Biological studies on a number of Moorland Tipulidae

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by

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ABSTRACT

The life-history and ecology of Tipula subnodicornis Zetterstedt have been studied on the Moor House National Nature Reserve, an area of upland blanket-bog with an altitude range of 1300-2780ft (396-845m). The annual life-cycle is maintained under different temperature conditions by adaptive responses to temperature and photoperiod during development. The optimum temperature for growth and the magnitude of response in growth rate to change in temperature both decrease during larval development. The growth phase is followed by an overwintering stage which is probably temperature independent but cannot be considered as a diapause as the metabolic rate does not drop. This phase can be ended by subjecting the larvae to an increased day length (18hr). In the field the increasing day length in spring synchronises pupation. In the autumn emerging species, T. pagana, which has a summer diapause, decrease in day length breaks the diapause and promotes development towards pupation. In this case it has been shown that the degree of synchronisation is directly related to the shortness of day length.

The population dynamics of T. subnodicornis have been studied and it was shown, by the method of k factor analysis, that overwinter mortality in the field is density dependent. Experimental manipulation of density in enclosures in the field and in culture indicated that the same was true for the early instars. A multivariate analysis on the factors affecting wing length, which was used as an indication of size and fecundity, showed that site and year were the most important influences in both sexes and that the effect of density was significant for the males. Wing length was not significantly correlated with altitude in either sex.

Contents

I. INTRODUCTION

This study has been concerned with the ecology of moorland craneflies, particularly Tipula subnodicornis Zetterstedt, and was carried out on the Moor House National Nature Reserve, No. 80, an area of upland blanket-bog.

There is considerable literature on the taxonomy of the Tipulidae in both hemispheres. In particular, Alexander (1920), Dobrotworsky (1968, 1971a,b,c), Edwards (1938, 1939), Mannheims(1940 onwards) and Coe (1950) have produced keys to the adults. Brindle (1960 and 1967) and Chiswell (1956) describe fourth instar larvae of most of the British Tipulidae.

Much of the work on craneflies has been concerned with the few species of economic importance. Tipula paludosa Meigen and T. oleracea Linnaeus occur on farm land and their damage to crops has been described by Rennie (1916, 1917), Loi (1965) and Ricou (1968) among others. White (1951) studied T. lateralis Meigen in relation to the damage it caused in watercress beds. The life-history and general biology of T. paludosa was described by Selke (1936) and Maerks (1943), while Milne et al. (1965) and Laughlin (1967) have related the abundance and growth rate of the species to environmental conditions (rainfall and temperature respectively).

Detailed studies on two other species, T. subnodicornis and Molophilus ater Meigen, have been carried out by Coulson (1962), Hadley (1969, 1971a&b) and Horobin (1971) on the Moor House Reserve. Community studies on craneflies have been carried out by Coulson (1959), Crips and Lloyd (1954) and Freeman (1964, 1967, 1968) and Freeman and Adams (1972), and the taxonomic works already referred to give further ecological information.

The work on T. subnodicornis and M. ater that was carried out on the Moor House Reserve formed the basis for this study which has been partly concerned with the fluctuations in the numbers of T. subnodicornis and partly with the synchronisation of the life-cycle. Horobin (1971) made use, as did Jordan (1962), Reay (1964) and Welch (1965) in their work on the rush moth Coleophora alticollela Zeller, of the fact that there is a considerable altitude range on the reserve, to study the effect of temperature on the development rate of a univoltine insect in the field. He had sites at 1400ft and at 2700ft and found that between the two sites there was a mean annual temperature difference of 1.2°C corresponding to an accumulated temperature sum of 438 C degree days (from 23 May 1968 - 21 April 1969 the accumulated temperature sums at the two sites were 2036 and 1408 C degree-days respectively giving a difference for the whole year in excess of 628 C degree days). Despite the temperature differences and the lack of a diapause in M. ater he found that by early April larvae at the two sites, and at intervening sites, were at the same stage of development in their annual life-cycle. As the rate of development in poikilotherms is usually temperature dependent (Andrewartha and Birch 1954), this was thought to be worth further investigation.

T. subnodicornis has a life-history very similar to that of M. ater, emerging on a number of the same sites a few days before M. ater in May, so it was thought also to be a suitable insect for investigation into the effect of temperature on the rate of development and the synchronisation of an annual

life-cycle. The work in this study on the timing of emergence in the field has been greatly facilitated by the presence of soil temperature data provided by Horobin (1971) for different altitude sites and by the records from the Grant multichannel recorder used during the International Biological Programme for measuring the temperatures registered by thermistor probes at different depths in blanket-bog. The daily readings from the Moor House Meteorological Station have provided information on year to year variation in temperature.

From 1953-1955 Coulson (1962) made a detailed population study throughout the life-cycle of T. subnodicornis on an area dominated by Juncus. In this study the same site has been used and additional sites on Juncus and Eriophorum dominated areas and blanket-bog have been started for comparative purposes. Data have been accumulated on the numbers of fourth instar larvae and adults present on these sites and the effect of density on mortality has been investigated under experimental conditions. Wing length, used extensively by Hemingsen (1956), Hemingsen and Birger Jensen (1957, 1960, 1972) and Hemingsen and Nielsen (1965) in other contexts, has been used to reflect the size of adults on each site, so fecundity as well as mortality has been estimated. The results from this study confirm the observations of Milne et al. (1965) for T. paludosa and Coulson (1962) for T. subnodicornis that drought in the early stages of development causes a high mortality. Evidence for density dependent effects on both mortality and fecundity has also been found and as this is also the case for M. ater (Horobin 1971) the two species may be compared.

Note :

1. The specific names of plants mentioned in this thesis are taken from Clapham et al.(1962) for flowering plants, and Watson (1955) for mosses and liverworts.
2. The statistical analyses are based on Bailey (1959) and Snedecor and Cochran (1967). When samples of less than thirty are compared by means of a t-test the degrees of freedom have been calculated by Bailey's method (page 51).

II. THE STUDY AREA

1. Description of the Moor House Reserve

The Moor House National Nature Reserve, Westmorland (N.R. 80 : Nat. Grid Ref. NY 758329) was described by Conway (1955). It consists of 3850 hectares of which the greater part is blanket bog lying on the eastern dip slope of the Pennine escarpment. Knock Fell (2604ft, 794m), Great Dun Fell (2780ft, 845m) and Little Dun Fell (2761ft, 842m) which form part of the summit ridge lie within the reserve while Cross Fell (2930ft, 893m), the highest peak of the Pennines, is just to the north of the reserve boundary. The River Tees forms the north and east boundary of the reserve and also divides Cumberland and Westmorland along this stretch. The main tributary of the Tees in its upper reaches is Trout Beck. The west scarp slope overlooks the Eden Valley and the two main streams on this slope,

Crowdundle Beck and Knock Ore Gill, are tributaries of the River Eden. Fig. 1 shows a map of the reserve showing relevant landmarks and the positions of the sites.

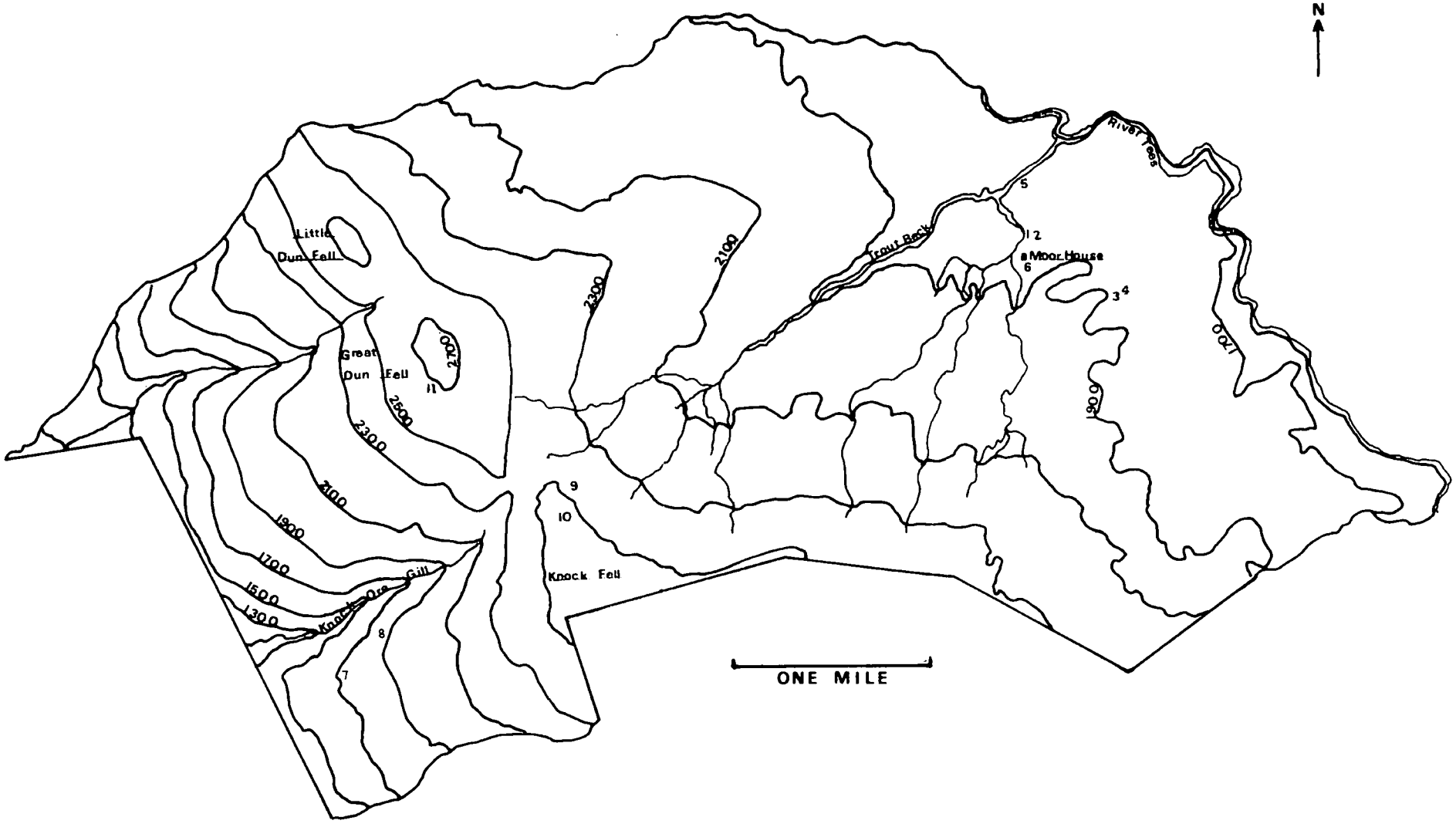
The geology of the reserve has been described by Johnson and Dunham (1963). The underlying rock consists of limestone and sandstone bands of the Carboniferous series. Dun Fell is capped by sandstone and there are considerable limestone outcrops on the west scarp. Limestone areas also occur on the dip slope; Moor House stands on one, but most of the area is overlaid by peat, commonly about 1.5m deep, but reaching a depth of 8m in places.

Peat occurs on all areas where waterlogging takes place and is a consequence of the low temperatures (mean annual temperature for 1953-1965 was 5.1°C) and high rainfall (mean annual rainfall for 1953-1965 was 1869mm). This gives rise to blanket bog with a characteristic flora. Sphagnum spp. are constants and Calluna vulgaris and Eriophorum vaginatum are dominant over large areas, while E. angustifolium is abundant in the wetter places, giving way to a total cover of Sphagnum on base poor flushed areas. Where the peat is shallow or disturbed Juncus squarrosus is often the dominant plant, possessing long roots which can reach up to 1m to the mineral soil.

The larger streams are bordered by beds of peaty or sandy alluvium and bare drift denoted by Johnson and Dunham (1963) as "Mixed Bottom Lands". These and the limestone outcrops support a varied flora in which Festuca ovina, Deschampsia caespitosa, Agrostis tenuis, Holcus lanatus, Carex spp., Achillea millefolium and Thymus drucei are common.

Fig. 1. Map of the Moor House National Nature Reserve showing the positions of the study areas.

Moor House site		Dun Fell sites	
1.	Netherhearth	7.	1700ft
2.	Above Netherhearth	8.	1900ft.
3.	Bog End (*Juncus*)	9.	2500ft
4.	Bog End (mixed moor)	10.	2550ft
5.	Trout Beck	11.	2700ft
6.	Behind House		


N
Little Dun Fell
Great Dun Fell
2100
2300
2700
2500
2300
2100
1900
1700
1500
1300
Knock Ore
Gill
Knock Fell
Trout Beck
River Tees
Moor House
1700
1900
1
2
3
4
5
6
7
8
9
10
11
ONE MILE

2. The Study Sites

The sites can be divided into two series; those on the west scarp slope at differing altitudes, and those on the east side in the immediate vicinity of Moor House at an altitude of approximately 1800ft (549m).

The Sites on the East Side :

(1) Netherhearth. This is a flat area of disturbed ground near mine workings. Juncus squarrosus and Festuca ovina are co-dominant, Agrostis tenuis, Nardus stricta and Gallium saxatile are common.

(2) Above Netherhearth. This site lies above and to the East of Netherhearth from which it is separated by a peat hag. Eriophorum vaginatum is dominant.

(3) Bog End (Juncus). This site lies on an old mine track at the edge of the blanket bog. The vegetation has been described by Welch (1964). J. squarrosus is dominant and Deschampsia flexuosa, Carex nigra, Polytrichum commune and F. ovina are constants.

(4) Bog End (Mixed-moor). This site lies to the north-east of the mine track on a slight slope. Calluna vulgaris and E. vaginatum provide high cover value. Sphagnum spp. are abundant and E. angustifolium is present.

(5) Trout Beck Bridge. This site lies on an area of level blanket bog on the east side of Trout Beck Bridge. It has been drained but still retains a high Sphagnum cover. C. vulgaris and E. vaginatum are co-dominant.

(6) Behind the House. This site lies immediately behind the house in the pasture. It is subject to flooding. J. squarrosus, F. ovina and N. stricta are widespread and in places P. commune and J. effusus are present. Sphagnum spp. occur in the wetter areas.

The Sites on the West Side :

These sites were inherited from Horobin (1971) and, with the exception of the 2550ft site, are described in his thesis. They form an ascending series on Dun Fell and the adjoining Knock Fell.

(7) 1700ft Site (508m). This is a very wet site. The underlying rock forms a flat ledge and the drainage is impeded. There are numerous semi-permanent pools in the area. The vegetation is dominated by J. squarrosus with E. angustifolium, Vaccinium myrtillus, Empetrum nigrum amd P. commune common.

(8) 1900ft (579m). This site lies on an extensive and gently sloping area dominated by J. squarrosus. V. myrtillus and Festuca spp. are also present.

(9) 2500ft Site (762m). This site lies in a shallow valley to the north of the summit of Knock Fell. It is protected and has a tendency to waterlogging. J. squarrosus dominates the vegetation.

(10) 2550ft Site (777m). This is an exposed site on the shoulder of Knock Fell. There is a limestone outcrop near and the vegetation indicates a mixed substratum. J. squarrosus and F. ovina are co-dominant and N. stricta, A. tenuis and P. commune are common. V. myrtillus is present.

(11) 2700ft Site (823m). This site is a restricted area where J. squarrosus is dominant and P. commune common. During the period over which it was studied the site became invaded by a band of E. angustifolium.

III. TEMPERATURE RECORDS ON THE RESERVE

The first sequence of published temperature records for the reserve was compiled by Manley (1936, 1942, 1943) who classified the climate as sub-arctic and noted that his records corresponded well with those at sea-level in Southern Iceland. He found that the mean temperatures at 1840ft were 5.5°F (3.1°C) lower than those based on an average from four lowland stations (Newton Rigg, 559ft; Appleby, 440ft; Houghall, 160ft; Durham, 330ft). He found that the maxima were on average 7°F (3.9°C) lower, but that the mean minima were only 3°F (1.7°C) lower, and that the mean daily range was less in the uplands than in the valleys.

Since 1951, Moor House and the summit of Great Dun Fell (2780ft) have been used as recording stations by the Meteorological Office and daily climatological readings have been taken.

From 1967 until 1970, Horobin (loc. cit.) used Cambridge mercury in steel thermographs to record soil temperatures at some of his sites. The thermometer bulbs, measuring 1.5cm in diameter, were positioned just below the soil surface. The clock-work mechanism of the recorder was capable of running for a fortnight but the charts were usually removed at weekly intervals when the calibration was checked with a mercury thermometer. During 1969 thermographs were used to record soil temperatures at 1700ft, 2050ft, 1900ft and 2700ft from April (May in the case of 2700ft) until August.

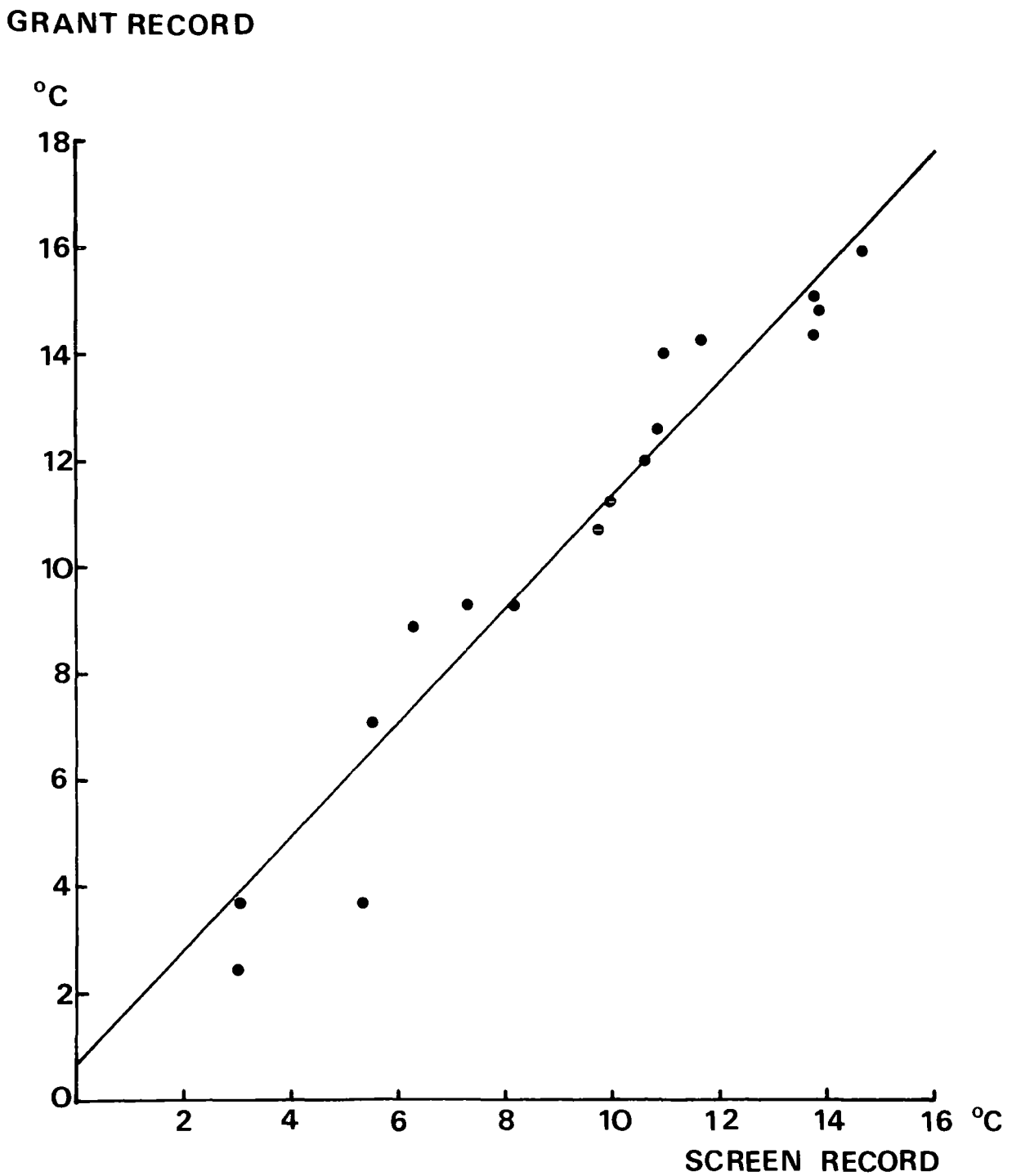
Horobin (loc. cit.) also made use of the sugar inversion method (Berthet 1960). This relies on the rate of inversion of sucrose to fructose and glucose being temperature dependent. The concentration of the end products is determined polarimetrically. He placed his sugar tubes, with 15ml of sucrose with buffer, in standard 2 x 1 inch glass tubes in slightly larger aluminium canisters close to, and at approximately the same depth as, the thermograph probes. He also placed sugar tubes at a similar depth on his other sites. The tubes were collected at fortnightly intervals in the summer and at monthly intervals in winter, and provide data from 1 October 1967 to 13 May 1970 at the 1700ft, 1900ft, 2500ft, 2700ft, Bog End (Juncus) Above Netherhearth and close to the Bog End (mixed-moor) sites.

As a control for the Berthet method, Horobin placed sugar tubes by the thermometers in the meteorological screen. He compared the mean temperatures derived from the meteorological data and from the Cambridge recorders with the means calculated from the sugar tubes in appropriate positions and obtained the regression $y = 0.87x - 0.4$ (where y is the true arithmetic mean temperature in ^{o}C and x is that derived from the sucrose method) with a correlation coefficient of $r = +0.98$, showing a close linear relationship. There is therefore a useful and reliable series of soil temperature data at sites of differing altitude on the reserve.

From the summer of 1968 until January 1972 a Grant recorder was used by participants in the International Biological Programme. This was set up on Syke Hill (1800ft, 550m) and recorded the temperatures registered by probes at different heights in the different types of vegetation and at various depths below the vegetation. These data are now being analysed in detail by Heal (pers. comm.) but I found that the data from a probe at a depth of 1.0cm in Juncus squarrosus litter correlated well with that from the meteorological screen when the weekly means from April to September 1967 were compared. The regression, Fig. 2, has the equation $y = 1.07x + 0.71$, where y is the temperature in ^{o}C derived from the Grant weekly means and x is that from the meteorological data. The correlation coefficient, $r = +0.98$, provides justification for using the Moor House data where soil temperatures would be more appropriate.

Fig. 2. The regression of the weekly mean temperature, recorded at a depth of 1.0cm in Juncus squarrosus litter, on the weekly mean obtained from the screen data during the period 20 April - 6 September 1969.

$y = 1.07x + 0.71$, $r = +0.98$, $p < 0.001$


GRANT RECORD
°C
18
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
°C
SCREEN RECORD

Discussion of the temperature recording methods

Macfadyen (1956, 1963) points out that the air temperature 1.5m above the ground in the Stephenson screen is not necessarily a close approximation to the temperature at or below the soil surface where the insect is living. Andrewartha (1944a) also makes this point and adds that the method, which has been used here, of adding the daily maximum and minimum and dividing by two to arrive at the mean does not give the true mean. However, as is shown in Fig. 2, over a weekly period the mean from the screen data rarely shows more than 1°C deviation from the mean derived from the Grant data, and the Grant recording has neither of the two drawbacks mentioned above in that the probe is within the microhabitat of the animal and that the mean is the true mean of 24 hourly recordings per day.

The thermograph chart and the chemical integration method give a continuous temperature record so the mean temperatures derived from them are not biased as is that arrived at by taking the maximum and minimum. These methods also have the advantage that the temperature being recorded is that of the insects' habitat.

IV. THE TIMING OF THE LIFE-CYCLE

Coulson (1962) described the development and annual life-cycle of T. subnodicornis under field conditions. Oviposition takes place from mid May until mid June during the period of adult emergence. The eggs take approximately three

weeks to hatch and give rise to first instar larvae. Towards the end of July first instar gives place to the second which lasts two to three weeks as does instar three. Most larvae have entered instar four by the last week in September. All larvae overwinter in instar four which is, like the other larval instars, an active feeding stage. Pupation lasts three weeks from about late April until mid May when the adults start emerging. Fig. 3, taken from Coulson (1962), gives a diagrammatic representation of the life-cycle in the field.

Coulson found that T. subnodicornis had a highly synchronised emergence period from mid May until mid June. At any one site the emergence took place over a three week period with two thirds of the emergence occurring within eleven days (S.D. = 5.5 days). Horobin (1971) found that both M. ater and T. subnodicornis emerged later at higher altitudes. In 1970, for instance, the mean date of emergence for T. subnodicornis at 2700ft was eight days behind that at 1700ft.

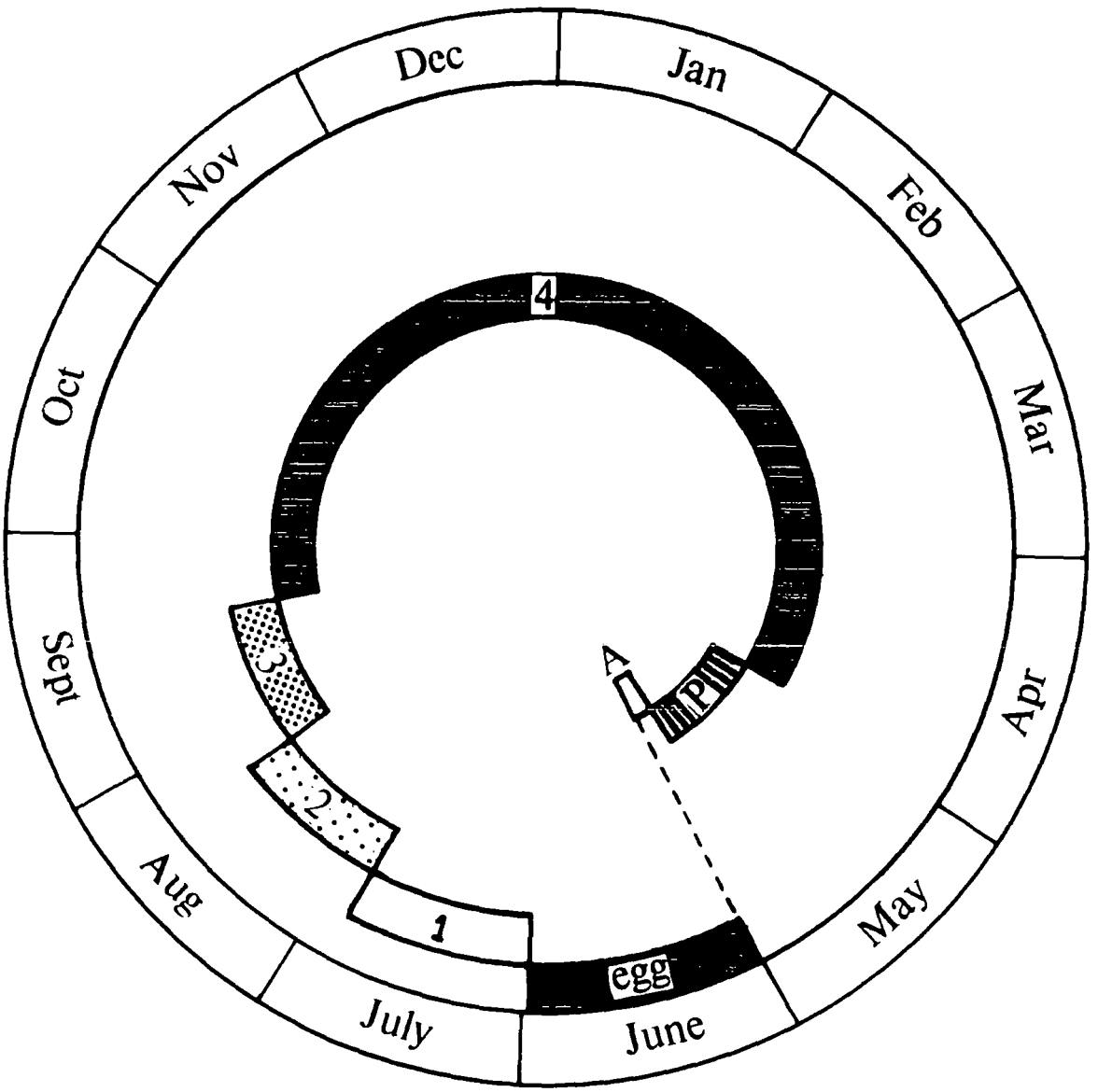
If development rate is linearly related to temperature it is possible to calculate the temperature sum in degree-days (calculated in this thesis as mean daily temperature above $0^{o}C$ multiplied by the number of days at that temperature) required for development, as has been done for the codling-moth Enarmonia pomonella L. (Glenn 1922)and Acronycta rumicis L. (Danilevskii 1965). The temperature sums at 1700ft and 2700ft on Dun Fell for the period 9 June 1969 - 13 May 1970 were 2068 and 1717 ^{o}C degree-days respectively. If the date of emergence were dependent on the yearly temperature sum alone this difference (17%) is too great to be compensated by the eight day difference

Fig. 3. The life-cycle of T. subnodicornis at Moor House (taken from Coulson 1962).

1 - 4 = larval instars

P = pupa

A = adult



TIPULA SUBNODICORNIS

in the emergence means which, assuming a high mean daily temperature of 10°C, could account for a maximum 80C degree-days. As T. subnodicornis lacks a diapause (Coulson 1962) there must be some factor other than temperature sum accumulation that influences the duration of the life-cycle. In order to investigate this situation the relationship between temperature and development rate at different stages of the life-cycle of T. subnodicornis has been studied both in the field and in the laboratory.

For convenience of study in the laboratory, the life-history is considered in five stages : egg; larval 1; larval 2; pupal; and adult. The first larval stage constitutes the period of growth between hatching and attaining maximum weight, and the second larval stage is that between achieving maximum weight and pupation. The field study has mainly centered on the timing of emergence.

V. EMERGENCE IN THE FIELD

Horobin (1971) found that when sods containing M. ater were transferred from one site to another, even as close to the emergence period as 15 days before the mean emergence date on the host site, the means for the transferred groups approximated much more closely to the mean on the host site than to those of the sites where they originated. For example, the mean date of emergence from sods transferred from 2700ft to 1400ft on 13 May 1970 was 29 May (s.e. $\pm$ 0.2). The mean date of emergence at 2700ft was 14 June (s.e. $\pm$ 0.2) and of controls on the host

site 28 May (s.e. ± 0.1). He found no correlation between the yearly temperature sum at each site and mean emergence date at that site, but suggested that larval development had finished by early spring and that pupation was initiated by the passing of a temperature threshold. This would occur earlier on lower and more sheltered sites and would explain the sequence on Dun Fell. As T. subnodicornis has a life-cycle similar to M. ater and emerges a few days before M. ater in the same sequence on Dun Fell it was thought interesting to compare the two.

1. Sampling method

The most accurate method to monitor the emergence pattern is to use emergence traps (Hadley 1969, Horobin 1971). However, in the present study the low densities of T. subnodicornis and the number of sites used made this impractical and an alternative method was sought.

Hadley (1969) and Horobin (1971) both used pitfalls to record the emergence of M. ater on a number of sites and Coulson (1962) used sticky traps for T. subnodicornis. Pitfall traps are not reliable indicators of population density (Mitchell 1963, Greenslade 1964) due to the catch being dependent in part on the activity of the insect as well as on the numbers present, and the same criticism applies to sticky traps. However, Hadley (1969) found that for the wingless and short-lived M. ater pitfall traps gave a valid representation of the emergence pattern. He compared direct population estimates, arrived at by suction trapping within $0.05m^2$ emergence traps, and indirect estimates obtained from both sticky traps and pitfalls on the same sites. He found that,

using eight pitfalls and eight sticky traps, the first and last days of the emergence, the range and the mean date were not significantly different from those obtained by the direct method.

As T. subnodicornis also has a short adult life and only the males are able to fly, it was thought probable that either sticky traps or pitfalls could be used to reflect the pattern of emergence in this study. In the first instance pitfall catch and sticky trap catches were compared, and in a later year a comparison between emergence from enclosures and the pitfall catch was made.

During this study each Moor House site had 20 1 lb jam jars placed (except at the Bog End (Juncus) site where there were two lines) in a grid of four lines of five. On the Dun Fell sites there were 10 jars in two rows of five at each site. Each jar was separated from its neighbour by approximately 2m and sunk with its rim flush with the soil surface and filled to a depth of about 2 cm with a weak detergent solution. The detergent acted as a wetting agent preventing the escape of insects once they had made contact with the water film. The traps were emptied daily on the Moor House site in 1970 and 1971 and on alternate days in 1972. On the Dun Fell they were emptied daily in 1971 and 1972 and on alternate days in 1970.

1a. Comparison between sticky trap and pitfall catches

In 1970 four sticky traps similar to those described by Broadbent (1948) were erected at the four corners of the

Netherhearth site. Each trap consisted of an aluminium cylinder 30cm in length and 13.7cm diameter. The cylinders were covered with polythene, held in place by clothes pegs, and covered with "Stick-tite", a tree banding preparation. In Table 1 the daily catches on both types of trap are compared. In Figure 4 the cumulative percentages of flies trapped are plotted for both pitfall and sticky traps. The mean date for pitfall catches, 30.70 $\pm$ 0.24 May, is significantly different from that for the sticky traps, 28.92 $\pm$ 0.41 May ($t = 3.16$, $p < 0.002$), but the first days are the same and although the last days are not, the patterns are very similar.

A possible explanation for the differences in the mean dates obtained by the two trapping methods might be provided by the fact that the sticky traps catch very few females. If males emerged earlier in the emergence period than females, as is the case with M. ater (Hadley 1969), the mean emergence date registered by the pitfall catch (in which both sexes are represented) would be later than that for the sticky trap catch where males almost exclusively are caught. It can be seen from Figure 4 that the male cumulative percentage pitfall catch follows the combined catch very closely and has an identical mean, indicating that the percentage of the total male catch on the ground is similar to that of the females at any period in time. This, however, does not invalidate the suggestion that males might be emerging earlier than females if a behavioural difference is involved.

Table 1. Comparison of catches on four sticky traps with those in twenty pitfalls at Netherhearth in 1970

Date	Pitfalls		Sticky traps	
	Male	Female	Male	Female
16 May	0	0	-	-
17	-	-	-	-
18	0	0	0	0
19	0	1	3	0
20	2	0	3	0
21	1	1	0	0
22	2	0	0	0
23	5	3	15	0
24	5	7	13	0
25	20	12	4	1
26	13	7	3	0
27	17	6	6	1
28	11	15	17	0
29	28	17	8	1
30	16	20	10	0
31	14	8	3	0
1 June	11	2	7	0
2	16	12	16	0
3	15	5	7	0
4	11	17	5	1
5	15	9	3	0
6	10	6	1	0
7	8	4	2	0
8	6	2	1	0
9	0	1	3	0
10	4	2	0	0
14	2	1	0	0
Totals	232	158	130	4

Mean emergence dates : pitfalls = 30.70 $\pm$ 0.24 May

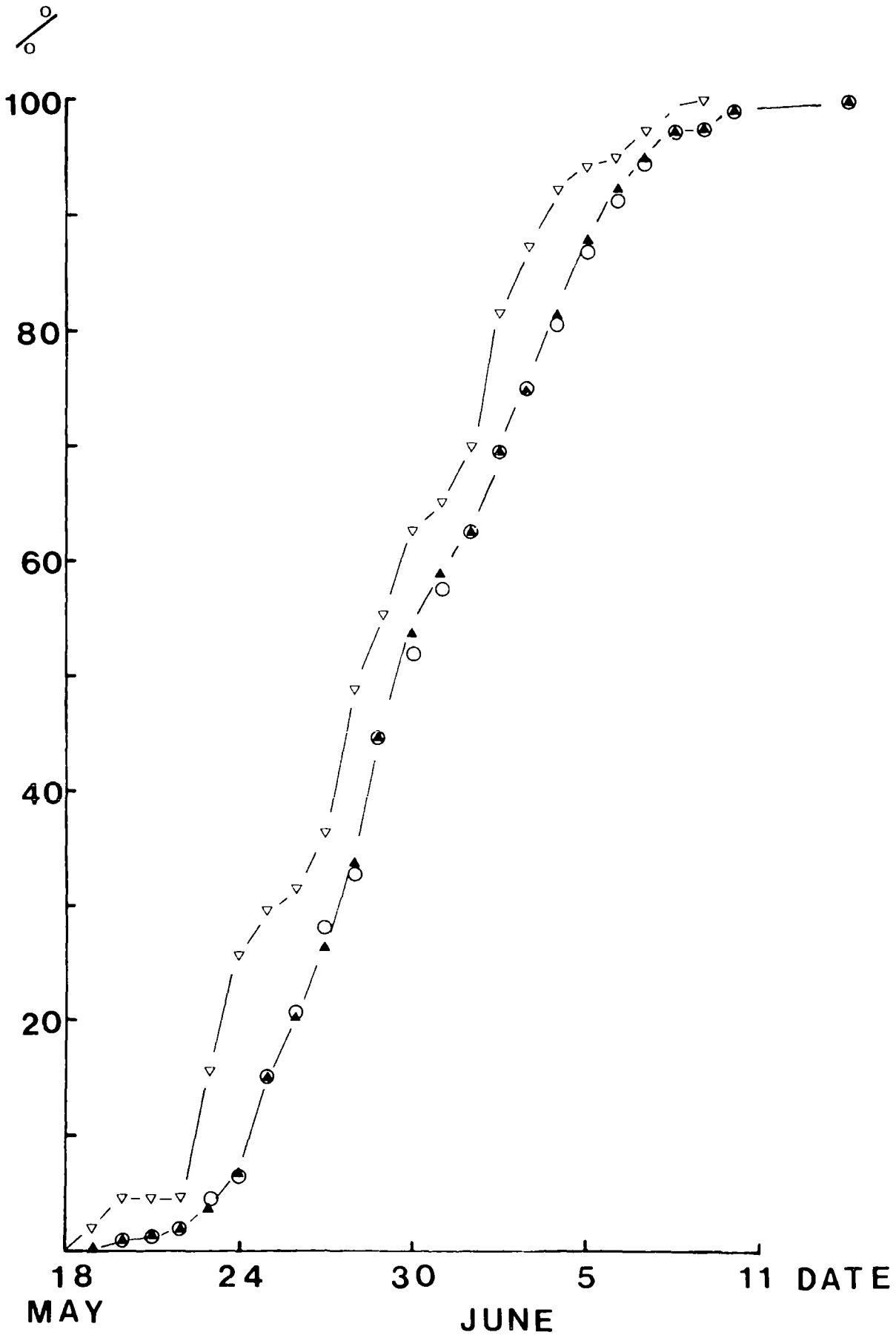
sticky traps = 28.92 $\pm$ 0.41 May

Fig. 4. The accumulated percentage pitfall and sticky trap catches of T. subnodicornis at Netherhearth in 1970 plotted against date.

▽ sticky trap (N = 134)

▲ pitfall, both sexes (N = 390)

○ pitfall, male (N = 232)


%
100
80
60
40
20
18
MAY
24
30
5
JUNE
11
DATE

1b. Comparison of emergence trap and pitfall catches

In 1972 ten 0.25m emergence traps were used to monitor emergence on Netherhearth. Each trap consisted of four galvanised steel sides, 50 x 30cm, set edge to edge in a square and sunk 10cm in the ground. The top of the trap was covered by fine nylon netting, hole diameter 2mm, secured by string. The emergence traps were visited daily, and the flies removed, except on 20 and 21 May, while the pitfall traps on the same site were emptied on alternate days.

The data from the two sets of catches are shown in Table 2. The mean date of emergence calculated from the emergence trap catch was 22.42 $\pm$ 0.30 May, and from the pitfall catch was 24.70 $\pm$ 0.39 May, a significant difference ($t = 4.63$, $p < 0.001$). When the cumulative percentage catch is plotted separately for each sex for each set of traps (Fig. 5), however, it can be seen that the correspondence between the female pitfall catch and the female emergence data is very close and that the traps give an accurate impression of the female emergence pattern on a site. When the mean dates are calculated for females alone they are not significantly different; 24.41 $\pm$ 0.52 May for the pitfall traps; and 23.75 $\pm$ 0.52 May for the emergence traps.

It can also be seen from the emergence trap results that the males do emerge earlier during the emergence period than the females. I would suggest that the reason that this is not reflected in the pitfall catch is due to a difference in male behaviour in the presence and absence of females. When there are few females, the males spend more time in

searching flight just above the vegetation than they do on the ground. It is only when there are large numbers of females present that substantial numbers of males descend to the vegetation and are at risk of falling into the pitfalls. This hypothesis explains why the male component of the pitfall catch follows the female catch so closely and why the male sticky trap catch gives an earlier mean emergence date than the pitfall catch.

The longer continuation of the pitfall catch present in both sexes can be accounted for by the life-spans of the adult. Coulson (1956) calculated from mark recapture experiments that the life expectation for the male was between 48 and 22hrs from the hour of capture, and that for the female between 32 and 15hrs.

On the basis of the comparisons made between pitfall and emergence trap catches it was decided that, as for M. ater, the pitfall catch gave an accurate representation of the emergence pattern for female T. subnodicornis. For the purposes of year to year and site to site comparison it was not thought necessary to make any adjustment to the calculated mean emergence date to allow for the earlier appearance of the males, but if an absolute date for the mean emergence for both sexes were required, the emergence trap data would indicate that this is two days before that calculated from the pitfall data.

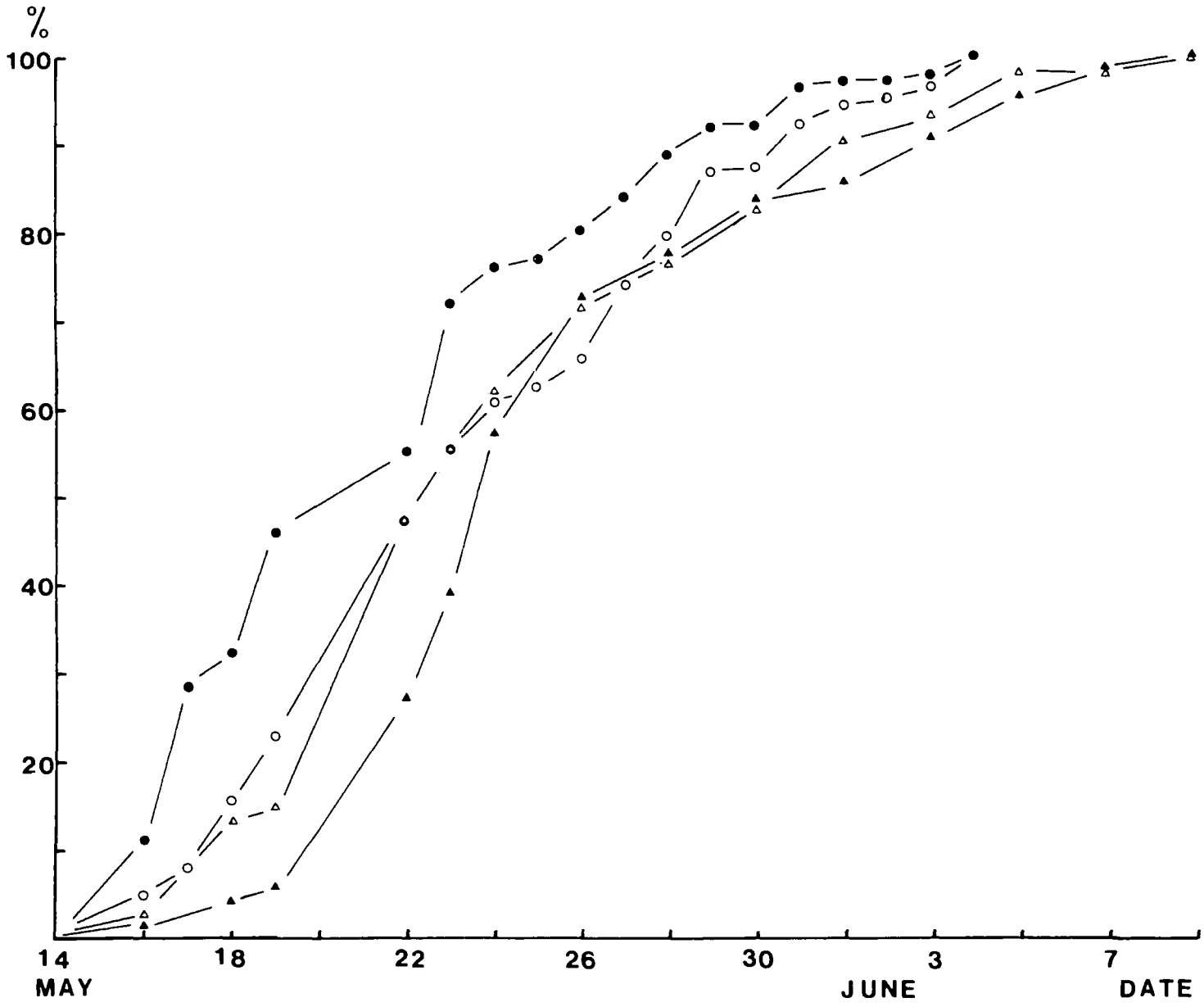
Fig. 5. The accumulated percentage pitfall and emergence traps catches of T. subnodicornis at Netherhearth in 1972.

▲ pitfall, male (N = 120)

△ ,, female (N = 68)

● emergence traps, male (N = 176)

○ ,, ,, female (N = 93)


%
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80
60
40
20
14
MAY
18
22
26
30
JUNE
3
7
DATE

Table 2. Comparison of the numbers of *T. subnodicornis* caught in eight $0.25m^2$ emergence traps with the catch in twenty pitfalls at Netherhearth in 1972

Date	Pitfalls		Emergence traps	
	male	female	male	female
14 May	0	0	0	0
15	-	-	-	-
16	1	3	20	5
17	-	-	30	3
18	2	13	8	7
19	1	2	24	7
20	-	-	-	-
21	-	-	* -	* -
22	15	39	*16	*22
23	8	10	30	8
24	12	8	7	5
25	-	-	2	1
26	10	11	6	3
27	-	-	8	8
28	4	6	6	5
29	-	-	6	7
30	4	8	0	0
31	-	-	7	5
1 June	2	9	2	2
2	-	-	0	1
3	3	3	2	1
4	-	-	2	3
5	3	6	0	0
6	-	-	0	0
7	2	0	0	0
8	-	-	0	0
9	1	2	0	0
10	-	-	0	0
11	0	0	0	0
12	0	1	0	0
Totals	68	121	174	93

*estimated from four intact traps

Mean emergence dates : pitfalls = 24.70 $\pm$ 0.39 May

emergence traps = 22.42 $\pm$ 0.30 May

2. Results from the pitfall data

The emergence data for the four Moor House sites from 1969-1972 and for the Dun Fell sites from 1970-1972 are shown in Tables I-IV in the appendix. Figs. I-III, also in the appendix, show the accumulated percentage daily catch plotted against the date for each site for 1970-1972 (the catches on Dun Fell in 1972 have been omitted due to the small sample size). In Table 3 the mean and median dates of emergence on the four Moor House sites for 1969-1972 are shown.

It can be seen from Table 3 and Figs. I-III that the emergence pattern takes the form of an approximately symetrical distribution where the mean is equal to the median. The deviation from the normal distribution is discussed in the next section, but, as it was in most cases small, the differences in mean emergence dates have been tested, using Student's t-test. From Table 4 it can be seen that mean emergence dates differ significantly on the same site from year to year, and on different sites,(with the exception of Netherhearth and Bog End (mixed-moor) in 1971 and 1972) within the same year.

As Horobin (1971) found no correlation between the mean emergence date of M. ater and the temperature sum accumulated during the life-cycle at each site and suggested that pupation was triggered by the passing of a temperature threshold in spring, it was decided to look at the relationship between the timing of the emergence period of T. subnodicornis and spring temperature. The effect of temperature during the emergence period has been considered separately from that of the earlier spring temperature.

Table 3. The mean and median emergence dates for the Moor House sites from 1969 - 1972

Year	Site	No. caught in 20 pitfalls*	Median date	Mean date	S.E.	Variance
1969	Netherhearth	110	9 June	8.1 June	±0.42	19.4
	Above Netherhearth	118	7 June	9.4 June	±0.28	9.1
	Bog End (*Juncus*)	104	31 May	31.8 May	± 0.45	20.7
	Bog End (mixed-moor)	50	2 June	2.8 June	±0.65	20.7
1970	Netherhearth	390	29 May	30.7 May	±0.24	21.8
	Above Netherhearth	447	1 June	1.3 June	±0.24	25.7
	Bog End (*Juncus*)	237	27 May	26.9 May	±0.30	27.1
	Bog End (mixed-moor)	257	29 May	29.8 May	±0.28	20.1
1971	Netherhearth	240	21 May	21.4 May	±0.40	38.4
	Above Netherhearth	254	25 May	23.9 May	±0.40	40.0
	Bog End (*Juncus*)	286	17 May	17.3 May	±0.33	30.9
	Bog End (mixed-moor)	169	20 May	20.5 May	±0.49	40.6
1972	Netherhearth	189	23 May	24.7 May	±0.39	30.0
	Above Netherhearth	125	25 May	27.4 May	±0.58	42.0
	Bog End (*Juncus*)	254	22 May	22.4 May	±0.40	40.6
	Bog End (mixed-moor)	147	24 May	24.9 May	±0.59	51.2

*In 1969 only 10 pitfalls were used

2a. The effect of temperature during the emergence period

The Netherhearth site has been chosen to compare the variation in emergence pattern from year to year because it provides a relatively complete set of data and it is near the meteorological screen whence the daily temperature data have been obtained. The percentage accumulated pitfall catch for each day has first been plotted against date and then against accumulated temperature in C degree-days, which have been calculated from the screen daily means (max + min/2), on normal probability paper (Figs. 6 - 9). It can be seen that plotting against accumulated temperature rather than date has a normalising effect. The 1972 emergence trap data have also been treated in the same way, Fig. 10, and it can be seen that the temperature effect is not just the result of increased activity on hotter days, but is also caused by more adults emerging.

Although the temperature during the emergence period modifies the normal distribution, the effect that this has in most years is small, and in no case does the date on which the mean in accumulated C degree-days falls differ significantly from the arithmetic mean date. This is shown in Table 5. The comparison between emergence periods based on mean dates is therefore felt to be legitimate.

Fig. 6. The accumulated percentage pitfall catch at Netherhearth in 1969 plotted against date and against accumulated C degree-days on normal probability paper.

● date

■ C degree-days from the day before the first fly was caught

(N = 110)

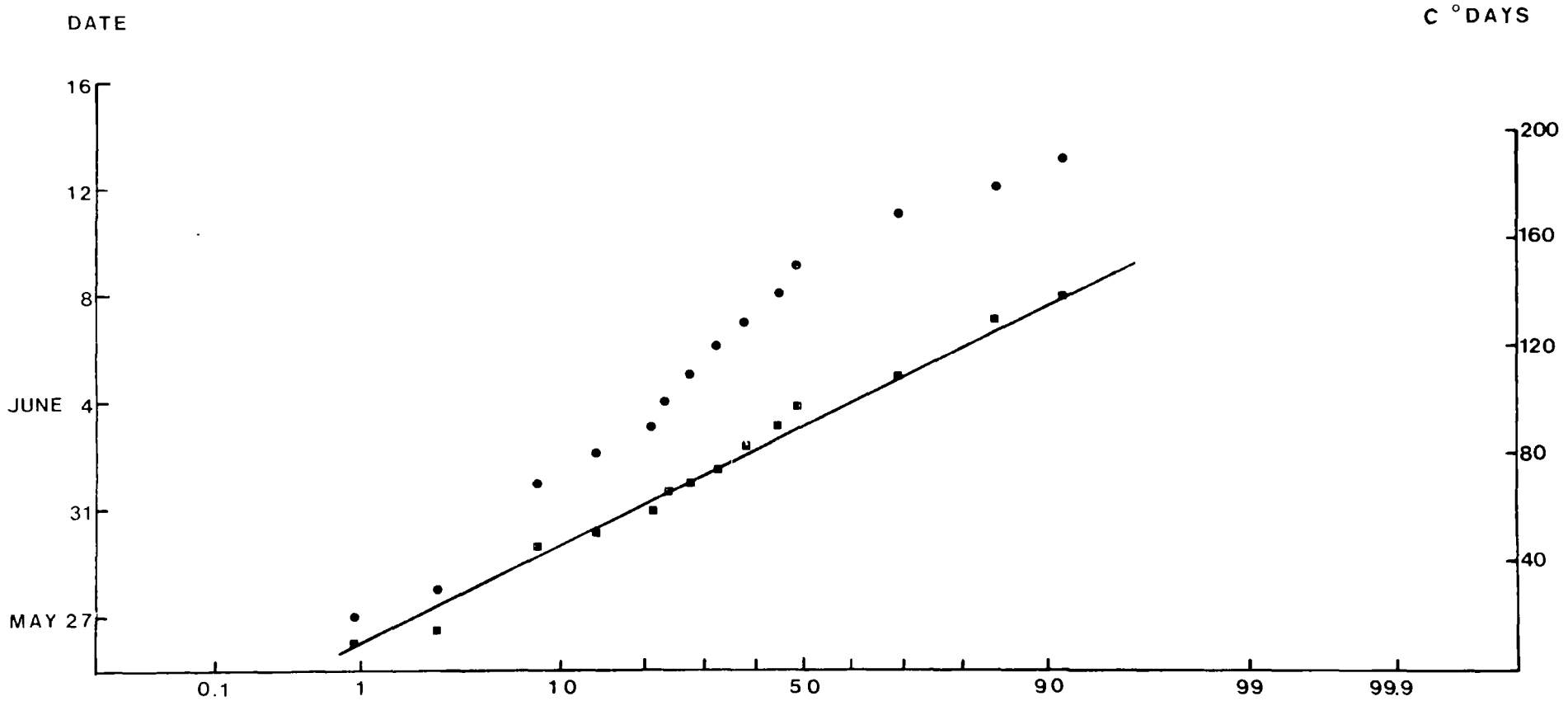

DATE
C °DAYS
16
12
8
JUNE 4
31
MAY 27
200
160
120
80
40
0.1
1
10
50
90
99
99.9

Fig. 7. The accumulated percentage pitfall catch at Netherhearth in 1970 plotted against date and against accumulated C degree-days on normal probability paper.

- ● date
- ■ C degree-days from the day before the first fly was caught

(N = 390)

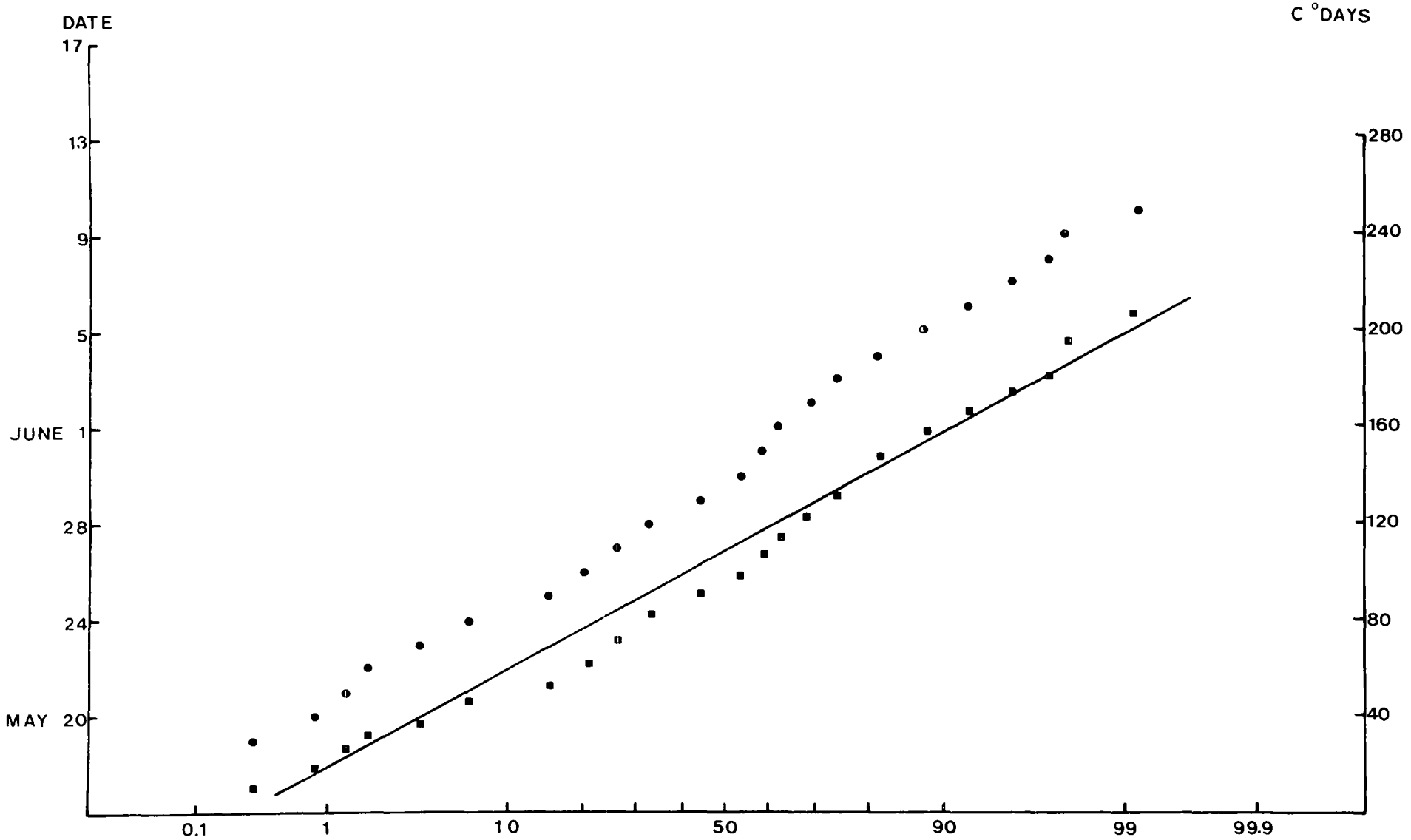

DATE
17
13
9
5
JUNE 1
28
24
MAY 20
C °DAYS
280
240
200
160
120
80
40
0.1
1
10
50
90
99
99.9

Fig. 8. The accumulated percentage pitfall catch at Netherhearth in 1971 plotted against date and against accumulated C degree-days on normal probability paper.

● date

■ C degree-days from the day before the first fly was caught

(N = 240)

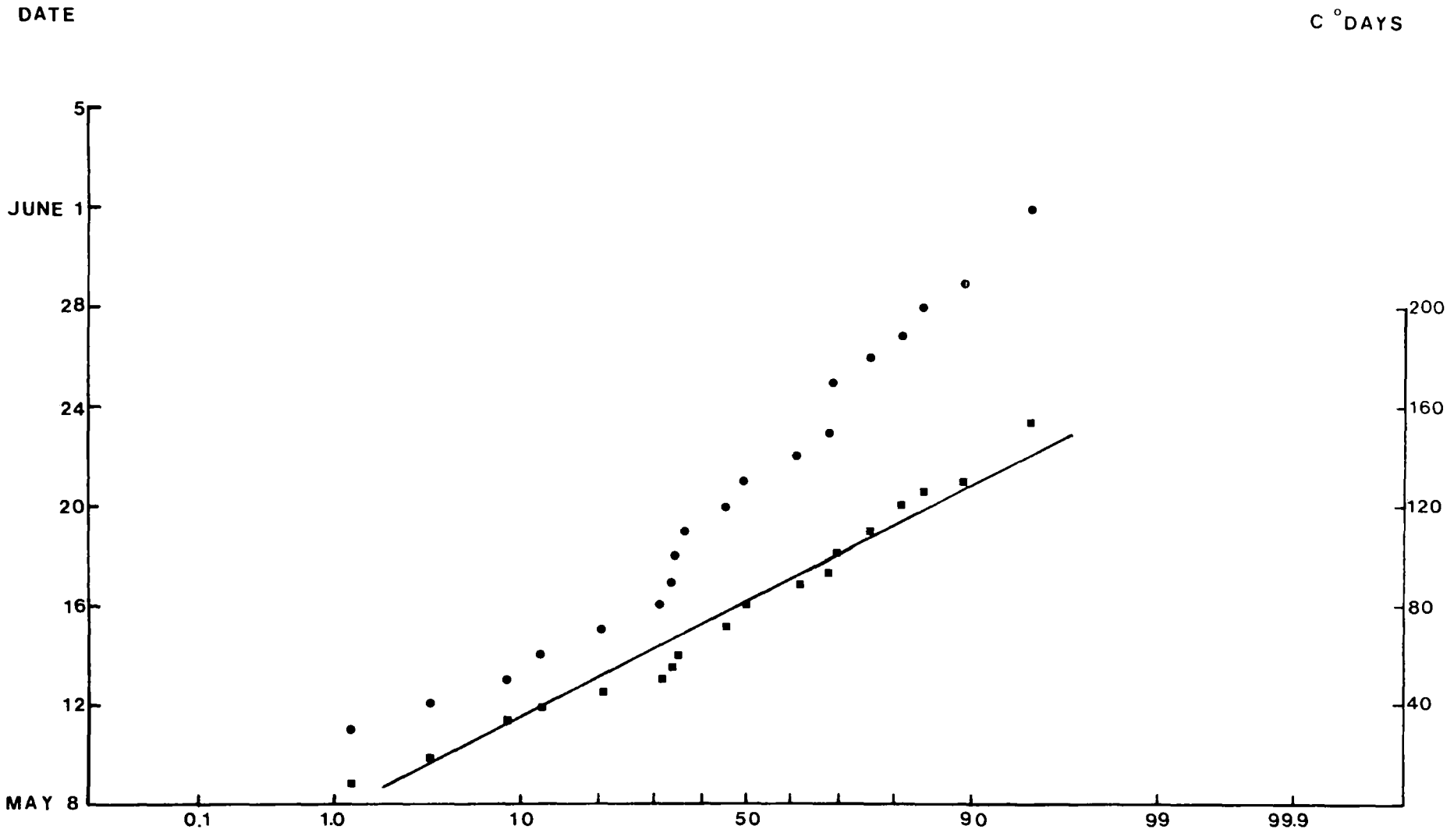

DATE
C °DAYS
5
JUNE 1
28
24
20
16
12
MAY 8
200
160
120
80
40
0.1
1.0
10
50
90
99
99.9

Fig. 9. The accumulated percentage pitfall catch at Netherhearth in 1972 plotted against date and against accumulated C degree-days on normal probability paper.

● date

■ C degree-days from the day before the first fly was caught

(N = 189)

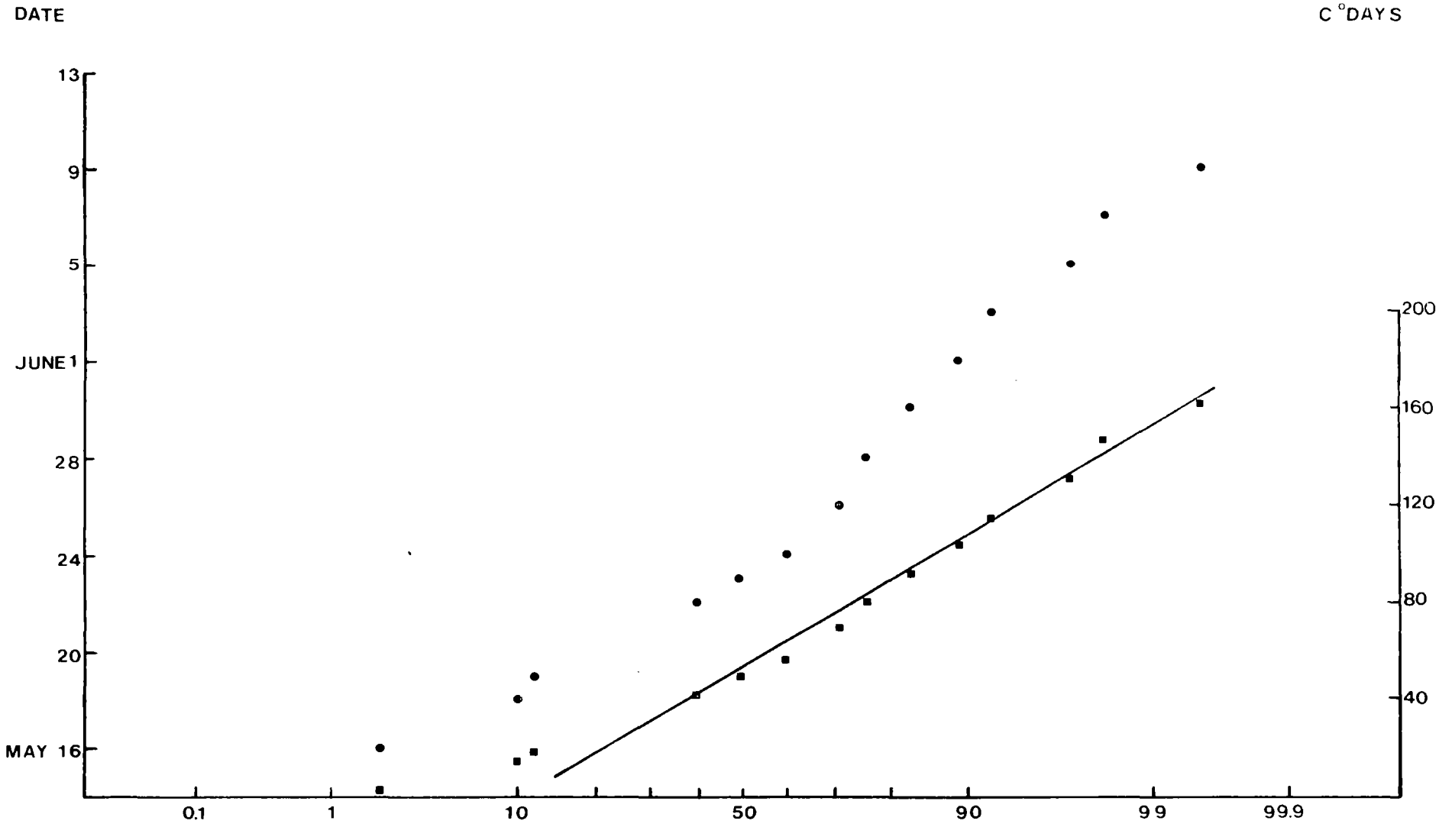

DATE
C °DAYS
13
9
5
JUNE 1
28
24
20
MAY 16
200
160
120
80
40
0.1
1
10
50
90
99
99.9

Fig. 10. The accumulated percentage emergence trap catch at Netherhearth in 1972 plotted against accumulated C degree-days on normal probability paper.

- ● date
- ■ C degree-days from the day before the first fly was caught

(N = 267)

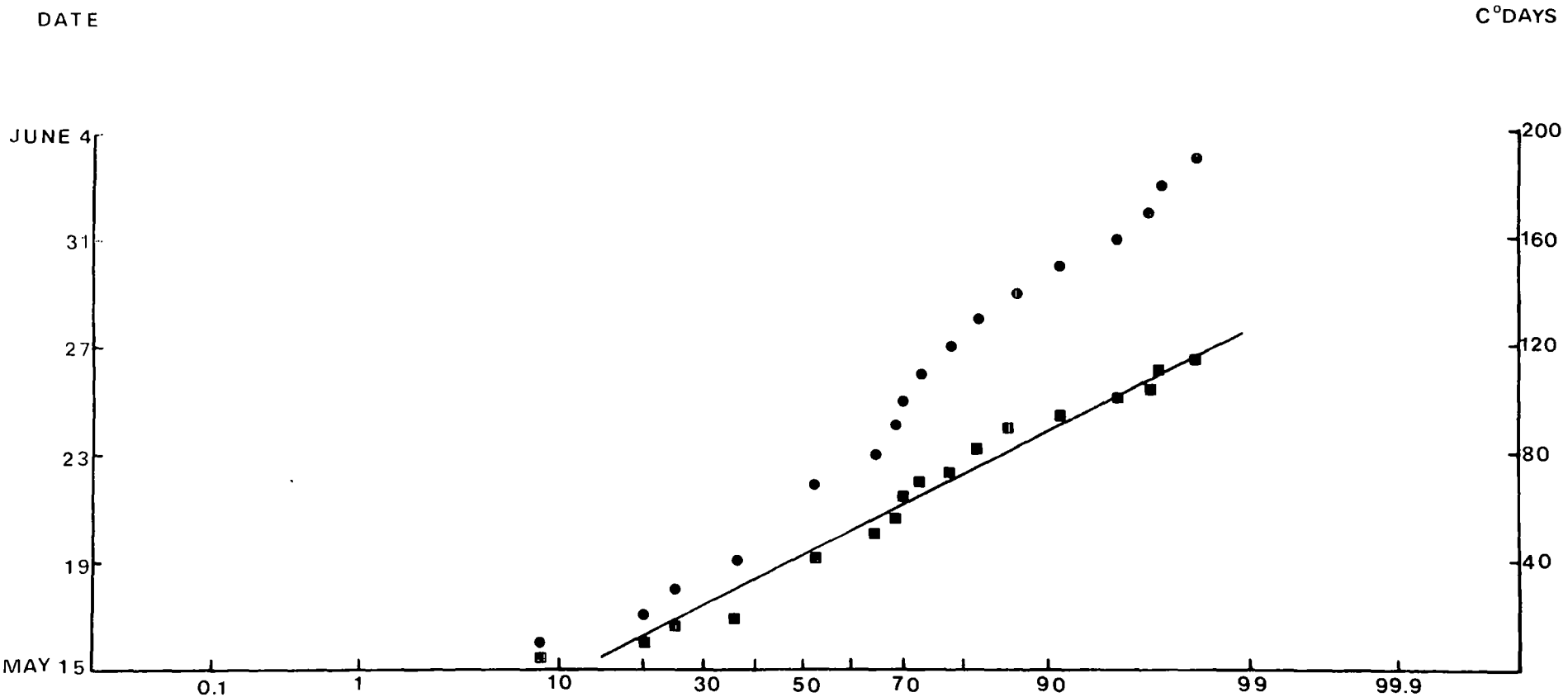

DATE
C°DAYS
JUNE 4
31
27
23
19
MAY 15
200
160
120
80
40
0.1
1
10
30
50
70
90
99
99.9

Table 4. The differences between mean dates of emergence in different years and between sites showing their level of significance

Year to year comparison on the same site :

Years being compared	Differences between years (days) Netherhearth	Above Netherhearth	Bog End (*Juncus*)	Bog End (mixed-moor)
1969-1970	9.4**	8.1**	4.9**	4.0**
1970-1971	9.3**	8.4**	9.6**	9.3**
1971-1972	3.3**	3.5**	5.1**	4.4**

Site to site comparison within the same year :

Sites being compared	Differences between sites (days) 1969	1970	1971	1972
Netherhearth - Bog End (*Juncus*)	8.3**	3.8**	4.1**	1.5*
Netherhearth - above Netherhearth	1.3*	1.6**	2.5**	2.7**
Netherhearth - Bog End (mixed-moor)	5.3**	0.9*	0.9n.s.	0.2n.s.
Bog End (*Juncus*) - above Netherhearth	9.6**	5.4**	6.6**	5.0**
Bog End (*Juncus*) - Bog End (mixed-moor)	2.0**	2.9**	3.2**	2.5**
Above Netherhearth - Bog End (mixed-moor)	6.6**	2.5**	3.4**	2.5*

* $p < 0.05$

** $p < 0.001$

Table 5. The mean temperature sum in C degree-days calculated from the beginning of emergence and the date by which this sum has been accumulated compared with the mean emergence date

Year	Mean accumulated C degree-days from the beginning of emergence	Date on which mean C degree-day falls	Mean date of emergence
1969	*92	7 June	8.1 June
1970	96	29 May	30.7 May
1971	80	20 May	21.4 May
1972	56	23 May	24.7 May

*The discrepancies between the calculated temperature sums for each year are probably due to the influence of temperature before the emergence period begins, as well as to difficulty in assessing the day on which emergence starts.

There is considerable variation in the spread of emergence between years (Table 3 shows variance) which is primarily caused by temperature differences. Fig. 11 shows the variance on the four Moor House sites plotted against the mean temperature, taken from the screen, for the emergence periods from 1969-1972. It can be seen that in general the variance decreases with the increase in mean temperature. The very low variances recorded in 1969 were probably due to the additional effect of the emergence period being later than usual. The synchronising effect of photoperiod is discussed in section VIII page 60, where it is shown that a delayed emergence period is likely to be more closely synchronised than an early one.

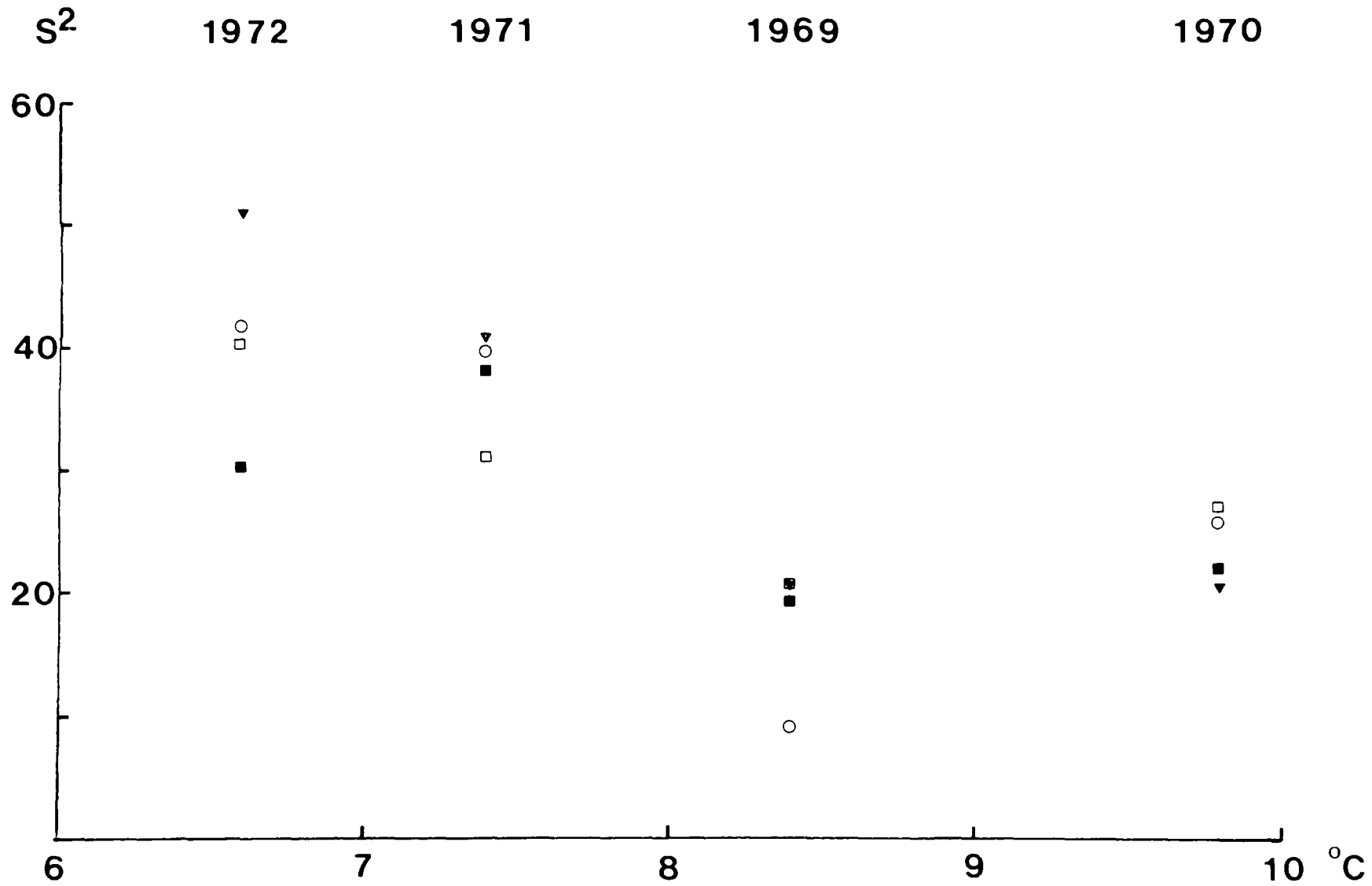
Fig. 11. The variances on the mean emergence dates on four Moor House sites plotted against the mean temperature (^{o}C) during the emergence period.

▼ Bog End (Mixed-moor)

o Above Netherhearth

□ Bog End (Juncus)

■ Netherhearth


S2
1972
1971
1969
1970
60
40
20
6
7
8
9
10
°C

2b. The effect of spring temperature on the mean date of emergence on one site from year to year

It can be seen from Tables 3 and 4 that the mean dates of emergence differ considerably from year to year and that the sequence of emergence from site to site, but not the time intervals between mean dates, remains consistent. Each year emergence begins on the Bog End (Juncus) site and ends at the Above Netherhearth site.

Using the Netherhearth data and the mean daily temperature records from the meteorological screen the temperature sum in C degree-days until the mean date of emergence has been calculated. This is shown in Table 6 and it can be seen that the temperature sum from 1 March to the mean emergence date is approximately the same each year. 1 March was chosen as a suitable date from which to calculate the temperature sum as laboratory data showed that development towards emergence was temperature dependent from approximately this date. It is also the date at which the mean daily temperatures in the field start to rise above zero. However, both of these reasons can give only an approximate date from which to calculate the temperature sum and it would not be expected that the sums calculated from year to year would correspond exactly even if the rate of development of T. subnodicornis in the spring were linearly related to temperature.

Table 6. The temperature sums from 1 March until the mean date of emergence at Netherhearth

Year	Mean date	Temperature sum in C degree-days
1969	8 June	300
1970	31 May	338
1971	21 May	297
1972	25 May	338

2c. The comparison of emergence on different sites in the same year

In 1970 Horobin (1971) used the Berthet temperature integration method for recording the soil temperatures at the 1700ft, 1900ft, 2500ft, 2700ft Bog End (Juncus), Bog End (mixed-moor) and Above Netherhearth sites. His temperature data with the calculated temperature sums in C degree-days are given below in Table 7. Due to the sugar tubes not being put down on the same date on the two sides of Dun Fell an approximation has been made to allow calculation of the temperature sum for each site for the same period of time. This consisted of regarding the period between 20 and 27 January 1970 as having a mean temperature equal to that between 27 January and 19 April 1970 (as the temperature is so low during this period this approximation does not affect the temperature sum greatly) and using Horobin's (1971)

Table 7. The mean emergence dates in 1970 and Horobin's (1971) mean temperature data derived from Berthet's method for the spring of 1970 together with temperature sums in degree °C days calculated from them

	Sites						
	1700ft	1900ft	2500ft	2700ft	Bog End (*Juncus*)	Bog End (Horobin's site)	Above Netherhearth
Mean emergence date	29.8 May	1.9 June	4.2 June	6.6 June	26.9 May	31.2 May	1.3 June
Mean temperatures from 20 Jan - 24 April on the Moor House sites and from 27 Jan - 19 April 1970 on the Dun Fell sites in °C	1.3	1.3	0.7	0.4	2.9	3.5	1.4
Mean temperatures from 24 April - 18 May on the Moor House sites and from 19 April - 13 May on the Dun Fell sites in °C	6.4	5.7	5.3	4.7	6.8	5.4	5.3
Temperature sums in C degree-days from 27 Jan - 13 May 1970 corrected to allow for the differences in dates between which the mean temperatures were taken	269.3	252.5	189.5	148.4	391.0	413.8	214.0

relationship between the mean obtained from the sugar inversion method and that from the screen data to correct for the period 13 - 18 May 1970. The mean soil temperature for the period 13 - 18 May 1970, 8.97°C, has been obtained by the substitution of the mean screen temperature of 7.4°C in the equation $y = 0.87x - 0.4$, where y is the mean in °C from the screen data and x is the mean in °C obtained from the Berthet method. The soil temperature has then been multiplied by five and 44.8Cdegree - days have been subtracted from each temperature sum at the Moor House sites. Table 7 gives the mean dates of emergence at three Moor House sites (the Bog End mixed-moor site used by Horobin was close to, but approximately 10ft above, my site on the west facing slope) and the four Dun Fell sites. Horobin's temperature data and the approximate temperature sums derived from them are shown in the same table. In Fig. 12 the mean date of emergence has been plotted against the temperature sum between 27 January and 13 May 1970. This gives the equation $y = 14.87 - 0.028x$, where the correlation coefficient is -0.809, $p < 0.05$. If the mean emergence date on each site is plotted against the uncorrected mean temperature data for April to mid May a correlation of $r = -0.917$, $p < 0.01$, is obtained and the regression has the equation $y = 32.53 - 4.46x$. This is shown in Fig. 13.

It is clear from these results that the mean emergence date is closely correlated with spring temperature, but the data do not indicate a constant temperature sum from 27 January to the mean date of emergence which was suggested by the results from the year to year comparisons at Netherhearth.

Fig. 12. The regression of mean emergence date in 1970 on accumulated temperature, in C degree-days from 27 January - 13 May 1970.

$$y = 14.87 - 0.028_x, \quad r = -0.809, \quad p < 0.05$$

(for the purposes of the regression 26 May is day 1 and subsequent dates are numbered from this date).

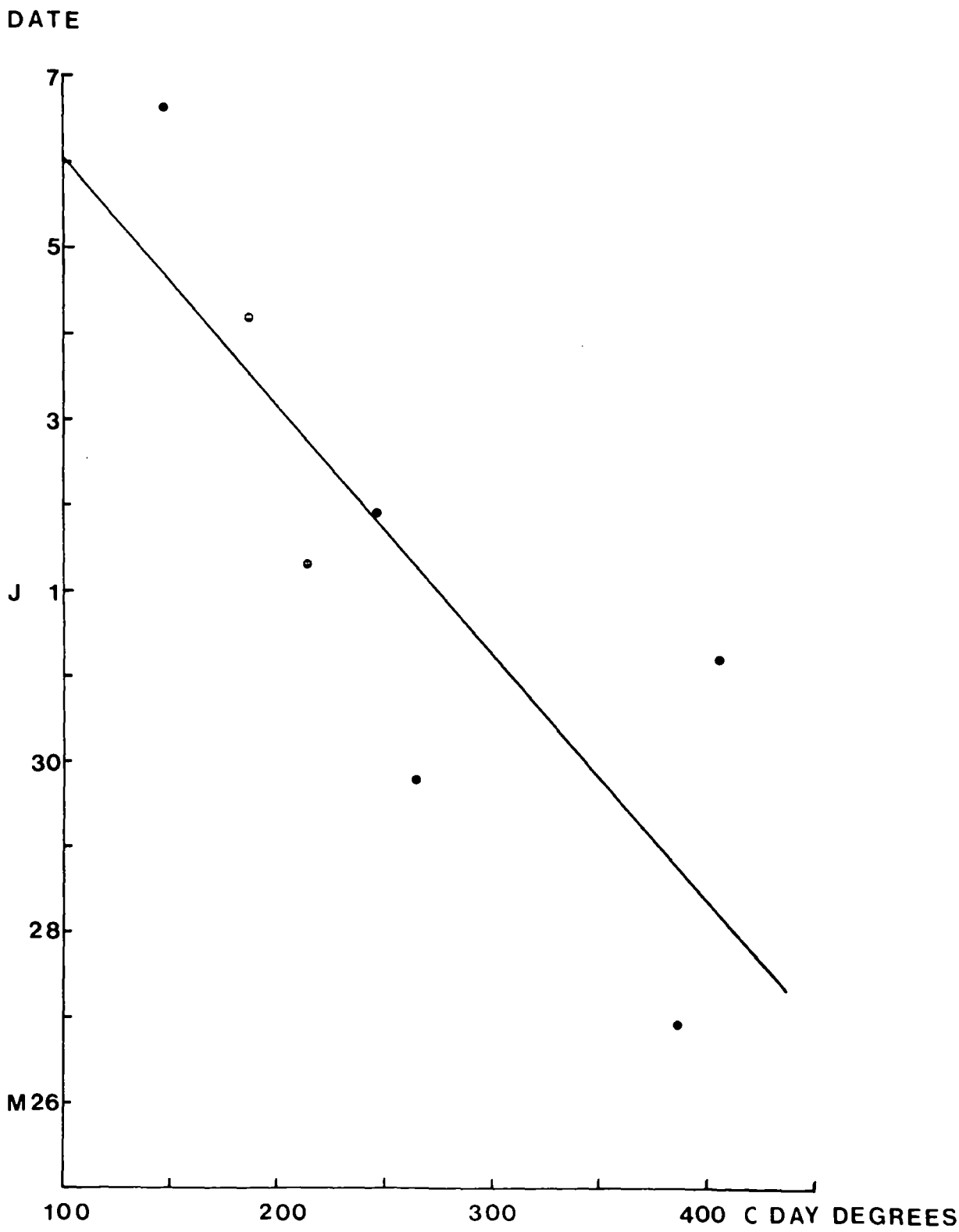
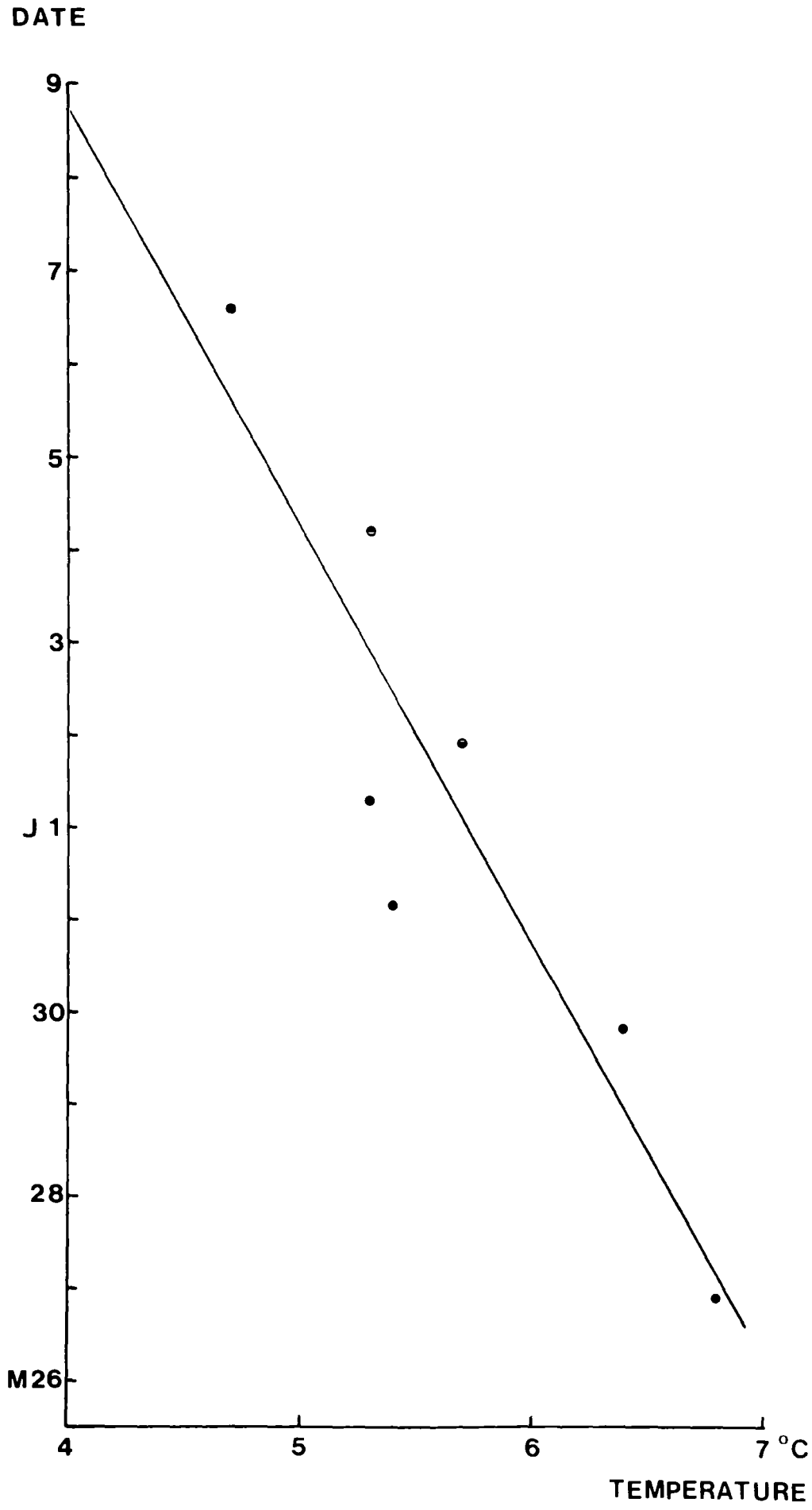

DATE
7
5
3
J 1
30
28
M26
100
200
300
400 C DAY DEGREES

Fig. 13. The regression of mean emergence dates in 1970 on mean temperature, from 19 April - 13 May 1970 on the Dun Fell sites and from 24 April - 18 May 1970 on the Moor House sites

$$y = 32.53 - 4.46x, \quad r = -0.917, \quad p < 001$$

(for the purposes of the regression 26 May 1970 is day 1 and subsequent dates are numbered from this date).


DATE
9
7
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J 1
30
28
M26
4
5
6
7 °C
TEMPERATURE

2d. Discussion

There are a number of reasons why, although development is temperature dependent, the emergence date might not depend on the accumulation of a specific temperature sum calculated as C degree-days above $0^{\circ}C$. In the first place, $0^{\circ}C$ may not be the threshold for development and development might continue below or be discontinued at a higher temperature. Glenn (1922, 1931) therefore used "effective day degrees" which were based on the temperatures above the threshold for development. In theory this threshold can be obtained graphically from experimental results at constant temperatures. If the rate of development is plotted against temperature extrapolation of the regression line back will cut the temperature axis at the "developmental zero". In practice, as Krogh (1914) pointed out, development usually continues at temperatures below this.

The second reason that temperature summation may not give consistent results is linked to the first in that the hyperbola is not usually the most appropriate description of the relationship between development rate and temperature (Andrewartha and Birch 1954), and that this applies most specifically in the region of the upper and lower development thresholds. Before a predictive model for the relationship between field temperatures and emergence date can be made, information on the type of curve that is the best expression of the relationship between development rate and temperature is required. This is best found under constant temperature conditions in the laboratory.

There is a further barrier to making accurate field predictions in that, as Laughlin (1967) found, development under field conditions may be at a higher rate than predicted from constant temperature experiments in the laboratory. It has been suggested that this is the result of the fluctuation of field temperature which in itself promotes development. Since Andrewartha and Birch (1954) disputed this suggestion there has been further work on this aspect (Messenger 1964) which will be discussed when the laboratory studies on T. subnodicornis are compared with the field results.

VI. The timing of emergence under controlled temperature conditions in the laboratory

1. Culture Methods

Fourth instar larvae were cultured in crystallizing dishes 100mm in diameter and 45mm in depth on a bed of washed sand approximately 1cm in depth. The sand was kept moist and liverworts and Juncus litter were added as food which was replaced when needed. Each dish was covered by polythene secured by a rubber band. Between 10 and 20 larvae were put in each dish and no problems of cannibalism arose.

Experiments were carried out either in constant temperature cabinets of .07m^3 capacity fitted with 8 watt fluorescent tubes or in constant temperature rooms fitted with 8 watt fluorescent tubes, (an 80 watt ceiling light in the 15°C room.). Each light was wired in series with a "Venerette"

time switch so that the photoperiod could be controlled automatically. The culture dishes were placed approximately 30cm below the 8 watt tubes in the cabinets and in the 10°C and 5°C rooms and approximately 2m below the 80 watt tubes in the 15°C room. In these positions they received illumination of 150 - 240 lux.

On 29 February 1972, 95 larvae were obtained by Berlese extraction of soil samples taken from the site behind the house. A total of 32 larvae, in three cultures, were put in the 15°C room, 42, in three cultures, in a cabinet at 10°C, and 21, in two cultures, were put at 7°C in a cabinet. The temperatures were monitored by thermographs and the cabinets were adjusted frequently so that they rarely showed more than 1°C divergence from the desired temperature. In all three cases the light regime was L : D, 18 : 6.

2. The effect of temperature on the development rate in the stage before pupation

The mean dates of pupation at the three temperature regimes are shown in Table 8 and the differences between means are shown to be significant, using a t-test.

Table 8. Comparison of mean dates of pupation of larvae brought in from the field on 29 February 1972 and kept at different constant temperatures in the laboratory

Temperature	No. of larvae used	No. of larvae pupating	No. of days (d) taken to pupate	't' for the differences in adjacent means
15°C	32	24	16.8 ± 0.71	10.5 $p < 0.001$
10°C	42	40	25.8 ± 0.49	
7°C	21	14	35.9 ± 2.76	3.6 $p < 0.001$

These data have been plotted as mean date of pupation against temperature in Fig. 14 where the relationship between the reciprocal x 100 of the number of days to pupation and temperature is also shown. The data correspond adequately to the hyperbola, $252 = y(x - 0.05)$, where y is the number of days before pupation and x is the temperature. Where y is the daily development rate x 100, this is converted to the linear equation $y = 0.4x - 0.02$ ($r = +0.999$, $p < 0.01$) indicating that between 7° and 15°C there is a close correlation between temperature and the rate of development towards pupation.

3. The effect of temperature on the development rate during pupation

Table 9 gives the mean number of days spent during pupation at different temperatures. The percentage daily development rate is plotted against temperature in Fig. 15. The sigmoid nature of the curve of the development rate plotted against temperature can be seen and the linear relationship;

Fig. 14. Time in days for larvae taken from the field on 29 February 1972 to pupate and the percent development per day plotted against temperature (^{o}C).

When y is percent development per day

the regression equation is

$y = 0.4x - 0.02$, $r = +0.999$, $p < 0.01$

o development time in days (Y)

● percent development rate per day $(\frac{100}{Y})$

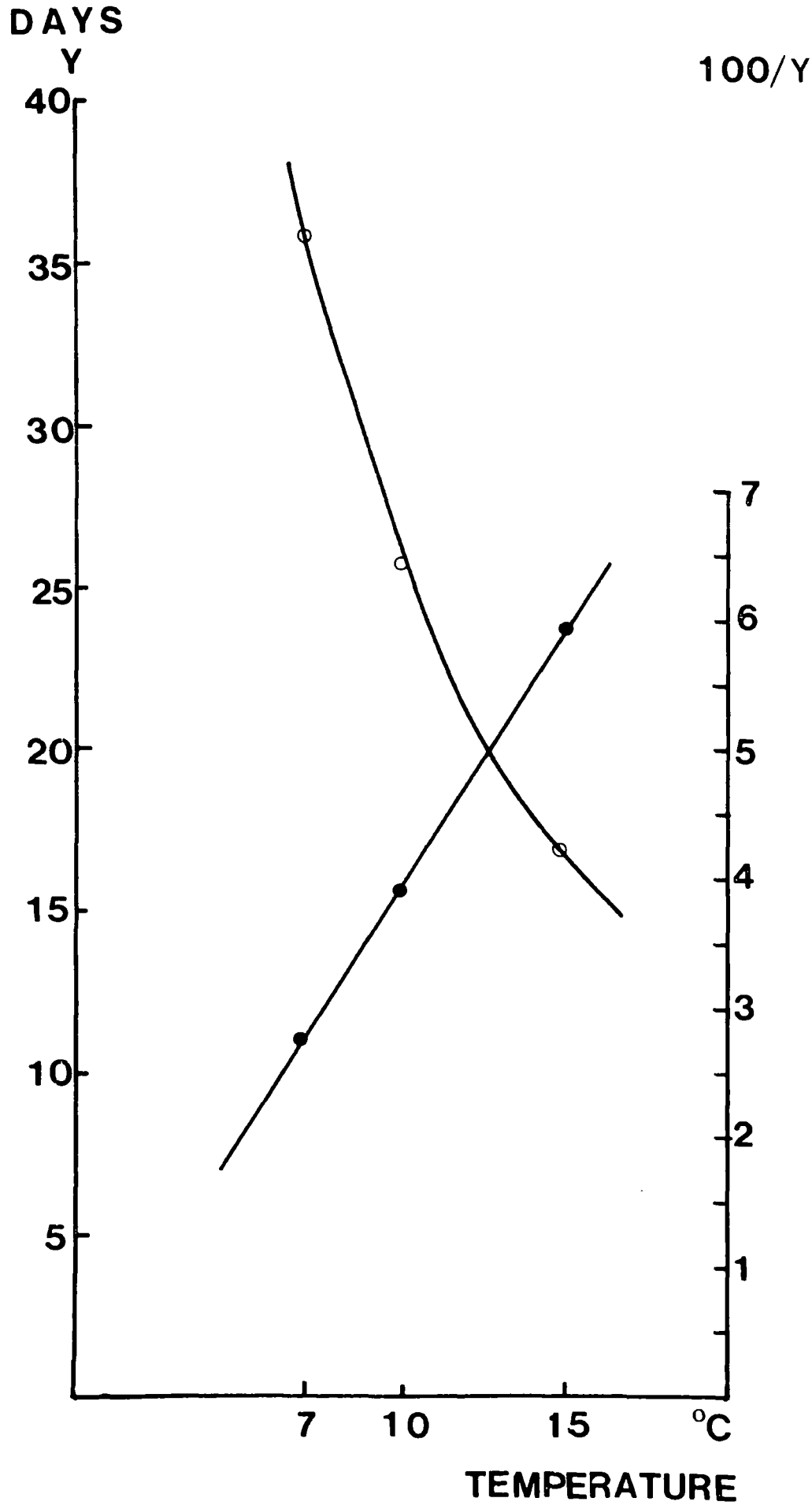
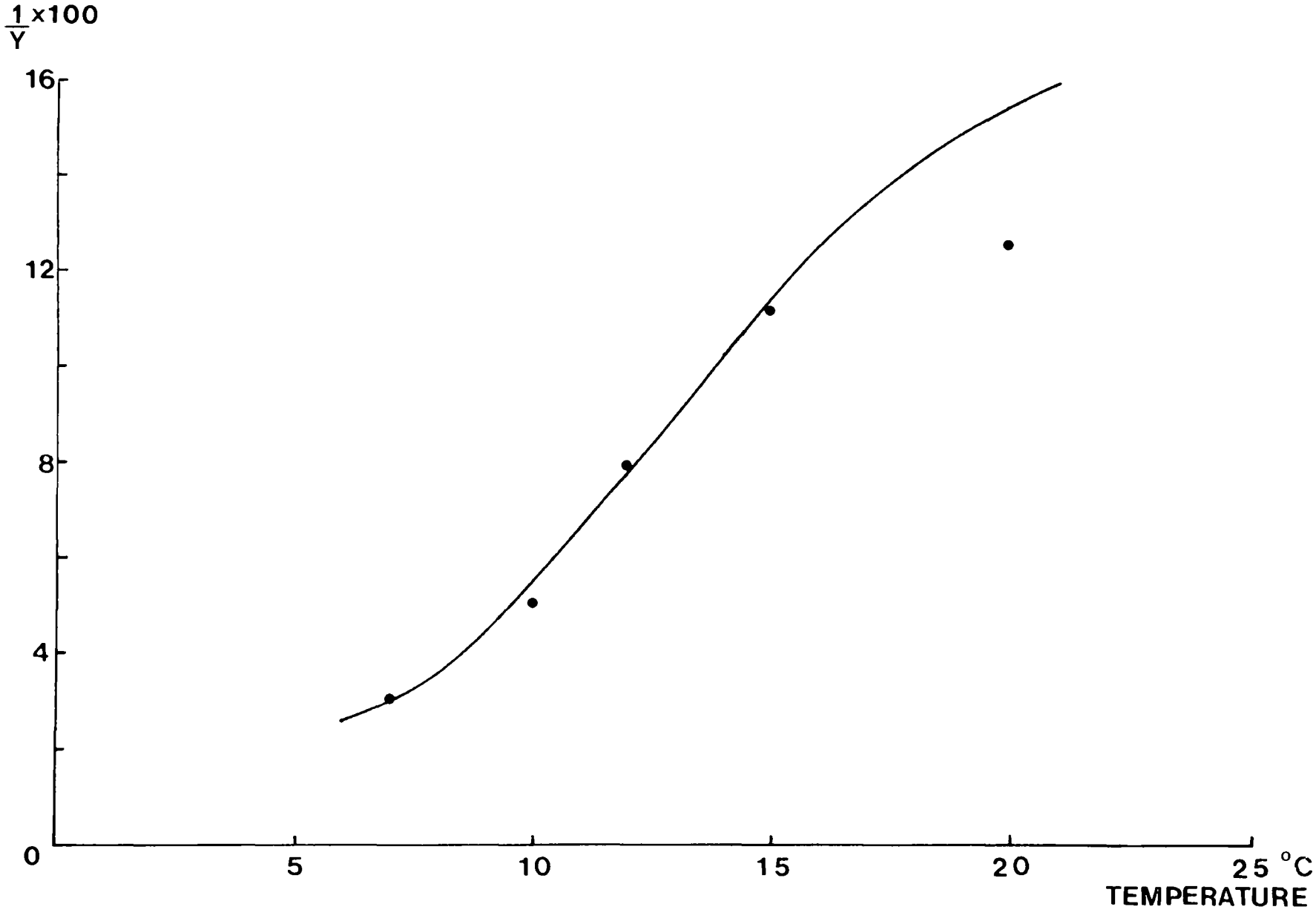

DAYS
Y
100/Y
40
35
30
25
20
15
10
5
7
6
5
4
3
2
1
7
10
15
°C
TEMPERATURE

Fig. 15. The percent daily development rate during pupation plotted against temperature (^{o}C).

The equation of the fitted curve is :

$$y = \frac{18.0}{1 + e^{3.4799 - 0.2636x}}$$


1/Y x100
16
12
8
4
0
5
10
15
20
25 °C
TEMPERATURE

$y = 1.21x - 6.89$, where y is the percentage daily development and x is the temperature, is restricted to between 10°C and 15°C. The Pearl-Verhulst equation (Davidson, 1944)

$$\frac{100}{Y} = \frac{18}{1+e^{3.4799 - 0.2636x}}$$

where Y is the time required for pupation and x is the temperature, fits the data over a greater temperature range, 7° - 15°C. However, considerably more data are needed before such an equation can be fitted precisely.

Table 9. Comparison of the duration of pupation at different constant temperatures

Temperature (°C)	No. of pupae used	No. of pupae died	Mean no. of days during pupation (d)	S.E.	't' for the differences between the adjacent means
20	10	2	8.00	±0.47)	
				)	1.92 n.s.
15	9	0	9.00	±0.22)	
				)	12.66 p<0.001 d.f. 13
12	6	0	12.67	±0.19)	
				)	10.07 p<0.001 d.f. 6
10	6	0	20.17	±0.72)	
				)	9.52 p<0.001 d.f. 7
7	8	3	32.60	±1.09)	
5	7	7	no emergence		

4. Discussion

If the relationship between development rate and temperature is known it is possible to calculate the mean emergence date of an insect (Glenn 1931) from the field

temperature data. If this is done for T. subnodicornis, assuming a linear relationship between development rate and temperature and a threshold of 0°C, the temperature sum obtained from the laboratory data is : 250 + 200 = 450 C degree-days for the period before pupation and that during pupation for larvae brought in from the field on 29 February 1972. This must be compared with the temperature sum accumulated at Netherhearth from 1 March until the mean emergence date each year which ranged between 296 and 338 C degree-days. The discrepancy might be lessened if the developmental zero was lower than 0°C (calculated from the linear relationship it was +0.05°C for the period before pupation and +5.7°C for pupation). It is also necessary to know whether such a threshold applies to the whole developmental period or to a specific phase such as moult or emergence. Although no flies emerged at 5°C, it was noticed that after thirty days the pupae were alive and darkened (usually a sign of maturity), but that they died soon after, indicating that the 5°C threshold applied to emergence rather than pupal development.

Alternatively, the percentage daily development at field temperatures could be calculated from the logistic equation which has already been shown to fit a greater temperature range than does the linear relationship for the pupation data. This is likely to give a much better approximation for development rates in the field because of the flattening of the curve in the region of the developmental zero. However, as Howe (1967) pointed out, it is necessary to have at least ten points on the

curve with additional points for 3°C on either side of the optimum before a curve can be fitted. The data for all stages of development in T. subnodicornis are not adequate for accurate equations of this type to be fitted.

Another reason that development in the field might be faster than expected is that the temperature fluctuates. Messenger (1964) found that for Therioaphis maculata Buckton the rate of development on a fluctuating temperature regime was faster at all temperatures than would be expected from constant temperature studies. That is, the rate of development at the mean of the fluctuating temperature was higher than the rate at the same constant temperature. He used the technique of hourly temperature summing determined from the constant temperature-development relationship so that curvature in this relationship was allowed for, and the observed increase in development rate at fluctuating temperatures could be attributed to the stimulation of the change in temperature alone.

Further data are needed on the relationship between development rate and temperature at temperatures below 7°C but despite discrepancies when field and laboratory data are compared it appears that the development of larvae towards pupation and during pupation in the spring is temperature-dependent. Contrary to Horobin's hypothesis for Molophilus ater, T. subnodicornis larvae are not fully developed by early spring and waiting for a temperature trigger to pupate. There is a period before pupation when further temperature dependent development takes place. Between 7°C and 15°C

a linear relationship describes the relationship between development rate and temperature, but more data would probably indicate that the logistic curve would be more appropriate, especially at field temperatures. The rate of development during pupation is also temperature dependent as it is in M. ater (Hadley 1971b), and this relationship is also probably best described by the logistic equation.

VII. THE EFFECT OF TEMPERATURE ON THE RATE OF DEVELOPMENT OF THE EGG AND OF TEMPERATURE AND PHOTOPERIOD ON THE RATE OF DEVELOPMENT IN THE PRE-WINTER LARVAL STAGES

Whether the linear or logistic relationship between rate of development and temperature is used, in the middle part of the favourable temperature range the development rate is approximately linearly related to temperature. Danilevskii (1965) shows that for a number of lepidopterous species the development rate is directly related to temperature over the temperature range encountered in the environment.

It has been suggested that in the spring the field temperatures are below the range over which the development rate of T. subnodicornis is linearly related to temperature. This would diminish the effect of temperature differences during this period but it is clear from the field data as well as from the laboratory experiments that the timing of emergence in spring is still positively related to temperature. As egg development and a large part of the larval development takes place during the summer months when the mean temperature is above 10°C, it would be expected that the rate of development

would be directly related to temperature during this period and, unless a diapause intervenes or larvae are inhibited from further development at some stage, an annual life-cycle cannot be maintained under differing temperature conditions. Accordingly, the response of egg development and larval growth rate to constant temperature over a range from 5 - 25°C has been examined in the laboratory. As photoperiod has also been shown to have an effect on growth rate in certain cases (Geyspitz and Zarankina 1963; Danilevskii 1965; Beck 1968) it was also decided in 1972 to compare the effect of long day L : D; 18 : 6, and short day L : D; 6 : 18, on the growth of larvae in culture.

1. The relationship between temperature and egg development rate

Method

Newly emerged males and females were allowed to copulate in covered crystallizing dishes. A sheet of damp crumpled tissue paper provided ridges from which the pair could hang while copulating and kept the humidity high. On the completion of copulation, decapitation of the females ensured that the eggs were laid in quick succession (Coulson 1962). These were picked up on the end of a brush and placed on damp tissue paper in Petri dishes. The dishes were then placed in constant temperature cabinets at 25°, 20°, 15°, 10° and 7°C.

Results

The mean number of days taken for the eggs to hatch at each temperature is shown in Table 10. The mortality increased with decrease in temperature.

Table 10. The number of days taken for eggs to hatch at different temperatures and the percentage mortality at each temperature

Temperature °C	Mean no. days to hatch	Spread of hatching (hours)	No. of eggs	% mortality
25	7	9.0	82	6.4
20	9	9.0	100	0
15	14	24.0	85	16.5
10	25	24.0	96	22.9
5	60	48.0	39	61.3

These data are shown in Fig. 16 where y, the mean hatching time, has been plotted against x, temperature in ^{o}C. For comparative purposes the reciprocal $\times$ 100 of the mean hatching time has also been plotted against temperature. This gives the linear relationship $y = 0.64x - 2.06$ ($r = +0.996$) where y is the percentage development per day and x is temperature in ^{o}C. Coulson (1962) also measured the time taken for eggs to hatch at different temperatures. His data are shown, but not included in the regression.

These data which, if they were more extensive, would probably be shown to be better expressed by a logistic

Fig. 16. The number of days taken during egg development and the percent development per day plotted against temperature (^{o}C).

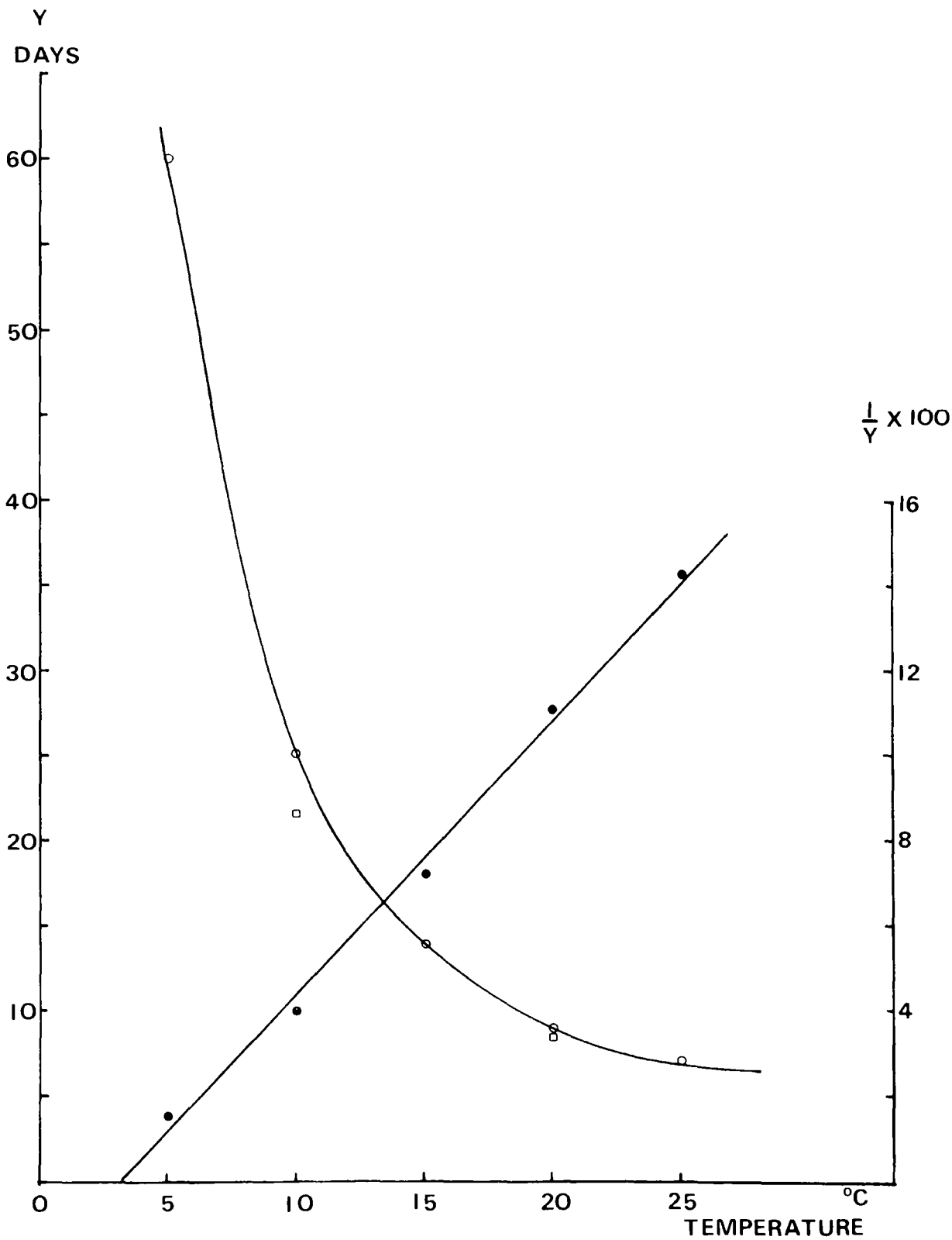
When y is percent development per day the regression equation is :

$y = 0.64x - 2.06$, $r = +0.996$, $p < 0.001$

o development time in days

□ ,, ,, ,, (Coulson 1962)

● percent development rate per day


Y
DAYS
60
50
40
30
20
10
0
5
10
15
20
25
°C
TEMPERATURE
1/Y X 100
16
12
8
4

curve correspond to the expected type of relationship between development rate and temperature. Although there is probably a departure from the linear relationship between development rate and temperature at 5°C, between 7°C and 25°C the relationship is close enough to be used predictively.

2. The effect of temperature on larval growth rates (1971)

2a. Method

During the emergence period in 1971 fertilised females were gathered in the field and enclosed, on damp filter paper, in crystallizing dishes. Under these conditions they laid most of their eggs within 12 hours. The eggs were then removed with a paint brush to damp filter paper in Petri dishes. The Petri dishes were kept at 15°C until the larvae hatched.

On hatching, the first instar larvae were transferred in groups of 20 to a culture medium of leafy liverworts on a base of wet sand in Petri dishes, and on reaching about 20mg the larvae were transferred to the same type of culture in crystallizing dishes. The liverworts consisted largely of Dyplophyllum albicans and Ptyllidium ciliare found around the Juncus bases at Netherhearth. Twenty Petri dishes were put at each of the following temperature regimes : 25°, 20°, 15°, 10° and 5°C. In all cases the photoperiod regime was L : D, 18 : 6, and the cultures were arranged so that they received the same amount of incident light (150 - 240 lux). The temperatures were monitored by Cambridge thermographs in

constant temperature rooms and by Castella thermohygrographs in constant temperature cabinets. When working normally neither the constant temperature rooms nor the cabinets deviated by more than $\pm$ 1°C from the set temperature.

At intervals of two to four weeks, larvae were taken from each of the sets of cultures and weighed.

2b. Results

The mean weights of the larvae at each temperature regime are shown in Table V in the appendix and plotted on a logarithmic scale against time in Fig. 17. It appears that the growth rates at temperatures from 10° - 20° C are not positively related to temperature over the weight range from 5 - 50mg. The larvae kept at 25°C grew faster than at the other temperatures initially, but all larvae died before 5 October 1971 and the peak mean weight attained was 62.5mg, as opposed to 97.8mg at 15°C.

Table 11 shows the number of days and the daily percentage rate of development at each temperature for the range in weight from 5 - 50mg.

Fig. 17. The mean weights (mg) of larvae reared at different temperatures (°C) in 1971 plotted on a logarithmic scale against time (days)

▲ 25°C

o 20°C

■ 15°C

□ 10°C

△ 5°C

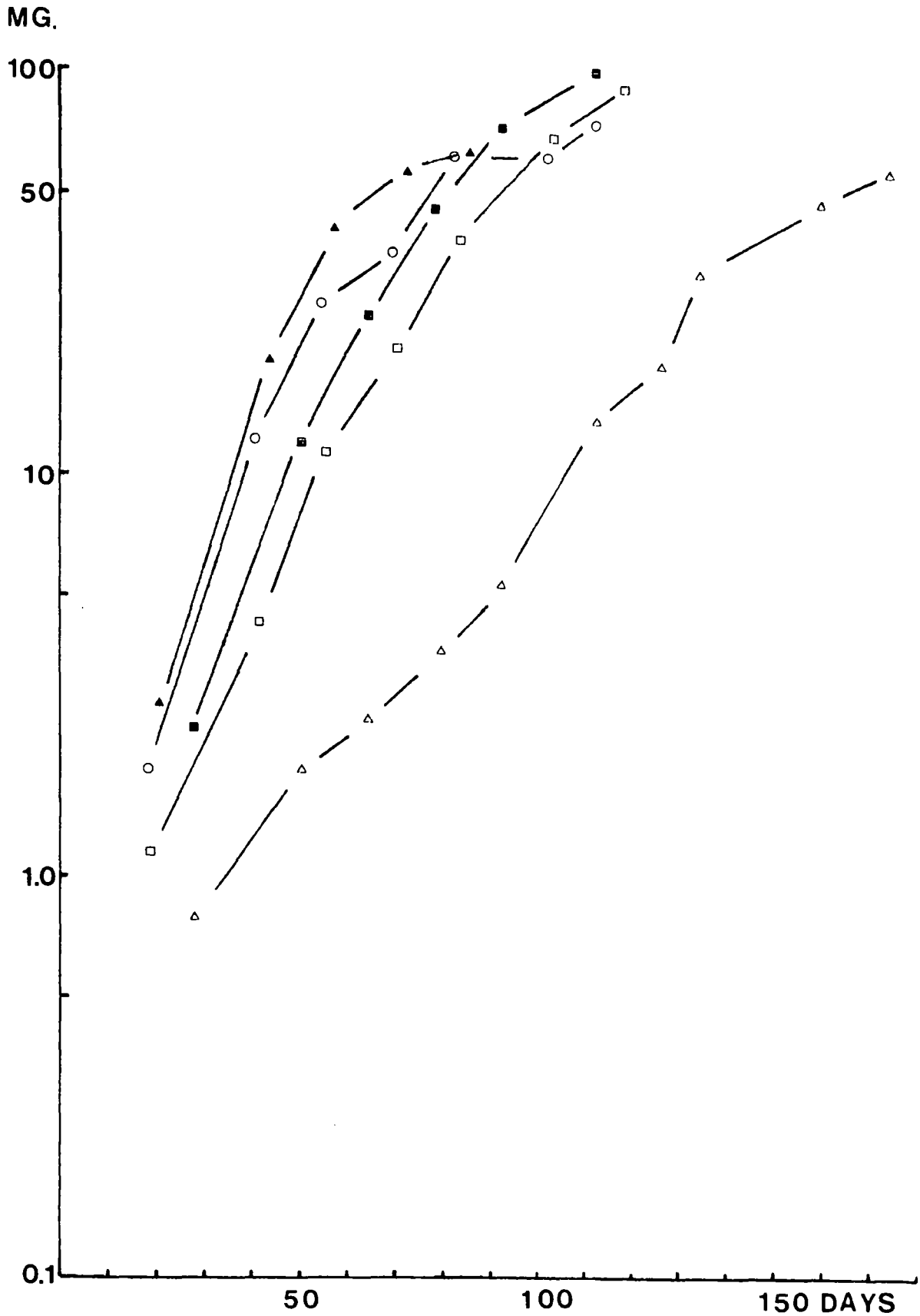

MG.
100
50
10
1.0
0.1
50
100
150 DAYS

Table 11. The number of days and the daily percentage rate of development for larvae on different temperature regimes in 1971 to grow from 5 - 50mg

Temperature (°C)	No. of days (Y) to grow from 5-50mg	100/Y
25	39	2.56
20	48	2.08
15	43	2.33
10	48	2.08
5	76	1.32

The lack of positive correlation between growth rate and temperature was unexpected and it was thought that the method by which the mean weights were obtained was unreliable. Selection from each set of cultures might not have been random if the larger larvae were more conspicuous, and high mortality in unfavourable cultures might have biassed the mean if, for example, mortality had been higher among the slower growing larvae. On these grounds it was decided to repeat the experiment in the following year, measuring growth of individual larvae. This method also has the advantage that confidence limits can be attached to the means.

3. The effect of temperature on larval growth rates (1972)

3a. Method

The eggs were allowed to hatch and the first instar

larvae were cultured as in 1971. The cultures were placed under similar temperature and light conditions as before, with the addition of another temperature regime, 7°C. After a week, 20 larvae from each of the culture sets at 25°, 20°, 15° and 10°C were weighed and put in individual cultures of liverwort on damp sand in standard 2 x 1 inch tubes. 20 larvae from the 7°C regime were set up in similar cultures the week after and 20 larvae from the 5°C regime the following week. The larvae were weighed at approximately 10 day intervals, longer at 7° and 5°C, and on reaching 20mg were transferred to 3 x 1½ inch tubes.

On 7 July 1972 two additional sets of cultures were set up at 10° and 20°C respectively, on a photoperiod of L : D, 6 : 18. The larvae used to start these cultures were obtained from the stock cultures at 10° and 20°C on the L : D, 18 : 6 photoperiod.

In all cultures the medium was renewed at irregular intervals whenever the food supply appeared to be less than abundant or to be fouled. Dead larvae were replaced by larvae from the stock cultures kept at each temperature and photoperiod.

3b. Treatment of 1972 results

Few of the original larvae in each set of cultures survived to pupate so it was decided to use the mean weight increments rather than actual weights for analysis. However,

Figs. 18 and 19 showing mean weight of larvae, grown at the photoperiod L : D, 18 : 6 and on different temperature regimes, plotted arithmetically and logarithmically respectively against date, are included for comparison with Fig. 17. The results are similar in that there appears to be little difference in the mean growth rates of larvae at temperatures between 10° and 20°C. The larvae at 25°C failed to survive beyond three weeks, possibly because of the malfunction of the thermostat which allowed the temperature to rise to 28°C during this period.

Laughlin (1960) found that in T. oleracea the growth curve was logarithmic during the first three instars and arithmetic in the fourth. In Fig. 20 the mean weights of a group of larvae on the L : D, 6 : 18 photoperiod and 10°C regime that survived to reach their maximum weights have been plotted against time. This shows that an initial logarithmic growth phase is followed by an arithmetic phase and that the change takes place between 10 and 20mg. In order to find whether this corresponded to a change in instar a small sample of larvae was weighed and assigned to instar by measurement of the spiracular disc (Coulson 1962). This is shown in Fig. IV and Table VI in the appendix and it appears that, as in T. oleracea, the change from logarithmic to an arithmetic growth rate occurs at the change from the third to fourth instar in the 16 - 25mg range. Accordingly, the weight of 20mg has been regarded as the division between third and fourth instar and increments of larvae weighing less than 20mg have been compared as the mean logarithmic daily weight increment and

Fig. 18. The mean weights (mg) of larvae reared at different temperatures (°C) but the same photoperiod (L:D; 18:6) in 1972 plotted against time (date)

○ 20°C

■ 15°C

□ 10°C

● 7°C

△ 5°C

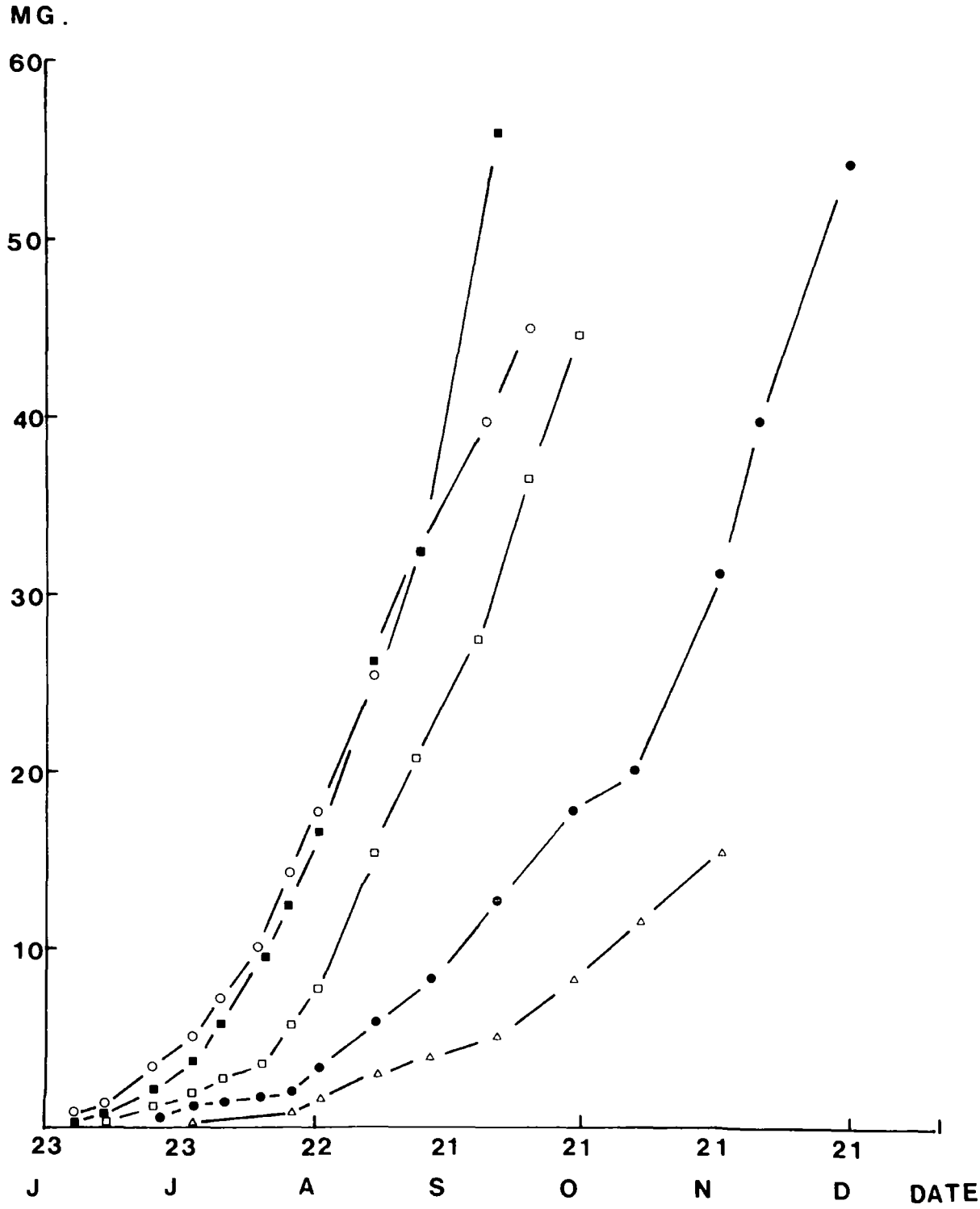

MG.
60
50
40
30
20
10
23 J
23 J
22 A
21 S
21 O
21 N
21 D
DATE

Fig. 19. The mean weights (mg) of larvae reared at different temperatures (°C) and the same photoperiod (L:D; 18:6) in 1972 plotted on a logarithmic scale against time (date).

○ 20°C

■ 15°C

□ 10°C

● 7°C

△ 5°C

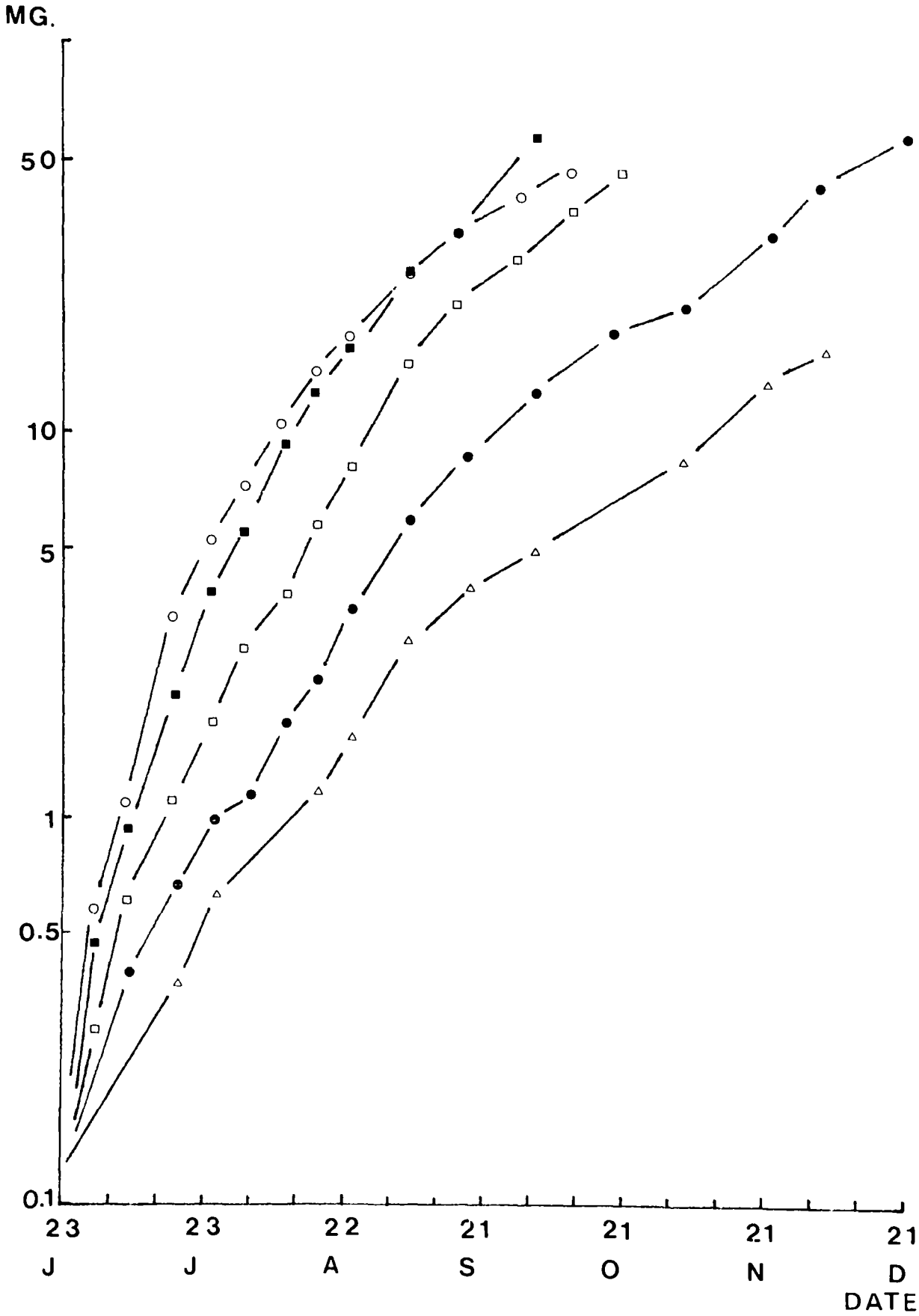
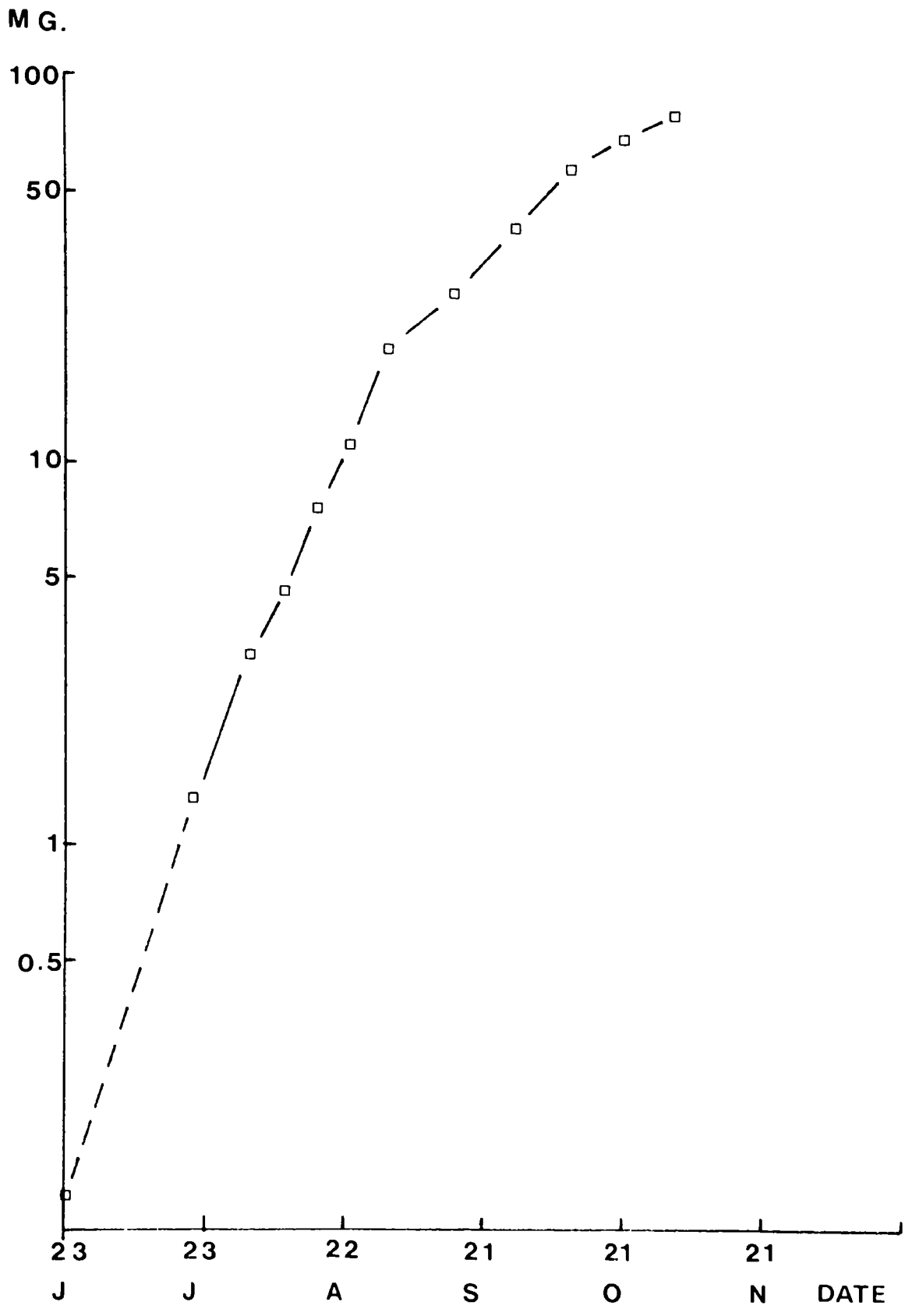

MG.
50
10
5
1
0.5
0.1
23 J
23 J
22 A
21 S
21 O
21 N
21 D
DATE

Fig. 20. The mean weight (mg) of eight larvae kept at 10°C and a photoperiod of L:D; 18:6 in 1972 plotted on a logarithmic scale against temperature.


MG.
100
50
10
5
1
0.5
23 J
23 J
22 A
21 S
21 O
21 N
DATE

increments of larvae weighing more than 20mg have been compared as mean daily weight increments, all the original weighings being in mg.

From Fig. 19 it appears possible that there are inflections in the growth curves other than at 20mg. This might have been an artifact produced by the substitution of larvae, but at 20°, 7° and 5°C there is an inflection at 3mg and this corresponds to the approximate weight at which larvae enter the third instar. So another division into weight ranges has been made at this point and the increments of larvae below 3mg are considered separately from those above. The 3 - 20mg range has been further divided into 3 - 10mg and 10 - 20mg ranges so that fourth instar or third instar larvae, in which the growth rate was slowing as a prelude to moult, are restricted to the heavier weight range.

From comparison of Figs. 18 and 19 it appears possible that the arithmetic growth phase was entered earlier at higher temperatures than at lower. In this case the logarithm of the increment would be negatively correlated with weight and would require correction. Table VII in the appendix shows the regression parameters for the regressions of the logarithm of the weight increment on the logarithm of the weight in mg. It can be seen that in a number of cases there is a significant though small regression coefficient. The data for the 10°C, L : D; 18 : 6 regime in the 10 - 20mg range have been corrected to allow for the negative relationship between the logarithms of increment and original weight. This has had the result of changing the mean logarithmic increment multiplied by 10^5 from 1581 ± 200 to 1598 ± 206. As this is a difference of 1.1% and not significant, it was decided that it was unnecessary to make this type of correction.

An analysis of variance, shown in Table VIII in the appendix, indicated that within each weight range the variation between the weight increments of one larva was no less than that between larvae. It was therefore decided to use all the available weight increments of each larva in each weight range.

Death of larvae is usually preceded by loss of weight. In order to eliminate this variation only the increments of larvae that entered the weight range above that being considered have been used. In the case of larvae weighing more than 20mg the increment for the weight before the maximum weight and subsequent increments have not been used.

3c. Results

Table 12 shows the mean of the logarithmic daily increments for the weight ranges below 20mg and the mean daily increments for weight ranges above 20mg for the larvae grown under different temperature conditions, but at the same photoperiod, L : D; 18 : 6. Survival of larvae at $5^{\circ}C$ was so low that only one set of data, that from the 0.12 - 3mg range, was available. The data have been examined in two ways; first, the differences in growth rate of larvae growing at each temperature have been compared in each weight range to see whether the growth rate decreases as the weight increases. Secondly, the growth rates at the different temperature regimes have been compared within each weight range. Students' t-test is used to indicate the significance of the differences.

Table 13 shows that at each temperature there is a significant drop in the logarithmic rate of growth between the first and third weight ranges and that the decrease in rate is greatest at 20°C. At the two higher temperatures, but not at 7° or 10°C, the decrease in rate between the 0.12 - 3mg and the 3 - 10mg ranges is significant.

Table 14 shows the differences between rates in the same weight range but at different temperatures. In the 0.12 - 3mg range the rate is positively related to temperature from 5 - 20°C but only the differences between 7° and 10°C and between 10° and 15°C are significant. In the 3 - 10mg range the rates have decreased and none of the differences between increments gained at adjacent temperatures are significant. However, the rates are positively related to temperature over the range from 7 - 20°C and the difference between the rate at 7°C and the rate at 15°C is significant. In the 10 - 20mg range the rate at 20°C drops below that at 15°C and the difference becomes significant in the range above 20mg. In this range the differences in growth rates between 7° and 15°C have decreased to the extent that none of them is significant.

Table 12. The mean logarithmic daily increment for larvae weighing less than 20mg and the mean daily increment for larvae weighing more than 20mg, the original weights being in mg, in each weight range and at each temperature regime

Weight range	Temperature °C	N	Mean daily log $\times 10^5$ increment (mg)	S.E.
0.12 - 3mg	5	42	1586	173
	7	67	1741	243
	10	61	2365	183
	15	29	3568	303
	20	22	4348	453
3 - 10mg	7	32	1347	133
	10	37	1861	286
	15	31	2214	197
	20	30	2237	409
10 - 20mg	7	21	935	165
	10	17	1581	200
	15	19	1976	227
	20	33	1531	155
			Mean daily increment (mg)	
20 + mg	7	23	0.680	0.0813
	10	49	0.886	0.0791
	15	25	1.080	0.2051
	20	60	0.582	0.0524

Table 13. Comparison of the logarithmic mean increments gained on the same temperature regime but in different weight ranges

Temperature	Wt. ranges being compared	Difference in mean daily $\log . 10^5$ increment, mg	t	p
7°C	0.12 - 3 & 3 - 10mg	394	1.42	n.s.
	3 - 10 & 10 - 20mg	412	1.94	n.s.
	0.12 - 3 & 10 - 20mg	806	2.74	<0.01, d.f.82*
10°C	0.12 - 3 & 3 - 10mg	504	1.49	n.s.
	3 - 10 & 10 - 20mg	280	0.80	n.s.
	0.12 - 3 & 10 - 20mg	784	2.89	<0.01, d.f.45
15°C	0.12 - 3 & 3 - 10mg	1354	3.75	<0.001, d.f.49
	3 - 10 & 10 - 20mg	238	0.79	n.s.
20°C	0.12 - 3 & 3 - 10mg	2111	3.46	<0.01. d.f.47
	3 - 10 & 10 - 20mg	706	1.61	n.s.

* Degrees of freedom have only been calculated when one or both the sample sizes are below 30

Table 14. Comparison of the logarithmic increments and increments gained within the same weight range and on the same photoperiod, L : D; 18 : 6, but on different temperature regimes

Wt. range	Temperatures being compared (°C)	Differences in mean daily log x 10^5 increment, mg (1)	t	p	
0.12 - 3mg	5 and 7	+ 155	0.52	n.s.	
	7 and 10	+ 624	2.05	< 0.05	
	10 and 15	+ 1203	3.41	< 0.01	
	15 and 20	+ 780	1.47	n.s.	
3 - 10mg	7 and 10	+ 514	1.63	n.s.	
	10 and 15	+ 353	1.01	n.s.	
	15 and 20	+ 23	0.05	n.s.	
	10 and 20	+ 376	0.75	n.s.	
	7 and 15	+ 867	3.64	< 0.01	
10 - 20mg	7 and 10	+ 646	2.48	< 0.02	(2) d.f.33
	10 and 15	+ 395	1.30	n.s.	
	15 and 20	- 445	1.62	n.s.	
		Mean daily increment, mg			
20 + mg	7 and 10	+ 0.2062	1.82	n.s.	
	10 and 15	+ 0.1935	0.88	n.s.	
	15 and 20	- 0.4977	2.35	< 0.05	d.f.27
	7 and 15	+ 0.3997	1.81	n.s.	

(1) + indicates that the rate is higher at the higher temperature
- that it is lower

(2) Degrees of freedom only calculated when one or both the sample sizes are below 30

Table 15. The number of days required to grow through each range at each temperature and the daily development rate at each temperature

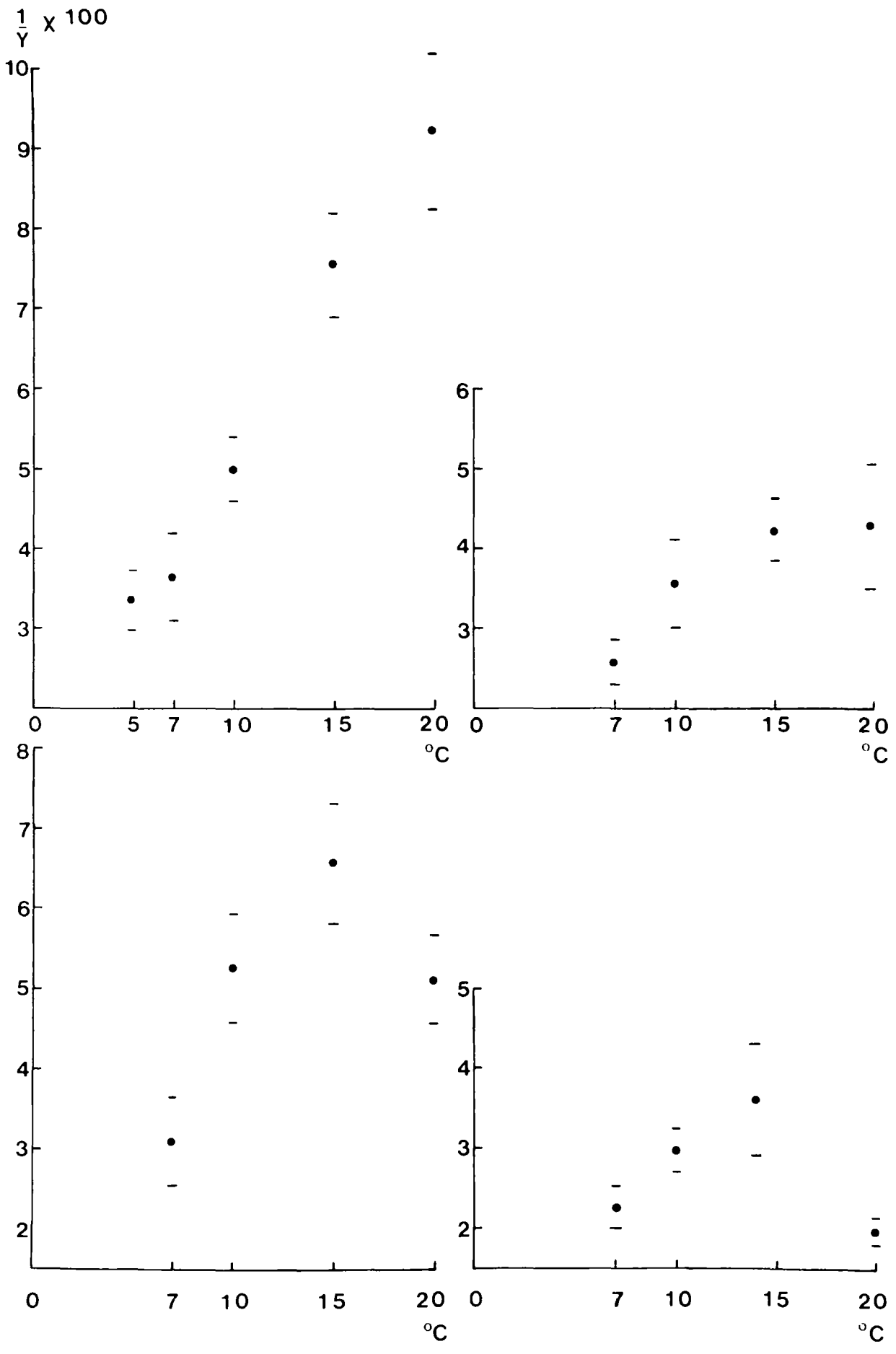
Weight range		Temperature regimes				
		5°C	7°C	10°C	15°C	20°C
1 - 3mg	Days	30.08	27.40	20.17	13.37	10.97
	$^{100}/_{d}$	3.37	3.65	5.02	7.57	9.23
	S.E. $^{100}/_{d}$	0.37	0.52	0.39	0.64	0.96
3 - 10mg	Days		38.82	28.10	23.62	23.38
	$^{100}/_{d}$		2.58	3.56	4.23	4.28
	S.E. $^{100}/_{d}$		0.25	0.55	0.38	0.78
10 - 20mg	Days		32.20	19.04	15.23	19.66
	$^{100}/_{d}$		3.11	5.25	6.56	5.09
	S.E. $^{100}/_{d}$		0.55	0.67	0.75	0.52
20 - 50mg	Days		44.12	33.86	27.78	51.55
	$^{100}/_{d}$		2.27	2.95	3.60	1.94
	S.E. $^{100}/_{d}$		0.27	0.26	0.68	0.17

For comparative purposes the logarithmic growth rates in the ranges below 20mg and the arithmetic rates in the range above 20mg have been re-calculated as the number of days spent in each range (the 0.12 - 3mg range has been converted to a 1 - 3mg range and the range above 20mg is considered to be from 20 - 50mg). The number of days in each stage has then been converted to the reciprocal to give a daily growth rate. This is shown in Table 15 and in Fig. 21; the percentage growth rate per day is plotted against temperature.

Fig. 21. The percent growth rate per day for larvae in four weight ranges plotted against temperature.

Upper left 1 - 3mg range Upper right 3 - 10mg range

Lower left 10 -20mg range Lower right 20 - 50mg range


1/Y x 100
10
9
8
7
6
5
4
3
0
5
7
10
15
20
°C
6
5
4
3
0
7
10
15
20
°C
8
7
6
5
4
3
2
0
7
10
15
20
°C
5
4
3
2
0
7
10
15
20
°C

All stages of the life-history are compared in Table 16 where the Q_{10} between 10° and 20°C and the Q_{10} between 7° and 15°C have been calculated for each stage. A visual impression of the comparative effect temperature has on developmental rates has been given by expressing all development rates as percentages of the rate at 10°C in each weight range. This is shown in Fig. 22.

Table 16. The Q_{10} between 10° and 20°C and between 7° and 15°C for each stage in the development of T. subnodicornis

Stage in development	Q_{10} between 10° and 20°C	Q_{10} between 7° and 15°C
Egg	2.78	*3.91
Larval 1 - 3mg	1.84	2.49
,, 3 -10mg	1.20	1.85
,, 10 -20mg	0.97	2.54
,, 20 -50mg	0.67	1.78
"Prepupal"	-	2.56
Pupal	2.52	5.91

*Calculated from regression line

Assuming that the development rate plotted against temperature over the favourable temperature range approximates to a logistic equation (Davidson 1944) it can be seen that the favourable range for development in T. subnodicornis larvae decreases with age. If the curve for the egg stage (Fig.16) is compared with that for the first weight range, the optimum

Fig. 22. The daily development rate at each temperature expressed as a percentage of the rate at 10°C for a number of stages in the life-history.

● egg

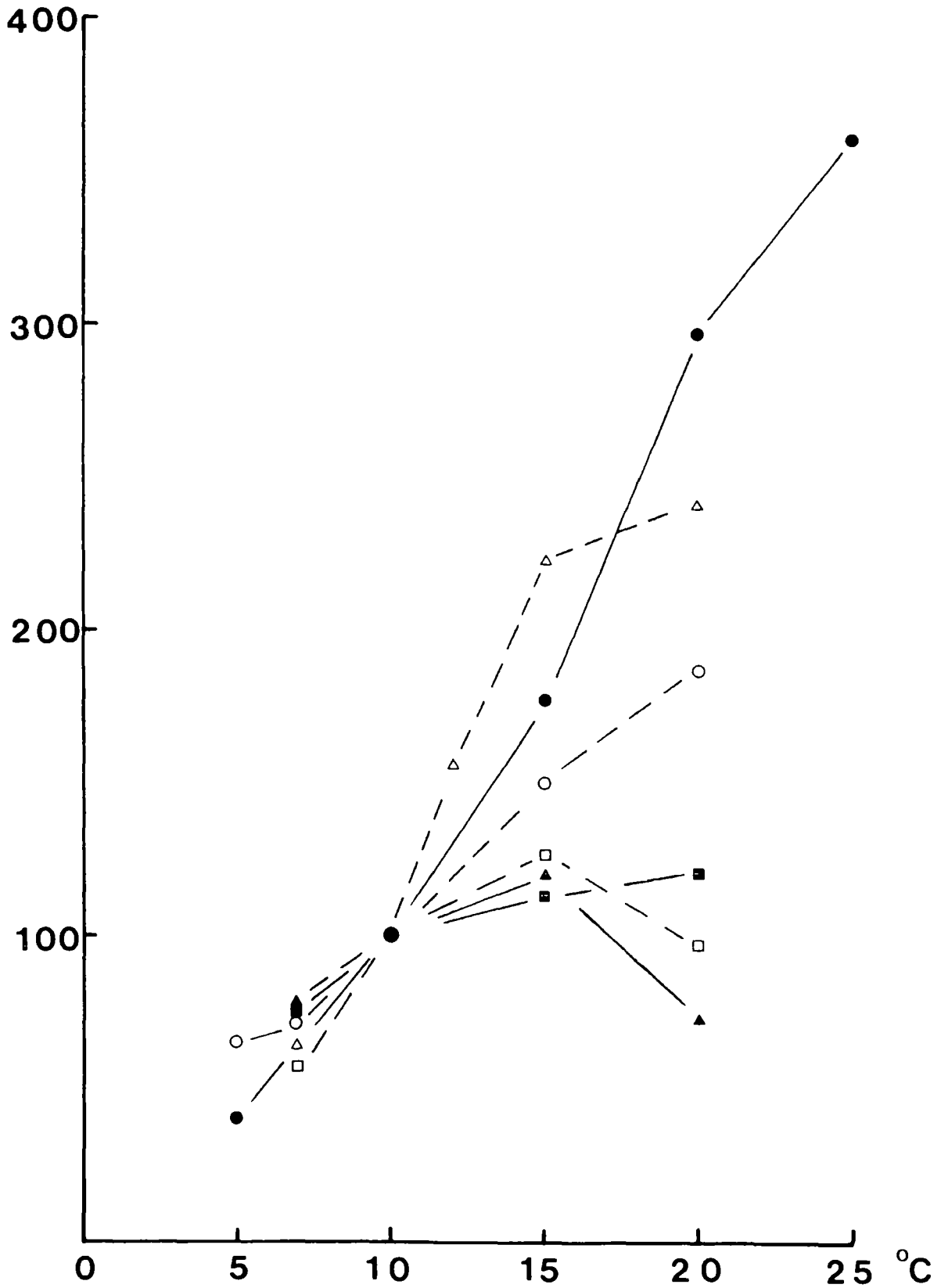
△ pupa

○ 1- 3mg

■ 3-10mg

□ 10-20mg

▲ 20-50mg


400
300
200
100
0
5
10
15
20
25
°C

temperature appears to have dropped. There are insufficient data to estimate the positions of the optima in either case but hatching of eggs occurs at 25°C whereas survival of larvae is very low at this temperature. In the 3 - 10mg range the optimum has dropped further and in the 10 - 20mg and 20 - 50mg ranges it can be seen to be below 20°C. The lower limiting temperature appears to be approximately 5°C throughout development. Hatching and pupation, but not emergence, can take place at 5°C and mortality in the larval stages at this temperature is high. The decrease in favourable temperature range during development is consistent with the results for Rhyzopertha dominica Fab. and Calandra oryzae L. (Birch 1945c) and may well be a more general feature of insect development. Andrewartha and Birch (1954) point out that there is no reason to suppose all stages in development have the same temperature optima and that, as they often take place under widely different environmental temperature conditions, this would be unlikely.

3d Discussion

The extent of the favourable developmental range and the positions of its upper and lower limits are related to the life-history and habitat of an insect as well as to the metabolic requirements inherent in biochemical reactions. In a multivoltine insect living in temperate latitudes it is important that the high summer temperatures should be fully utilised and it would be expected that an insect such as Pieris brassicae L. (Danilevskii 1965) would develop most

rapidly at comparatively high temperatures. It would also be expected that their response to rise in temperature, manifested by increase in growth rate, would be great.

In a univoltine insect without a diapause, and relying on a synchronised emergence period, it would be an advantage for the response to temperature, and the range over which the response is made, to be small. During the life-history of T. subnodicornis there is a low optimum temperature and a comparatively narrow favourable range for development.

Another feature of adaptive significance is the decrease in the differences between growth rates at different temperatures within the favourable temperature range during development. This is reflected in the drop in Q_{10} throughout larval development. From Table 16 it can be seen that the Q_{10} between 10° and 20°C declines throughout the embryonic and larval growth period. This is also true for the Q_{10} between 7° and 15°C except in the 3 - 10mg range where it can be seen from Fig. 22 that the growth rate at 15°C is lower than would be expected. The decrease in Q_{10} during larval development may also be common in insect development. Geyspitz and Zarankina (1963) comment on this feature in the development of Dasychira pudibunda L. reared at different temperatures, and in T. subnodicornis it has the effect that for the greater part of the life-history the development rate responds only slightly to rise in temperature.

It appears that the development of T. subnodicornis is adapted so that the temperature differences in the environment will, for the greater part of its life-cycle, have little effect on the development rate and therefore on the timing of the life-

history. This partly explains how the annual life-cycle can be maintained over a considerable range of latitude and altitude. However, as the Q_{10} for the temperature range from 7 - 15°C, which approximates to the range of mean daily temperatures at Moor House during the summer, is above unity for most of the development period, these adaptations cannot account fully for the degree of synchrony shown in the life-cycle.

4. The effect of photoperiod on growth rate

Results

Table 17 shows the mean logarithmic daily weight gains in the ranges below 20mg and the mean daily weight gains for larvae above 20mg at 10° and 20°C on photoperiods of L : D; 18 : 6, and L : D; 6 : 18. Student's t-test has been used to test the significance of the differences in growth rates between the two photoperiod regimes.

The differences between the growth rates on the two photoperiod regimes are only significant on two occasions : in the weight range above 20mg at 20°C and in the 0.12-3mg range at 10°C. However, except in the 10 - 20mg range at 10°C, the growth rate is faster at both temperatures on the short day regime. The significant difference between the rates in the 0.12 - 3mg range at 10°C might be due to the effect of new culture media on the larvae set up on the L : D; 6 : 18 regime; but the increased growth rate in the fourth instar on the short day regime at 20°C, supported by a similar but not significant increase at 10°C, may be a response to short photoperiod.

Table 17. Comparison of the rates of growth on long day, L : D; 18 : 6, and short day, L : D; 6 : 18, photoperiods at 10° and 20°C

Temperature	Wt. range	L : D; 18 : 6 N	Mean log x 10^5 daily increment	Variance	L : D; 6 : 18 N	Mean log x 10^5 daily increment	Variance	t	p	
20°C	3 - 10mg	30	2237	5,017,322	15	2462	1,094,479	0.46	n.s.	
	10 - 20mg	33	1531	793,214	22	1566	603,818	0.15	n.s.	
			Mean daily increment in mg			Mean daily increment in mg				
	20 + mg	60	0.5815	0.1647	69	0.7709	0.3835	2.08	< 0.05	
10°C			Mean log x 10^5 daily increment			Mean log x 10^5 daily increment				
	0.12 - 3mg	61	2365	2,034,827	21	2955	571,371	2.4	< 0.02	d.f.68
	3 -10mg	37	1861	3,022,308	35	2341	1,911,158	1.3	n.s.	
	10 -20mg	17	1581	682,985	19	1401	275,429	0.77	n.s.	
			Mean daily increment in mg			Mean daily increment in mg				
	20 + mg	49	0.8857	0.3069	25	1.0468	0.2873	1.21	n.s.	

This experiment needs to be repeated starting the cultures on the different photoperiods at the same date and, as far as possible, with larvae of the same starting weight. However, it appears likely that short day length promotes growth in fourth instar larvae. Such a response to photoperiod might affect larvae in the field that have not completed their growth by the winter.

Discussion

The mechanism by which day length affects growth rate is not clear. The simplest explanation is that a feeding rhythm which corresponds to dark, as does that of Barathra brassicae L. (Danilevskii 1965), or light, is prolonged by the extension of the appropriate phase. Larvae of Agrostis occulta L. (Danilevskii 1965), for instance, grow fastest and have the shortest larval development time on continuous illumination. Growth rate drops and development time grows longer as day length is decreased. However, this type of relationship does not always hold as Geyspitz and Zarankina (1963) have shown in their study on Dasychira pudibunda. Here the growth rate was at a maximum between 3 and 6hrs and a minimum at 16hrs daylight. Between 3 and Ohrs light there was a considerable drop in the growth rate indicating that a more complex reaction than a feeding response triggered by darkness was taking place.

From the experimental results for T. subnodicornis it can be seen that the larvae on the L : D; 6 : 18 at 10°C photoperiod were growing at the same rate as those on the

L : D; 18 : 6 photoperiod at 15°C and it is suggested that the short photoperiod might, in the field, compensate to a certain extent for the drop in temperature in the autumn. If the increase in growth rate were a response involving the feeding rhythm, the increased rate of development would apply only to those larvae that were still growing. Those that had achieved maximum weight would be unaffected, so the response to photoperiod might provide a mechanism by which larvae growing in colder habitats could complete their growth by the onset of winter.

5. The effect of temperature on larvae taken from the field in the autumn

One further investigation into the temperature effect was carried out on late fourth instar larvae in 1972.

Twenty larvae were taken from the field on 14 November 1972 and cultured at 15°C. On 28 November another twenty were collected and these were put at 10°C. Both sets of larvae were kept on a photoperiod of L : D; 6 : 18 until 14 December 1972 when they were transferred to an L : D; 18 : 6 photoperiod at 15°C. The photoperiod change was made in order to bring about rapid and synchronised pupation which only occurs on long day length. This reaction is discussed in the next section.

Results

Fourteen flies emerged from each culture. Those that had been on the 15°C regime pupated at a mean of 24.8 ± 1.3 days after the transfer to long photoperiod and the

larvae that had been on the 10°C regime pupated at a mean of 20.8 ± 1.0 days after the transfer. The individual pupation dates are shown in Table IX in the appendix. This result indicates that from late November T. subnodicornis development is not positively correlated with temperature when the larvae are kept on a short photoperiod. The difference in the two means ($t = 2.44$, d.f. 24, $p < 0.02$) shows that there is a slight (20%) retardation effect at the higher temperature.

Conclusion

The observations outlined above are of a very preliminary nature and the experiment needs to be repeated with larger numbers of larvae and over a range of temperatures; however, it appears possible that when growth has been completed T. subnodicornis larvae may go through a stage where development is temperature independent or possibly, as is often the case in diapause, continues at a faster rate at lower temperatures. In this it resembles Phyllopertha horticola L. (Laughlin 1963) which, although it also has a winter diapause, enters an apparently temperature independent phase in the third instar.

The concept of diapause and "diapause development" will be discussed later when the relationship between photoperiod and development in the fourth instar is examined.

VIII THE EFFECT OF PHOTOPERIOD ON DEVELOPMENT IN FOURTH INSTAR *T. SUBNODICORNIS* AND *T. PAGANA* LARVAE AFTER THE COMPLETION OF GROWTH

1. The effect of photoperiod on late fourth instar larvae of *T. subnodicornis*

It has been shown that the growth of *T. subnodicornis* larvae in the field might be roughly synchronised by the narrow range over which growth rate increases with temperature and by an active feeding response to short photoperiod. These adaptations would allow larvae to be at approximately the same stage of development by late autumn, but do not account for the absence of pupation in a warm winter. The larvae from the experiment on the relationship between development rate and temperature reared at 15°C and a L : D; 18 : 6 photoperiod in the laboratory started pupating on 20 October 1973, having experienced a temperature sum of 1785C°-days since hatching on 23 June 1973 and it is possible that larvae developing in the New Forest, where *T. subnodicornis* is also found, would have experienced a similar temperature sum by the end of October. It was also noticed in the laboratory cultures that pupation on the L : D; 18 : 6 regimes was not closely synchronised (14 larvae at 15°C pupated over a period of 42 days and 14 larvae at 10°C pupated over 52 days with standard deviations of 14 days rather than the 5 days found in the field) and that pupation on the L : D; 6 : 18 regime was very retarded. From these indications it was thought that photoperiod might affect development in the fourth instar in the stage when active growth has ceased, and it was decided to examine the reaction of late fourth instar larvae to photoperiod in the laboratory.

Method

Larvae were collected from the field on 15 December 1971 and on 29 February 1972. The larvae were cultured, as previously described in the section on the effect of temperature on the stages before pupation, and all cultures were kept at 10°C. On 15 December 1971 thirty one larvae were put on a photoperiod of L : D; 18 : 6 and fifty nine larvae were put on L : D; 6 : 18. On 29 February 1972 forty two larvae were put at a photoperiod of L : D; 18 : 6 and thirty two larvae at L : D; 6 : 18. The cultures were checked on alternate days thereafter and pupae removed.

Results

The mean number of days to pupation in each set of cultures is shown below in Table 18 and the distribution of the pupation periods is shown in Fig. 23.

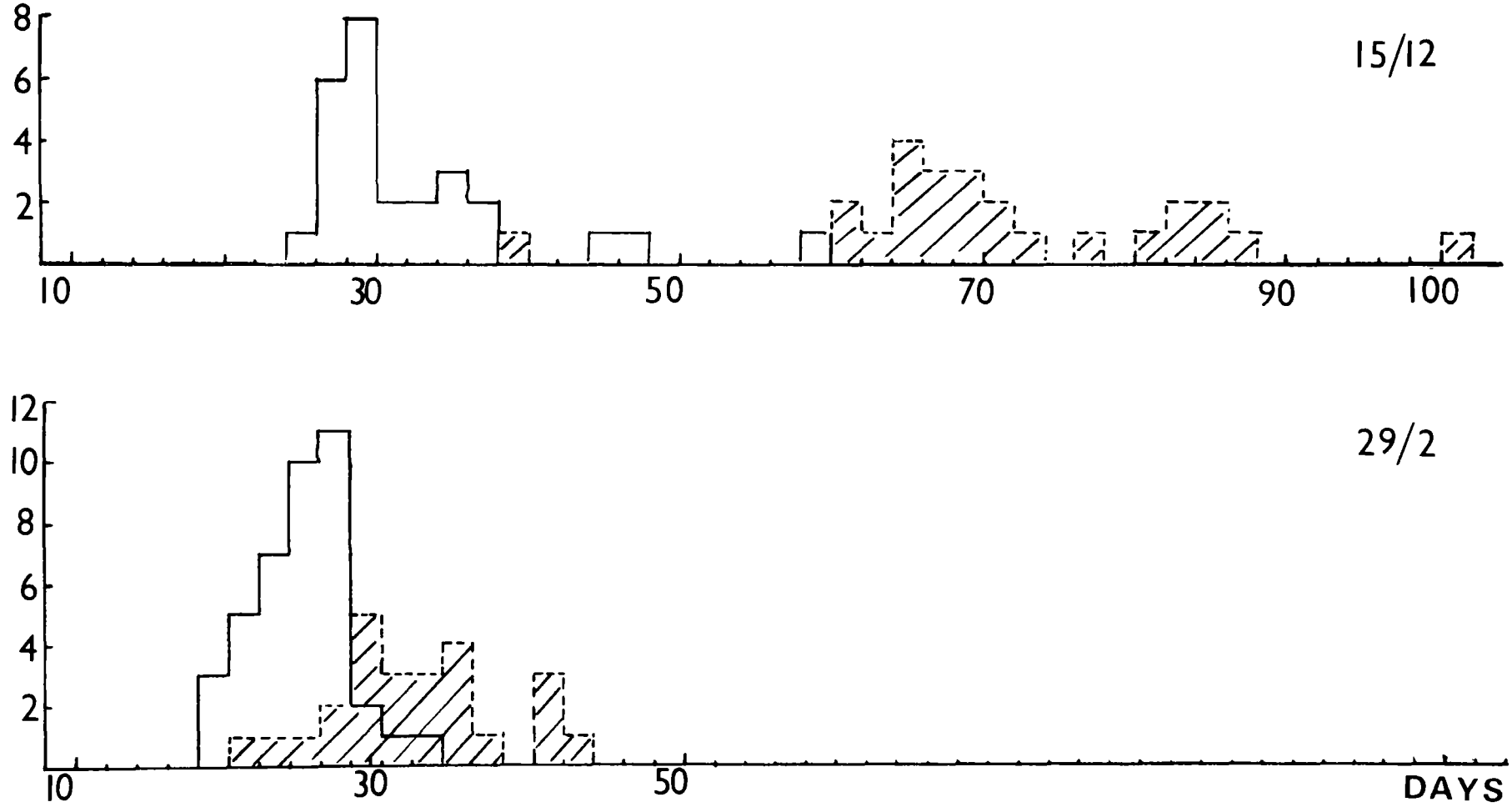
Table 18. The effect of photoperiod on the timing of pupation in the winter and early spring in T. subnodicornis kept at 10°C

Date	Light regime L : D	No. of larvae	No. died	Mean no. days to pupation	S.E.	Variance
15 Dec 71	18 : 6	31	7	33.2	1.5	55.3
,,	6 : 18	59	34	72.1	2.4	143.3
29 Feb 72	18 : 6	42	2	25.8	0.5	9.8
,,	6 : 18	32	7	32.6	1.1	31.0

Fig. 23. The distribution of dates of pupation for T. subnodicornis on long (L:D; 18:6) and short (L:D; 6:18) photoperiods. Upper histogram shows pupation dates of cultures set up on 15 December 1971 and lower histogram shows pupation dates of cultures set up on 29 February 1972.


L:D; 18:6


L:D; 6:18


NOS.
PUPATING
8
6
4
2
15/12
10
30
50
70
90
100
12
10
8
6
4
2
29/2
10
30
50
DAYS

Before Christmas short photoperiod had a marked effect in retarding pupation even when the larvae were kept at, what would be in the field, high spring temperatures. By 29 February 1972 the photoperiod effect was much smaller. The means of the number of days to pupation on the two light regimes, although significantly different ($t = 5.6$, $p \leq 0.001$), were only seven days apart, and the variance for the short day regime, although significantly different from that of the long day regime ($F = 3.2$, $p < 0.01$) had decreased considerably.

It appears from these results that fourth instar T. subnodicornis larvae develop slowly towards pupation at 10°C on a short day photoperiod. This process is accelerated and pupation synchronised by a long day regime. This would have considerable adaptive significance in the field, making it possible for larvae to maintain an annual cycle by restraining larvae from pupating during a warm winter and synchronising the emergence period. The mechanism of the photoperiod effect will be discussed later when the reaction of an autumn emerging tipulid, T. pagana Meigen has been described.

2. The effect of photoperiod on the termination of diapause in T. pagana

In addition to looking at the photoperiod reaction in T. subnodicornis an autumn emerging species, T. pagana, was studied for comparison. T. pagana lays its eggs, which hatch throughout the winter and early spring, in October at Moor House. Growth is very rapid until late June when the

larvae cease to eat and become relatively inactive. Pupation takes place in September. In the period between June and September the metabolic rate drops and unlike the over-wintering stage in T. subnodicornis, in which feeding and activity continue, the larvae are considered to be undergoing a true diapause in the sense of Harvey (1962).

In 1971 a preliminary experiment indicated that the diapause in T. pagana was broken by a short (L : D; 6 : 18) as opposed to a long (L : D; 18 : 6) photoperiod and that pupation was not triggered by drop in temperature as suggested by Horobin (1971). In 1972 a further experiment designed to find the critical photoperiod was set up.

Method

Cultures of T. pagana larvae were set up on 10 July 1972 when the larvae were already in their passive state. The culture method used was similar to that for fourth instar larvae of T. subnodicornis with the exception that the mosses from which the larvae were collected were substituted for liverworts. Twenty to thirty larvae were put at 15°C on the following light regimes : L : D; 18 : 6, L : D; 16 : 8, L : D; 14 : 10, and L : D; 12 : 12.

Results

The number of days until the mean emergence date on each regime is shown in Table 19 and the distribution of

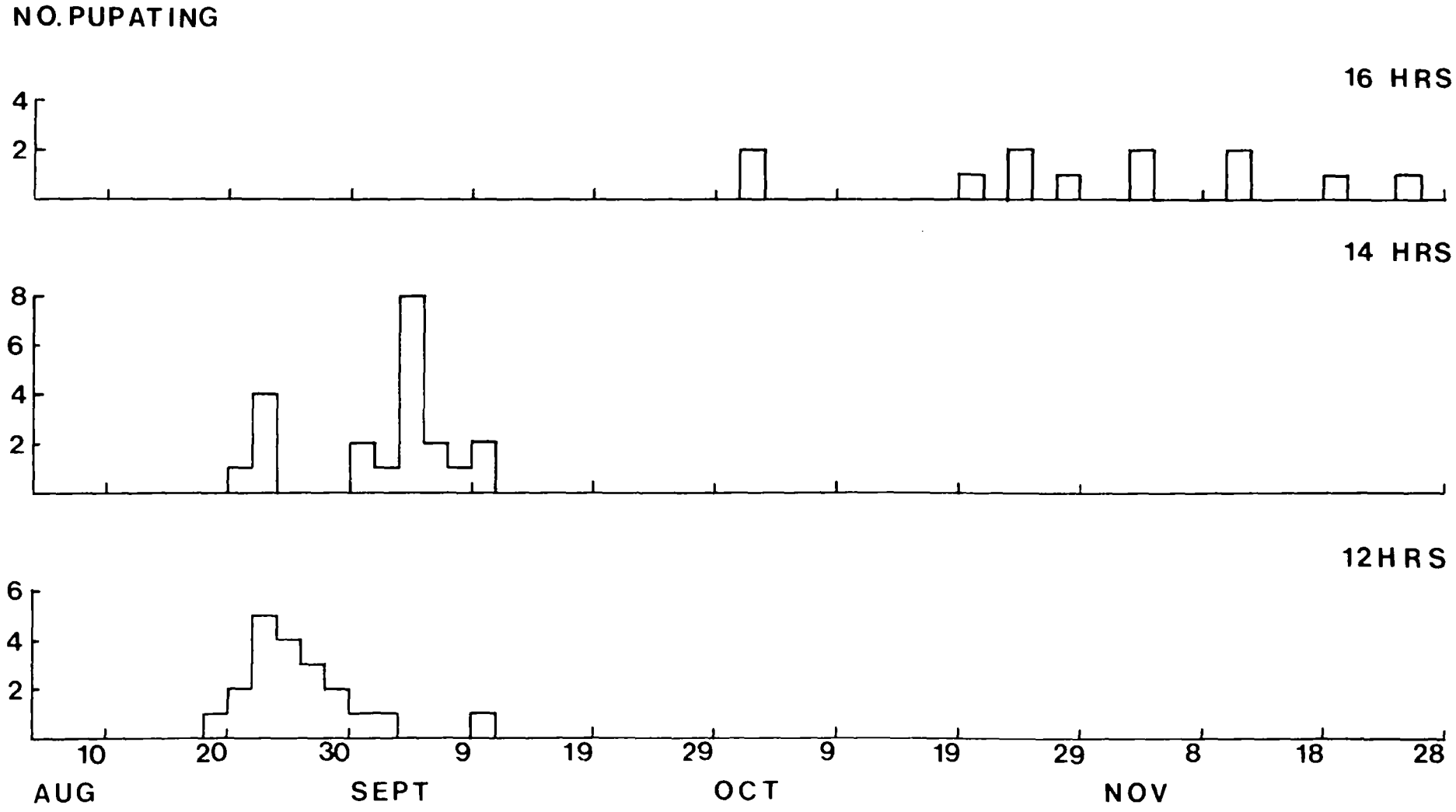
emergence is shown in Fig. 24. It can be seen that the critical day length for the initiation of emergence is in the region of 16hrs. It can also be seen that the emergence date becomes progressively earlier (the difference between the L : D; 14 : 10 regime and the L : D; 12 : 12 regime is significant, $t = 4.06$, d.f. 3 7, $p < 0.001$) with decrease in photoperiod, but that the difference between the mean dates on the 16hr and on the 14hr regimes is much greater than that for the 14 and 12hr regimes. The variance about the mean emergence date is also related to the photoperiod and decreases as the time taken until emergence grows shorter.

Table 19. The mean number of days to emergence for T. pagana larvae cultured under different photoperiod conditions and a constant temperature of 15°C

Light regime L : D	No. larvae	No. died	Mean no. days until emergence	S.E.	Variance
12 : 12	24	3	47.5	0.98	20.0
14 : 10	29	8	54.0	1.28	34.1
16 : 8	29	17	113.1	4.62	255.9
18 : 6	25	3	No pupation after 197 days	-	-

It can be seen from the results that T. pagana, unlike T. subnodicornis, is prevented from pupating by inappropriate photoperiod. The effect of the L : D; 16 : 8 photoperiod is very similar to that of L : D; 6 : 18 on

Fig. 24. Distribution of emergence dates for T. pagana in laboratory cultures set up at 15°C and at three different photoperiods on 10 July 1972.


NO. PUPATING
16 HRS
4
2
14 HRS
8
6
4
2
12HRS
6
4
2
10
20
30
9
19
29
9
19
29
8
18
28
AUG
SEPT
OCT
NOV

T. subnodicornis in that the synchrony of emergence has been lost. It is clear from the decrease in variance with the decreased photoperiod that the shortening day length will have the effect, not only of breaking diapause, but of synchronising the emergence in the field. The effect that decreasing photoperiod between 14 and 12hrs has on advancing the mean emergence date will have adaptive significance in the field by promoting the emergence of flies that have been slow in breaking diapause.

3. Discussion

Beck (1968) remarks that "the importance of photoperiodism in the seasonal development and ecological adaptations of univoltine species is little appreciated and has been investigated in very few forms". Considerable work has been carried out on the initiation and termination of diapause, especially in the Lepidoptera (Danilevskii 1965) in multivoltine species. Diapause is defined as a period when development is "spontaneously" arrested (Shelford 1929) in contrast to the situation when unfavourable conditions impose restrictions on the metabolism. The diapause state is characterised by a decrease in activity and a drop in metabolic rate and may occur automatically as a stage in the life-history, as in the egg stage of the grasshopper Austroicetes cruciata Sauss. (Andrewartha 1943b), or it may be triggered by some aspect of the environment, such as a specific day length. Either summer or winter can constitute an unfavourable period, but it is more usual for polycyclic

insects in temperate climates to have their growth period during the warmer part of the year and to react to short day length by going into diapause. In this way the least vulnerable stage is subjected to the winter temperature and any problem of food shortage is avoided.

In a univoltine insect such as T. pagana the reaction to photoperiod performs two functions. Short day length both breaks diapause and synchronises emergence. Probably the main function of diapause in this case is that it is broken by a precisely timed signal which synchronises emergence. It has not been demonstrated but it is probable that larvae do not enter diapause until they are fully grown and that under an 18hr day they diapause, according to the temperature they have experienced in the field, over a considerable time period; alternatively, they may enter diapause a fixed number of days after the final larval moult as does Phyllopertha hortiola (Laughlin 1963). In T. subnodicornis the photoperiod reaction is less familiar in that the larvae are not technically diapausing through the winter (the reasons for supposing T. pagana to be in diapause and T. subnodicornis not will be discussed in the next section on respiration). However, the synchronising function of photoperiod is very similar to the situation in T. pagana. It is interesting to note that T. subnodicornis reacts to long day length and T. pagana to short day length. As the two species are in the same genus it is likely that the physiological response is similar in the two cases and that the photoperiod responded to is a product of the selection pressure of the life-history and the environment. Danilevskii (1965) has shown that even within one species (Acronycta rumicis L.) the critical day length for diapause initiation can change from 15 to 20hrs over a latitude range of 43° to 55°N.

IX Preliminary model for the life-cycle of T. subnodicornis

In most univoltine insects that have been studied (Danilevskii 1965, Beck 1968) the yearly cycle which takes place over a wide geographical range involving exposure to widely different temperature regimes is made possible by a diapause, defined as a stage in the life-history when there is a "spontaneous" drop in the metabolic rate (Shelford 1929). In T. subnodicornis adaptations to both temperature and photoperiod ensure a yearly life-cycle without the intervention of diapause. The lengthening photoperiod in spring also has the effect of synchronising the emergence period and this second attribute is not an aspect that has been investigated extensively.

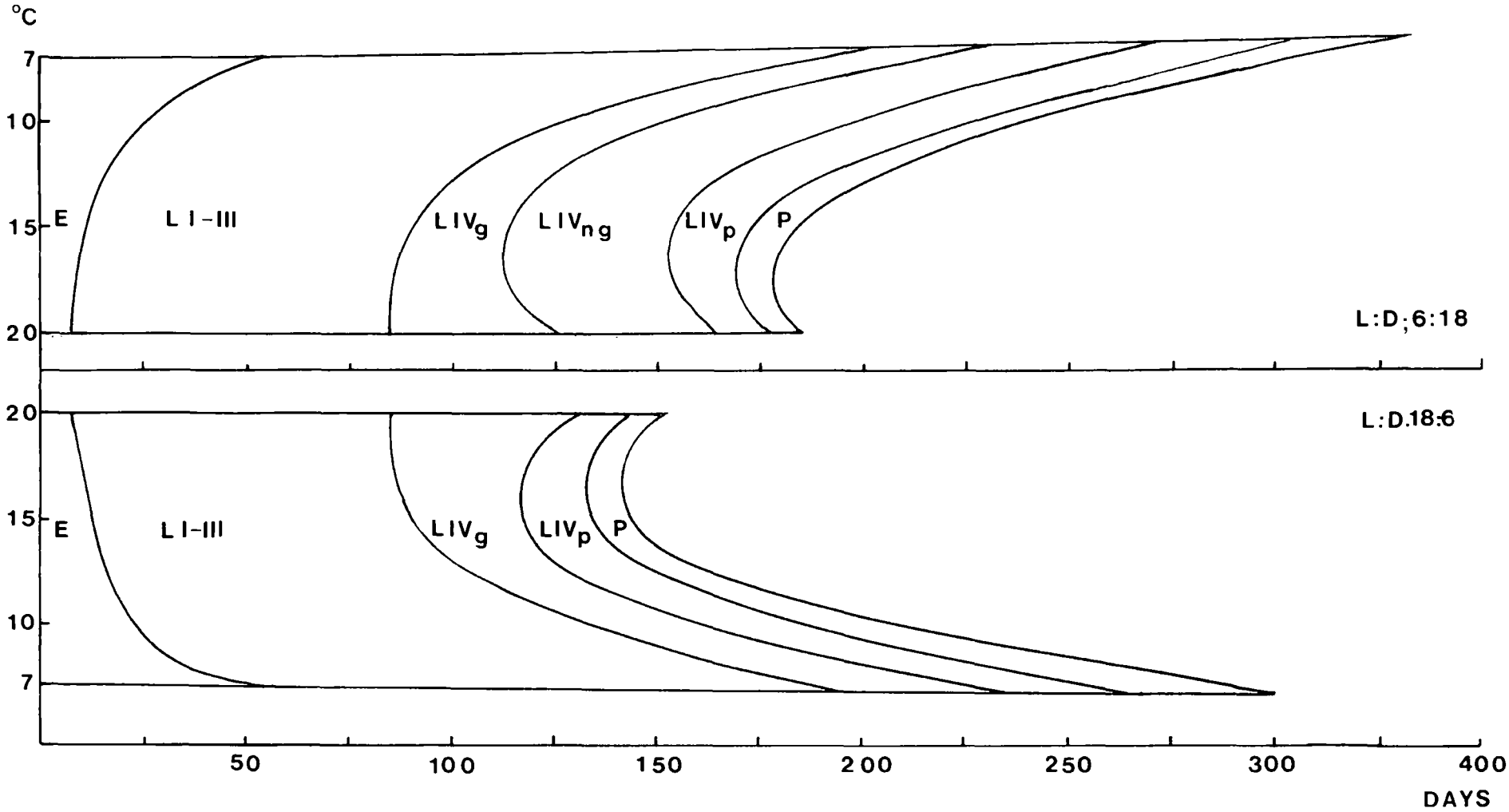
Development of the egg, early instars and pupae of T. subnodicornis responds to an increase in temperature over a comparatively wide range of temperature. In the third and fourth instars the optimum temperature for development drops and the increase in rate in response to rise in temperature over the favourable temperature range decreases. There may also be a response to shortening day length such that larvae which are still growing increase their growth rate (see p. 55). These adaptations allow larvae developing in the field, under a range of temperature conditions, to finish their growth period before the onset of winter.

It is suggested that the completion of growth is followed by a period which is either temperature independent or proceeds more quickly at lower temperatures. The onset of this phase prevents larvae from warm areas progressing towards

pupation before Christmas. This stage takes place under a period of short day length and can be broken by putting the larvae onto a long photoperiod. In the field larvae would enter this phase between early November and January. By the beginning of March the day length of 10hrs no longer inhibits temperature dependent development and larvae can progress to pupation. The mean pupation date, and, in consequence, the mean emergence date will be directly related to the temperature from March onwards. Fig. 25 shows the duration of different stages of the life-history under a range of temperature conditions and long and short day length in the laboratory.

Fig. 25. The duration of the life-history at different temperatures and under short (L:D; 6:18) and long (L:D; 18:6) photoperiods in the laboratory.

E	=	egg
L_{I-III}	=	first three instars
$L_{IV}g$	=	fourth instar, growth period
$L_{IV}ng$	=	fully grown fourth instar, temperature independent phase
P	=	pupa


°C
7
10
15
20
E
L I-III
LIVg
LIVng
LIVp
P
L:D;6:18
20
15
10
7
E
L I-III
LIVg
LIVp
P
L:D.18:6
50
100
150
200
250
300
400
DAYS

X. RESPIRATION RATES IN THE LARVAL STAGES OF *T. SUBNODICORNIS* AND *T. PAGANA*

Introduction

The respiration rates were measured to give a comparative indication of the metabolic rate under different conditions. In the case of *T. subnodicornis* it was thought that a possible explanation for the growth rates being so similar under widely different temperature conditions in the field was that the larvae were acclimatised to the temperature at which they were developing. This theory was tested by bringing larvae into the laboratory, keeping them on different temperature regimes for about three weeks, and then comparing the respiration rates.

As it was thought that the stage before pupation in *T. pagana* constituted a true diapause, the respiration rates of larvae in July were compared with those of over-wintering *T. subnodicornis* larvae. A further experiment was made to see whether there was a difference in the respiration rates of *T. pagana* larvae on a long day, diapause inducing photoperiod, and a short day, pupation initiating photoperiod.

Measurement of respiration rate

Respiration rates were measured in Warburg manometers filled with Brodies' fluid (Dixon 1951). 10ml reaction flasks were used and kept at constant

temperature by immersion in a thermostatically controlled water bath. Each larva was weighed and placed, unrestrained, in a reaction flask. 0.1ml of 2N potassium hydroxide was added to the central well to absorb carbon dioxide and 0.2ml of distilled water was put in the flask to keep the larva damp. The respiration rates were measured over periods of 6 - 10hrs for each larva.

1a. Method - T. subnodicornis

All measurements were carried out between the end of October and mid December. The acclimatisation temperatures used were 15° and 5°C and all the respiration rates were measured at 15°C. Larvae were brought in from the field in early December and kept at the appropriate acclimatisation temperature until testing. Their respiration rates were compared with those of larvae taken straight from the field in late October and with those of larvae that had been reared at 15° and 5°C in the laboratory. Rearing and acclimatisation were carried out under an L : D; 18 : 6 photoperiod regime and the rate of respiration was measured during the photophase.

1b. Results

The respiration rates of each group of larvae are shown below in Table 20. The mean respiration rates of individual larvae are shown in Table X in the appendix.

Table 20. The respiration rates at 15°C of larvae that have been reared or acclimatised on different temperature regimes

Acclimatisation regime	No. of larvae	Mean live weight (mg)		S.E.	Mean resp. rate $\mu l O_2/hr/g$ wet wt.	S.D.
1. 5°C from hatching	11	29.2	±	1.8	220.7	± 64.2
2. 15°C from hatching	9	84.1	±	5.1	138.3	± 35.0
3. Brought from field kept at 15°C from :						
1 December - 17 Dec 1972	8	84.6	±	8.2	142.3	± 5.0
4. Reared at 15°C and acclimatised at 5°C from :						
16 Sept - 27 Oct 1972	4	55.2	±	7.6	188.9	± 34.6
5. Brought in from field and acclimatised at 5°C from :						
24 Nov - 17 Dec 1972	6	86.1	±	7.0	143.3	± 5.3
6. Straight from field :						
20 and 26 October 1972	12	63.8	±	4.6	167.6	± 35.0

There is a significant difference between the respiration rates of the larvae reared at 5°C (group 1) and those reared at 15°C (group 2) ($t = 3.6$, d.f. 16, $p < .001$), but it is more likely that this is an effect of size difference (Bertalanffy 1957) rather than due to acclimatisation to two different temperature regimes. (When the regression of respiration rate per hour per g wet weight (y) against wet weight in mg (x) for the twenty one larvae that had been reared or acclimatised at 5°C was made, the following equation was obtained : $y = 242.4 - 0.989x$. On the basis of this regression the respiration rates for larvae with mean weights of 29.2mg and 84.1mg should be 213.5 and 159.3µl of O_2 per g per h respectively, neither of which are significantly different from the actual figures recorded.)

The difference between the two groups brought in from the field (groups 3 and 5 , where the weights are comparable)and acclimatised at 5° and 15°C respectively, is not significant; and if the two groups that have been acclimatised at 5°C (4 and 5) are compared with those that have been reared and acclimatised at 15°C (2 and 3), the rate is still not significantly different ($t = 1.85$, $p > 0.05$).

1c. Conclusion

When invertebrates are wholly or partly acclimatised to low temperature they often display a higher initial respiration rate when they are moved to a higher temperature than animals that have been kept at this temperature (Bullock 1955). However, Scholander et al. (1953) found

no evidence of this type of reaction in tropical and arctic insects and from the data above it seems unlikely that T. subnodicornis shows acclimatisation. In the case of T. subnodicornis, however, the larvae were not restrained during tests and it is possible that their activity masked the small differences in respiration rates due to the differences in basal metabolic rates. Another criticism is that most of the tests were carried out when the larvae had finished growth. If immobilized larvae were used, and their respiration rates throughout the year were measured, it might be found that acclimatisation occurred during the growth period. However, from the experimental data on growth and the timing of the stages in the life-history, there is no necessity to invoke acclimatisation to explain the synchrony of development.

It can be seen from the comparison of the larvae in the various weight ranges that diapause does not occur. The drop in respiration rate per g wet weight shown by the older larvae can be accounted for in terms of increased weight alone.

2a. Method - T. pagana

T. pagana larvae were taken from the field on 16 July 1972 and divided into two groups which were cultured as previously described (p. 63). Both groups were kept at 15°C and one set of cultures was placed on a photoperiod regime of L : D; 18 : 6, while the other was put on an L : D; 10 :14 regime. The respiration rates of larvae from both groups were measured on 27 July 1972 during the photophase of both light regimes.

2b. Results

The respiration rates at 15°C of larvae from the two photoperiod regimes are shown below in Table 21.

The mean respiration rate of the larvae from the long photoperiod was 21.8 ± 2.9$\mu l O_2$ per hour per g wet weight whereas the mean respiration rate of the larvae on the short photoperiod was 38.5 ± 9.6$\mu l O_2$ per hour per g wet weight. These means are not significantly different. The effect of size on the respiration rate is very small ($y = 30.88 - 0.05x$, where x is the wet weight of the larva in mg and y is the respiration rate in $\mu l O_2$ per g wet weight per hour).

2c. Conclusion

It can be seen that the respiration rate of the T. pagana larvae is about a fifth of that of T. subnodicornis at the same stage in their life-cycle. As the larvae of the two species are similar in weight and have been kept and tested under the same temperature conditions, it can be assumed that T. pagana undergoes diapause at the end of its larval growth period and that T. subnodicornis does not. This view is confirmed by the behaviour of the two species. T. subnodicornis remains active and continues eating through the winter while in the summer T. pagana ceases to eat and withdraws to a refuge, often found between thick mosses. Even when exposed to light its movement is very limited.

Table 21. The mean respiration rates at 15°C of *T. pagana* larvae kept for 10 days on two different photoperiods L : D; 18 : 6 and L : D; 10 : 14

Larvae from the L : D; 18 : 6 regime			Larvae from the L : D; 10 : 14 regime		
	Live wt. mg	$\mu l O_2$/larva/hr	$\mu l O_2$/g w.wt/hr	Live wt. mg	$\mu l O_2$/larva/hr	$\mu l O_2$/g w.wt/hr
1.	41.6	0.82	19.7	87.3	3.15	35.9
2.	52.3	1.59	30.3	98.6	2.10	21.3
3.	57.1	0.80	13.9	87.3	2.85	32.6
4.	45.8	0.47	10.3	47.0	3.77	80.2
5.	49.7	1.14	22.9	54.8	1.24	22.2
6.	80.8	1.23	15.3			
7.	57.2	2.28	39.8			
8.	44.1	0.82	18.5			
9.	62.5	1.57	25.2			

If T. pagana undergoes diapause it would be expected that the respiration rate would rise when diapause is terminated and progress towards pupation begins (Endelman 1951 in Lees 1955). That this has not been recorded in T. pagana may be due to the measurements being carried out before diapause had been broken. The larvae pupated between 28 July and 5 August 1972 and it is possible that larva no.4 is the only larva in the group from the short photoperiod that had ended diapause. Further information on this and the growth stages of the life-cycle is needed.

XI MORTALITY RATE THROUGHOUT THE LIFE-HISTORY OF *T. SUBNODICORNIS*

Information on mortality rate at different stages in the life-history of *T. subnodicornis* has been gained from observations in the field and laboratory. As explained below, the number of samples that could be sorted was limited so the population study in the field has been concentrated on the fourth instar and adults. Coulson (1962) showed the pattern of mortality throughout the life-history on one site. In this study several sites have been compared.

1a. Sampling method for larvae

An approximation to stratified random sampling was made by dividing each site into eight equal areas and sampling from each area. A corer of 1.9cm radius was used to sample for eggs and first instar larvae and a corer of 5.7cm radius was used for the later stages.

Throughout the study the size and number of cores taken were related to the number of samples that could be sorted in the time available. Coulson (1962) used a flotation method in which cores were macerated in magnesium sulphate solution (sp.gr.1.23) to extract first instars and eggs. In this study, where the densities were lower and a number of sites were being compared, the method was found to be too time-consuming to process enough samples to give useful figures on egg density and hatching success. An attempt to adapt the wet funnel regimes, used by Hadley (1966) and Horobin (1971) for extracting *Molophilus ater*, also proved unsuccessful, so first instar estimations were made on only a few occasions.

It was found that during heat extraction for the later instars in Berlese funnels almost as many larvae died within the core as were extracted, so hand sorting was used. This was found to be an efficient method for fourth instar larvae. In the autumn of 1970 forty cores, radius 5.7cm, were hand sorted and 34 larvae removed. Further careful sieving and washing yielded only one further larva which was dead. Subsequent checks by double sorting samples indicated that this level of efficiency was maintained.

Coulson (1962) found that, at the densities at which he was studying them, larvae showed no significant tendency to aggregate, so he used the mean as the best estimate of the variance. During this study a high density site on Knock Fell was found in spring 1972 and sampling between 28 February 1972 and 24 March 1972 confirmed that in the spring fourth instar larvae are distributed randomly. The comparison of the data with those for the equivalent Poisson distribution is shown in Table 22.

Further tests on distributions at lower densities also failed to show significant deviation from the appropriate Poisson distribution. 60 cores taken from blanket-bog in autumn 1970 with a mean of 0.567 larvae per core gave a χ^2 value of 0.28, d.f. 2, $p > 0.1$ and 165 cores (0.436 larvae per core) from a set of Juncus sites chosen as having a density of approximately 40 larvae/m^2 gave a value of 2.06, d.f. 2, $p > 0.1$.

Table 22. The distribution of T. subnodicornis larvae in 83 cores, 102cm in area, taken from Knock Fell on 28 February 1972 and 9 March 1972, compared with a Poisson distribution having the same mean

Mean no. larvae/sample = 1.313, $e^{-\bar{x}}$ = 0.269

No.larvae/sample	0	1	2	3	4	5	6	7
Observed	27	29	17	1	4	4	0	1
Expected	22.3	29.3	19.3	8.4	2.8	0.7	0.1	0.0

χ^2 0.98+0.00+o.26 +0.36 = 1.6, d.f.1 , $p > 0.1$

As most of the population data in this study were collected from larvae in the fourth instar, the variance has been assumed to be equal to the mean, and standard errors have been calculated on this basis for all population estimates in the fourth instar. Spring and autumn larval densities for the period of this study and for 1969 are shown in Table XI in the appendix.

1b. Sampling method for adults

Adult flies were caught each year on each site in pitfall traps, the numbers and dispositions of which are described on p. 15. The pitfall catches at the Moor House sites for the period of this study and for 1969 are shown in Table XII in the appendix. The use of pitfalls to monitor emergence has already been discussed (p. 14). Their use to compare density between sites is more open to criticism (Southwood 1966).

The difference in activity level at sites of different altitude was appreciable in that it was very rare to see males flying above 2500ft and it is possible that the activity of the females too was curtailed on the colder sites. In addition, Greenslade (1964) demonstrated that for carabids the pitfall catch is influenced by the surrounding vegetation. This is relevant to this study in which the two main vegetation types, blanket-bog and Juncus or Eriophorum sward have such different growth characteristics.

The value of using the pitfall catch as a comparative density measurement has been examined by comparing the pitfall catches with the spring larval densities which should represent the maximum possible number of adults/m^2 on each site. The sites used are those on the east side and therefore at approximately the same altitude, but as it was thought likely that female catch was less affected by weather than the male catch, correlations have been carried out for both the total catch and the female pitfall catch. In the first pair of correlations all sites, except the Behind House site in 1972 which was flooded during most of the emergence period, have been included. In the second pair the blanket-bog sites and the Behind House site in 1972 have been omitted, and in the third pair the 1969 results have been left out as well. During 1969 numbers of flies varying between 1307 and 2881 (6/m^2 and 13/m^2 respectively) were removed from each site, and as this constituted a large part of the calculated population, the pitfall catch must have been diminished as a consequence. The results of these correlations and the regression parameters, derived at the same time for adult pitfall catch and spring larval density, are shown in Table 23.

Table 23. The regression parameters and the correlation coefficients derived from plotting pitfall catches against spring larval densities

	N	Regression coefficient	Constant	Correlation coefficient	P
Total pitfalls (against larval density)					
1. All sites	20	2.43	124.2	+ 0.377	n.s.
2. *Juncus* and *Eriophorum* sites 1969-1972	14	3.64	119.1	+ 0.695	<0.01
3. *Juncus* and *Eriophorum* sites 1970-1972	10	3.72	121.4	+ 0.705	<0.05
Female catch (against larval density)					
1. All sites	20	0.71	87.89	+ 0.205	n.s.
2. *Juncus* and *Eriophorum* sites 1969-1972	14	1.36	83.03	+ 0.593	<0.01
3. *Juncus* and *Eriophorum* sites 1970-1972	10	1.42	82.65	+ 0.718	<0.02

The positive constant which appears in all the regression equations is possibly the result of a behavioural difference at low densities when the increased time spent searching for a mate means that both sexes are at risk for longer than usual.

It can be seen that the total pitfall catch, rather than the female catch alone, in two out of three cases, gives a higher correlation coefficient and that the omission of the

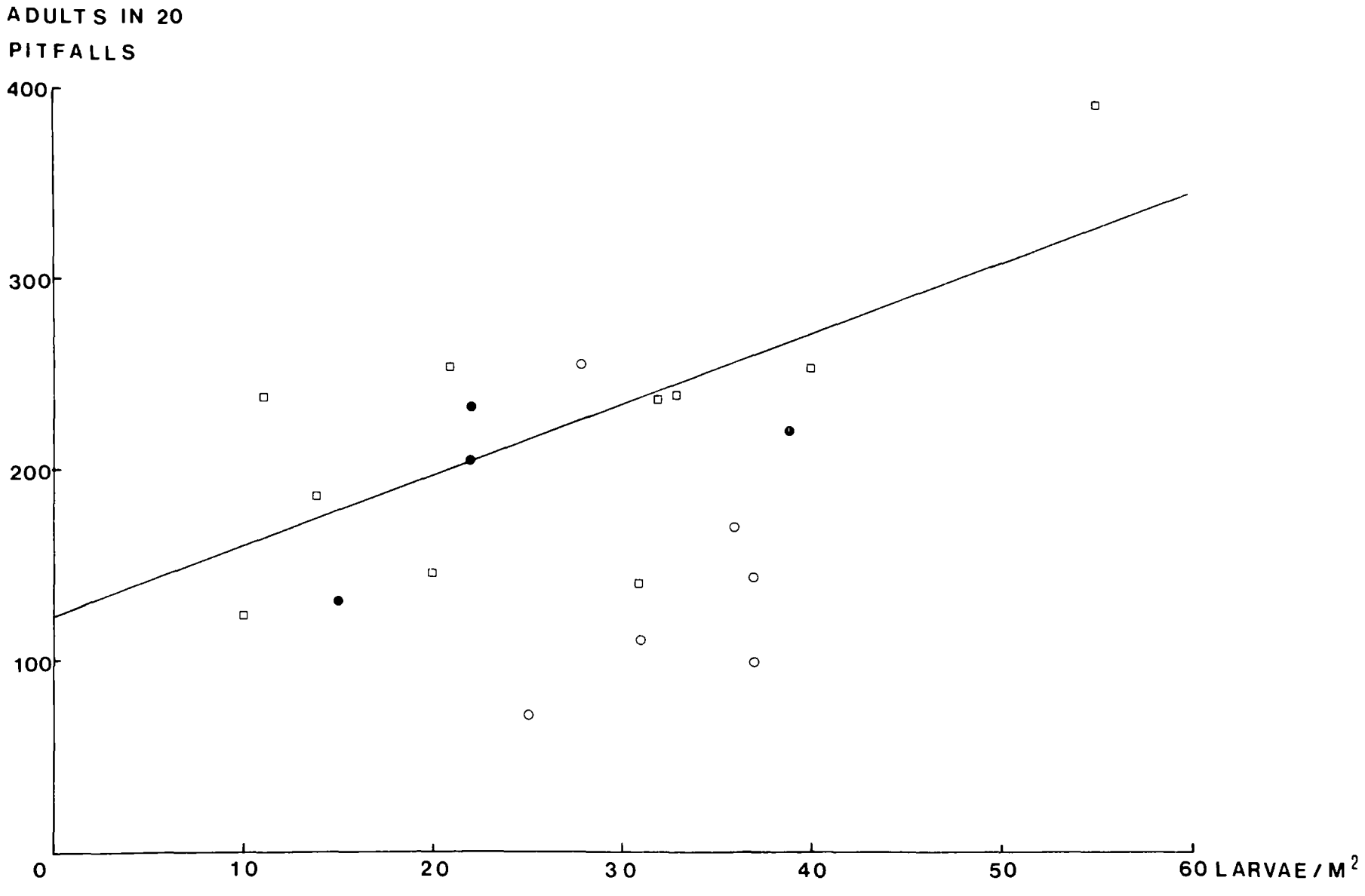
Fig. 26. The regression of pitfall catch on *Juncus* areas on spring larval density from 1969 - 1972. The blanket-bog densities are also shown but not included in the regression.

$y = 3.72x + 121.4$, $r = +0.705$, $p < 0.01$

● 1969 *Juncus* sites

○ Blanket bog

□ 1970, 1971 and 1972 *Juncus* sites


ADULTS IN 20
PITFALLS
400
300
200
100
0
10
20
30
40
50
60 LARVAE / M 2

blanket-bog figures also improves the correlation. Whether the latter effect is the result of the differences in vegetation types or whether it is due to a difference in the mortality rates during pupation on the two types of site has not been assessed. Fig. 26 shows the distribution of the data and it is concluded that the pitfall catch gives an adequate estimate of the number of adults per m^2 when the relationship $y = 3.72x + 121.4$ (where y is the number of adults per 20 pitfalls and x is the spring larval density when the altitudes of the sites are approximately the same and the vegetation is a Juncus or Eriophorum sward).

2. Mortality rate in the egg stage

Unlike the eggs of M. ater (Hadley 1971a) those of T. subnodicornis are resistant to dessication, being encased in a tough chorion. This may also offer protection against invertebrate predators though Coulson (1962) found 17% of eggs had a pierced chorion in 1955 and 4% in 1954. The fertility of eggs was high; of 363 eggs kept in the laboratory at room temperature, only 41 (11%) failed to hatch. An examination of 18 cores taken from the Knock Fell site on 22 June 1972 yielded 72 larvae and 8 eggs, only three (4% of the total) of which failed to hatch, while cores taken from Netherhearth on 1 July 1972 yielded 179 larvae and 2 (1%) infertile eggs. The two sets of data combined indicate that the hatching success is about 98%, but it is possible that the larvae were more easily seen during extraction than the eggs, and that eggs could have been removed and completely destroyed by predators.

3. Mortality rate in the first instar

Coulson (1962) showed that during the life-cycle the heaviest mortality takes place during the first instar. This would be expected in an insect with an annual life-history producing a large number of eggs (Deevey 1947). Coulson found that between 28 June 1954 and 8 July 1954 there was an 82% mortality (18,000 eggs/m^2 to 3,300 larvae/m^2). This type of mortality rate was found on Knock Fell in 1972. An estimated 13,750 eggs per m^2 gave rise to 4,130 larvae/m^2, sampled on 22 June 1972, a 70% mortality, and by 28 July 1972 the density had dropped to 329 larvae per m^2, a 98% mortality. Coulson (loc.cit.) considered that drought and the condition of the ground are very important factors in the survival of the early stages of T. subnodicornis and it is known that a wet autumn promotes the survival of T. paludosa (Milne et al. 1965).

3a. The effect of experimental manipulation of density on the first instar in the field

In 1971 ten 0.25m^2 enclosures were set up at Netherhearth before the beginning of emergence. Each enclosure was formed by sinking four 20 x 50cm galvanised strips into the ground to a depth of 10cm so as to form a square. The corners were reinforced with "lawn edging" and fine nylon net, hole diameter 1mm, was placed over the top and secured with string. During the emergence period the number of females emerging from each trap was supplemented

with fertilised females from outside until traps 1 - 6 had received ten each and traps 7 - 10 eighty each. On 4 July 1971 four cores (1.9cm radius) were taken from each trap and sixteen were taken from the area surrounding the traps.

Results

The numbers of first instar larvae per m^2 on 4 July 1971 within and without the enclosures are shown in Table 24. The number of adult females per m^2 has been calculated from the spring larval density and the number of eggs per m^2 has been calculated from the regression $y = 110.5x - 808$, where y = egg number and y = female wing length, made during 1969 (M.Sc. study). The mean wing length of the females on Netherhearth in 1971 was 10.2mm so the mean fecundity was considered to be 319 eggs per female.

The densities of larvae in the two sets of traps have been tested, assuming that the number of larvae extracted from each plot is proportional to the number of females introduced. $\chi^2 = 4.7$, d.f. 1, $p < 0.05$, indicating that this was not the case and that survival at the higher density was less than expected. This result was corroborated by the data from the area outside the enclosures where the density of females was calculated to be approximately 6 per m^2. When the three densities are tested together $\chi^2 = 48.98$, d.f. 2, $p < 0.001$. It was therefore considered that mortality in the first instar is higher at higher densities.

Table 24. The densities of first instar larvae within and without the enclosure at Netherhearth on 4 July 1971

	Adults ♀/m^2	Approx. no. eggs/m^2	No. of 11.3cm cores	No. first instar/core	S.E.	No. first instar/m^2	S.E.	Percentage survival
Outside traps	6 *	1,914	16	0.88	±0.23	779	± 204	40.7
Traps 1 - 6	40	12,760	24	1.54	±0.30	1,363	± 266	10.7
Traps 7 - 10	320	102,080	16	8.25	±1.38	7,301	±1221	7.2

* calculated from the spring larval density

4. The effect of high densities on the survival of the first three instars in the laboratory

The cultures of newly hatched larvae were set up in Petri dishes, as described in an earlier section, on 25 June 1970. Ten cultures were set up with ten larvae each, eight cultures with fifty larvae each, and six with a hundred larvae each. All cultures were put at 12°C. The liverworts were replaced and the sand kept damp, but otherwise the larvae were left undisturbed until 10 September 1970 when they were counted.

Results

The numbers of larvae surviving in each culture after a two and a half month period are shown in Table 25.

Table 25. The numbers of larvae surviving at the end of two and a half months in cultures set up with different densities of newly hatched larvae on 25 June 1970

	Numbers surviving		
Replicate no.	10 larvae/culture	50 larvae/culture	100 larvae/culture
1	4	2	0
2	1	0	0
3	3	0	0
4	4	1	0
5	1	1	1
6	1	0	0
7	1	2	
8	0	0	
9	7		
10	3		
Totals of survivors	25	6	1
Percentage survival	25	1.5	0.17

Two χ^2 tests have been carried out, the first based on the assumption that survival in the cultures should be in proportion to the number of larvae introduced at the beginning of the experiment, the second based on the assumption that each culture has a carrying capacity and that equal numbers of larvae will survive per Petri dish at each density regime. In the first case $\chi^2 = 186.04$, d.f. 2, $p < 0.001$; in the second $\chi^2 = 18.5$, d.f. 2, $p < 0.001$. It appears that there is a highly significant density-dependent effect and that overcompensation occurs so that smaller numbers actually survive at high densities. A further test was carried out to test the significance of the differences between adjacent pairs of density regimes, again based on the assumption that there was no difference in the numbers surviving per Petri dish. When the ten larvae per dish regime was compared with the fifty larvae/dish ($\chi^2 = 7.95$, d.f. 1, $p < 0.01$), and when the fifty larvae/dish regime was compared with the hundred larvae/dish regime ($\chi^2 = 2.33$, d.f. 1, n.s.). The lack of a significant difference between the last two figures can be interpreted as that the overcrowding at fifty larvae per dish has effects so drastic that they cannot readily be exceeded.

5. Mortality rate in the fourth instar

5a. Winter mortality in the field

The differences between the autumn and spring larval densities shown in Table XI for each site have been tested using Student's t-test. The percentage overwinter mortality at each site in each year is shown in Table 26 and the level of significance denoted.

Table 26. Autumn and spring larval densities on each site for each year showing the overwinter mortality

		Autumn		Spring		
Year	Site	No. of cores	No. larvae /m^2	No. of cores	No. larvae /m^2	% mortality
1969	Netherhearth	40	64	36	55	14
-1970	Above Netherhearth	40	34	80	32	6
	Bog End (*Juncus*)	50	35	60	33	6
	Bog End (mixed-moor)	50	37	60	28	24
1970	Netherhearth	40	17	60	11	35
-1971	Above Netherhearth	40	20	60	21	0 (-5)
	Bog End (*Juncus*)	30	26	60	20	23
	Bog End (mixed-moor)	80	60	60	36	40 *
	Trout Beck	19	88	85	31	65 **
1971	Netherhearth	30	49	40	12	75.5 ***
-1972	Above Netherhearth	72	116	40	10	90 ***
	Bog End (*Juncus*)	30	36	40	42	0 (-17)
	Behind House	90	107	60	51	52.3 ***
	Bog End (mixed-moor)	30	23	40	37	0 (-61)
	Trout Beck		30	20	25	17

* $p < 0.05$; ** $p < 0.02$; *** $p < 0.001$.

The t-tests were carried out on the differences in the mean no. larvae per core shown in Table XI.

These results indicate that in the 1970-1971 winter mortality was high on the blanket-bog sites whereas in the 1971-1972 winter

mortality occurred largely on the Juncus sites and that none of the sites suffered a significant decline in the 1969-1970 winter. There are not, however, sufficient data to be able to attribute mortality to specific combinations of site and weather conditions. It is interesting that significant mortality occurs in the exceptionally mild winters of 1970-1971 and 1971-1972, but not in 1969-70, but it is probably not valid to make a direct comparison between the air temperatures in each year as between 1 November 1969 and 31 March 1970 there were seventy eight days of snow cover. Oke and Hannel (1966) showed that a snow fall of 12.5cm had such an insulating effect that although the snow surface dropped to -17.3°C, the earth surface below remained at 0°C. On a cleared area the soil showed a temperature gradient from the surface to a depth of approximately 50cm. Oke and Hannel give an example where, when the air temperature was -11.3°C (a realistic minimum temperature for Moor House) the temperature just below the surface was -7.2°C, at a depth of 5cm it was -5°C, and at 10cm it was -3°C.

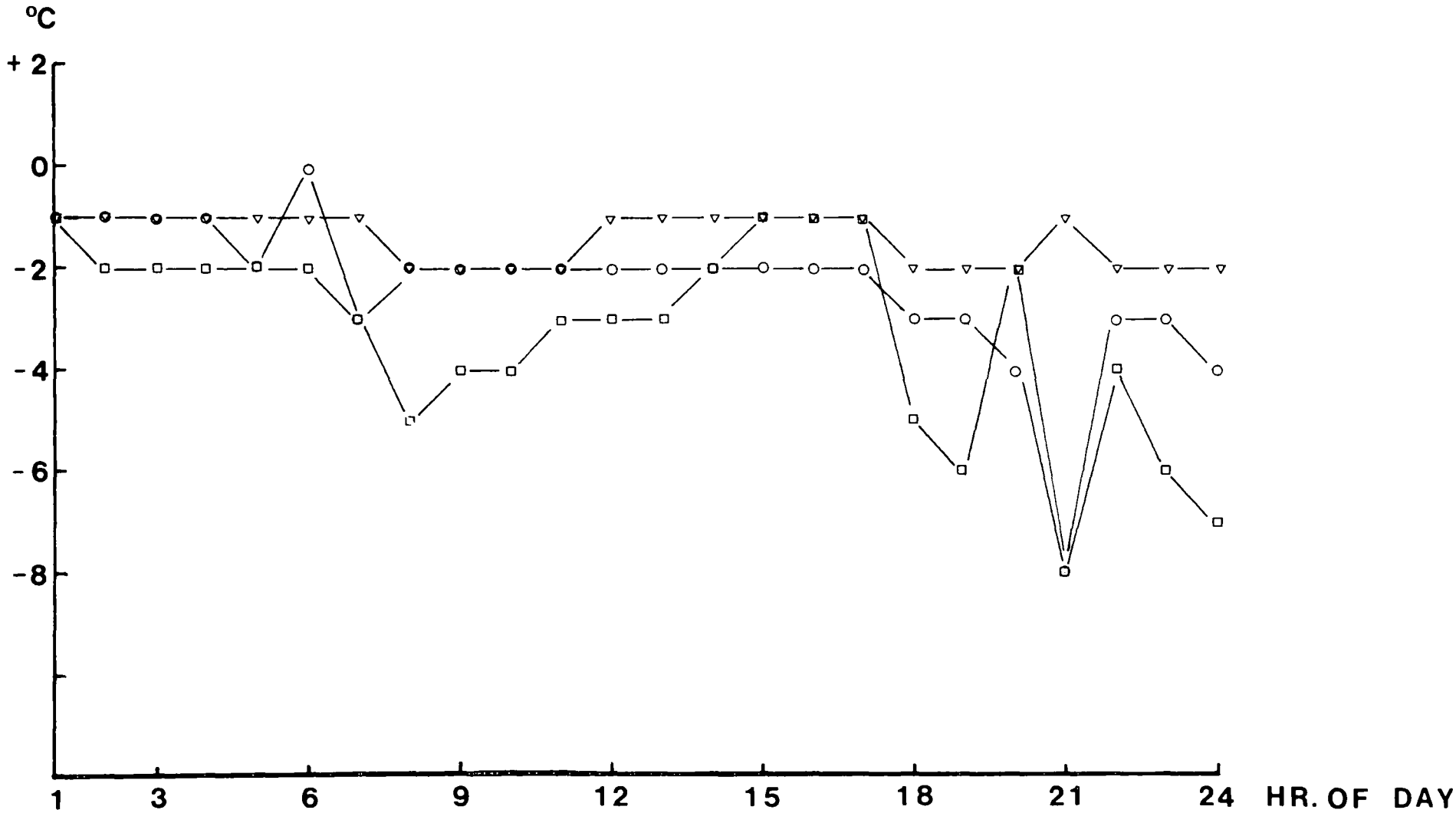
Fig. 27 shows the Moor House Grant recordings for three thermistor probes in different positions on blanket-bog for 5 January 1969 when snow was absent. It indicates what a considerable buffering effect the vegetation and a depth of 1cm has on low temperatures. -9°C was recorded in the middle of an Eriophorum tussock, but at -1cm in Juncus litter the temperature did not fall below -2°C. It therefore seems possible that a short downward migration

Fig. 27. Grant recordings of hourly temperature readings for thermistor probes in blanket-bog on 5 January 1969.

□ In Eriophorum tussock

○ - 2cm in Calluna litter

▽ - 2cm in Juncus litter


°C
+ 2
0
-2
-4
-6
-8
1
3
6
9
12
15
18
21
24
HR. OF DAY

would allow T. subnodicornis to avoid most frosts, and Ricou (1968) found that overwintering T. paludosa larvae showed this type of behaviour, moving to a depth of 1cm below the frost level which, during his study, did not penetrate below 7cm. However, both he and Freeman (1967) showed that T. paludosa had a high mortality when exposed to temperatures below 0°C in the laboratory and, as T. subnodicornis cannot avoid being exposed to such temperatures on occasion, the cold-hardiness of the larvae was examined in the laboratory.

5b. The effect of temperatures below freezing on fourth instar larvae in the laboratory

Fourth instar larvae were brought in from the field during the winter and exposed to -4°C for a number of days. The effect of acclimatisation was tested by keeping the larvae for a month, some at 15°C and some at 5°C, before exposure to low temperature. The results are shown in Table 27.

Table 27. The mortality of acclimatised and unacclimatised fourth instar larvae at -4°C

Date Collected	No. of days acclimatised	No. of days at -4°C	No. of larvae surviving	No. of larvae dying	% mortality
29 Oct	direct from field	32	0	32	100
16 Mar	,, ,, ,,	3	24	0	0
10 Sept	30 at 5°C	9	12	8	40
10 Sept	30 at 15°C	9	4	7	64

These results show that T. subnodicornis larvae are resistant to temperatures below 0°C. The effect of acclimatisation at 5°C for thirty days is better but is not significantly different from a 15°C regime (χ^2 = 0.78, d.f. 1, n.s.) but the experiment should be repeated with larger numbers of larvae and at a lower acclimatisation temperature. Horobin (1971) showed that in the case of T. paludosa survival of larvae at -4.0°C was considerably improved when larvae had been acclimatised at 6.0°C and 2.0°C rather than at 15°or 10°C and that some larvae could withstand 10hrs at -6.0°C when they had been cultured at 2.0°C for the previous week.

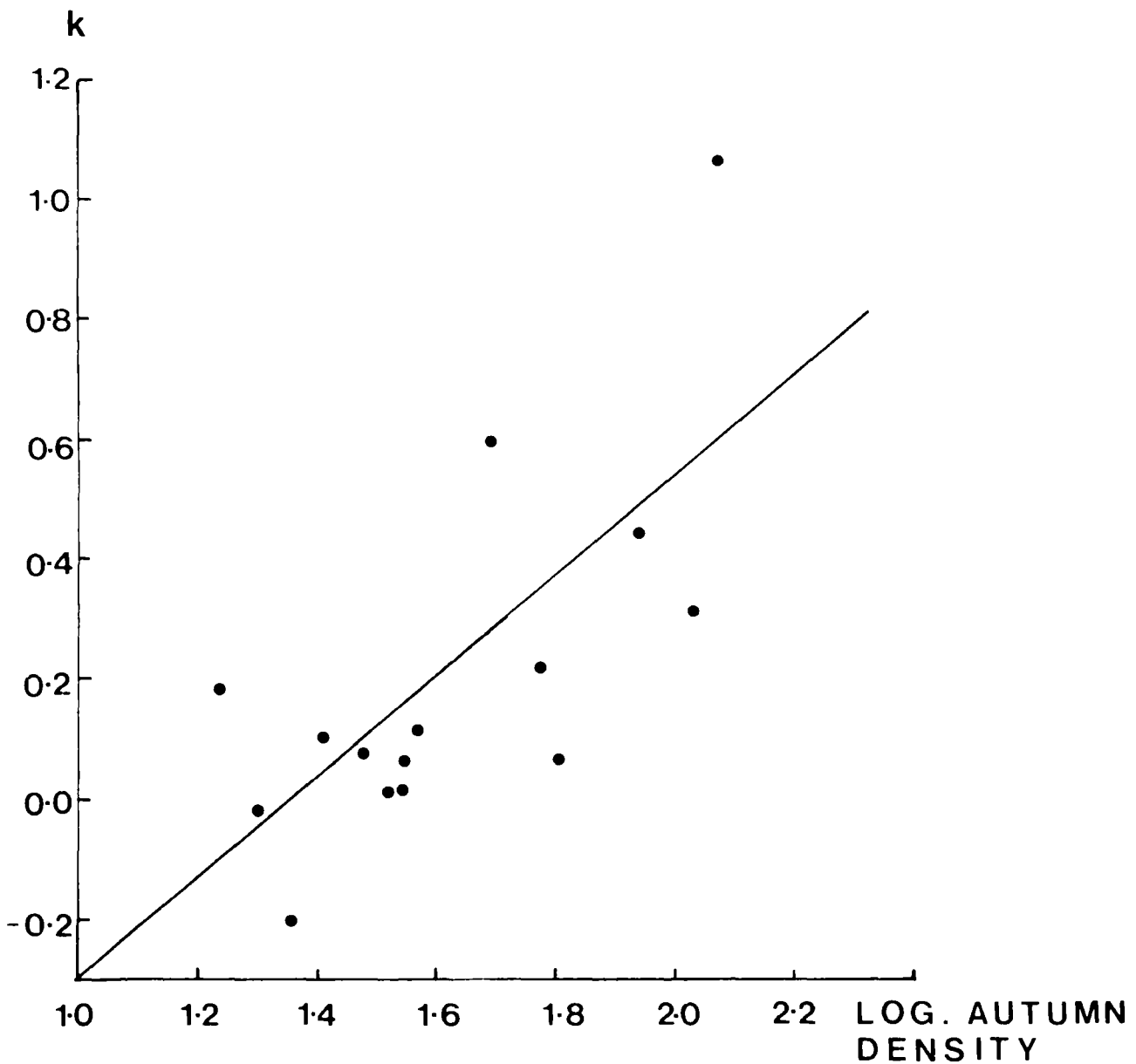
The Grant records show that, during the 1968-1969 and 1969-1970 winters (there is a break in the records in February 1969 but they are otherwise continuous), the temperature at a depth of -2cm below never dropped below -2°C so larvae in similar positions were not likely to have been subjected to lethal temperatures.

5c. Density dependent mortality in the fourth instar

The overwinter mortality has been examined for density effects. Using Varley and Gradwell's (1960) method, the logarithm of the autumn density minus the logarithm of the spring density (k) has been plotted against the logarithm of the autumn density (Fig. 28). The regression coefficient obtained (+0.841) is significantly different from zero ($t = 3.70$, $p < 0.01$). The logarithms of the autumn and spring

Fig. 28. The regression of k (overwinter mortality) on the logarithm of the autumn density

$$y = 0.841x - 2.628$$


k
1·2
1·0
0·8
0·6
0·4
0·2
0·0
-0·2
1·0
1·2
1·4
1·6
1·8
2·0
2·2
LOG. AUTUMN DENSITY

densities when plotted against each other both yield regression coefficients that are significantly different from unity ($t = 3.50$, $p < 0.01$ and $t = 2.62$, $p < 0.02$ respectively) and it can therefore be concluded that overwinter mortality is positively related to density.

5d. Overwinter mortality on Knock Fell in 1972

Other mortality factors such as disease or parasitization were not obvious on the Moor House sites. Coulson (1962) describes a black discoloration of the epidermis which he attributed to fungal attack, but as it can be induced in the laboratory by puncturing the cuticle it could be the result of disease or physical damage rather than the appearance of the infection itself. Both during his study, when eight larvae were afflicted in a sample of 102, and during most of this study, very few blackened larvae were found and it was not thought to be an important mortality factor until a much higher density of infected larvae was found on the Knock Fell site in spring 1972. On 9 March 1972 seventeen larvae from a sample of fifty five (30%) were found to be discoloured. Of these seventeen larvae, eleven were found dead (none of the normal larvae found in the same sample were dead). The area was sampled three times; on 28 February 1972 before the mortality occurred, on 9 March 1972 when the dead larvae were found, and on 24 March 1972. Between the first and the last date the population dropped significantly ($t = 2.64$, $p < 0.01$) showing a 45% mortality which could be accounted for adequately by the percentage of dead and blackened larvae found in early March. The data are presented in Table 28.

Table 28. The mortality of fourth instar larvae on Knock Fell in spring 1972

Date	No. of samples	No.larvae /core	No.larvae alive	No.larvae dead	Density (m^2)	Percentage mortality since the previous sampling
28 Feb	42	1.28	54	0	125	-
9 Mar	41	1.07	44	11	105	16
24 Mar	40	0.70	28	0	69	34

These results indicate that the blackening was closely linked to overwinter mortality on a high density site, but as the cause of the discoloration was not clear, it is not possible to say whether it could act as a density-dependent effect. It seems unlikely that it is due to a fungal attack as efforts at culture have failed (P. Lehmann pers.comm.). If the blackening were caused by a virus infection or by physical damage undergone by larvae at high densities chewing each other it could be the manifestation of a density-dependent process. On the other hand, physical damage, and thus the blackening, might be the result of a sandy substratum or frost. Further investigation is needed.

5e. Year to year variation in autumn density

Table 29 shows the autumn densities for each year on the sites that were sampled in each of the three years.

Table 29. The autumn densities in different years at each site with the significance of the difference from the year before indicated by an asterisk

Site	No. larvae/m^2 1969	1970	1971
Netherhearth	64	17**	49*
Above Netherhearth	34	20	116**
Bog End (Juncus)	35	26	36
Bog End (mixed-moor)	37	60	23*
Trout Beck	-	88	30*

*$p < 0.05$; **$p < 0.002$. The other figures are not significantly different from those of the previous year.

These results indicate that although high densities were never attained, there were significant differences from year to year in fourth instar densities on each site and there was considerable variation in the mortality rate between hatching and the fourth instar in different years on each site. The low autumn densities on the Juncus and Eriophorum sites in 1970 contrast with the high Bog End (mixed-moor) and Trout Beck densities and corroborate Coulson's (1962) finding that a dry summer leads to very low survival on Juncus areas. (The rainfall in May and June 1970 was 157mm (64%) of the mean for the period 1961-1970 which was 245mm).

6. Mortality rate during pupation

The mortality rate during pupation cannot be directly calculated because the estimates of adult densities in this study are not sufficiently accurate. However, there is evidence of differential mortality between the sexes either late in the fourth instar or during pupation and emergence. Inequality in the sex ratio has been noticed in a number of tipulid species (Coulson 1962, Freeman 1964, Hadley 1969). Coulson found a 1 : 1 larval sex ratio in T. subnodicornis on dissection in March and attributed the preponderance of males in the adult population to the greater longevity of the male which he estimated from mark recapture data. Freeman, on the other hand, found that the inequality of the sex ratio among adult T. luna corresponded to a bimodality in larval head capsule and suggested that the sex ratio was already unequal in the fourth instar.

In the present study 167 males and 68 females emerged from the traps at Netherhearth in 1972 giving a ratio of 2.46 males : 1 female. Searching for pupal cases within the traps revealed 100 male and 39 female cases, giving a ratio of 2.57 males : 1 female. The technique of estimating the sex ratio (Coulson 1962) or emergence pattern (Laughlin 1967) from pupal cases has been used for T. paludosa and it was felt from the emergence trap data that an accurate estimate of the sex ratio could also be made by the same method for T. subnodicornis. Between 21 May and 1 June 1970, 272 pupal cases were collected on the Bog End (Juncus) site. 204 of these were male and 68 female, a ratio of 3 : 1 and a significant departure from the 1 : 1 sex

ratio (χ^2 = 68, $p < 0.001$, d.f. 1). It was therefore concluded that there was a real inequality in the sex ratio of emerging adults and that this was due to differential mortality in the very late larval stage or during pupation and emergence rather than to a larval inequality established in the last instar as in T. luna. Further evidence to support this view was derived from the laboratory cultures in which 293 fourth instar larvae gave rise to 121 males and 142 females. This result does not differ significantly from a 1 : 1 ratio (χ^2 = 1.68, $p > 0.1$, d.f. 1) and indicates that in a favourable environment differential mortality does not occur to the extent that it does in the field.

7. Conclusion

There is both field and experimental evidence to indicate that mortality in a number of crane-flies is closely linked to weather conditions at specific stages in the life-history. The egg and first instar appear to be particularly susceptible to drought and Milne et al. (1965) correlated poor survival of T. paludosa with drought in the early autumn and showed experimentally that the egg or hatching stage was more vulnerable than the first instar. Coulson (1962) suggested that drought caused the population crash of T. subnodicornis in 1955 and showed that in this case the hatching success was normal and that the first instar succumbed. The high first instar mortality was confirmed in this study when a 98% mortality was found by 28 July 1972 on Knock Fell and the

low densities of larvae on Juncus sites after the dry summer in 1970 agree with his finding that after the drought in 1955 the densities of larvae on the Juncus areas were drastically reduced whilst those on blanket-bog were relatively unaffected.

Overwinter mortality has been measured and it is not thought that, over the period of this study, it was caused primarily by low temperature as the larvae appeared to be sufficiently cold-hardy to survive temperatures encountered a few centimetres below the ground surface.

The effect of density on mortality has been examined experimentally for the early instars and in the field for fourth instar larvae. It has been shown that both in the early instars and in the overwintering stage mortality is higher at high densities. First instar larvae in culture were often seen biting each other, but a chewed larva was usually dead by the time it was observed. Laughlin (1958) found a considerable degree of cannibalism in T. oleracea larvae and this may well account for mortality of crowded first instar T. subnodicornis larvae in the field. In the later instars there was no evidence of the larvae in culture damaging each other, so it would seem unlikely that this could be a factor in the over-winter mortality in the field. It is more likely that during cold periods those larvae that fail to find a refuge are at risk. It has been shown that the larvae need migrate to a depth of only a few centimetres in Juncus litter to avoid extreme low temperature, but the number of positions where conditions are suitable during a period of alternate thawing and freezing conditions may be limited. If this were the case, a marked density effect would be expected.

Further effects of density, on the size of larvae, have also been observed, and are discussed in the following section which deals with wing length. The possibility that numbers of T. subnodicornis on a site could be limited by the food supply is examined in the next section.

XII. Analysis of gut contents for T. subnodicornis and T. variipennis Meigen

Coulson (1962) found that there was a significantly higher density of T. subnodicornis larvae in samples containing Diplophyllum albicans and Ptilidium ciliare than in samples from which liverworts were absent when he sampled the Eriophorum sward at Netherhearth in 1954. He also found that liverworts constituted the majority of identifiable remains in the faeces. Freeman (1967), on the other hand, studied the feeding of ten species of tipulid larvae and found no evidence of selection for food within groups of larvae taken from the same type of habitat. He therefore concluded that competition for food was not an "important factor in their ecology". As the densities of T. subnodicornis on areas of the Moor House Reserve are on occasion very high, and the supply of liverworts limited, a further analysis of the larval diet was made. The 2550ft site on Knock Fell was chosen as a suitable area to sample on the grounds that not only was there a high density of T. subnodicornis, but that T. variipennis was also present so that any selectivity in the two species could be compared.

Method

The hand-sorting technique has already been described (p. 78) and it has been shown that the distribution of T. subnodicornis larvae in samples taken from Knock Fell on 28 February and 9 March 1972 did not differ significantly from a Poisson distribution (p. 79). A smaller number, 70, of T. variipennis larvae was found in the same samples. Their distribution was also found not to differ significantly from a Poisson (χ^2 = 5.54, d.f. 2, $p > 0.05$). A test based on the null hypothesis that the two species are not associated in their distribution was carried out. This is shown in Table 30 and the significant result indicates that the two species are positively associated and in a position to compete with each other.

In addition to searching for larvae in the soil cores an estimate of the percentage area of the ground covered by vegetation was made. This was as follows : 52.7% grass, 21% Juncus squarrosus, 21.3% moss, 1.8% dicotyledon, and 0.3% liverwort.

Table 30. 2 x 2 contingency table drawn up to test whether T. subnodicornis and T. variipennis were associated in 123 cones, radius 5.7cm

T. variipennis	T. subnodicornis		
	Present	Absent	Total
Present	23	7	30
Absent	33	60	93
	56	67	123

χ^2 = 15.5, $p < 0.001$

The guts of 35 T. subnodicornis and 13 T. variipennis larvae were removed and the contents teased out on a slide and examined wet, with no further preparation, under high power.

Results

The categories that the plant tissues and other gut contents have been divided into, and the number of occurrences in each category, have been listed below in Table 31. Only in cases where the characteristic epidermal cells were present have pieces of tissue without chlorophyll been classified as leaf, and only where root hairs were present were tissues listed as root. This leaves a large proportion of the gut contents in both species that can only be classified as miscellaneous plant tissue. It is not, therefore, possible to compare the proportions of the vegetation available and the proportions in the gut.

As no attempt to assess the size of pieces ingested was made, it was thought more relevant to compare the number of occurrences in the guts of each of the two species rather than to compare the proportions of the different tissues in the guts. χ^2 has been calculated separately for each category on the basis that the type of vegetation should occur in the same number of guts, proportionally, for both species. The results of this analysis are shown in the last column of Table 33. The number of T. variipennis guts containing grass and higher plant tissue is significantly greater than that of T. subnodicornis, and it can be seen from Table 31 that mosses constitute a higher

percentage of all the pieces examined from the T. subnodicornis than they do of the T. variipennis guts. These differences may be the result of the difference in mandible size in the two species (that of T. subnodicornis is two thirds the length of that of T. variipennis) and are consistent with the habitat preferences of the two. T. subnodicornis is found primarily on peat and T. variipennis is found primarily on alluvial soils or mixed peat and alluvial areas (Coulson 1959). As both species are polyphagous and the food is apparently abundant, it is unlikely that either species is directly limited by the food supply or that they come into competition for this resource. However, at high densities the difference in their primary food choice would allow them to co-exist.

Table 31. The number of occurrences of different types of plant tissue in 35 T. subnodicornis and 13 T. variipennis guts. The number of guts containing the tissue in the two species are compared by means of a χ^2-test and the result from this is shown for the two categories where $p < 0.05$

Type of plant tissue	T. subnodicornis				T. variipennis				
	No. of pieces in 35 guts	%	No. of guts with tissue	%	No. of pieces in 13 guts	%	No. of guts with tissue	%	χ^2
Grass leaf	78	27.5	22	62.9	136	50	13	100	4.87*
Root	48	16.9	15	42.9	43	15.8	9	69.2	n.s.
Unidentified higher plant tissue	43	15.1	16	45.7	57	21.0	12	92.3	6.66**
Dicotyledon leaves	4	1.4	1	2.9	9	3.3	1	7.7	n.s.
Mosses	85	29.9	17	48.6	16	5.9	6	46.2	n.s.
Liverwort	8	2.8	5	14.3	5	1.8	2	15.4	n.s.
Fungal mycelia	5	1.8	3	8.6	3	1.1	1	7.7	n.s.
Unidentified material and miscellaneous non-plant material	13	4.6	5	14.3	3	1.1	1	7.7	n.s.
Totals	284	100			272	100			

*$p < 0.05$, **$p < 0.01$; d.f. = 1 in both cases

XIII. Variation in size and fecundity in *T. subnodicornis* in the field and under experimental conditions

When the fecundity of *T. subnodicornis* was being studied in 1969 (M.Sc. dissertation) it proved impossible to find adequate numbers of teneral females on each site. The counting of eggs in individual females was also time-consuming so a parameter that would reflect egg number was sought. Wing, tibia and tarsus lengths were measured for a sample of teneral females and these measurements correlated with egg numbers and $\sqrt[3]{\text{egg numbers}}$/female. It was found that the relationship between wing length and $\sqrt[3]{\text{egg numbers}}$ gave the highest correlation coefficient ($r = +0.613$, $p < 0.001$).

In the present study some parameter that reflected fecundity was again sought so that this means of population change could be studied. It is generally accepted (Hemmingsen and Birger Jensen 1960) that the relationship of the size of the part of an organism with another is best expressed by such an equation as : $\log y = \log x\ b + \log a$, where y and x are measurements of body lengths, b is the slope and a the intercept on the y axis. In the case of the wing measurement it would be expected that wing area would be proportional to the weight of a fly and therefore a more relevant measurement than wing length. However, as the measurement of area would have been a complex procedure, it was decided to determine whether wing length alone could be used to indicate weight. Femur length, the only conveniently measured parameter not investigated in 1969, has also been related to weight.

1. The relationship of wing and femur length with dry weight

Flies that were used for dry weight estimates were collected from the site and killed by a short exposure to ethyl acetate. They were then brought back to the laboratory, measured under a low power microscope with a scale in the eyepiece, and dried to constant weight in a vacuum oven at 40^{o}C. The results of the correlations between wing length, femur length, the logarithms of these measurements and dry weight, $\sqrt[3]{\text{dry weight}}$ and the logarithms of these measurements for flies caught on the 1900ft site on Dun Fell are shown in Table 32. Male flies have been used to avoid the complication of the uncertainty as to how many eggs the females have laid. The normality of wing length distribution for flies on a site has been checked by plotting the wing lengths of 199 males and 222 females from pitfalls at the 2500ft site in 1967 on normal probability paper. This is shown in fig. V in the appendix.

Table 32. The regression parameters and correlation coefficients derived from relationships between length of femur and wing and dry weight of 33 male T. subnodicornis taken from 1900ft

y	x	regression coefficient (b)	S.E.b	constant (a)	r
log wing length	log dry wt	0.1672	± 0.0364	- 0.0291	+ 0.636
log femur length	log dry wt	0.566	± 0.1352	+ 0.453	+ 0.601
wing length	$\sqrt[3]{\text{dry wt}}$	3.493	± 0.7815	+ 6.256	+ 0.626
femur length	$\sqrt[3]{\text{dry wt}}$	2.610	± 0.6398	+ 3.705	+ 0.591
wing length	dry wt	0.441	± 0.1032	+10.021	+ 0.609
femur length	dry wt	0.324	± 0.0848	+ 6.542	+ 0.566

It can be seen from the correlation coefficients above that femur length does not have such a close relationship to dry weight as does wing length and that the relationship between wing length and dry weight is only slightly improved by expressing the measurements as logarithms. On the basis of the degree of significance of these correlation coefficients it was decided that wing length could be used as a measure of size on a site.

There is however some indication that wing length might be an unsuitable measurement to choose when sites at

different altitudes are being considered. Byers (1969) came to the conclusion that wing length reduction was a characteristic of cold adapted insects and found tipulids a particularly good example of this phenomenon. Hemmingsen and Nielsen (1965), in their study on T. excisa Schummel, found that in both sexes for a given body length the wing lengths of Alpine flies were an average of 5.25% longer than those of Lappland flies, and although the same authors found no correlation between wing length and altitude in the Alpine race of T. excisa, this could have been due to the comparatively small sample size. Further correlations for the other sites on Dun Fell have been carried out to determine whether a correction for altitude is required. The effect of altitude on wing length has also been examined in the multivariate analysis on p. 111.

2. The effect of altitude on the relationship between wing length and dry weight

Correlations between wing length and dry weight have been made from samples of male flies collected from the 2700ft, 2500ft and 1700ft sites in addition to those for the sample from the 1900ft site. The regression parameters and correlation coefficients are shown in Table 33.

Table 33. The regression parameters and correlation coefficients for the regressions of male wing length on dry weight for different sites on Dun Fell

Site	N	Regression coefficient (b)	S.E.b	a	S.E.a	Correlation coefficient
1700ft	13	+ 5.71	± 1.92	+ 9.64	± 0.73	+ 0.667
1900ft	33	+ 4.41	± 1.04	+10.02	± 0.47	+ 0.609
2500ft	16	+ 6.59	± 1.54	+ 9.02	± 0.53	+ 0.746
2700ft	32	+ 3.17	± 1.01	+10.02	± 0.40	+ 0.498

There is no significant difference between the regression coefficients in Table 33, the highest value for t when sites are compared is for the difference between the regression coefficients for 2700ft and 2500ft where $t = 1.86$ ($d.f. = 45$, $p \geq 0.05$) so the data for the four sites have been combined, giving the equation $y = 0.786x + 9.70$ ($r = +0.62$, $p < 0.001$) where y is the wing length and x is the dry weight of the male. From these results it was decided that wing length could be used to reflect the mean weight of males on sites of different altitude and that as there were no significant differences between regression coefficients or constants for the sites under consideration, the effect of altitude on wing length could be ignored. Further correlations were then carried out on the relationship between mean male and female wing lengths at each site.

Table 34. The mean wing length of male and female T. subnodicornis caught in pitfalls on the different altitude sites on Dun Fell

	1967		1970		1971	
17	♂ wl S.E.	♀ wl S.E.	♂ wl S.E.	♀ wl S.E.	♂ wl S.E.	♀ wl S.E.
1700ft	11.15 ± 0.08	9.11 ± 0.11	12.45 ± 0.11	10.11 ± 0.10	12.57 ± 0.12	10.18 ± 0.10
1900ft	11.89 ± 0.04	9.69 ± 0.04	12.48 ± 0.05	10.12 ± 0.04	12.63 ± 0.06	10.48 ± 0.03
2500ft	10.05 ± 0.07	9.54 ± 0.09	11.48 ± 0.08	9.51 ± 0.09	-	-
2700ft	11.70 ± 0.06	9.52 ± 0.10	11.48 ± 0.05	9.23 ± 0.06	12.01 ± 0.06	9.78 ± 0.09

Table 35. The mean wing lengths of male and female T. subnodicornis caught in pitfalls on the Moor House site

	1969		1970		1971		1972	
	♂ wl S.E.	♀ wl S.E.	♂ wl S.E.	♀ wl S.E.	♂ wl S.E.	♀ wl S.E.	♂ wl S.E.	♀ wl S.E.
Netherhearth	11.82±0.026	10.19±0.045	11.48±0.054	9.5±0.062	12.24±0.08	10.21±0.076	12.01±0.071	9.87±0.062
Above Netherhearth	11.66±0.051	10.20±0.033	11.12±0.071	9.24±0.046	11.85±0.10	10.26±0.08	11.79±0.102	9.75±0.078
Bog End (Juncus)	11.53±0.032	9.66±0.035	11.24±0.069	9.25±0.080	11.72±0.084	9.60±0.06	11.76±0.074	9.82±0.048
Bog End (mixed-moor)	11.60±0.060	9.68±0.170	11.13±0.040	8.89±0.057	11.50±0.08	9.09±0.07	11.32±0.072	9.26±0.082
Behind the House	11.99±0.035	10.38±0.032	-	-	11.93±0.10	10.24±0.06	11.53±0.106	9.67±0.068
Trout Beck	-	-	11.9±0.055	94.1± 0.055	10.90±0.10	92.2 ±0.09	-	-

3. Comparison of mean male and mean female wing lengths

During the emergence period each year adult T. subnodicornis was caught, as previously described, in pitfalls. After counting, each day's catch was preserved in 70% alcohol and at a later date wing lengths were measured in the laboratory. In addition to the flies trapped between 1970 and 1972 Horobin's collections from Dun Fell, made in 1967, and my data from 1969, have been used.

The mean wing lengths of males and females on each site are shown in Tables 34 and 35. As there was a possibility that the correlations between wing lengths in the two sexes might vary on the two slopes of Dun Fell, it was decided to compare the data for the West side and the East side separately. The regression parameters and correlation coefficients for the sites on the West side and the East side of Dun Fell are shown in Table 36 and Fig. 29.

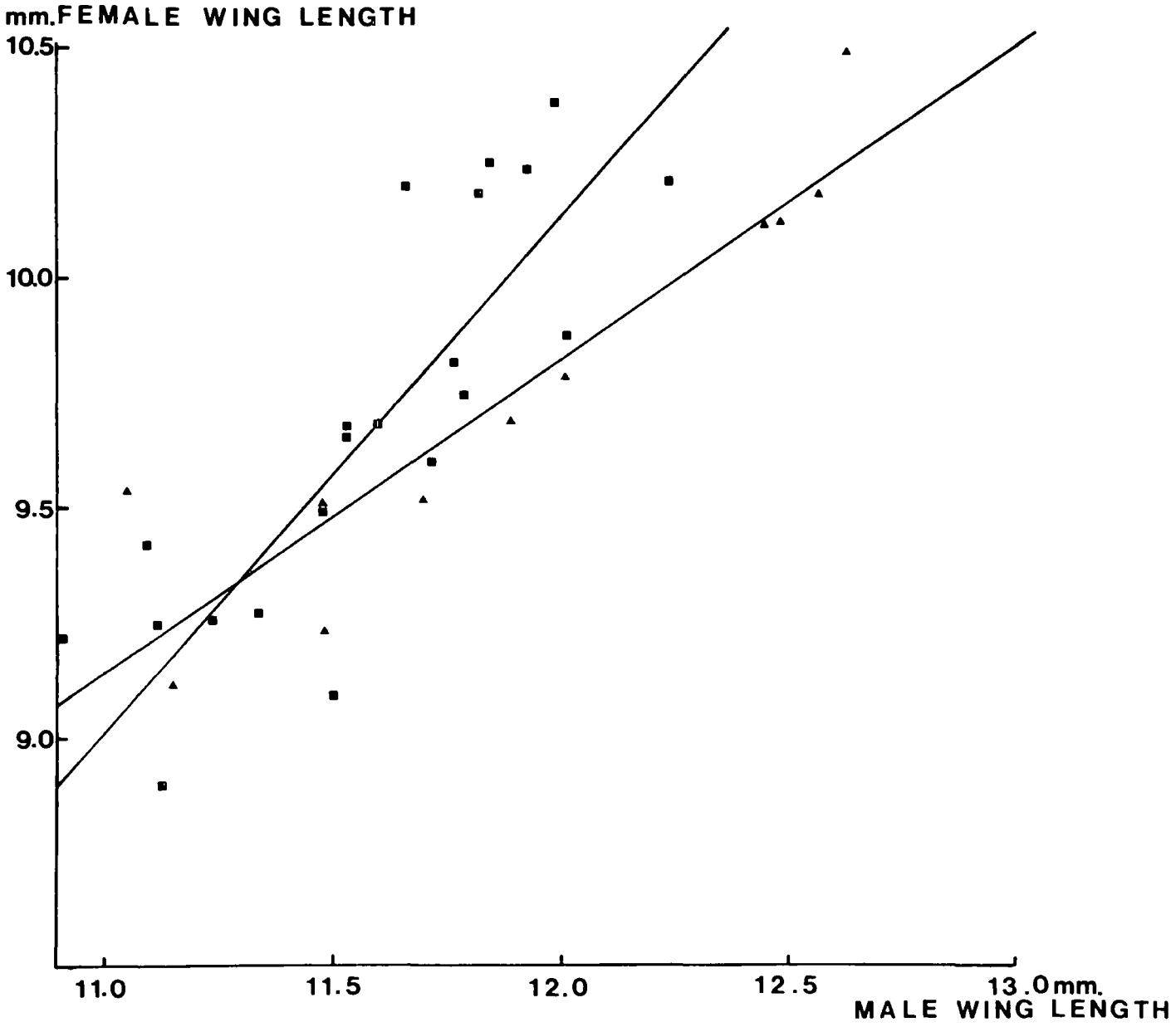
Table 36. The regression parameters for the regression of mean female wing length against male wing length for the sites on the West and East side of Dun Fell

	N	Regression coefficient (b)	S.E.b	a	S.E.a	Correlation coefficient	
West side	11	+0.673	±0.0953	+1.743	±1.136	+0.920	$p < 0.001$
East side	21	+1.082	±0.156	-2.848	±1.812	+0.846	$p < 0.001$

Fig. 29. The regressions of female wing length on male wing length on the two sides of Dun Fell.

■ East side $y = 1.082x + 2.848$, $r = +0.846$, $p < 0.001$

▲ West side $y = 0.673x + 1.743$, $r = +0.920$, $p < 0.001$


mm.FEMALE WING LENGTH
10.5
10.0
9.5
9.0
11.0
11.5
12.0
12.5
13.0mm.
MALE WING LENGTH

Both the regression coefficients and the constants are significantly different on either side of Dun Fell ($t = 2.24$ d.f. 30, $p < 0.05$ and 2.15 d.f. 30, $p < 0.02$) respectively. The information therefore has not been combined, but it was concluded that the relationships between male and female wing length on the two sides were closely correlated for the wing length of either sex to be used as an indication of size on a site from the appropriate side of Dun Fell.

4. Multivariate analysis on the factors affecting wing length

Further information on the variation of wing length from year to year and from site to site has been extracted by means of a multivariate analysis. The programme used was a Stepwise Regression, coded BMD02R (Dixon 1968).

The effect of the following variables on wing length has been tested : year, site, altitude and density. It was thought that autumn or spring larval density might bear a closer relation to the weight of the adult than the pitfall catch which, if there has been any mortality, will not represent the density during the larval growth period. As there were no larval density measurements for the West side, the two sides have, in the first instance, been considered separately. The blanket-bog sites have not been used, and the Behind House site in 1972, when it was flooded, has been omitted. A list of variables entered on each run is shown below in Table 37. The larval densities were taken from Table XI in the appendix and the adult densities from the pitfall data in Tables XII and XIII in the appendix.

Table 37. The independent variables entered in three regressions in which first the male and then the female wing length is the dependent variable

Variable entered	West side	East side	Combined
1. Year*			
1967	+	-	+
1969	-	+	+
1970	+	+	+
1971	+	+	+
1972	-	+	+
2. Site*			
Netherhearth	-	+	+
Above Netherhearth	-	+	+
Bog End (Juncus)	-	+	+
Behind House	-	+	+
1700ft	+	-	+
1900ft	+	-	+
2500ft	+	-	+
2700ft	+	-	+
3. Density			
spring larval	-	+	-
autumn larval	-	+	-
no. females/20 pitfalls	+	+	+
no. males/20 pitfalls	+	+	+
total/20 pitfalls	+	+	+
4. Altitude			

+ variable entered; - variable omitted

*Year and site were coded on a 0 or 1 matrix indicating individual sites and years.

During computation variables were introduced to the equation in order of significance. These are listed with the regression coefficients and their level of significance, at the stage when the last significant, or nearly significant, variable has been entered, in Table 38. It can be seen that the year and the site have been selected as the most important variables affecting wing length and that density also has a significant effect on the male wing length. On the east side where autumn and spring densities have been measured as well as pitfall catches, spring density has been selected as having the most significant effect. On the west side altitude has the expected effect of producing a negative regression coefficient, but it is not significant. When all sites are combined, year 1971 and site 1900ft have the effect of producing long-winged flies of both sexes, whereas the Bog End (Juncus) site produced small winged flies. Both sexes are shorter-winged at higher densities, but the effect on the males is greater. The Above Netherhearth site produces short-winged males and the 2700ft site short-winged females, and in 1969 female wing length is longer than usual.

In order to remove the effect of the non-significant factors on the analysis, two more regressions have been made using only the significant factors. The final equations took the form :

$$\underset{(mm)}{\text{Male wing length}} = 12.016 + x_1 0.371 - x_3 0.496 - x_4 0.333 + x_5 1.008 - x_6 0.00$$

$$r^2 = +0.689$$

$$\underset{(mm)}{\text{Female wing length}} = 9.854 + x_1 0.443 + x_2 0.546 - x_3 0.544 + x_5 0.684 - x_6 0.0014$$

$$r^2 = +0.769$$

where x_1 and x_2 are the year effect of 1971 and 1969 respectively, x_3, x_4 and x_5 are the respective effects of the sites; Bog End (Juncus), Above Netherhearth and 1900ft, and x_6 is the effect of the density measured as the total pitfall catch per 20 traps on each site.

The main factors affecting wing length appear to be year and site. The year effect is presumably caused by some aspect of the weather, such as drought or temperature. The altitude effect, although not significant, is in the direction that supports the possibility that low temperatures reduce the size of flies. Further data are required before the appropriate aspect of the year effect can be discovered. This also applies to the site effect which could be due to a wide range of factors. The density effect is also significant. This finding is supported by experimental evidence from the wing length measurements made on the flies emerging from the enclosures set up at different densities at Netherhearth, which will be described in the next section.

Table 38. The independent variables, selected in order of significance, which influence wing length in T. subnodicornis

1. East side

a Male wing length (mm); constant = 11.7897, multiple r = 0.979

Variable	Regresssion coefficient (b)	S.E.b	F(d.f.1&8)	p
Year 1971	+ 0.1473	± 0.04903	9.02	< 0.05
Year 1970	- 0.3178	± 0.07199	19.48	< 0.01
Site, Behind House	+ 0.2887	± 0.06255	21.30	< 0.01
Site, Netherhearth	+ 0.3739	± 0.05155	52.61	< 0.01
Density, Spring larval	- 0.00798	± 0.002306	11.97	< 0.01

b Female wing length (mm); constant 10.2085, multiple r = 0.952

Variable	Regression coefficient (b)	S.E.b	F (d.f.1&10)	p
Year 1972	- 0.3951	± 0.09402	17.66	< 0.01
Year 1970	- 0.7239	± 0.09151	62.57	< 0.01
Site, Bog End (Juncus)	- 0.4639	± 0.09151	25.69	< 0.01

2. West side

a Male wing length (mm); constant = 13.4754, multiple r = 0.778

Variable	Regression coefficient (b)	S.E.b	F (d.f.1&8)	p
Year 1967	- 0.6834	± 0.2535	7.27	< 0.05
Altitude	- 0.000611	± 0.00029	4.43	> 0.05

b Female wing length (mm); constant 9.8564, multiple r = 0.851

Variable	Regression coefficient (b)	S.E.b	F (d.f.1&7)	p
Year 1971	+ 0.2774	± 0.21418	1.68	> 0.05
Site 1900ft	+ 0.6086	± 0.20226	9.06	< 0.05
Density, male pitfalls	- 0.00253	± 0.00128	3.91	> 0.05

3. East side + West side

a Male wing length (mm); constant 12.0647, multiple r = 0.825

Variable	Regression coefficient (b)	S.E.b	F (d.f. 1&19)	p
Year 1971	+ 0.3348	± 0.1306	6.57	< 0.05
Site, Bog End (Juncus)	- 0.4780	± 0.1826	6.85	< 0.05
Site, Above Netherhearth	- 0.3270	± 0.1630	4.02	> 0.05
Site, 1900ft	+ 1.0281	± 0.2397	18.39	< 0.001
Density, male and female pitfalls	- 0.00203	± 0.000614	11.01	0.001

b Female wing length (mm); constant 9.7883, multiple r = 0.883

Variable	Regression coefficient (b)	S.E.b	F (d.f.1&18)	p
Year 1971	+ 0.4423	± 0.1158	14.59	< 0.01
Year 1969	+ 0.5245	± 0.1347	15.17	< 0.01
Site, Bog End (Juncus)	- 0.5163	± 0.1382	13.97	< 0.01
Site, 2700ft	- 0.1102	± 0.1739	0.40	> 0.05
Site, 1900ft	+ 0.5058	± 0.1814	7.77	< 0.05
Density, male pitfalls	- 0.001895	± 0.000961	3.62	> 0.05

5. The relationship between wing length and larval density under experimental conditions

The traps that were set up on Netherhearth in spring 1971 were left in position throughout the year and during the emergence season in 1972 they were again netted. Emerging adults were removed each day and their wing lengths measured to give an indication of the size attained in each set of traps. The number of flies removed from each set of enclosures, and from the 20 pitfalls at Netherhearth, their mean wing lengths and the densities of the first instars are shown in Table 39.

Table 39. Densities at which traps were set up in spring 1971 and the mean wing lengths of the resultant adults emerging in 1972

		Males			Females		
Traps	1st instar/m^2 1971	N	Wing length in mm	S^2	N	Wing length in mm	S^2
Outside*	779	68	12.01	0.344	122	9.87	0.470
1 - 6	1,363	106	11.78	0.515	43	9.36	0.365
7 - 10	7,301	56	11.27	0.808	39	9.17	0.504

*Estimated from the spring larval density

S^2 = variance

The significance of the differences in the mean wing lengths of the flies from the different densities is tested in Table 40.

Table 40. t-tests on the significance of the differences between mean wing lengths of T. subnodicornis reared under different density regimes

	Difference in mean ♂ wing length (mm)	t	p	Difference in mean ♀ wing length (mm)	t	p
Between traps 1 - 6 and 7 - 10	0.51	3.70	<0.001	0.19	1.3	n.s.
Between traps 1 - 6 and the outside of the traps	0.23	2.31	<0.02	0.51	4.59	<0.001

Unlike the multivariate analysis, which indicated a significant density dependent effect only in the case of the male wing length, the results above show that the wing length in both sexes decreases with increase in density. There is a significant effect between the traps at different densities as well as between the traps and the exterior, indicating that there was a real density effect rather than that the traps themselves provided an unfavourable environment.

It is noticeable that the number of flies emerging from the two sets of traps, 149 and 95, are very similar when compared as densities per m^2 (100 per m^2 and 95 per m^2 respectively). This might indicate a "carrying capacity" (Coulson (1956) gives early May larval densities of 145 and 111 per m^2 for the same area) of 100 adults per m^2, but this result may have been brought about by emigration rather than mortality. Rennie (1917) found that when placed at high density T. paludosa crawled out of cages.

Conclusion

It is concluded that high density is not only associated with increased mortality but also with reduction in wing length in adults. As wing length is correlated with weight and fecundity it is assumed that at high densities there will be a reduction in fecundity. The reduction of mean fecundity associated with a decrease of mean female wing length from 9.87mm to 9.17mm would be from approximately 280 eggs/female to 205 eggs/female (M.Sc. dissertation). Although this is a 27% decrease in the numbers entering the next generation it is unlikely that reduction in numbers at this stage will have a great effect on the regulation of adult density.

As the larvae are polyphagous, it seems unlikely that the food supply would prove limiting on a site. It is possible that the density effect is brought about by contact between larvae as in Bupalus piniarius (Klomp and Gruys 1965; Gruys 1970).

General discussion

This study has largely been concerned with two aspects of the biology of T. subnodicornis ; the synchronisation of the annual life-cycle and the fluctuation in numbers in the field. The influence of temperature and photoperiod on the timing of the life-history has been examined both in the field and the laboratory. The variation of population density from year to year and from site to site has been observed in the field and the effect of density on mortality has been observed under experimental conditions.

The response to temperature is such that both the increase of growth rate with temperature and the temperature range over which this increase is shown, diminish during larval development. The reduced response to temperature has been shown to occur in the moth Dasychira pudibunda by Geyspitz and Zarankina (1963) and the reduction in the range over which the response is made is brought about in other insects such as Calandra oryzae and Rhizopertha dominica (Birch 1944) as it is in T. subnodicornis by the drop in the optimum temperature for development. Laughlin (1963) found that during the development of Phyllopertha horticola the lower temperature threshold dropped during development so that although during the first instar larvae showed a slower growth and lower survival rate at 12°C, in the second instar the rate of development was as fast at 12°C as at 16° and 18°C. Although the position of the lower threshold has not been determined for T. subnodicornis, the situation is analagous in that in the fourth instar the growth rate at 20°C is below that at 15° or 10°C.

Laughlin suggested that the drop in threshold temperature was an adaptation to the falling autumn temperature in the field. In the case of T. subnodicornis the drop in the optimum temperature for development would enable the larvae in the colder areas to complete their growth not long after those in warmer habitats. The next phase in development is temperature independent, or possibly inversely related to temperature, and all larvae should be in this stage by the end of the winter.

It is suggested that the main response to photoperiod in T. subnodicornis comes in the fourth instar when the growth period has finished, but that there may be a secondary response during the growing period when larvae kept on a short photoperiod grow more quickly than those on a long photoperiod. This could be an adaptation promoting the development of larvae that have not completed their growth by autumn due to their early development having been retarded by low temperature.

The primary photoperiod effect lies in the response of the full grown larvae to lengthening day which promotes and synchronises pupation. The temperature independent phase takes place on a short day length and, like some diapause conditions (Beck 1968), can be broken by the appropriate photoperiod. If larvae are taken from the field in mid December and kept at 10°C they can be prevailed upon to pupate forty days earlier on an eighteen hour day than on a six hour day. By the end of February this effect has almost disappeared and the mean dates of pupation are only seven days apart on the two light regimes. The variance is, however, still significantly greater on the short day regime and this suggests that the photoperiod effect may be additive

so that by the end of February, although the day length is long enough to sychronise pupation to a certain extent, a longer photoperiod has a greater effect. This type of situation exists in T. pagana where both the mean pupation date and the variance decrease with shorter day length, and appears to be similar to the effect found in the lacewing Chrysopa carnea Stephens(Tauber and Tauber 1973) where the duration of the overwinter reproductive diapause shows an inverse linear relationship with day length. In the two tipulids studied it could be a useful adaptation acting to accelerate the pupation of any larvae that have been delayed in development or have failed to receive earlier photoperiod stimulation.

Most Tipulidae are characterised by their lack of resistance to desiccation and many species within the group are confined to areas where the humidity is high. This limitation in habitat could be expected to impose severe restrictions on the abundance of the species. However, in the two species studied, T. subnodicornis and T. pagana, there are adaptations in the life-histories that allow them to exist over a wide temperature range (therefore latitude and altitude), so suitable habitats can be exploited over a large area.

Coulson and Whittaker (in press) suggest that the fauna at Moor House consists of two components; the moorland community which has affinities with the fauna of northern Scandinavia, and the grassland community which consists largely of species common at lower altitudes. T. subnodicornis belongs to the first group and T. pagana to the second. It is appropriate that the two species, both showing adaptations that allow the annual cycle to be maintained

over a considerable latitude range, should both exist in an area where the two communities are at the limits of their respective ranges.

T. subnodicornis is particularly interesting in that it lacks a diapause. There is a considerable body of research on the effect of temperature on the distribution and abundance of animals (Andrewartha and Birch, 1954; Krebs 1972). The ability of an animal to exist over a wide temperature range is usually attributed to the presence of different genetic strains, acclimatisation (Bullock 1955; Fry 1958) or, in the case of insects, a diapause (Danilevskii 1965). However, in a number of univoltine insects that have been investigated (Geyspitz and Zarankina 1963; Laughlin 1963), further adaptations have been discovered, and it is suggested that a physiological approach to the life-histories of other univoltine species would illuminate their ecology.

Andrewartha and Birch (1954) put forward the theory that over the geographical range of a species the variation in habitat and climate could act in such a way that there is no necessity to invoke density dependent regulation of populations. They suggested that for an insect frequent catastrophes provoked by weather conditions usually kept numbers low, and although a succession of favourable years might allow a great increase in numbers, this occurrence would usually be rare. Extinction of the population, on the other hand, would be avoided due to the variation of the natural habitat which provides refuges where the prevailing unfavourable conditions could be avoided and whence emigration could take place when the environmental stress relaxed.

Nicholson (1954b), again using an insect, Lucilia cuprina Wied., as an example, propounded the converse of this theory in suggesting that populations are usually restrained by intraspecific competition and that only when there is a catastrophic decline in numbers is the full reproductive potential of the individual realised.

Cragg (1961) commenting, with reference to T. subnodicornis, that "the variability of the moorland habitat .... accounts, with the sometimes violent climatic fluctuations, for the marked variations in abundance", found no immediate reason for regulation to be significant when extinction of local populations might be of frequent occurrence. During the present study, however, there have been strong indications that density dependent regulation does occur even at the low densities encountered on the Moor House sites between 1969 and 1972.

It has been shown experimentally that survival in the first instar and later stages can be density dependent. The traps at Netherhearth showed that density dependent mortality had taken place when sampled for first instar larvae, and the next spring the two sets of traps both yielded the equivalent of 100 adults per m^2 despite the initial densities having been in the ratio of 1:8. Observation of overwinter mortality in the field also indicates a density dependent relationship, and the possibility of disease or damage inflicted intraspecifically (causing the blackening of larvae) remains to be explored. Fecundity may also be affected by density, but as estimation of fecundity was approached by the circuitous method of measuring wing length, this needs to be investigated further. Even a 25% decrease in

fecundity (e.g. from 400 to 300 eggs) would have little effect on the numbers of adults in the next generation if followed by the usual very high first instar mortality.

It has been shown that the first instar is the stage in which the greatest mortality occurs and also that it is the stage which is most vulnerable to adverse weather conditions (Coulson 1962). Very large differences in the mortality rates in the first instar cause fluctuations in the population density that give the impression that the numbers are kept down by recurrent catastrophes. However, it is suggested that both in the first instar and at the later stages, especially the over-wintering stage, density dependent mortality takes place, and that this buffers the effect of extrinsic factors such as the weather.

Using wing length as an indication of size it has been shown that weight and fecundity (in the female) are related to year and site. As the information from the altitude sites and laboratory experiments make it seem unlikely that the weight attained during growth is directly related to temperature, some other aspect of the environment must be sought to explain the between-year variation on a site. Meats (1967) found that the growth rate in T. oleracea and T. paludosa was related to the difficulty of extracting water from the soil, and rainfall, therefore, might be a component of the weather worth further investigation. It was felt that there was not enough information from the present study to attempt analysis of this year-to-year variation, so the situation has been left in that of Laughlin's (1967) where he could find no explanation for the mean peak weight differences in T. paludosa.

The between site differences suggest that some aspect of the diet is influencing the weight gain, especially as the blanket-bog sites on the East side produce consistently small flies of both sexes. This would be in agreement with Ricou's (1967) finding for the equally polyphagous T. paludosa which attains a higher weight and fecundity when fed on a supplement of dandelion (Taraxacum officinale) or wild chicory (Cichorium intybus) than it does on supplements of clovers or grasses.

Another aspect of wing length that was investigated was its relationship with altitude. T. subnodicornis shows wing reduction in the female, and in this is typical of many mountain species that show wing reduction in one or other of the sexes (Mani 1962). This is thought by Byers (1969) to be a response to cold conditions when, because flight is not possible, there is an absence of selective pressure on mutant forms with reduced wings. It might be supposed that in a species which already has a flightless female, the male would show progressive reduction with altitude. However, although the male flies infrequently at the higher altitude sites on Dun Fell, on warm days flight is quite possible, and while there is selective advantage in the male being able to fly, wing reduction is not likely to occur.

Summary

1. The life-cycle and population dynamics of Tipula subnodicornis have been studied in the laboratory and in the field on the Moor House Nature Reserve, an area of Pennine moorland consisting largely of blanket-bog, between 1969 and 1972.

2. The study sites can be divided into two groups; one group consisted of sites at different altitudes from 1700ft to 2700ft on the western scarp slope of Dun Fell, the other of sites at approximately the same altitude (1800ft) but on different vegetation types on the eastern dip slope.

3. Soil temperature measurements were made at each of the sites on the west side of Dun Fell from October 1967 until May 1970 using a mercury in steel thermograph. During this period the Berthet sucrose inversion method was used to give the monthly means at the altitude sites and sites on the west side. From summer 1968 until January 1972 the participants in the International Biological Programme had a Grant recorder registering hourly temperature readings for probes in a number of positions on blanket bog. The daily meteorological readings from the screen at Moor House were available during the study period.

4. Molophilus ater and T. subnodicornis both undergo an annual life-cycle at 1400ft and at 2700ft. The ability of T. subnodicornis to maintain an annual cycle over a wide temperature range was thought to be worth investigation.

5. The emergence period in the field was monitored by pitfall traps each year. The mean date of emergence calculated from the pitfall catch was compared with those calculated from sticky traps and

emergence traps and it was shown that the pitfall data represented the emergence pattern on a site adequately.

6. It was found that the duration (as measured by the variance) of the emergence period and the timing of the mean date of emergence were dependent on temperature. Emergence was delayed at the higher altitude sites and following a cold spring.

7. The relationship between emergence date and temperature was confirmed in the laboratory. Both the rate of development before pupation and the rate of development during pupation were positively linearly related to temperature over small temperature ranges but the relationship is probably better expressed by the Pearl-Verhulst logistic equation.

8. The relationship between the rate of development of the egg and temperature was also positive and approximately linear between $7^{\circ}C$ and $25^{\circ}C$ and can be expressed by the equation $y = 0.64x - 2.06$ (where y is percentage development per day and x is temperature in $^{\circ}C$).

9. Development rate in the early larval stages was also found to be positively related to temperature; over a range of temperatures from 5° to $20^{\circ}C$. During larval development the optimum temperature dropped from $25^{\circ}C$ (or above) in the egg to below $20^{\circ}C$ in the later instars. Q_{10} between 20° and $10^{\circ}C$ and between 15° and $7^{\circ}C$ drops from 1.84 to 0.66 and from 2.49 to 1.78 respectively during larval development so that temperature has progressively less influence on growth rate.

10. Fourth instar larvae on a short photoperiod, L:D; 6:18, grew 20 - 30 percent faster at 10° and $20^{\circ}C$ than on a long photoperiod, L:D; 18:6, at the same temperatures.

11. At the end of the growth period a temperature-independent phase intervened. This took place under short day conditions and eventually ended spontaneously. However, long photoperiod had the effect of completing the stage and promoting development towards pupation. As day length in the field acts at the same moment on all larvae, this would have the effect of synchronising pupation.

12. Tipula pagana larvae enter a diapause when fully grown. This diapause continued indefinitely under long photoperiod (18:6; L:D) and was terminated by a decrease in photoperiod to L:D; 16:8. Pupation occurred earlier in response to a shorter photoperiod (L:D; 12:12) and in the field this reaction would tend to increase the degree of synchronisation of the emergence period.

13. A model for the control of the timing of the life-history of T. subnodicornis is suggested.

14. No evidence of acclimatisation was found from the measurement of the respiration rate in T. subnodicornis.

15. Comparison of the respiration rates of late fourth instar larvae of T. subnodicornis and T. pagana supported other evidence that T. pagana underwent diapause during July and August.

16. The larval density of T. subnodicornis was assessed on a number of sites by taking soil cores which were later hand sorted. Low densities and the failure to find a suitable extraction method restricted the study to fourth instar larvae.

17. Adult densities were assessed by pitfall catches at each site. It was decided, after correlation of pitfall catch with spring larval density ($r = +0.70$, $p < 0.001$) that pitfall estimates gave an adequate representation of the adult densities on areas of the same vegetation type.

18. Egg hatching success in T. subnodicornis was estimated to be 98 percent in the laboratory. There was an 82-97 percent mortality in the first instar in the field.

19. Density dependent mortality occurred in the first instar in artificially stocked enclosures in the field and in laboratory cultures in which the larvae were set up at different densities and left for $2\frac{1}{2}$ months.

20. Overwinter mortality in T. subnodicornis in the field averaged 34 percent in 1970-1971 and 39 percent in 1971-1972, but only 12 percent in 1969-1970. The Juncus sites were worse affected in 1971-1972 than in 1970-1971 whereas the mortality on the blanket-bog was heavy in 1970-1971.

21. Laboratory studies indicated that fourth instar larvae could survive several days at $-4^{\circ}C$ and data from the Grant recorder showed that at -2cm below the surface in Juncus litter the temperature did not drop below $-2^{\circ}C$ when the temperature in an Eriophorum tussock was at $-9^{\circ}C$. From this it was concluded that overwinter mortality was not likely to be (largely) dependent in low temperature.

22. Using Varley and Gradwell's (1960) method, density dependent mortality in overwintering larvae in the field was demonstrated.

23. The 55 percent mortality between 28 February and 24 March 1972 at a high density site on Knock Fell and the blackened condition of many larvae are described and the cause of this mortality is discussed.

24. The greatest between year variation in autumn density was between 1970 and 1971 at the Above Netherhearth site (20 larvae per m^2 and 116 larvae per m^2) and numbers never reached Coulson's (1956) estimates of 600 larvae per m^2 in September.

25. The mortality during pupation is not easily assessed, but the sex ratio changed from 1:1 in the fourth instars to 3:1 or 2.5:1; males : females in the emerging adults on two sites in 1971 and 1972.

26. Gut analyses were carried out on samples of T. subnodicornis and T.variipennis from the Knock Fell site. Both species were polyphagous and it seemed unlikely that the food supply could be limiting in either case. T.variipennis ate a significantly higher proportion of grass and higher plant tissue, but fewer mosses than did T. subnodicornis. This might be associated with the larger mandible size of T.variipennis.

27. Wing length and femur length were found to be significantly correlated with dry weight for male T. subnodicornis ($r = +0.61$ and 0.57 respectively, $p < 0.001$ in both cases).

28. Wing length was not significantly correlated with altitude but male and female wing length on each site were closely related ($r = +0.92$ for the west side and $r = +0.85$ for the east side; $p < 0.001$ in both cases).

29. A multivariate analysis indicated that the main factors affecting wing length were site and year. It is suggested that the site effect might be dietetic and the year effect might be due to weather.

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*Not consulted in the original.

A P P E N D I X

TABLE I. The daily catch of *T. subnodicornis* in ten pitfalls on each Moor House site in 1969

Date	Netherhearth		Above Netherhearth		Bog End *Juncus*		Bog End (mixed moor)	
	male	female	male	female	male	female	male	female
23 May	0	0	0	0	1	1	0	0
24	0	0	0	0	1	2	0	0
25	0	0	0	0	4	1	0	1
26	0	0	0	0	0	5	0	1
27	1	0	0	0	1	2	4	1
28	1	1	0	0	4	4	1	1
29	0	0	0	0	4	2	0	0
30	0	0	1	1	5	7	1	1
31	0	0	0	0	5	1	1	2
1 June	2	4	1	1	3	4	4	0
2	3	3	1	1	8	7	2	1
3	6	3	6	2	4	1	11	2
4	2	0	2	0	3	1	0	1
5	2	3	4	12	4	2	3	1
6	2	3	3	8	1	0	0	0
7	3	3	7	11	2	4	0	0
8	1	7	2	6	0	4	0	4
9	3	1	4	7	1	2	1	0
10	-	-	0	19	0	2	3	1
11	17	17	0	11	0	0	0	0
12	3	3	0	6	0	1	0	1
13	3	4	0	2	0	0	1	0
16	4	5	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0
Totals	53	57	31	87	51	53	32	18

TABLE IIa. The daily catch of *T. subnodicornis* in twenty pitfalls on each Moor House site in 1970

Date	Netherhearth		Above Netherhearth		Bog End *Juncus*		Bog End (mixed moor)	
	male	female	male	female	male	female	male	female
16 May	0	0	0	0	0	0	0	0
17	-	-	-	-	-	-	-	-
18	0	0	0	0	1	5	0	0
19	0	1	0	1	2	2	0	0
20	2	0	0	0	3	2	0	1
21	1	1	0	0	6	3	2	0
22	2	0	0	0	6	2	2	0
23	5	3	1	2	7	3	2	5
24	5	7	1	6	8	8	3	9
25	20	12	3	7	16	6	9	15
26	13	7	7	8	11	5	3	12
27	17	6	6	13	20	8	18	9
28	11	15	7	29	10	15	7	22
29	28	17	9	23	6	3	6	8
30	16	20	14	27	9	4	6	11
31	14	8	12	9	5	5	10	11
1 June	11	2	11	13	5	3	7	15
2	16	12	24	53	2	4	2	15
3	15	5	3	13	2	3	1	3
4	11	17	11	30	3	10	0	6
5	15	9	17	11	5	6	0	16
6	10	6	11	7	0	0	0	5
7	8	4	4	9	2	4	1	6
8	6	2	9	12	1	5	0	4
9	0	1	0	4	0	0	0	0
10	4	2	2	5	0	0	0	1
14	2	1	3	4	1	0	2	2
17	0	0	3	2	0	0	0	0
23	0	0	0	1	0	0	0	0
28	0	0	0	0	0	0	0	0
Totals	232	158	158	289	131	106	81	176

TABLE IIb. The catch of *T. subnodicornis* in ten pitfalls, inspected on alternate days, on each site on Dun Fell in 1970

Date	1700ft		1900ft		2500ft		2700ft	
	male	female	male	female	male	female	male	female
22 May	2	2	0	2	0	0	0	0
25	4	10	4	7	0	0	0	0
27	12	7	12	4	3	0	0	0
29	4	10	9	17	8	2	0	0
31	7	9	17	21	16	4	1	0
2 June	8	11	40	72	15	10	3	5
4	6	7	33	76	7	10	36	25
6	10	2	30	30	24	24	83	47
8	0	0	5	7	13	26	62	45
10	0	0	2	1	4	7	45	30
12	0	0	0	0	2	2	4	7
15	0	0	0	0	0	0	3	1
19	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0
Totals	53	58	152	237	92	85	237	160

Fig. I. The accumulated percentage pitfall catch at each site in 1970 plotted against date.

▲	Netherhearth	△	1700ft
▼	Above Netherhearth	▽	1900ft
●	Bog End (*Juncus*)	○	2700ft
■	Bog End (mixed-moor)		

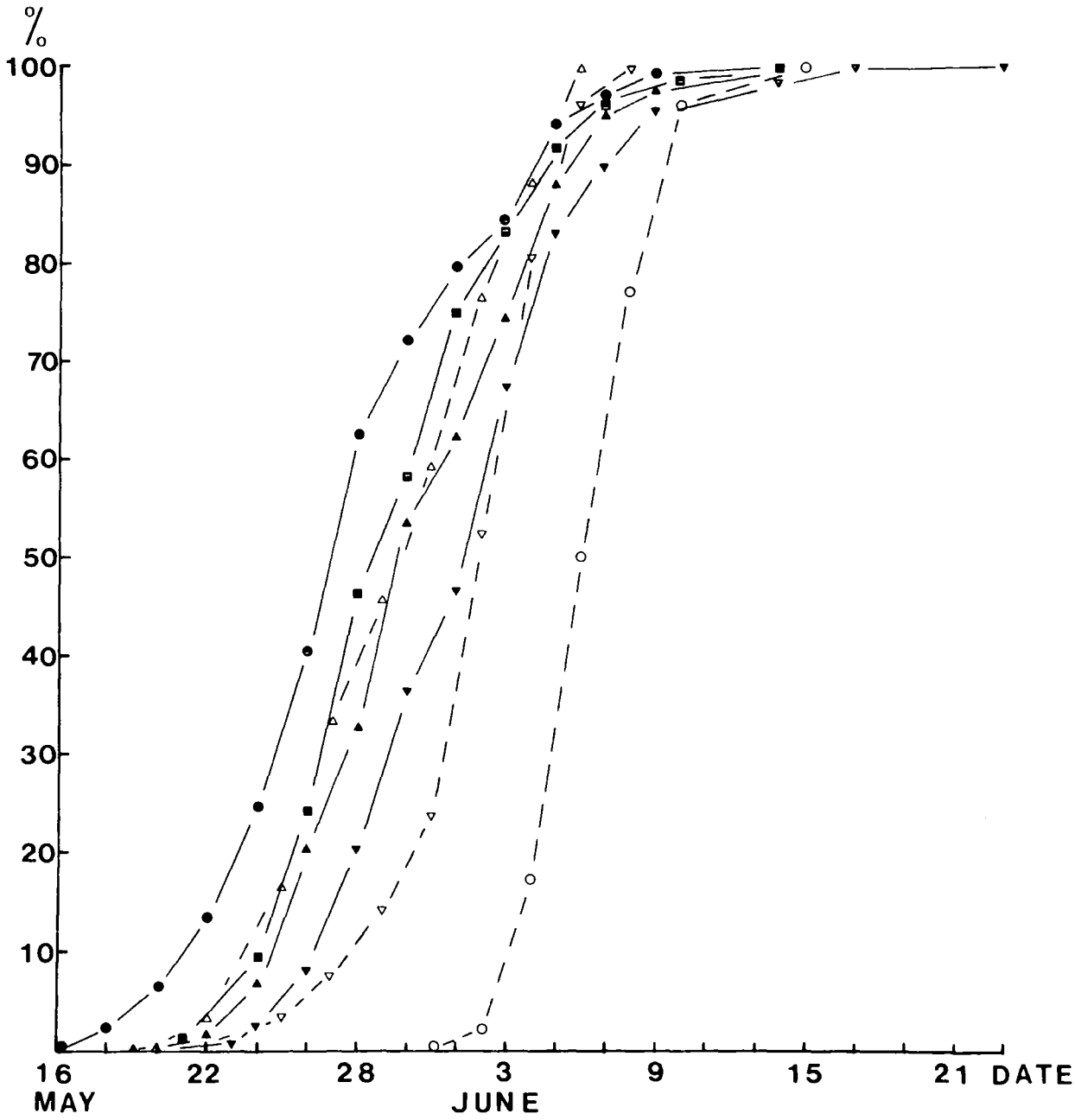
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TABLE IIIa. The daily catch of *T. subnodicornis* in twenty pitfalls* on each Moor House site in 1971

Date	Netherhearth		Above Netherhearth		Bog End (*Juncus*)		Bog End (mixed moor)	
	male	female	male	female	male	female	male	female
3 May	0	0	0	0	0	0	0	0
5	0	0	0	0	1	0	0	0
11	0	3	0	2	14	29	6	4
12	3	3	0	2	1	5	1	1
13	6	6	1	3	4	9	2	3
14	7	3	2	11	11	13	6	11
15	12	9	6	9	0	12	3	3
16	18	6	9	3	18	21	9	4
17	5	1	8	2	1	4	7	5
18	1	1	0	2	7	11	1	1
19	2	3	2	4	11	10	1	8
20	10	10	3	9	7	11	3	5
21	5	6	4	6	7	15	0	5
22	17	12	9	9	9	16	2	17
23	9	7	2	6	9	2	7	2
24	0	0	4	4	1	2	3	0
25	2	0	3	1	-	-	-	-
26	3	14	13	14	1	4	1	7
27	6	7	10	9	4	4	8	9
28	4	3	4	9	1	1	2	4
29	4	6	22	7	4	1	2	6
30	-	-	-	-	-	-	-	-
31	-	-	-	-	-	-	-	-
1 June	11	2	8	8	2	2	2	3
4	5	8	6	10	0	1	2	1
7	0	0	3	5	0	0	1	1
10	0	0	0	0	0	0	0	0
Totals	130	110	119	135	113	173	69	100

* 30 pitfalls on the Bog End (*Juncus*) site.

TABLE IIIb. The daily catch of T. subnodicornis in ten pitfalls on each Dun Fell site in 1971

Date	1700ft		1900ft		2700ft	
	male	female	male	female	male	female
8 May	0	0	0	0	0	0
12	4	7	9	8	0	0
13	0	2	4	6	0	0
14	2	2	5	3	0	0
15	1	9	6	16	3	1
16	2	2	14	9	3	0
17	1	0	1	5	0	0
18	0	1	4	9	1	0
19	1	2	4	9	2	0
20	0	3	4	13	8	2
21	0	2	8	12	5	2
22	1	4	7	17	6	2
23	7	5	12	15	4	0
24	0	1	0	1	2	4
25	2	1	1	3	4	2
26	0	2	1	9	3	13
27	2	0	3	23	15	9
28	0	0	3	5	12	5
29	0	0	1	5	8	13
30	0	0	2	13	12	15
31	0	0	1	3	5	4
1 June	0	1	2	2	7	8
2	0	0	1	11	2	20
3	0	0	0	6	5	14
4	0	0	1	5	6	10
5	1	0	0	1	3	7
6	0	0	0	0	0	1
7	0	0	0	0	0	2
8	0	0	0	0	0	4
9	0	0	0	1	0	3
10	0	0	0	1	0	1
11	1	0	1	0	0	2
12	0	0	0	0	0	0
13	0	0	0	0	0	0
14	0	0	0	0	0	0
15	0	0	0	1	1	0
16	0	0	0	0	0	0
Totals	25	44	95	214	117	144

Fig. II. The accumulated percentage pitfall catch at each site in 1971 plotted against date

▲	Netherhearth	△	1700ft
▼	Above Netherhearth	▽	1900ft
●	Bog End (*Juncus*)	○	2700ft
■	Bog End (mixed-moor)		

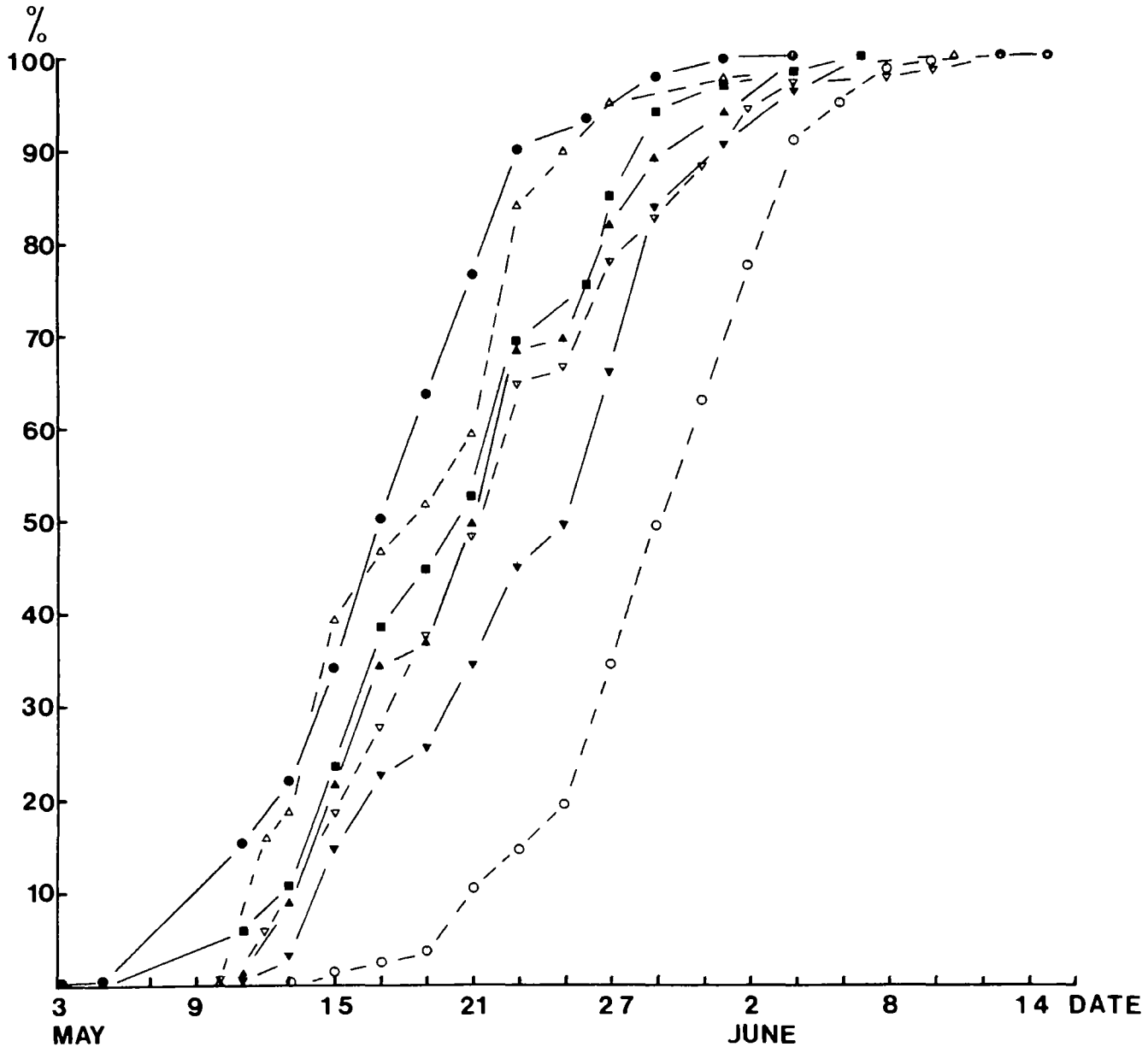
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TABLE IVa. The catch of *T. subnodicornis* in twenty pitfalls usually inspected on alternate days, on the Moor House sites in 1972

Date	Netherhearth		Above Netherhearth		Bog End (*Juncus*)		Bog End (mixed moor)	
	male	female	male	female	male	female	male	female
10 May	0	0	0	0	0	0	0	0
12	0	0	0	0	0	10	1	2
16	1	3	1	1	5	20	0	2
18	2	13	0	3	4	25	1	3
19	1	2	1	2	2	4	3	1
22	15	39	7	19	37	46	17	29
23	8	10	3	8	5	14	1	4
24	12	8	9	4	10	12	8	10
26	10	11	5	3	6	11	23	4
28	4	6	2	3	1	1	4	0
30	4	8	4	5	14	12	8	3
1 June	2	9	1	9	1	3	0	2
3	3	3	5	4	0	5	1	0
5	3	6	5	8	0	0	1	5
7	2	0	5	2	0	1	0	2
9	1	2	2	2	1	1	5	2
12	0	1	0	2	1	2	0	2
14	0	0	0	0	0	0	0	3
18	0	0	0	0	0	0	0	0
Totals	68	121	50	75	87	167	73	74

TABLE IVb. The daily catch of *T. subnodicornis* in ten pitfalls on each site on Dun Fell in 1972

Date	1700ft		1900ft		2700ft	
	male	female	male	female	male	female
14 May	0	0	0	0	0	0
18	0	3	1	4	0	0
19	0	0	0	0	0	0
20	1	0	1	0	0	0
21	0	4	0	1	0	0
22	0	1	1	3	0	0
23	0	3	2	7	0	0
24	0	3	3	8	0	0
25	0	1	0	1	0	0
26	0	0	0	0	2	0
27	0	1	0	1	0	0
28	0	0	1	0	0	0
29	0	1	1	6	0	0
30	0	0	0	1	3	1
31	1	2	0	0	0	0
1 June	1	2	0	1	0	0
2	0	3	0	2	0	0
3	0	0	0	0	1	3
4	0	0	1	4	1	1
5	0	0	0	3	3	2
6	0	1	1	1	0	1
7	0	0	0	1	1	1
8	0	1	0	2	2	3
9	0	0	0	2	5	2
10	0	0	0	0	2	1
11	0	0	0	1	2	1
12	0	0	0	1	2	6
13	0	0	0	0	3	2
14	0	0	0	0	1	5
15	0	0	0	1	1	3
16	0	0	0	1	0	4
17	0	0	0	0	0	3
18	0	0	0	1	0	0
19	0	0	0	0	0	0
Totals	3	26	12	53	29	39

Fig. III. The accumulated percentage pitfall catch at each of the Moor House sites in 1972 plotted against date.

▲ Netherhearth

▼ Above Netherhearth

● Bog End (*Juncus*)

■ Bog End (mixed-moor)

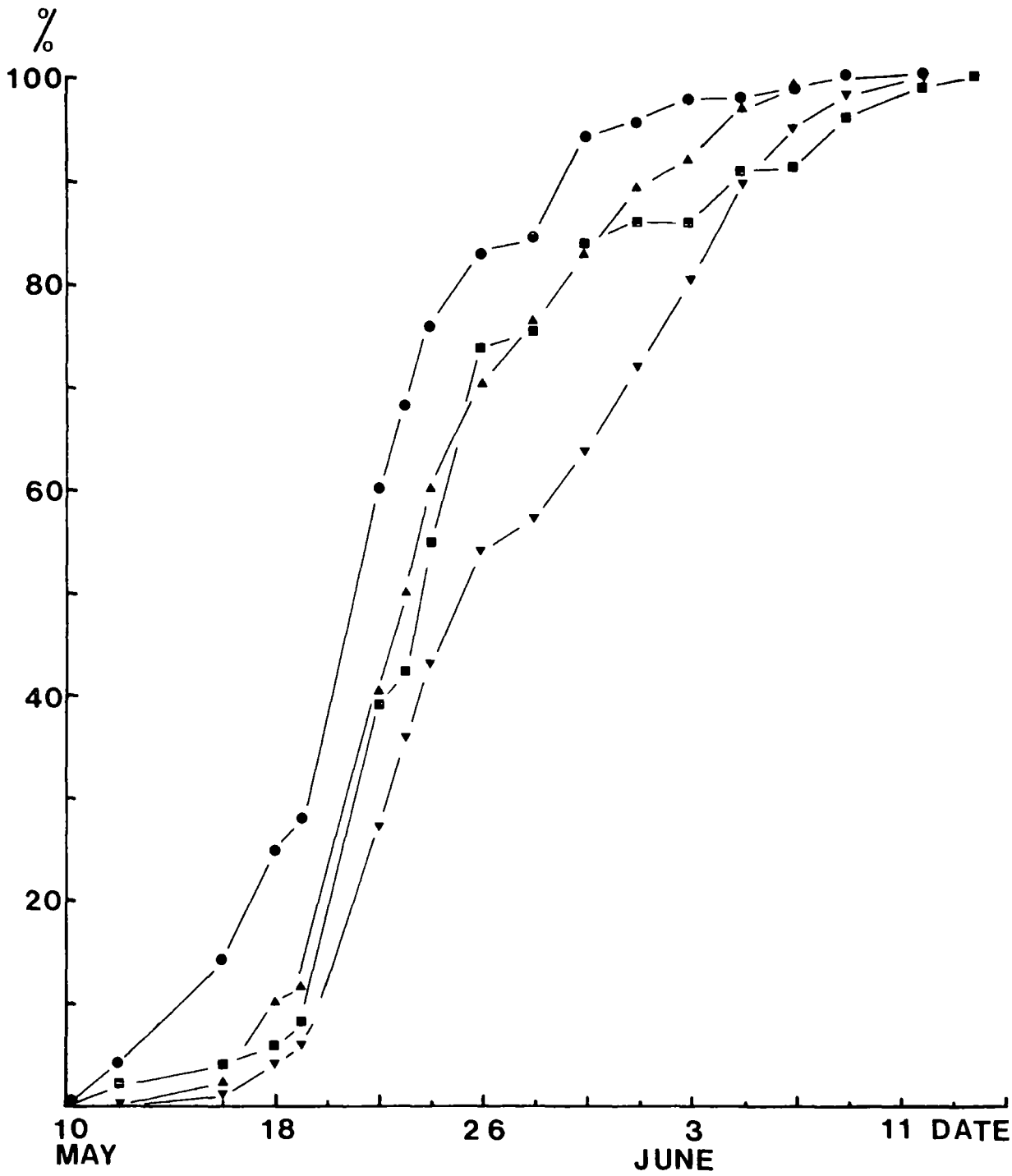
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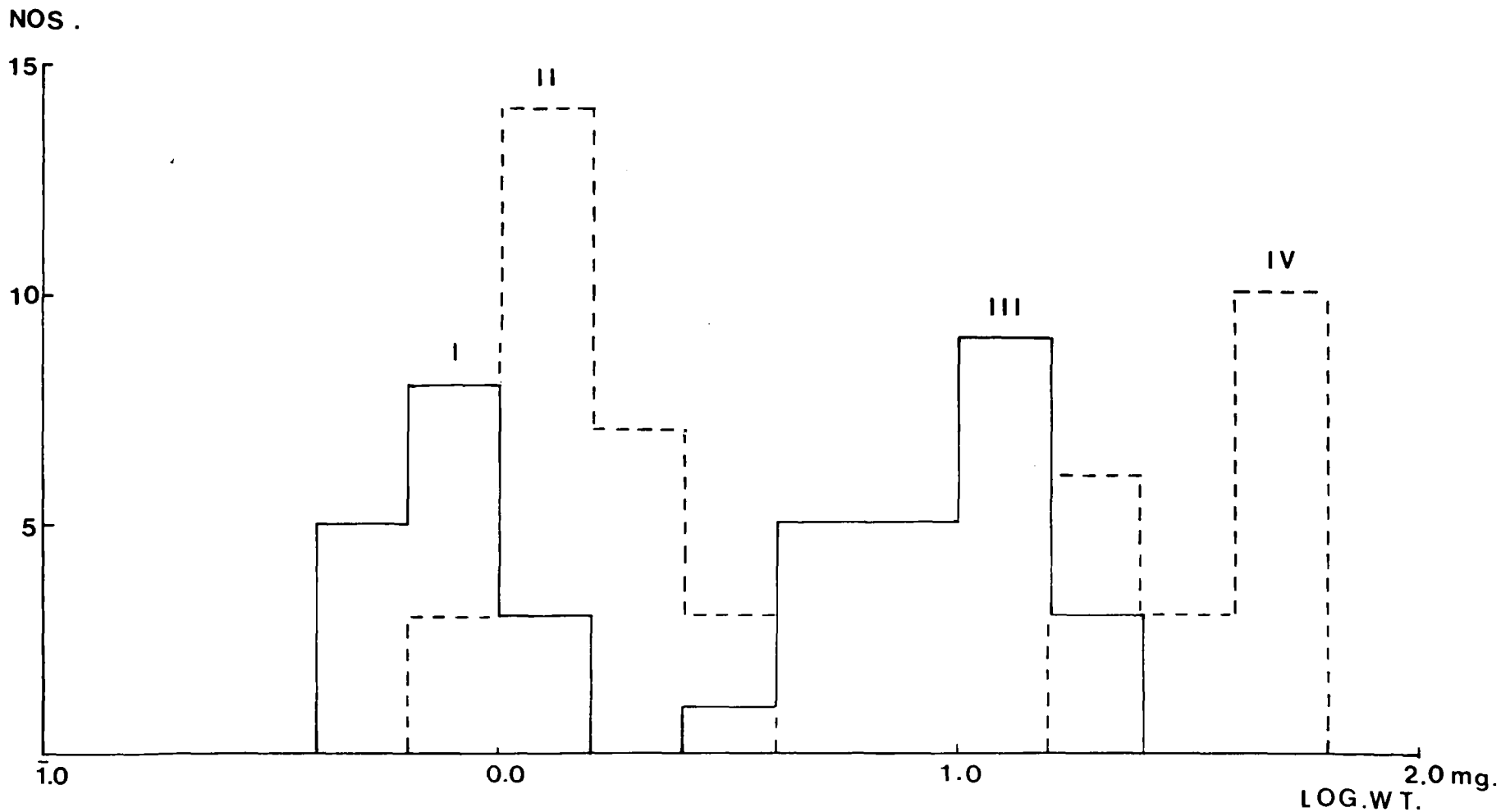
TABLE V. The mean weights of larvae reared on different temperature regimes in 1971

Date when weighed	25°C N	25°C Mean wt mg ± S.E.	20°C N	20°C Mean wt mg ± S.E.	15°C N	15°C Mean wt mg ± S.E.	10°C N	10°C Mean wt mg ± S.E.	5°C N	5°C Mean wt mg ± S.E.
12 July	9	2.66 ± 0.54	10	1.85 ± 0.035	9	2.32 ± 0.21	10	1.17 ± 0.073	6	0.79 ± 0.032
4 Aug	12	19.35 ± 1.94	12	12.06 ± 1.61	14	11.9 ± 1.22	14	4.28 ± 0.303	14	1.86 ± 0.17
18	18	40.71 ± 3.86	17	27.53 ± 2.39	17	24.76 ± 2.38	20	11.42 ± 1.35	13	2.49 ± 0.22
31	-	-		-	16	44.73 ± 4.46	-	-	-	-
2 Sept	17	56.92 ± 4.25	14	35.46 ± 3.30	-	-	18	20.38 ± 1.15	14	3.65 ± 0.24
15	13	62.52 ± 5.55	12	61.80 ± 5.37	12	71.18 ± 9.20	14	38.72 ± 4.71	8	5.26 ± 0.84
5 Oct	-	-	13	60.31 ± 3.17	8	97.83 ± 10.34	13	68.32 ± 1.44	17	13.37 ± 1.40
19	-	-	8	73.03 ± 2.74	17	84.55 ± 5.92	12	79.08 ± 6.25	13	18.63 ± 2.22
27	-	-	-	-	-	-	-	-	7	31.44 ± 4.54
22 Nov	-	-	-	-	-	-	-	-	10	46.99 ± 2.78
6 Dec	-	-	-	-	-	-	-	-	10	54.82 ± 1.08

TABLE VI. Distribution of weights and spiracular disc diameter in a sample of larvae

Instar	I	II		III		IV	
	wt (mg)	wt(mg)	diam.sp. disc(mm)	wt(mg)	diam.sp. disc(mm)	wt(mg)	diam.sp. disc(mm)
	0.48	0.69	0.88	3.04	1.75	18.0	2.60
	0.55	0.86	0.88	4.06	1.88	18.1	2.56
	0.58	0.87	0.86	5.62	1.69	18.2	2.60
	0.60	1.04	1.06	5.74	1.88	19.0	2.56
	0.60	1.10	0.88	6.14	1.88	23.5	2.88
	0.66	1.10	1.00	6.30	2.12	24.1	2.80
	0.69	1.12	0.88	7.76	1.56	27.0	2.75
	0.77	1.16	1.00	7.82	2.12	33.2	2.63
	0.78	1.21	1.06	8.78	1.62	35.4	2.75
	0.83	1.21	1.00	8.86	1.88	36.5	2.56
	0.88	1.27	0.86	9.30	1.56	39.9	2.75
	0.92	1.28	0.88	10.00	1.63	45.3	2.56
	0.97	1.28	0.86	10.30	1.81	45.4	2.62
	1.01	1.31	0.86	11.25	1.88	46.8	2.63
	1.04	1.37	0.94	11.95	1.69	49.4	2.56
	1.06	1.43	1.00	13.05	1.88	54.5	2.80
		1.48	1.00	13.30	1.62	55.0	2.75
		1.59	1.00	14.0	1.62	58.2	2.56
		1.60	1.00	14.45	1.75	58.9	2.63
		1.69	1.00	14.60	1.88		
		1.70	1.06	17.05	1.94		
		1.83	1.00	21.00	1.75		
		1.92	1.06	21.80	1.75		
		2.03	1.00				
		2.84	1.00				
		3.34	1.06				
		3.56	0.94				

Fig. IV. The distribution of weights within each larval instar for a sample of 85 larvae.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I
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2.0 mg.
LOG.WT.

TABLE VII. Regression parameters for the regression of log increment against log weight (increment against weight for larvae above 20mg) for larvae in the weight ranges specified kept at different temperatures and in two different photoperiods

Wt.range	Temperature °C	L:D; 18 : 6, N	a	byx	t	L:D; 6 : 18, N	a	byx	t
0 - 3mg	5	42	+0.0229	-0.0057	-0.52	-	-	-	-
	7	67	+0.0468	-0.0026	-2.31*	-	-	-	-
	10	61	+0.0247	-0.0009	-0.58	21	+0.0442	-0.0121	-0.98
	15	29	+0.0644	-0.0254	-2.00*	-	-	-	-
	20	22	+0.1079	-0.0584	-2.62*	-	-	-	-
3 - 10mg	7	32	+0.0005	+0.0048	+0.51	-	-	-	-
	10	37	+0.0222	-0.0021	-0.09	35	+0.0060	+0.0100	+0.10
	15	31	+0.0765	-0.0309	-2.68**	-	-	-	-
	20	30	+0.0491	+0.0410	+1.37	15	+0.0496	-0.0140	-0.73
10 - 20mg	7	21	+0.0398	-0.0137	-0.67	-	-	-	-
	10	17	+0.1376	-0.0563	-2.65**	19	+0.0407	-0.0122	-0.68
	15	19	+0.0820	-0.0296	-1.11	-	-	-	-
	20	33	+0.1283	-0.0519	-3.42**	22	+0.1330	-0.0535	-2.49*
Above 20mg	7	16	+0.546	+0.0058	+0.49	-	-	-	-
	10	49	+0.709	+0.0046	+0.80	25	0.705	+0.0104	+1.03
	15	25	+1.606	-0.0131	-0.98	-	-	-	-
	20	64	0.537	+0.0012	+3.26**	60	0.506	+0.0021	+6.33**

't-tests have been carried out on the difference of the slope from zero. * p 0.05, ** p 0.01

TABLE VIII. Analysis of variance on the daily log weight gains (daily weight gains in mg for larvae heavier than 20mg) comparing the variation for an individual and between individuals

Wt range	Temp. °C	Photoperiod L:D	Source of variation	Sum of sqs log x 10^3	d.f.	Mean sq log x 10^3	F
0-3 mg	5	18: 6	Between larvae	226304	15	15087	1.36
			For one larva	289170	26	11122	
	7	18: 6	Between larvae	176780	14	12627	0.26
			For one larva	2437037	51	47785	
	10	18: 6	Between larvae	261094	18	14505	0.64
			For one larva	958620	42	22824	
	10	6:18	Between larvae	96380	15	6425	1.92
			For one larva	20022	6	3337	
	15	18: 6	Between larvae	345250	14	24661	0.87
			For one larva	398465	14	28462	
3-10mg	7	18: 6	Between larvae	44284	10	4428	0.71
			For one larva	130740	21	6226	
	10	18: 6	Between larvae	215121	11	19556	0.56
			For one larva	872910	25	34916	
	10	6:18	Between larvae	187828	13	14448	0.65
			For one larva	461826	21	21992	
	15	18: 6	Between larvae	78275	11	7116	0.48
			For one larva	282993	19	14894	
	20	18: 6	Between larvae	202857	10	20286	0.31
			For one larva	1252167	19	65904	
10-20mg	7	18: 6	Between larvae	28168	10	2817	0.33
			For one larva	86301	10	8630	
	15	18: 6	Between larvae	132195	9	14688	2.99
			For one larva	44220	9	4913	
	20	18: 6	Between larvae	134201	15	8947	1.27
			For one larva	119627	17	7037	
	11	6:18	Between larvae	47091	12	3924	0.44
			For one larva	79627	9	8847	
Above 20mg	7	18: 6	Between larvae	0.433	3	0.144	0.732
			For one larva	1.576	8	0.197	
	10	18: 6	Between larvae	2.401	13	0.185	0.533
			For one larva	11.426	33	0.346	
	10	6:18	Between larvae	1.132	10	0.1132	0.262
			For one larva	6.050	14	0.4322	

Continued overleaf..

TABLE VIII. (Contd.)

Wt range	Temp °C	Photoperiod L:D	Source of variation	Sum of sqs log x 10^3	d.f.	Mean sq log x 10^3	F
Above 20mg (Contd.)	15	18: 6	Between larvae	11.237	7	1.605	1.781
			For one larva	13.518	15	0.901	
	20	18: 6	Between larvae	3.129	13	0.241	1.696
			For one larva	6.955	49	0.142	
	11	6:18	Between larvae	3.1588	13	0.2430	1.637
			For one larva	6.6809	45	0.1485	

TABLE IX. Dates of pupation of larvae brought in from the field and kept at two different temperature regimes on a photoperiod of L:D; 6:18 before being transferred to 15°C and a photoperiod of L:D; 18:6 on 14 December 1972

Pupation Date	Larvae brought in from field 14 Nov 72 and kept at 15°C until 14 Dec 1972		Larvae brought in from field on 28 Nov 72 and kept at 10°C until 14 Dec 1972	
	♂	♀	♂	♀
28 Dec	0	0	1	0
30	0	0	2	0
1 Jan	0	0	0	1
3	1	3	1	1
5		1	1	1
7	1	2	1	3
9	1	1	1	0
11	0	0	1	0
13	*11p	0	0	0
15	1	1	0	0
17	1	0	0	0

* started to pupate but failed to shed larval skin completely

TABLE X. Respiration rates of T. subnodicornis larvae at 15°C

	larval wt (mg)	µl O_2/hr /animal	µl O_2/hr /g wet wt
Larvae reared in the laboratory			
1. Reared at 5°C			
	42.9	15.27	355.9
	25.0	6.35	254.0
	17.2	5.55	322.5
	34.3	9.74	284.0
	51.7	8.30	160.5
	32.3	5.58	172.9
	16.7	2.93	175.5
	29.6	4.05	136.9
	19.8	4.32	218.3
	13.6	2.62	192.8
	37.6	5.80	154.4
4. Reared at 15°C acclimatised at 5°C for 41 days			
	75.3	17.06	226.6
	38.6	7.79	201.8
	54.3	10.55	194.3
	52.7	6.99	132.6
Larvae brought in from the field			
5. Acclimatised at 5°C for 23 days	109.8	16.08	146.4
	61.4	8.22	133.9
	93.6	14.39	153.6
	94.7	15.05	158.9
	72.8	9.97	137.0
	84.1	10.97	130.2
3. Acclimatised at 15°C for 17 days	74.9	11.38	152.0
	76.2	11.62	152.7
	73.7	11.87	161.0
	100.7	14.80	147.0
	76.6	11.32	148.0
	67.1	9.05	135.0
	71.5	8.49	118.6
	136.4	16.89	123.7
6. Tested immediately	73.7	10.92	148.1
	70.4	10.47	148.7
	59.6	8.10	135.9
	83.8	13.99	166.9

Continued overleaf....

TABLE X. (Contd.)

Larvae reared in the laboratory				Larvae brought in from the field			
	larval wt (mg)	µl O_2/hr /animal	µl O_2/hr /g wet wt		larval wt (mg)	µl O_2/hr /animal	µl O_2/hr /g wet wt
2. Reared at 15°C				6. Tested immediately (Contd.)			
	92.0	14.3	155.8		96.0	12.91	134.4
	61.4	8.1	131.9		45.6	7.72	169.3
	97.1	14.5	148.8		47.3	6.58	139.1
	83.6	10.4	124.1		48.4	11.50	237.6
	78.2	9.2	117.4		53.7	7.71	143.5
	77.9	9.8	125.4		58.1	13.47	231.8
	117.3	15.2	129.3		81.6	16.58	203.2
	73.8	10.5	142.1		48.5	7.45	153.5
	75.9	12.9	170.3				

TABLE XI. Fourth instar larval density measurements made in spring and autumn each year on the Moor House sites

Date	Site	No. of cores 5.7cm* radius	Mean larvae /core	larvae /m^2	S.E.
Spring 1969					
Jan - Apr	Netherhearth	40	0.325	40	11
	Above Netherhearth	40	0.175	22	8
	Bog End (Juncus)	40	0.175	22	8
	Behind House	40	0.125	15	7
	Bog End (mixed moor)	40	0.300	37	11
Winter 1969					
9 Dec	Netherhearth	40	0.65	64	13
24 Jan	Above Netherhearth	40	0.35	34	9
4 Nov	Bog End (Juncus)	50	0.36	35	8
20 Jan	Bog End (mixed moor)	50	0.38	37	8
Spring 1970					
5 Apr	Netherhearth	36	0.56	55	12
17 Mar	Above Netherhearth	80	0.33	32	6
5 Apr	Bog End (Juncus)	60	0.33	33	7
5 Apr	Bog End (mixed moor)	60	0.28	28	7
Winter 1970					
1 Sep & 10 Nov	Netherhearth	40	0.18	17	7
1 Sep	Above Netherhearth	40	0.20	20	7
20 Oct	Bog End (Juncus)	30	0.27	26	9
26 Aug & 26 Nov	Bog End (m.moor)	80	0.61	60	9
22 Sep	Trout Beck	19	0.89	88	21
Spring 1971					
23 Mar	Netherhearth	60	0.12	11	4
31 Mar	Above Netherhearth	60	0.22	21	6
10 Feb	Bog End (Juncus)	60	0.20	20	6
13 Feb	Behind House	60	0.32	31	7
5 Apr	Bog End (mixed moor)	60	0.37	36	8
10 & 16 Mar	Trout Beck	85	0.32	31	6
Winter 1971					
14 Oct	Netherhearth	30	0.50	49	13
14 Oct - 9 Dec	Above Netherhearth	72	1.18	116	13
4 Oct	Bog End (Juncus)	30	0.37	36	11
30 Oct	Behind House	90	1.09	107	11
9 Nov	Bog End (mixed moor)	30	0.23	23	9
9 Nov	Trout Beck	40	0.30	30	8
Spring 1972					
13 Apr	Netherhearth	40	0.13	12	5
13 Apr	Above Netherhearth	40	0.10	10	5
22 Mar	Bog End (Juncus)	40	0.43	42	10
22 Mar	Behind House	60	0.52	51	9
22 Mar	Bog End (mixed moor)	40	0.38	37	9
13 Apr	Trout Beck	20	0.25	25	11

* 5.1cm in 1969

TABLE XII. Number of adults caught in 20 pitfalls on each of the Moor House sites in each year

	Year	Site	♂ catch	♀ catch	Total
*	1969	Netherhearth	106	114	220
	1969	Above Netherhearth	62	174	236
	1969	Bog End (Juncus)	102	106	208
	1969	Bog End (mixed moor)	64	36	100
	1969	Behind House	56	74	130
	1970	Netherhearth	231	158	390
	1970	Above Netherhearth	94	143	237
	1970	Bog End (Juncus)	131	106	237
	1970	Bog End (mixed moor)	81	176	257
	1970	Trout Beck	149	211	360
	1971	Netherhearth	130	110	240
	1971	Above Netherhearth	119	135	254
	1971	Bog End (Juncus)	53	93	146
	1971	Bog End (mixed moor)	69	100	169
	1971	Trout Beck	37	73	110
	1971	Behind House	36	104	140
	1972	Netherhearth	68	121	189
	1972	Above Netherhearth	50	75	125
	1972	Bog End (Juncus)	87	167	254
	1972	Bog End (mixed moor)	73	74	147
	1972	Trout Beck	34	36	70
	1972	Behind House	50	104	154

* For 1969 the total figures have been multiplied by 2 as there were only 10 pitfalls at each site

TABLE XIII. The numbers of T. subnodicornis caught in ten pitfall traps on the altitude sites on Dun Fell

Year	1700ft			1900ft			2500ft			2700ft		
	♂	♀	total	♂	♀	total	♂	♀	total	♂	♀	total
1967	86	51	137	303	293	596	200	222	422	156	50	206
1970	53	58	111	152	237	389	92	85	177	237	160	397
1971	25	47	72	91	207	298	-	-	-	117	145	262
1972	3	27	30	12	52	64	-	-	-	29	38	67

Fig. V. The distribution of male and female wing lengths of T. subnodicornis caught on the 2500ft site in 1967 plotted on normal probability paper

■ male wing length (N = 199)

□ female wing length (N = 222)