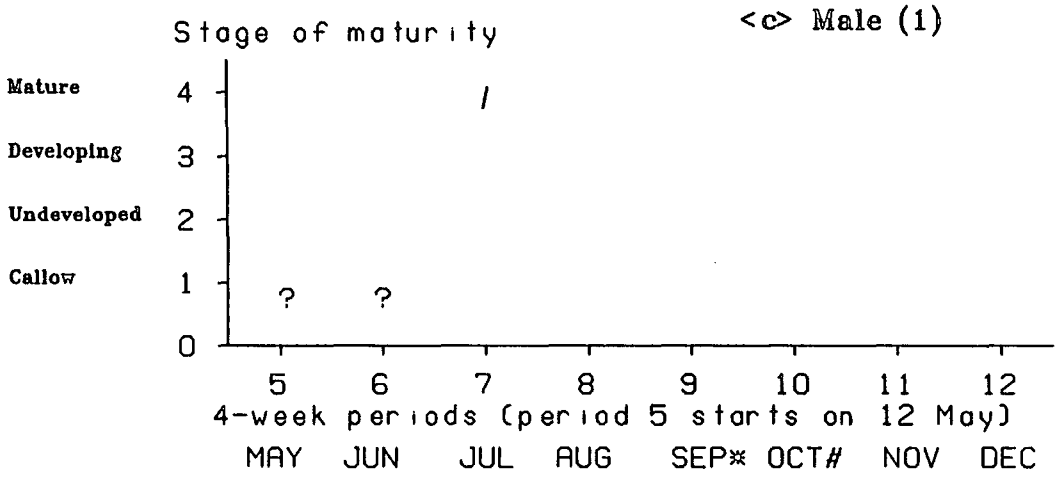


<b> Male (2)



data are for 1 week
¤ data are for 3 weeks

<Fig.4.15.3> Stages of maturity of <u>Pterostichius</u> <u>niger</u> caught in successive 4–week periods in grassland



Frequencies are plotted

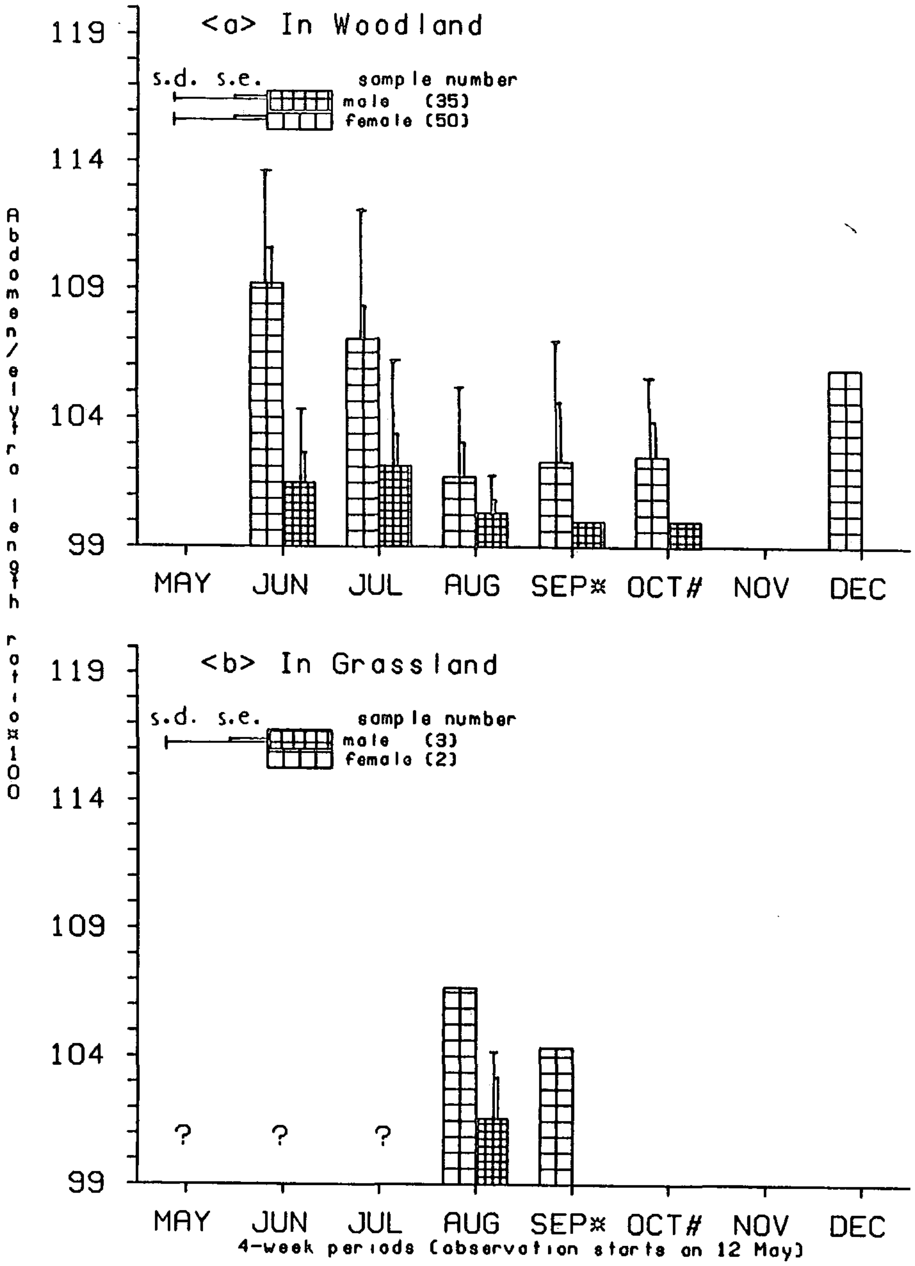
? indicates no observation

<c> Male (1)

data are for 1 week
¤ data are for 3 weeks

<Fig.4.15.4> Abdomen/elytra length ratio in 4-week periods

Pterostichus niger

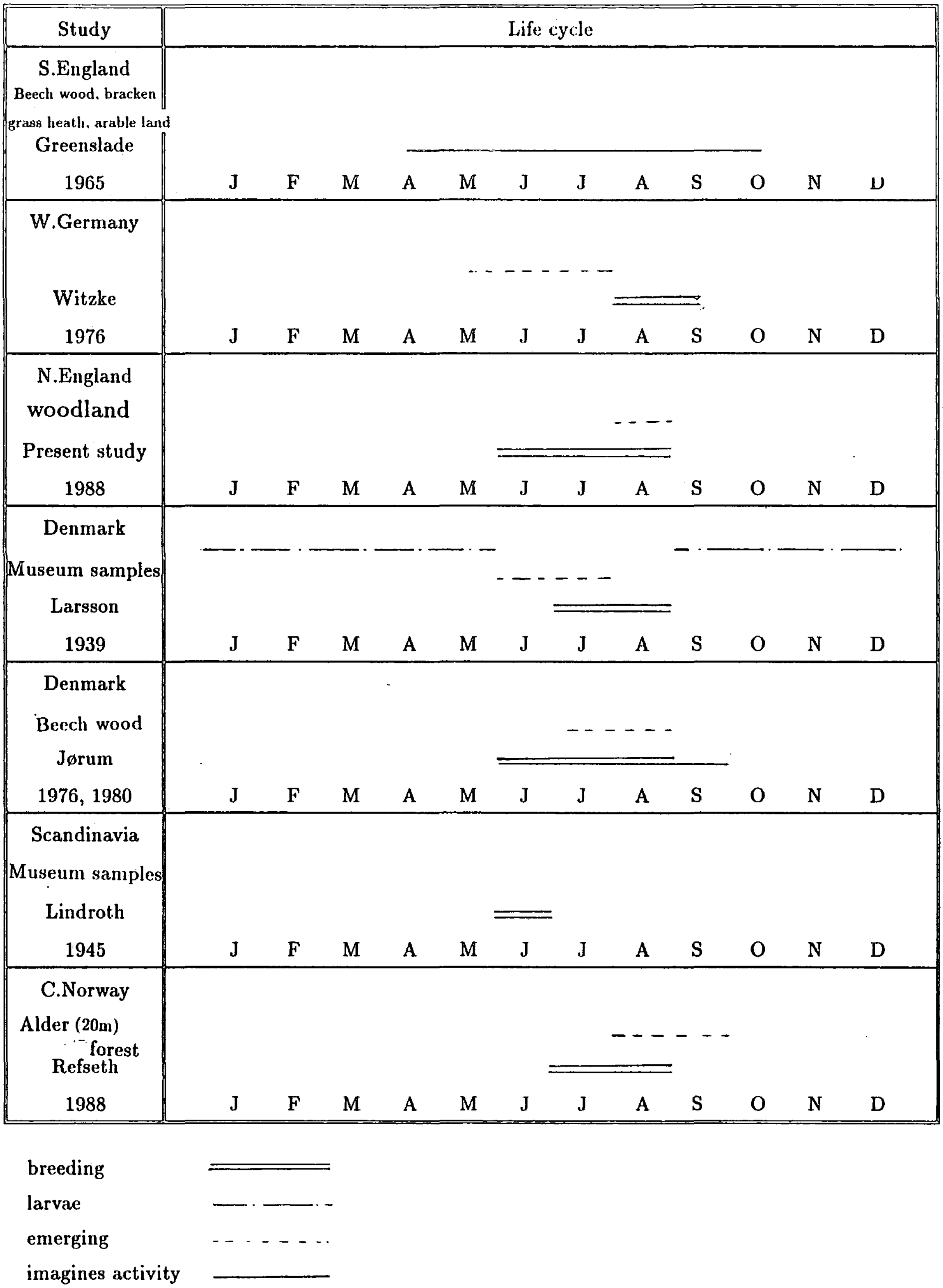


※ Data are for 3 weeks

Data are for 1 week

? indicates no observation

<Fig. 4.15.5> The results of previous and present study of life cycle of *Pterostichus niger*



4.16 Pterostichus nigrita Paykull

PREVIOUS INFORMATION

This species inhabits shady and damp environments (Greenslade 1965), usually near water (Lindroth 1974).

Pterostichus nigrita has been classified as a member of the group of "spring breeders with no larval dormancy, with emergence in autumn and obligatory dormancy in the adult" (Thiele 1977). The species has been studied experimentally by Thiele (1966, 1968) and Ferenz (1975). For females the photoperiod, firstly by short-day for previtellogenesis and then by long-day for vitellogenesis, terminates the adult hibernation prior to breeding in the next spring. However, males can mature (with formation of spermatozeugma) only by the stimulation of the short-day photoperiod. Ferenz (1975) suggested that;

1. the critical photoperiod for female maturation is different phenologically between low and high latitudes.

The critical short-day photoperiod for previtellogenesis

- 15.5h light/day: 51°N (Köln in West Germany)
- 19.5h light/day: 66°N (Messaure, northern Sweden)

The critical long-day photoperiod for vitellogenesis is, however, only a little different:

- 13.1h light/day: 51°N
- 14.0h light/day: 66°N

which means at the end of July and at the beginning of April, irrespective of longitude (Refseth 1986) <Fig.4.18.2>.

Ferenz (1975) also reported that when the Messaure population is compared with the Köln population, the larvae from polar populations

2. develop faster in all temperatures;
3. have a low mortality in low temperatures;
4. have a high growth rate in high temperatures. (See Table 4.18.1, Table 4.18.2.).

Ferenz concluded that the polar population of *P. nigrita* was able to survive a sudden cold spell and, during optimum temperatures, could compensate for periods of reduced development.

Fig.4.16.2 shows the results of previous field studies of the life cycle of this species. In southern England (Greenslade 1965), *P. nigrita* has been observed to overwinter as an adult. Periods of maximum activity occur in March–April and in October. In Denmark (Larsson 1939), the maximum activities have been observed in May–June (with the appearance of mature females in late April–July) and late August–early October (relating to emergence). In Scandinavia (Lindroth 1945), the maximum activities have occured in May–June and September (emergence).

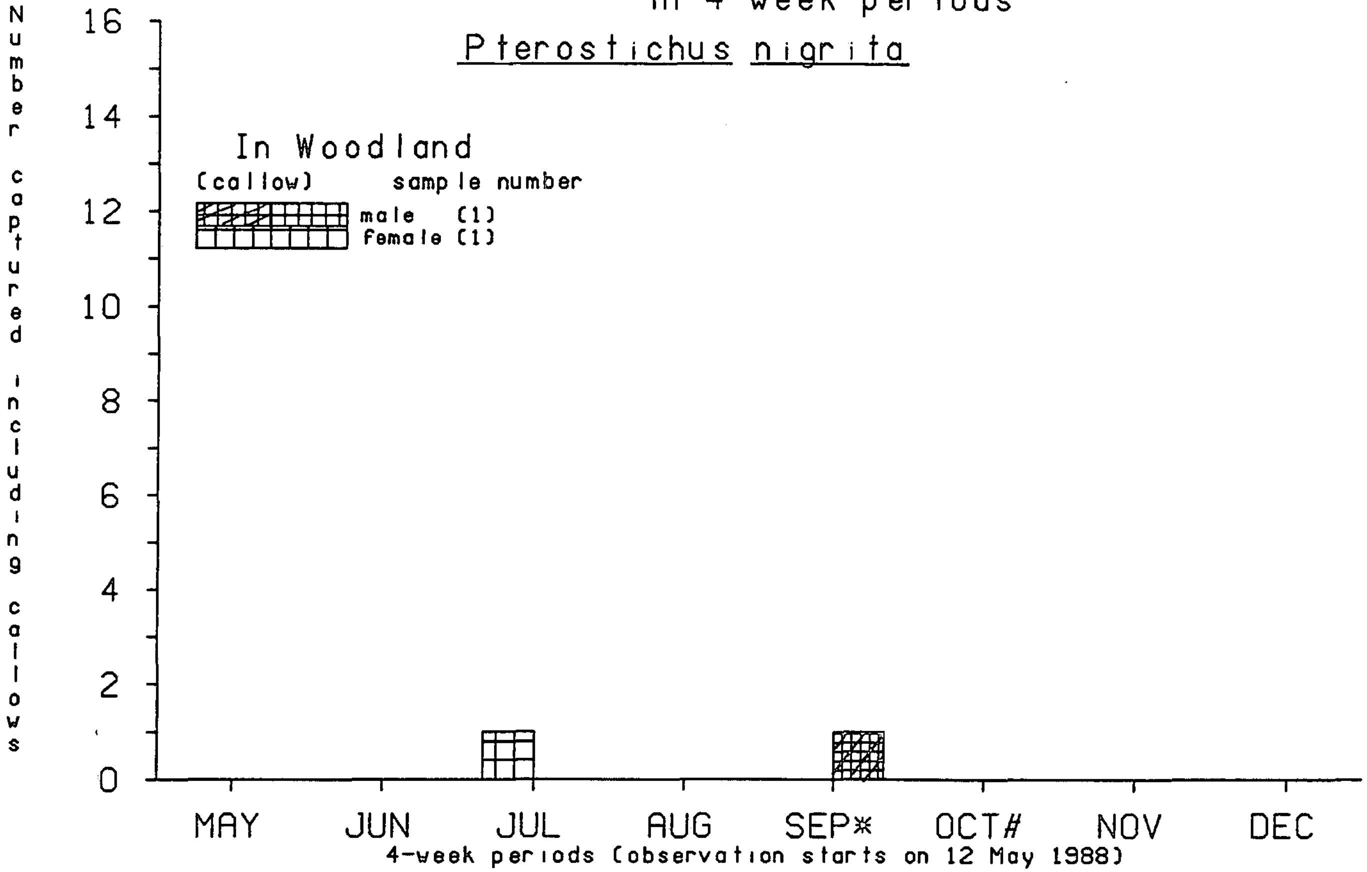
RESULTS AND DISCUSSION

P. nigrita was captured only in the Durham woodland in July and September <Fig.4.16.1>. One male callow was observed in September. The emergence in the Durham woodland in September was similar to the results found in Denmark and Scandinavia and earlier than the time of emergence found in southern England. (The present data are not of sufficient quantity to permit discussion of the breeding season of *P. nigrita*.)

When the previous studies are compared with the present study, it is found that, generally, the emergence seasons peak in the same periods. Emergence occurs mainly in September in each of the various geographical areas. The breeding seasons in spring become shorter as the environment becomes more severe, i.e. the breeding starts later and ends sooner. When the starting times of the breeding seasons are compared with the starting times of the vegetation growth periods, they are found to be almost simultaneous. It is therefore possible that the starting of breeding is controlled by the vegetation growth periods in addition to photoperiodical signal. (See Fig.4.16.2 with Table 4.0.2). Consequently, shorter developmental periods for larvae are found in the more severe environments. This has been proved by the work of Ferenz (1975), in which the population in northern Sweden was shown to have a higher growth rate in high temperature than that of Köln <Table 6.1>.

The end of the breeding season occurs earlier as the environment becomes more severe. When the times of the end of the breeding seasons are compared with those of the vegetation growth periods at each area, it is observed that the breeding ends about four months before the end of the vegetation growth periods. The autumn emergences begin about four months after the start of breeding in the spring and end one month before the end of the vegetation periods. The earlier end of breeding seasons in spring and the consequent earlier occurrence of emergence in autumn seems to allow for the longer duration of preparation for overwintering and breeding of the following spring soon after overwintering. The more severe the environment, the stronger is the synchronization between the changing of temperature and the occurrence of the breeding and emergence seasons. Experimental study is necessary to investigate the sensitivity of populations to temperature at increasingly harsh environments.

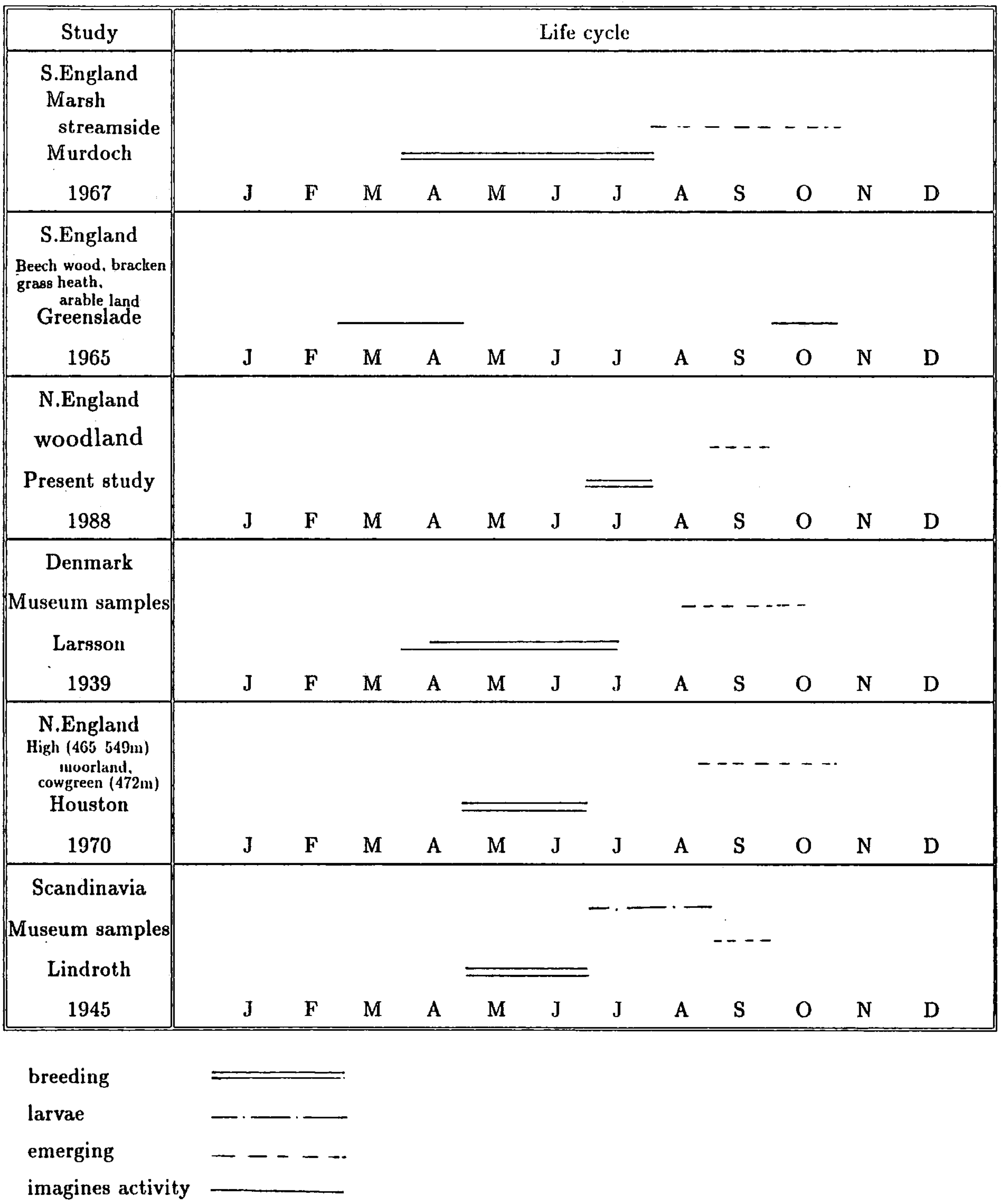
<Fig.4.16.1> Frequency of capture (including re-capture) in 4-week periods



※ Data are for 3 weeks

Data are for 1 week

<Fig.4.16.2> The results of previous and present study of life cycle of *Pterostichus nigrita*



4.17 Pterostichus strenuus Panzer

PREVIOUS INFORMATION

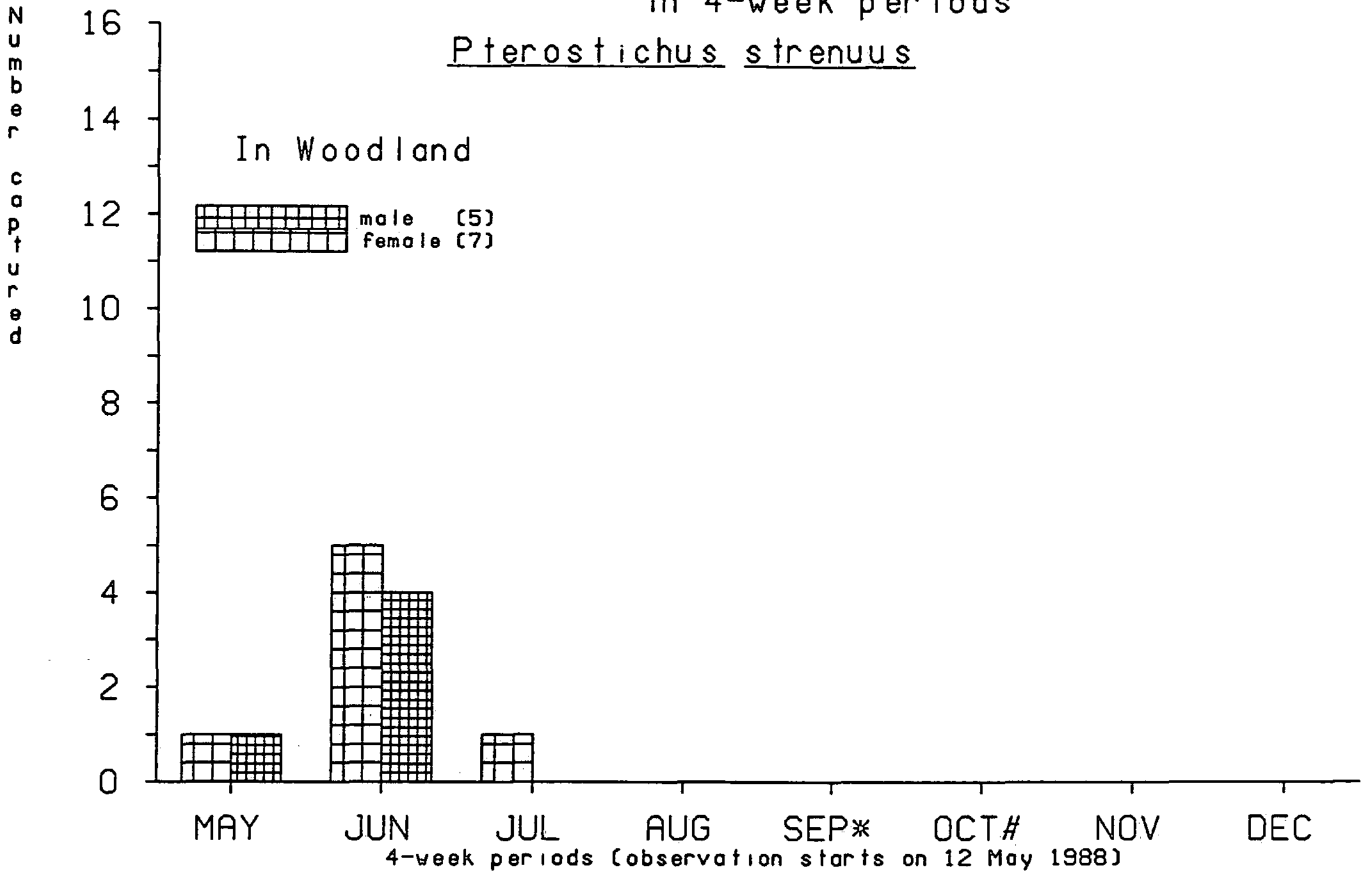
Pterostichus strenuus inhabits shady places, usually in damp deciduous forests, on clayish soil and amongst moss and leaves. (Lindroth 1974).

Fig.4.17.3 shows the results of previous field studies of the life cycle of this species. The life cycle of *Pterostichus strenuus* in marshlands and streamside areas in southern England includes spring breeding, with summer larvae (Greenslade 1964). Autumn emergence follows, with further breeding during the next spring from March to July after hibernation (Murdoch 1967). The life cycle is similar on high moorland in northern England (Houston 1970): emergence occurs in September–October and breeding occurs in April–June. In Denmark, the peak of captures is observed in April (Larsson 1939).

RESULTS AND DISCUSSION

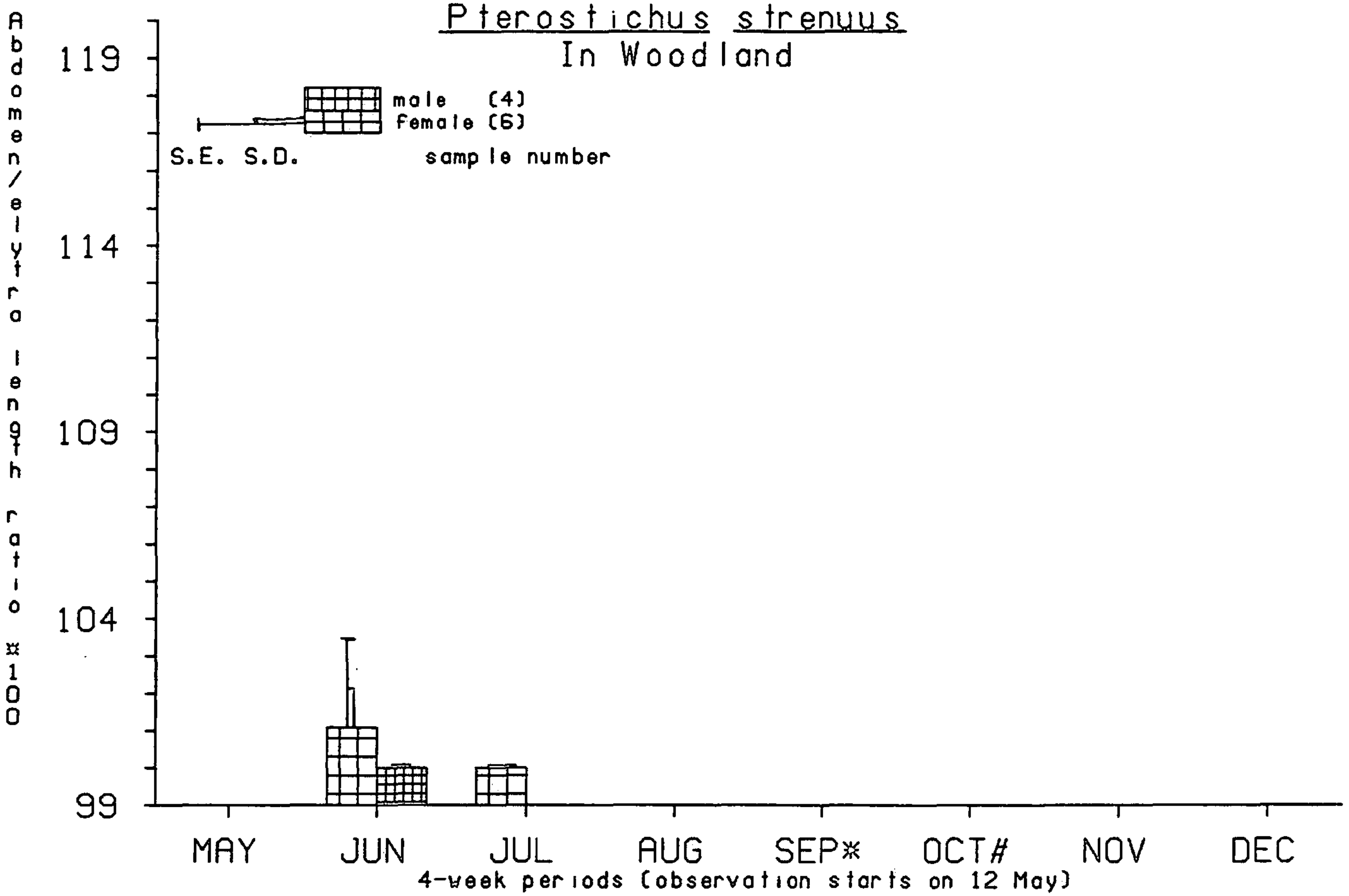
Captures were made in the present study at the Durham woodland from May to July, with a peak in nt<Fig.4.17.1>. A large average ratio of female abdomen/elytra length was found in June <Fig.4.17.2>. The *P. strenuus* population at the Durham woodland seems to have had a spring breeding period with a peak in June. The timing of the breeding season is consistent with that found in previous studies in southern England (Murdoch 1967) and the highlands of northern England (Houston 1970).

<Fig.4.17.1> Frequency of capture (including re-capture) in 4-week periods



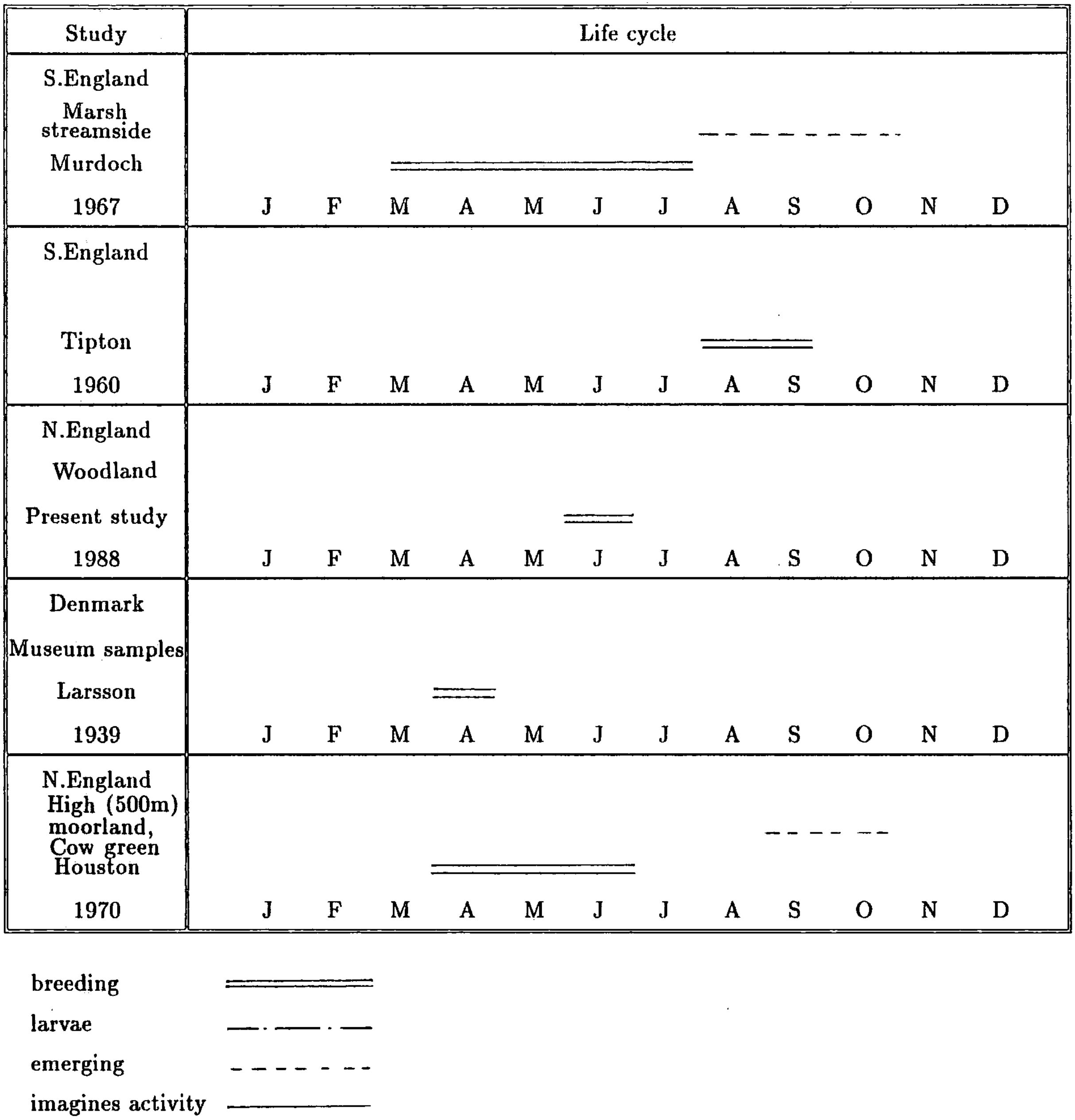
※ Data are for 3 weeks
Data are for 1 week

<Fig.4.17.2> Abdomen/elytra length ratio in 4-week periods



¤ Data are for 3 weeks
Data are for 1 week

<Fig. 4.17.3> The results of previous and present study of life cycle of *Pterostichus strenuus*



Many of the species included here will be considered further in chapter 5 during a discussion of the composition of the Carabid community. All species will then be grouped in chapter 6 into four categories according to the seasons of breeding and emergence.

Chapter V

Composition of the Carabid Community

Table 5.1 lists the species for which two or more individuals were caught in each of the two habitats. Table 5.2 shows the number of species, the diversity index and the equitability of the two habitats in 4-week periods. These parameters (Lloyd and Ghelardi 1964) provide information on the structure of the Carabid community.

In general, the Durham Carabid community had a larger equitability and a larger number of species in the woodland than in the grassland. The reason for this seems to be that the grassland has a less diverse range of microhabitats than the woodland. The number of species in the woodland Carabid community displayed a peak associated with a large equitability in July. The large equitability of the woodland community in that month was influenced strongly by a decreasing number of individuals of the dominant species, *Pterostichus madidus.* The equitability indicates that the community was close to the species composition distribution of the "broken-stick" model of MacArthur (1957). A comparison of the results of species number, diversity index and equitability in the two habitats in August and September shows that the grassland Carabid community is more strongly dominated by *Pterostichus madidus* than is the woodland community.

Fig.5.1 shows the capture duration and median of the duration of activity of each species in the woodland in order of elytra length (the best measure available of body size). Each of the two dominant species had two separate periods of activity. (The medians of the durations of activity of the dominant species are taken as the medians of the active periods of the breeding seasons; see also Loreau (1988)). The following were observed:

1. the dominant species in the Carabid community were medium-sized imagines;
2. smaller-sized species tended to remain more active in late autumn and in winter than the larger species;
3. There were two groups of the woodland Carabid beetles, one of which has an average elytra length of more than 7mm (7 species) — the *large body group* — and the other of less than 6mm (7 species) — the *small body group.* (These average elytra lengths correspond to body lengths greater than approximately 11mm and less than 11mm respectively).
4. In the *large body group*, when the seasonal changes of capture number are compared between species, there may be a tendency that the Carabid beetles of smaller body size have a peak of activity earlier in the year. (However, this tendency is not observed significantly in the distribution of the medians of the periods of activity : $T_B = 0.2$, $p > 0.10$). The larger Carabid beetles are most active in August; later in the year the smaller individuals of this *large body group* remain active.

   Examples of the timing of capture peaks are:

   - in June: *Pterostichus madidus* (breeding), *Nebria brevicollis* (emergence) *Pterostichus melanarius*
   - in July: *Pterostichus niger, Pterostichus melanarius, Abax parallelopipedus*
   - in August: *Cychrus caraboides, Carabus violaceus, Pterostichus ma-*

  didus (emergence)

  - in September: *Nebria brevicollis* (breeding).

5. In the *small body group*, a similar tendency is observed, but with the distinction that the individuals of the largest species (*Calathus piceus*) were most active in July.

   Examples of this are;

   - June: *Loricera pilicornis*
   - July: *Patrobus atrorufus, Calathus piceus, Leistus rufomarginatus*
   - August: *Leistus rufescens*
   - October: *Leistus ferrugineus.*

A lack of sufficient data precludes a similar division of the grassland Carabid beetles.

When the results for the Carabid *large body group* of Durham are compared with those of Loreau's (1988) study in beech wood in Belgium <Fig.5.2> and the Southwood (1978) study in woodland and grassland areas in southern England <Fig.5.3>, then:

1. although no tendency was found in the present work for a shift in the median of the period of activity in the *large body group*, the results of Loreau and Southwood did show evidence for such a shift: $r_s = 0.577$, $p < 0.05$ (Loreau 1988), $r_s = 0.503$, $p < 0.01$ (Southwood 1978: from Loreau reference) but
2. the *small body group* activity in Durham seems to be different from that of the previous two studies, which show intense activity in spring and early summer

for the majority of the *small body group* and few medium or large species in autumn and winter.

3. the period of activity is more restricted in summer for the Durham Carabid community than for the Belgium and southern England community. Short, active seasons of various species were observed in June, July and August; consequently each season does not have the the strong characteristics described by Southwood (1978), i.e. in the Durham woodland and grassland, the *small body group* were not clearly spring breeders and the *large body group* also were not clearly autumn breeders.

Reasons for the previous results noted in point 1 above are suggested by Loreau from his study with relation to prey:

- There is a gradient of size (or biomass, or catchability) in the various prey types, to which the Carabid species are adapted through different specializations according to their size.
- The periods of Carabid beetle activity and the periods of their prey activity coincide with each other.
- The activity of Carabid beetles and their prey are correlated with each other in dominant species (*Pterostichus oblongopunctatus* and *Carabus problematichus*).

The disagreement of the results of the present work with those of the previous studies may be due to insufficient data.

An explanation of point 2 is implied by the study of Loreau (1988). The activities of small species do not have a strong relation with prey availability. For example, *Notiophilus biguttatus* activity was found to be related to the availability of collembolan prey in Belgian forest in which *N. Biguttatus* was abundant2; both were active in August. However, the Loreau results in beechwood showed different activity peaks between *N. biguttatus* (peak in April and May) and collembolan (peak in summer). It is suggested here that the smaller insects at the Durham site, being in the lower position of the food web, develop and mature faster than larger insects: their life cycle may therefore be more flexible in order to avoid predators (e.g. large insects).

One reason for the restricted activity stated in point 3 may be the presence of lower temperatures. Average temperature: 9.9°C (2.2°C–17.5°C) at Lembeek (the data from Uccle) in Belgium; 9.9°C (3.4°C–16.5°C) at Berkshire in southern England; 8.5°C (2.2°C–14.9°C) at Durham.

Recall the results of Chapter 4 (*Results for Each Species*), from which four species in Durham were observed to remain active in winter. These were

- *Leistus ferrugineus*
- *Leistus rufomarginatus*
- *Notiophilus biguttatus*,

and

- *Nebria brevicollis*
- *Pterostichus madidus*
- *Pterostichus niger.*

The first three species are in the *small body group* and the last three species are the smallest species in the *large body group.*

It is therefore concluded that smaller species tend to remain active in winter. One reason for this may be the avoidance of large insect predators that are active from late summer to autumn.

<Table 5.1> List of species for the two habitats

(Species of more than two are listed)

Species name	Woodland							Grassland			
Number of 4-week periods	5	6	7	8	9	11	12	8	9	11	12
Abax parallelepipedus	○	○	○	○	○			○	○		
Amara curta									○		
Benbidium bipustulatus					○	○	○	○		○	○
Calathus melanocepharus								○	○		
Calathus piceus		○	○	○	○			○			
Carabus violaceus	○	○	○	○	○			○	○		
Clivina fossor	○	○	○					○			
Cychrus caraboides		○	○	○	○						
Leistus ferrugineus		○		○		○					
Leistus rufescens			○	○	○						
Leistus ruformarginatus	○	○	○		○	○	○				
Loricera pilicornis	○	○	○	○	○			○		○	
Nebria brevicollis	○	○	○	○	○	○	○	○	○	○	○
Notiophilus biguttatus	○	○	○			○	○				
Patrobus atrorufus		○	○	○	○						
Pterostichus madidus	○	○	○	○	○	○	○	○	○	○	
Pterostichus melanarius	○		○					○			
Pterostichus niger		○	○	○	○	○	○	○	○		
Pterostichus nigrita			○		○						
Pterostichus strenuus	○	○	○								
Trechus obtusus		○		○	○	○		○	○	○	
Total 21	10	15	16	12	14	8	6	12	8	5	2

<Table 5.2> List of the diversity index of carabidae species and the species number by 4-week periods in the two habitats

Habitat	number of 4-week periods	Diversity index	Equitability	species number
Wood land	5	1.73	0.43	10
	6	2.55	0.53	15
	7	3.47	0.99	16
	8	2.20	0.51	12
	9	2.25	0.46	14
	11	2.77	1.19	8
	12	2.30	1.11	6
Grass land	8	1.20	0.24	12
	9	1.01	0.30	8
	11	1.84	0.92	5
	12	0.65	0.90	2

Equitability=s'/s

s : species number observed

s': hypothetical species number by the MacArthur model (1957)

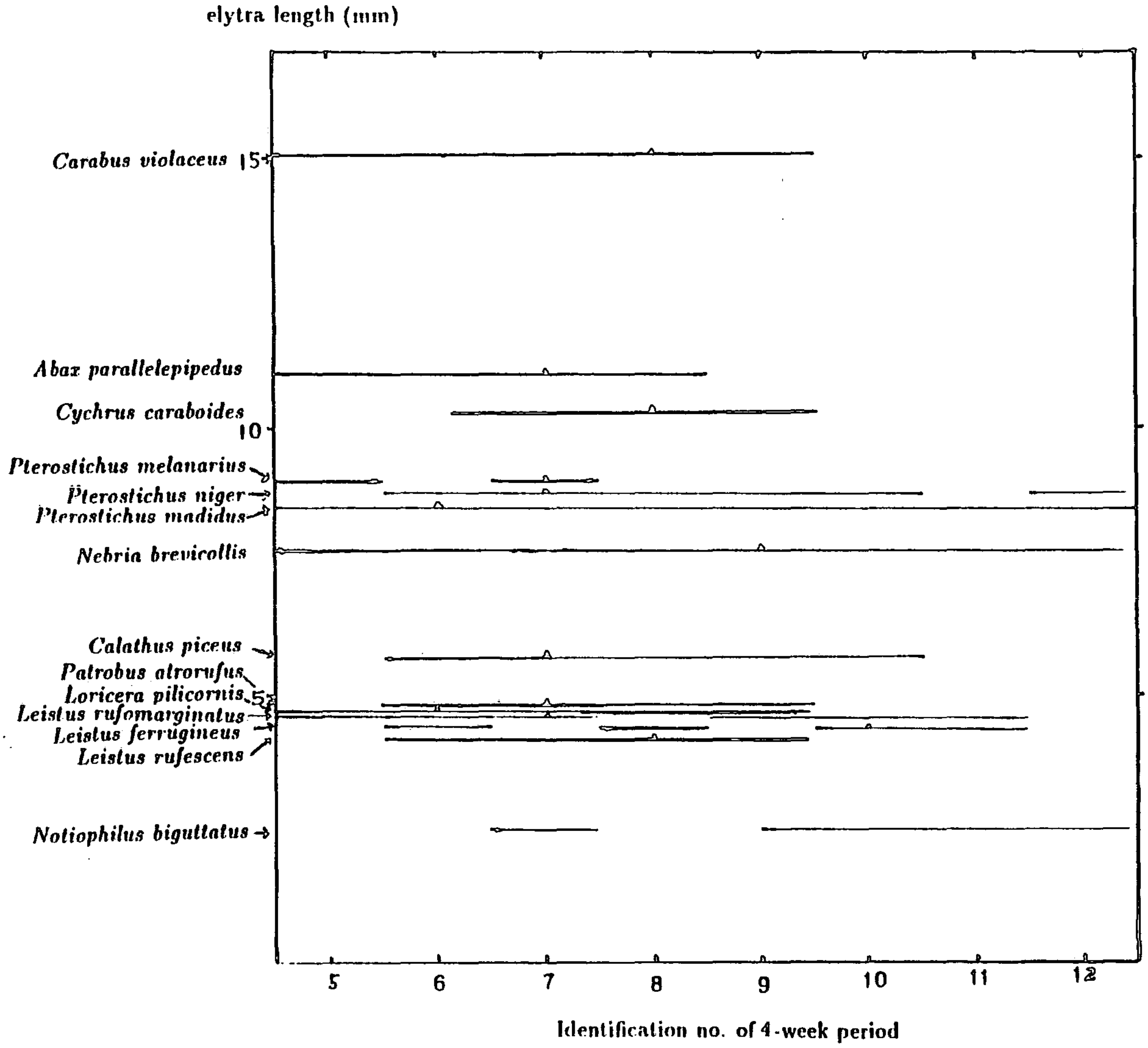
$$\pi_r = \frac{1}{s}\sum_{i=1}^{r} 1/(s-i+1)$$

$$M(s') = -\sum_{r=1}^{s} \pi_r \log_2 \pi_r$$

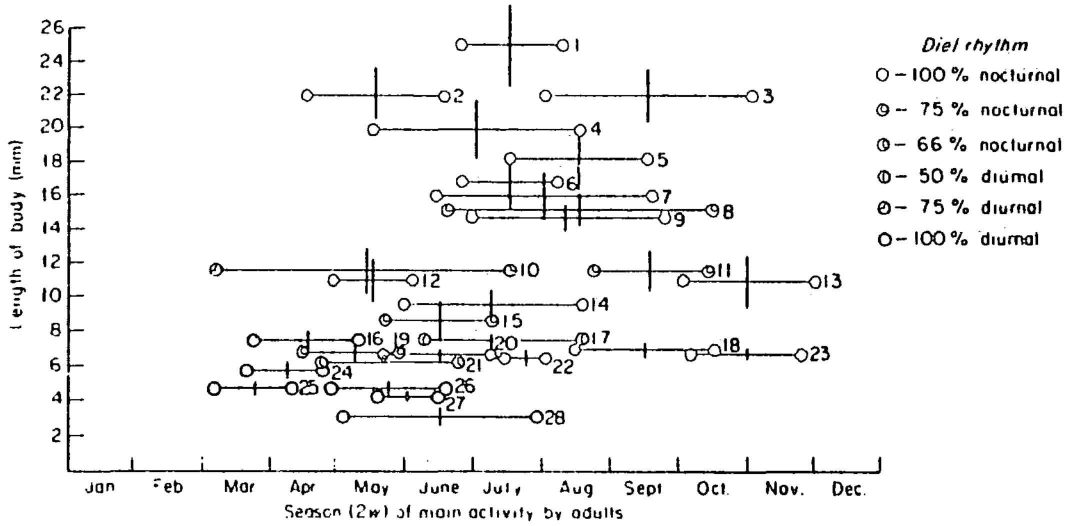
from table by M. Lloyd and R. J. Ghelardi (1964)

<Fig.5.1> Active period of each species in Carabid community in the woodland relating with their average elytra lengths

▵ indicates the median of theactive period of each species. For the dominant species (*Pterostichus madidus* and *Nebria brevicollis*), ▵ is taken as the median of the active period of the main breeding season.

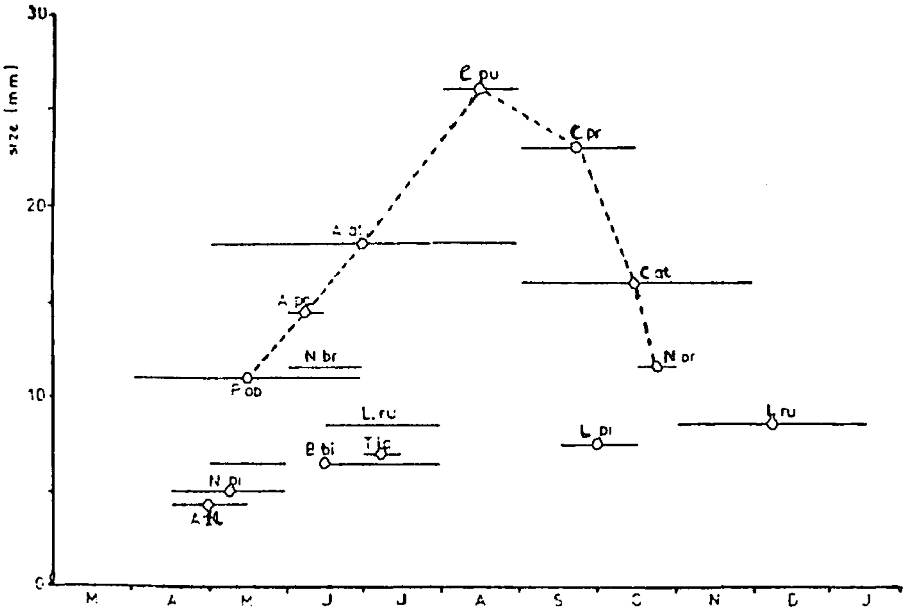


<Fig.5.2> Species packing in ground beetles (Carabidae) in terms of maximum adult activity, adult size and diel periodicity. Data for woodland-grassland area at Silwood Park in southern England from P.J.M.Greenslade (1961,1963,1965). Reference by Southwood (1978). The numerals identify species as follows:



1, *Carabus violaceus*; 2, *Carabus nemoralis*; 3, *Carabus problematicus*; 4, *Abax parallelepipedus*; 5, *Pterostichus niger*; 6, *Cychrus rostratus*; 7. *Pterostichus melanarius*; 8, *Pterostichus madidus*; 9, *Harpalus rufipes*; 10, *Pterostichus caerulescens*; 11, *Calathus fuscipes*; 12, *Nebria brevicollis* spring; 13, *Nebria brevicollis* autumn; 14, *Calathus piceus*; 15, *Harpalus affinis*; 16, *Loricera pilicornis*; 17, *Amara lunicollis*; 18, *Calathus melanocephalus*; 19, *Agonum dorsale*; 20, *Stomis pumicatus*; 21, *Amara communis*; 22, *Synuchus nivalis*; 23, *Leistus ferrugineus*; 24, *Notiophilus rufipes*; 25, *Notiophilus substriatus*; 26, *Notiophilus biguttatus*; 27, *Asaphidion flavipes*; 28, *Bembidion lampros*.

<Fig.5.3> Size as a function ofperiod of activity in the 13 main species in the beechwood in Belgium. The dashed line joins the successive niche centres of the large species. Species are mentioned by their abbreviation;



P. ob. = *Pterostichus oblongopunctatus*; A. pa. = *Abax parallelus*; A. at. = *Abax ater*; C. pu. = *Carabus purpurascens*; C. pr. = *Carabus problematicus*; C. at. = *Cychrus attenuatus*; N. br. = *Nebria brevicollis*; A. fl. = *Asaphidion flavipes*; N. bi. = *Notiophilus biguttatus*; B. bi. = *Badister bipustulatus*; T. la. = *Trichotichnus laevicollis*; L. pi. = *Loricera pilicornis*; L. ru. = *Leistus rufomarginatus*.

Chapter VI

Discussion and Summary

Consider the shifts of the life cycles of Carabid beetles.

The Carabidae community has been studied at adjacent woodland and grassland habitats in Durham, north-east England from 12 May to 23 December, 1988. Some seventeen Carabid species have been included in the present study. The species are here divided into four groups according to life cycle, using the classification scheme of Thiele (1977).

(1) Autumn breeders with a thermic hibernation parapause at the larval stage and no dormancy in the course of adult development

- o *Calathus melanocephalus*
- o *Calathus piceus*
- o *Carabus violaceus*
- o *Cychrus caraboides*
- o *Leistus rufescens*
- o *Leistus rufomarginatus*
- o *Pterostichus madidus*
- o *Pterostichus melanarius*
- o *Pterostichus niger*

(2) Autumn breeders with a thermic hibernation parapause for the larvae and a photoperiodic aestivation parapause for the adults

- *Leistus ferrugineus*
- *Nebria brevicollis*
- *Patrobus atrorufus*

(3) Spring breeders with no larval dormancy but with an obligatory dormancy in the adults (parapause) governed mainly by photoperiod

- *Loricera pilicornis*
- *Pterostichus nigrita*
- *Pterostichus strenuus*

(4) Species with unstable conditions of hibernation and potentially lacking dormancy

- *Abax parallelopipedus*
- *Notiophilus biguttatus*

When the life cycles of various species within a given group are considered together with the local environmental conditions typical of the Durham site, the results of the present study are found to be consistent with a shift in the pattern of life cycles observed during previous studies at increasingly severe geographical locations.

The four groups are now considered in turn.

Group (1)

As environmental conditions become more severe, this group shows:

1. a shift of the breeding season

   from autumn

   (a) to summer
      - *Calathus melanocephalus*
      - *Carabus violaceus*
      - *Cychrus caraboides*
      - *Leistus rufomarginatus*
      - *Pterostichus melanarius*
      - *Pterostichus niger*

   (b) to spring
      - *Pterostichus madidus*

   and

2. a shift of the emergence season

   from spring

   (a) to summer
      - *Carabus violaceus*
      - *Cychrus caraboides*
      - *Leistus rufescens*
      - *Pterostichus madidus*
      - *Pterostichus melanarius*

and

(b) to autumn

- *Calathus melanocephalus*
- *Leistus rufomarginatus*
- *Pterostichus madidus*
- *Pterostichus niger*

3. Univoltine autumn breeders are replaced initially by a mixture of univoltine and semivoltine breeders, and finally by semivoltine spring breeders. *Leistus rufescens* is an exception, for only a univoltine life cycle has been observed (See Fig.4.9.4).

The larval development of *Pterostichus melanarius* is inhibited by low temperature (thermic hibernation parapause as obligation) at the 3rd larval stage (Thiele and Krehan 1969, Krehan 1970); the same is observed for *Pterostichus niger* (Witzke 1976). This explains why lower temperatures and protracted winters delay the emergence period from spring to summer. It also explains why a biennial life cycle is found at the more severe environmental locations; maturation cannot be completed in the shorter time available after the delayed emergence. Consequently a fraction of the population which matures more slowly, or has emerged later in the emergence season than others in the population, must be semivoltine and can begin to oviposit earlier than the next new imago generation. This applies to

- *Pterostichus madidus*: in the present study and the results from upland in northern England (Houston 1970),

- *Pterostichus melanarius*: in the Netherlands (van Dijk 1972, 1973, 1979) and
- *Carabus violaceus*: in the present study in the Durham woodland.

In the more severe environmental locations, a larger proportion of a population must follow a semivoltine life cycle. On the other hand, the breeding seasons have been shown to shift to earlier seasons in the year under more severe conditions. Faster maturation is then expected in the severe environments. Experimental studies in the laboratory should be performed to examine this prediction. In the same way that Ferenz experimented on *Pterostichus nigrita* (1975), animals caught at various geographical areas should be examined under a range of temperature conditions in order to determine the time required to reach maturity.

Group (2)

The three species included in this group have been found to display:

1. a slight shift of breeding
   - in late summer and autumn: for *Patrobus atrorufus*
   - during autumn: *Nebria brevicollis, Leistus ferrugineus.*
2. a shift of emergence season from May to June: all species of this group
3. a change of life cycle from univoltine late summer–autumn breeding to a mixture of univoltine and semivoltine summer breeding.

It should be noted that *Patrobus atrorufus* populations in the extreme environments (e.g. upland in northern England and central Norway) have shown a shift of life cycle from a mixture of univoltine and semivoltine summer–early autumn breeding (e.g. upland of northern England and possibly the Durham woodland) to semivoltine spring breeding (e.g. upland in central Norway). They also show a shortening of the summer emergence season

- from June–September: upland in northen England;
- to July–August: central Norway

The larvae hibernate at low temperatures (Thiele 1969,1971)

- for *Nebria brevicollis* from the 1st to 3rd larval stage, but
- for *Patrobus atrorufus* at the 3rd larval stage.

Metamorphosis requires a rising temperature at the end of the 3rd instar for larvae of both species. However, the time of the emergence of imagines is fixed at the period May to June, in contrast with a shift of the emergence season by group (1) species from spring to summer which requires the same condition for metamorphosis. By comparing the results of the previous and present studies and the monthly average temperature of each of tthe geographical areas, emergence seems to be more strongly controlled by temperature than that found for group (1). See Fig.5.4 and Table 4.0.2.

For example, for the start of emergence

- about 13°C: for *Patrobus atrorufus*
- about 12°C: for *Nebria brevicollis*

except for the *Patrobus atrorufus* population in extreme conditions, i.e. central Norway and upland in northern England. The onset of aestivation interrupts maturation and is controlled by photoperiodicity and temperature (Thiele 1969, 1971). In the experimental conditions, short-day photoperiodicity for the start of egg-ripening was found at 16.0–17.0h light/day for *N. brevicollis* and *P. atrorufus*. This is supported by the previous field studies at various geographical locations. The start of reproduction is determined by additional temperature requirements for *Nebria brevicollis*: lower temperatures inhibit maturation less, therefore the animals in the more severe environmental areas breed earlier than those in the warmer areas. The experimental results of Thiele (1971) are in agreement with those of the previous field studies.

For the populations of *Patrobus atrorufus* of Scandinavia and uplands in northern England <Fig.4.13.5>, the breeding season moves from August to June as the altitude becomes greater. Refseth (1986) found that the population with an earlier breeding season (June) has already begun to mature in May before the photoperiodical signal turns to short-day. Refseth also suggested that the Scandinavian population may be a different race phenologically to the species in other western European areas. Although experiments have not been carried out, Refseth (1986) has proposed a correspondence between the breeding season and the end of the vegetation growth period for the species *Patrobus atrorufus* and *Patrobus assimilis* for several altitude points in central Norway. The results show that temperature has a strong influence which may be direct or indirect. A lower temperature causes a greater acceleration of maturation for the semivoltine *P. atrorufus*.

Group (3)

Throughout the various geographical regions, the life cyles of carabid beetles of this group show:

1. spring and/or early summer breeding

2. an autumn emergence season

3. a univoltine life cycle.

The species *Pterostichus nigrita* and *Pterostichus strenuus* match this general description and show a fixed emergence season in autumn (mainly September) and a spring breeding season which starts later and ends earlier with harsher conditions.

Loricera pilicornis does not fit clearly into this description. (See below.)

The spring breeding and the summertime larval development are explained by the results of experiments which have shown that the female maturation of *Pterostichus nigrita* is controlled by photoperiod. The critical photoperiod signals are, for example:

for previtellogenesis: short-day photoperiod

- 15.5h light/day 51°N
- 19.5h light/day 66°N

for vitellogenesis: long-day photoperiod

- 13.1h light/day 51°N
- 14.0h light/day 66°N.

The critical photoperiod for previtellogenesis is the end of July, while the critical photoperiod for vitellogenesis is the beginning of April, irrespective of geographical location. (See Fig.6.2.) However, the results of the previous and present field studies of *Pterostichus nigrita* show a later starting of breeding in harsher environments. It may therefore be concluded that the start of the breeding season is controlled directly or indirectly by temperature in addition to the photoperiodical signal.

The previous studies for *Pterostichus strenuus* show that breeding began at approximately the same time in the various geographical study areas <Fig.4.17.3>.

Ferenz (1975) has suggested that the larvae of *P. nigrita*, which lives in more severe environments, develop faster in the shorter warm seasons <Table 6.2>. However, the comparisons of the results of the field studies in various areas for both *P. nigrita* and *P. strenuus* show that the time from the start of oviposition to the start of emergence is approximately four months. They do not show a quickening of larval development in harsher environments compared with that in milder environments.

Loricera pilicornis <Fig.4.11.5>: As environments become more severe this species shows:

1. a shift of the breeding season for study areas with average temperatures:
    - up to and including that prevailing at the upland in northern England <Table 4.0.3>: a shift of the breeding season from twice per year (in spring and autumn) to once per year (in spring–early summer), with a shortening duration of activity.
    - towards the more severe environments of central Norway: the breeding season starts earlier in the year.
2. a shift of the emergence season from summer (July) to autumn (September)
3. a univoltine life cycle.

The time between the start of breeding and the start of emergence is approximately two to three months.

The following suggestions are therefore made:

1. the signals for the start of maturation for the Scandinavian *L. pilicornis* population are different to those for the populations in the other European areas, or
2. after the signals, maturation occurs faster for the Scandinavian population.

Group (4)

As conditions become more severe, this group shows:

1. breeding seasons which reduce in number from three to one per year. For example <Fig.4.3.5>:
   - three breeding seasons per year: in the Netherlands (van der Drift 1951);
   - two per year: in Köln in West Germany (Löser 1970, 1972 and Lauterbach 1964 at low regions, slopes with southern exposure and warmer years);
   - one per year: highlands in northern England (Houston 1970) and in West Germany (Löser 1970, 1972) and Lauterbach (1964) at high regions, slopes with northern exposure and colder years.

   Such restrictions are caused by a lowering of the temperature with the geographical location (Löser 1970, 1972 and Lauterbach 1964).

As the active seasons for these species become shorter, the number of emergence seasons can reduce from two to one per year (Löser at Köln).

2. the breeding seasons also reduce in number from three to one.

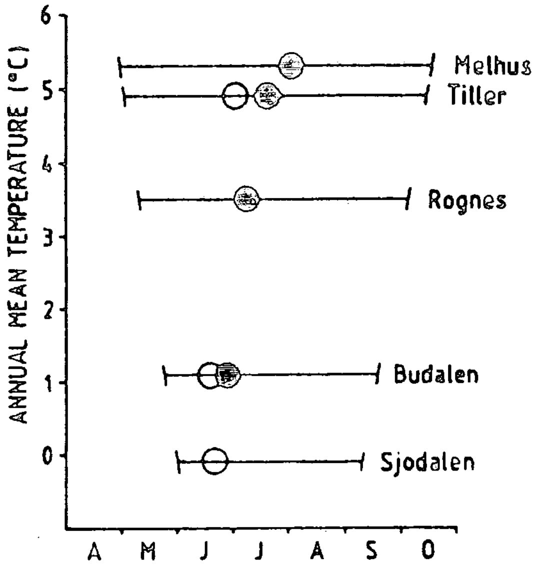
<Tabe 6.1> Mortality in the pre-adult stages of *P. nigrita* from two different regions in % of initial population. From Ferenz (1975).

Temperature °C	Central Europe (Köln 50°N)	Lapland (Messaure 66°N)
10	87	42
15	11	28
20	18	12
25	12	16
30	63	66

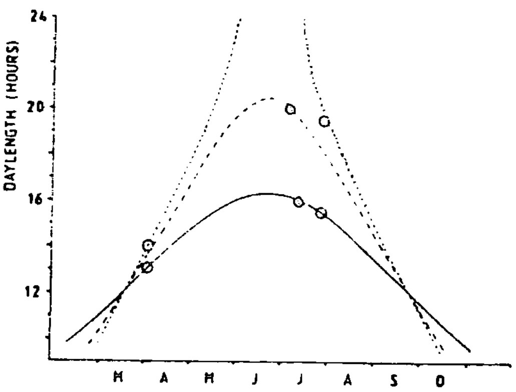
<Tabe 6.2> The duration of larval development of *P. nigrita* from two different regions; mean number of days, with standard deviation. From Ferenz (1975).

Temperature °C	Central Europe (Köln 50°N)	Lapland (Messaure 66°N)	Reduction rate of duration of development
10	136.9±9.3 (n=13)	99.6±7.7 (n=29)	27%
15	44.4±2.9 (n=89)	42.0±2.8 (n=36)	4%
20	31.5±1.8 (n=41)	28.7±1.6 (n=44)	9%
25	23.2±1.3 (n=44)	19.9±1.7 (n=42)	13%
30	25.7±4.0 (n=37)	19.8±2.1 (n=17)	23%

<**Fig.6.1**> The duration of the vegetation periods at the study sites in relation to the annual mean temperatures with the times of breeding of *P. atrorufus* (filled circles) and *P. assimilis* (open circles) indicated. From Refseth (1986).



<**Fig.6.2**> The seasonal variations in the daylength (excluding twilight) at three selected latitudes: —: Bodø(67°N), —: Trondheim (63°N), —:Köln (51°N). The critical photoperiods for maturation in *P. nigrita* (open circle) and *P. atrorufus* (closed circles) at different latitudes are indicated. From Refseth (1986).



Communities of Carabid beetles have been studied at adjacent woodland and grassland habitats in Durham, north-east England. Fieldwork was performed during the period 1988 May 12 to December 23.

Of a total of 25 Carabid species identified, 21 were observed in woodland and 15 in grassland. A subset of some 17 species was considered in Chapters 4 and 5.

The biological seasons of the adult individuals of the 17 species were investigated using the data collected on frequency of capture (including the peak(s) of capture and the relative proportions of the two sexes), the distances of movement and the stages of maturity. A measurement of the length of the mandible tip was used as the principal indication of the age of a given individual. The stages of maturity were determined using the approximate distributions of the observed ages of individuals within a species, together with the data on the ratio of the length of the abdomen to that of the elytra, and the volume and number of eggs.

Also examined was the composition of the community of Carabid species using the data on equitability and the relation of activity to the body size. The dominant species in the Durham woodland and grassland have been found to be *Pterostichus madidus* and *Nebria brevicollis.* Generally, the equitability of the Carabid community in the woodland was greater than in the grassland.

Frequent comparisons of the present work have been made with the results of the studies of Carabid beetles at various habitats at many locations in north-west Europe. The results of the Durham study are apparently consistent with the relationship between the time of occurrence of the breeding and emergence seasons and the relative severity of the local environment.

Bibliography

Baars, M. A., Dijk, T. S. van, 1984. Population dynamics of two Carabid beetles at a Dutch heathland. II. Egg production and survival in relation to density. *J. Anim. Ecol.* **53**, 389–400.

Boer, P. J. den, 1958. Activiteitsperioden van loopkevers in Meijendel. *Entomol. Ber. Amst.* **18**, 80–89.

Briggs, J. B., 1965. Biology of some ground beetles (Coleoptera, Carabidae) injurious to strawberries. *Bull. Entomol. Res.* **56**, 79–93.

Bruun, I., 1967. *Climatological summaries for Norway. Standard normals. 1931–60 of the air tempeature in Norawy.* Det Norske Meteorogiske Institutt, Oslo.

Butterfield, J. E. L., 1986. Changes in life-cyle strategies of *Carabus problematichus* over a range of altitudes in northern England. *Ecol. Entomol.* **11**, 17–26.

Darlington, P. J., 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monographs* **13**, 37–61.

Davies, L., 1987. Long adult life, low reproduction and competition in two sub-Antarctic carabid beetles. *Ecol. Ent.* **12**, 149–162

Desender, K., 1988. Spatial distribution of Carabid beetles in a pasture. *Rev. Ecol. Biol. Soc.* **25** (**1**), 101–113.

Dijk, T. S. van, 1972. The significance of the diversity in age composition of *Calathus melanocephalus* L. (Col. Car) in space and time at Schiermonnikoog. *Oecologia (Berl.)* **10**, 111-136.

Dijk, T. S. van, 1973. The age-composition of *Calathus melanocephalus* (L.) analysed by studying marked individuals kept within fenced sites. *Oecologia (Berl.)* **12**, 213–240.

Dijk, T. S. van, 1979. On the relationship between reproduction, age and survival in two Carabid beeles: *Calathus melanocephalus* (L.) and *Pterostichus coerulescens* (L.). *Oecologia (Berl.)* **40**, 63-80.

Ferenz, H. J., 1975. Anpassungen von *Pterostichus nigrita* an subarktische Bedingungen. *Oecologia (Berl.)* **19**, 49–57.

Ferenz, H. J., 1975. Photoperiodic and hormonal control of reproduction in male beetles, *Pterostichus nigrita*. *J. Insect Physiol.* **21**, 331–341.

Ferenz, H. J., 1977, Two-step photoperiodic and hormonal control of reproduction in the female beetle, *Perostichus nigrita*. *J. Insect. Physiol.* **23**, 671–676.

Forsythe, Trevor, G., 1987. The relationship between body form and habitat in some Carabidae (Coleoptera). *J. Ecol. Lond.* **211**, 643–666.

Fusskåhl. B., 1972. The invertebrate fauna of the Kilpisjarvi area, Finnish lapland. 9. Carabidae, with special notes on ecology and breeding biology. *Acta Soc. Fauna Flora Fenn.* **80**, 99–119.

Geiler, H., 1960. Zur Ökologie und Phänologie der auf mitteldeutschen Luzerne destander vorkommenden Insekten unter bederer Bericksichtigung der Coleoptera. *Z. angew. Ent.* **47**, 128–136.

Gilbert, O., 1956. The natural histories of four species of *Calathus* (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. *Oikos* **7**, 22–47.

Green, A., 1975. Biology of five species of *Cychrini* (Coleoptera, Carabidae) in the Steppe region of southern Washington (U.S.A.) *Melanderia* **19**, 1–49.

Greenslade, P. J. M., 1963. Further notes on aggregation in Carabidade (Coleoptera), with special reference to *Nebria brevicollis* (F.). *Entomol. Mon. Mag.* **99**, 109–114.

Greenslade, P. J. M., 1964. The distribution, dispersal and size of a population of *Nebria brevicollis* (F.) with comparative studies on three other Carabidae. *J. Animal. Ecol.* **33**, 311–333.

Greenslade, P. J. M., 1965. On the ecology of some British carabid beetles with special reference to life histories. *Trans. Soc. Brit. Entomol.* **16**, 149–179.

Heerdt, P. F. van, Blockhuis, B., Haaften, C. van, 1976. The reproductive cycle and age composition of a population of *P. oblongopunctatus* Fabricius in the Netherlands (Coleoptera: Carabidae). *Tijdschr. Entomol.* **119**, 1–13.

Heydeman, B., 1962. Der Einfluß des Deichbaus an der Nordsee auf Larven unt Imagines von Carabiden unt Staphyliniden. *Ber. 9. Wanderversamm. Deut. Entomol.* 237–274.

Houston, W. W. K., 1970. "Ecological studies on moorland ground beetles Coleoptera: Carabidae" Durham Univ. Ph.D. thesis

Houston, W. W. K., 1981. The life cycle and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst (Col. Carabidae) on moorland in northern England. *Ecol. Entomol.* 6, 263–271.

Jacobsen, M., 1974. Insect pheromones. in Rockstein, M. (ed.), *The physiolosy of insecta. VolIII* 2nd ed., Academic Press, London.

Jørum, P., 1980. Life cycles and annual activity patterns of *Pterostichus melanarius* and *P. niger* in a Danish beech wood. *Ent. Medd.* 48, 19–25.

Krebs, C. J., 1985. *Ecology. The experimental analysis of distribution and abundance*.3rd ed. Harper, London.

Kålåss, J.A., 1985. Species composition and seasonal activity patterns of Carabidae (Col.) in a smal deciduous forest in western Norway. *Fauna norv. Ser. B* 32, 28–32.

Kirk, V. M., Dupraz, B. J., 1972. Discharge by a female ground beetles, *Pterostichus lucublandus* (Coleoptera, Carabidae),used as a defense against males. *Ann. Entmol. Soc. Am.* 65, 513.

Larsson, S. G. 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. *Entomol. Meddr.* 20, 277–560.

Lauterbach, A. W., 1964. Verbreitungs und aktivitätsbistimmende Faktoren bei Carabiden in sauerländischen Wälden. *Abhandl. Landesmus. Naturkunde Münter* 26, 1-103.

Lindroth, C. H., 1945. Die Fennioscandischen Carabidae. *Göteborgs Kungl Vetensk. Vitterh. Samh. Handl. (Ser. B4)* **1-2**, Spezieller Teil, 1–709 .

Lindroth, C. H., 1949. Die Fennioscandischen Carabidae. *Göteborgs Kungl Vetensk. Vitterh. Samh. Handl. (Ser. B4)* **3**, Allgemeiner Tail, 1–911 .

Lindroth, C. H., 1974. "Handbooks for the identification of British insects. (Vol.IV part2)" Royal entomological society of London, London.

Lindroth, C. H., 1985. *Fauna Entomologica Scandinavica. The Carabidae (Coleoptera) of Fenoscandia and Denmark. vol 15.* E. J. Brill Scandinavian Science Press Ltd., Leiden Copenhagen.

Lloyd, M., Ghelardi, R. J., 1964. The table for calculating the 'Equitability' component of species diversity. *J. Animal Ecol.* 33, 217–225.

Loreau, M., 1985. Annual activity and life cycles of carabid beetles in two forest communities. *Holarctic Ecol.* 8, 228–235.

Loreau, M., 1986. Niche differentiation and community organization in forest carabid beetles. pp465–485. in Boer, P. J. den, Luff, M. L., Mossakowski, D. and Weber, F. (eds.), *Carabid beetles: their adaptation and dynamics.*, Gustav Fisher, Stuttgart.

Loreau, M., 1988. Determinants of the seasonal pattern in the niche structure of a forest community. *Pedobiologia* **31**, 75–87.

Loreau, M., 1987. Vertical distribution of activity of carabid beetles in a beech forest floor. *Pedobiologia* **30**, 173–178.

Löser, S., 1970. Brutfürsorge und Brutpflege bei Laufkäfern der Gattung *Abax*. *Verh. Deut. Zool. Ges. Wörzburg* **1969**, 322–326.

Löser, S., 1972. Art und Ursachen der Verbreitung einiger Carabidenarten (Coleoptera) im Grenzraum Ebene-Mittelgebridge. *Zool. Jb. Syst.* **99**, 213–262.

Luff, M. L., 1973. The annual activity pattern and life cycle of *Pterostichus madidus* (F.) (Coleoptera, Carabidae). *Entomol. Scand.* **4**, 259-273.

Luff, M. L., 1974. Adult and larval feeding habits of *Pterostichus madidus* (F.) (Coleoptera, Carabidae). *J. Nat. Hist.* **8**, 403–409.

Luff, M. L., 1986. Aggregation of some Carabidae in pitfall traps. pp385–397: in Boer, P. J. den, Luff, M. L., Mossakowski, D. and Weber, F. (eds.), *Carabid beetles: their adaptation and dynamics.*, Gustav Fisher, Stuttgart.

MacArthur*

Meteorological office, 1976. *Averages of temperature for the United Kingdom 1941 - 1970 (Met O 883)*, Hobbs the Printers Ltd, Southhampton

Milliron, H. E., 1967. A successful method for artificially hibernating *Megabombus fervidus* (F.) and notes on a related species. *Can. Ent.* **99**, 1321–1332.

Moor, B. P., 1979. Chemical defence in Carabid and its bearing on phylogeny. pp193–208: in Erwin, T. L., Ball, G.E., Whithhead, D. R. and Halpern, A. L. *Carabid beetles: Their evolution, natural history, and classification*. Dr.W. Junk bv Publishers, London.

Moroney, M. J., 1956. *Facts from figures.* 3rd ed., Penguin Book., London.

Müller, G., 1970. Der Sexual-Index bei Carabiden als ökologisches Kriterium. *Entomol. Berichte*, 12–18.

Murdoch, W. W., 1967. Life history patterns of some British Carabidade (Coleoptera) and their ecological significance. *Oikos* **18**, 25–32.

Paarman, W., 1979. Ideas about the evolution of the various annual reproduction rythms in carabid beetles of the different climatic zones. *Miscell. Papers L. H. Wageningen* **18**, 119–132.

Penney, M. M., 1966. Studies on certain aspects of the ecology of *N. brevicollis* (F.) (Coleoptera, Carabidae). *J. Animal Ecol.* **35**, 505–512.

Penney, M. M., 1969. Diapause and reproduct in *Nebria Brevicollis* (F.).

*MacArthur, R. H., 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci., Wash. 43, 293-295.

J. Animal Ecol. **38**, 219–223.

Refseth, D., 1980. Differences in seasonal activity pattern and breeding time of *Patrobus atrorufus* in central Norway. *Holarctic Ecol.* **3**, 87–90.

Refseth, D., 1984. The life cycles and growth of *Carabus glabratus* and *C. violaceus* in Bulalen, central Norway. *Ecol. Enotmol.* **9** 449–455.

Refseth, D., 1986. Phenological adaptations in *Patrobus assimilis* and *P. atrorufus*. *Fauna norv. Ser. B* **33**, 57–63.

Refseth, D., 1988. Annual patterns of activity, reproduction and development in some Norwegian Carabidae (Coleoptera). *Fauna norv. Ser. B* **35**, 21–30.

Rijnsdorp, A. D., 1980. Pattern of movement and dispersal from a Dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae). *Oecologia (Berl.)* **45**, 274–281.

Schøtz–Christensen, B., 1965. Biology and population studies of Carabidae of Corynepheretum. *Natura Justlandica* **11**, 1–173.

Seber, G. A. F., 1982. *The estimation of animal abundance —and related parameters.* 2nd ed., Charles Griffin, Oxford.

Southwood, T. R. E., 1962. Migration of terrestrial arthoropod in relation to habitat. *Biol. Rev.* **37**, 171–214.

Southwood, T. R. E., 1966. *Ecological methods.* Methuen and Co. Ltd., London.

Southwood, T. R. E., 1978. The components of diversity. pp19–40: in Mound, L. A., and Waloff, N.,(eds.)) *Diversity of insect faunas, Symp. Roy. Entomol. Soc. no.9*, Blackwell, Oxford.

Southwood, T. R. E., 1978. *Ecological Methods with particular reference to the study of insect populations* 2nd ed., Chapman and Hall, Cambridge.

Sokal, R. R., Rohlf, F. J., 1969. *Biometry.* Freeman, San Francisco.

Sota, T., 1985. Activity patterns, diets and interspecific interactions of coexisting and autumn breeding carabids: *Carabus yaconinus* and *Laptecarabus kumagai* (Coleoptera, Carabidae). *Ecol. Entomol* **10**, 315–324

Szyszko, J., 1977. Male–to–female ratio in *Carabus arcensis* Herbst (Coleoptera, Carabidae) in various forest habitats. *Bulletin de l'academie polonaise des sciences série des sciences biologiques cl. II. Vol. XXV, No.6* 371–375pp.

Thiele, H.-U., 1969. The control of larval hibernation and of adult aestivation in the carabid beetles *Nebria brevicollis* F. and *Patrobus atrorufus*

Stroem. *Oecologia (Berl.)* **2**, 347–361.

Thiele, H.-U., Krehan, I., 1969. Experimentelle Untersuchungen zur Larvaldiapause des Carabiden *Pterostichus vulgaris*. *Entomol. Exper. Appl.* **12**, 67–73.

Thiele, H.-U., Krehan, I., 1971. Die steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren. *Zool. Jb. Syst.* **98**, 341–371

Thiele, H.-U., 1975. Interactions between photoperiodism and temperature with respect to the control of dormancy in the adult stage of *Pterostichus oblongopunctatus* F. (Coleoptera, Carabidae). I. Experiments on gonad maturation under different climatic conditions in the laboratory. *Oecologia (Berl.)* **19**, 39–47.

Thiele, H.-U., 1977. *Carabid beetles in their environment. A study on habitat selection by adaptation in physiology and behaviour. Zoophysiology and Ecology 10.* Springer, Berlin.

Tipton, 1960. ReadingUniv. Ph.D. Thesis. Some aspects of the biology of the beetles Nebria brevicollis (F.) and Feronia caerulescens (L.)

Vlijm, L., Dijk, T. S., Wijmans,S. Y., 1968. Ecological studies on carabid beetles. III. Winter mortality in adult *Calathus melanocephalus* (Linn.). Egg production and locomotory activity of the population which has hibernated. *Oecologia (Berl.)* **1**, 304–314.

Walker, M. A., 1985. The pitfall trap study on Carabidae and Staphylinidae (Coleoptera) in county Durham. *Entomol. Mon. Mag.* **21**, 9–18.

Weber, F., Hemmer, J., Klenner, M., Niesing, H., 1986. Life history phenomena in a subpopulation of *Carabus auronitens* F. from the Westphalian lowland. 439–464pp. in Boer, P. J. den, Luff, M. L., Mossakowski, D., Weber, F. (eds.), *Carabid beetles.* Gustav Fischer, Stuttgart.

Wilson, D. S., 1975. The adequacy of body size as a niche difference. *Amer. Nat.* **109**, 769–784.

World Meteorological Organizatione, 1971.(Climatological Normals (CLINO) for CLIMAT and CLIMAT SHIP STATIONS for the period 1931 - 1960 (WMO/OMM-No.117.TP.52)?, Geneva - Switzerland

Zant, T. van, Poulson, T. L., Kane, T. C., 1976. Body-size differences in carabid cave beetles. *Amer. Nat.* **12**,229–234.

Zordo, I. de, 1979. Phänologie von Carabiden im Hochgebirge Tirols (Obergurgl, Österreich) (Insecta: Coleoptera) *Ber. nat. med. Ver. Insbruck* **66**, 73–83.

Appendix A

A list of all species and the number in each habitat

(1) For field observation <Table A.1>

(2) For dissection <Table A.2>

Table A.1 List of all species and the number in each habitat for field observation

Species name	Grassland	Woodland	
Duration of data collesion	31/7-23/12	31/7-23/12	12/5-23/12
Sex	F M T	F M T	F M T
Abax parallelepipedus	5 2 7	10 9 19	28 28 56
Amara curta	2 0 2		
Amara familiaris	0 1 1	1 0 1	1 0 1
Amara plebia	1 0 1		
Badister bipustulatus		- - 1	- - 1
Benbidium guttula	8 1 9	2 2 4	2 2 4
Calathus melanocephalus	1 1 2		
Calathus piceus		1 0 1	7 1 8
Carabus violaceus	2 1 3	5 12 17	8 20 28
Clivina fossor	- - 3		
Cychrus caraboides		5 8 13	10 13 23
Elaphrus riparius		- - 1	- - 1
Leistus ferrugineus		4 2 6	4 3 7
Leistus rufescens		2 4 6	4 7 11
Leistus rufomarginatus		3 3 6	6 8 14
Loricera pilicornis	3 7 10	5 7 12	13 15 28
Nebria brevicollis	27 10 37	42 40 82	52 60 112
Notiophilus biguttatus		- - 9	26 5 31
Patrobus atrorufus	1 0 1	6 12 18	15 20 35
Pterostichus madidus	155 266 421	164 166 330	300 240 540
Pterostichus melanarius	6 13 19		3 1 4
Pterostichus niger	2 3 5	21 17 38	51 37 88
Pterostichus nigrita		0 1 1	1 1 2
Pterostichus strenuus			7 5 12
Trechus obtusus	18 13 31	1 2 3	1 2 3

Table A.2 List of all species and the number in each habitat for dissection

Species name	Grassland			Woodland		
Sex	Female	Male	Total	Female	Male	Total
Abax parallelepipedus	1	0	1	8	1	9
Calathus melanocepharus	4	0	4	1	0	1
Calathus piceus	1	0	1	19	3	22
Carabus violaceus				5	1	6
Cychrus caraboides				3	5	8
Leistus ferrugineus				3	2	5
Leistus rufescens				1	0	1
Leistus rufomarginatus				1	0	1
Loricera pilicornis	2	0	2	5	0	5
Nebria brevicollis	5	1	6	24	14	38
Notiophilus biguttatus				2	2	4
Patrobus atrorufus	2	0	2	3	1	4
Pterostichus madidus	33	24	57	45	20	65
Pterostichus melanarius	6	0	6	1	0	1
Pterostichus niger	0	1	1	8	2	10

Appendix B

The comparison of elytra lengths

Table B shows the measurements of elytra lengths for each species. The elytra lengths for both sexes of each species have also been considered in the additional information section of Chapter 4 (*Results for Each Species*), during which comparisons of the results of statistical tests were discussed.

Elytra lengths were measured to provide a comparison of body size. (Measurements of the whole body length are imprecise because live individuals extend the joints between head, thorax and abdomen when captured).

The females of six of the the species of Carabid beetles measured in Durham had elytra lengths that were significantly larger than those of the males. No species were found in which the elytra lengths of the males were significantly larger than those of the females.

Table B. List of elytra length of each species in the two habitat

Habitat	Woodland		Grassland		Comparison
Sex	Female	Male	Female	Male	
Abax parallelepipedus	10.877	11.147	10.980	11.20	$\wedge \; \genfrac{}{}{0pt}{}{<}{<} \; \wedge$
Calathus melanocephalus			4.700	4.500	$\vee$
Calathus piceus	5.804	4.900	5.700	—	$\genfrac{}{}{0pt}{}{\vee}{\vee} \; >$
Carabus violaceus	15.662	14.783	15.650	15.800	$\vee \; \genfrac{}{}{0pt}{}{>}{<} \; \wedge$
Cychrus caraboides	10.217	10.359			$\wedge$
Leistus ferrugineus	4.457	4.285			$\genfrac{}{}{0pt}{}{\vee}{\vee}$
Leistus rufescens	4.220	4.171			$\vee$
Leistus rufomarginatus	4.767	4.550			$\vee$
Loricera pilicornis	4.728	4.714	4.450	4.617	$\vee \; \genfrac{}{}{0pt}{}{\gg}{\gg} \; \wedge$
Nebria brevicollis	7.985	7.449	7.526	7.090	$\genfrac{}{}{0pt}{}{\vee}{\vee} \; \genfrac{}{}{0pt}{}{\gg}{>} \; \genfrac{}{}{0pt}{}{\vee}{\vee}$
Notiophilus biguttatus	3.615	3.086			$\genfrac{}{}{0pt}{}{\vee}{\vee}$
Patrobus atrorufus	4.982	4.684	4.367	—	$\vee \; >$
Pterostichus madidus	8.458	8.249	8.712	8.455	$\genfrac{}{}{0pt}{}{\vee}{\vee} \; \genfrac{}{}{0pt}{}{\ll}{\ll} \; \genfrac{}{}{0pt}{}{\vee}{\vee}$
Pterostichus melanarius			9.460	8.577	$\genfrac{}{}{0pt}{}{\vee}{\vee}$
Pterostichus niger	8.761	8.830	10.250	10.350	$\vee \; \genfrac{}{}{0pt}{}{<}{\ll} \; \wedge$

Key to Comparison: the symbols represent the results of comparison between sexes and habitats in each species (Data from Chapter 4, additional information section)

In each cell	
Woodland female	Grassland female
Woodland male	Grassland male

$\gg$: significantly larger, $>$: insignificantly larger

Appendix C

The study of pheromones

During the field studies, several species were found to secrete pheromones. In the insect world, pheromones are signals for

1. reproductive behaviour (sex and assembling pheromones),
2. alarm and defence,
3. territory and trail-marking,
4. social regulation and recognition,
5. control of caste, differentiation.

The roles under 2. are observed for social insects (e.g. termites, ants, bees and wasps).

1.: sex pheromone is a prerequisite to successful courtship and mating. In most cases, a sex pheromone produced by a species is specific for the opposite sex of that same species.

RESULTS

Table C shows the results of the Durham field observations of pheromones.

<Table C> List of the species which were observed to secrete pheromone in the Durham woodland and grassland

Species	sex	Habitat	Date of observation	Oviposition season from the results deduced in Chapter 4.
Abax parallelepipedus	M	W	7/7	June–Sep.
Carabus violaceus	M, F	W	27/6, 23/7 (F), (M)	June, Aug.–Oct.
Loricera pilicornis	F	W	23/6	June–July
Nebria brevicollis	F	W	3/7	Sep.–Nov.
Patrobus atrorufus	F	W	9/7	July–Sep.
Pterostichus madidus	M	W	7/7	June, Aug.
Pterostichus niger	F	W	7/7, 25/7	June–Aug.

Appendix D

A study of defence mechanisms

Defensive behaviours were observed in three species during the Durham field studies.

Thiele (1977) divided the defence mechanisms of Carabid beetles into three:

1. Mimicry: this is confined to members of the Lobiini tribe. They may imitate certain species of the Chrysomelidae of subfamily Alticinae (flea beetles), which are poisonous.

2. Biochemical defenec "weapons": Carabids, in common with all members of the suborder Adephaga under order Coleoptera, possess pygidal glands which produce defensive secretions.

The chemical compounds of the principal groups of defence chemicals are reported by Moore (1979). (See Table D.1.)

3. Sound productions: the species *Carabus irregularis* stridulate by rubbing the two inner surfaces of the elytra (Bauer 1973, 1975). Other reports have been made for the subfamily Cicindelinae (Freitag and Lee 1979), genus Scaphinotus (North American Cychrines) (Bagnall 1906, Greeene 1975), *Cychrus caraboides* (Thiele 1977), *Elaphrus cupreus, E. riparius* (Bauer 1973, 1975)

The stridulation was observed always under stressful situations. From observations and experiments, Bauer suggested that stridulation and chirping is a warning signal (1973, 1975, 1976: referenced by Thiele 1977).

Table D.1 Defence chemical compound and moods of discharge

Principal groups of compounds detected: 1, hydrocarbons; 2, formic acid; 3, higher saturated acids; 4, unsaturated acids

Generus name	Chemical compounds	Modes of discharge
Abax	4	Oozing
Calathus	1, 2	Spraying
Carabus	4	Spraying
Cychrus	4	Spraying
Loricera	3	Oozing
Nebria	4	Oozing
Notiophilus	3	Oozing
Pterostichus	1, 4	Spraying

<Table D.2> Results of observation of defence mechanisms in the Durham woodland and grassland

Species name	Sex	Date	Modes of discharge
Abax parallelopipedus	M	21/7	Oozing when captured
Carabus violaceus	M	19/7	Oozing when captured
	M, F	Often	Spraying of stimulative liquid
Cychrus caraboides	M	25/7	Spraying of stimulative liquid
	M, F	Often	Hissing by squeezing of abdomen
Loricera pilicornis	M	3/7, 19/7	Oozing when captured
Patrobus atrorufus	F	2/8, 10/8	Oozing when captured