Ecological investigations on certain dung-inhabiting coleoptera, with special reference to the beetles of the genus aphodius (illiger)

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ECOLOGICAL INVESTIGATIONS ON CERTAIN DUNG-INHABITING COLEOPTERA, WITH SPECIAL REFERENCE TO THE BEETLES OF THE GENUS APHODIUS (ILLIGER).

By

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-being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1957.

ECOLOGICAL INVESTIGATIONS ON CERTAIN DUNG-INHABITING COLEOPTERA, WITH SPECIAL REFERENCE TO THE BEETLES OF THE GENUS *APHODIUS* (ILLIGER.).

This work was undertaken on an area of moorland in the northern Pennines, between 1954 and 1956. Here 16 species of dung-inhabiting beetles of the genus *Aphodius* were found.

The adult taxonomy of two closely related species, *A. prodromus* and *A. sphacelatus*, was examined in detail; and the larval stages of three previously unknown species were identified.

The biology of several species was studied, enabling the author to discover some of the factors which separated them ecologically.

Attempts were made to assess the place of *Aphodius* beetles in the utilisation of sheep dung, and with this end in view the distribution, form and condition of dung on several types of vegetation were examined. Observations were also made on dung-inhabiting lumbricid worms and dipterous flies which were the other organisms of importance in the utilisation of dung. The worms were most effective in removing dung, but their activities varied on the different types of vegetation. Dipterous larvae were of second importance, and were not appreciably affected by vegetation type. Averaged over the whole year, only one-fifth of the sheep droppings were infested by *Aphodius*. The beetle infestation was not affected by vegetation type.

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Contents.

ECOLOGICAL INVESTIGATIONS ON CERTAIN DUNG--INHABITING COLEOPTERA, WITH SPECIAL REFERENCE TO THE BEETLES OF THE GENUS *APHODIUS* (ILLIGER).

I. Introduction.

This work was undertaken with the object of increasing our knowledge of the biology of the dung-inhabiting beetles of the genus *Aphodius*. As these animals occurred commonly in dung, an attempt was made to determine how closely several of the species were related ecologically. A general impression was obtained of the relationship of these beetles to other organisms living and feeding in dung, and it was attempted to assess the importance of these biotic agents in utilising dung.

The investigation was carried out mainly on the Moor House Nature Reserve where good facilities were available for field work. Here sheep were relatively unrestricted in their movements, so that the deposition of dung was natural. These conditions could only be found on an upland area, for the intensive farming which occurs on lowland calls for strictly controlled grazing.

II. The Areas of Study.

Most of the detailed observations in this study were carried out on the Moor House National Nature Reserve (Nat. grid; 54°41′ N., 2°23′ W). This is situated in the north-west corner of Westmorland, covering 10,000 acres (c. 4,000 hectares). It includes part of the summit ridge of the northern Pennines, the steep escarpment on the west side, and a broad stretch of the dip slope to the east (Conway, 1955). The mountain tops of Little Dun Fell (2761 ft.), Great Dun Fell (2780 ft.), and Knock Fell (2604 ft.) are covered largely by an impoverished grassland and *Eriophorum* moor, while lower and further to the east is a large area of eroded blanket bog with *Calluna* as the dominant plant. In the north-eastern corner of the Reserve, the blanket bog is still actively developing, *Sphagna* of several species forming an important component of the plant cover.

Drainage of the eastern slopes of the

Reserve is effected by the headwaters of the R. Tees. The smaller becks intersect the peat and provided slopes too steep for much peat development, so that a mixed vegetation of Juncus, Eriophorum, Polytrichum, Nardus and other plants is established. The larger streams have built up alluvial areas of sand, gravel, and peat, on which a Fescue-bent grassland has developed. Further variation is given to the vegetation complex where small outcrops of the underlying limestone reach the surface, here a closely knit turf of Agrostis and Festuca is found.

The sheep grazing provided by these different vegetation types is very variable. Where Calluna or Eriophorum are dominant, the grazing is very poor, and the grassland of the summit ridge appears to be little better. Where Juncus squarrosus is prominent the grazing is more intensive throughout the year. The new growth of J. squarrosus is particularly valuable as a spring bite for the sheep before the grasses begin to shoot, and these areas also provide food after grasses have ceased to grow under conditions of summer drought. The grassland of the alluvial flats and the areas of limestone outcrop support the greatest density of sheep throughout their stay on the moor.

Comparative observations of the seasonal succession of beetles of the genus *Aphodius* were made in the intensive agricultural area around Durham City.

For taxonomic purposes collections of *Aphodius prodromus* and *A. sphacelatus* were made in many parts of Co. Durham, while a study of the altitudinal distribution of *A. lapponum* involved visits to a number of widely dispersed localities in the northern Pennines.

The climatic conditions of the Moor House reserve have been studied by Manley (1936, 1942, and 1943), who concluded that the climate was sub-arctic, being similar to that operative in parts of southern Iceland at sea-level. The average annual rainfall and temperature were probably higher than in southern Iceland, but the amount of sunlight was somewhat less. The average annual rainfall was estimated to be 70 inches at Moor House, but much of this rain is of little importance biologically, for it falls between late autumn and early spring when the moor is usually saturated. The activity of flying insects at Moor House is largely confined to the period late April to September, and a consideration of rainfall during this period bears a more direct relationship to the activities of the animals. The year 1954 was particularly wet, the May to September period having 47% more rain than the average of 33.2in. The summer of 1955 was dry, the rainfall being 16% below average over the same period, but this was followed by another wet season with 20% above average. The percentage deficit for 1955 gives but a poor indication of the drought conditions which existed during that summer. In August, streams dried up almost entirely, and the soil on limestone areas was dry to the touch at a depth of two inches. Even in late September after several inches of rain had fallen with but little evaporation, the peat was still dry below the first inch. During this drought the grasslands ceased to produce fresh grazing and the sheep were forced to seek food on areas where <u>J. squarrosus</u> was a prominent member of the vegetation.

III. Taxonomic and General Literature.

Most groups of the British Coleoptera are well known taxonomically, and considerable attention has been given to the Lamellicornia. Fowler's (1895) 'British Coleoptera' forms the standard work from which all of the later keys have been developed, and from the point of view of general information it was found to be the most useful. The information on *Aphodius* given in Joy's (1932) 'Practical Handbook of British Beetles' is very similar to Fowler, but in that it uses only characters of the dorsal surface it is imprecise and restrictive in use. Britton (1956) collected together most of the taxonomic information on the British members of the genus, but difficulty is still experienced with some of the characters which have been employed. This key also suffers from one serious defect which prevents *A. constans* being identified at all. During the study recourse was made to several foreign keys, the illustrations of Reitter (1908) were useful provided that the colours were ignored, while Janssens (1951) went into a wealth of structural detail. Hansen (1925) and Landin (1946) provided information which allowed A. prodromus and A. sphacelatus to be separated satisfactorily. Schmidt (1922) keyed all of the known Aphodius species.

The nomenclature used in the present study follows that of Britton.

As with most insect groups the larval stages of Aphodius have received much less attention than the imagos. In the 19th century Schiodte (1873) made a start by describing the larva of A. rufipes, the mouthparts being figured in detail. Rosenhauer (1882) followed with descriptions of five species found in Britain. Madle (1935-36) made a more satisfactory advance when he described and keyed 13 species, of which 12 occurred in Britain. British coleopterists were helped when van Emden (1941) translated most of Madle's key and added one species. Even with this translation the larval taxonomy is poorly known for 25 British species remain to be described.

Although much has been written about the inhabitants of herbivore dung, it has not been possible to make much direct comparison between the literature and the present study. Lawrence (1954), Hammer (1941), and Mohr (1943) were chiefly concerned with the Diptera, the beetles receiving only incidental mention. Svendsen (1955) worked with the Lumbricidae which occurred late in the succession of dung inhabitants, and Aphodius beetles were not mentioned.

Several authors have worked specifically on Aphodius, Hafez (1939) with A. lividus, Madle (1934) with A. rufipes, and Carne (1956) with A. howitti. Even here comparison with the present study was limited, for each author worked in very different environmental conditions. Hafez studied A. lividus in Eygpt in the dung of camels, horses, buffaloes and cows. The climatic conditions were such that dung became desiccated within a few days, and it is not known whether it is a specific character of this species to carry through its immature stages in the vegetative mat beneath dung, or whether this procedure was forced on the species because of the climate.

Madle worked with *A. rufipes*, a species which occurred uncommonly at Moor House, however, the life-cycle on the moorland area corresponded closely with Madle's findings. Schmidt (1935) described in general terms the life-cycles of *A. fimetarius* and *A. fossor*, and considered the distribution of some members of the genus in a more detailed manner than Kolbe (1905). Recently, Carne described the life-cycle of *A. howitti*, which is a pest of improved grasslands in parts of Australia. The behaviour and population dynamics of the species were studied in detail. The scarcity of *Aphodius* beetles on the moorland area was such as to prevent much progress being made along these lines.

IV. The Taxonomy and Distribution of *Aphodius*.

The beetles of the genus *Aphodius* are members of the Lamellicornia, a sharply defined section of the Coleoptera. They are distinguished by their antennae terminating in a distinct large club composed of between three and seven lamellae. In the Lucanidae, which includes the Stag beetles, these lamellae are fixed, but in the Scarabaeidae they are freely moveable, a feature which is immediately noticed on watching an Aphodius beetle examining its environment. The family Scarabaeidae are distributed throughout the world, but with the exception of the genus Aphodius, they are poorly represented in Europe. They are most commonly found in warmer and tropical climates. This can be seen from Table I, which shows the distributions of some of the coprophagous members of the Lamellicornia (Kolbe, 1905).

The genus Aphodius can be said to have a world-wide distribution, and Table I illustrates that it flourishes in the Palaearctic. Many species are almost cosmopolitan, for instance A. fimetarius can be found at sea-level in Britain and at over 8300 feet in the Tyrolean Alps, it occurs in North America, Europe, Asia and even in Australasia, although it may have been introduced there. Other species are more restricted in that they are confined to some broad climatic zone. A. alpinus is found in cool countries, at high

Table I.

The Distribution of some Coprophagous Lamellicornia.

(Compiled from Kolbe, 1905.)

	Total species	Region Pal.	Aeth.	Ind.	Austr.	Neotr.	Nearc.
Geotrupinae							
Geotrupes	63	37	-	7	-	13	10
Bolboceras	142	10	32	30	40	23	7
Pleocominae							
Pleocoma	8	-	-	-	-	-	8
Troginae							
Acanthocerus	55	-	-	1	-	53	1
Trox	137	24	34	10	24	31	21
Aphodiinae							
Ataenius	76	2	-	2	4	55	18
Aphodius	490	274	90	25	12	37	70
Onthophaginae							
Onthophagus	879	126	422	164	89	65	13
Pinotinae							
Canthidium	99	-	-	-	1	98	-
Pinotus	85	-	-	-	-	84	2
Coprinae							
Copris	106	9	50	30	-	9	6
Canthoninae							
Canthon	149	-	-	-	-	139	14
Scarabaeinae							
Scarabaeus	95	9	82	5	-	-	-
Phanaeinae							
Phaneus	98	-	-	-	-	92	7

Schmidt (1922) listed a further 196 Aphodius species, very few of which were found in the Palaearctic.

latitudes in Lapland, Finland, Sweden and Iceland, or in the Alps of southern Europe, but it is absent from the warmer plain of central Europe.

There appears to be no correlation

between vegetational type and the species distribution as in the case of many other insect groups, but this may be because the food of the organism is dung. It is possible that subtle differences in dung constitution may be of importance to some *Aphodius* species. It has been suggested that in Britain *A. constans* shows a preference for areas with calcareous soils (Whicher, pers. com.), if this is so it could be a reflection of slight differences in dung constitution because of the grasses growing on calcareous soils.

V. The British Species of Aphodius.

At present 42 species of *Aphodius* are recognised as British (Britton). The paucity of this fauna becomes obvious when compared with neighbouring European countries, for Paulian (1941) records 75 species for France, Reitter 63 for Germany, while Belgium has a list of 56 (Janssens). Denmark which is only one quarter the size of the British Isles, and which is topographically much less variable, boasts a fauna of 42 species (Hansen).

The distribution of individual species

Table II.

The Species of <u>Aphodius</u> found at Moor House and Durham.

	Moor House	Durham
A. fossor	*	*
A. foetens	*	
A. fimetarius	*	*
A. scybalarius	*	*
A. ater	*	*
A. constans	*	*
A. rufus		*
A. lapponum	*	
A. tenellus	*	
A. pusillus		*
A. merdarius	*	*
A. conspurcatus	*	*
A. prodromus	*	*
A. sphacelatus	*	*
A. contaminatus	*	*
A. luridus	*	
A. rufipes	*	*
A. depressus	*	*

has not been studied thoroughly in Britain, the information given by Britton hardly improves on that of Fowler. Notes on the relative abundance of different species suffer from the limitation that collectors have been more active in the southern parts of Britain. For instance, Britton records <u>A. erraticus</u> as being 'common,' but this is not true for either of the areas used in this study for the species was never taken. The same applies to <u>A. scybalarius</u> which was only taken four times.

All of the species are not generally distributed, for instance, A. lapponum occurs in the northern parts of the country on high ground while A. consputus is restricted to the south-east corner of England.

Table II shows the species found at Moor House and Durham during the study. Of these, only single specimens of A. foetens, A. scybalarius, A. fossor and A. luridus have been found at Moor House. The same applies to A. pusillus and A. scybalarius at Durham.

VI. The Taxonomy of A. prodromus and A. sphacelatus.

Three species of the sub-genus Melinopterus (Muls.) occur in Britain, one of these A. consputus is restricted to the south-east corner of England, while A. prodromus and A. sphacelatus are recorded as being ubiquitous both here and on the continent. The latter two species are structurally similar and difficulty was experienced in separating them on the characters given in the commonly used British keys.

The taxonomic characters given in the

several keys studied are listed below.

A. prodromus

1/. The males have the apical spine on the anterior tibia truncated and with a short backwardly directed tooth. (Fowler, Joy, Janssens, Reitter, Paulian and Britton.)

2/. The superior apical spine of the posterior tibia is typically shorter than the metatarsus. (Janssens, Reitter, Paulian, Schmidt, and Landin.)

3/. The length of the metatarsus is equal to the three following tarsal joints together. (Janssens, Schmidt, and Paulian)

4/. The 7th elytral stria is considerably longer than the 8th anteriorly. (Landin and Hansen)

5/. The base of the pronotum is not bordered throughout. (Landin.)

6/. The frontoclypeal suture is absent. (Britton)

A. sphacelatus

1/. The males have the apical spines of the anterior tibia pointed.

2/. The superior apical spine of the posterior tibia is equal to the metatarsus.

3/. The length of the posterior metatarsus is less than the three following joints united.

4/. The 7th elytral stria is just longer than or equal to the 8th anteriorly.

5/. The base of the pronotum is obviously bordered throughout.

6/. The frontoclypeal suture is distinct.

The characters listed above were examined in relation to each other, most reliance being put on point 4/.

On this basis character 1/ was found to be satisfactory. Character 2/ was of little practical value, for of 100 A. prodromus, 53 had the superior spine of the posterior tibia equal in length to the metatarsus, a characteristic of A. sphacelatus.

In order to examine the efficacy of character 3/, the hind metatarsus and the first three tarsal joints were measured on 100 animals of each species. In addition the maximum thoracic width of each animal was recorded. The distributions of the ratios of three tarsal joints to the metatarsus in both species are shown in Table III.

Table III.

Leg Ratios of A. prodromus and A. sphacelatus.

Leg ratios.	No. of animals.	
3 tarsal joints / metatarsus	A. prodromus	A. sphacelatus
0.889 - 0.938	0	1
0.939 - 0.988	4	2
0.989 - 1.038	6	11
1.039 - 1.088	21	16
1.089 - 1.138	23	17
1.139 - 1.188	22	19
1.189 - 1.238	15	14
1.239 - 1.288	7	11
1.289 - 1.338	1	6
1.339 - 1.388	1	2
1.389 - 1.438	0	1
Mean leg ratio	1.1185	1.1860

The difference between the mean leg ratios was significant statistically ($P < .01$), confirming that on average, the length of the three tarsal joints was longer relative to the metatarsus in A. sphacelatus than in A. prodromus. The ratios appeared to vary with the size of the animal, so each ratio was compared with the maximum thoracic width of the animal. The results are shown in Table IV, and are illustrated in Fig. 1.

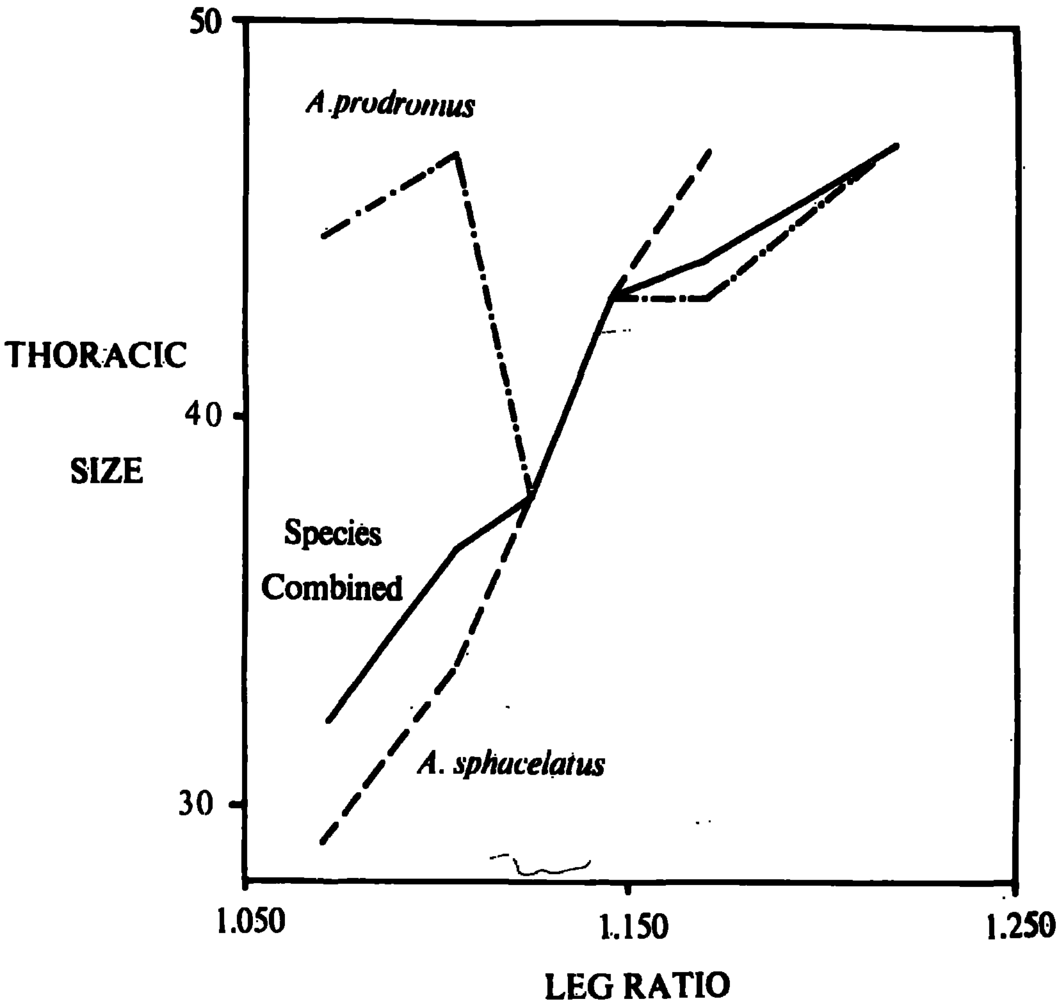


Fig. 1. The relationship between the size of animal and the ratio of the hind metatarsus to three tarsal joints in A. prodromus and A. sphacelatus.

Table IV.

Correlation of Thoracic Width and Leg Ratios in A. prodromus and A. sphacelatus.

Thoracic width		Leg ratios		
Size group	Mean size	All animals	A. prodromus	A. sphacelatus
29-34	32.5	1.2279	1.1198	1.2689
35-36	35.5	1.1822	1.1097	1.2043
37-38	37.5	1.1690	1.1771	1.1641
39-40	39.6	1.1236	1.1231	1.1242
41-43	42.0	1.1172	1.1202	1.1057
44-53	47.0	1.0827	1.0827	...

When both species were combined, there was an inverse correlation between thoracic width and the leg ratio. However, on separating them the correlation broke down. There was a significant difference between the leg ratios of the small animals of the two species ($P < .001$). Thus character 3/ was valid in that there was a difference between the two species, but variation was so great that the character was of no practical importance.

Character 5/ was found to be correct but inconvenient to use, for the difference was difficult to observe.

Character 6/ was useful, but in some small specimens of A. prodromus slight indentations were found on the head which could have represented the frontoclypeal suture.

Britton (pers. com.) on examining the value of character 4/, stated that it appeared to be satisfactory for British specimens of both species, but some animals from Algeria which appeared to be A. sphacelatus, had the 8th elytral stria short as in A. prodromus. The aedeagi of these specimens were intermediate between those of the two species, but in some respects were identical with those of A. sphacelatus. Britton suggested that A. prodromus and A. sphacelatus might be one polymorphic species.

VII. The Larval Taxonomy.

The taxonomy of the immature stages of the genus Aphodius is poorly known. Only cursory attention has been given to the egg, pupal, and first two larval stages. What information there is available about the third instar larvae is scattered and incomplete.

In all, 12 of the 18 species occurring

at Moor House and Durham have been identified in the third larval instar. It has been possible to check and confirm 7 of the known species, and in addition *A. lapponum*, *A. sphacelatus* and *A. tenellus* have been definitely identified. All of the commonly occurring species on the two areas were known.

Characters of importance in the taxonomy of the larvae are, 1/ the number of hairs on the lateral callus of each segment of the abdomen, and 2/ the structure of the 'raster,' or last abdominal sternite. The arrangement of the spines on the raster serves as a character of specific importance in the present stage of knowledge. Figs. 2, 3, and 4 show diagrammatically the rasters of 6 species not illustrated by Madle. The drawings were made from the postero-ventral position, Madle's technique being followed for the sake of uniformity. The position of the hairs on the raster have not been drawn with the accuracy of the spines, as they were not examined from the point of view of specific characters. The figures were of third larval instars, slight differences occurring in other stages at least in

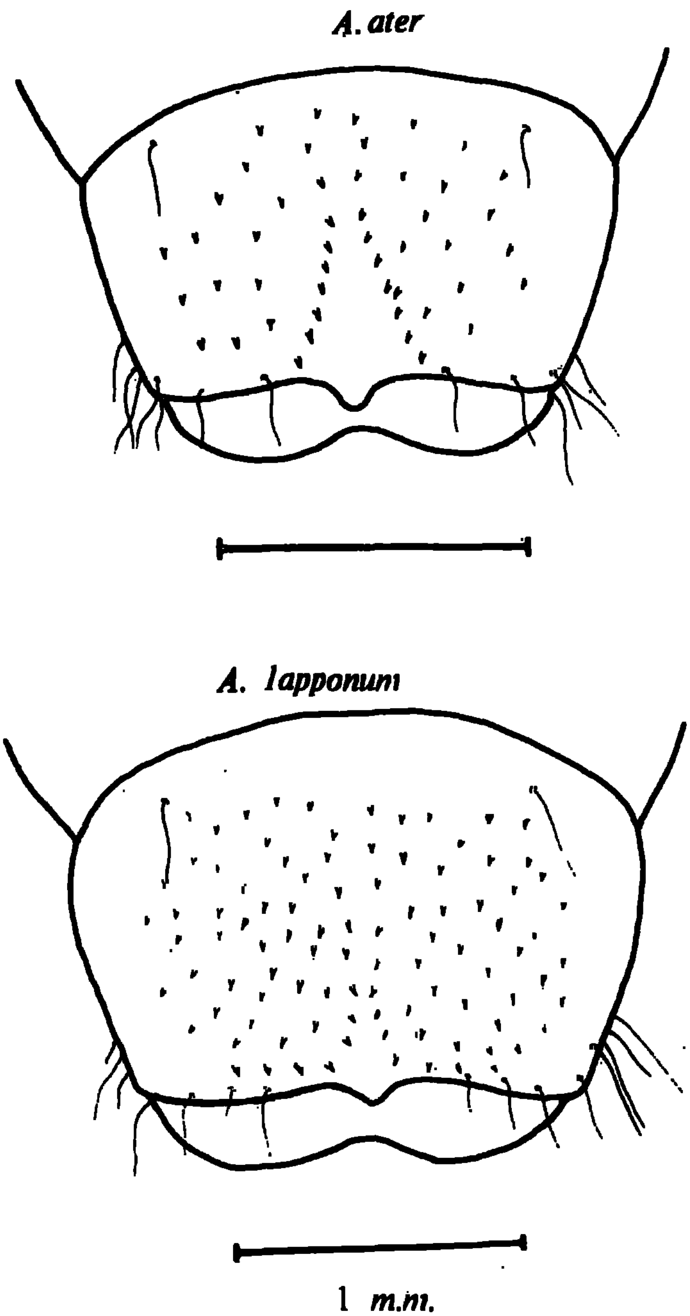


Fig. 2. The 'rasters' of third instar larvae of <u>A. ater</u> and <u>A. lapponum</u>.

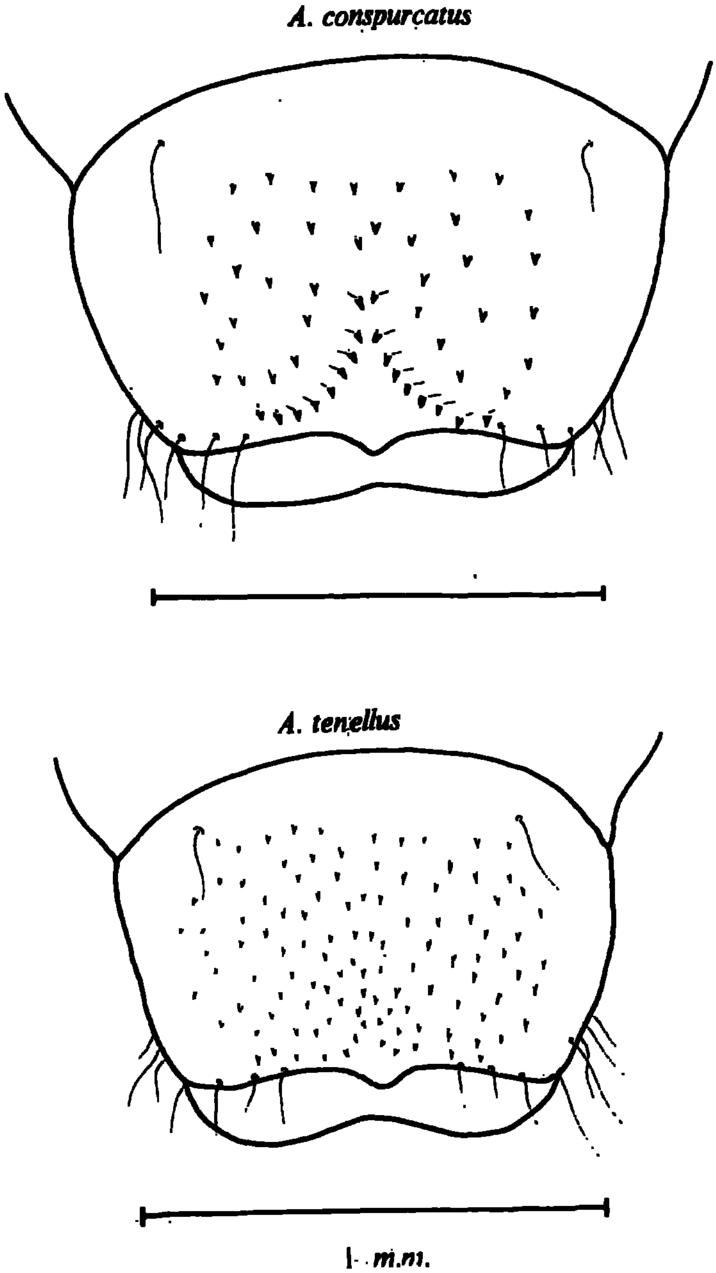


Fig. 3. The 'rasters' of third instar larvae of <u>A. conspurcatus</u> and <u>A. tenellus</u>.

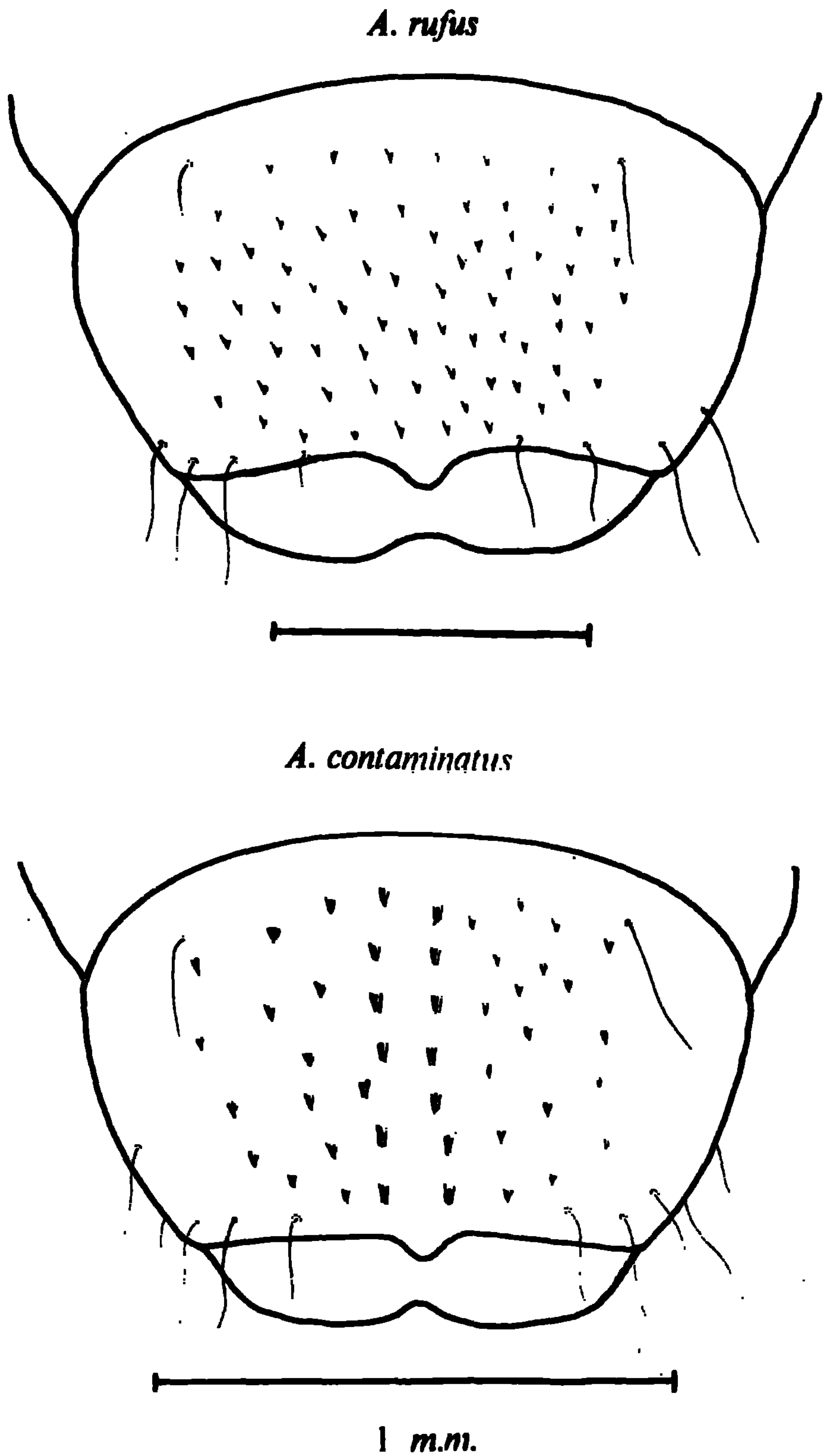


Fig. 4. The 'rasters' of third instar larvae of A. rufus and A. contaminatus.

some species.

In *A. lapponum* the extent of the space separating the raster into two lateral halves varied (Fig. 2.), so that in some animals it was obvious while in others it was obscure. The size of the spines forming the shallow 'V' posteriorly was sometimes similar to that of the other spines, but sometimes they were obviously stouter. As with most of the other species, *A. lapponum* had two setae on each lateral callus of the abdomen. In the third instar at least, the base of the mandibles was light in colour forming a distinct contrast to the reddish-brown head capsule.

The raster of *A. tenellus* had little to distinguish it from that of *A. lapponum* (Fig. 3.) except for its smaller size. In all of the specimens examined, spines of only one size were involved. In this species there were two setae on each lateral callus of the abdomen.

The stronger median spines of *A. contaminatus* varied in size and position which affected the appearance and extent of the median bare area (Fig. 4.).

The raster of *A. sphacelatus* was not

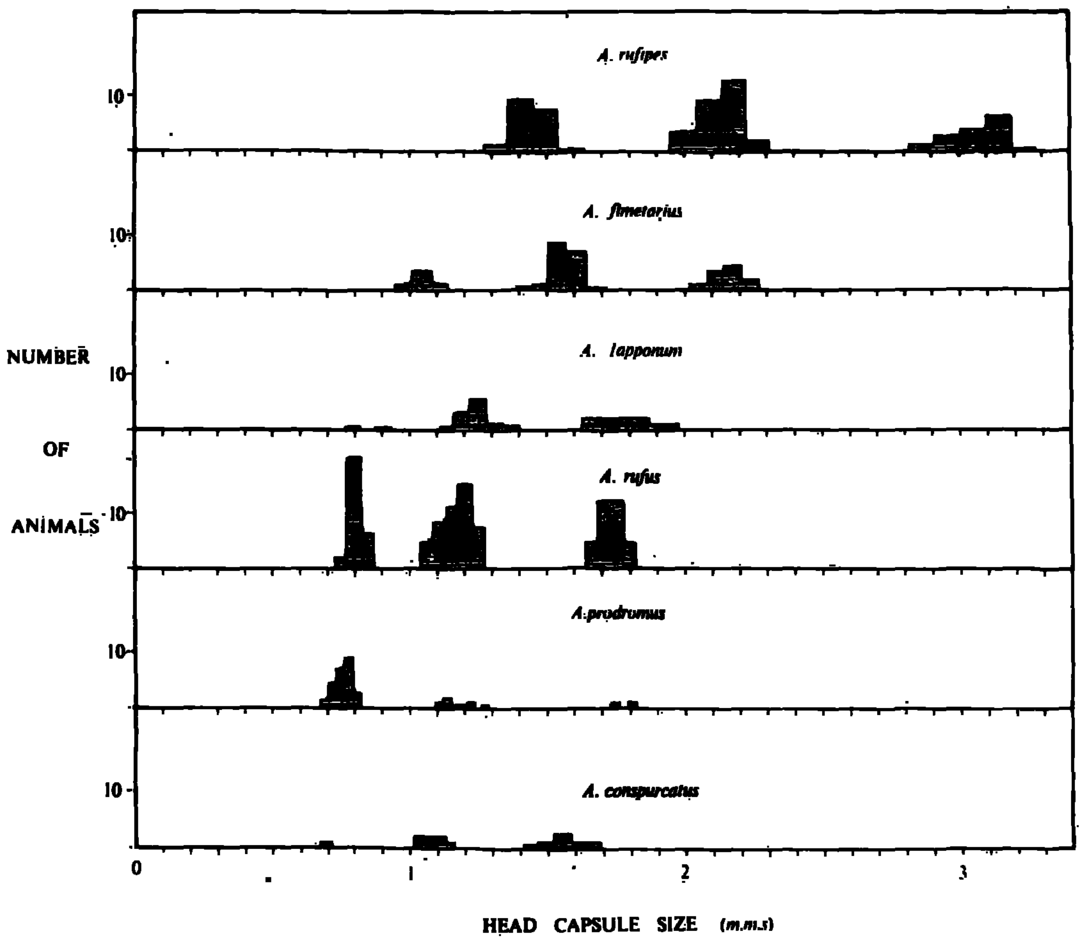


Fig. 5. Larval head capsule sizes for several <u>Aphodius</u> species.

figured, as few specimens were available for examination. However the raster was not obviously patterned, the spines being of one strength only. Each lateral callus of the abdomen carried two setae, and the head capsule was yellowish-brown with dark brown 'eye-spots', situated postero-externally to the antennae.

The specimens which were obtained from A. prodromus cultures did not correspond to the description given by Madle. However it would not be justifiable to state dogmatically that Madle's identification was incorrect, for very few specimens were obtained from satisfactory cultures. The animals believed to be A. prodromus did not have a marked 'V' of strong spines on the raster and had two setae on each lateral callus of the abdomen. The raster resembled that of A. sphacelatus but there was a suggestion of stronger central spines and a trace of a central bare area as in A. contaminatus. The head capsule was yellowish-brown as in A. sphacelatus, but no specimens had the dark brown 'eye-spots' of that species. The few larvae which Madle measured had head capsules in the third instar of 1.82-1.85mm.

The measurements made by the present author varied between 1.65-1.82mm (Table V.).

Table V.

Larval Head-capsule Measurements (mms.).

Species	Larval instars.					
	1st		2nd		3rd	
	min.	max.	min.	max.	min.	max.
A. rufipes	1.32	1.59	1.99	2.27	2.88	3.25
A. fimetarius	0.98	1.12	1.42	1.69	2.06	2.25
A. lapponum	0.79	0.91	1.13	1.38	1.66	1.96
A. rufus	0.75	0.86	1.08	1.25	1.68	1.82
A. prodromus	0.60	0.82	1.11	1.29	1.65	1.82
A. conspurcatus	0.69	0.69	1.03	1.15	1.44	1.66
A. sphacelatus			1.06	1.23	1.53	1.88

In that A. prodromus and A. sphacelatus are very closely related taxonomically, it seems unlikely that the larvae should differ so conspicuously as would be the case if Madle's identification were correct. The one specimen listed in the British Museum as A. prodromus was of no value, it had been kept in 70% alcohol and had disintergrated.

Fig. 5 shows the head capsule measurements which were carried out, and Table V lists the size range found for each instar. These figures supplement those produced by van Emden.

VIII. The Distribution of A. prodromus and A. sphacelatus.

Examination of material collected at Moor House and Durham revealed only small numbers of A. sphacelatus among the A. prodromus. In view of the reported abundance of A. sphacelatus, an intensive search was carried out in an attempt to find it in numbers. At Bishop Auckland, Coundon, and Aycliffe collections were made which revealed large proportions of A. sphacelatus (Fig. 6.). Table VI shows the relative abundance of A. sphacelatus in collections which were made in Co. Durham, while Table VII shows the results of collections made in various other parts of Great Britain. It is clear that the two species do not have similar distributions. In Co. Durham collections of three types were discernible, in the Bishop Auckland to Aycliffe area A. sphacelatus was common, sometimes being more abundant than A. prodromus. About Durham, A. sphacelatus occurred regularly but was uncommon, rarely forming 10% of the two species combined. In the third type of collection only a few specimens of A. sphacelatus occurred, such collections were made at Cleadon, Coxhoe, Trimdon, and Sedgefield. It is of interest to note

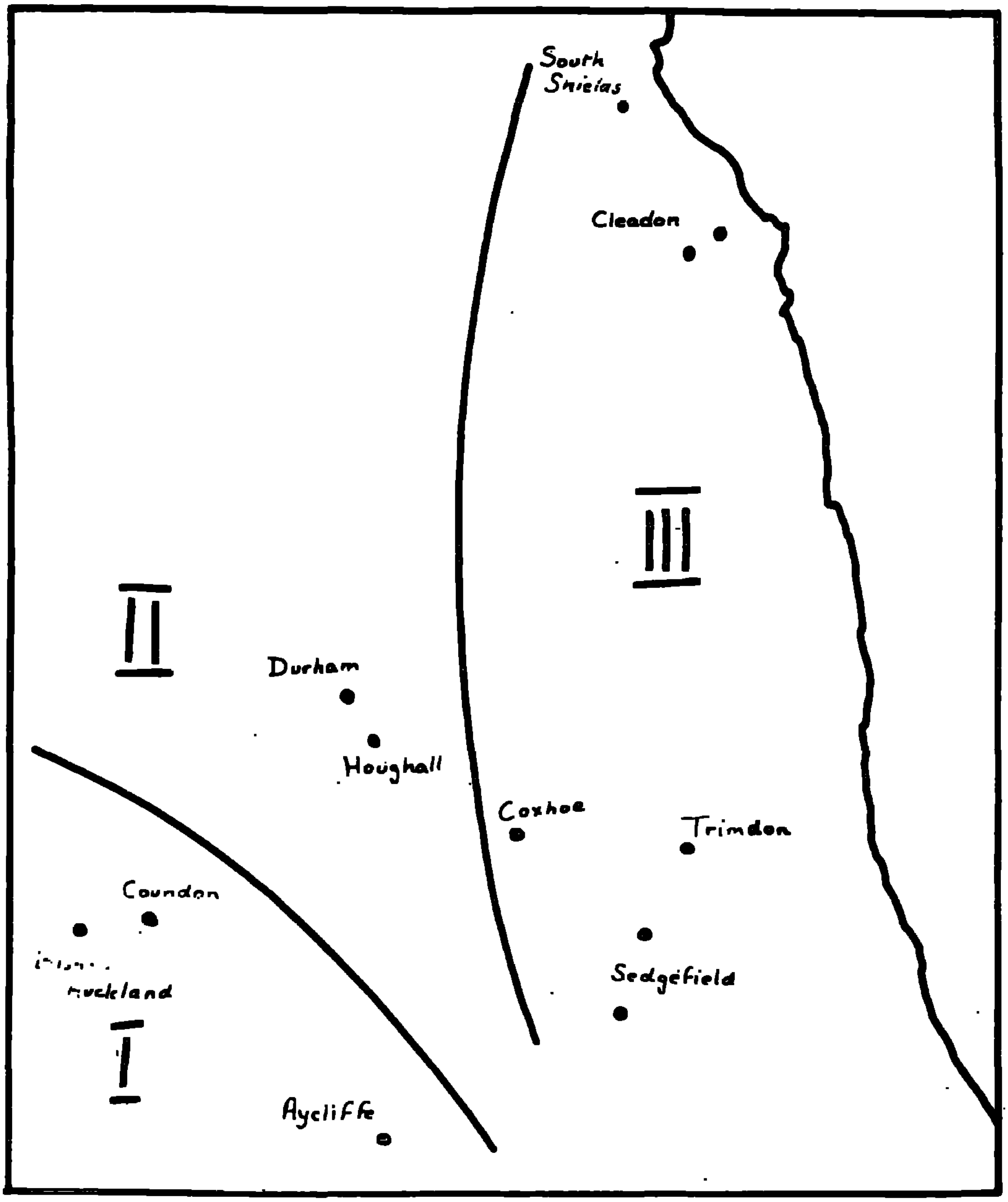


Fig. 6. Sites where A. prodromus and A. sphacelatus were collected in Co. Durham.

Table VI.

Collections of A. prodromus and A. sphacelatus in Co. Durham.

Locality	Date	No. of A. prodromus	No. of A. sphacelatus	% A. sphac.
Group I.				
Bishop	9-4-56	47	79	63
Auckland	18- 4-56	210	75	26
	2-11-56	30	18	38
	12- 3-57	66	140	68
	18- 3-57	44	258	85
	25- 3-57	27	25	48
	1- 4-57	116	63	35
	8- 4-57	74	20	21
Coundon	9- 4-56	79	19	19
	12- 3-57	7	33	82
Aycliffe	11- 4-56	121	46	28
Group II.				
Durham	26- 3-56	55	10	15
City	18- 4-56	228	4	2
	13-10-56	142	0	0
Houghall	26- 3-56	42	1	2
	26- 3-56	170	16	9
	4- 4-56	154	3	2
	4- 4-56	346	19	5
	16- 3-57	65	0	0
	16- 3-57	40	0	0
Group III.				
Cleadon	27- 3-56	81	2	2
	28- 3-56	84	2	2
	12- 4-56	89	0	0
	30- 3-57	42	0	0
Sedgefield	2- 4-57	59	0	0
	2- 4-57	86	0	0
Trimdon	29- 3-57	51	0	0
Coxhoe	29- 3-57	99	0	0

that collections made in 1957 were completely devoid of A. sphacelatus except in the Bishop Auckland area. The figures obtained from the

Table VII.

Collections of A. prodromus and A. sphacelatus.

Locality	Date	No. of A. prodromus	No. of A. sphacelatus	% A. sphac.
Hassock Sussex	30- 9-56	57	0	0
Inverness	10-10-56	50	210	81
	3-11-56	68	167	71
Swansea	10- 9-56	89	8	8
Beddgelert Caernarvon	19- 4-56	4	44	92
Moor House	27- 4-56	160	25	13
	7- 5-56	33	10	23
	6- 6-56	66	29	30
	9- 4-57	18	3	14
	15- 4-57	24	3	11

Durham area suggested that this difference might have been of significance ($P < .05$).

It can be seen that the activity period of the two species was not identical. In the 1957 collections at Bishop Auckland A. sphacelatus predominated in early March, A. prodromus becoming relatively more common in late March and April. This accounts for the very different estimates of the relative abundance of each species which was obtained at Coundon. It is not thought that a time difference of this sort accounted for the absence of A. sphacelatus in the collections of group III, for the sampling was carried out over a sufficiently wide range of dates for it to have been found if it occurred in these areas. The figures in Table VII show divergence among the estimates similar to the Co. Durham figures. No satisfactory explanation can be offered for the difference in the distributions of these two species.

The difference in the period of activity and distribution of these two animals suggested that they were not components of a polymorphic species.

IX. The Distribution of A. lapponum.

A. lapponum is a member of the boreo-British coleoptera described by Lindroth (1935). This group comprises 15 species whose distribution outside of Britain is confined to Scandinavia and the extreme north of Europe. Most of them occur also in Siberia, and a few are circumpolar. The group is peculiar in that its members occur neither in the central European plain nor in the mountains of that region.

Besides A. lapponum the group is composed of six species of the Carabidae, five of the Staphylinidae, and single species of three other families. A boreo-British distribution of this type is not confined to the coleoptera, but is well-marked in quite a number of Phanerogams (Wilmott, 1930), and mosses (Cardot, 1930). Among vertebrate animals the Snow Bunting (Plectrophenax nivalis) has a boreo-British distribution.

Lindroth attempted to determine the source of origin, and the time and manner in which the present distribution came about, by a consideration of the ecological requirements of the 15 species of beetle.

As the main part of the distribution of the boreo-British coleoptera lies outside of Britain and is entirely to the north, Lindroth concluded that immigration to the British Isles must have come from the north, presumably from Scandinavia.

Lindroth assumed that all of the boreo-British coleoptera arrived in this country at a similar time and in a similar way. He transferred the significance of the distribution of Pelophila borealis, and the isolation of

Nebria nivalis from Man, to other members of the boreo-British coleoptera. This was certainly not justifiable, for unlike P. borealis, A. lapponum has a widespread distribution in the British Isles, and it is certainly not as remote from Man as N. nivalis. In fact its abundance and distribution bear no resemblance to the appearance of a relict fauna.

Lindroth's conclusions that the boreo-British coleoptera could only have arrived in this country before the last glaciation (Wurm) cannot be upheld for A. lapponum. He ruled out the arrival of these species in recent times, or during the period following the last glaciation when the Dogger Land was in existence. The reasons offered for this were that certain species of the group were not equipped ecologically to make the journey over the Dogger Land, and those which were, failed to establish themselves in central Europe.

While A. lapponum may have survived the last glaciation on nunataks and in the southern part of the British Isles, for larger herbivores remained in the country throughout the period, the

Table VIII.

The Distribution of A. lapponum in the Northern Pennines in 1956.

Eastern slopes.

Locality.	Height (in feet)	A. lapponum	Other Aphodius	% A. lapponum
Killhope	2000	94	8	93
Hartside	1900	56	6	86
Alston Moor	1550	42	21	67
Lanehead	1450	17	46	27
W. of Alston	1450	0	42	0
W. of Alston	1450	2	35	5
E. of Alston	1350	0	76	0
Alston—	1300	0	66	0
—Nenthead	1200	0	94	0
E. of Alston	1050	0	106	0
Allendale moor	900	0	94	0

Western slopes

Locality.	Height (in feet)	A. lapponum	Other Aphodius	% A. lapponum
Rundale Beck	1600	38	0	100
	1500	36	4	90
	1400	40	6	87
	1200	3	33	9
	1100	4	43	8
Dufton Pike	1300	27	36	43
	1400	27	28	49
Crowdundle Beck	1400	35	13	73
	1200	16	66	19
	1100	6	48	11
	1000	0	56	0

All of the collections were made during July.

present distribution of A. lapponum in this country labels it as an upland species (Table VIII).

This being so it is thought that the species may have experienced difficulty in surviving the warmer conditions prevailing in Britain during the post glacial climatic optimum. However, if the species could have survived these conditions, then immigration could have taken place before the last glaciation or across the Dogger Land. In either event the species may have become established in central Europe, only to be eliminated there during the climatic optimum.

If the species was unable to withstand the conditions of the post glacial climatic optimum, then immigration in recent times with Man and his animals seems likely, indeed, it is almost certain that this method of colonisation occurred in Iceland. Lindroth's contention that A. lapponum may have survived the last glaciation in Iceland in the complete absence of larger herbivores by living in carrion and rotten vegetation is not thought to be likely. While Brundin (1934), Kearns (1929), and Cragg (pers. com.) have found Aphodius species to be attracted to carrion, there is no evidence of breeding in such situations.

X. The Distribution of A. rufus.

A. rufus does not occur at Moor House, and was not found in any situation above 1000 ft. It seemed to be associated with good meadowland. 75 animals of this species were collected at Durham, and were kept for several days in dung at 8°C. Two groups of 25 animals were then set up in culture (for method see later), one was left at Durham and the other was taken to Moor House. The remaining 25 animals were placed in 500cc of fresh sheep dung on grassland at Moor House, the whole being surrounded by a metal emergence trap to prevent the animals escaping. After 30 days all three cultures were examined, larvae were found only in the Durham culture, a careful search showing that no eggs had been laid in the Moor House experiments. The ease with which this species was usually cultured suggested that the failure of the Moor House experiments was of significance. The absence of competition from other organisms in the experiments, suggested that the failure to produce eggs must have been a response to some climatic factor.

Dissection of the animals after these experiments were completed, did not offer any explanation of the results, for the activity period of the adult beetles was nearly over, and the few animals which remained alive were in poor condition their reproductive systems and fat bodies were completely degenerate.

XI. Culture methods.

The material used for the identification of larvae was mainly obtained from cultures kept in the laboratory grounds. Tins 18 cm deep and 11 cm in diameter were used, small punctures were put in the sides 2 cm from the top, and approximately 6 cm of fine soil were placed in each tin. The soil was covered with fresh dung and up to 40 animals of a given species were added. After several weeks the culture was dismantled, the soil and dung being searched for adult beetles and larvae. A culture was considered to have been successful if large numbers of larvae were obtained from it, but when only a few larvae were found it was thought that they could possibly have hatched from eggs laid in the dung before it was collected. When species did not respond to the culture conditions described above, variations were tried with several types of dung, soil and sand. Glass topped vessels were also used in order to avoid upsetting diurnal rhythms which may have affected egg-laying.

The success of the methods largely depended upon the species, A. rufus and A. rufipes produced eggs readily under most conditions, but all attempts to get eggs from A. merdarius and A. constans were unsuccessful. Where species produced eggs readily on some occasions, as in A. fimetarius, A. conspurcatus and A. lapponum, it is thought that the cultures which failed must have been set up with animals not in a physiological state to reproduce. Dissection of A. fimetarius adults from a culture which failed, showed that nearly all of the specimens were spent, most of the reproductive system being degenerate.

The difficulty experienced in separating the adults of A. prodromus and A. sphacelatus made it of particular importance to identify the larvae. Both species were unresponsive to all of the culture conditions offered. Eventually plots of dung known to be infested by the beetles were taken from the field together with the turf beneath to a depth of 15 cm, and were kept under observation. No young stages were ever found in them. Other infested plots were marked and left in situ, a few of these were examined at fortnightly intervals using previously undisturbed droppings on each occasion. The same negative results were obtained. The larvae of A. conspurcatus, whose adults occurred together with A. prodromus and A. sphacelatus, were found abundantly in these droppings.

There appeared to exist a definite inhibition towards laying eggs under some culture conditions. A. prodromus adults were kept in tins containing 6 cm of moist sand, covered with 100 cc of fresh sheep dung. The beetles were prevented from escaping by a glass plate over the tin. After 21 days, during which time no eggs were laid, the animals were dissected revealing that most of the females were packed with eggs in numbers rarely found in animals from the field (Table IX). All of the culture specimens had been fertilised for spermatozoa were found in the spermathecae.

Table IX.

Egg Counts from A. prodromus.

	No. of well-developed eggs. 5-8	9-12	13-16	17-20	21-24	25-28	29-32	Average
Culture specimens	1	3	6	8	3	7	2	15
Field specimens	29	26	2	0	0	0	0	9

In order to supplement the information obtained from culturing methods, larvae were collected in the field, and were reared to emergence.

XII. Preservation of Aphodius adults and larvae.

Carne (1951) suggested several preservatives for Scarabaeid larvae, but previous experience led the present author to preserve both larvae and adults in Pampel's fluid. Larvae kept for four years remained in perfect condition for taxonomic purposes, while the alimentary canal and reproductive system of adult beetles remained in good condition for at least two years. 70% alcohol was inadequate as a preservative for these animals. The British Museum larval collection was preserved in 70% alcohol and was largely useless for taxonomic purposes as the tissues disintergrated on touch.

XIII. The General Biology of Aphodius Species.

1. The Egg Stage.

The eggs of a number species have been identified. Generally speaking they are oval or spherical, of yellow or whitish colour and translucent, without any adornments such as filaments or fins which are so frequently found in other dung living insects. The eggs of A. rufipes, A. depressus, A. lapponum and A. prodromus were yellowish white in contrast to those of A. fimetarius which were pearly white. A. fimetarius eggs also differed in being almost spherical, while those of the other species mentioned were distinctly oval.

Observation indicated that the eggs were not resistant to desiccation, for they collapsed within a short time if kept on dry rather-than damp filter paper.

Not all of the dung inhabiting species of Aphodius laid their eggs in dung. Table X indicates the egg-laying situations of several species in the field and laboratory. In Eygpt, A. lividus laid eggs in dung, while A. howitti oviposited in soil cavities irrespective of whether dung was available or not. The eggs of _A. fimetarius_ were found in cow dung placed on the walls of tunnels made by the beetles as well as in the end pockets of these tunnels, here no doubt they were very liable to predation. However in pellets of sheep dung the procedure was different, a small cavity was scooped out of the dung, a single egg was laid in it and the opening was smoothed over sealing it off from the exterior.

Table X.

Aphodius Egg-laying Situations.

Species	In culture	In field	Eggs laid
A. rufipes	soil	soil	in groups
A. depressus	soil	soil	in groups
A. lapponum	soil, dung	dung	singly
A. ater	dung	dung	singly
A. fimetarius	dung	dung	singly
A. rufus	soil, dung	dung	singly
A. tenellus	dung	dung	singly
A. prodromus	soil		singly
A. sphacelatus	soil		singly

Most of the species in Table X laid their eggs singly, but _A. rufipes_ and _A. depressus_ deposited them in batches of as many as twelve. In this respect they resembled _A. howitti_.

Dissection of female _A. prodromus_ showed that as many as 33 partly developed eggs could be carried in the ovaries, but these animals were kept in the laboratory and failed to produce any eggs in culture, specimens taken straight from the field never contained more than 16 partly developed eggs. If only completely developed eggs were counted, 14 proved to be the maximum in culture and field caught specimens. Eggs considered to be fully developed were egg-shaped and pearly white after pickling in Pampel's fluid, while partly developed eggs were translucent and often distorted by the proximity of other eggs in the ovary. The maximum number of fully developed eggs found in A. depressus was eleven, corresponding closely to the largest batch discovered in the field.

Corpora lutea such as were found by Gilbert (1956) in Calathus, were never seen in A. prodromus and A. depressus, but were noted in A. tenellus. These corpora lutea were composed of the debris of nurse cells left behind when a batch of eggs had been laid. Only specimens of A. tenellus collected in the spring showed corpora lutea, specimens pickled in the autumn did not possess them. They may have been identifiable only because a cessation of egg-laying occurred in this species at the onset of winter. If this was not the case then it can only be assumed that corpora lutea do not develop in A. prodromus and A. depressus. Certainly the development of eggs in these two species did not appear to be strictly in batches, for eggs in all stages were found within a single ovary. There does not appear to be any advantage in developing eggs in batches if they are to be laid singly as in A. prodromus. Where a large number of fully developed eggs were found in a beetle, the number never exceeded the number of ovarioles. Thus where eggs were developed in batches, the maximum number of eggs per batch could be estimated by counting the ovarioles. The number of ovarioles per ovary varied between 4 and 6 in A. depressus, while in A. prodromus the number was between 5 and 7. Each ovary in A. tenellus was composed of 5 or 6 ovarioles. Hafez stated that A. lividus laid up to 40 eggs, but did not say whether they were developed a few at a time or in batches. A. howitti laid eggs in two batches, the primary oviposition had a mean of 34.6 eggs, while the second had a mean of 15.4 eggs. It is not thought that any of the species studied by the present author laid so many eggs, and it is certain that no species laid batches averaging 35 eggs.

Carne found that *A. howitti* had a fully developed batch of eggs on emergence, this was examined in detail with *A. tenellus* in the present study, and it was found that all specimens had undeveloped ovaries on emergence.

Eggs of *A. lividus* hatched between 2 and 4 days after laying, at 25°C. The hatching times for *A. rufipes* in the laboratory, at temperatures fluctuating between 10-18°C, showed a mean value of 8 days for 132 eggs. The mean hatching time for 23 eggs of *A. rufus* under similar conditions was 5 days. Eggs of *A. howitti* hatched within 5-14 days in the field. In some species the eggs did not hatch in so short a time. Eggs of *A. fimetarius* and *A. contaminatus* overwintered in dung, but it is not known whether this was a diapause effect or a simple temperature effect. Eggs of the former species which were laid in the spring had a short incubation period.

2. The Larval and Pupal Stages.

Before hatching the larvae can be seen

through the translucent pellicle of the egg, the body acutely folded over with the terminal sternite of the abdomen lying between the posterior pair of legs, in an attitude slightly more cramped than that taken up after hatching. The larvae are fleshy animals with only thin chitin covering the body except on the head which is strong, carrying complex mouthparts.

The larvae of the various species differ conspicuously in their feeding habits. Those which live in dung certainly ingest it, although examination of their faeces did not reveal what they did with it. Hafez suggested that the larvae utilised the nitrogen rich vegetable and bacterial albumen contained in the dung.

A. prodromus larvae were never found in dung in the field, and it is thought that they lived on organic matter found in the soil. Eggs of this species were placed in soil without dung, but with grass roots and some growing vegetation. After thirty days several thriving larvae were found. Larvae of A. howitti lived on growing vegetable matter, but fed on dung if they came

Table XI.

Larval Feeding Situations.

Species	Feeding situation
A. rufipes	dung
A. depresseus	dung
A. lapponum	dung
A. ater	dung
A. fimetarius	dung
A. tenellus	dung
A. conspurcatus	dung
A. prodromus	soil (presumed)
A. sphacelatus	soil (presumed)

upon it while foraging.

Before larvae completed feeding and evacuated the gut for the prepupal stage, some of those which fed in dung (Table XI.) moved out and buried in the soil, where they prepared cavities in which to pupate (Table XII). Such larvae when taken from the soil often had soil particles in the gut, it seems that they may have had to ingest the soil in order to make progress through it. Carne found that A. howitti also burrowed in this way.

In dung it was most usual to find larvae in small sealed cavities which they enlarged as they grew. Once established in such cavities the larvae were safe from predation except from those animals which could burrow through the dung. This category of predators included other *Aphodius* larvae, as well as larger Staphylinids (*Philonthus* spp.), and Cantharid larvae. Several instances of cannabalism were observed among *Aphodius* larvae. On one occasion, a 300 cc sheep dropping containing 16 third instars of *A. rufipes* was carefully broken down, 180 cc of dung was left, and 19 cavities were found of which 6 communicated in pairs. In one of the communicating cavitites a broken head capsule of a third instar was found.

Table XII.

Site of Pupation.

Species	Site
A. rufipes	soil
A. depressus	dung, soil
A. lapponum	dung, soil
A. ater	dung
A. fimetarius	dung
A. tenellus	dung
A. conspurcatus	soil

It is not known to what extent cannabalism occurred in the species studied, but Carne found larval combat to be one of the major causes of mortality in *A. howitti*. Most of the mortality resulted from fighting which occurred when larvae came into contact while foraging on the soil surface at night. Their thin body cuticle was readily punctured by their heavily sclerotised mouthparts, and damaged larvae were very liable to attack by bacteria.

The site of pupation where known is listed in Table XII. The species which pupated in the soil were similar to A. howitti and A. lividus.

3. The Length of the Immature Stages.

The length of the immature stages varied with the time of year in many species. The third larval instars of A. tenellus may exist in the prepupal stage for several months if the eggs were laid in the spring, but this stage lasted only several days when eggs were laid in the autumn.

Between 10-15° C, the first two instars of A. rufipes lasted an average of 4.5 days (mean of 32 animals), the feeding stage of the third instar varied between three and seven weeks. In all species the first and second instars were short relative to the third instar. In A. lividus the first two larval instars lasted only a few days. The pupal stage in A. rufipes lasted between 10-18 days at varying temperature, but Madle found that the animals died if the stage was prolonged too long by low temperature.

No Aphodiussspecies known passes the winter in the pupal stage. Pupae of A. lividus emerged within 6-8 days at 23-25° C. Five pupae of A. conspurcatus lasted for between 19 and 29 days at 15° C. Similarly five specimens of A. tenellus emerged between 21 and 31 days.

4. The Overwintering Stage.

Carne found that A. howitti overwintered

Table XIII.

The Overwintering Stage.

Species	Stage
A. rufipes	prepupa
A. depressus	adult
A. lapponum	adult
A. ater	adult
A. fimetarius	adult, egg
A. tenellus	adult, egg?
A. conspurcatus	adult, egg?
A. prodromus	adult
A. sphacelatus	adult
A. contaminatus	egg, adult (rare)

in the third larval instar. This was found to be the case with A. rufipes, but most of the species studied overwintered in the adult stage (Table XIII). A. contaminatus was of interest in that it overwintered almost entirely as eggs.

5. The Adult Stage.

On emerging from pupae the adult cuticle takes some time to harden. Usually these 'callow' beetles remain in the pupal cavities, but on one occasion a callow A. lapponum was found on fresh sheep dung. Table XIV shows the hardening period of specimens of A. conspurcatus and A. tenellus at 15°C.

Table XIV.

The Hardening Period.

Species	No. of days.						
	2	3	4	5	6	7	8
A. tenellus	2	5	3	2	3	1	1
A. conspurcatus	0	0	1	1	2	1	0

Almost all species of Aphodius are associated with dung for feeding, even if they do not use it as a breeding medium. Mohr recorded the occurrence of A. distinctus in enormous numbers even though the immature stages were never found, A. femoralis and A. bicolor also visited dung only in order to feed. Dung was not essential for the completion of the life-cycle of A. howitti, even though a dung feed increased the output of eggs. Among the species found at Moor House, A. prodromus and A. sphacelatus came to dung only to feed.

That Aphodius adults feed on dung or its contents cannot be disputed, for Carne stated that the dyes flourescein and methylene blue were taken up by the gut of the insect if it was mixed with dung. Examination of the faeces of the beetle merely reveals material similar to herbivore dung only in smaller particles. Swan (1934) noted that the adults of A. howitti had poorly sclerotised mouthparts which could only deal with semi--liquid food, and this appeared to be the case with the British species which were examined.

Aphodius beetles were strongly attracted to the dung of horses, cattle, and sheep, only a few specimens were obtained from pig dung, while infested carnivore dung was never found.

Carne found that entry to cattle dung was made from beneath while beetles entered horse dung at any point, but it was noted that Sphaeridium adults behaved very differently to Aphodius on cow dung, for they were not averse to entering from the upper surface.

Dissection of A. depressus obtained from sheep dung, revealed that a large proportion of the animals contained no trace of food in the gut (90 out of 285). Attempts to relate this condition to the state of egg development and fat content proved to be impossible. The animals could not clear the gut entirely during the time between collection and pickling, although it was found that A. prodromus removed from dung contained only traces of food after two days, and after five all of the animals were free of all food traces.

Copulation was frequently seen in the field when a dung pad was opened, but leisured observation of it was impossible for the animals parted immediately on disturbance. The male mounted the female by clinging to her thorax and abdomen, the antennae of both animals touching. Movements of the male's hind legs appeared to play a part in the pre-copulatory activities if not actually during copulation. On only one occasion was copulation observed away from dung, and this occurred between two specimens of A. prodromus in a closed tin after capture. Carne stated that A. howitti copulated in and on soil as well as in dung pads.

Hafez found that A. lividus searched for fresh dung at night, and Carne found the same thing for A. howitti. In this latter species the factors determining the time and period of flying activity were examined in detail. Flight initiation was positively correlated to the sunset, but to subject the animals to similar falling light intensity at any other time did not stimulate the animals to fly. Carne suggested that the beetles must possess some form of 'physiological clock.' Humidity did not affect flight, but a wind of more than 10 m.p.h. stopped it entirely. It was found that little or no flying activity took place after dark at Moor House. Fresh dung laid out at dusk was invariably free of beetles the following morning. A. rufipes and A. lappomum were known to fly at night, so that it was concluded that the climatic conditions were not suitable for night flying at Moor House. Temperature may well have prevented flying activity during darkness for much of the year. Carne found that a temperature of 60°F or more was associated with conspicuous flying activity in A. howitti, but the minimum temperature exceeded 50° F on only 17 nights during the whole of 1955 at Moor House, and it was not until June of that year that the daily maximum temperature reached 60° F. At no time could flying activity be said to be conspicuous at Moor House, indeed, flying beetles were rarely seen. Observation suggested that sunshine increased flight activity, no doubt radiant heat from the sun allowed flight to take place at a lower air temperature than when the sky was overcast.

A considerable part of the year was spent in the adult stage, particularly in species which overwintered as adults. A. prodromus did this, and it was found that the mortality suffered by it during Oct.-Mar. inclusive, amounted to 40%. This mortality occurred at field temperatures but it must be pointed out that predators were excluded during October and March when turves containing the animals had to be enclosed in order to ensure that the beetles did not leave.

Some species of Aphodius lived for more than a year in the adult stage, this was demonstrated for *A. fimetarius*, *A. ater*, and *A. prodromus*.

Dissection of overwintering *A. lapponum* and *A. tenellus* adults showed that their guts were completely devoid of any trace of food, irrespective of whether they had remained in their pupal cavities, or whether they had been active in dung.

6. The Number of Generations per Year.

Carne stated emphatically that *A. howitti* had only one generation per year, Hafez did not commit himself about *A. lividus* but implied that there was more than one generation and that there may have been several. Mohr found there was one generation of *A. fimetarius* and Madle found only one in *A. rufipes*. This would appear to be the general situation, but the position is confused by some of the adults being so long-lived. Schmidt suggested that there may be two or three generations of *A. fimetarius*, but no indication of this was found at Moor House.

It seemed possible that *A. tenellus* may manage more than one generation per year. Dung dropped in Sept. fed larvae and adults emerged before Nov. These adult beetles lived alongside adults which emerged the previous autumn but which did not produce eggs until the spring. It is not known whether beetles emerging in early autumn could lay eggs which could complete the life-cycle before the winter.

7. Sex Ratios.

Examination of the sex ratios by rearing pupae was carried out for A. rufipes, in this case 39 males emerged compared with 45 females. The numbers were insufficient to say whether the sex ratios differed from the normal 1:1. Carne showed that in A. howitti females predominated over males in excess of the ratio 6:4. Schmidt found similar deviations from the 1:1 ratio in A. distinctus (46% males) and A. prodromus (40% males).

Regular collections of beetles from sheep dung showed that the sex ratios here changed significantly with time ($P < .01$). In A. ater, A. depressus, and A. lapponum males predominated in the early part of the season, but gradually females became more common. The reason for this was not known, but it seemed likely that females may have stayed longer in dung for feeding and egg-laying, while males may have frequented dung less when all of the females had been fertilised.

Over the whole season, the numbers of male *A. ater* collected in regular samples did not differ significantly from the number of females. However, in 1955 and 1956, more female *A. lapponum* were found in dung (1955; 61% females: 1956; 57% females). This difference in the male to female ratio was significant from the 1:1 ratio ($P < .001$). It is not known whether this difference represented a real difference in the sex ratios at emergence or whether the difference was behavioural. In view of the findings of Carne and Schmidt the former opinion does not seem to be unlikely.

8. The Enemies of *Aphodius*.

No comprehensive work has been done on this aspect, only superficial observations have been made. Mohr and Hafez recorded attacks on *Aphodius* adults and larvae by various Staphylinidae and Histeridae, and Carne recorded a fungal parasite *Cordyceps*, but there are no records of Hymenopterous parasites. Campbell (1936) recorded *Aphodius* adults from the stomachs of several species of British birds, including Crows, Thrushes and Plovers. Occasionally the author has seen Elaterid and Cantharid larvae holding crushed *Aphodius* adults and larvae, while adults frequently carry mites believed to be of the genus *Parasitus*. These mites attach themselves by the mouthparts to areas of thin cuticle, and suck the body fluids of the beetle.

9. The Abundance of *Aphodius* Beetles.

A study of the literature indicated that several authors found *Aphodius* occurring in very different sorts of abundance to that found by the present author at Moor House. Carne's work showed that *A. howitti* sometimes reached enormous numbers, he estimated that the density of adults was sometimes more than 50,000 per m^2 in dung. Admittedly this species had reached pest proportions, but even so other workers also found *Aphodius* to be much more common than in the present study. Mohr found *A. distinctus* infested dung to a density of over 800 adults to an average sized cattle dropping, and Hafez found 100 *A. lividus* in 500 cc of dung commonly.

Occasionally this species was sufficiently common to destroy the dung as a habitat for dipterous larvae. Again, Hammer stated that *Aphodius* adults could be so common that their activities within droppings could make the dung 'quiver'.

Such high infestations never occurred in dung at Moor House, although the activities of the beetles may have been sufficient to cause occasional food shortage for the dipterous larvae. Only once was a dropping found which was so heavily infested as to give this quivering appearance. This occurred in horse dung at Durham during October, when *A. contaminatus* adults were active. 210 beetles were removed from 300 cc of the dropping. A careful search of several adjacent fields showed that there was no other suitable dung in the neighbourhood, which is thought to be the reason for this extremely high infestation.

Hammer maintained that the activities of *Aphodius* and *Sphaeridium* were of the utmost importance to dipterous larvae living in dung. These were able to utilise the food available in droppings more completely when an aeration system was formed by the tunneling activities of the beetles. At Moor House, Diptera seemed able to utilise the sheep dung satisfactorily irrespective of whether beetles were involved in infestation or not. An adequate air supply in sheep dung was probably available without such tunneling activities, for the droppings were smaller, of a more solid consistency, and were usually well supplied with crevices.

10. The Abundance of *A. howitti*.

The differences between the biology of *A. howitti* and the species which occurred at Moor House, may give some indication of the characteristics of *A. howitti* which have enabled it to become a very common animal, indeed to become so numerous as to be a pest of agricultural importance.

Carne showed that dung was of secondary importance to *A. howitti*, for it could complete its life-cycle in the absence of it. To be able to feed generally on vegetable matter must have been an important factor affecting its abundance, its habit of feeding on grasses and clover is the reason for it being classified as a pest. Feeding on growing vegetable matter was not a characteristic of the species of *Aphodius* at Moor House. Only

A. prodromus was known to do this in the larval stage.

None of the Moor House species were ready to lay eggs on emergence from the pupal cavity, and a dung feed appeared to be necessary before the eggs became fully developed. In this respect they differed from A. howitti, the ability to lay eggs immediately after emergence and copulation without feeding, would effectively reduce mortality by predation on beetles full of eggs, and so would be of importance in the development of large populations. A third point which may have been of importance in promoting dense populations of A. howitti may have been its fecundity, which was greater than that of any other Moor House species.

XIV. Taking Samples of Adult Beetles.

In order to obtain an adequately detailed picture of the seasonal replacement of the species of Aphodius, some method of sampling had to be devised which would give an estimate of the relative numbers of each species active at any given time. It was only possible to study the seasonal changes using the adult stage, as the egg, larval, and pupal taxonomy was so poorly known.

Adult beetles of the genus were found in a number of situations. They were most easily found in dung but they were also discovered in soil, particularly while overwintering, just after emergence in some species, and while egg-laying in others. Occasionally they were found walking across turf, although this was usually near to dung during periods of flight activity. It was not practicable to take representative samples from all of these situations, and as beetles which were overwintering or which had just emerged from pupae cannot be described as active, they were ignored. It was also impracticable to sort soil cores from beneath every dropping in order to search for egg-laying beetles, so samples were only taken from dung and the surface of turf immediately beneath it. On one occasion 15 soil cores were taken which yielded one adult beetle as opposed to 23 found in the dung above the cores.

Sheep dung was used for the study of the seasonal succession, largely because it was more densely infested than the horse dung, which was almost free of beetles between late June and early September.

The method of sampling dung was different in 1955 and 1956. Dung was sorted by breaking it up and washing it through sieves in 1955. The beetles and larger particles of dung could then be separated in dishes of water. Only dung infested by beetles was sampled. It was found that to sort a fixed number of droppings was not satisfactory, for they varied from a few cubic centimetres to over 500 cc, and on occasions the number of beetles per dropping ranged from 1 to 40. A dropping containing 40 beetles could affect the estimated proportions of the species so markedly that 50 occupied droppings had to be examined to give a reliable estimate of the proportions. It was not practicable to sort such large quantities of dung but the difficulty was overcome by taking a fixed quantity of dung from each dropping. The criteria finally adopted were to sample only dung which was infested by beetles, the first beetle found was taken, together with 50 cc of the dung or the whole dropping if it was less than that volume.

In order to determine how many sample units of this type would be necessary to obtain a reliable estimate of the species proportions, 100 samples were taken and compared randomly in batches of 20, 30, 40, 50, 60, 70, 80, and 90. Figures 7 and 8 show the extreme values of the mean and standard deviation of 10 random samples of the <u>A. ater</u> distribution, calculated for each of the above mentioned batches. It was considered that it would be necessary to take 50 samples in order to obtain reasonably fixed proportions.

However local differences in species proportions still affected the estimates given by a series of 50 sample units in a number of cases. Table XV shows an extreme example of this which occurred on two grassland areas half a mile apart at Moor House.

Table XV.

Species Proportions on Two Grassland Areas at Moor House on 26 May, 1955.

	Area A		Area B	
	Numbers	% of total	Numbers	% of total
A. lapponum	129	67.0	93	44.0
A. ater	41	21.5	66	31.5
A. depressus	19	10.0	40	19.0
A. tenellus	3	1.5	10	4.5
A. fimetarius	2	1.0	2	1.0
	192		211	

In 1956, the form and condition of the

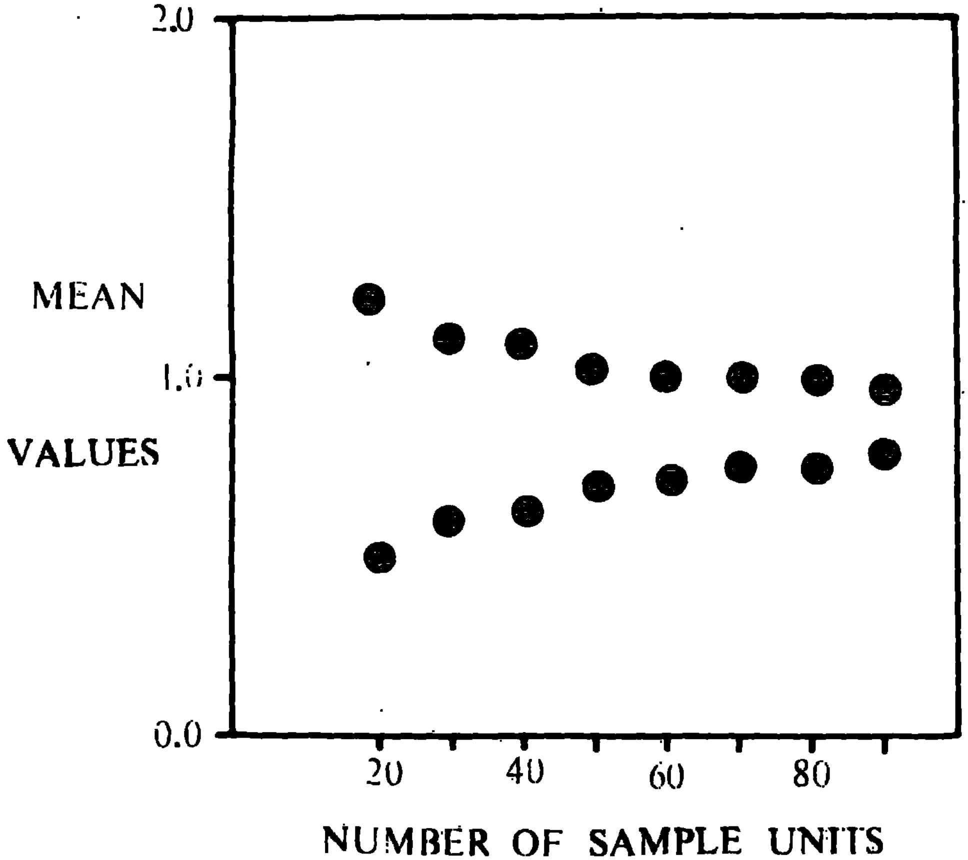
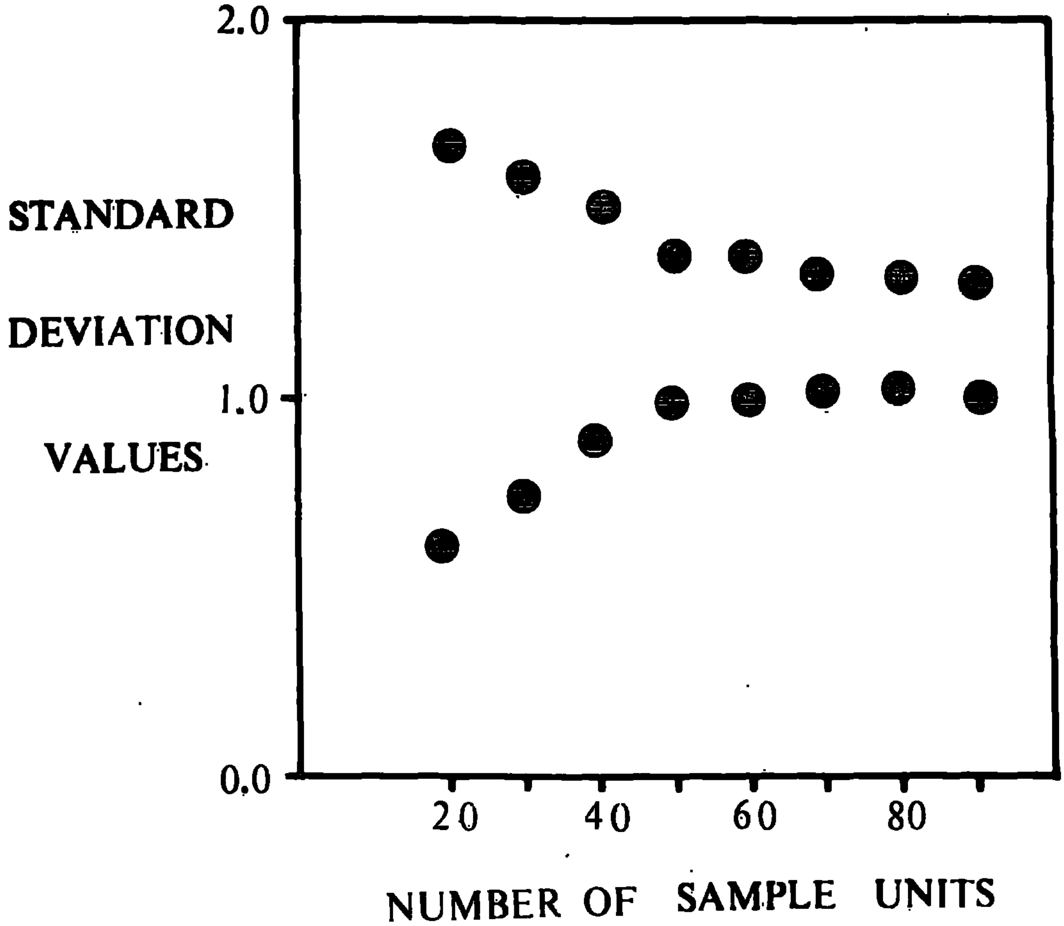


Fig. 7.



2.0
STANDARD
DEVIATION
1.0
VALUES
0.0
20
40
60
80
NUMBER OF SAMPLE UNITS

Fig. 8.

habitat were studied in greater detail, and for this reason the sampling method used in 1955 had to be abandoned. Handsorting was used, and beetles were removed from the entire droppings. In order to reduce the effect of local aggregations, sampling areas were scattered over a considerable area. The additional labour involved in studying the droppings in detail, meant that sampling had to be carried out less frequently. This resulted in the collection of smaller numbers of beetles, making the estimates of the seasonal succession less precise.

As was expected the numerical distribution of beetles in this type of sample was not random. There were several reasons for this, perhaps the most important being that dung of any age was sampled, small or large numbers of beetles were taken depending upon whether the dung was in an early, full, or late stage of infestation. Secondly, weather conditions preventing or reducing beetles activity could affect the number of beetles infesting dung of certain ages. The size of droppings available for sampling varied, and the attractive powers of large and small droppings were found to be different. Another factor contributing to the non-random distribution of the beetles may have been that the older dung became unavailable to a newly emerging species because it was no longer attractive. Again, if a species showed preference for dung of a particular age, this would produce aggregation of that species in the samples. Mohr maintained that A. fimetarius

Table XVI.

Infestation of Dung by A. fimetarius.

	A. fimetarius	Other Aphodius species	Total Aphodius beetles
In dung less than 1 wk. old	8	1262	1270
In dung more than 1 wk. old	11	282	293

did not colonise cow dung until it was four days old, this was not the case with sheep dung at Moor House, for it came to dung as quickly as any other species, but stayed longer (Table XVI) (P<.001). It was also possible that dung varied intrinsically in its physical and chemical composition, affecting its attractiveness.

Finally the non-random condition would be exaggerated if the age distribution of the dung sampled varied considerably from day to day. However, as sheep were not restricted in their movements this possibility was not considered to be very serious.

The conditions producing sample aggregation mentioned above, caused even more severe aggregation when horse dung was sampled, for the dung was suitable for infestation for a shorter period of time.

XV. The Distribution of Sheep Dung.

Habitat disposition is of importance to every organism, and perhaps even more so to an animal whose habitat is transitory, irregular in distribution and density. For these reasons the defaecation habits of the sheep were studied during 1956. Vegetational types of several kinds were examined and it was found that the density of droppings varied on each. Observation suggested that, with the exception of certain areas which the sheep used habitually as resting places, the disposition of dung also gave an indication of the feeding activities of the sheep.

An area where the vegetational cover was variable over a relatively small area was studied in detail. Grassland on limestone outcrops and alluvial flats formed one of the vegetational types studied, and areas where *Juncus squarrosus* was prominent formed another. Moorland where *Eriophorum* was dominant over *Calluna*, was distinguished from *Calluna* dominant areas. All of these vegetational types were in juxtaposition in the locality about the house, and it was probable that the sheep population which grazed them formed an entity, thus allowing comparison of dropping densities on the different vegetational types. Areas where *Festuca* and *Agrostis* grasses were prominently interspersed with *J. effusus* covered a considerable part of the study area, but were not examined in detail. Observation suggested that less dung was dropped here than on grassland without *J. effusus*, but the dropping rate was greater than on *J. squarrosus* areas. The only other extensive vegetational type which was not studied was the grassland found on the summit ridge.

The deposition of dung was studied by examining numerous fixed areas at regular intervals.

Each sampling area was of 100 m^2, demarcated by stakes or marked stones. A sample of this size was chosen in order to reduce local aggregation of droppings because of the association of yearlings or mothers and lambs, and in order to obtain a sufficient number of droppings from the less intensively grazed parts of the moor. Thirty of these areas were established on grassland, thirty on the J. squarrosus areas, and 15 on both the Callunetum and Eriophoratum (Fig. 9).

XVI. The Grassland Sample Sites.

The thirty areas of grassland varied considerably in structure, condition, and in the amount of grazing they offered the sheep. Sites 1-6 inclusive were situated on limestone outcrop while the remainder were based on alluvium. Site 18 was an area of very poor grassland consisting of part of a river bed in the process of recolonisation, no continuous turf had been established, only tufts of Nardus and Festuca were found. Areas 19-22 inclusive were similar except that the grasses had formed a continuous turf. Very little soil had developed and the areas were subject to severe and rapid drying out. Unpalatable Nardus and the

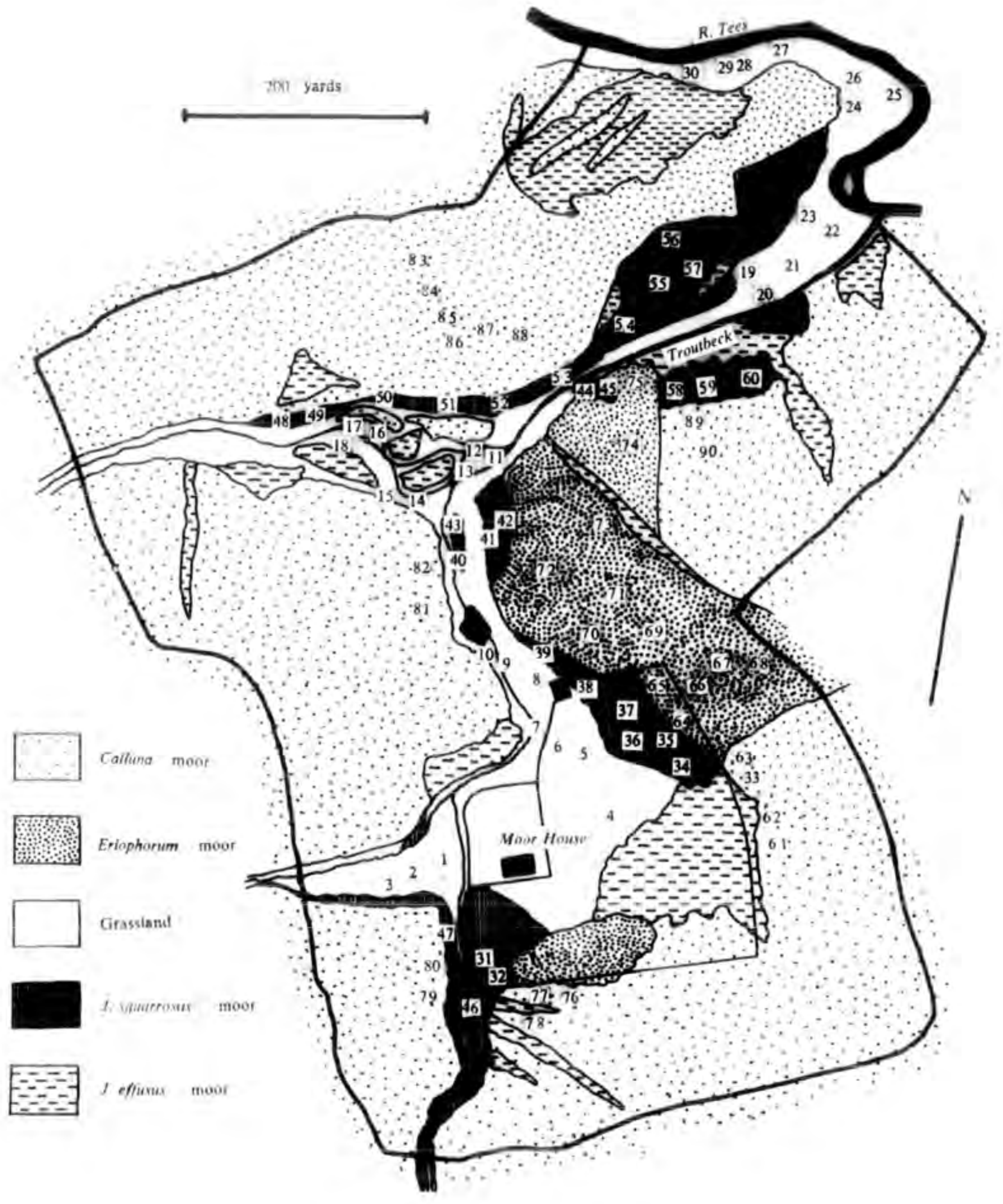


Fig. 9. The position of sample sites on the study area.

lichen Cladonia were common plants on these areas, the latter typifying the rather xerophytic conditions. As a consequence of the edaphic conditions, grass growth was poor providing little grazing for sheep. Area 23 was similar to sites 19-22 except that it was kept moist by run-off from the moor, consequently there was a better grass growth here. Sites 12 and 13 were also based on alluvium but a rich soil 6-12 inches deep had developed in which moles and earthworms were particularly active. Here the grasses produced better grazing for the sheep. Site 15 also had a deep soil, and this together with run-off from the moor, provided moist conditions under which a lush grass growth developed. This area offered good grazing for sheep, a fact indicated by the number of droppings found on it. Sites 1-6 did not produce as much grass as was expected. Here the soil was shallow being only 2-4 inches deep, and the porosity of the limestone made for rather xerophytic conditions which probably explains the poor grass growth.

Thus it can be seen that there was great variation among the thirty grassland sites, however as the variability was representative of a broad range of vegetational covers grouped together as grassland, the figures obtained from these areas were of significance.

XVII. Sites on J. squarrosus areas.

Juncus squarrosus was frequently the dominant plant on narrow peat slopes situated between the moor and the grassland. Other plants which may have been of value to the sheep on these areas were Eriophorum, Nardus, and Polytrichum. Occasionally J. effusus and Sphagna were also found.

The slopes of these areas provided shelter for the sheep, with the result that the number of droppings found there might have emphasised the apparent value of these areas for sheep grazing.

XVIII. The Calluna-Eriophoretum Sites.

The major part of the study area was covered by Callunetum and Eriophoretum. Areas 61-75 were on Eriophoretum while 76-90 were situated on Callunetum. On these areas other plants which played a prominent part in the vegetation cover were Polytrichum, Cladonia, J. squarrosus, Eriophorum angustifolium, Sphagna and other mosses.

XIX. The Deposition of Dung throughout 1956.

Counts of the number of droppings deposited throughout the period 17 Apr. -- 5 Nov. are shown in Fig. 10. The grassland histogram is based on intervals of 15 days, while those for J. squarrosus and Calluna-Eriophoretum areas were calculated on a basis of 30 days. One period of 15 days was used for both of the latter vegetational types in August when sheep were gathered about the house in large numbers for shearing. This aggregation of sheep accounts for the sharp peak on each of the three histograms.

Three factors were thought to be operative in the early part of the season in bringing about the increased number of droppings,

1/ the number of sheep on the area increased during May and June,

2/ the increased grazing activities of the lambs as they grew and were weaned,

and 3/ the amount of fodder available increased

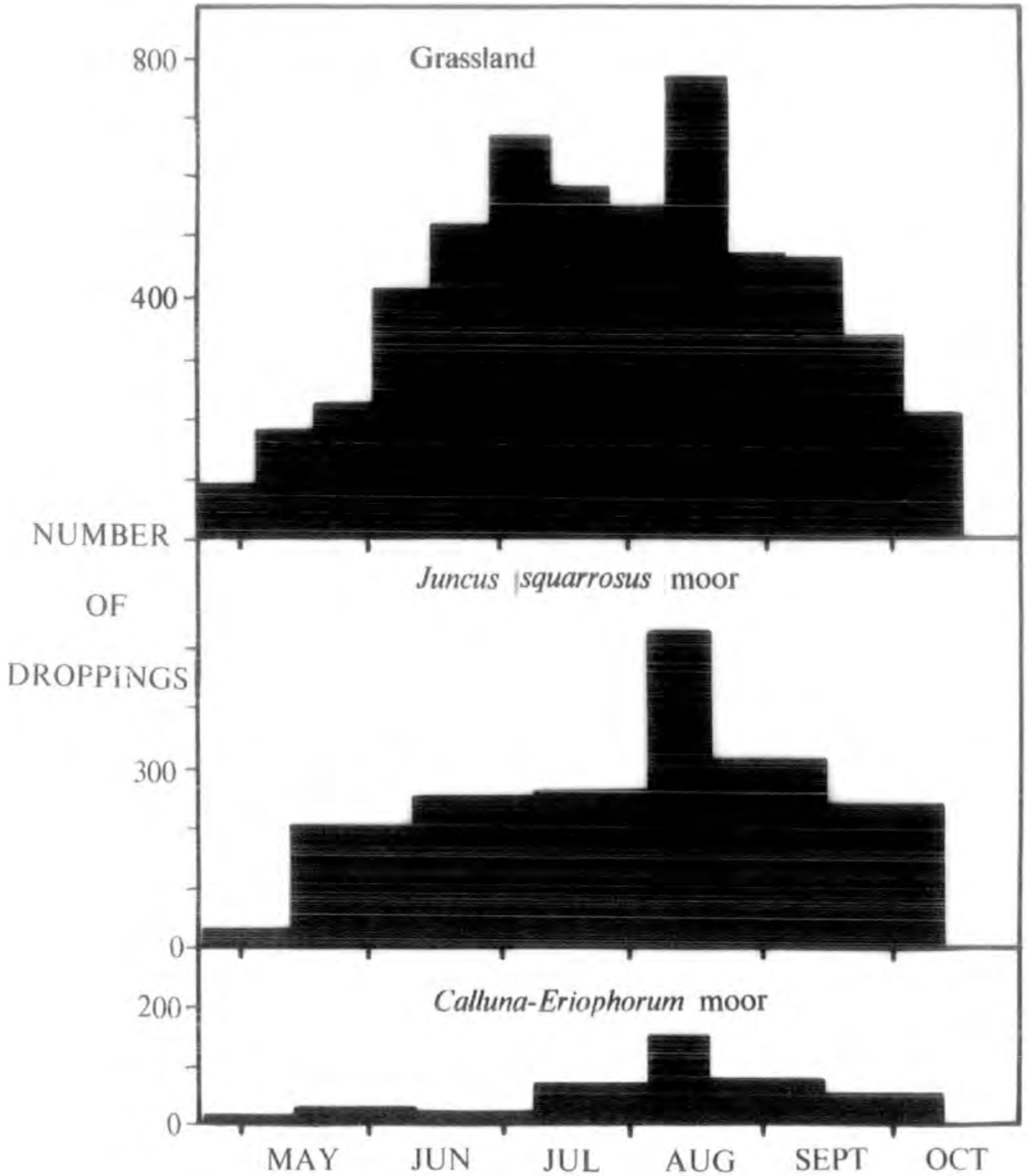


Fig. 10. The numbers of sheep droppings deposited on the sample sites of three vegetational types during 1956.

as plant growth accelerated.

It was not until mid-May that there was extensive plant growth. The decreasing number of droppings in Sept., Oct., and Nov. was the result of the gradual removal of sheep from the reserve.

XX. The Distribution of Droppings on the Grassland Areas.

The range in the type of grassland over the thirty sample sites was paralleled by the variability in the number of droppings found on them (Table XVII). No information was available which was of use in assessing the value of the grazing provided by each sample site, so that it was not possible to determine what degree of correlation there was between sheep feeding and the number od droppings. However, on areas where there was good grass growth the numbers of droppings were always high, and conversely where there was a poor turf of Nardus interspersed with Festuca the numbers of droppings were always low. This is illustrated in Table XVIII, on average each sample site would be expected to have 3.3% of the total droppings found on each sampling date. However on the productive grassland of areas 12,

Table XVII.

Sheep Droppings on Grassland Sample Sites in 1956.

Sample Sites.	7 May	24 May	8 Jun	22 Jun	4 Jul	17 Jul	2 Aug	17 Aug	29 Aug	18 Sept	2 Oct	18 Oct	1 Nov	Total
1	1	1	10	18	15	16	25	25	28	40	8	17	6	210
2	5	15	7	28	24	24	27	23	21	21	17	13	9	234
3	1	2	6	16	13	7	12	20	14	23	12	3	7	136
4	0	6	7	13	10	2	15	29	15	18	14	40	15	184
5	12	6	10	11	25	10	14	32	21	24	21	18	4	208
6	10	10	6	6	10	6	21	22	15	15	15	15	14	165
7	3	5	7	8	21	12	25	30	25	16	19	9	6	186
8	9	6	24	14	20	6	19	38	20	13	16	6	7	198
9	0	0	7	6	12	12	17	14	21	8	10	10	7	124
10	2	1	2	3	11	4	10	21	6	24	7	8	5	94
11	0	1	0	4	13	20	16	9	12	18	14	8	4	119
12	5	11	19	18	26	32	34	31	36	38	21	17	12	300
13	4	19	8	12	25	41	24	14	37	35	27	11	4	261
14	1	2	14	14	8	11	27	23	14	26	14	12	6	172
15	8	33	28	33	43	53	69	81	22	60	25	20	13	488
16	4	5	3	6	17	24	28	22	8	19	9	13	12	170
17	7	13	23	25	33	39	54	38	21	41	21	19	7	341
18	0	1	4	3	10	13	17	14	7	26	10	7	4	116
19	8	2	10	22	12	21	19	25	15	24	12	9	15	194
20	1	6	6	10	11	15	16	20	11	16	18	7	2	139
21	1	5	3	3	3	5	18	19	2	9	3	4	1	76
22	0	2	0	3	5	5	5	20	6	11	11	3	1	72
23	4	3	7	7	12	8	9	11	13	13	16	2	6	111
24	2	11	4	19	13	26	20	25	9	16	23	15	8	191
25	3	2	6	8	5	21	15	30	8	15	6	8	2	129
26	0	7	7	20	18	19	20	31	11	11	10	16	3	173
27	1	7	8	21	11	25	20	18	12	28	14	6	3	174
28	0	4	2	10	5	17	11	15	18	24	11	12	4	133
29	1	2	1	16	12	23	6	12	21	11	4	10	1	120
30	1	8	7	25	26	31	21	21	44	38	16	17	9	264
	90	196	246	402	469	548	634	733	513	631	424	349	197	5482

Table XVIII.

Percentage of Total Droppings on Each Grassland Sample Site.

Sample Sites.	7 May	24 May	8 Jun	22 Jun	4 Jul	17 Jul	2 Aug	17 Aug	29 Aug	18 Sept	2 Oct	18 Oct	1 Nov	Average
1	1.1	0.5	4.1	4.5	3.2	2.9	3.9	3.4	5.4	5.8	1.9	4.9	3.0	3.9
2	5.6	7.6	2.8	6.9	5.1	4.4	4.2	3.1	4.1	3.1	3.4	3.7	4.6	4.3
3	1.1	1.0	2.4	4.0	2.8	1.3	1.9	2.7	2.7	3.6	2.8	0.9	3.6	2.5
4	0.0	3.0	2.9	3.2	2.1	0.4	2.4	3.9	2.9	2.6	3.3	11.4	7.6	3.4
5	13.5	3.0	4.1	2.7	5.3	1.8	2.2	4.3	4.1	3.5	4.9	5.2	2.0	3.8
6	11.2	5.1	2.4	1.5	2.1	1.1	3.3	3.0	2.9	2.2	3.5	4.3	7.1	3.0
7	3.4	2.5	2.8	2.0	4.5	2.2	3.9	4.1	4.9	2.3	4.5	2.6	3.0	3.4
8	10.1	3.0	9.7	3.5	4.3	1.1	3.0	5.2	3.9	1.9	3.8	1.7	3.6	3.6
9	0.0	0.0	2.8	1.5	2.6	2.2	2.7	1.9	4.1	1.2	2.4	2.9	3.6	2.6
10	2.3	0.5	0.8	0.7	2.3	0.7	1.6	2.9	1.2	3.5	1.7	2.3	2.5	1.8
11	0.0	0.5	0.0	1.0	2.8	3.6	2.5	1.2	2.3	2.6	3.3	2.3	2.0	1.7
12	5.6	5.6	7.7	4.5	5.5	5.8	5.3	4.3	7.0	5.6	4.9	4.9	6.1	5.5
13	4.5	9.6	3.3	3.0	5.3	7.5	3.8	1.9	7.2	5.1	6.4	3.2	2.0	4.8
14	1.1	1.0	5.7	3.5	1.7	2.0	4.2	3.1	2.7	3.8	3.3	3.4	3.0	3.1
15	9.0	16.7	11.4	8.2	9.2	9.7	10.8	11.0	4.3	8.8	5.9	5.7	6.6	8.9
16	4.5	2.5	1.2	1.5	3.6	4.4	4.4	3.0	1.6	2.8	2.1	3.7	6.1	3.1
17	7.9	6.6	9.3	6.2	7.0	7.1	8.5	5.2	4.1	6.0	4.9	5.4	3.6	6.2
18	0.0	0.5	1.6	0.7	2.1	2.4	2.7	1.9	1.4	3.8	2.4	2.0	2.0	2.1
19	9.0	1.0	4.1	5.5	2.6	3.8	3.0	3.4	2.9	3.5	2.8	2.6	7.6	3.5
20	1.1	3.0	2.4	2.5	2.3	2.7	2.5	2.7	2.1	2.3	4.2	2.0	1.0	2.5
21	1.1	2.5	1.2	0.7	0.6	0.9	2.8	2.6	0.4	1.3	0.7	1.1	0.5	1.4
22	0.0	1.0	0.0	0.7	1.1	0.9	0.8	2.7	1.2	1.6	2.6	0.9	0.5	1.3
23	3.4	2.0	2.9	1.7	2.6	1.5	1.4	1.5	2.5	1.9	3.8	0.6	3.0	2.0
24	2.3	5.6	1.6	4.7	2.8	4.7	3.1	3.4	1.8	2.3	5.4	4.3	4.1	3.5
25	3.4	1.0	2.4	2.0	1.1	3.8	2.4	4.1	1.6	2.2	1.4	2.3	1.0	2.4
26	0.0	3.6	2.8	5.0	3.8	3.5	3.1	4.2	2.1	1.6	2.4	4.6	1.5	3.2
27	1.1	3.6	3.2	5.2	2.3	4.6	3.1	2.5	2.3	4.1	3.3	1.7	1.5	3.2
28	0.0	2.0	0.8	2.5	1.1	3.1	1.7	2.0	3.5	3.5	2.6	3.4	2.0	2.4
29	1.1	1.0	0.4	2.6	4.2	0.9	1.6	4.1	1.6	0.9	2.9	0.5	4.0	2.2
30	1.1	4.1	2.8	6.2	5.5	5.6	3.3	2.9	8.5	5.6	3.8	4.9	4.6	4.8

15, and 17, the percentages were always in excess of this, but the percentage of total droppings on areas 18, 20, 21 and 22, rarely reached the expected figure.

XXI. The Distribution of Droppings on *J. squarrosus* Areas.

x/ Table IXX shows the numbers of droppings deposited on the sample sites during 1956. As on the grassland the variation in numbers was considerable, but was not so readily explainable. It was realised early in the season that site 33 would not have much dung deposited upon it, for it was a small patch of *J. squarrosus* surrounded by moorland. However areas 52, and 55, also had little dung deposited on them and no explanation can be offered for these low figures.

XXII. The Distribution of Droppings on the Calluna-Eriophoretum Areas.

The numbers of droppings found on the 30 Calluna-Eriophoretum sample sites are shown in Table XX. Much of the variability in the numbers of droppings can be explained in terms of vegetational differences between the sites. Areas 76, 77, and 78, consisted almost entirely of *Calluna* which was

Table XIX.

Sheep Droppings on *J. squarrosus* Sample Sites in 1956.

Sample Sites.	15 May	13 Jun	9 Jul	9 Aug	23 Aug	25 Sept	24 Oct	Total
31	0	13	12	36	32	40	18	151
32	4	32	24	6	36	22	32	156
33	0	3	6	4	6	14	2	35
34	1	10	12	8	24	30	28	113
35	3	39	18	16	12	8	18	114
36	8	12	8	16	10	20	28	102
37	3	12	12	8	18	14	26	93
38	11	4	4	6	12	10	16	63
39	3	11	14	16	10	10	6	70
40	0	12	12	10	8	36	16	94
41	0	10	4	10	34	36	34	128
42	7	16	26	30	14	20	4	117
43	6	22	6	18	14	14	10	92
44	1	10	14	20	30	12	20	107
45	3	12	18	20	10	12	4	79
46	3	14	16	16	8	12	10	79
47	7	8	18	32	16	54	14	149
48	7	34	28	10	20	56	28	183
49	1	16	12	18	10	14	2	73
50	1	25	32	22	28	44	20	172
51	0	24	12	24	18	24	6	108
52	0	0	4	12	8	8	2	34
53	1	4	0	24	10	12	10	61
54	5	8	10	20	24	52	18	137
55	1	10	0	10	4	16	4	45
56	1	9	8	16	20	16	14	84
57	7	30	14	22	36	36	22	167
58	0	6	20	60	18	28	16	148
59	0	18	26	32	12	28	12	128
60	5	17	30	22	22	24	20	140
	89	441	422	564	524	722	460	3222

Table XX.

Sheep Droppings on Calluna-Eriophorum Sample Sites in 1956.

Sample Sites.	15 May	13 Jun	9 Jul	9 Aug	23 Aug	25 Sept	24 Oct	Total
61	0	1	0	3	5	5	3	17
62	0	0	1	9	12	4	0	26
63	0	0	0	5	14	5	4	28
64	0	6	2	4	2	9	7	30
65	0	2	2	2	6	10	1	23
66	4	4	0	1	6	0	2	17
67	1	1	1	1	3	0	1	8
68	1	2	0	1	2	2	3	11
69	0	2	1	5	4	1	1	14
70	0	3	1	2	5	6	0	17
71	0	0	1	6	13	6	1	27
72	4	4	4	4	7	3	0	25
73	0	2	0	1	7	0	1	11
74	3	2	4	11	12	7	5	41
75	0	0	4	2	3	3	1	13
76	0	0	0	0	0	1	0	1
77	0	1	1	1	0	0	1	4
78	1	1	0	2	2	1	1	8
79	2	2	0	1	0	2	0	7
80	0	1	0	6	1	1	1	10
81	1	9	3	8	8	8	7	44
82	0	2	1	3	3	2	1	12
83	2	0	0	0	1	1	0	4
84	0	0	0	0	1	1	1	3
85	0	1	1	2	3	16	8	31
86	1	1	0	6	3	8	4	23
87	0	1	0	3	3	12	12	31
88	0	1	0	2	2	8	4	17
89	2	10	10	25	22	19	20	108
90	0	2	1	4	0	4	11	22
	22	61	38	120	150	144	101	636

so thick and bushy that sheep rarely visited there, which explains the low dung counts. Areas 83 and 84 were situated on the crown of the moor, and the low dung counts recorded from these sites were probably the result of the sheep's preference for the edges of the moor. The large number of droppings on site 81 occurred because of the juxtaposition of a patch of J. squarrosus, almost all of the 44 droppings being found within two metres of the Juncus patch. Site 89 was a typical area of Callunetum, the very large number of droppings deposited there being the result of several sheep using it as a night resting place throughout the summer.

XXIII. The Time of Sampling.

The dung deposited on the sample sites was examined at regular intervals throughout the period that sheep were on the reserve. During 1956, the first sheep were returned to the moors on 17 Apr., and the last were removed in the early days of Nov. Observations made in 1955 had suggested that fortnightly sampling of the grassland areas would be sufficiently frequent to account for all of the droppings deposited in that time. This proved to be the case except on one occasion when very heavy rain severely washed away freshly dropped dung at the beginning of a fortnightly period. When sampling was carried out two weeks later only small quantities of whitish fibres indicated the position of these droppings. On the other vegetational types most dung remained recognisable for several months, and for this reason sampling was carried out at four-weekly periods, each sampling date being one week after alternate sampling dates on the grassland. All dung was removed from the sites after examination.

XXIV. The Examination of Dung.

In addition to counting the number of droppings the volume of each plot of dung was estimated. This was done by estimating the volume against tins of known size, in this way every dropping was placed in a size group each of which ranged over 25 cc. These estimates were accurate up to 200 cc., and above this size were probably accurate within a range of 50 cc. Volume was chosen as a measure of quantity in preference to weight, as it varied much less if weather conditions allowed a crust to develop on the dropping.

Attempts to estimate the age of each plot of dung from its external appearance and

Table XXI.

Estimation of the Age of Droppings.

24 May - 7 Jun.

Site No.	No. of droppings		Site No.	No. of droppings	
	<1 wk. old	>1 wk. old		<1 wk old	>1 wk old
1	9	1	16	0	3
2	4	2	17	10	13
3	2	4	18	4	0
4	4	3	19	3	7
5	4	6	20	3	0
6	4	2	21	3	3
7	5	2	22	0	0
8	8	16	23	1	6
9	3	4	24	4	0
10	2	0	25	3	3
11	0	0	26	4	3
12	12	7	27	5	3
13	1	7	28	0	2
14	7	7	29	1	0
15	20	8	30	3	4
Total <1 wk. old 129					
Total >1 wk. old 117					

texture was difficult because weather markedly affects the appearance of the dung. On the grassland, dung was distinguished as less than one week, or more than one week old. These broad age groups were thought to be reasonably accurate.

Table XXI shows the estimated age of all droppings on the grassland sample site on the stated date. Even though the proportions varied so much on individual sample sites the number of droppings in each age group was similar, as would be expected if the age estimates were accurate.

Where dung was examined at four-weekly intervals, the age estimates were restricted to the groups 'less than two weeks old', and 'more than two weeks old'. These estimates were not so accurate as those made on grassland.

In addition to estimating the age and volume of the droppings, two types of dung were distinguished, those deposited as loose pellets, and those which maintained a compact form. This distinction was made as <u>Aphodius</u> adults reacted very differently to the two types. Before removal from the area each dropping was hand-sorted for <u>Aphodius</u> and <u>Sphaeridium</u> adults, the smaller Staphylinid and Palpicorn beetles were ignored as they were too numerous and too active to be collected adequately while hand-sorting. On selected dates the incidence of lumbricid worms and dipterous larvae was noted.

XXV. Overwintered Dung.

The severe climatic conditions which are usually operative on the Moor House reserve during the winter months serve to reduce animal activity in dung to a mimimum. Occasionally lumbricid worms were found to be active in dung during February, and on sunny days at this time of year adult Borborid flies have been seen in numbers on fresh horse dung. Generally speaking all droppings were frozen solid until March. Sheep dung which was found in early April of 1956 had all overwintered, and there had been very little animal activity in it. Examination of this dung revealed eggs of Spiders, a few lumbricid worms and their cocoons, and occasionally overwintering adults of <u>A. tenellus</u> and Elaterid beetles.

Fig. 11 shows the abundance and size of overwintered sheep droppings on the sample sites of three vegetational types. Comparison of these distributions with those of dung dropped in Aug. and Sept. made it clear that considerable erosion

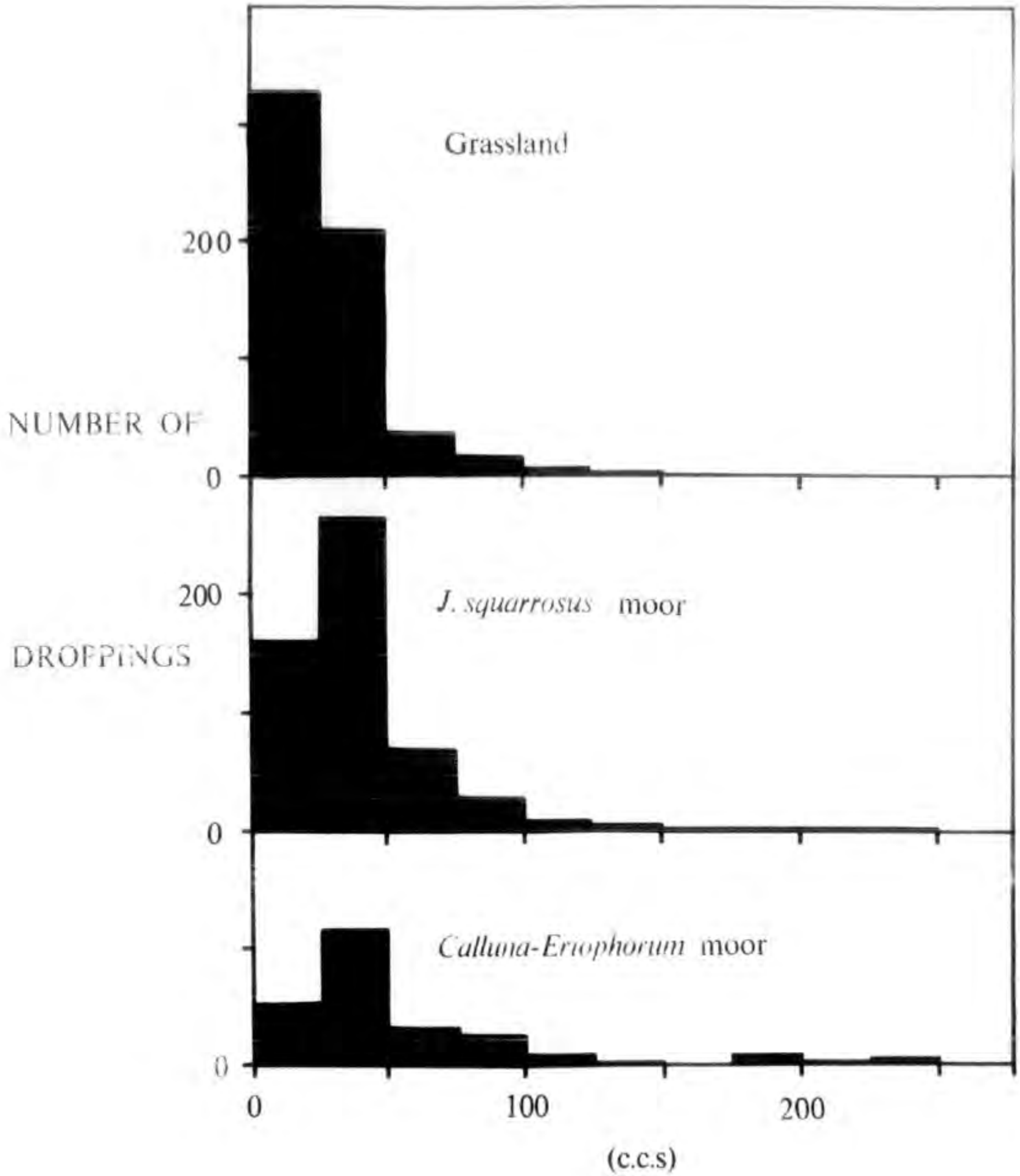


Fig. 11. The amount of dung which lasted the winter on the sample sites of three vegetational types.

of dung took place during the winter months.

On the grassland a large proportion of the overwintered dung fell into the size group 0-25 cc, being represented only by a trace of dung. The distributional differences between the grassland and the other areas was the result of different erosion intensity. Dung on grassland was more exposed to wind and rain when lying on a short turf, than if it was protected by the taller growth of J. squarrosus, Calluna, and Eriophorum.

XXVI. The Duration of Dung.

In order to make a comparison of the relative duration of dung on different vegetational types, a coarse analysis was carried out using the counts of droppings which overwintered from 1955, and the total droppings deposited on the sample sites during 1956. Making the assumption that similar numbers of droppings were deposited in 1955 and 1956, a rough estimate of the average duration was obtained as in Table XXII. These estimates take no account of variation in average duration throughout a year, and must be biassed towards average dung duration in winter.

However it is considered that the estimates were of significance between the vegetational types. All four estimates were significantly different from each other ($P<.01$). The long average duration period for dung on Eriophoretum and Callunetum supported the belief that some droppings might last for more than one year on these areas.

Table XXII.

Average Dung Duration.

Vegetation type	Droppings deposited 1956	Droppings overwintered	Average duration (in days)
Grassland	5482	603	$\frac{603 \times 365}{5482} = 39$
J. squarrosus	3156	549	$\frac{549 \times 365}{3156} = 64$
Eriophoretum	308	99	$\frac{99 \times 365}{308} = 119$
Callunetum	325	150	$\frac{150 \times 365}{325} = 167$

An estimate of summer dung duration was obtained from the <u>J. squarrosus</u> sites during July, August, and September. Over this period only 50 m was cleared of dung on each sample site. At the end of September a dung count was carried out on the uncleared parts of the sample sites. Comparison of the total numbers of droppings deposited upon 50 m^2., with the number remaining on an equivalent area after the same period of time, allowed a coarse estimate of summer dung duration to be made. The figures and sampling dates are shown in Table XXIII. The estimate based on the

Table XXIII.

The Duration of Dung on *J. squarrosus* Areas.

Sampling dates	Days after 12-6-56	No. of droppings on $50m^2$.	Days after 12-6-56	No. of droppings on $50m^2$.
9-7-56	27	211	-	-
8-8-56	57	282	-	-
22-8-56	71	262	-	-
25-9-56	105	361	105	632
Totals		1116		632

total figures and the whole experimental period was

$$\frac{632 \times 105}{1116} = 60 \text{ days.}$$

As it is believed that no dung disappeared within a month, a better estimate may be obtained using only the first 71 days of the experiment, thus,

$$\frac{632-361}{1116-361} \times 71 + 34 = 61 \text{ days.}$$

These estimates compared very closely with those obtained from a study of overwintered dung.

In Table XXIV the size distribution of droppings left for the 105 days of the experiment were compared with the size distribution of the droppings removed on four occasions during the same

Table XXIV.

Weathering of Dung in Summer on J. squarrosus Areas.

Dropping size (in ccs)	Droppings deposited on 50 m^2 in 105 days	Droppings found on 50 m^2 after 105 days.
0- 50	473	160
50-100	413	230
100-150	111	123
>150	119	118
Totals	1116	632
Mean dropping size	71 cc.	101 cc.

period. The distributions were similar above 100 cc, but the average dropping size was very different. The destructive forces of the physical and biotic environment act upon a dropping as a unit rather than in proportion to its size. This explains the difference found in the mean size of the droppings in the experiment. Small droppings were the first to disappear.

In 1956, an experiment was carried out on the duration of sheep dung on grassland of a limestone outcrop. Ninety plots of 100 cc were laid out on the 6 Jun. and were subsequently examined on 14 Jul., 22 Aug., and 20 Sept.. The size distribution of the plots on these dates are shown in Fig. 12, while Fig. 13 shows the mean dropping size and disappearance of droppings on the four dates. It was estimated that 50% of the droppings disappeared within 100 days, and that 50% of the dung disappeared within 60 days. Table XXV shows the extent of animal activity in these droppings on 22 Aug.

Table XXV.

Animal Activity in Experimental Plots on 22 Aug.

	No. of plots.		
	Infested	Previously infested	Not attacked
Dipterous larvae	2	1	58
Lumbricid worms	22	35	4
Aphodius larvae	6	0	55

Sixty fresh plots of 100 cc of dung were laid out on Eriophorum at the same time as those on the limestone outcrop. The disappearance rate on the Eriophoretum was slow, all plots being recognisable after 115 days, and the mean

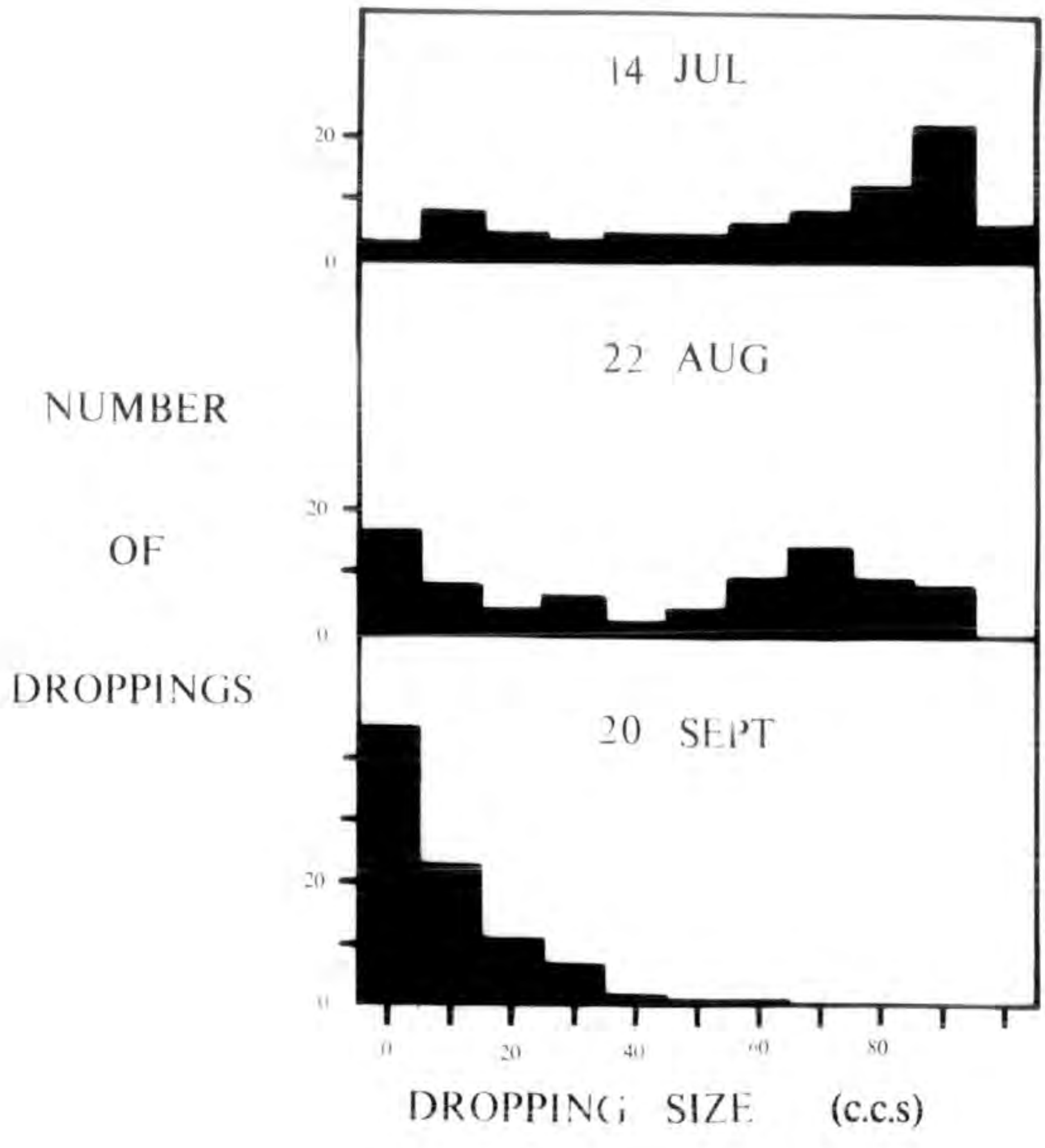


Fig. 12. The disappearance of sheep dung from the grassland of a limestone outcrop.

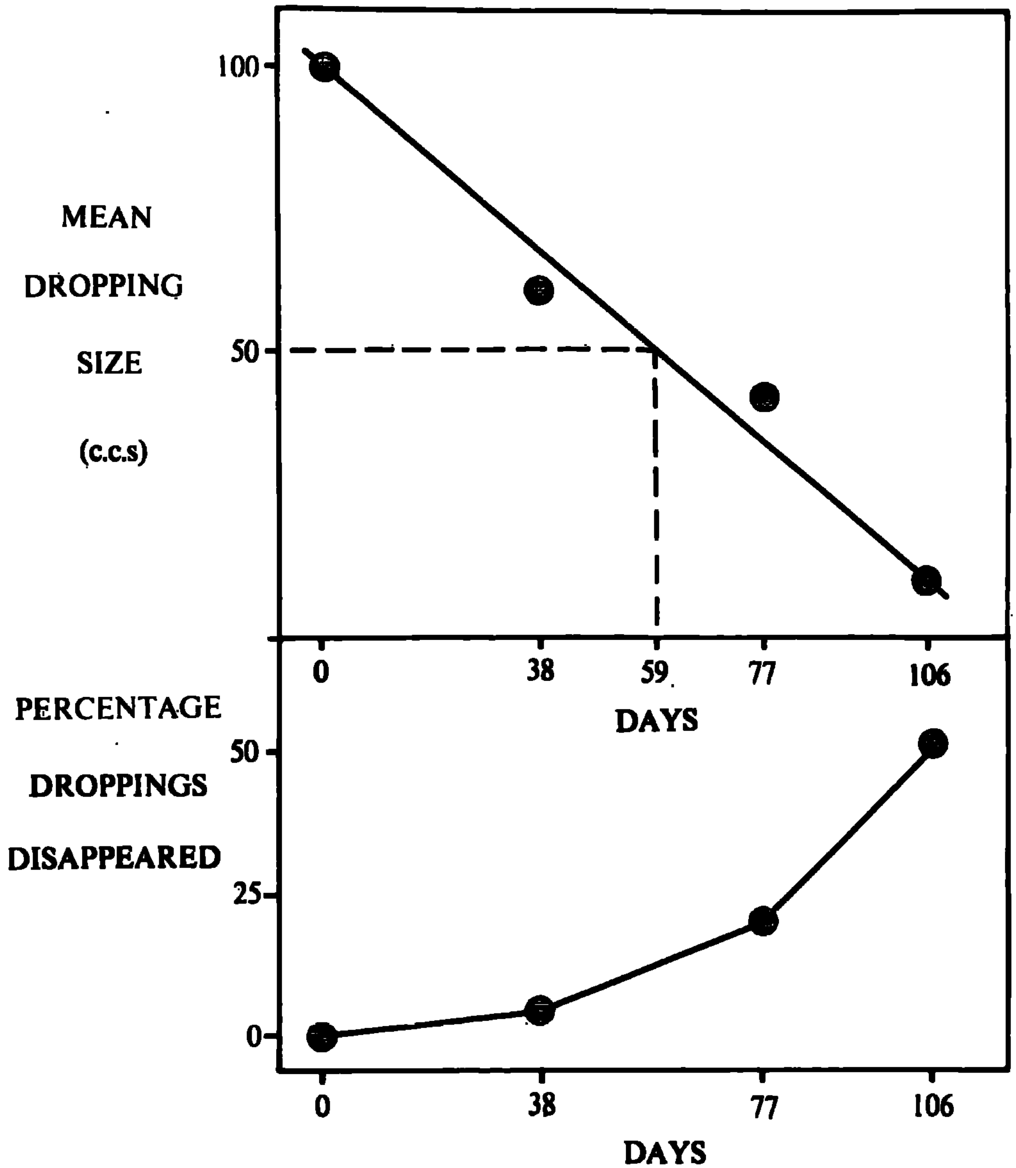


Fig. 13. The removal rate of sheep dung from the grassland of a limestone outcrop.

size of these droppings was 86 cc. The extent of the animal activity in these droppings on 29 Aug. is shown in Table XXVI. It can be seen that 40% of the plots showed evidence of the activity of

Table XXVI.

Animal Activity in Experimental Plots on 29 Aug.

	No. of plots		
	Infested	Previously infested	Not attacked.
Dipterous larvae	1	19	35
Lumbricid worms	0	4	51
Aphodius larvae	8	3	44

dipterous larvae. It is suggested that this figure gives a better indication of the extent of dipterous infestation than those shown in Table XXV, for on these areas the intensive activity of lumbricid worms largely destroyed the evidence of previous occupation by Diptera. The different intensity of infestation by lumbricid worms, reflected their relative densities on the two areas. Svendsen (1955) found several species of earthworm to be common on limestone outcrop areas, while Dendrobaena octaedra and Bimastis eiseni occurred in only small numbers in the peat. The tables illustrate that 10-20% of these droppings were occupied by larvae of A. lapponum.

There can be little doubt that on the grassland areas, removal of dung was largely effected by lumbricid worms, dipterous larvae may also have been of considerable importance, but their effect was difficult to assess from the results obtained.

XXVII. The Size of Sheep Droppings.

It was found that the mean dropping size increased as the season progressed (Fig. 14, Table XXVII). As the method was liable to some subjective variation, an intensive check on size was carried out at the beginning of the season and in early August. These checks showed that the increase was genuine.

The increase in average dropping size was largely the effect of the increased size of lamb droppings, together with a reduction in the frequency with which the young animals defaecated. Until July the percentage of small droppings was high relative ~~to that~~ found from August onwards.

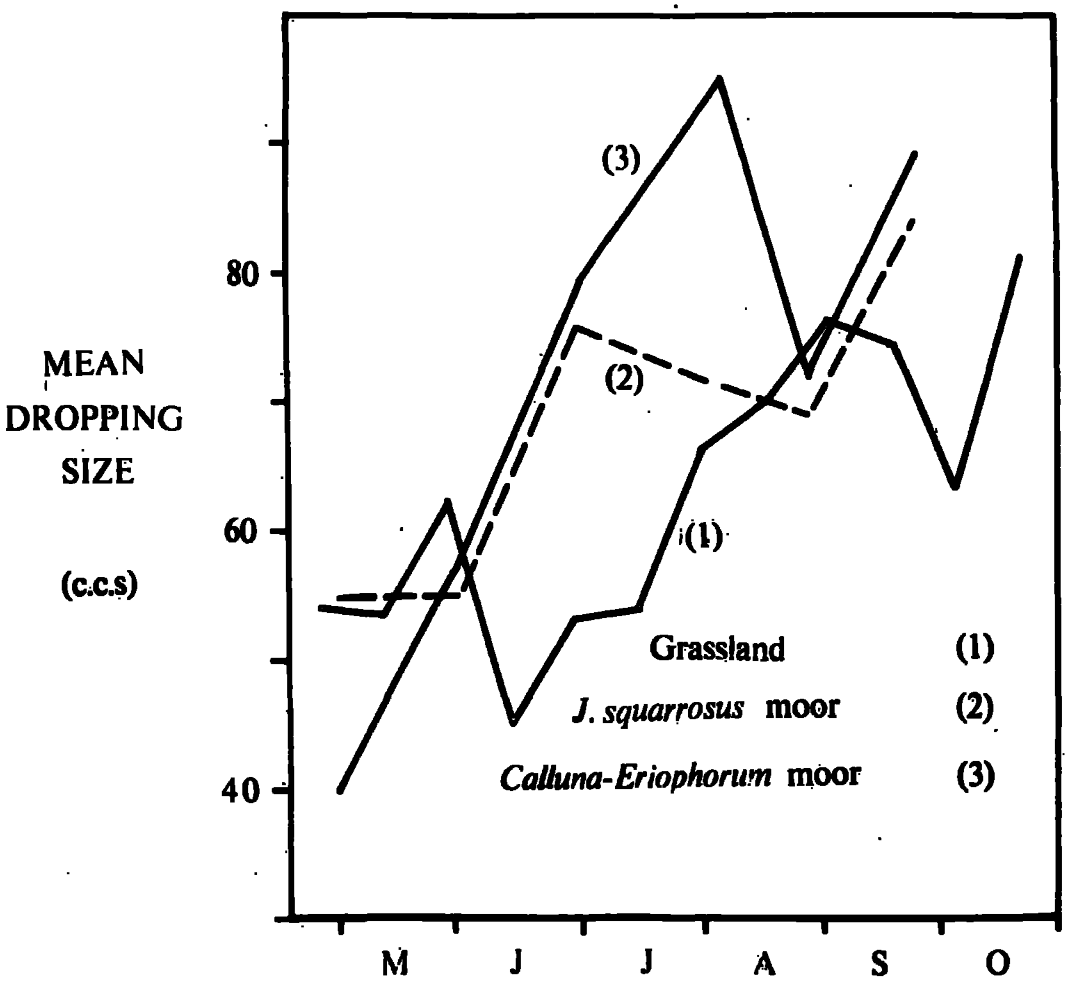


Fig. 14. The change in mean sheep dropping size during the summer of 1956.

Table XXVII.

The Size Distribution of Plots During the Season.

Dropping size (cc.)	Before 22 Jun.	After 2 Jul.	% of total before 22 Jun.	% of total after 2 Jul.
0- 25	155	186	16.6	6.9
25- 50	441	892	47.3	33.0
50- 75	178	667	19.1	24.7
75-100	74	475	7.9	17.6
100-125	36	148	3.9	5.5
125-150	25	129	2.7	4.8
>150	23	203	2.5	7.5

Droppings on grassland only.

Fig. 10 shows the quantity of dung dropped on each of the vegetational types throughout the year. It can be seen that more droppings were deposited on the areas in the second half of the summer, and this, together with the increased dropping size resulted in greater quantities of dung being found in the latter part of the year (Fig. 15).

Table XXVIII shows the average quantities of dung deposited on the several vegetation types, together with the extreme values.

XXVIII. Variation in the Type of Dung throughout the Year.

It has already been mentioned that Aphodius beetles reacted differently to droppings in the

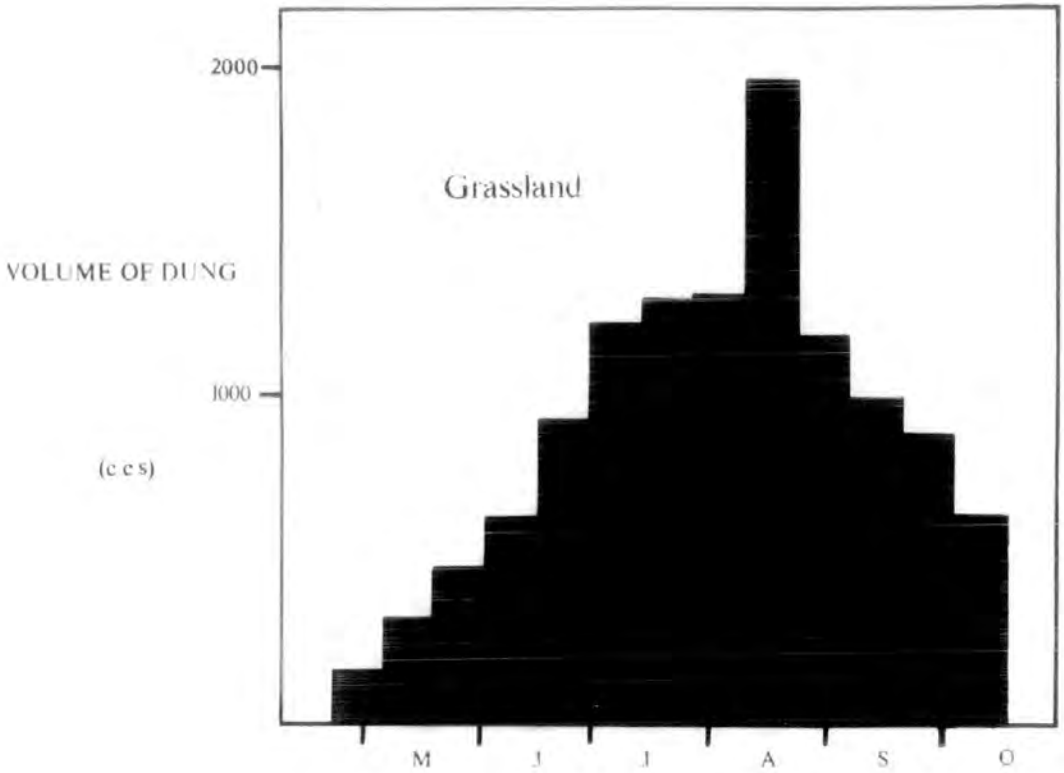


Fig. 15. The volume of dung deposited on the grassland sample sites during 1956.

Table XXIX.

The Quantity of Dung on Several Vegetational Types in One Year. (in cc./m^2.)

Vegetation types.	Average for 30 areas	Extreme estimates.			
		Site	Quantity	Site	Quantity
Grassland	119	15	304	22	52
J. squarrosus	78	48	234	52	33
Callunetum and Eriophoretum	18	85	35	76	2

N.B. Site 89 on Callunetum had 102 cc/m^2 of dung on it during 1956. This area was abnormal, sheep using it as a resting place.

form of loose pellets and those which were compact. Thus it was of interest to find that the proportions of the two forms varied throughout the year (Fig. 16). The reason for the increase in 'pellet-form' droppings as the season progressed was obscure. The large proportion of 'pellet-form' droppings in the first column of the histogram was caused by numerous small lamb droppings.

On average 'pellet-form' droppings were smaller than 'compact' droppings. The size distributions of the two types on grassland over the whole year are shown in Table XXX. The difference in mean dropping size was highly

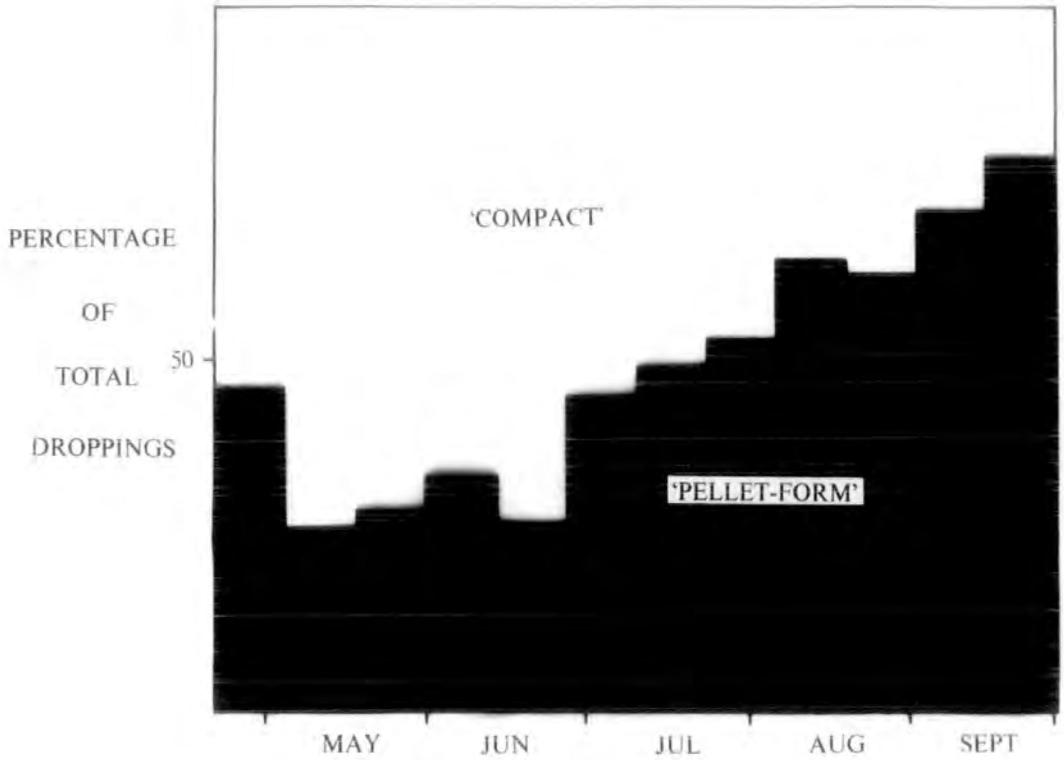


Fig. 16. The change in sheep dung type during 1956.

Table XXX.

Size Distribution of Two Dung Types.

Size (cc.)	'Pellet-form'	'Compact'
0- 25	350	203
25- 50	888	863
50- 75	486	506
75-100	265	325
100-125	69	136
125-150	54	111
150-200	44	126
200-250	6	45
250-300	4	19
300-350	2	3
>350	3	6
Mean dropping size	53 cc	69 cc.

The

significant statistically ($P<.001$), the difference arising very largely in the size group 0-25 cc.

XXIX. The Infestation of Dung by Beetles.

Table XXXI shows the percentages of droppings on grassland which were infested by beetles on the sorting dates. It can be seen that the proportion of infested plots fell after the first two months of the summer season. This was not only the consequence of more dung being available later, for the actual number of occupied plots fell.

Fig. 17g. shows the percentage of occupied

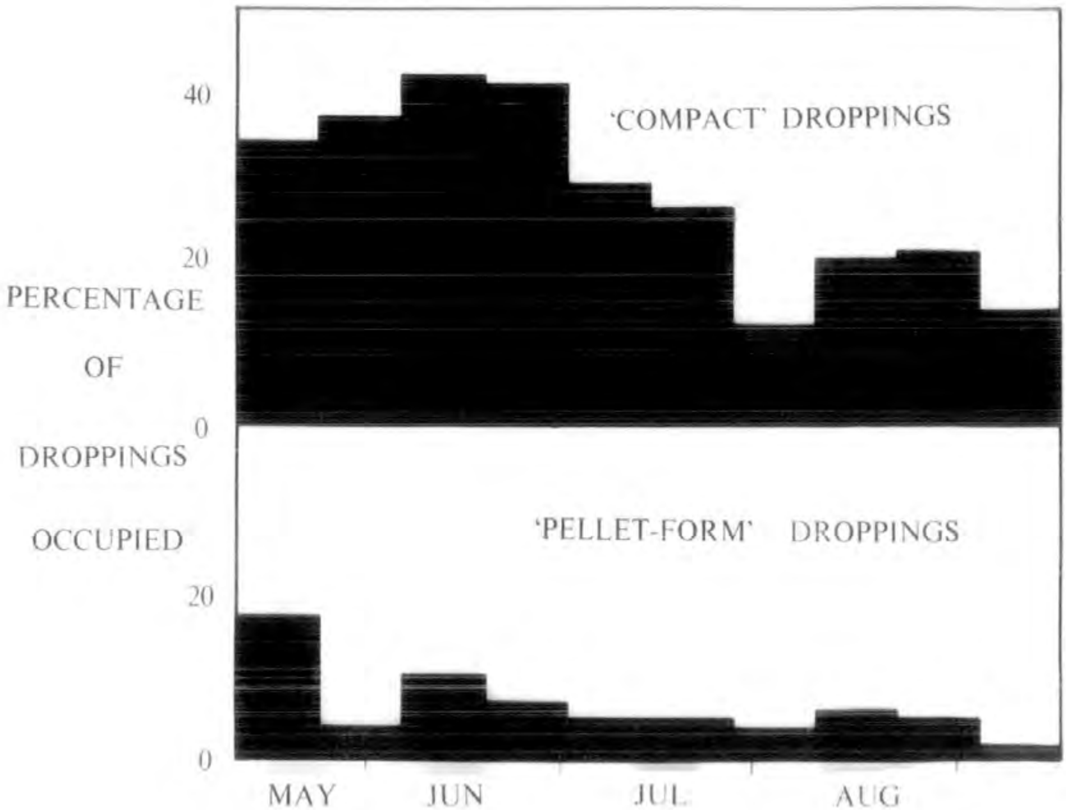


Fig. 17. The percentage of sheep droppings infested by Aphodius beetles during 1956.

Table XXXI.

The Infestation of Dung by Beetles.

Date	Occupied droppings	Unoccupied droppings	% infestation
7 May	22	89	24.7
22 May	56	185	30.3
6 Jun.	82	231	35.5
21 Jun.	113	419	26.9
5 Jul.	108	529	20.5
21 Jul.	90	683	13.2
4 Aug.	50	592	8.3
20 Aug.	90	560	16.1
4 Sept.	51	776	6.6
19 Sept.	42	483	8.7

plots when dung was considered as two types, obviously the compact droppings were more attractive to beetles than those of the pellet-form. Table XXXII shows the average percentage

Table XXXII.

The Average Percentage Infestation of Dung.

Dung type	Total droppings	Occupied droppings	% infestation
'compact'	2343	589	25.1
'pellet-form'	2171	99	4.5

occupation for the two types of dung over the whole season.

XXX. The Size Distribution of Infested Dung.

The size of droppings which were infested by beetles was compared with the size distribution of all droppings (Table XXXIII). It can be seen that

Table XXXIII.

Infestation and Dropping Size.

Size (cc)	No. of droppings	% of droppings	No. of droppings infested.	% of droppings infested.
0- 25	621	11.7	14	2.2
25- 50	1965	37.2	171	26.9
50- 75	1194	22.6	156	24.5
75-100	748	14.2	129	20.3
100-150	457	8.6	93	14.6
150-200	199	3.8	44	6.9
> 200	102	2.0	29	4.6
	5286		636	
Mean dropping size	62 cc		81 cc	

there was a considerable difference in the mean size of the two distributions. On average, infested droppings were 19 cc larger than all of the droppings together, a difference which was highly significant statistically ($P<.001$). Table XXXIII shows that the difference between the two distributions was largely the result of fewer small droppings (less than 50 cc.) being infested than expected. Generally speaking larger droppings proved to be more attractive to beetles, this can be seen from Table XXXIV which shows that the number of beetles per plot increased with the dropping size.

Table XXXIV.

Beetle Infestation and Dropping Size.

Dropping size (cc.)	0- 50	50-100	100-150	>150
'compact' type 1 wk. old				
May-Jun.	2.59	3.68	4.25	6.50
Jul.-Sept.	1.78	2.37	2.31	2.30
'compact' type 1 wk. old	1.58	1.56	1.76	2.87
'pellet-form' droppings	1.60	1.54	2.10	1.16
	No. of beetles per occupied plot.			

When the two dung types were distinguished, the infested droppings were still significantly larger than their respective total distributions ($P < .001$). However comparison of the size distributions of infested 'pellet-form' and 'compact' droppings, showed no significant difference ($P > .06$).

XXXI. <u>The Age of Infested Droppings.</u>

The figures in Table XXXV suggested that

Table XXXV.

The Age of Infested Plots of Two Types of Dung.

Dung type	Less than one week old	More than one week old	Total
'compact'	406	145	551
'pellet-form'	73	12	85

on average, dung up to one week old was more attractive or suitable for beetles than dung aged between one and two weeks. The implication is that many beetles leave infested dung when it becomes one week old. About 26% of the infested 'compact' droppings were estimated to be more than one week old, while only 14% of the infested 'pellet-form' droppings were in the second age group. The difference in the proportions of each dung type which were infested in the second week, was statistically significant ($P < .001$). Thus it appears that, on average, the 'pellet-form' droppings were suitable for infestation over a shorter period than the 'compact' form. This was to be expected, for the structure of the 'pellet-form' droppings makes them more liable to desiccation.

It was believed that ~~the~~ most of the infested droppings remained suitable for beetles for a week, so that by splitting the dung into two age groups as above, it was possible to get a more accurate estimate of the actual proportion of plots which were attacked at some time. Thus the proportions found to be infested on oexamination (Table XXXII) can be corrected as in Table XXXVI,

Table XXXVI.

The Actual Proportions of Droppings Infested by Beetles.

Dung type	% droppings occupied on examination	% infested droppings less than one week old	Estimate of % droppings occupied
compact	25.1	73.7	2(25.1 x .737) = 37%
pellet-form	4.5	85.9	2(4.5 x .859) = 7.8%

thus it was estimated that 37% of the 'compact' droppings were infested by beetles, while only 8% of the 'pellet-form' droppings were attacked. Table XXXVII shows estimates of the proportions (of the proportions) of dung which were infested in alternate weeks of 1956 on grassland. Occasionally a high percentage infestation was achieved among 'compact' droppings.

The size distribution of infested droppings, when considered in two age groups showed no great difference (Table XXXVIII). There was some indication that infestation of the smallest droppings rarely lasted for longer than a week.

Table XXXVII.

Estimates of the Proportion of Dung Infested by Beetles.

Date	Compact droppings No. per week	No. infested <1 wk. old	% infested	Pellet-form droppings No. per week	No. infested <1 wk. old	% infested
7 May	23	11	48	22	6	28
22 May	66	51	77	26	2	8
6 Jun.	80	57	71	35	7	20
21 Jun.	142	70	49	67	10	15
6 Jul.	201	73	36	62	6	10
21 Jul.	218	44	20	123	8	6
5 Aug.	142	19	13	154	7	5
20 Aug.	85	47	56	195	17	9
19 Sept.	114	28	25	212	7	3

Table XXXVIII.

The Size of Infested Plots of Different Age.

Size (cc)	<1 wk. old.	>1 wk. old.	% infested plots <1 wk. old.	% infested plots >1 wk. old.
0- 25	13	1	2.7	0.6
25- 50	124	47	25.9	29.9
50- 75	117	39	24.4	24.8
75-100	106	23	22.1	14.6
100-125	36	14	7.5	8.9
125-150	33	10	6.9	6.4
>150°	50	23	10.4	14.6
Totals	479	157		

XXXII. The Seasonal Succession of Aphodius Adults in Sheep Dung.

The adult beetles of the genus *Aphodius* show a well-marked seasonal succession which was studied in some detail in sheep dung in the Moor House area. Supplementary observations were made on the contents of horse dung during early spring and late autumn when sheep were not present. For the purpose of general comparison, qualitative observations of the succession were made at Durham in 1955.

At Moor House in the second week of March, 1957, recently dropped horse dung was found to contain small numbers of actively feeding *A. conspurcatus*. This was the earliest record of adult beetle activity obtained from Moor House. A month later *A. tenellus* was found to have joined *A. conspurcatus* in horse dung. Only small numbers of these two species were involved in spring activity, *A. prodromus* and *A. sphacelatus* were the first species to appear in large numbers. In 1955, the appearance of these species coincided with the return of sheep to the reserve, but in 1956, activity started several days before sheep dung was available, with the result that horse dung was heavily infested.

Quantitative observation of the seasonal succession of adults in sheep dung at Moor House is presented graphically in Fig. 18. The figure covers the periods of activity in 1955 and 1956, the histograms being constructed from estimates of the percentage frequency of each species at approximately 14 day intervals. The method of taking samples was different in the two years as has already been described. In 1955, quantitative sampling did not begin sufficiently early to demonstrate the importance of A. prodromus and and A. sphacelatus at the beginning of the season, and in 1956 the dominance of these two species was not shown particularly well because A. ater had appeared in considerable numbers before sheep dung was available for sampling. In mid--Apr. 1956, A. prodromus and A. sphacelatus constituted 70% and 20% of the total beetles found in horse dung.

It can be seen from Fig. 18 that A. prodromus and A. sphacelatus had a similar period of activity in dung, disappearing at the end of June. A. ater appeared a week later than the first two species but persisted much longer,

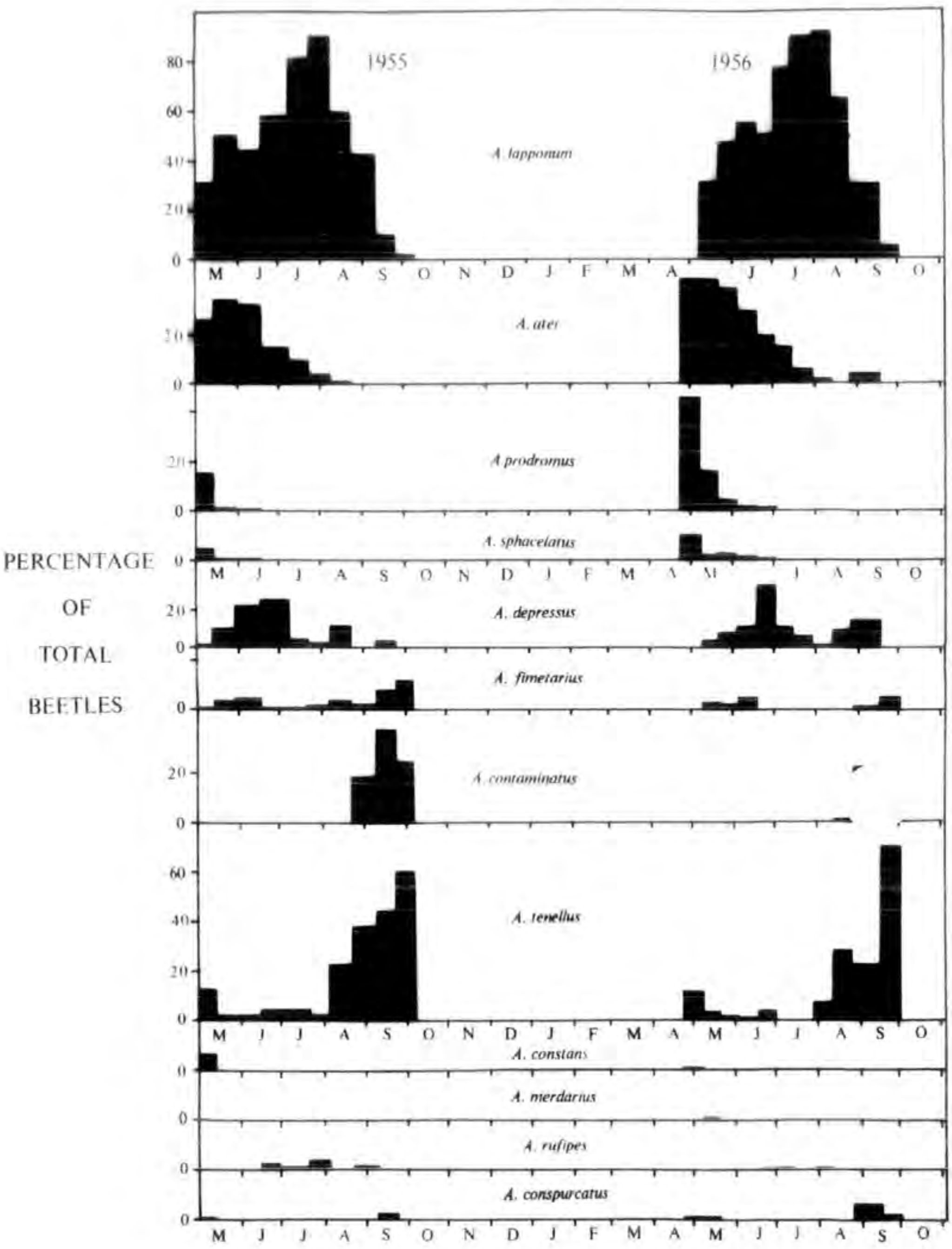


Fig. 18. The seasonal succession of Aphodius beetles in the adult stage.

still being found in August and September.

A. lapponum made its appearance in the second week of May, rapidly becoming the commonest beetle, a position which it maintained until late Sept. In late Jul. and early Aug. 80-90% of the beetles found in dung were of this species.

A. depressus had a similar period of activity to A. lapponum but was never so important numerically.

A. contaminatus appeared in the dung from late Aug. until the sheep were removed at the beginning of Nov., a few specimens were obtained from horse dung during the first half of Nov.

Consideration of the common species of Aphodius at Moor House is concluded with A. tenellus. Adults of this species were found throughout the period in which activity was possible at Moor House, and it became the commonest beetle when A. lapponum declined.

The figure also shows the occurrence of the less common species at Moor House. A. fimetarius was found throughout the season in 1955 but not in 1956. It is believed that this was because the graphs for 1956 were based on fewer animals than those of 1955. This fact probably accounts for the absence of _A. tenellus_ from the samples of Jul. 1956. The estimates for this month were based on 539 and 205 animals in 1955 and 1956 respectively.

XXXIII. The Seasonal Succession at Durham.

Qualitative observations at Durham revealed certain conspicuous differences from the seasonal succession of adult beetles at Moor House. Both _A. lapponum_ and _A. tenellus_ were absent from the lower area, but were partially replaced by _A. rufus_ and _A. fossor_. _A. conspurcatus_ occupied a similar position in the succession of both areas, being found in early spring and autumn. The appearance of _A. prodromus_ and _A. sphacelatus_ occurred between 12 Mar. and 30 Mar. in the three years of study, that is between four and six weeks earlier than at Moor House. At Durham _A. ater_ did not follow so rapidly after these two species, appearing in early Apr. Whilst being common, _A. ater_ never formed such a large proportion of the beetles active in Durham.

A. fossor was the dominant species during late May and June, this making way for _A. rufus_ and _A. rufipes_ in Jul. and Aug. _A. rufipes_ played a more important part in the succession at Durham than at Moor House where it could be said to be an uncommon species. The relative abundance of A. depressus and A. fimetarius at Durham was the reverse of that found at Moor House, for the latter species could always be found in some numbers throughout the summer on the lower area.

A. contaminatus had a similar period of activity in both areas.

A conspicuous difference in the successions at Moor House and Durham was the re-appearance of A. prodromus and A. sphacelatus at the lower area, large numbers were found in horse dung during the second week of October and they remained active until mid-November.

A. constans and A. merdarius played similar parts in the successions of both areas, they were uncommon and found only in April, May and June.

XXXIV. The Relative Abundance of Aphodius Species at Moor House.

The numbers of adult beetles removed from samples of sheep dung throughout the seasons of 1955 and 1956 are shown in Table XXXIX. The

Table XXXIX.

The Relative Abundance Of Beetles At Moor House.

Species	No. of beetles 1955	No. of beetles 1956	% of total 1955	% of total 1956
A. lapponum	1753	865	51.6	50.6
A. ater	696	420	20.4	24.6
A. depressus	322	134	9.4	7.8
A. prodromus	78	99	2.3	5.7
A. tenellus	300	91	7.8	5.3
A. sphacelatus	34	29	1.0	1.6
A. fimetarius	91	27	2.6	1.5
A. contaminatus	80	23	2.4	1.3
A. conspurcatus	7	7	0.2	0.4
A. merdarius	12	6	0.4	0.4
A. rufipes	27	5	0.8	0.2
A. constans	29	1	0.9	0.1
A. luridus	1	0	0.1	0.0
Totals	3430	1707		

relative abundance of each species was remarkably similar in both years, and it is suggested that the similarity would have been even more conspicuous if the sampling method used had been the same in each year. The figures for 1956 provided a more reliable estimate of the relative abundance of each species, for the method of sampling ensured the removal of all beetles from a fixed area at regular intervals. This was not so for beetles collected in 1955.

The contributions to the table made by A. ater and A. prodromus considerably under--estimated their importance in 1955, for sampling started some time after these species became active in sheep dung. Conversely, the importance of A. tenellus and A. contaminatus was over-emphasised, for towards the end of the season the scarcity of infested dung made it necessary to search greater areas to obtain adequate samples.

Half of the animals were of one species namely A. lapponum, A. ater was also common making up 20-25% of the total. Six other species, A. depressus, A. prodromus, A. tenellus, A. contaminatus, A. sphacelatus and A. fimetarius, were commonly found at some time during the season. The remaining five species could be said to be uncommon at Moor House.

XXXV. The Number of Adults on a Fixed Area.

Fig. 19 shows the numbers of adults found in sheep dung on 3,000 m² of grassland in 1955 and

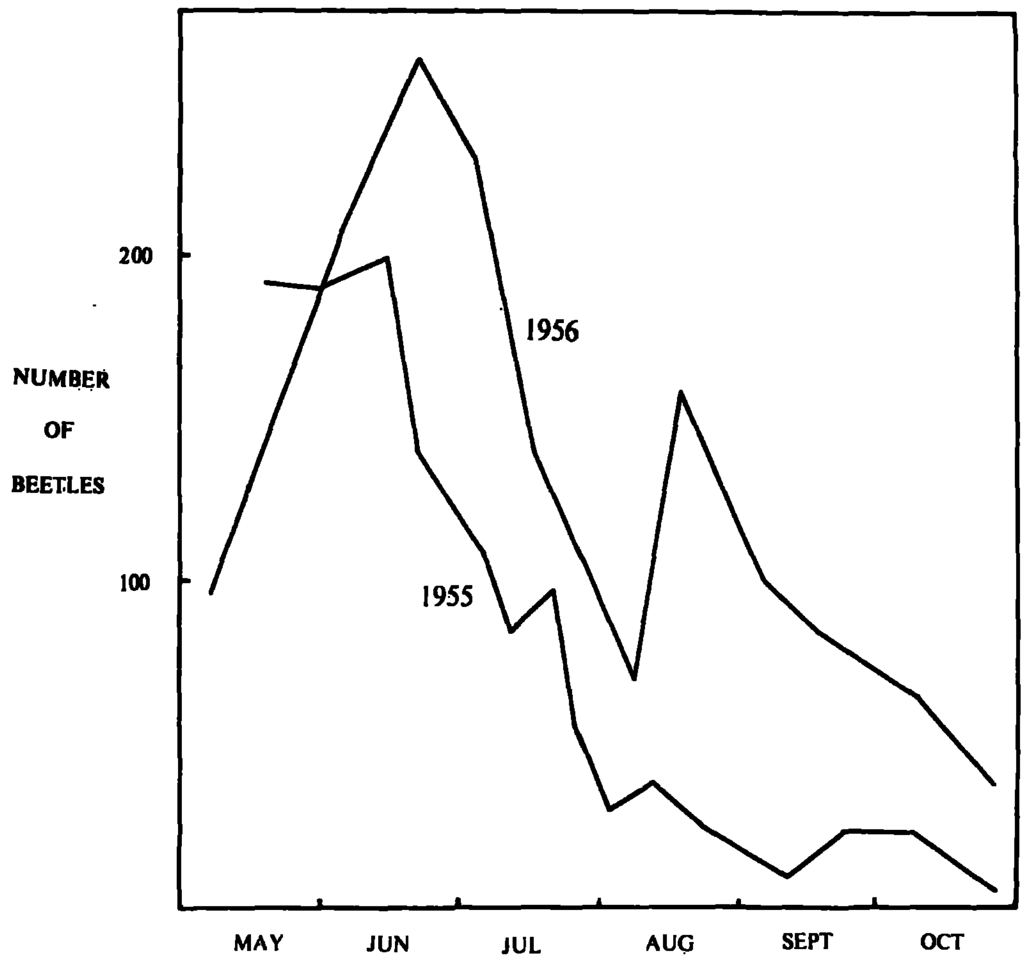


Fig. 19. The number of adult <u>Aphodius</u> beetles found in dung on 3,000 m^2 of grassland during 1955 and 1956.

1956. The figures for 1955 gave a more detailed curve, as samples were taken at weekly instead of 15 day intervals. The samples were taken differently in the two years, which probably accounts for the greater part of the difference between the curves. The 1955 figures were obtained by sorting 50 cc of dung from each dropping, while in 1956 the whole dropping was sorted. In addition, beetles were taken from dung more than one week old in 1956, this was not so in 1955.

However, it seems likely that the greater number of beetles in the latter part of 1956 relative to the same part of 1955 might represent a genuine difference. Such a difference would be readily explicable in terms of the effect on dung of the drought occurring at that time during 1955. Figs. 20 and 21 show the abundance of beetles in dung for several species.

If these enormous changes in adult population were typical for every year, then it indicates that there can be no food shortage or scarcity of egg-laying situations for adult beetles in the latter part of the year, for the amount of dung available at that time was greater than in the early part of the year.

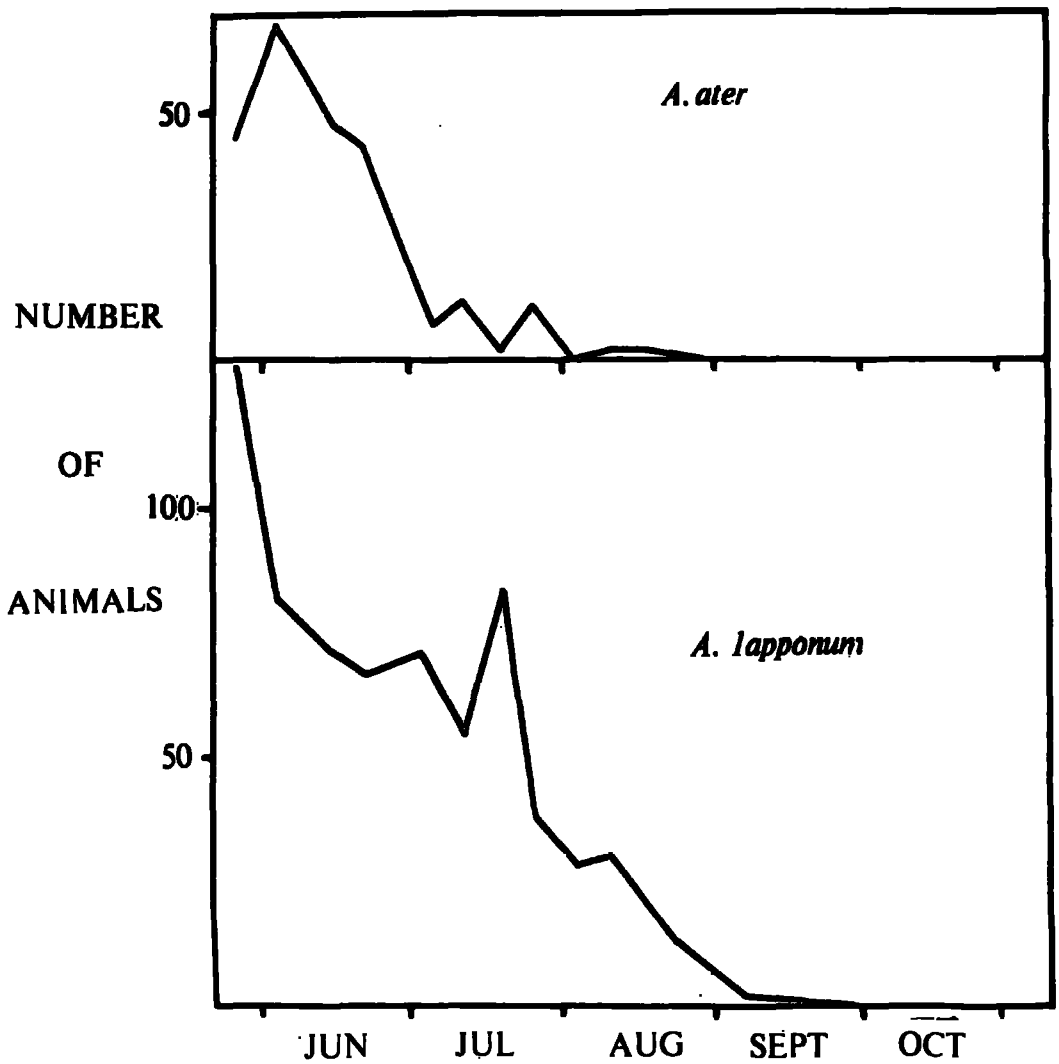


Fig. 20. The numbers of adult A.ater and A. lapponum found in dung on 3000 m² of grassland during 1955.

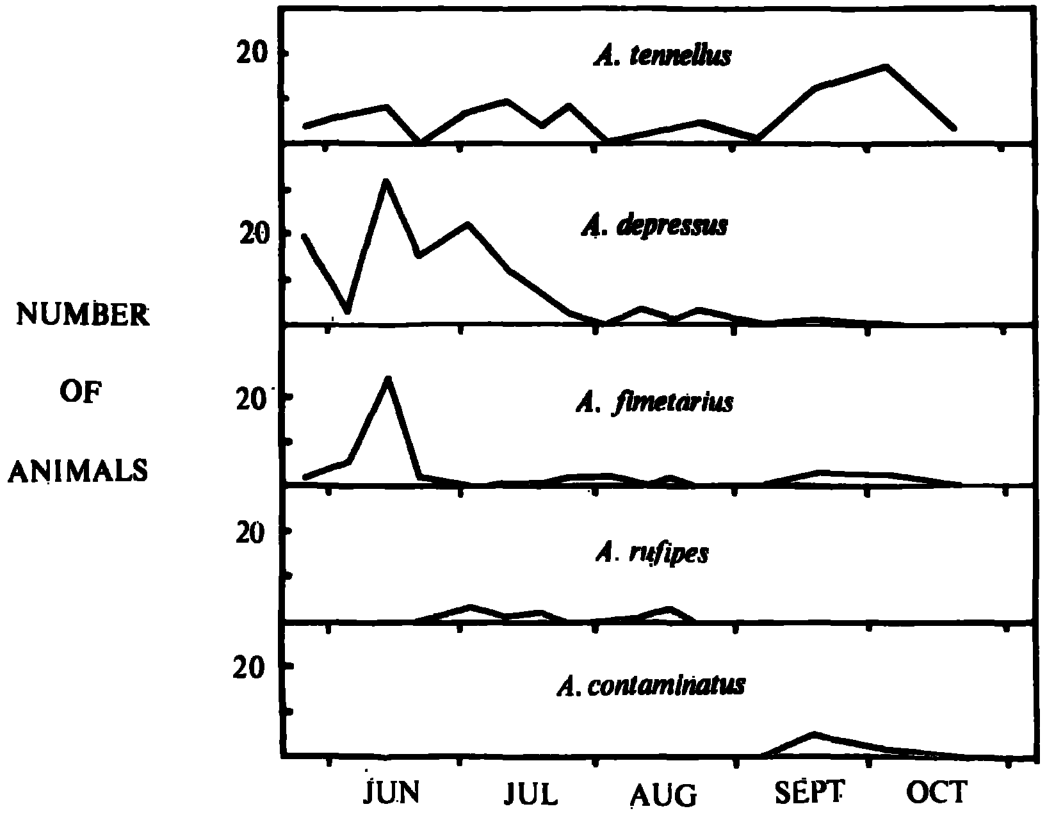


Fig. 21. The numbers of adult beetles of several species found on 3000 m^2 of grassland during 1955.

XXXVI. The Attractiveness of Different Dung Types.

The olfactory senses of the beetle were undoubtedly of the greatest importance in searching for dung, but probably sight and later touch played their part. The attractive power of dung has not been studied, but qualitative differences between dung types was easily demonstrated. At Houghall near Durham when *A. rufus* and *A. fossor* were found in large numbers in cow dung (100 *A. fossor* to 63 *A. rufus*), only the former was found in sheep dung in an adjacent field. At Moor House on 3 June equal quantities (2,500 cc) of infested horse and sheep dung were sorted for beetles with the result shown in Table XL.

Table XL.

Species Proportions and Number of Adult Beetles in Equal Quantities of Horse and Sheep Dung.

Species	Sheep dung (2500 cc) Nos.	Sheep dung (2500 cc) % of total	Horse dung (2500 cc) Nos.	Horse dung (2500 cc) % of total
A. lapponum	85	49	11	28
A. prodromus	0	0	16	40
A. ater	78	45	5	13
A. tenellus	3	2	2	4
A. fimetarius	5	3	3	8
A. depressus	2	1	2	4
A. merdarius	0	0	1	3
	173		40	

N.B. Dung of both types was taken from the same area.

A number of other comparative collections were made which illustrated the apparent preference of some species for certain types of dung (Table XLI.).

Table XLI.

Random Collections of Adult Beetles Taken from Sheep and Horse Dung, Showing Differences in Species Proportions in the Two Types of Dung.

	Sheep dung	Horse dung
Moor House 7 Sept. 1955.		
A. contaminatus	10	45
A. rufipes	0	2
A. lapponum	10	2
A. fimetarius	2	1
A. tenellus	15	0
Moor House 21 Sept. 1955.		
A. contaminatus	6	38
A. rufipes	1	1
A. lapponum	2	0
A. fimetarius	1	0
A. tenellus	15	1
A. conspurcatus	0	1
Moor House 5 Oct. 1955.		
A. contaminatus	13	13
A. rufipes	0	1
A. lapponum	1	0
A. fimetarius	5	0
A. tenellus	16	1
A. conspurcatus	1	25

Caution must be exercised in interpreting the results of this latter table, because of local variation in the species complex. On 6 Sept. 1955, A. contaminatus was common at one site but was completely absent from an adjacent site (Table XLII).

Table XLII.

Differences in Species Proportions in Sheep Dung in Adjacent Fields at Moor House, 6 Sept. 1955.

	Site A	Site B
A. contaminatus	0	10
A. tenellus	11	15
A. lapponum	20	10
A. fimetarius	0	2
A. depressus	2	0

N.B. All animals collected within 60 yards of each other.

In conclusion it can be said that A. prodromus, A. sphacelatus, A. contaminatus and A. conspurcatus showed a preference for horse dung, while A. lapponum A. ater and A. tenellus prefered sheep dung.

Taking horse dung as 100% attractive to A. howitti. Carne found the attractiveness of cow and sheep dung to be 26-54% and 16-18% respectively for this species.

XXXVII. The Number of Beetles Infesting Droppings of Different Type and Size.

It has already been demonstrated that 'pellet-form' droppings were not very attractive to *Aphodius* beetles. Further evidence of this was obtained when the number of beetles per occupied plot was examined (Table XLIII.). The difference

Table XLIII.

Beetle Density and Dung Type.

Dung type	No. of beetles	No. of occupied plots	Beetles per occupied plot
'compact'	1499	585	2.56
'pellet-form'	163	98	1.60

between the number of beetles per dropping was highly significant ($P < .001$).

It was also found that the density of beetles in infested droppings varied with the size of the dropping. Table XXXIV shows an analysis of this. It was particularly clear in 'compact' droppings less than one week old in the early part of the year. The figures for the 'pellet-form' droppings were not significant, the number of beetles involved being rather small.

An experiment carried out during 1955 also showed that the number of beetles per plot increased with the size of the dropping. In this experiment plots of fresh dung of known volume were exposed to infestation for 24 hours. In all nine replications were carried out, only seven of them being infested. Each replication consisted of 8 droppings of 100 cc, 4 droppings of 200 cc, and 2 of 400 cc. On completion of the experiment 5,600 cc of dung in each size group had been sorted, with the result shown in Table XLIV. The differences were not significant, but both experiments indicated that the attraction of beetles to dung was mainly to the dropping as a unit, but larger droppings may have exerted (have exerted) a greater attraction to beetles.

Table XLIV.

Beetle Infestation and Dropping Size.

Dropping size (cc.)	100	200	400
No. of plots	56	28	14
No. of beetles	46	28	18
Beetles per plot	0.8	1.0	1.3

The experiment using plots of dung of known size was repeated, the dung being left for longer periods. During Aug. 1955, conditions were hot and dry, so that after four days plots of 100 cc had lost the moist texture which beetles enjoy. The results of the experiment are shown in Table XLV.

Table XLV.

Beetle Infestation After Four Days.

Dropping size (cc.)	4 plots of 100 cc.	2 plots of 200 cc.	1 plot of 400 cc.
1st replication	3	5	9
2nd replication	1	3	7
Total	4	8	16
Beetles per plot	0.5	2.0	8.0

It can be seen that the number of beetles per plot increased markedly with the size of the dropping. This in all probability resulted because the smaller plots dried out. However it is not thought that the results of the experiments carried out in 1956 were influenced much by this effect, for the conditions were too cool and wet for severe drying to occur on anything but rare occasions.

XXXVIII. <u>Variation of Infestation with Dung Density.</u>

In the early part of the 1956 season it was noticed that where dung was scarce, the number of beetles found in droppings was higher. This was examined in detail for the period 21 Apr. to 23 May on the grassland areas. As few 'pellet-form' droppings were infested, only 'compact' droppings were considered in the analysis. The sample sites

Table XLVI.

Beetle Infestation and Dung Density.

Dung density groups	1	2	3	4
No. of sampling sites	42	9	6	3
No. of droppings	49	51	50	46
Occupied droppings	21	18	17	12
No. of beetles	168	133	73	66
Aver. droppings per 100 m^2.	1.2	5.7	8.3	15.3
Beetles per 100 m^2.	4.0	14.8	12.1	22.0
% plots infested	43	35	34	26
Aver. beetles per plot	3.4	2.6	1.5	1.4
Aver. beetles per occupied plot	8.0	7.4	4.3	5.5

were ranked according (according) to the density of droppings on them, and were then split into four groups with approximately equal numbers of droppings in each. The results are summarised in Table XLVI. It can be seen that the proportion of plots occupied, the average number of beetles per plot, and the average number of beetles per occupied plot, were all higher where the density of dung was low. This implied that the dispersing, dung-seeking beetles were more randomly distributed than the droppings. However, it should be noted that where dung was more dense, more beetles were found per 100 m^2. It was not possible to carry out the analysis using individual species, as insufficient material was available. Similar calculations were carried out for each sampling date, but the general increase in dung density was sufficient to prevent such aggregation occurring.

XXXIX. Other Animal Occupants of Dung.

Of the other beetles which were found in dung, small Staphylinids and Palpicorns of the genus Cercyon were the most common. The taxonomy of both these groups is uncertain, and to study them would have been a full-time research problem. For this reason these animals were rarely collected, and little is known of their place in the utilisation of sheep dung. They were certainly very numerous, and their larvae were commonly found in dung. In order to get some idea of the numbers which appeared in heavy infestations, a dropping of 300 cc was carefully sorted for the adult stages, 403 Cercyon adults and 162 Staphylinids were counted. Generally speaking _Aphodius_ did not occur in dung without these other beetles, it may only have been a consequence of their abundance but they were always present in dung before _Aphodius_.

Sphaeridium of two species were taken at Moor House during 1956. All of the specimens were _S. scarabaeoides_ except two which were _S. lunatum_. They were uncommon, only 45 specimens being taken while 1700 _Aphodius_ adults were collected. Thirty _Sphaeridium_ were taken on 23 May. only occasional specimens being collected on other dates.

Geotrupes was a conspicuous but relatively rare member of the dung fauna, occurring less frequently than _Sphaeridium_.

As is usual in the succession of animals which infest dung, the Diptera were the first to appear at Moor House. Sphaerocerids of the genus _Borborus_ were so common that sometimes their lemon coloured eggs filled every crevice of the dung. _Scopeuma stercorarium_ was particularly common from May to August.

Before _Aphodius_ adults completely vacated dung, the dipterous eggs began to hatch.

larval stages, and lumbricid worms. The method of study was not designed to estimate the relative importance of these groups in their role as dung removers, but some tentative conclusions can be drawn from observations made during the three years of study.

By careful examination of the dung it was possible to identify the previous tenants fairly accurately. Dipterous larvae left a dropping with part of it perforated by many closely-set borings. Aphodius adults produced a few broad and irregular tunnels, while the larvae produced characteristic spherical cavities. On the other hand lumbricid worms tunneled in dung rather like Aphodius adults but also removed dung from the under-surface of the dropping in a manner which was readily recognisable. Using these characteristics it was possible to make some estimate of infestation rates of the three groups of animals. However, on occasions when worm activity was intense it was sufficient to obliterate the evidence of previous occupation by fly larvae and beetles. This sometimes occurred in the months of Jul., Aug., and Sept., when lumbricid worms were most active (see p. 81, Table XXV.). The infestation by Diptera differed from that of lumbricid worms in that it was more intensive in the early part of the year. This difference is illustrated in Table XLVII, compiled from two counts made on the grassland sample sites. Undoubtedly dung was suitable for a

Table XLVII.

Infestation of Dung by Lumbricid Worms and Dipterous Larvae on Grassland Sample Sites.

	No. of droppings Infested	No. of droppings Total	Percentage infested
6 Jun. 1956			
Lumbricid worms	8	211	4
Dipterous larvae	62	211	29
16 Aug. 1956			
Lumbricid worms	172	733	24
Dipterous larvae	17	733	2

period longer than 15 days, so that the proportion of dung attacked by lumbricid worms in the table is not a good representation of what happened under natural conditions. A number of counts were made by Svendsen (1955) during his work on the area which give a better indication of the extent of infestation of dung by worms (Table XLVIII). The present author carried out one count comparable to Svendsen's figures during late June 1956, for three vegetational types (Table XLIX). The dung

Table XLVIII.

Infestation of Sheep Dung by Lumbricid Worms in Aug. 1953.

(from Svendsen, 1955)

	No. of droppings		Percentage
	Infested	Total	infested
Grassland	43	127	34
Calluna-Eriophoretum	61	211	29

was arbitrarily separated into two groups from its appearance, that which was estimated to have

Table XLIX.

Infestation of Sheep Dung by Lumbricid Worms and Dipterous Larvae in Jun. 1956.

	No. of overwintered droppings			No. of recent droppings		
	Infested by			Infested by		
	Diptera	Worms	Total	Diptera	Worms	Total
Grassland	0	27	30	91	9	150
J. squarrosus areas	6	43	61	40	5	60
Calluma-Eriophoretum	8	37	58	13	1	26

overwintered, and that which was not more than two months old. It can be seen that there had been little lumbricid activity in the recent dung, while half of the overwintered dung had been attacked at some time. This together with the large proportion of recent droppings infested by Diptera confirms the conclusions drawn from Table XLVII.

The infestation of dung by Aphodius on the three vegetational types was only examined in the adult stage. It can be seen that the percentage ~~infestation~~ infestation over the whole year was similar for the three types when allowance was made for the fact that sampling was carried out at monthly intervals on the *J. squarrosus* and Calluna-Eriophoretum areas (Table L.).

Table L.

Infestation of Dung by Aphodius on Different Vegetational Types.

	Occupied droppings	Total droppings	Percentage occupied
Grassland	636	3544	18
J. squarrosus areas	133	823	16
Calluna-Eriophoretum	46	287	16

XI. Discussion.

Between the years of 1944 and 1952 a discussion of considerable length took place in biological journals on the importance and meaning of what came to be called 'Gause's hypothesis'. The argument started at a symposium of the British Ecological Society on 'the ecology of closely related species', when several definitions of the hypothesis were presented. It was unfortunate that in the papers which were quoted as containing the hypothesis Gause made no statement which resembled any of the definitions used by later authors (Gause, 1934a, 1934b). However in the report of the symposium (Anon., 1944) Gauses's hypothesis was stated as 'two species with similar ecology cannot live together in the same place'. Elton, Lack and Varley supported the postulate at this meeting, Elton (1946) and Lack (1947) subsequently publishing their views. Moreau (1948) in a study of ecological isolation in a tropical avifauna supported Elton's contention that ecological separation manifested itself by less species per genus being present in a community than would be expected on chance. Williams (1947, 1951) examined statistically some of the figures presented by Elton and Moreau and concluded that their interpretation of results was incorrect, for more species per genus occurred in these communities than would be expected on chance. Williams concluded that closely related species tended to occur together because they were more suited to similar environmental conditions and to similar extra-generic competition. The advantages of these factors were believed to outway the disadvantage of interspecific competition between close relatives, even though as Darwin (1859) wrote, 'As the species of the same genus usually have, ..., much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between species of distinct genera.' Gilbert, Reynoldson and Hobart (1952), examined the definitions of Gause's hypothesis in detail, and it is now generally agreed that most of the argument revolved about terms used in slightly different ways by each group of protagonists. Nevertheless it is of great interest to discover in what way closely related species are separated ecologically as well as taxonomically.

In 1924 Clements wrote that, 'The opinions and hypotheses arising from observation are often interesting, and may even be of lasting value, but ecology can be built upon a lasting foundation solely by means of experiment.....' While agreeing with Clements on this, observation leading to the formulation of hypotheses must necessarily be a precursor to experimentation. The present study has progressed little further than the observation stage.

Species of the genus Aphodius appeared to be closely related ecologically as well as taxonomically, for most of them were commonly found in herbivore dung, a superficially similar habitat, but just as many of the arguments of Elton and Williams depended upon the degree of detail used in describing the habitat, so it was with the apparent similarity of the dung beetles' habitat. The beetles reacted differently to horse, cow and sheep dung, and even dung of one herbivore varied considerably in form, condition and suitability for beetles. Further the beetles did not spend all of their lives in dung, so that the habitat had to be extended to include soil and peat, making for still more variability in the habitat.

Seasonal succession separated many of the species ecologically. This was seen particularly well in the adult stage, for of the eight species which formed at least 10% of the species complex at any one time during the breeding season, never more than four were common at the same time.

Besides temporal differences of this sort, the species behaved differently. The species varied in their egg-laying habits and larval stages. Even A. prodromus and A. sphacelatus which were very close taxonomically, were found to have slightly different periods of activity in the adult stage together with differences in distribution. It was found that several species showed distinct preferences for specific types of dung, a situation which emphasised the separation of the species. Presumably the olfactory senses had a part to play in dung type selection of this sort. That odours could prove to be attractive to one species while another was unaffected was shown by Kearns.

Insufficient knowledge of the detailed biology of the Aphodius species was discovered to allow a study of their populations at Moor House. The reasons for this were several, for instance the aggregation of the organisms to dung presented formidable sampling problems. Neither of the methods adopted in this study were suitable for population work for only adults were sampled, and the numbers obtained were probably indicative of the extent of activity rather than actual numbers of organisms.

Secondly, the abundance of the beetles and their immature stages was not great. The methods used by Carne in his study of A. howitti would not have yielded any results at Moor House, for while he found that heavy infestations of larvae reached 6170 animals per m^2 and 250 adults usually emerged from the same area. The density of Aphodius larvae at Moor House probably averaged less than 1 per m^2 even on the grassland.

The scarcity of the animals in the field together with the difficulty experienced in culturing the beetles, restricted experimental work on the larval stages, and little was discovered of the beetles' enemies. However the very scarcity of the beetles themselves posed some interesting questions. At only one period during the season did the beetles attack most of the dung, 75% of the 'compact' droppings being infested. Even at this time most of the 'pellet-form' droppings were uninfested and there can have been no food shortage for adult beetles. However, it was possible that larvae hatching from eggs laid at this time may have experienced difficulty in finding an adequate supply of food, for droppings which were heavily infested by adults were so riddled by tunnels that they were liable to rapid desiccation. Towards the end of the season beetle infestation of droppings was so low that it is believed that food shortage could not have affected the beetle populations. There is no doubt that in a population study of Aphodius species, the availability of the habitat and food supply could not be measured in terms of the number of droppings. Initially, account would have to be taken of the availability and attractiveness of each dropping at the time at which adult beetles were active.

The two years of study provided great climatic extremes, but no obvious differences in the beetles populations were noticed, in fact the two years were remarkable for the similarity of the results obtained.

Even though _A. lapponum_ is restricted in this country to upland areas, it was the most common _Aphodius_ species found at Moor House. This change from being the dominant species to complete absence occurred over a distance of only several miles and an altitudinal distance of 1000 ft. This suggested limitation by the physical environment, for it was considered unlikely to be the result of a change in the suitability of the dung. Where closely related species occur together in the same habitat for a considerable part of their life--cycles, factors of the physical environment are probably of primary importance in determining their relative abundance in any locality.

The abundance and utilisation of many commodities can be used to give an indication of the turnover of materials in Nature. Sheep dung was one such commodity at Moor House, the abundance of dung gave some indication of the value of different vegetational types as food for sheep, while the rate at which dung was consumed on these areas was an index of the abundance and variety of species available to utilise it as food. Per unit area, grassland produced the most food for sheep and also supported greater numbers of organisms capable of utilising the dung. Areas of J. squarrosus came second to the grassland, while areas of Calluna-Eriophoretum made a very poor third. Three groups of animals played important parts in utilising the dung, lumbricid worms, dung fly larvae, and dung beetles. It was found that only the worms were influenced directly by the vegetation type. The activities of the other organisms were linked more directly to the dung, their ability to fly releasing them from the limitations imposed upon the worms by the soil type. The percentage infestation of dung by Aphodius adults was seen to be similar for the three vegetational types studied, and the same appeared to apply to the dipterous flies. Lumbricid worms were most abundant on grassland, being found less commonly on areas of J. squarrosus, while very few specimens were taken on Calluna-Eriophoretum.

It is considered that Aphodius was relatively unimportant as an agent in removal of dung compared with lumbricid worms and dipterous larvae. The latter were most efficient in the early part of the season, while lumbricid worms reached the peak of their activity later in the year.

Factors of the physical environment such as wind, rain, and frost, also played a major part in dung removal, their effect not being similar on the three vegetational types. The short turf of the grassland areas provided less protection against the elements than did *Juncus*, *Calluna* and *Eriophorum*.

In conclusion it can be said that grassland produced greater quantities of sheep fodder per unit area than Calluna-Eriophoretum, and the same was probably true for areas of *J. squarrosus*. Removal of dung from these areas was effected by factors of the physical environment together with a number of biotic agents. Of the latter, lumbricid worms were the most important, their effect being greatest on grassland. Dipterous larvae were of second importance, rivalling the effect of worms on the Calluna-Eriophoretum areas. *Aphodius* came third in importance, infesting dung irrespective of the vegetational type.

XLI. Summary.

1. Most of the work was carried out between 1954 and 1956 on the Moor House National Nature Reserve in the northern Pennines, comparative observations being made near Durham.
2. The biology of several species of *Aphodius* were studied in some detail, which enabled the author to discover some of the factors which separated ecologically these closely related species.
3. Attempts were made to assess the place of *Aphodius* beetles in the utilisation of sheep dung. With this end in view observations were also made on dung-inhabiting dipterous flies and lumbricid worms.
4. The genus *Aphodius* has a world-wide distribution and is particularly well-represented in the Palaearctic. There are 42 British species of the genus, 16 of which were found at Moor House.
5. The taxonomy of *A. prodromus* and *A. sphacelatus* was examined in detail.
6. The larval taxonomy of the genus *Aphodius* is poorly known, only 17 of the British species being described. Seven of the known species

were confirmed, and A. lapponum, A.tenellus and A. sphacelatus were definitely identified. Doubt was cast on the published description of the larval stages of A. prodromus.

7. Although A. prodromus and A. sphacelatus were very closely related taxonomically, slight differences in the adult period of activity were found, and A. sphacelatus was more restricted in its distribution in Co. Durham.

8. A. lapponum is an upland species in Britain and is a member of the boreo-British coleoptera. Lindroth maintained that this species arrived in this country before the Wurm glaciation. The present author considered that this conclusion was not valid, and that the species could have arrived in post-glacial or even recent times.

9. Egg-laying behaviour, larval feeding habits, and the site of pupation were described for several species, and information was given for the length of some of the immature stages. There was one generation per year in all species, with the possible exception of A. tenellus. Most of the species overwintered in the adult stage, but A. rufipes spent this time as a prepupa, and A. fimetarius and A. contaminatus

overwinter partially as eggs. The sex ratios of _Aphodius_ species were sometimes different from the 1:1 ratio, females frequently being more numerous than males.

10. A comparison of the biology of _Aphodius_ species found at Moor House and the biology of _A. howitti_ led to the enumeration of the factors which may have been important in the development of this species as a pest. Its independence of dung and high fecundity coupled with the fact that eggs were ripe on emergence, were considered to be factors of importance.

11. Although these closely related species of _Aphodius_ were living in a similar habitat, namely dung, many differences were found in their biology which separated them ecologically. The seasonal succession in the adult stage was particularly effective in this respect, never more than 4 species being common at the same time.

12. Adult beetles were found to be more common in dung during the first half of the summer. A study of the relative abundance of species at Moor House showed that _A. lapponum_ comprised 50% of the animals taken. _A. ater_ comprised 25% of the adults caught.

13. Sheep dung as a habitat for _Aphodius_ beetles

was studied in some detail. The form and condition of dung was observed throughout 1956, and the effect of age, size, type, and density were examined in relation to the beetles. Adult beetles began to leave sheep dung after several days, so that dung 'more than one week old' contained less beetles than that 'less than one week old'. On average larger droppings contained more beetles, and 'compact' droppings were more suitable for beetles than 'pellet-form' droppings. At the beginning of the season more beetles per dropping were found where dung density was low.

14. The removal of sheep dung by physical and biotic agents was examined on three vegetational types, grassland, Juncus squarrosus and Calluna-Eriophoretum. Dung remained recognisable longest on Calluna and Eriophorum, and disappeared most rapidly on grassland. Weathering by the physical elements was more intensive on grassland than on the other areas which had taller vegetation. Biotic agents in the form of lumbricid worms were most active on grassland. Worms were also found more often on J. squarrosus areas than on Calluna and Eriophorum where they were uncommon. Dipterous fly larvae and Aphodius were the other

major dung removers. Both groups of animals were not restricted in their activities by the soil type as were the worms. Infestation of dung was similar on all three vegetational types when Aphodius was considered, on average 18% of all droppings were attacked by beetles. Infestation by Diptera was more intensive than this. It was concluded that lumbricid worms were the most important organisms removing dung, Dipterous larvae came next, and beetles third.

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