THE FOOD OF THE RED GROUSE, LAGOPUS LAGOPUS SCOTICUS, WITH PARTICULAR ATTENTION TO THE ARTHROPOD COMPONENT IN THE DIET.

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CONTENTS

INTRODUCTION

The aim of this study is to resolve the controversy which has arisen concerning the role of arthropods in the diet of the red grouse; Lagopus lagopus scoticus. According to earlier workers, eg. Collinge (1924-27), the diet of the red grouse is supplemented by animal material, often insects. In more recent studies however, prior to 1975, the arthropod component of the diet was considered to be of little importance. (Jenkins, Watson and Miller 1963, 1967; Miller, Watson and Jenkins 1970; Moss 1967, 1969, 1972; Savory 1974). These more recent studies were carried out on the low altitude, dry, heath-type moors (c. 150-300m), typical of the Banchory area in north-east Scotland. In 1975 however, a paper was published by Butterfield and Coulson which reported that adult red grouse ate arthropods at much higher levels than had previously been thought. Their study was carried out at the Moor House National Nature Reserve; an area of blanket bog in the high Pennines. They suggested that arthropods could be an important source of nutrients to the red grouse on high altitude blanket bog. In the same paper by Butterfield and Coulson, it was reported that the level of arthropods consumed by the adult red grouse on another area of dry, low-altitude, heath-type moor; Muggleswick Common, County Durham, was very much lower.

This study examines the role of the arthropods in the diet of the red grouse at a variety of sites of different altitude, from low altitude heath-type moors to high altitude blanket bog. The sites cover a range of altitude from 280m to 550m .

The examination of the diet was carried out by faecal analysis. Undigested cuticular fragments of plants can be identified in the faeces by the appearance of cell walls and the patterns of cells. Arthropod fragments can also be distinguished. Sampling was carried out from May to August 1979. At the same time, pitfall traps were used at the sites to give an indication of arthropod abundance.

The adult red grouse feeds primarily on *Calluna*. Savory (1974) found that the shoot tips and flowers of *Calluna* formed at least 90% of the diet by dry weight for most of the year. In June, July and August, the diet was supplemented by the flowers, leaves and seeds of many other plants and the proportion of *Calluna* dropped to 60-80%. Plants frequently taken to supplement the diet included: *Vaccinium myrtilus*, *Erica tetralix*, *Erica cinerea* and *Rumex acetosella*.

Eastman and Jenkins (1970), from the monthly analysis of faeces, found that the proportion of *Calluna* fragments averaged 74%, remaining fairly constant throughout the year. Recent studies by Jenkins, Watson and Miller 1963, 1967; Miller, Watson and Jenkins 1970; Moss 1967, 1969, 1972, fail to mention any arthropod component in the diet of the adult red grouse.

Eastman (1964) found arthropod fragments in adult droppings from May to October but only at very low levels. At Garrol Hill, a well- drained, nutrient- poor area near Banchory, Kincardineshire, the invertebrate component of the diet was only 0.14%. On a second moor in the same area; Tilquhillie, which is mineral-rich and much wetter than Garrol Hill, the invertebrate component was even lower, forming 0.05% of the food items examined.

Savory (1974) gives similarly low figures for arthropods found in the crops of birds shot in the Kerloch area, north-east Scotland. Arthropoda were found during the months from April to July; by mean percentage dry weight, the arthropod component was highest in July at 0.9% and for the other three months was $\leqslant 0.2\%$.

This evidence conflicts with earlier studies. Collinge (1924-27) found from the analysis of crops, that animal material formed 22% by weight of the food consumed. Wilson and Leslie, in the Committee of Inquiry on Grouse Disease (Lovat 1911), state that insects are taken as a substitute for heather. They record that,

" Occasionally one finds that even an adult bird has eaten scores of small black gnats."

Butterfield and Coulson (1975), using faecal analysis on material collected from the Moor House National Nature Reserve, found high levels of insect material in adult red grouse droppings. The remains of the tipulid, Tipula subnodicornis, Zetterstedt, were abundant in droppings collected during May, whilst in late May to early June, fragments of the smaller tipulid, Molophilous ater, Meigen, were found. In 3% of the cases, it was found that tipulid remains formed over half of the items in the droppings. During the period from mid May to early June, 98% of the droppings analysed were found to contain fragments of adult tipulids.

Butterfield and Coulson (1975) also found evidence of selection for insects by the adult red grouse. The crop of an adult bird shot at Moor House in mid October 1970, was found to contain 495 adults of the rare tipulid, Tipula gimmerthali Lackschewitz, representing an ingestion of 12g live weight. A few small pieces of Calluna and Vaccinium myrtilus were also present in the crop. The virtual lack of plant material and the high number of rare tipulids of restricted habitat indicates a degree of selectivity on the part of the red grouse.

In late April and early May, the red grouse hens lay eggs which are incubated for 3 weeks. After the chicks hatch, they are cared for by both parents, at the same time, territorial activity almost ceases. It has been suggested that the adult birds may take the chicks to wet flushes to feed and the family often leave the territory from June to August while the chicks grow and the adults moult.

Evidence concerning the diet of red grouse chicks is less equivocal than that of the adult birds. Savory (1975), examined 211 crops of red grouse chicks up to 5 weeks old and found that Calluna shoot tips and arthropods were the only foods that the chicks took frequently. Calluna made up the bulk of the diet by dry weight; 85%, followed by the arthropod component which was 4.1% by dry weight. The frequency of occurrence of Calluna and arthropods in the droppings was 99% and 88% respectively.When the chicks reached the age of 2-3 weeks, the quantity of arthropods in their diet dropped markedly. Their diet was supplemented with such plants as Vaccinium, Juncus squarrosus, Carex and Pohlia mutans. Savory found that Diptera made up the largest part of the invertebrate component in the diet; Tipulidae being the most important family, in particular, Molophilous ater. This finding agrees with that of Grimshaw, in the Committee of Inquiry on Grouse Disease (Lovat 1911), who also found this species in the crops of red grouse chicks.

The environmental conditions at the four sampling sites in this study are very different and consequently the insect species available to the red grouse at the sites also vary markedly. By comparison with lowland Britain, the fauna at Moor House is sparse in numbers, however this reduction does not occur equally in all the animal groups. The Diptera are well represented at Moor House. Nelson (1965) recorded that 96% of all invertebrates caught on sticky traps were Diptera, whilst they formed 63% of the catch in liquid-filled pitfall traps and 60% of the total species taken. The dominance of the Diptera is typical of Arctic and sub-Arctic fauna and the success of the group in such conditions relates to their preference for and adaptation to wet or semi-aquatic environments. They are also able to remain active at low temperatures.

Richards (1926) recorded a much more diverse insect fauna associated with the low altitude Calluna heaths than is found at Moor House. On low altitude heaths the Coleoptera and the Lepidoptera outnumber the Diptera in the number of species.

At Moor House many of the insects have sub-Arctic affinities. The short active season of the sub-Arctic results in the majority of insect species using the spring rise in temperature or lengthening photoperiod to initiate pupation. On the blanket bog at Moor House, this results in a vast 'spring' emergence, with little additional emergence through the year. In contrast, insect species with southern affinities, frequently the low altitude forms, show a much more even distribution of emergence during the spring and summer months.

The availability of insects to red grouse at the four sampling sites therefore differs not only in species composition but also in the time of year at which they emerge.

MATERIALS AND METHODS

I (i) Collection of Droppings

Red grouse produce two types of droppings; soft caecal droppings which are deposited as amorphous residues and secondly hard droppings of distinctive shape from the main gut. These hard droppings contain recognisable, undigested cellular fragments. Both types of droppings are distinct from one another and from other droppings found on the site. Only hard droppings were collected for analysis.

Droppings were collected from the four main study areas at approximately weekly intervals from May to July 1979, with a final collection in mid August. On each occasion, 30 adult red grouse droppings were collected. Fresh droppings were collected by walking over the moor, through the territories of many birds, taking one dropping from each group of faeces. Fresh droppings can readily be told from old ones; the former are usually yellow-green in colour although the colour may vary with the food eaten, and are partially coated with white urates. Older droppings are brown in colour, lacking in urates, with exposed woody fibres.

Red grouse chick droppings are recognisable by their small diameter. When chick droppings were found, they were collected as a paired sample with the adult dropping to allow a comparison between the two.

A single collection of droppings was also made at other sites of varying altitude and climatic conditions.

in the North York Moors in late June 1979, and in the Swaledale area of Yorkshire in early July 1979. These additional sites were chosen to include a range of moorland types, from dry low altitude heath-type moors to high altitude blanket bog. The data from the additional sites provide furthur information on the arthropod levels in droppings from different moorland types and can be compared with the data from the four main sites.

I (ii) The Analysis of Droppings

Each dropping was reduced to a length of 3cm before analysis. The dropping was then soaked in water and its contents spread over a Petri dish. The dropping was examined using a microscope and for every dropping, the items in four $1cm^2$ areas were identified as far as was possible. In each dropping , a minimum of 100 items was identified. The chick droppings were treated in a similar manner. In this way, the contents of each dropping were attributed to various categories, eg *Juncus squarrosus*, Arthropoda etc.

The different types of fragments were identified by the appearance of the epidermal cell walls and the patterns formed by groups of cells; each species having characteristic cell shapes and patterns. To facilitate identification, reference slides of epidermal tissues were made from plants collected from the sampling areas.

Some items were in an advanced state of digestion and could not be identified, others were woody items which could not be assigned to any particular category. These items were included in an ' Unidentified ' category.

Arthropod fragments are easily distinguished from the plant material in droppings. Insect cuticle is a different colour and frequently bears bristles. The most heavily cuticularised parts of the arthropods survive the digestive process and are the parts that are most frequently found, eg. legs and palps. Insect wings and the eggs of some Tipulidae can also be distinguished. The soft parts of the arthropods however, are easily digested and are not recognisable in the droppings.

II Pitfall Traps

Pitfall traps were used to obtain a measure of arthropod abundance at the four main sites. Ten pitfall traps were laid in a straight line at 2m intervals at each site. The contents of the traps were emptied and identified at approximately weekly intervals.

III Measurement of Soil Moisture Content

The four main sites cover an altitude range from 280 - 550m, consequently the hydrology of the areas varies considerably. In order to obtain a measure of the soil moisture , 10cm soil cores were taken at each site. The cores were air dried and the percentage weight loss due to water was calculated. At the Waskerley site, the feeding area is intersected by drainage ditches and the soil moisture content is markedly different from that of the main feeding area. Soil cores were also taken from these wet flushes.

The values of soil moisture content are not absolute, the measurements were made for comparative purposes.

DESCRIPTION OF SITES

Four different sampling areas were chosen so that, among them they included a range of altitude and consequently different climatic conditions. This enables a comparison to be made between the diets of the red grouse living in different environmental conditions.

Ten furthur sites were selected from which to make a single collection of grouse droppings, again these sites included a range of altitude and climatic conditions.

Site 1: Bogend, Moor House National Nature Reserve.
Nat. Grid Ref : NY 758328
Altitude : 551m

The Moor House Reserve lies on the high Pennines. Most of the land is covered by deep peat and the area has an average rainfall of 1981mm. The annual average temperature is low; 5°C, and as a consequence of this and the high rainfall, the peat soils are almost permanently waterlogged. The vegetation at Bogend is ' blanket bog ', with *Calluna*, *Eriophorum* and *Sphagnum* as co-dominant species.

Soil moisture content : 89%

Site 2 : Muggleswick Common High, Co. Durham.
Nat Grid Ref : NZ 003449
Altitude : 476m

This is an exposed site at the highest point of Muggleswick Common. The vegetation is dominated by Calluna, interspersed with small patches of Vaccinium myrtillus. There are areas of bare peat with pools of standing water.

Soil moisture content: 68%

Site 3 : Waskerley, Co. Durham.

Nat. Grid Ref. : NZ 014446

Altitude: 411m

This site is very near Muggleswick Common. The vegetation is dominated by Calluna, with some patches of Juncus effusus. The area is intersected by drainage channels which contain standing water. These wet flushes are dominated by Sphagnum and J. effusus, with some Calluna, J. squarrosus and Polytrichum. This site was chosen to see if the wetness of the area, although at a lower altitude than Bogend or Muggleswick High, had any effect on the levels of arthropods eaten.

Soil moisture content, main area : 57%

Soil moisture content, wet flushes : 73%

Site 4 : Muggleswick Common Low, Co. Durham.

Nat. Grid Ref. : NZ029499

Altitude : 280m

This is a sheltered area at the bottom of Muggleswick Common. The vegetation is dominated by Calluna with bracken, Pteridium, approaching co-dominance. There are some small patches of Vaccinium myrtillus.

Soil moisture content : 34%

The data for these four sites and the remaining sites in the North York Moors and Swaledale area are summarised in Table 1.

Table 1 : Description of Sampling Sites.

Site	Grid ref.	Altitude (m)	Annual Rainfall (mm)	Peat Depth (cm)	Vegetation
Bogend	NY758328	551	2010	7100	Blanket bog
Muggleswick Common High	NZ003449	476			*Calluna*
Waskerley	NZ014446	411	950	7	*Calluna* *J. effusis*
Muggleswick Common Low	NZ029499	280			*Calluna*, bracken
Yarlsey Moss	NZ750007	305	1020	13	*Calluna*
Bolton Cross	NZ701017	427	900		*Calluna* *Eriophorum*
Kildale	NZ620111	274	880	8	*Calluna*
Job Cross	NZ692110	250	910	10	*Calluna* *Eriophorum*
High Tranmire	NZ762117	213	910	10	*Calluna*, grasses
Murk Mire Moor	NZ797025	240	780	7100	*Calluna* *J. effusis*
Beldom Bottom	SD967940	488	1500	7100	Blanket bog
Golden Groves	SE044945	457	1100	25	Blanket bog
Bollihope Common	NY993316	502			Blanket bog
Apedale	SE239944	396	1180	6	*Calluna* *J. effusis*

RESULTS

I. Comparison of the levels of arthropod fragments in adult droppings at Bogend, Muggleswick High, Waskerley, and Muggleswick Low.

(i.) Mean percentage of arthropod fragments; Fig. 1.

The values for the mean percentage of arthropod fragments in adult droppings are similar for Bogend and Waskerley, both peaking at c. 10% in mid June. At both sites, the levels show a rapid rise from 0% to their peak values in the space of two weeks. Similarly, for both sites, the levels fall off to c. 1% by the end of June. The period over which arthropods were eaten in any quantity at these sites was the three weeks around mid June.

The data for Muggleswick High show an earlier peak and at a lower value; 3% in early June and the peak is less pronounced than those of the two previous sites.

The level of arthropod fragments in droppings at Muggleswick Low did not rise above 1%, with a small peak at the end of June, after which the level fell off to 0%.

(ii.) Percentage frequency of occurrence of arthropod fragments in droppings; Fig. 2.

The graphs show that the values for Waskerley and Bogend peak during mid June, at which time 85-90% of the droppings examined were found to contain arthropod fragments. It is during this period that the peaks in the mean percentage of arthropod fragments in droppings occurred. Fig. 1.

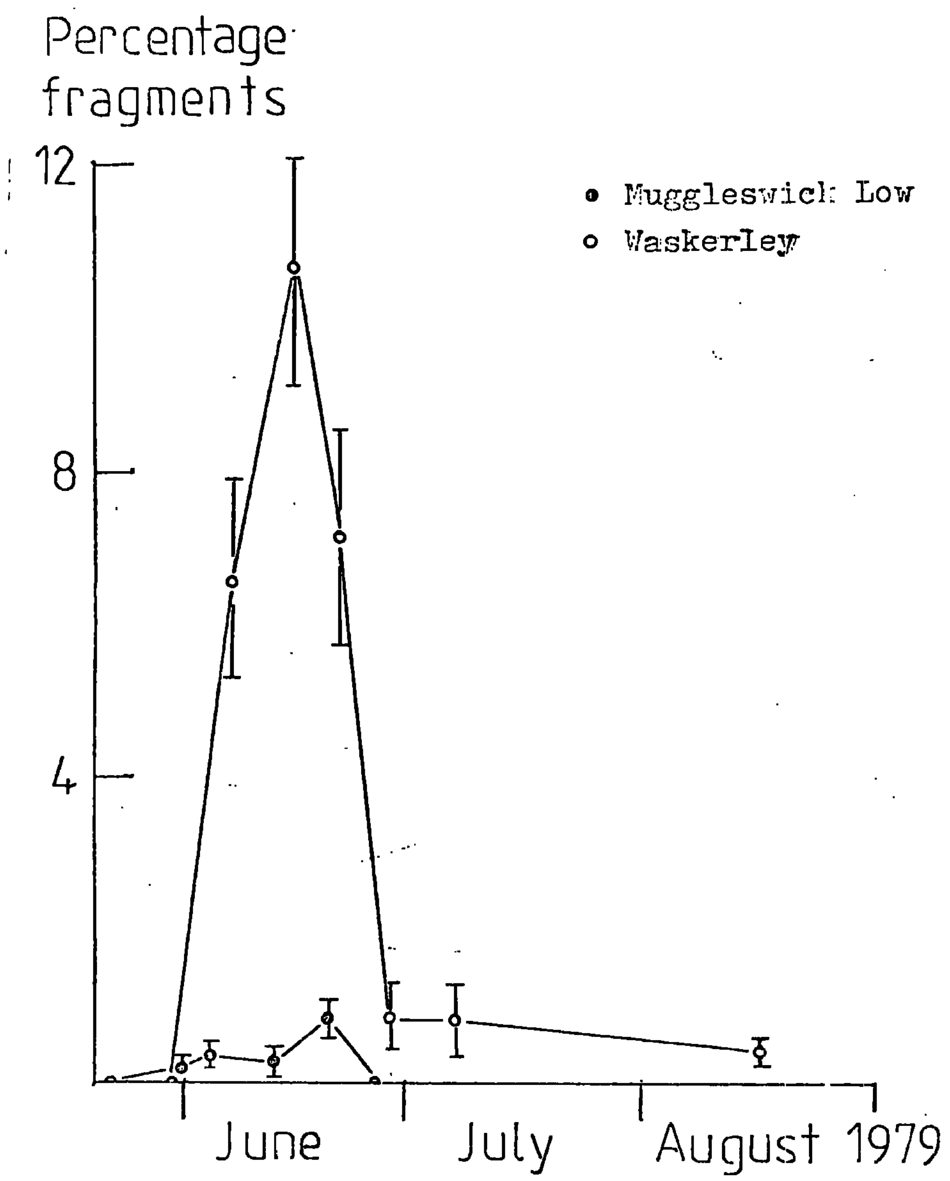
The Muggleswick High data show a less pronounced peak spread over a longer period, with a value c. 55%.

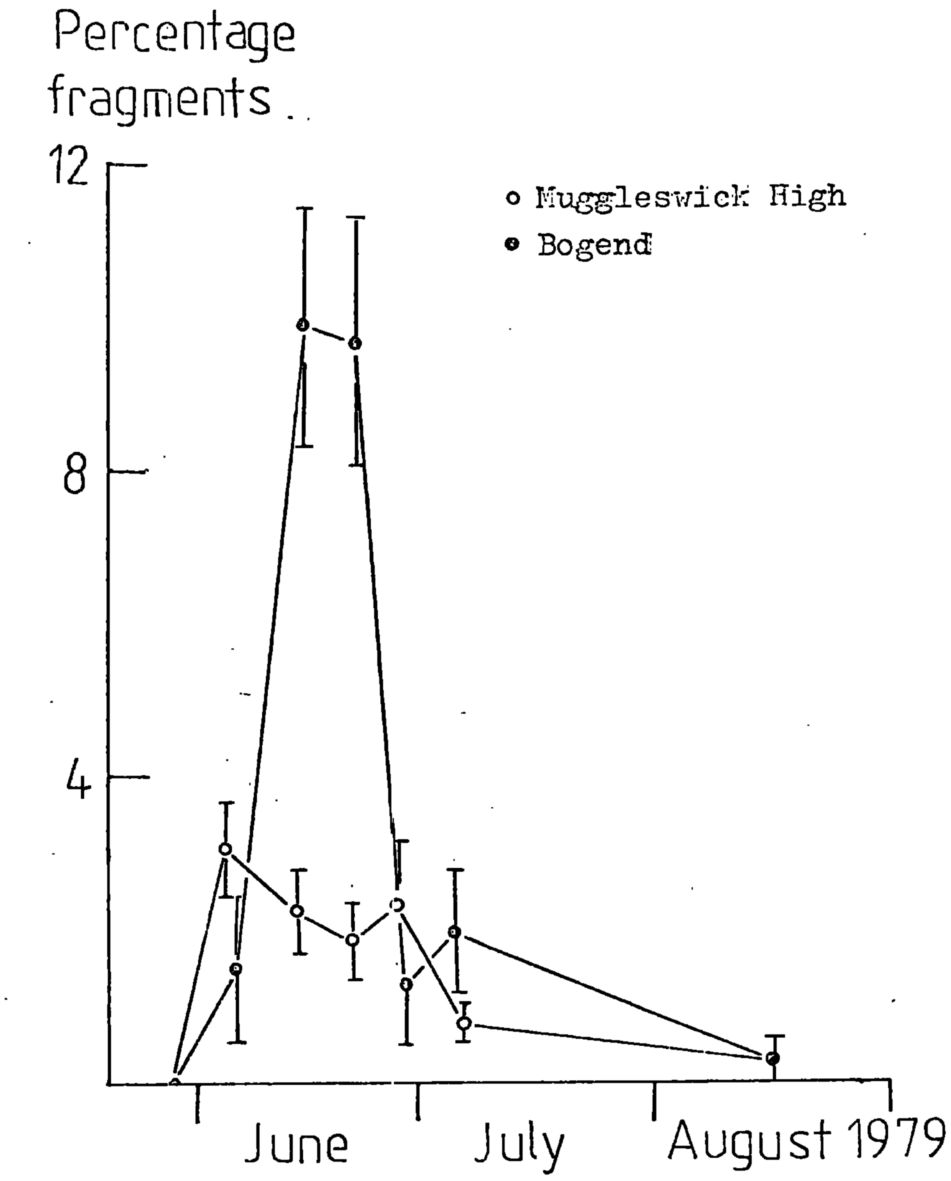
At Muggleswick Low, the values peak in late June, at which time c. 35% of the droppings examined were found to contain arthropod fragments. This value fell off to 0% by the beginning of July.

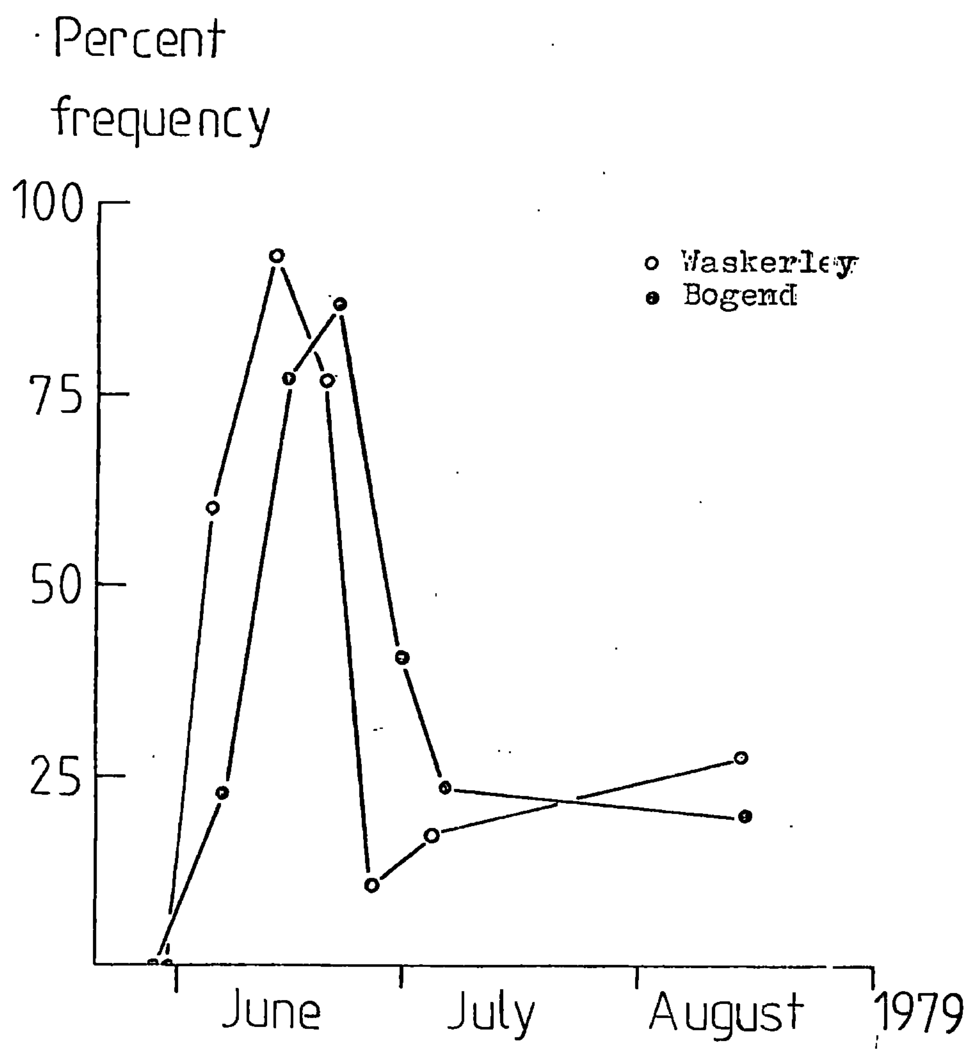
(iii.) Abundance of arthropod fragments in adult droppings.

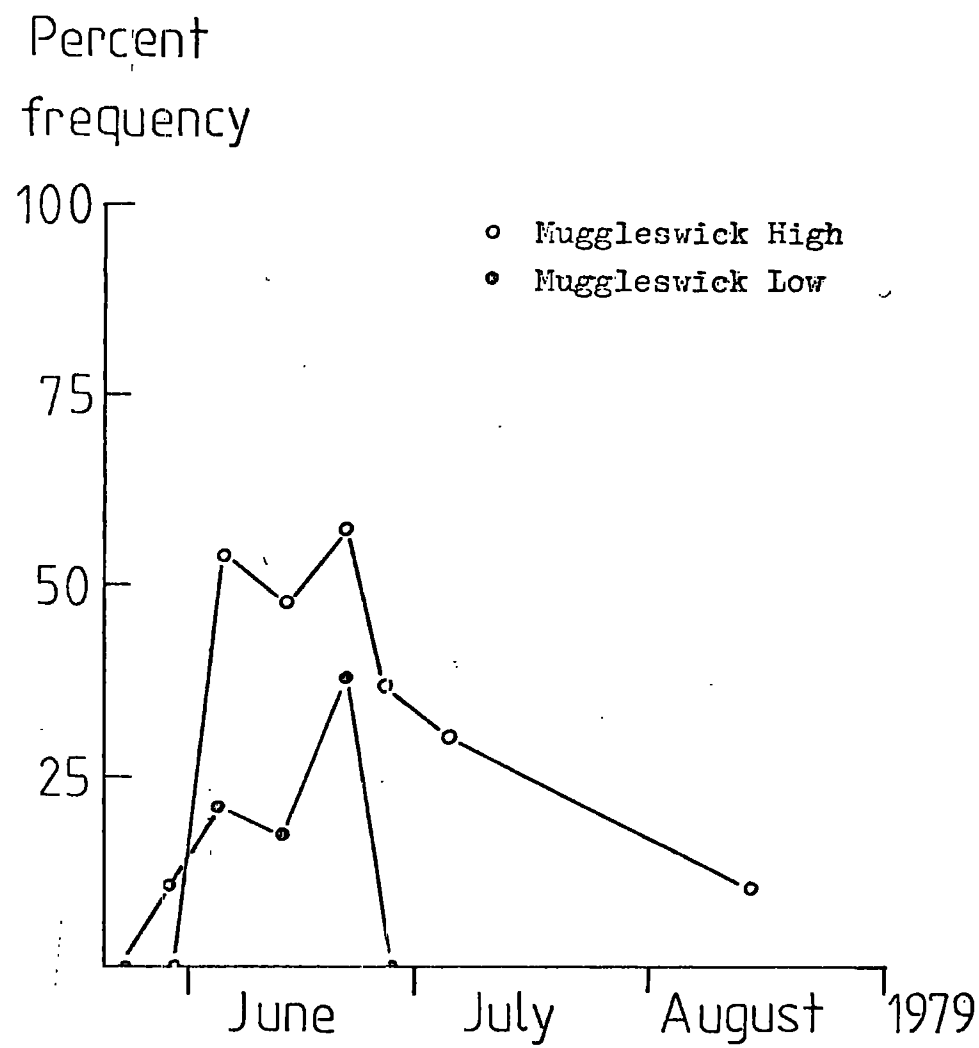
Appendix 1 shows the abundance of arthropod fragments found in adult droppings at the four sites. In all cases the abundance of arthropod fragments in droppings reached its peak in mid June.

The pattern which has emerged in the previous two comparisons of arthropod levels in adult droppings, (Figs. 1&2), at the four sites, also appears in this case. The abundance of arthropod fragments in adult droppings is highest at Bogend and Waskerley, lower at Muggleswick High, and lower still at Muggleswick Low.


Percentage fragments
12
8
4
Muggleswick Low
Waskerley
June
July
August 1979


Percentage fragments
12
8
4
Muggleswick High
Bogend
June
July
August 1979


Percent
frequency
100
75
50
25
Waskerley
Bogend
June
July
August
1979


Percent
frequency
100
75
50
25
Muggleswick High
Muggleswick Low
June
July
August
1979

II. (i.) Calculation of the biomass of the arthropod food available to the red grouse.

A comparative measure of the biomass of arthropod food available to the red grouse during the period in which the droppings were collected, was calculated from the pitfall data (Appendix 2). The arthropod groups were in some cases divided into size classes when the pitfall catches were examined. The following categories were used:

Carabids 1	≤ 15mm in length
Carabids 2	> 15mm " "
Staphylinids 1	≤ 15mm " "
Staphylinids 2	> 15mm " "
Diptera 1	≤ 10mm " "
Diptera 2	> 10mm " "
Diptera 3	Tipulidae

It became apparent after the identification of some of the fragments found in droppings, that some arthropod groups were taken more frequently than others.

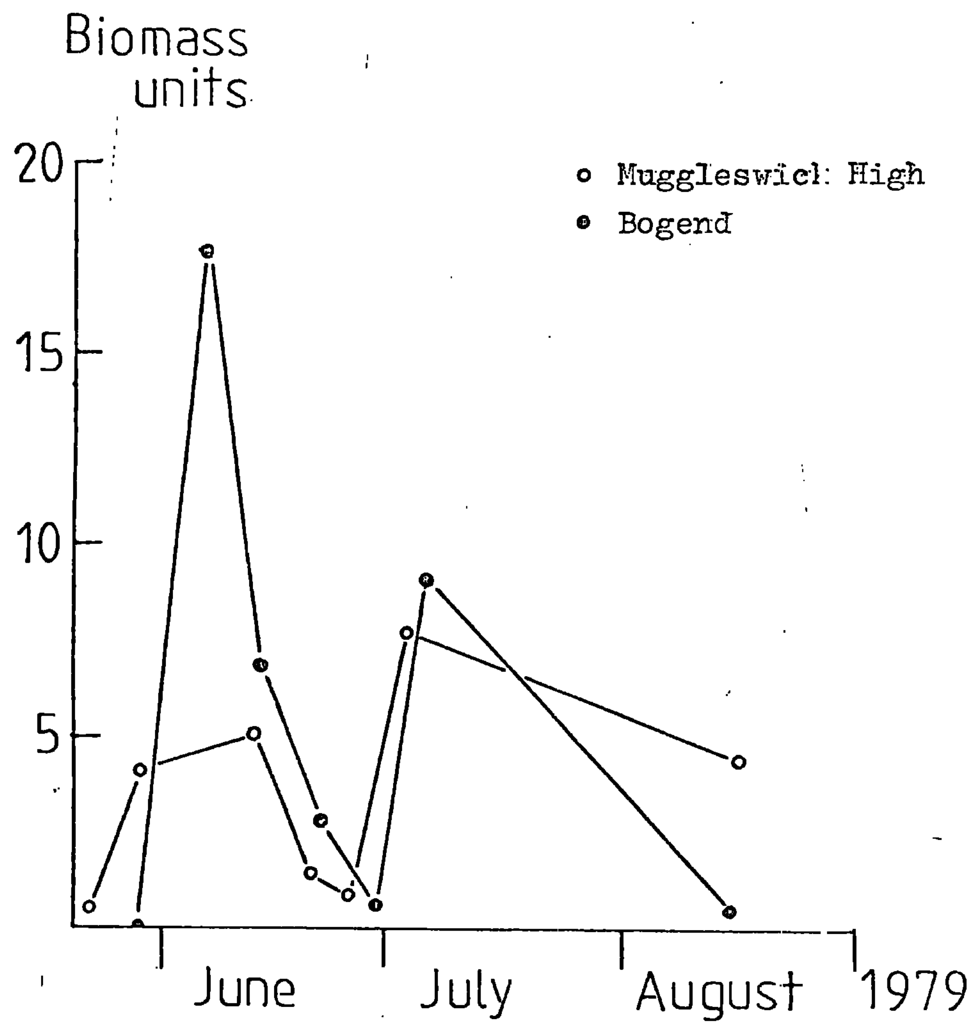
The groups used in the calculation of available biomass were; Diptera 3, lepidopteran larvae, weevils (Curculionidae) and Carabids 1. There was no evidence to suggest that the grouse had been taking Carabids 2; the larger carabid beetles. Diptera 2 was not included as the insects in this group were mainly dung-flies (Cordilurinae), which move too fast for grouse to catch.

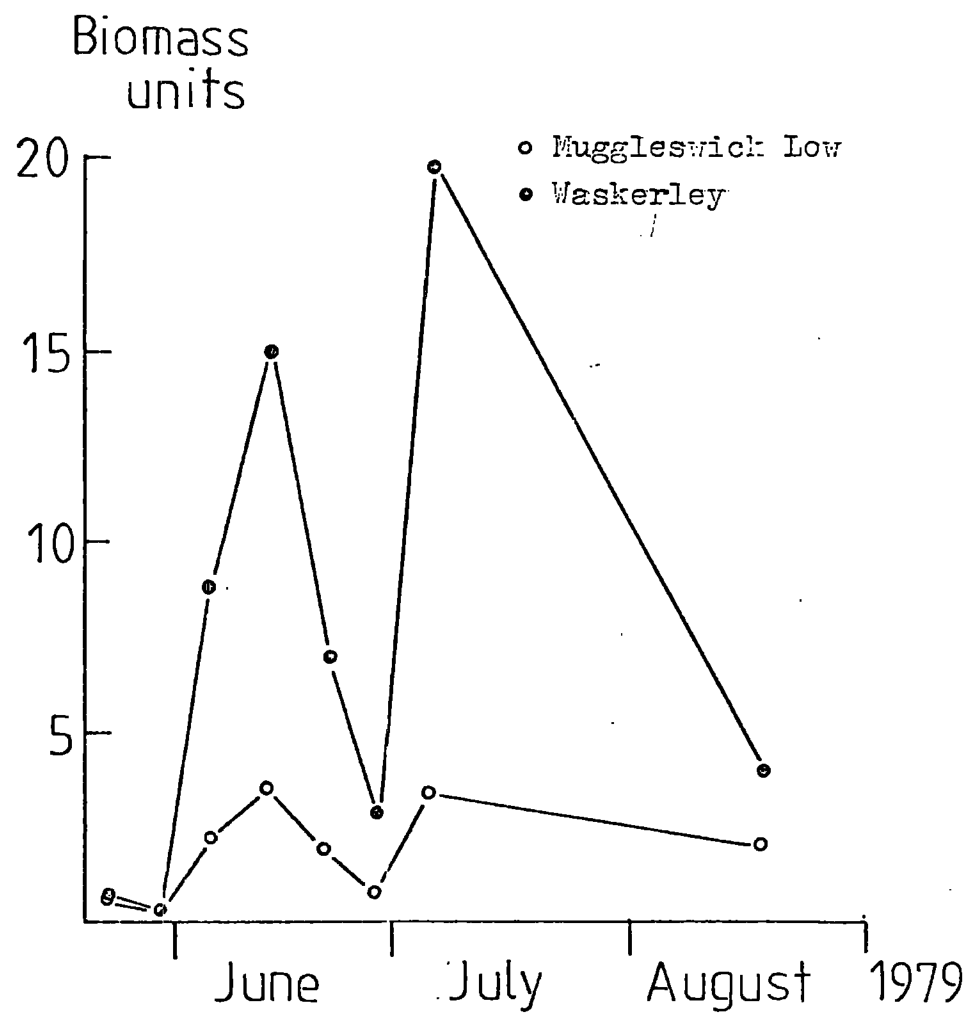
The values for Carabids 1 were divided by five, because these beetles are 'trap happy'. Each biomass value was calculated from a pitfall catch corrected to captures of a 7 day period.

II. (ii) <u>Comparison of the arthropod biomass at the four sites. (Fig 3.)</u>

The arthropod biomass was highest at Bogend and Waskerley; these sites showed pronounced peaks in mid June. This is the period when the level of arthropod fragments in the droppings was at its highest. The Waskerley site showed a second large peak in early July. This was due almost entirely to <u>Limonia</u> <u>dilutior</u>, a tipulid of highly localised distribution.

The arthropod biomass at Muggleswick High and Muggleswick Low did not show a pronounced peak in mid June and the biomass was lower than at the previous two sites.


Biomass units
20
15
10
5
Muggleswicl: High
Bogend
June
July
August
1979


Biomass units
20
15
10
5
Muggleswic:h Low
Waskerley
June
July
August
1979

III. <u>Comparison of the percentage of arthropod fragments in adult droppings with the arthropod biomass at the four sites. (Figs. 4 & 5)</u>.

(i.) <u>Bogend</u>

The rise in the numbers of arthropod fragments in the droppings follows the increase in the arthropod biomass in mid June. Similarly, the decrease in arthropod fragments in the droppings follows the fall off in arthropod biomass.

(ii.) <u>Muggleswick High</u>

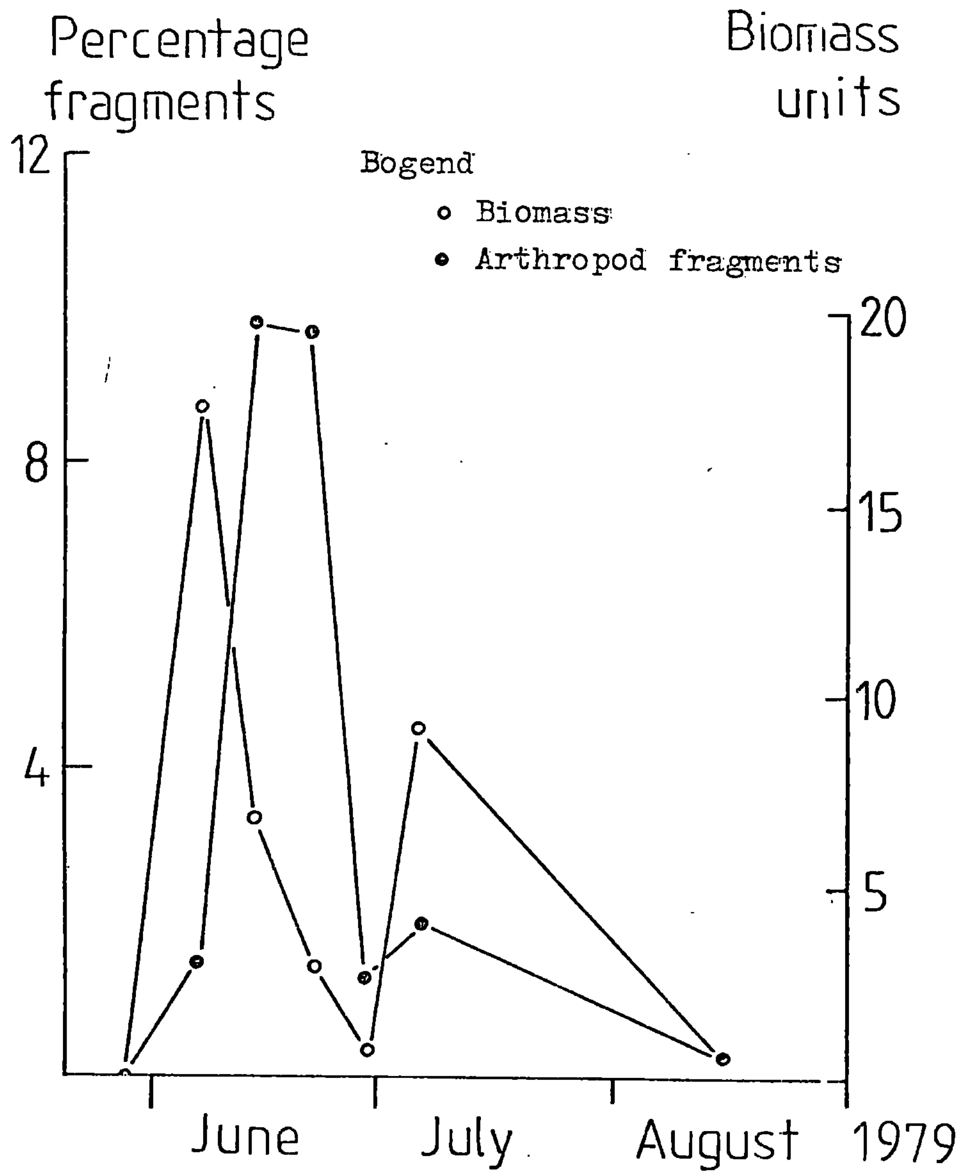
The small peak of arthropod fragments in adult droppings takes place within the peak of arthropod biomass during early to mid June. Although the arthropod biomass rises again in early July, there is no corresponding increase in the level of arthropod fragments in the droppings.

(iii.) <u>Waskerley</u>

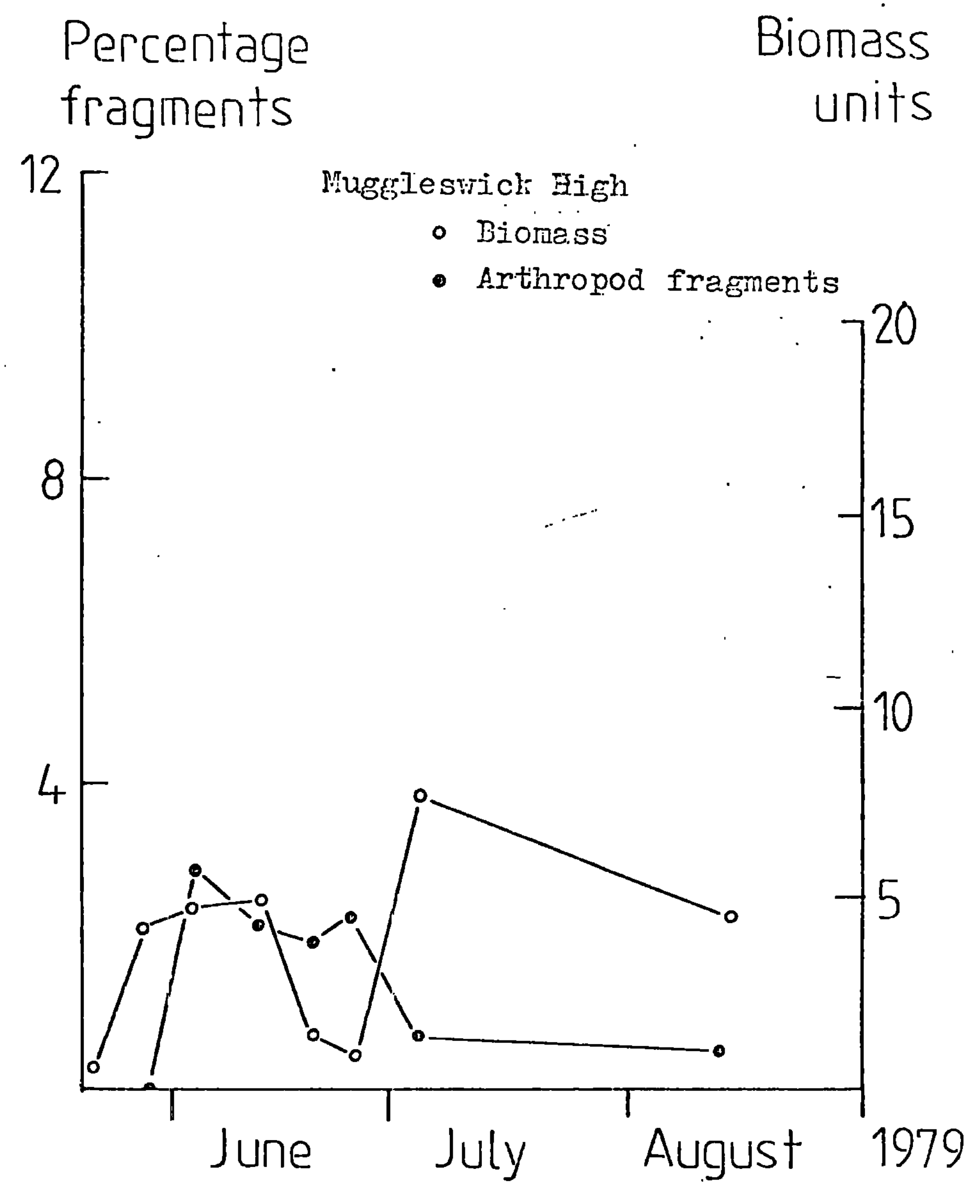
The peak of arthropod biomass occurs during early to mid June after which it decreases. This pattern is closely followed by the levels of arthropod fragments in the droppings which peak in mid June, subsequently decreasing to <1% in July and August. During July, the arthropod biomass rises rapidly to a second peak. As previously mentioned, this rise in biomass can be attributed to <u>Limonia dilutior</u>. This tipulid has a localised distribution and consequently the high value for the biomass in July is not representative of the whole area.

(iv.) Muggleswick Low

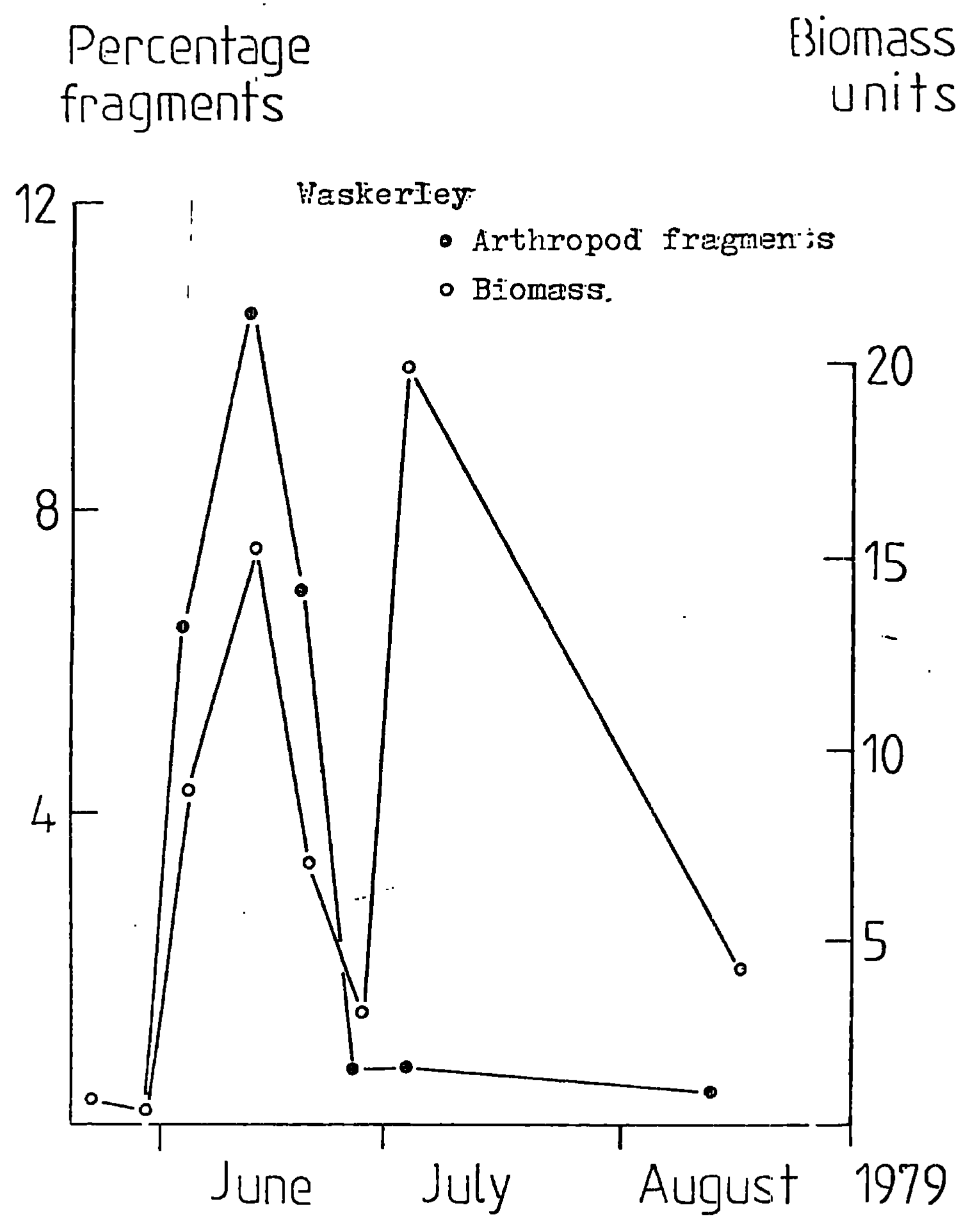
The arthropod levels in the droppings at this site never rose above 1% and were found only between the end of May and the end of June. This was the period when the arthropod biomass was at its highest.

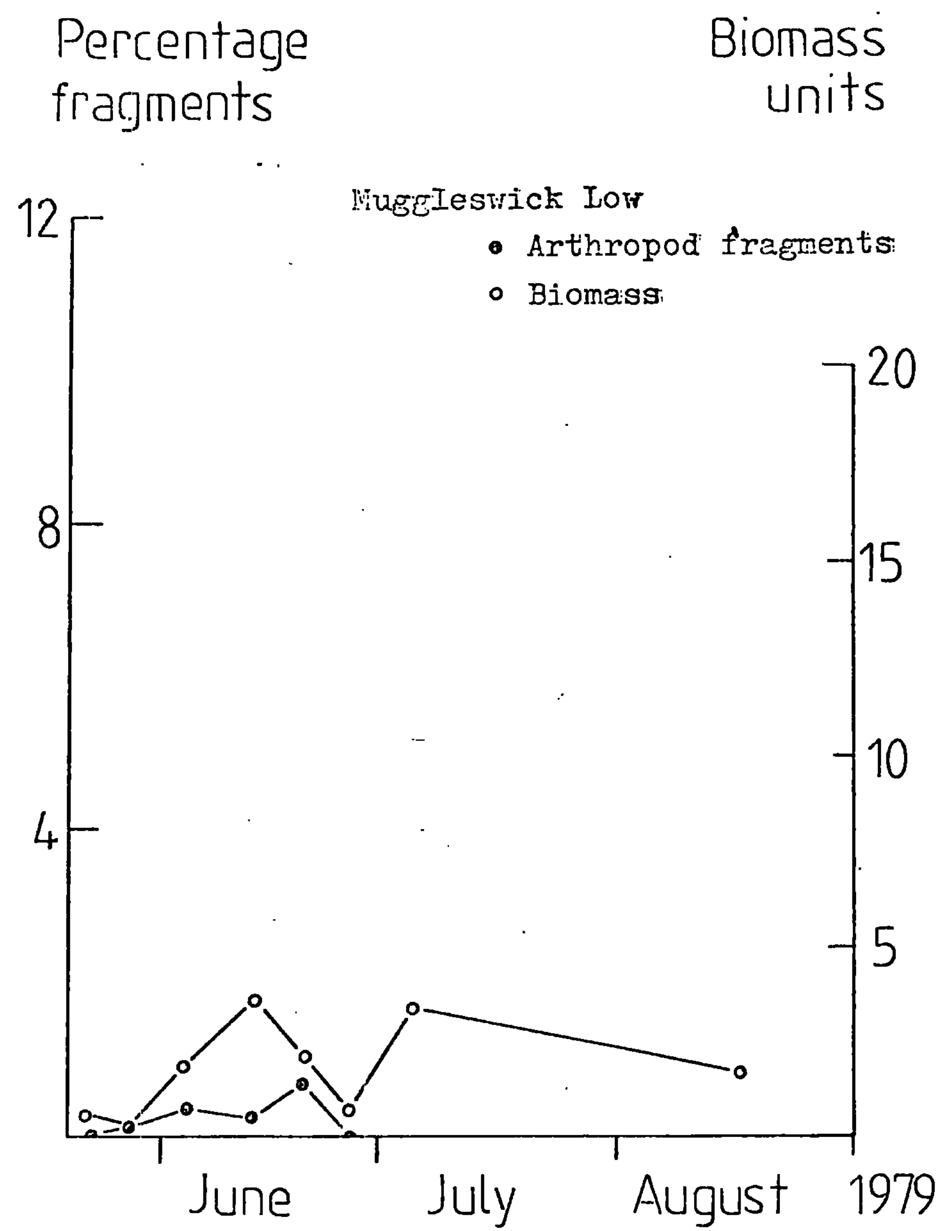


Percentage fragments
Biomass units
Bogend
Biomass
Arthropod fragments
12
8
4
20
15
10
5
June
July
August
1979



Percentage fragments
Biomass units
Muggleswick High
Biomass
Arthropod fragments
12
8
4
20
15
10
5
June
July
August
1979


Percentage fragments
Biomass units
Waskerley
Arthropod fragments
Biomass.
12
8
4
20
15
10
5
June
July
August
1979


Percentage fragments
Biomass units
Muggleswick Low
Arthropod fragments
Biomass
12
8
4
20
15
10
5
June
July
August
1979

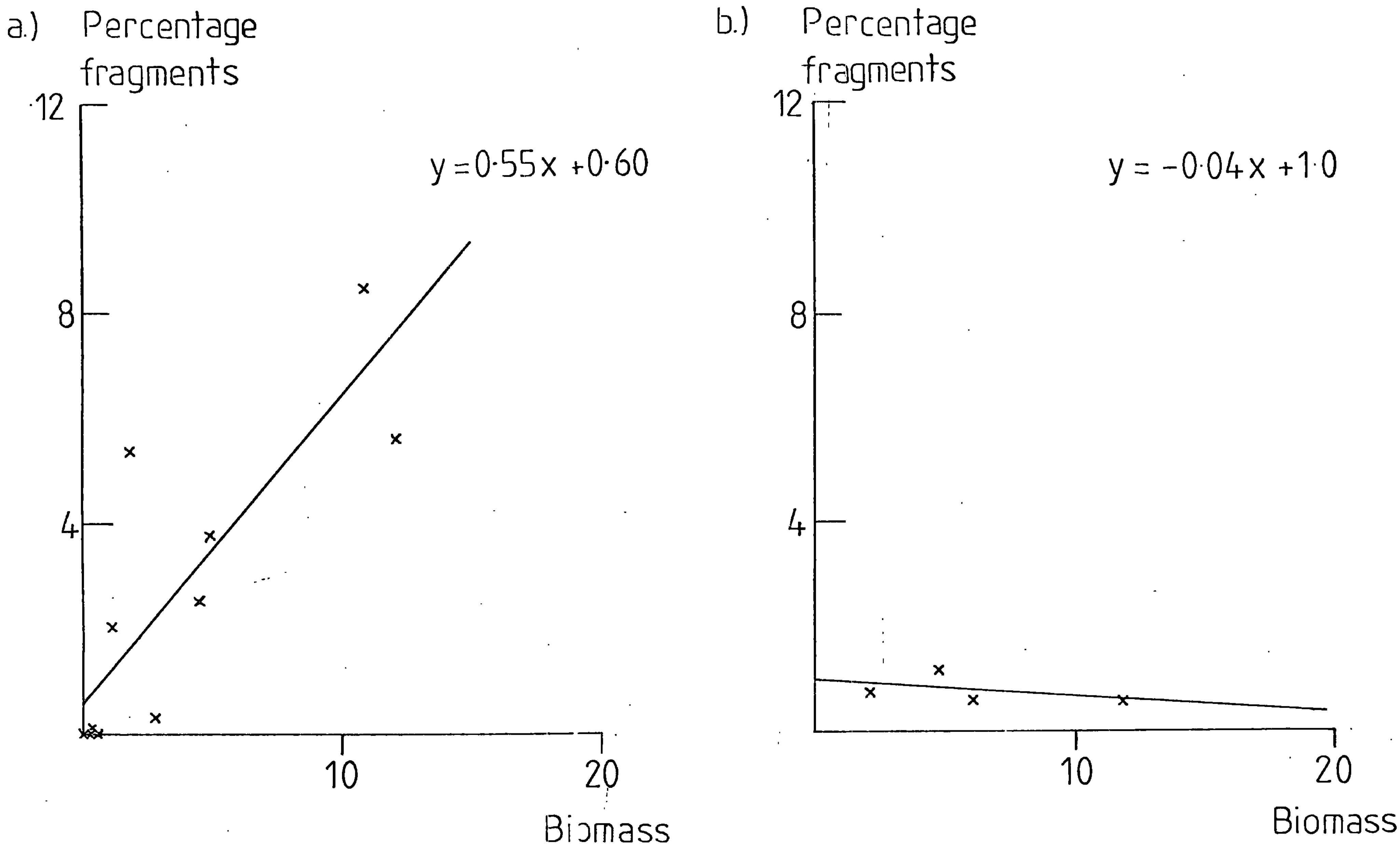
IV. The relationship between the available arthropod biomass and the levels of arthropod fragments in the adult droppings.

Fig. 6 illustrates the relationship between the biomass of arthropod food available to the red grouse and the levels of arthropod fragments in the adult droppings at all four sites. The two graphs show the different relationships during the months of May and June, and July and August.

During May and June, as the available biomass increased, the level of arthropod fragments in the droppings increased accordingly. The increase of the arthropod fragment levels with the available biomass is significant ($r = 0.830$, $p < 0.01$).

In July and August, although there was arthropod biomass available, the levels of arthropod fragments in the droppings were low. The relationship is not significant ($p < 0.05$).

The relationships between arthropod fragment levels and the available biomass in May and June, and July and August, are significantly different from each other, ($t = 4.807$, 13 d.f. $p < 0.001$).


a.)
Percentage fragments
12
8
4
y = 0·55x + 0·60
10
20
Biomass
b.)
Percentage fragments
12
8
4
y = −0·04x + 1·0
10
20
Biomass

V. Identification of arthropod fragments in adult and chick droppings at the four sites.

(i.) Bogend

Throughout June, fragments of tipulids were found in the adult droppings. In particular, fragments of *Tipula subnodicornis* and *Tricyphona immaculata* were identified. Beetle fragments were also identified in adult droppings during this period. In late June and early July, parts of lepidopteran larvae were found.

The chick droppings were found to contain tipulid remains throughout June, in particular, parts of *Molophilous ater* and *Tricyphona immaculata* were identified in droppings collected at the end of June.

(ii.) Muggleswick High.

Tipulid remains were identified in adult droppings collected throughout June. Fragments of weevils, carabid beetles and a stonefly (Plecoptera) were identified in the same droppings. Lepidopteran larvae remains were found to be present in early July.

The chick droppings contained fragments of chrysomelid beetles in early to mid June, whilst in late June, fragments of two different tipulid species were identified; *Limnophila meigeni* and *Tipula varipennis*. Lepidopteran larvae remains were also identified.

(iii.) Waskerley.

Beetle remains were identified in adult

droppings throughout June. Tipulid remains, possibly *Tipula varipennis*, were present in early and mid June. Fragments of weevils and lepidopteran larvae were identified in droppings collected in late June and early July.

The chick droppings contained fragments of beetles, tipulids and weevils throughout June and early July.

(iv.) *Muggleswick Low*

Tipulid and beetle remains were identified throughout June, in particular, fragments of *Tipula subnodicornis* were identified in adult droppings collected in late May and early June.

The chick droppings were found to contain fragments of beetles, tipulids and lepidopteran larvae.

VI. The analysis of droppings from the additional sites in Swaledale and the North York Moors.

The sampling areas in the North York Moors and Swaledale can be broadly classified into low altitude heath-type moors and high altitude areas of blanket bog, respectively. Although only a single collection of droppings was made at these sites, the droppings were analysed in a similar way to, and can be compared with, those collected from the four main sites. These sites therefore provide additional information on the arthropod levels in droppings over an altitude range.

Table 2 illustrates the range of levels of arthropod fragments in adult droppings collected from moors of different altitude. The pattern in the additional sites is similar to that seen in the data from the four main sites. The values for the low altitude moors (<350m), were very low and lay within the range of 0- 0.3%. The percentage frequency of occurrence of fragments was similarly low, ranging from 0- 13%. (Appendix 4). On the higher moors, (>350m), increased levels of arthropod fragments were found. The levels of arthropod fragments fell in the range of 0.7-9.0%. The percentage frequency of occurrence of fragments ranged from 17-77%.

When the χ^2 test was applied to the data to test the difference in arthropod fragment levels between moors of altitudes up to 350m and moors at altitudes above 350m, the result was significant ($\chi^2 = 14$, 1 d.f. $p < 0.001$). In general, the arthropod fragment levels increased with the altitude of the moor. Within the altitude range, there are a few anomalies, eg. the exceptionally high value of Apedale. This site is a particularly wet area and although at a lower altitude, it is probably a richer source of arthropods than many of the sites at a higher altitude. Variations in the arthropod fragment levels in the droppings within the altitude range may therefore be caused by localised wet conditions on the sampling area. This is also seen at Waskerley, a site intersected by wet flushes and although it is at a lower altitude than Bogend, the two areas have similar levels of arthropod fragments in the droppings.

Identification of arthropod fragments.

Lepidopteran larvae remains were present in droppings from all the high altitude sites. Beetle remains and stonefly fragments were also identified in droppings collected from Golden Groves. At low altitude sites, beetle, weevil and lepidopteran larvae remains were identified. Tipulid remains were identified in droppings collected from Job Cross and High Tranmire.

Table 2

Site	Altitude (m)	% arthropod fragments and standard error
High Tranmire	213	0.3 + 0.18
Murk Mire Moor	240	0 0
Job Cross	250	0.3 + 0.18
Kildale	274	0.1 + 0.18
Muggleswick Low	280	0 0
Yarlsey Moss	305	0.1 + 0.18
Apedale	396	9.0 + 1.64
Waskerley	411	1.0 + 0.36
Bolton Cross	427	0.7 + 0.36
Golden Groves	457	1.0 + 0.55
Muggleswick High	476	2.0 + 0.73
Beldom Bottom	488	2.0 + 0.55
Bollihope Common	502	3.0 + 0.91
Bogend	551	2.0 + 0.91

VII. Comparison of the arthropod fragment levels in adult and chick droppings at each site.

The adult and chick droppings were collected as a paired sample in every case. The comparison between the levels of arthropod fragments in adult and chick droppings is shown in Figs. 7 & 8.

(i.) Bogend

The chick droppings at this site were found to contain very high levels of arthropod fragments, especially when the chicks were very young. The value of 44% arthropod fragments in mid June, was the highest value found in chick droppings at any of the four sites. In mid June, the level of arthropod fragments was approximately nine times that of the adult droppings. This value declined rapidly to 0% by early July.

(ii.) Muggleswick High

The maximum value of arthropod fragments found in chick droppings was 38% in mid June. The values appear to reach a peak, however, because hatching occurs over a period of a few weeks, and because the age of the chick droppings was not ascertained, the peak may be due to the collection of droppings from newly hatched chicks throughout the hatching period. As the chicks grew older, the level of arthropod fragments in their droppings declined. The value for the peak of arthropod fragments in chick droppings is approximately five times that of the adult droppings over the same period.

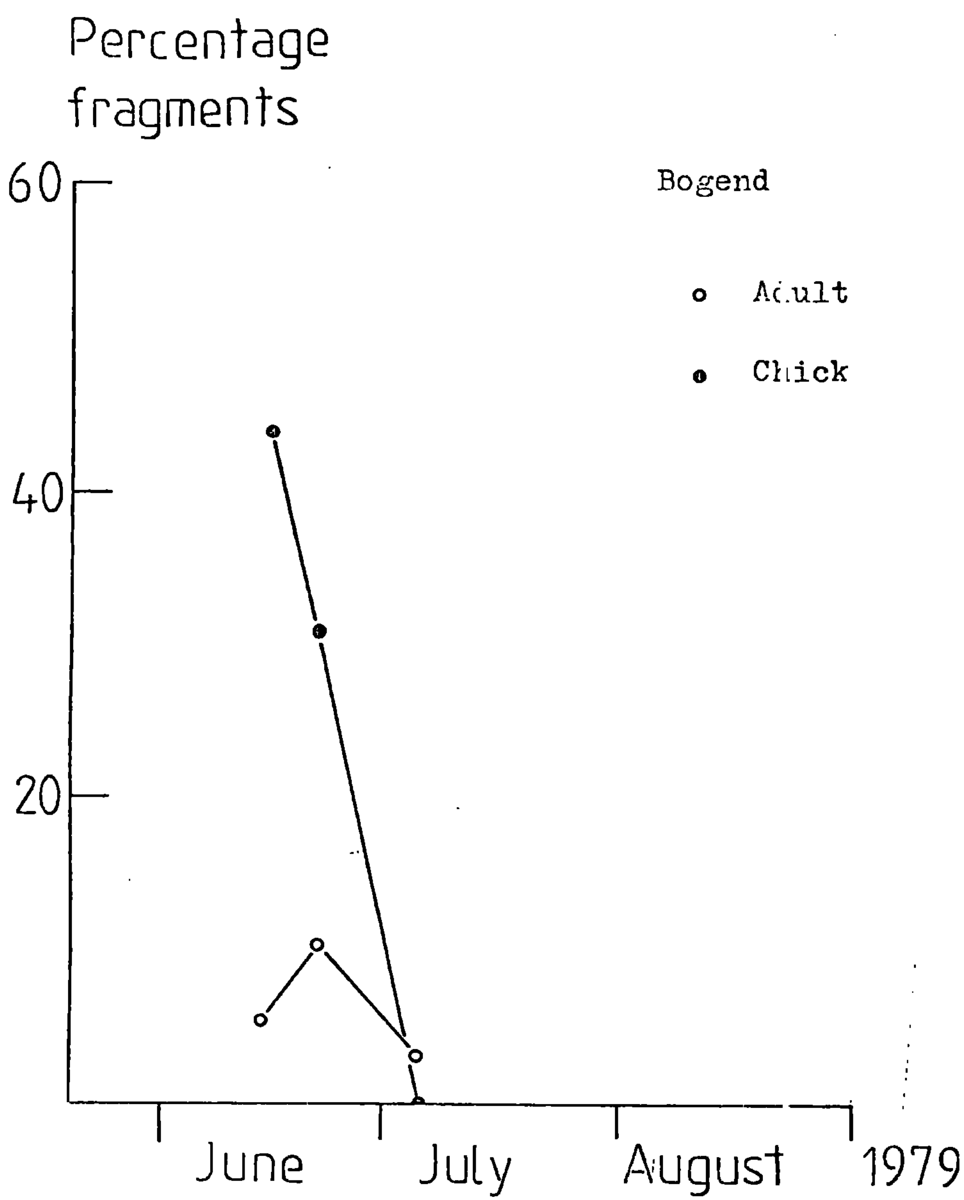
(iii.) <u>Muggleswick High</u>

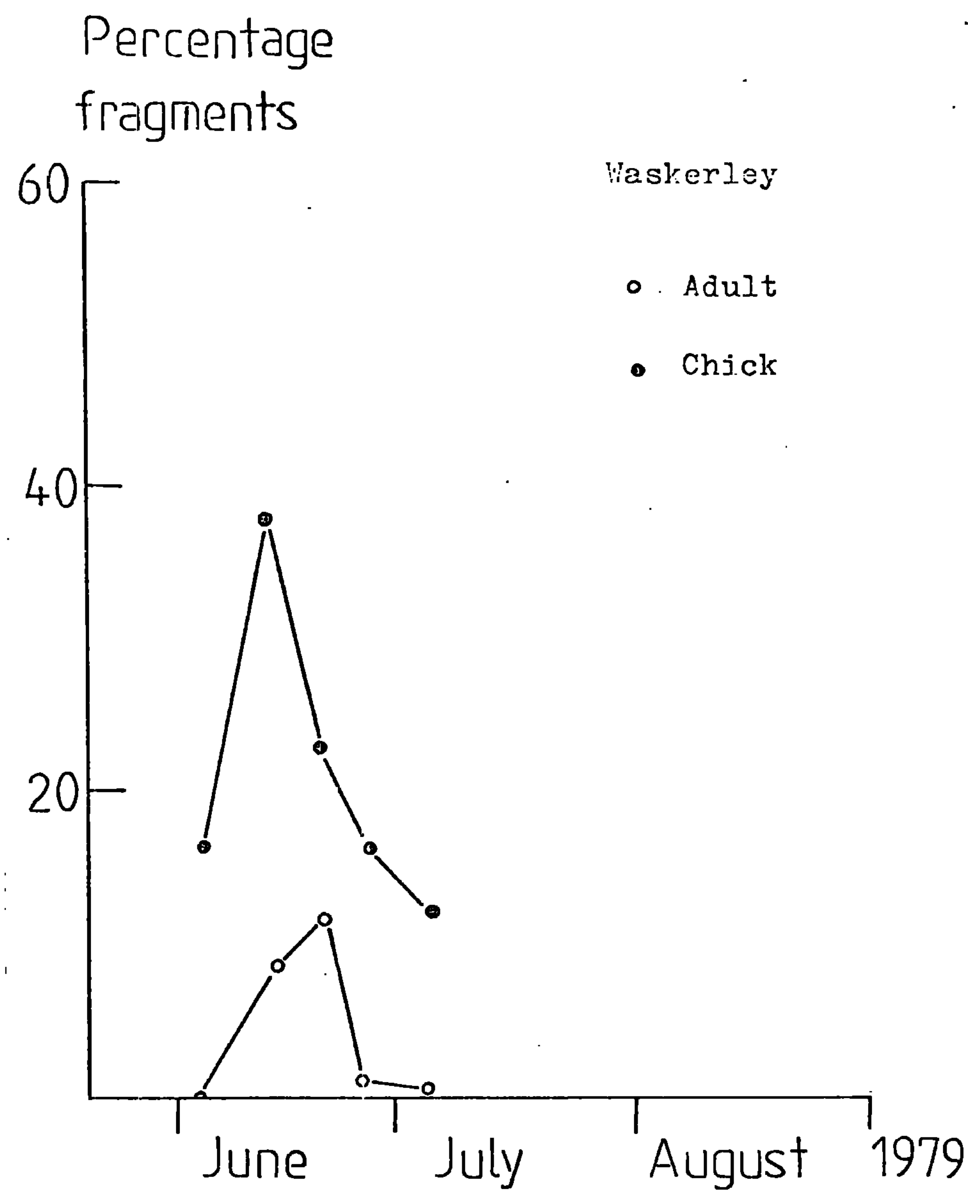
The highest value for the levels of arthropod fragments in chick droppings was 17%; the peak occurred over the same period in the second half of June as the peak in the adult droppings. The peak of the chick droppings may be due to the collection from newly hatched chicks, as explained above. The chick value at its peak is five to six times greater than that of the adult droppings over the same period. In a similar way to the other three sites, the level of arthropod fragments in chick droppings declined rapidly as the chicks grew older.

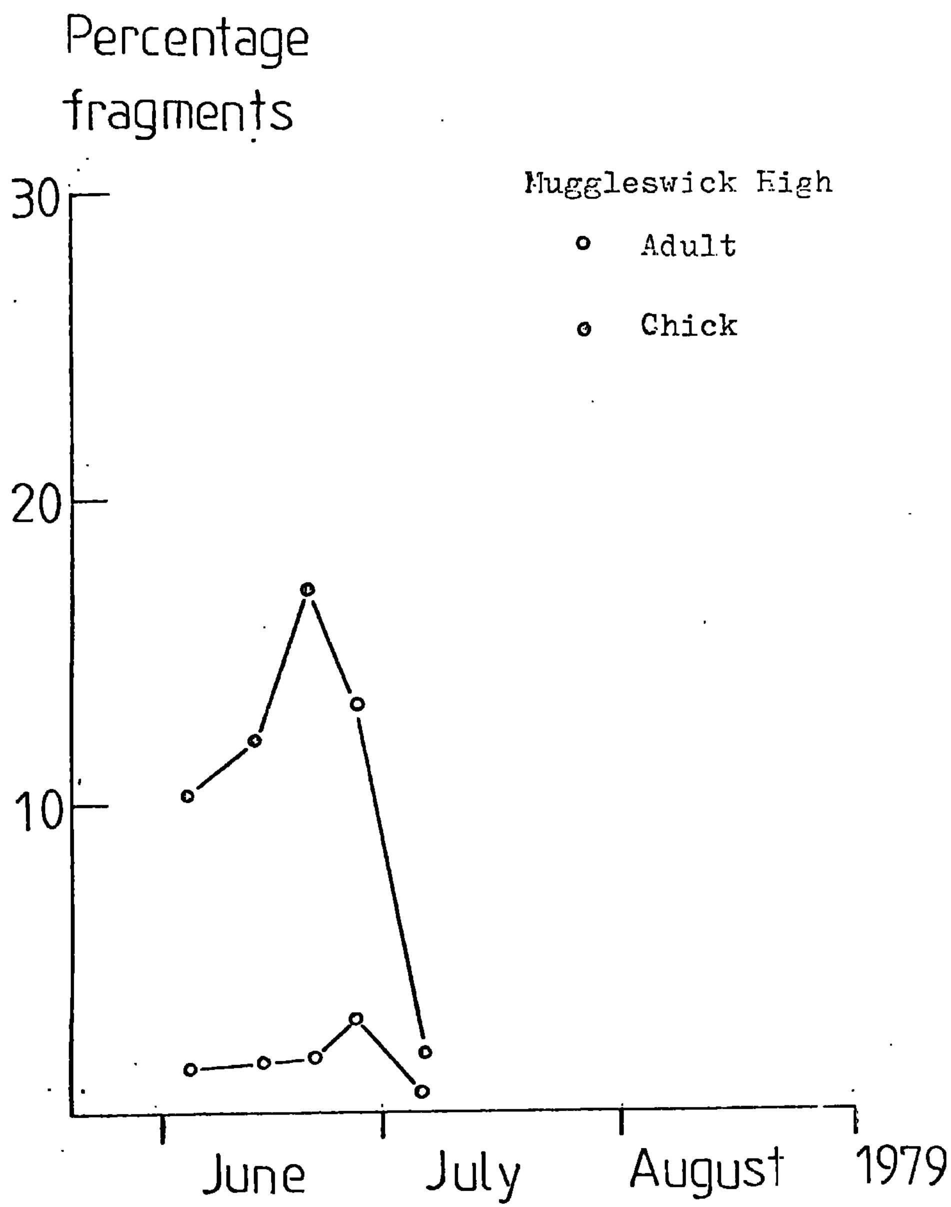
(iv.) <u>Muggleswick Low</u>

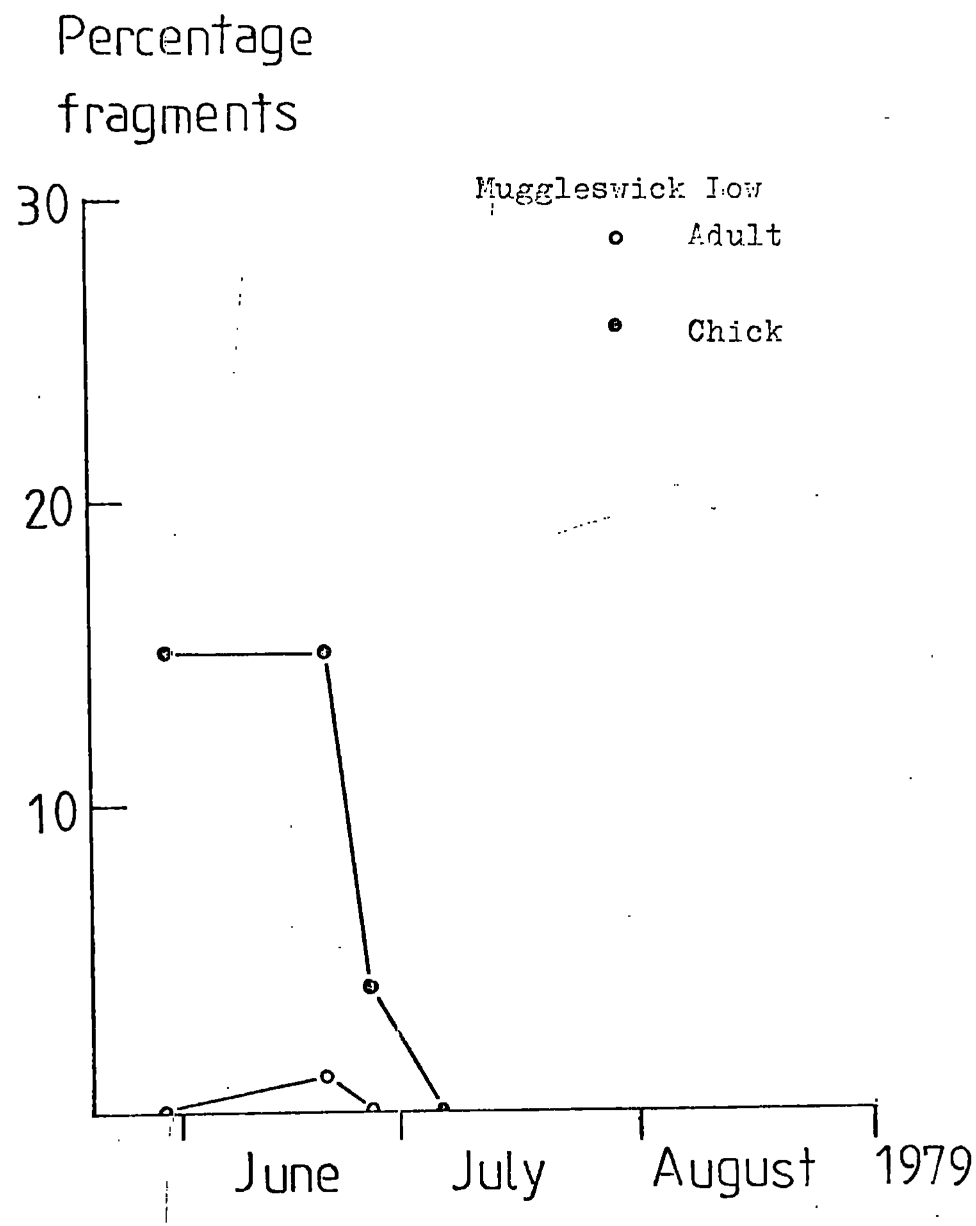
The chick droppings collected from this site contained levels of arthropod fragments of 15% for the first half of June. This value was more than fifteen times that of the adult droppings, which were negligible at this site. The levels of arthropod fragments in chick droppings declined rapidly in the second half of June, to reach 0% by early July.

The levels of arthropod fragments in chick droppings were very much higher than those of the adults at all four sites. A pattern similar to that of the levels of arthropod fragments in adult droppings emerged; with the levels highest at Bogend and Waskerley and lowest at Muggleswick Low.


Percentage fragments
60
40
20
Bogend
Adult
Chick
June
July
August
1979


Percentage fragments
60
40
20
Waskerley
Adult
Chick
June
July
August
1979


Percentage fragments
30
20
10
Muggleswick High
Adult
Chick
June
July
August
1979


Percentage fragments
30
20
10
Muggleswick Low
Adult
Chick
June
July
August
1979

VIII. The vegetational components in the diet of the red grouse (Appendix 3).

Table 3 summarises the *Calluna* data at the four sites.

(i). Bogend

The diet of the red grouse at Bogend was supplemented by *Eriophorum*, *Polytrichum* and small amounts of *J. sqarrosus*, which was taken in late June and in August. *Vaccinium* was absent from the droppings.

(ii). Muggleswick High

J. squarrosus was present in the droppings on two occaisions; in mid June and in mid August. The levels of *Calluna* remained very steady throughout the summer.

(iii). Waskerley

During mid June, the diet was supplemented by significant amounts of *Polytrichum*. *J. sqarrosus* formed a larger part of the diet at this site than at any of the others and in August, its value rose to 55%, causing the *Calluna* value to fall to 35%.

(iv). Muggleswick Low

J. squarrosus appeared in the droppings in mid August, where it formed a large part of them. *Eriophorum* was present in small amounts, $<1\%$, during May.

This was replaced by Vaccinium and Polytrichum in June and July.

The differences in the amounts of supplementary plants eaten at the four sites, reflect the vegetational compositions of the areas. The wetter sites, Waskerley and Bogend, support more Juncus squarrosus and Eriophorum than the drier Muggleswick sites.

Table 3.

Site	% *Calluna* and *Erica* in May, June & July 1979	% *Calluna* and *Erica* in July 1979	Main supplementary plants
Bogend	82	84	*Polytrichum* *Eriophorum*
Muggleswick High	86	85	*Polytrichum* *Eriophorum*
Waskerley	81	35	*Polytrichum* *J. squarrosus*
Muggleswick Low	87	68	*Polytrichum* *Vaccinium*

DISCUSSION

The controversy which has arisen concerning the role of arthropods in the diet of the red grouse can be explained when the type of moor on which the studies were made, is taken into account. From the results of this study, it has become apparent that the role of arthropods in the diet varies widely in different environmental conditions.

The level of arthropod fragments in droppings collected from low, (< 350m) dry moors was negligible In contrast to this, the droppings collected from high, (> 350m) blanket bog moors, contained very much higher levels of arthropod fragments. On high altitude moors where the conditions are cold and wet, such as Bogend and Bollihope Common, levels of ≤ 10% of the items counted in adult droppings were identified as arthropod fragments. This contrasts sharply with the conditions of the low, dry moors, such as Muggleswick Low and the sites in the North York Moors, where the levels of arthropod fragments did not exceed 1%.

From the identification of arthropod fragments in red grouse droppings, it would appear that adult tipulids, caterpillars, weevils and carabid beetles are frequently eaten. The cold, wet conditions of high altitude blanket bog favour the survival of the Tipulidae. The eggs and young larvae of many species of tipulids are very susceptible to dessication, consequently on dry moors, their distribution is restricted to any localised wet areas. At Moor House, sixty six species of tipulids have been found, some of which occur at high densities, (Coulson 1959). Molophilous ater, a small cranefly, occurs at larval densities of 1000-3000 per m^2 over most of the blanket bog. Both sexes of this cranefly have only vestigial wings and are therefore unable to fly and move by crawling slowly through the vegetation. The other arthropods taken frequently by the red grouse; weevils, carabid beetles and caterpillars, are also slow-moving and hence easier to catch than many other groups of the Diptera, which are winged and strong fliers.

When the levels of arthropod fragments in the droppings collected from Bogend in this study are compared to the figures given by Butterfield and Coulson (1975), the figures in this study are noticeably lower. In some of the droppings (3%), collected in 1974 at Bogend, arthropod fragments formed over 50% of the items counted. None of the droppings examined in this study contained >35% of arthropod fragments. The difference in the values between the two studies can be explained when the numbers of insects caught in the pitfall traps are examined. At the peak emergence of the tipulids in June at Bogend in 1970, a weekly catch from ten pitfalls was 50 - 60 tipulids. In this study, during the peak emergence of the tipulids, the highest number caught in one week in ten pitfalls was 13. The low number of tipulids is a result of the very severe winter of 1978/79, in which the snow cover extended into May. It is likely that the numbers in other insect groups have similarly been reduced.

Butterfield and Coulson (1975) reported that no larval or pupal remains were found in droppings collected in 1974. In this study, caterpillar remains were frequently found in both adult and chick droppings, particularly in the second half of June and early July. In years of high tipulid numbers, the red grouse may not take caterpillars however, in a year when tipulid numbers are severely reduced, the caterpillar may serve as an additional source of nutrition.

When the levels of the available biomass of arthropods are compared at the four sites, a pattern similar to that of the levels of arthropod fragments in droppings at the four sites, emerges. The available biomass was highest at Bogend and Waskerley, both sites where the cold, wet conditions favour the survival of tipulids. The biomass level at Muggleswick High was intermediate between Muggleswick Low and Bogend and Waskerley.

Although the Muggleswick High site is situated at a higher altitude and has a higher soil moisture content than the main area at Waskerley, the wet flushes at the latter site have a very high soil moisture content and are probably the main source of arthropods at the site. During June, adult and chick droppings were more frequently found around the wet flushes than on the main Calluna area. This suggests, as has previously been proposed, that the adults take the chicks to feed in the wet flushes where they find a local abundance of arthropods. The movement off the main Calluna area to the area of standing pools of water, was also noticeable at the Muggleswick High site during June. It is apparent that the wetness of an area, even when at a lower altitude, can affect the levels of arthropods eaten.

The level of available biomass was lowest at Muggleswick Low, where the dry conditions do not favour the survival of tipulids. These dry, low altitude areas were the types of moor on which the studies of the earlier workers were carried out. From the data obtained in this study, the available biomass of arthropod food would be expected to be low on such areas and this explains why the reports have contained no mention of any arthropod component in the diet of the red grouse.

The relationship between available arthropod biomass and the level of arthropod fragments in droppings shows two distinct phases. Firstly in May and June, the levels of arthropod fragments rose as more biomass became available. Secondly, in July and August, although the biomass was available, the grouse stopped eating arthropods at Muggleswick Low and at the other sites, arthropod fragments were present in droppings only at very low levels.

The levels of arthropod fragments in chick droppings are very much higher than the adult levels at all four sites. The arthropods taken by the chicks were similar to those eaten by adults; slow-moving arthropods such as caterpillars, weevils and tipulids. Beetle fragments, in particular chrysomelid beetles, were frequently present in chick droppings. The small, inactive cranefly, Molophilous ater is easily caught by the chicks and the peak emergence of this tipulid in early June, as well as the emergence of Tipula subnodicornis in late May, coincides with the period of hatching and maximum growth of the red grouse chicks. As the chicks grew older, the proportion of arthropod fragments in their droppings decreased. The decrease coincided with the period when the birds began to move back from the wet flushes onto the main Calluna area in July.

Animal food is a richer source of most vitamins, especially Vit. B 12 which is essential for growth, than plant material (Bolton 1963). Arthropods could be especially important for very young chicks because the caecum, which is thought to be the site of vitamin synthesis, does not function during the first few days of life.

Previous studies on red grouse populations have indicated that numbers are related to the amount of food present (Miller, Jenkins and Watson 1966), and that experimental changes in their food can increase breeding density in the spring and their breeding success in the summer (Miller, Watson and Jenkins 1970). Superficially, the red grouse may appear to have a vast excess of food available, however they are highly selective feeders, especially for nitrogen and phosphorus (Miller 1968, Moss 1972). Arthropods are a very rich source of these elements.

The main disadvantage of faecal analysis is the tendency to underrate the importance of the more easily digested foods. The major part of the bodies of insects such as tipulids and caterpillars is digested completely and only the heavily cuticularised parts of the animal appear in the faeces. The digestibility of animal protein is usually much higher than protein in plants (Bolton 1963). An average value for the digestion of animal protein derived from Bolton's figures is 87% whereas the highest value obtained by Moss and Parkinson (1972), for the digestion of heather protein by adult red grouse in spring was 48%. Animal protein contains a balance of essential amino acids which is closer to the optimum for growing chicks than most vegetable proteins (Bolton 1963). The concentrations of some of the amino acids in the protein of heather shoots are below these optimum concentrations.

Not only is the digestibility of animal protein higher than that of plants, but the concentrations of certain elements, eg. nitrogen and phosphorus, are also higher. When compared with the composition of <u>Calluna</u> shoots, the tipulids have appreciably higher concentrations of both elements (Butterfield and Coulson 1975). For example, <u>Tipula subnodicornis</u> has nine times more nitrogen, seven times more phosphorus, six times more sodium and nearly twice as much potassium, weight for weight, than <u>Calluna</u> shoots. The differences between <u>Molophilous ater</u> and <u>Calluna</u>, especially in the case of nitrogen are also appreciable. In general, moorland invertebrates have markedly higher levels of potassium and nitrogen than moorland plants. (Coulson and Whittaker 1975). Arthropods therefore represent important sources of these nutrients, particularly when the concentrations of these are low in most moorland plants.

Moss (1972), showed that red grouse select highly for nitrogen and phosphorus and that these elements appear to be the main limiting elements in the bird's heather diet. Savory (1975), also found that the red grouse selected heather with a relatively high concentration of nitrogen and phosphorus, compared with the available heather.

Whilst the first emergence of tipulids usually occurs during egg laying in the red grouse, the peak of emergence comes after most clutches have been completed. Tipulids are therefore unlikely to be of much importance in determining the quality of the eggs. Savory (1975), found that in captive red grouse, the total weight of eggs laid was significantly related to the amount of food eaten before laying but not to food intake during laying. The rate of production of eggs however was related to the amount of food eaten during as well as before laying.

The arthropod component in the diet could however, play an important part in the replacement of nutrients used in egg production and in maintaining the health of the grouse. Arthropods are eaten during the period when the birds moult, at this time the birds shelter in the taller heather which is older and less nutritious. Arthropods are a concentrated source of nutrients during this period.

The arthropods also form an important part of the diet of the red grouse chicks which eat them in much larger quantities than the adult birds.

A furthur study is required to investigate the nutritional value of the arthropods in comparison to that of the vegetational component in the diet. The role of nitrogen, potassium and calcium in particular should be examined with regard to their role in maintaining the health of the red grouse.

In conclusion, the importance of the arthropod component in the diet of the red grouse, depends on the type of moor on which the birds are feeding. On the low, dry moors, the kind of arthropods which are taken by the red grouse are likely to be low in numbers and consequently the arthropod component in the diet is negligible. This is the result reported in the earlier studies on the low, dry moors of north-east Scotland. In contrast to this, high altitude blanket bog supports large populations of tipulids; these and other slow-moving insects are suitable prey for the red grouse and represent an important source of nutrients, especially phosphorus and nitrogen. This is the result reported by Butterfield and Coulson (1975), for Bogend. A range of intermediate values exists between the extremes of high altitude blanket bog and the low, dry *Calluna* moors. The role of arthropods in the diet of the red grouse therefore depends on the regional differences in the abundance of suitable arthropod prey.

SUMMARY

1. From previous studies, the diet of the adult red grouse, *Lagopus lagopus scoticus*, is considered to be composed of 70 - 90% *Calluna* for the greater part of the year; the value for *Calluna* in this study fell within this range.

2. The diet is on occasion supplemented with other material. A controversy has arisen concerning the role of arthropods in the diet. The conflicting reports were carried out on different types of moors; firstly low, dry moors, where the arthropod component in the diet was found to be negligible and secondly high altitude blanket bog where the arthropod component formed in 3% of the cases over half of the items examined in the droppings.

3. During the summer of 1979, the diet of the red grouse was examined by faecal analysis at four sites at different altitudes and environmental conditions, ranging from 280 - 550m. Adult and chick droppings were examined for arthropod remains. A measure of arthropod abundance was made at each site using pitfall traps.

4. The arthropods taken by adults and chicks were the slow-moving groups; tipulids, carabid beetles, weevils and lepidopteran larvae. The biomass of such groups was found to be higher on the high altitude and wet

sites than on the low dry moors.

5. Droppings were collected on one occasion from additional sites over an altitude range. The levels of arthropod fragments in adult droppings from high moors (> 350m) were significantly higher than the corresponding levels from the low, dry moors (< 350m). ($\chi^2 = 14$, $p < 0.001$)
There is a significant correlation between the available biomass and the levels of arthropod fragments found in adult droppings during May and June, ($r = 0.830$, $p < 0.01$), but not during July and August when the levels of arthropod fragments in the droppings remained low.

6. The levels of arthropod fragments in chick droppings were very much higher than those in the adults. At the peak of arthropod fragments in chick droppings, the values were between five and fifteen times higher than the adult values. The levels in the chick droppings declined after the first few weeks of life.

7. Arthropods have higher levels of nitrogen, potassium and calcium than moorland plants and represent a concentrated source of these nutrients to red grouse on high altitude areas of blanket bog.

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APPENDIX I

Abundance of arthropod fragments in adult droppings.

Bogend

Date	No. droppings examined	0.1-1%	.1-5%	5.1-10%	10.1-30%	>30%	% with arthropods
2.5.79	30	0	0	0	0	0	0
17.5.79	30	0	0	0	0	0	0
28.5.79	30	0	0	0	0	0	0
6.6.79	30	2	5	0	0	0	23
14.6.79	30	2	4	3	12	2	77
21.6.79	30	2	8	5	11	0	87
28.6.79	30	6	5	0	1	0	40
5.7.79	30	0	5	1	1	0	23

Abundance of arthropod fragments in adult droppings.
Muggleswick High

Date	No. droppings examined	0.1-1%	1.1- 5%	5.1-10%	10.1-30%	> 30%	% with arthropods
10.5.79	30	0	0	0	0	0	0
22.5.79	30	0	0	0	0	0	0
29.5.79	30	0	0	0	0	0	0
4.6.79	30	1	8	6	1	0	53
13.6.79	30	3	6	4	1	0	47
20.6.79	30	7	7	2	1	0	57
26.6.79	30	2	4	3	2	0	37
4.7.79	30	4	4	1	0	0	30

Abundance of arthropod fragments in adult droppings.
Waskerley

Date	No. droppings examined	0.1-1%	1.1-5%	5.1-10%	10.1-30%	>30%	% with arthropods
10.5.79	30	0	0	0	0	0	0
22.5.79	30	0	0	0	0	0	0
29.5.79	30	0	0	0	0	0	0
4.6.79	30	0	5	4	9	0	60
13.6.79	30	1	8	5	13	0	93
20.6.79	30	2	8	7	6	0	77
26.6.79	30	0	1	2	0	0	10
4.7.79	30	2	2	0	1	0	17

Abundance of arthropod fragments in adult droppings.

Muggleswick Low

Date	No. droppings examined	0.1-1%	1.1-5%	5.1-10%	10.1-30%	>30%	% with arthropods
10.5.79	30	0	0	0	0	0	0
22.5.79	30	0	0	0	0	0	0
29.5.79	30	0	1	0	0	0	3
4.6.79	30	4	2	0	0	0	20
13.6.79	30	2	3	0	0	0	17
20.6.79	30	5	6	0	0	0	37
26.6.79	30	0	0	0	0	0	0
4.6.79	30	0	0	0	0	0	0

APPENDIX II

Bogend Pitfall Data.

	Date						
	17–28.5.79	6.6.79	14.6.79	21.6.79	28.6.79	5.7.79	7–14.8.79
Spiders	37	82	95	185	119	125	32
Harvestmen	0	0	2	8	4	14	30
Hemiptera	8	8	1	2	5	2	0
Staphylinids 1	2	3	4	6	7	7	1
Staphylinids 2	2	0	0	1	1	0	0
Carabids 1(<15mm)	0	4	4	4	3	0	4
Carabids 2(>15mm)	0	2	2	1	1	1	0
Other beetles	0	1	0	0	0	4	0
Beetle larvae	0	0	0	1	1	0	1
Diptera 1 (<10mm)	570	171	19	12	18	5	6
Diptera 2 (>10mm)	10	13	9	11	36	95	4
Diptera 3 *	0	6	13	3	3	5	0
Dipteran larvae	0	0	0	1	0	0	0
Hymenoptera	53	53	21	39	25	25	10
Weevils	0	0	0	0	0	0	0
Lepidoptera	0	0	0	0	0	0	1
Orthoptera	0	0	0	0	4	25	11
Lepidopteran larvae	0	1	0	0	0	2	0

* Tipulids

Muggleswick High Pitfall Data.

	16–22.5.79	29.5.79	4.6.79	13.6.79	20.6.79	26.6.79	4.7.79	9–16.8.79
Spiders	23	23	23	73	51	48	69	12
Harvestmen	0	0	1	4	13	37	33	3
Hemiptera	5	9	10	6	7	2	3	1
Staphylinids 1	3	4	4	15	21	6	1	5
Staphylinids 2	0	1	0	0	0	0	1	0
Carabids 1 ≤ 15mm	3	1	6	16	10	6	18	7
Carabids 2 > 15mm	0	0	4	18	18	1	3	5
Other beetles	0	1	0	0	3	0	0	0
Beetle larvae	0	1	2	3	4	3	3	0
Diptera 1 ≤ 10mm	13	35	83	54	22	45	45	30
Diptera 2 > 10mm	1	2	0	6	3	16	37	1
Diptera 3 *	0	0	0	0	0	0	3	1
Dipteran larvae	0	0	1	1	1	0	0	0
Hymenoptera	4	16	13	17	8	4	12	14
Weevils	1	0	0	0	0	0	1	1
Lepidoptera	0	1	3	1	3	2	1	0
Orthoptera	0	0	0	0	0	0	1	8
Lepidopteran larvae	0	1	1	1	0	0	1	1
Plecoptera	0	0	0	0	0	1	0	0

* Tipulids

Waskerley Pitfall Data.

	16–22.5.79	29.5.79	4.6.79	13.6.79	20.6 79	26.6.79	4.7.79	9–16.8.79
Spiders	21	14	37	130	156	55	87	11
Harvestmen	1	0	0	4	7	3	7	21
Hemiptera	5	17	19	11	11	11	6	6
Staphylinids 1	20	8	11	9	13	5	7	11
Staphylinids 2	0	0	0	0	0	0	1	0
Carabids 1 ≤ 15mm	4	2	7	16	9	7	5	2
Carabids 2 > 15mm	1	1	2	9	12	4	2	3
Other beetles	0	1	0	2	3	0	1	0
Beetle larvae	0	1	3	1	1	0	2	0
Diptera 1 ≤ 10mm	123	154	116	71	48	41	53	28
Diptera 2 > 10mm	3	1	7	9	6	3	6	13
Diptera 3 *	0	0	4	3	4	2	20	1
Dipteran larvae	0	0	0	0	0	0	0	0
Hymenoptera	3	13	15	18	12	11	12	65
Weevils	0	0	1	0	3	1	3	1
Lepidoptera	0	0	0	0	1	1	0	0
Orthoptera	0	3	0	0	5	1	17	12
Lepidopteran larvae	0	0	1	4	0	0	1	1
Plecoptera	0	0	1	1	1	3	2	0

* Tipulids

Muggleswick Low Pitfall Data.

	16-22.5.79	29.5.79	4.6.79	13.6.79	20.6.79	26.6.79	4.7.79	9-16.8.79
Spiders	21	22	34	97	75	55	64	20
Harvestmen	1	0	2	6	5	3	4	9
Hemiptera	21	10	24	16	11	4	16	5
Staphylinids 1	3	2	0	13	2	1	3	3
Staphylinids 2	0	1	0	0	0	0	0	0
Carabids 1 ⩽15mm	3	1	4	15	7	4	11	8
Carabids 2 >15mm	1	1	7	16	17	6	7	7
Other beetles	0	0	1	2	0	1	4	0
Beetle larvae	1	0	1	2	3	5	1	4
Diptera 1 ⩽10mm	617	165	49	48	55	55	51	21
Diptera 2 >10mm	1	12	7	3	8	9	17	2
Diptera 3 *	0	0	0	0	1	0	2	3
Dipteran larvae	1	0	0	0	1	0	0	1
Hymenoptera	30	66	64	97	45	39	46	17
Weevils	0	1	7	17	3	1	6	0
Lepidoptera	0	0	1	0	1	0	1	0
Orthoptera	0	0	0	1	4	0	0	5
Plecoptera	0	0	0	0	0	1	1	0
Lepidopteran larvae	0	0	0	0	0	0	0	0

* Tipulids

APPENDIX III

Analysis of adult red grouse droppings.

Site: Bogend

a = percentage fragments and standard deviation

b = frequency of occurrence in 30 droppings (%)

Date	*Calluna Erica* a	b	*Vaccinium* a	b	*Eriophorum* a	b	*Polytrichum* a	b	*J. squarrosus* a	b	Arthropoda a	b	Unidentified a	b
2.5.79	86 ±7	100	0	0	5 ±7	40	0	0	0	0	0	0	9	100
17.5.79	87 ±6	100	0	0	4 ±6	50	0	0	0	0	0	0	9	100
28.5.79	85 ±10	100	0	0	6 ±10	40	0	0	0	0	0	0	9	100
6.6.79	85 ±6	100	0	0	3 ±5	37	1.5 ±3	27	0	0	1.5 ±5	23	10	100
14.6.79	73 ±13	100	0	0	3 ±3	33	4 ±4	70	0	0	10 ±9	77	10	100
21.6.79	73 ±11	100	0	0	6 ±4	97	2 ±4	43	0	0	10 ±9	87	9	100
28.6.79	82 ±5	100	0	0	2 ±2	70	2 ±4	40	2 ±3	43	1 ±4	40	11	100
5.7.79	85 ±6	100	0	0	2 ±3	57	2 ±6	13	0	0	2 ±5	23	9	100
14.8.79	84 ±3	100	0	0	0	0	0	0	4 ±2	97	0.3 ±1	20	12	100

Analysis of red grouse droppings.

Site: Muggleswick High

a = percentage fragments and standard deviation

b = frequency of occurrence in 30 droppings (%)

Date	*Calluna* *Erica*		*Vaccinium*		*Eriophorum*		*Polytrichum*		*J. squarrosus*		Arthropoda		Unidentified	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
10.5.79	90 ±2	100	0	0	0	0	0	0	0	0	0	0	10	100
22.5.79	83 ±9	100	0	0	0	0	6 ±8	70	0	0	0	0	11	100
29.5.79	89 ±3	100	0	0	0	0	1 ±1	17	0	0	0	0	10	100
4.7.79	85 ±5	100	0	0	0	0	2 ±3	20	0	0	3 ±4	53	10	100
13.6.79	86 ±6	100	0	0	1 ±2	17	2 ±3	27	0	0	2 ±3	47	9	100
20.6.79	85 ±5	100	0	0	2 ±2	50	1 ±1	20	1 ±3	3	2 ±3	57	9	100
26.6.79	84 ±6	100	0	0	2 ±4	30	1 ±2	10	0	0	2 ±4	37	11	100
4.7.79	88 ±3	100	0	0	1 ±2	20	0	0	0	0	1 ±1	30	10	100
15.8.79	85 ±9	100	0	0	0	0	0	0	3 ±9	30	0.5 ±2	10	11	100

Site: Waskerley

Analysis of red grouse droppings.

a = percentage fragments and standard deviation

b = frequency of occurrence in 30 droppings (%)

Date	*Calluna Erica*		*Vaccinium*		*Eriophorum*		*Polytrichum*		*J. squarrosus*		Arthropoda		Unidentified	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
10.5.79	89 ±3	100	0	0	0	0	0	0	0	0	0	0	11	100
22.5.79	85 ±9	100	0	0	1 ±4	17	0	0	5 ±9	27	0	0	9	100
29.5.79	82 ±12	100	0	0	0	0	1 ±3	17	6 ±10	33	0	0	11	100
4.6.79	82 ±8	100	0	0	0	0	0	0	2 ±4	27	7 ±7	60	9	100
13.6.79	69 ±11	100	0	0	0	0	10 ±8	83	1 ±2	27	11 ±8	93	9	100
20.6.79	79 ±8	100	0	0	0	0	2 ±3	60	1 ±2	33	7 ±7	77	11	100
26.6.79	80 ±7	100	0	0	0	0	4 ±3	57	4 ±7	33	1 ±2	10	11	100
4.7.79	85 ±5	100	0	0	0	0	2 ±3	57	2 ±4	57	1 ±2	17	10	100
13.8.79	35 ±15	100	0	0	0	0	0	0	55 ±9	100	0.5 ±1	27	9	100

Analysis of red grouse droppings.

Site: Muggleswick Low

a = percentage fragments and standard deviation

b = frequency of occurrence in 30 droppings (%)

Date	*Calluna Erica*		*Vaccinium*		*Ericphorum*		*Polytrichum*		*J. squarrosus*		Arthropoda		Unidentified	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
10.5.79	90 ±3	100	0	0	1 ±1	47	0	0	0	0	0	0	9	100
22.5.79	90 ±2	100	0	0	0	0	0	0	0	0	0	0	10	100
29.5.79	90 ±4	100	0	0	0	0	1 ±4	10	0	0	0.1 ±1	10	9	100
4.6.79	85 ±9	100	0	0	0	0	6 ±8	63	0	0	0.4 ±1	20	9	100
13.6.79	89 ±4	100	0	0	0	0	1 ±2	27	0	0	0.3 ±1	17	10	100
20.6.79	82 ±4	100	0	0	0	0	6 ±3	100	0	0	0.8 ±1	37	11	100
26.6.79	86 ±3	100	1 ±3	37	0	0	2 ±3	100	0	0	0	0	11	100
4.7.79	87 ±3	100	2 ±3	50	0	0	0	0	0	0	0	0	11	100
15.8.79	68 ±12	100	1 ±2	46	0	0	0	0	21 ±12	90	0	0	10	100

APPENDIX IV

Analysis of red grouse droppings.

a = percentage fragments and standard deviation

b = frequency of occurrence in 30 droppings

Site	Date	*Calluna Erica* a	*Calluna Erica* b	*Vaccinium* a	*Vaccinium* b	*Polytrichum* a	*Polytrichum* b	*J. squarrosus* a	*J. squarrosus* b	Arthropoda a	Arthropoda b	Unidentified a	Unidentified b
Beldom Bottom	2.7.79	86 ±3	100	2 ±2	63	0	0	0	0	2 ±0.5	23	10	100
Golden Groves	2.7.79	87 ±5	100	1 ±2	17	0	0	1 ±4	10	1 ±0.5	17	10	100
Bollihope Common	2.7.79	83 ±6	100	2 ±2	50	0	0	2 ±3	43	3 ±0.9	53	10	100
Apedale	2.7.79	78 ±8	100	0	0	0	0	4 ±5	67	9 ±1.6	77	9	100
Yarlsey Moss	23.6.79	88 ±3	100	1 ±3	37	0	0	0	0	0.1 ±0.2	7	11	100
Bolton Cross	23.6.79	87 ±3	100	2 ±2	47	0	0	0	0	0.7 ±0.4	30	10	100
Kildale	23.6.79	88 ±3	100	0	0	1 ±2	33	0	0	0.1 ±0.2	7	11	100
Job Cross	23.6.79	88 ±3	100	0	0	1 ±2	23	0	0	0.3 ±0.2	13	11	100
High Tranmire	23.6.79	87 ±3	100	1 ±2	37	1 ±2	40	0	0	0.3 ±0.2	13	11	100
Murk Mire	23.6.79	89 ±3	100	1 ±2	27	0	0	0	0	0	0	10	100