SLUGS IN GARDENS: THEIR NUMBERS, ACTIVITIES AND DISTRIBUTION. PART 2*.

By H. F. BARNES AND J. W. WEIL, *Rothamsted Experimental Station*

(With Plates 3–5 and 11 Figures in the Text)

CONTENTS

8. FEEDING HABITS

Although the feeding habits of slugs have not received particular attention by the authors, there has been ample opportunity, especially while collecting at night, to acquire some definite information concerning their customary habits in this direction. The mere mention of one or more species feeding on a particular plant or substance is not meant to convey the impression that other species do not have the same habit; it simply indicates that the species mentioned caught the eye.

The most striking feature has been the apparently infinite variety of food which seems to appeal to their taste. This being so, it seems remarkable that almost any edible bait which may be placed in a garden will attract slugs: one would have thought that they would not have bothered to go towards it, there being so much alternative food all around. But they do.

Another point is that most species and individuals normally feed at or near the surface of the ground. This accounts for the fact that the lower leaves of such plants as cabbages, leeks, onions and so on which frequently touch the ground are more often damaged than the hearts and other portions farther from the soil. One species however, i.e. *Agriolimax reticulatus*, is prone to feed higher up on plants and there are also species which feed underground, e.g. *Milax gracilis* on potato tubers; but even in this species large numbers of individuals feed on the surface of the ground.

Healthy living plants: leaves. Naturally on some occasions slugs have been found after dark in the act of eating the leaves of living healthy plants. For example, *Arion hortensis* has been seen eating young leaves of primulas during the winter and spring months, particularly when they are under a covering of fallen leaves. Large *Arion ater* have been observed eating coarse grass, and their yellow-coloured young have seemed to be partial to brassicas, campanulas and saxifrage during the early part of the year. Likewise *Arion subfuscus* has been seen eating lettuce, cabbage and campanula leaves. *Agriolimax reticulatus* has been found eating the leaves of many plants including grass, lettuce, cabbage, winter greens, scarlet runner bean, Michaelmas daisy, potato, etc.

Healthy living plants: crowns, rhizomes and tubers. Slugs are, by their low feeding habits particularly fond of feeding on the crowns of plants, e.g. *Arion hortensis* on the crowns of primulas. Tubers and rhizomes of plants are also frequently attacked. Thus *Milax gracilis*, *M. sowerbyi* and *Agriolimax reticulatus* have been observed feeding on the tubers of potato and rhizomes of Jerusalem artichoke, particularly when the tubers have been left exposed on the surface of the ground.

The authors consider that *reticulatus* is not a primary pest of potato tubers and does not often start an attack on them. It is, however, a severe secondary pest and is quick to follow, and greatly increase, initial damage done to tubers by other pests, including the slugs *Arion hortensis* and the *Milax* species. Evidence supporting this opinion was obtained by keeping *reticulatus* provided with undamaged potato tubers. After several nights the

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tubers were still undamaged. On the other hand, when slices of potato or tubers with slug holes in them were given to *reticulatus*, there were obvious traces where the slugs had been feeding after only one night. *Milax gracilis* and *sowerbyi*, on the other hand, bored into potato tubers the first night. In the presence of puff-balls, however, *M. sowerbyi* did not attack the potato tubers but preferred the fungi. It is desirable that more critical experiments be carried out before dismissing *reticulatus* as a primary pest of tubers. In any case, it is a very serious secondary one.

Healthy living plants: fruit. As is well known *reticulatus* loves a ripe strawberry. Luckily, with this exception, most fruits are higher from the soil and so out of the reach of slugs. Unfertilized fruit of vegetable marrow has also been seen to attract slugs of various species.

Fungi, algae, lichens and mosses. Among the larger fungi, the puff-ball must have, during part of the summer, formed a favourite item of the diet of the slugs, to judge from the numbers of *Limax maximus*, *Arion hortensis*, *A. subfuscus*, *Milax gracilis* and *M. sowerbyi* seen feeding upon groups of immature specimens. Toadstools of various kinds have also been observed to be eaten by slugs during the early autumn.

In the autumn and winter large numbers of slugs, especially very small specimens of *hortensis* and *subfuscus*, have been observed feeding assiduously on the bark of fallen twigs and larger felled branches which have been laid on the ground. It is presumed the slugs were feeding on the smaller fungi, algae, lichens and mosses which were growing on this bark.

Plant material which has fallen from plants and trees. Throughout the different seasons of the year, various plant material drops to the ground from plants and trees. Thus catkins fall in the spring. Slugs of most species have been seen feeding on walnut catkins and the male catkins of golden willow (*Salix alba* var. *vitellina*). A little later various petals fall. Again slugs have been found apparently feeding greedily on fallen petals and flowers of red chestnut, apple and pear. Still later, fruit in all stages of growth falls at intervals to the ground Such fallen fruitlets and fruit whether sound or in different stages of over-ripeness and decay, as well as diseased fruits, seem equally attractive to many slugs. Hawthorn fruit, pears, apples and plums have all been noticed in this category. Lastly, in the autumn the fallen leaves of deciduous trees and shrubs provide a rich provender for slugs of all kinds, as well as good shelter.

All such material sooner or later develops fungi and algae on it as decay sets in, but the slugs do not wait for this to happen before starting their meals.

In addition, numerous slugs have been found devouring lawn cuttings on surrounding paths, and there have always been increased numbers of slugs found on any lawn the night after it has been cut compared with those seen on other nights.

Dying, rotting and diseased vegetable matter. One of the most noticeable facts about the feeding habits of slugs is their apparent preference for damaged vegetable matter rather than healthy plant tissues. Far more slugs have been seen feeding on wilting, drooping and wind-torn and otherwise slightly damaged leaves than on really healthy ones. This has been particularly noticeable with regard to onion, leek, daffodil and *Brassica* leaves. This may be partly due to the low feeding habits of slugs, but, even in the case of *Agriolimax reticulatus* which feeds higher up on plants, it is very noticeable how it picks out the withering and dying blossom and leaves of such plants as sweet pea and scarlet runner bean in preference to the healthy flowers and leaves. This is particularly so in the autumn. Also more slugs have been seen feeding on rotting vegetable marrows than on healthy ones. *Arion ater* seems very fond of rotting marrow.

Lastly in this section, at all seasons of the year the rotting vegetation or garden rubbish heaps, and old *Brassica* stems left lying on the ground, have been a great source of food supply in addition to being good shelter. All the slugs sheltering in such heaps do not spread out every night from them to nearby growing vegetation; many individuals have stayed on the heaps all night apparently finding plenty of food.

In drier weather, however, more slugs seem to disperse from garden rubbish heaps so long as the neighbouring soil is sufficiently moist to allow movement. *Milax sowerbyi* appears to linger longer and be less ready to move away from the heaps. It seems that this species is content to feed on much more dry material than, for example, *Agriolimax reticulatus*. Slugs also tend to leave the rubbish heaps more freely as the material forming the heaps rots down.

Flesh. Milax gracilis has frequently been observed eating the remains of squashed slugs of its own and other species. On one occasion it fed in some numbers on some slugs that had been killed by metaldehyde bran baits the previous night. The results were fatal.

Faeces. Another striking feature of the feeding habits of slugs in gardens has been the extent to which they are attracted to and feed on faeces. Several species, especially *Arion subfuscus*, *Milax gracilis*, *M. sowerbyi* and to a less extent *Arion hortensis*, and many individuals have been observed feeding on dog faeces in the various gardens visited. Similarly, slugs have been seen feeding on the faeces of cats, rabbits and hedgehogs.

Bones. The same species, which are especially attracted to faeces, i.e. *Arion subfuscus*, *Milax gracilis*, *M. sowerbyi* and to a less extent *Arion hortensis*, are attracted to and feed on meat and fish bones which have been given to dogs and cats respectively. This habit, together with the scatophagous one just mentioned, led us to experiment with meat and bone meal

as a slug attractant. The result was that this meal proved to be a significantly better attractant than bran for *gracilis*.

Miscellaneous substances. Miscellaneous substances on which numerous slugs have been observed feeding in gardens after dark include the following: damson and other plum stones thrown out after jam making; apple, vegetable marrow and potato peelings; porridge which had been thrown out because the milk used in making it had curdled; and dog biscuits.

Other miscellaneous substances have been used in bait trials. Those to which slugs have been readily attracted, and observed feeding upon, include bread, flour, ground rice, Quaker oats, cattle cake, cotton cake, linseed cake, middlings, yellow maize meal, castor meal, biscuit meal and, of course, bran. Other substances have also acted as attractants and possibly have provided nourishment to some extent. Among these may be enumerated sugar-beet pulp, used tea leaves and coffee grounds.

Conclusions. These observations amply prove the varied taste of slugs and that it includes healthy and decaying vegetation, plant products uncooked and cooked, cooked and uncooked meat and bones, as well as animal faeces. In an average garden which is not too scrupulously tidy and well cultivated the vast bulk of the slugs' food consists of material that would not be used for human consumption or pleasure. This explains why, although slugs are so numerous in gardens, only on comparatively few occasions are they accused of being, and are in fact, serious pests.*

9. MATING TIME AND BREEDING SEASON

Out of 34,956 slugs belonging to nine species observed and collected after dark in gardens and other places during 1942, only 288 belonging to four species were found in congress. On no occasion were specimens of *Arion ater*, *A. circumscriptus*, *Milax sowerbyi*, *Limax maximus* and *L. flavus* seen mating. These account for 2515 out of the total of 34,956. Of the remaining four species which were on occasion found mating, only 16 out of 12,010 *Arion hortensis* and two out of 6613 *Milax gracilis* were in congress. On the other hand, 50 out of 3590 *Arion subfuscus* and 220 out of 10,228 *Agriolimax reticulatus* were found mating.

In 1943 mating was observed to much the same extent, only 262 slugs belonging to four species, out of the total of 38,416 belonging to nine species, being seen in congress. Again *reticulatus* was observed mating most frequently followed by *subfuscus* and then by *hortensis* a long way behind. But no *gracilis* were found mating, whereas four out of 967 *ater* were.

At first sight these data seem too scanty to draw any conclusions, but further thought shows that they are not in reality so poor. It must be remembered that the duration of the collecting was only a fraction of the hours of darkness. Taking this point into consideration, as well as the fact that the method of collecting precluded all searching under leaves, etc., a most natural place for congress to take place in, the apparently scanty data seem sufficient to draw at least tentative deductions concerning the mating time and breeding season.

Tables 13 and 14 give the numbers and proportions of slugs seen mating after dark in the open during 1942 and 1943 respectively. The numbers seen mating do not bear a constant relationship to the total numbers seen or collected.

Table 13. *Number of slugs seen mating in the open after dark*, 1942

	Arion hortensis	*Arion subfuscus*	*Milax gracilis*	*Agriolimax reticulatus*
Jan.	0/ 197	0/ 80	0/ 89	0/ 193
Feb.	—	—	—	—
Mar.	0/ 1,000	0/ 156	2/ 547	2/ 825
Apr.	0/ 1,157	0/ 370	0/ 283	18/ 1,190
May	0/ 580	0/ 343	0/ 727	14/ 565
June	0/ 55	0/ 254	0/ 129	4/ 264
July	0/ 215	10/ 531	0/ 302	14/ 751
Aug.	0/ 846	24/ 672	0/ 617	12/ 1,685
Sept.	0/ 1,215	12/ 325	0/ 866	56/ 1,487
Oct.	8/ 1,936	4/ 344	0/1,045	62/ 1,659
Nov.	2/ 1,778	0/ 195	0/ 726	4/ 701
Dec.	6/ 3,031	0/ 320	0/1,282	34/ 908
Total	16/12,010	50/3,590	2/6,613	220/10,228

It can be seen that comparatively few *Arion hortensis* mate out in the open during the hours of darkness. From the appearance of young specimens in samples taken at all periods of the year, it would appear that breeding occurs all the year round. But it is probable that most mating and breeding takes place in the autumn and winter months. It is possible that the actual peak of mating in 1942 was in the month of October when two out of every 484 slugs seen were in congress.

It would appear that *Arion subfuscus* mates freely out in the open after dark during the four months July–October. In these months during 1942 two in every 75 were found in congress and none out of 1718 during the rest of the year. The peak of mating apparently was in August and September when two out of every 56 and 54 respectively were in congress. In 1943 two in every 58 were found mating in July–September and none out of 3676 during the rest of

* It may be mentioned incidentally that *Agriolimax reticulatus* has formed the only food of a slow-worm (*Anguis fragilis*), which has been kept in captivity, from May 1942 to September 1943. This animal seems to have been adequately fed, having sloughed its skin twice between May and October (1942) and it survived the following winter. No food was given it between the end of November and mid-March. Since September 1943 up to the end of March 1944 *Arion hortensis* has formed the main diet of the slow-worm with apparently no ill effects.

the year. The peak was in August and September when two out of every 32 and 46 respectively were found in congress. Baby specimens of this species have been most abundant during December–February, while comparatively few have been encountered in the summer months. It seems likely therefore that breeding is much more restricted in this species than in *Arion hortensis*.

Agriolimax reticulatus mates still more freely out in the open after dark. Mating time in this species has been observed taking place every month of the year. Young have also been observed throughout the year. But still there seems to be a definite peak in the mating season. Thus, during 1942 in September two in every 53 and in October two in every 54 found after dark were in congress. In 1943 the most favoured months were August and October, during each of which months two in every 42 individuals found were mating. It is thought that December 1942 when two in every 53 were mating was rather exceptional, and that it is not the rule for the peak of mating to take place in this month. It would appear that conditions favouring the congress of *reticulatus* occur all the year round and that in September and October these conditions occur more frequently than at other times of the year or, another explanation, that there is a rhythm by means of which most of the slugs reach maturity in these two months.

Table 14. *Number of slugs seen mating in the open after dark*, 1943

	Arion ater	*Arion hortensis*	*Arion subfuscus*	*Agriolimax reticulatus*
Jan.	0/155	2/ 1,711	0/ 349	4/ 666
Feb.	0/ 37	0/ 781	0/ 186	2/ 355
Mar.	0/ 80	0/ 721	0/ 198	10/ 307
Apr.	0/120	4/ 955	0/ 433	12/ 356
May	0/203	0/ 1,388	0/1,323	22/ 931
June	0/144	0/ 277	0/ 869	2/1,873
July	2/ 70	0/ 201	8/ 516	22/1,092
Aug.	2/ 37	0/ 385	18/ 294	42/ 880
Sept.	0/ 23	4/ 1,042	8/ 183	18/ 787
Oct.	0/ 40	0/ 2,692	0/ 173	68/1,445
Nov.	0/ 29	0/ 809	0/ 79	12/ 317
Dec.	0/ 29	0/ 332	0/ 66	0/ 126
Total	4/967	10/11,294	34/4,669	214/9,135

Arion ater has only been seen mating twice, once in July and once in August, both during 1943. It is probable that this species does not usually mate in the open after dark. The breeding season is clearly shown, by the appearance of the young, to be in the autumn and winter.

The only other species of slug found in congress after dark in the open has been *Milax gracilis*. Only one pair has been observed mating (17 March 1942) under these circumstances. It is considered that it is not the rule for this species to mate out in the open or after dark. Actually two other pairs have been found in congress, one under leaves and the other under a tarpaulin, on each occasion at 13.30 hr. (i.e. in daytime) on 7 and 11 November 1942. It should be mentioned that extremely few searches have been made during daytime, and that those that have been made have been more in the nature of glances rather than systematic searchings.

Similarly, *Milax sowerbyi* has never been seen in congress out in the field. But congress has been observed three times, all in October 1942; twice in Petri dishes on the laboratory bench, after samples collected after dark had been separated into their component species, and once in the insectary where the slugs were being kept in flower-pot saucers covered with other saucers. Congress on each occasion was taking place in daytime and was of several hours' duration. In one case it had started by 8.00 hr. and was still continuing at 17.00 hr. One pair which had mated on 1 October was in congress again on 27 October.

It would appear from these few observations that these two *Milax* species do not mate out in the open at night, but may do in the daytime under cover. It is possible that October is the peak month for *sowerbyi* and November for *gracilis*.

From what few data are available concerning mating, it would seem that the peak periods of mating in slugs are closely linked up with those of activity, which are themselves closely connected with the periods during which the slugs are largest. These points will be discussed in the next section.

10. WEIGHTS

(*a*) *Weights in relation to amount of food eaten*

The only available data of the amount of food eaten by slugs were derived from a small potato patch (10 × 10 yd.). Observations showed that the entire crop had been destroyed, literally only potato skins remaining. The coring method of sampling showed that the absolute population was in the neighbourhood of 60 per sq.yd. (or 300,000 per acre) and that 70% of the population was *Milax gracilis*.

In order to get information on the weights of slugs, a series of weighings was made in November and December 1942 by the following method. All the specimens of any one species collected in a single sample were weighed together and the weight per 100 calculated. The slugs as usual were kept overnight in an hermetically sealed tin and they were weighed the next morning immediately after the sample had been sorted into its component species. It was found that at this season of the year the mean weight of 100 *Arion hortensis* was 21 g., of 100 *Agriolimax reticulatus* 40 g. and of 100 *Milax gracilis* 43 g.

It is obvious that the slug population on the potato patch consumed almost the entire potato crop, which could hardly have been less than 5 tons per acre.

Using the weight of *gracilis* given above, it appears that each slug ate approximately 30–40 times its own weight. The estimate of 300,000 slugs per acre is probably too low for this patch, since this figure would indicate a population of only 6200 slugs (or about 5–6 lb. weight) on the 100 sq.yd. studied, and in two months at least 2000 slugs were removed from it without apparently decreasing the population. If the population was higher, as seems likely, this estimate of total food consumed by each slug would be too high.

A mixed sample of several species of slugs from a garden in mid-November indicated that 10,000 specimens weighed approximately 6 lb., and it has just been shown that *gracilis* weighs approximately 1 lb. per 1000. From such figures it is easy to appreciate that the weight of slugs per acre may be in the neighbourhood of 180–300 lb. and that the weight of food consumed per year must be considerable. The manurial value of an equivalent weight of livestock per acre is appreciable but the value of slugs' faeces as fertilizer is not known, neither have the proportions of their different types of food been ascertained quantitatively. Furthermore, the value of aeration of the soil by slugs is not known.

(*b*) *Weights throughout the year*

It was realized that to obtain any really useful data regarding the weights of slugs, weighings would have to be made at all seasons of the year. At the same time the weights of slugs in some gardens might be different from those of slugs in other gardens. If such series of weights were obtained, information would in all probability be gained regarding the growth rate, as well as the proportion of young to old, of the various species.

Table 15. *Calculated weights per* 100 *individuals, April* 1943–*January* 1944 *in all gardens*

Species	Numbers weighed	No. of weighings	Range in wt. (g.)	Mean wt. (g.)
Arion hortensis	9291	117	6– 40	19
Agriolimax reticulatus	8126	152	10– 86	33
Milax gracilis	9102	107	14– 95	32
Arion subfuscus	3960	106	17–258	99
Milax sowerbyi	2105	103	56–269	122

Therefore starting in April 1943 systematic weighings have been made of nearly all the samples taken in the course of the activity study (Table 15). It will be seen that *hortensis* is the lightest slug, followed by *reticulatus* or *gracilis*, then by *subfuscus* with *sowerbyi* the heaviest of the five species. This corresponds with their order in size (see Part 1, § 2).

In addition to these species, the weights of *Arion ater*, *Limax maximus*, and *Arion circumscriptus* were noted less regularly. On only two occasions (both in May), the last-named species was weighed. The weight per 100 worked out at 29 and 57 g. based on 17 and 7 individuals. In the case of *ater* 659 individuals were weighed, the largest weighing 21 g. (This species has been recorded elsewhere as reaching a weight of over 34 g.) In the case of *maximus* 83 individuals were weighed, the largest in this species weighing 20 g. *Maximus* appears to be biggest in May–July, whereas *ater* reaches its largest size in August–September and *circumscriptus* during the winter months.

It has been shown earlier in this paper and elsewhere (Barnes, 1944) that the behaviour of slugs as regards the general trends of activity after dark, as indicated by the method of sampling used by the authors, is practically the same whether the samples are taken in one garden frequently or one garden once in a month. The same trends of seasonal activity are observable in all Harpenden gardens visited whether the species is particularly numerous or otherwise.

Fig. 19 shows that the same general seasonal trend in weight of *Agriolimax reticulatus* is obtained whether one weighs samples collected infrequently in single gardens or frequently in one garden or at irregular intervals in many gardens. The data for the weights of slugs in the back garden of No. 5 are given in Table 16. The full data, which are voluminous and of which copies are kept in both the Entomology and Statistical Departments at Rothamsted Experimental Station, demonstrate that the same is true for *Arion hortensis* and *subfuscus*, *Milax gracilis* and *sowerbyi*. In other words, the method for obtaining the seasonal trends in weight of the different species is just as reliable as the one adopted in Part 1 for discovering the seasonal trends in numbers active. But just as the peaks of activity are higher and at slightly different times in some gardens, so in some gardens the slugs are usually heavier than in others.

The population of *reticulatus* is lightest in June and increases in weight steadily until the autumn and apparently is heaviest in April (Fig. 19). Fig. 20 shows the seasonal weights of four other species. *Arion hortensis* reaches its lowest weight during June and July and increases steadily during the autumn. The curve of *Milax gracilis* is very similar. Samples of these two species and *Agriolimax reticulatus* (Fig. 19) usually contain small and large specimens at whatever season of the year they are taken. The curve of weights of *Arion subfuscus* is different. In this case, the weights are lowest in the spring and autumn and rise steadily from April to a maximum in August. The subsequent fall in weight is equally pronounced. The curve for *Milax sowerbyi* shows a marked increase in weight during May and early June, but then the weights decrease suddenly and in late June, July and early August they reach their minima. But in the autumn the main increase in weight is apparent. By observation, the largest *sub-*

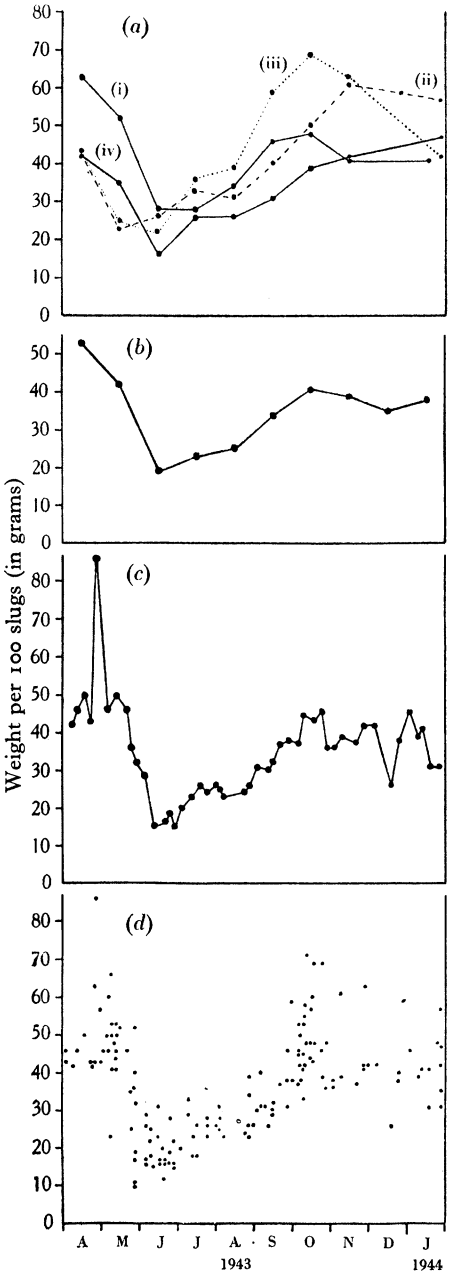


Fig. 19. The seasonal weight of *Agriolimax reticulatus* (*a*) in the back gardens of (i) No. 10 Douglas Road, (ii) No. 15, (iii) No. 11 and (iv) No. 7 Moreton End Lane; (*b*) the monthly average in the back garden of No. 5 Moreton End Lane; (*c*) per sample in the same garden; (*d*) scatter diagram of the weights per sample in all gardens. The weights are expressed as the weight in grams per 100 individuals.

Table 16. *The weights in grams per* 100 *individuals, April* 1943–*January* 1944, *No.* 5 *Moreton End Lane back garden*

(The numbers of slugs from which the weights are derived are to be found in Appendix 1.)

	Arion hortensis	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*
1943					
9 Apr.	17	30	27	71	42
13	14	26	29	80	46
18	18	43	29	—	50
23	16	70	32	75	43
27	14	53	27	91	86
5 May	13	51	30	75	46
13	18	67	28	93	50
22	14	70	27	144	46
26	14	79	26	120	36
30	10	63	26	138	32
5 June	13	73	26	125	29
13	14	73	24	93	15
21	—	87	24	67	16
24	—	94	22	—	19
28	—	82	20	—	15
3 July	—	124	23	—	20
11	—	138	29	—	23
16	—	128	19	—	26
24	11	123	22	76	23
1 Aug.	9	122	23	—	26
4	12	143	17	67	25
7	14	159	20	71	23
26	11	132	20	88	24
28	12	135	28	135	26
4 Sept.	12	111	22	94	31
10	13	132	24	126	30
16	14	119	28	137	32
21	15	111	30	185	37
28	16	119	31	164	38
5 Oct.	16	53	32	172	37
10	26	56	32	165	45
10	18	111	32	200	33
17	20	—	33	164	43
23	21	80	39	181	46
28	22	38	40	160	36
2 Nov.	24	71	40	200	36
10	20	58	31	150	39
21	21	36	32	200	37
28	20	56	32	167	42
7 Dec.	21	17	34	—	42
18	22	38	36	—	26
25	23	39	38	150	38
1944					
3 Jan.	22	21	33	175	46
9	26	33	39	100	39
12	25	29	34	100	41
18	26	25	39	133	31
26	26	32	35	—	31

fuscus slugs occur in the middle of the summer when few small ones are visibly active. Similarly, of the *sowerbyi* collected during May 1943 most were noticed to be a fair size, but then young ones started appearing and the large ones disappeared. In the autumn the majority were seen to be large, and although young ones were also present, especially in the later autumn months, they were always outnumbered by the large individuals.

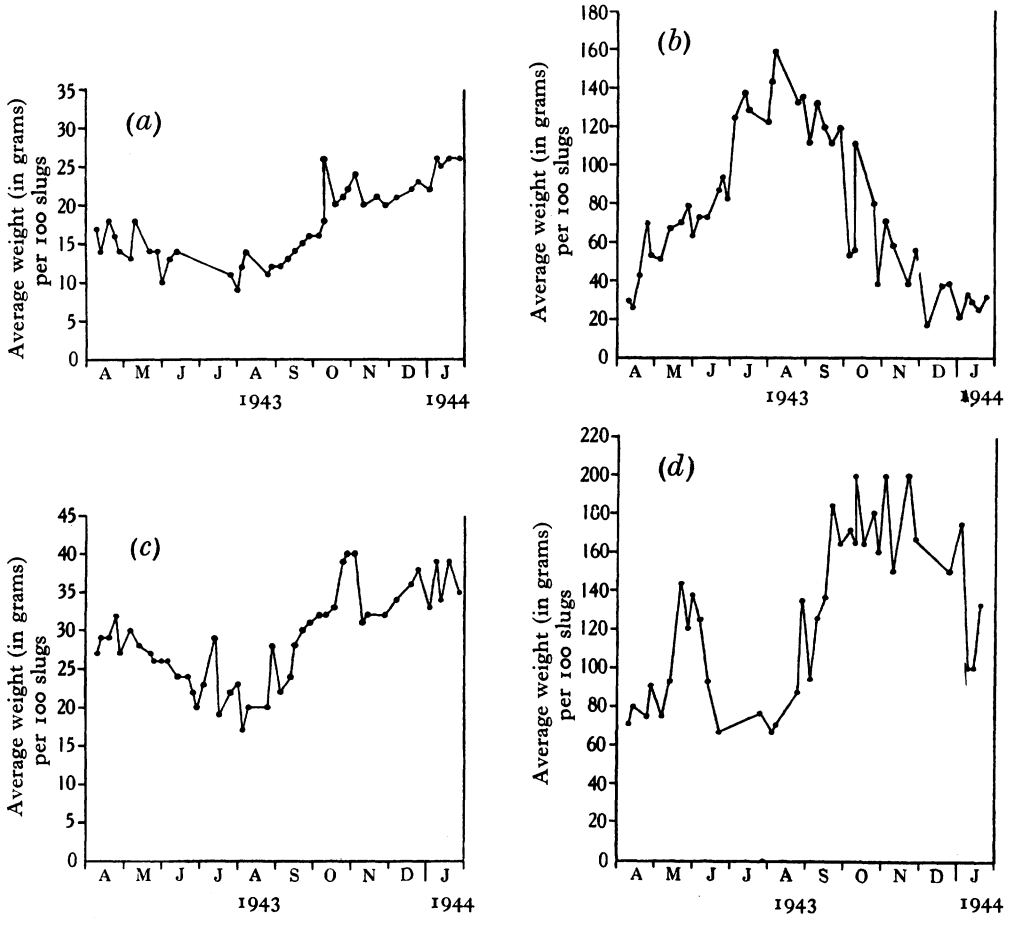


Fig. 20. The seasonal weight of (*a*) *Arion hortensis*, (*b*) *Arion subfuscus*, (*c*) *Milax gracilis* and (*d*) *Milax sowerbyi* in the back garden of No. 5 Moreton End Lane.

(*c*) *Weights in relation to seasonal activity*

Fig. 21 shows the monthly average weights of five species in relation to the monthly average numbers found active after dark. The data refer in each case to the back garden of No. 5 Moreton End Lane. As a rule the slugs are heaviest soon after the greatest numbers are found active. In other words, increased numbers active usually foretell an increase in the average weight of slugs. Further investigations, involving the weighing of slugs individually, are in progress in order to establish more exactly the relation of weight to numbers active.

(*d*) *Weights in relation to the mating season*

It has already been shown that the different species have different mating habits and consequently after dark the collection of slugs visible out in the open only yields mating data for *Agriolimax reticulatus*, *Arion subfuscus* and, to a much less extent, *A. hortensis*.

Fig. 22 shows the monthly average activity and weight as well as the total number seen mating, of *Arion subfuscus* and *Agriolimax reticulatus* in all gardens visited. The peak of numbers active in *reticulatus* and *subfuscus* is quickly followed by the peak in numbers found mating, and this occurs when the slugs are heaviest. The peaks of mating in 1942 and 1943 were in the same months, whereas the

peaks of activity were slightly earlier in 1942 than in 1943. This regularity in mating season would be expected, as mating is a biological function of the species, whereas the numbers active are closely associated with the weather conditions. On the other hand, the peaks in weight are dependent on both activity and physiological development.

From these figures, the height of mating is not followed quickly by a relatively large increase in the numbers found active, i.e. the resulting young. It might be imagined that the method of collecting does not result in the young slugs being collected. But the young of all species have been collected, even tiny specimens. An explanation is that the young

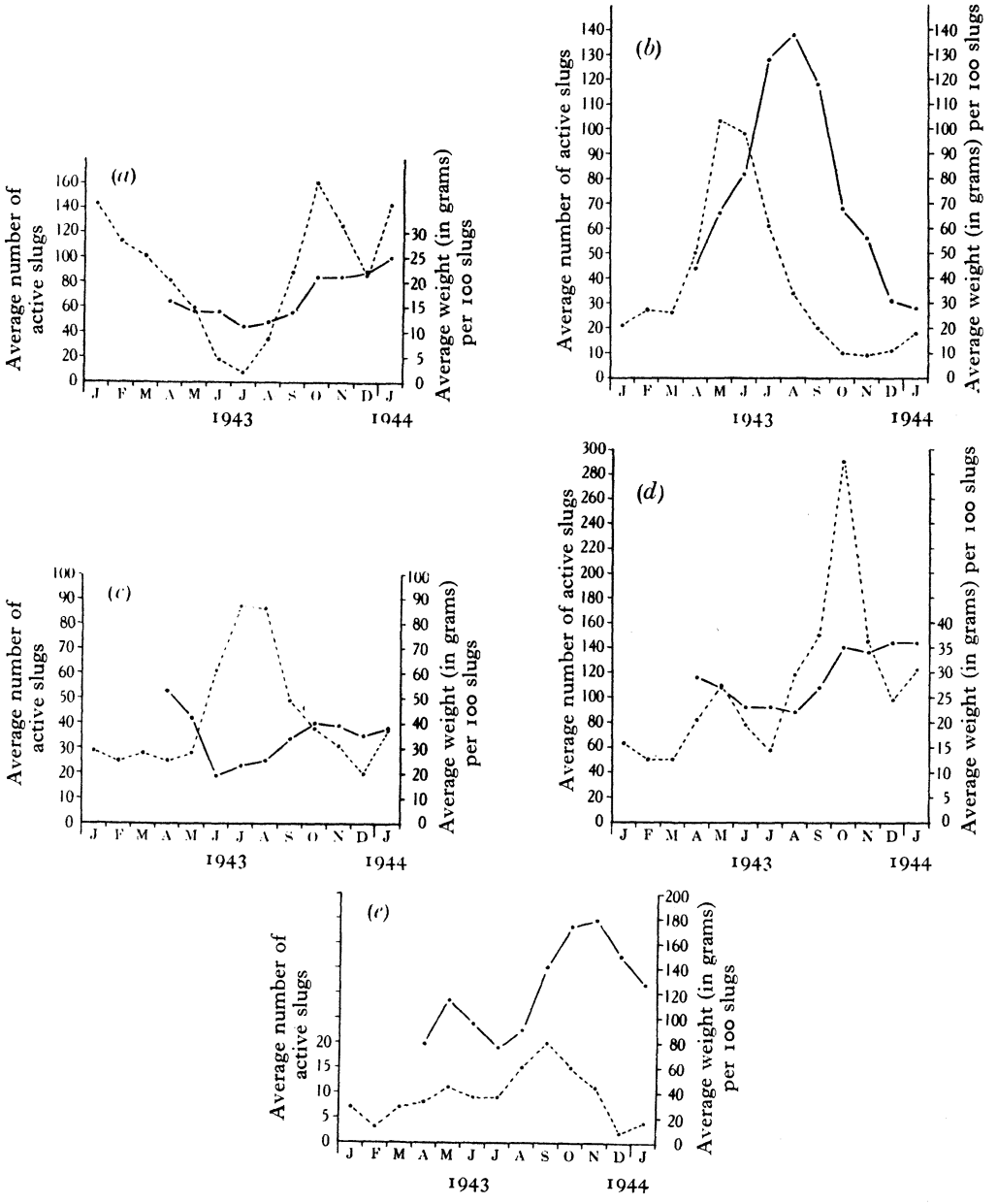


Fig. 21. The monthly average weight (——) in relation to the monthly average numbers found active after dark (----) in the back garden of No. 5 Moreton End Lane. (*a*) *Arion hortensis*, (*b*) *Arion subfuscus*, (*c*) *Agriolimax reticulatus*, (*d*) *Milax gracilis*, (*e*) *Milax sowerbyi*.

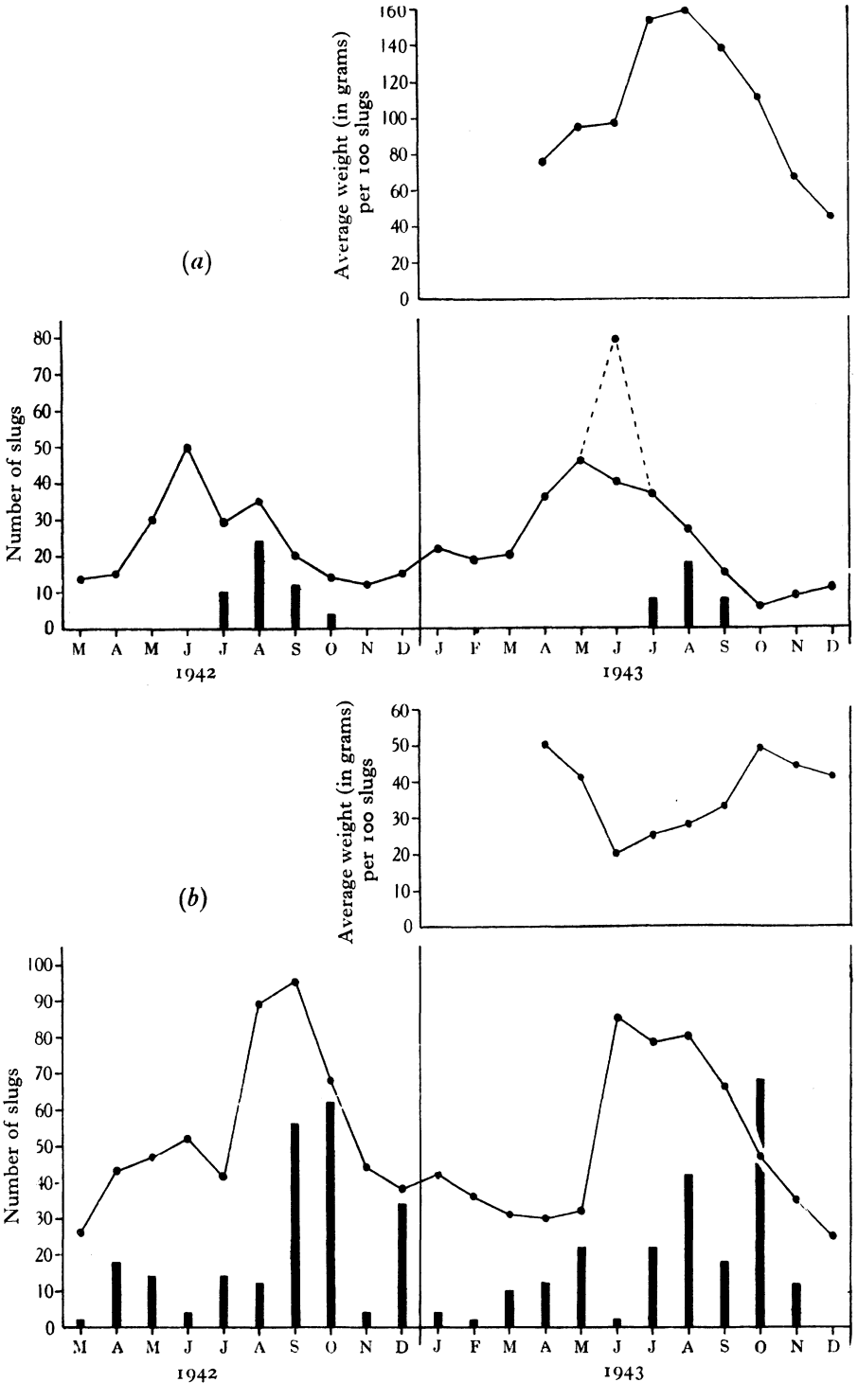


Fig. 22. Monthly activity, weight and total numbers seen mating (histograms) of (*a*) *Arion subfuscus* and (*b*) *Agriolimax reticulatus* in all gardens visited.

are not active out in the open after dark to the same extent as the older individuals at the times the collections have been made. But other workers have found that a long time may lapse between copulation and oviposition and also between oviposition and hatching.

The data for the mating of *Arion hortensis* are too sparse to allow of any deductions being made regarding this species.

(*e*) *Weights in relation to damage*

In assessing the damage liable to be done by slugs, their weights, the numbers active and the specific composition of the slug fauna should be taken into account, as well as any particular choice of food shown by any of the species and the season of the year.

From Fig. 21 (in which the monthly average weights of the five common garden species are shown in relation to the monthly average numbers found active after dark), it is obvious that with the exception of *Arion subfuscus* slugs are neither numerous nor large during midsummer. Observation (§ 8) has shown that this species is prone to feed on fungi and animal faeces, although occasionally it has been seen eating lettuce, cabbage and campanula leaves. Taken as a whole, however, this species cannot be considered as a serious menace.

The other four species—*Arion hortensis*, *Agriolimax reticulatus*, *Milax gracilis* and *M. sowerbyi*—are at their heaviest in the spring and in autumn, but with the exception of *hortensis* are much more numerous in the autumn than in the spring. This means that when new growth starts to appear in the spring, gardens in which *hortensis* is a common species will probably suffer considerable damage in mild seasons (e.g. 1943), particularly to crowns of such plants as primulas and to rhizomes, for example, of Jerusalem artichokes which have been left overwinter in the ground.

On the other hand, in the autumn, when there is normally a large amount of superfluous unwanted and rotting vegetation available, a much larger slug population can usually be tolerated than in the spring when there is a comparative shortage of plant material, especially when new growth is retarded by bad weather. But the autumn is the season of the year when certain slugs exhibit a definite food preference. In particular, *gracilis* and *hortensis* show a distinct partiality towards potato tubers and the latter species the crowns of carrots in addition. It is obvious that *gracilis* reaches its height of abundance in September and October, and it is this time of the year when the specimens are heaviest and the potato crop is available in the ground. Consequently, if *gracilis* is present to any extent in the slug fauna of a potato-growing area, great damage is liable to be incurred. Table 17 gives the percentage specific composition of collections made in the potato patches in four gardens, where serious damage to potatoes had been previously reported. In each area there was a high slug population. In the first two the present collector (H. F. B.) took the samples, whereas in the latter two the complainants collected following our instructions. It will be seen that in each area there was a high proportion of *gracilis* or *hortensis*.

Table 17. *Percentage composition of slug fauna in four garden areas in which the potato crop suffered great slug damage to the tubers*

	24 Douglas Road, Harpenden	14 The Pleasance, Harpenden	66 Norton Road, Heysham, Lancs	Marchurst, Shipbourne Tonbridge
Arion ater	1	0	0	0
A. circumscriptus	0	1	0	0
A. hortensis	61	17	29	12
A. subfuscus	1	2	0	0
Milax gracilis	31	69	66	84
M. sowerbyi	1	1	0	0
Agriolimax reticulatus	7	11	6	4

It is realized that *reticulatus* and *circumscriptus*, in addition to the *Milax* species and *hortensis*, have in the past frequently been associated with tuber damage. But in our experience *gracilis* is outstanding as a primary pest of potato tubers followed by *hortensis* as a fair second. *A. circumscriptus* has not been found in sufficient numbers to cause any considerable damage. *Reticulatus* in our experience is not a boring slug, and prefers to feed on green vegetable matter, e.g. potato leaves and haulms. Even when offered potato tubers, it has preferred to leave the tubers unattacked. But when once the tubers have been damaged by other agencies, e.g. cutworms, *Milax* spp., wireworms, etc., *reticulatus* will feed on them. Therefore we consider this species as liable to cause secondary damage to the potato crop.

Until further evidence is forthcoming as the result of more exact determination and abundance of the slug species involved in potato losses, we are forced to the conclusion that *Milax gracilis*, and to a much less extent *Arion hortensis*, is responsible for the major primary damage to potatoes and that *Agriolimax reticulatus* sometimes increases the losses caused by primary pests.

11. DISTRIBUTION OF SPECIES IN THE DISTRICT

One of the most interesting facts that has been brought out by this study is that the slug faunas in adjacent gardens are frequently extremely different. In other words, the fauna in one garden is no criterion of what may be expected to occur in the neighbouring gardens, either as regards total population or the relative numbers of the different species. Table 18 shows the numbers of individuals of *Arion ater*, *A. subfuscus*, *A. hortensis*, *Milax gracilis*, *M. sowerbyi* and *Agriolimax reticulatus* found in nine adjacent gardens in October 1942. The totals* include all the species found. It will be seen that most individuals of *A. ater* were found in No. 15 and there are indications that the numbers increase from No. 5 to garden No. 15 and then drop again. In the cases of *A. hortensis* and *M. gracilis* there is a decrease in numbers as one goes from No. 5 to No. 15, but then the numbers increase again. The distribution of *M. sowerbyi* is different. This species is most abundant in No. 9 and only just present in Nos. 13–21. Lastly, *A. subfuscus* and *A. reticulatus* appear to be randomly distributed throughout these gardens.

Tables 19 and 20 give the figures month by month in Nos. 5, 7, 9, 11, 13 and 15 for *A. hortensis* throughout 1942 and 1943. The peculiar distribution appears to be constant for the two years.

These tables show that in spite of the seasonal rise and fall in numbers which are very noticeable the distributions are maintained. Ideally in a distribution study all the localities should be sampled on the same day and at the same time, but this is impossible for one collector. Samples collected within any particular month, however, may be compared provided due precautions are taken in choosing the nights on which to collect, since the figures of seasonal activity have already shown that there is not very much change in numbers within a month. Similar tables can be drawn up for *Agriolimax reticulatus*, *Milax gracilis* and *sowerbyi*, *Arion ater* and *subfuscus* from Appendix 1 and these confirm the distributions shown in Table 18.

This series of observations spread over two years shows that the numbers of certain species have remained different from garden to garden, certain gardens having more individuals active than others throughout the year at any point on the seasonal activity curve of the particular species. In addition, the relative proportions of one species to another have remained different. For example, the relative proportions of *Arion hortensis* to *A. subfuscus* are consistently higher in No. 5 back garden than in No. 15 throughout the seasons, notwithstanding the very different numerical abundance from month to month (Fig. 23). In addition, these curves are further evidence of the adequacy of the sampling technique.

Table 18. *Distribution of species and total numbers in Moreton End Lane back gardens, October* 1942

Back garden No.	*Arion ater*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	Total*
5	1	185	19	93	15	63	376
7	8	56	18	73	18	95	272
9	4	60	13	36	87	75	277
11	6	11	39	17	19	94	186
13	12	9	19	5	0	56	101
15	37	4	19	6	1	50	120
17	5	35	14	9	0	59	124
19	7	30	13	33	1	49	132
21	1	123	5	38	3	92	265

Table 19. *Monthly distribution of* Arion hortensis, 1942, *in Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Jan.	84	57	25	—	—	3
Feb.	—	—	—	—	—	—
Mar.	66	32	25	—	9	4
Apr.	52	38	2	12	6	2
May	66	65	12	6	3	2
June	18	13	—	—	2	1
July	24	11	0	1	0	0
Aug.	81	10	7	0	0	0
Sept	150	50	20	8	0	1
Oct.	185	56	60	11	9	4
Nov.	162	105	89	48	19	18
Dec.	187	164	109	37	22	22

Table 20. *Monthly distribution of* Arion hortensis, 1943, *in Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Jan.	143	69	56	23	—	20
Feb.	113	72	18	10	—	4
Mar.	101	82	16	7	—	3
Apr.	81	54	60	4	—	16
May	59	34	22	2	3	9
June	18	5	5	0	—	3
July	8	3	0	1	—	0
Aug.	34	6	3	2	—	0
Sept.	88	38	2	(5)	—	1
Oct.	160	65	82	21	17	13
Nov.	125	44	81	15	—	23
Dec.	86	—	47	—	—	27

They indicate that the fluctuations in numbers from collection to collection (see Part 1, Figs. 3, 6) are due more to weather changes than to sampling, in that the fluctuations in the ratios are much less pronounced. The latter fluctuations are probably chiefly made up of the sampling error and any differential effect of weather changes on the two species.

The marked distributions shown to exist must be due to some definite cause. The most obvious controlling agencies of animal populations include food supply, natural enemies and the physical conditions obtaining in the habitat.

In the first place owing to the varied tastes of slugs it is not easy to believe that food is the limiting factor. In this connexion it should be mentioned that, although the numbers of *A. hortensis* in No. 15 Moreton End Lane are the lowest, the average weights of this species during the four months (October–January) were distinctly bigger in this garden than in No. 5

There remains the probability that some soil condition is responsible for these remarkable distributions. It seems probable also that these conditions are deep rooted rather than superficial.

The *p*H of the soil was tested, but there was no clear-cut gradation in the acidity or alkalinity of the surface soil. Thanks to the kindness of Mr R. G. Warren of the Chemistry Department at Rothamsted Experimental Station figures were obtained for the organic carbon in the soil as shown below (Table 21). It will be seen that this cannot account for the slug distribution.

Neither can the amount of cultivation and care a garden receives be held wholely responsible, although this does affect the total numbers from sample to sample at certain times of the year but not the relative abundance of the species.

Mechanical analysis of the soils, which was done for us in the Physics Department at Rothamsted

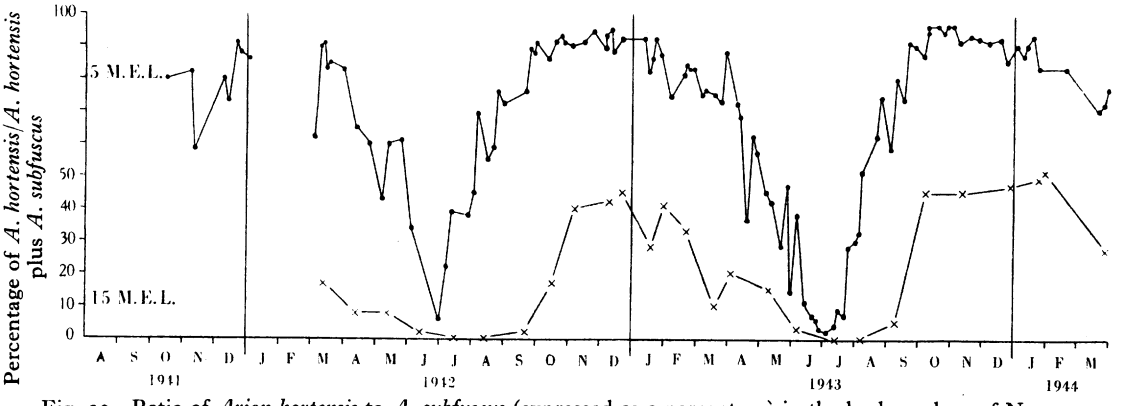


Fig. 23. Ratio of *Arion hortensis* to *A. subfuscus* (expressed as a percentage) in the back gardens of Nos. 5 and 15 Moreton End Lane.

Moreton End Lane where this species was so much more abundant. In fact, the weight data indicate that the fewer the slugs collected the bigger and heavier the specimens. But the relative numbers have remained constant.

No evidence has pointed to the possibility that natural enemies control the slugs differentially with such regularity in the various gardens. Again, our experience indicates that weather, even in the severe winter of 1941–2, has no lethal effect on slugs.

The back gardens in Moreton End Lane vary in the numbers of trees, for example Nos. 5 and 15 have a considerable number, especially No. 5, while in Nos. 9, 11 and 13 the largest trees are a few young fruit trees. Thus there is no gradient of shade from garden to garden. Each garden has completely mixed flora of ornamental and the usual culinary plants. Thus there is no reason to connect the observed distribution of slugs with the flora. As regards lay-out the gardens are roughly the same—each having a rockery, rubbish heap, rose beds, perennial borders, vegetable patches, lawn, paths and so on.

Table 21. *Organic carbon in Moreton End Lane back gardens*

Back garden No.	% organic carbon
5	3·13
7	2·62
9	2·78
11	2·67
13	2·56
15	3·02

Experimental Station, thanks to the courtesy of Dr R. K. Schofield, revealed no appreciable differences. Table 22 gives these figures on the oven-dry basis.

The same types of distribution are similarly apparent in the front gardens of the same properties. The front and back gardens are usually separated by gravel or concrete narrow paths between the wooden fences demarking the property and the houses. Table 23 gives the numbers of the same six species in six of the nine front gardens.

Harpenden is situated in the part of Hertfordshire that is made up of chalk overlaid by clay with flints.

River valleys are cut through the clay with flints, exposing the chalk on the flanks of the valleys. Luton Road lies on the course of an old stream bed which is here represented by a valley flat made up of river gravel and alluvium. Moreton End Lane, a turning off Luton Road, goes up the side of this valley and, higher up, the lane passes on to the clay with flints. It is not yet known how much cover there is over the chalk along the flank of the valley between the river gravel at the bottom and the clay with flints at the top.

In order to test whether the underlying geological formation was connected with the species distribution, samples were taken during 1943 in the gardens

Table 22. *Mechanical analysis of the soil in six Moreton End Lane back gardens*

No.	5	7	9	11	13	15
Coarse sand	15·9	17·5	18·3	18·1	21·2	14·2
Fine sand	38·1	37·1	35·8	34·6	33·7	39·5
Silt	22·7	20·5	19·3	18·7	16·3	20·5
Clay	18·3	17·3	18·5	21·7	21·0	19·5
Carbonates:						
Air-dry soil	2·3	2·4	2·6	2·8	2·6	2·4
Loss by solution	1·2	1·4	1·4	1·1	1·1	1·2
Difference	+1·5	+3·8	+4·1	+3·0	+4·1	+2·7
Total	100	100	100	100	100	100

Table 23. *Distribution of six species of slugs in six front gardens in Moreton End Lane, October* 1942

No. of front garden	*Arion ater*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*
5	0	114	16	97	2	60
7	6	43	13	24	7	60
9	0	6	6	5	10	90
11	3	23	13	7	7	109
13	8	4	12	10	2	80
15	12	6	10	13	1	62

in the neighbouring roads, which go over the same formations. Figs. 24–29 show the numbers of *Arion ater*, *A. hortensis*, *A. subfuscus*, *Milax gracilis*, *M. sowerbyi* and *Agriolimax reticulatus* which were obtained in May and June 1943.

Arion ater (Fig. 24) was found in greater numbers in Moreton Place gardens, which back on to the wooded railway embankment, but was practically absent from those in Douglas Road and on the east side of Luton Road. The distribution of this species may be associated with the amount of coarse grass both in and near the particular garden. Thus there is an uncultivated patch of grass just west of the top of Moreton Place and the largest numbers of *ater* are to be found in near-by gardens. But this may not be the whole explanation, since the gardens on the south side of Douglas Road adjoin a meadow. The age of the garden may also be a factor. Thus the gardens of Moreton End Lane and Moreton Place are of more recent origin than those on the east side of Luton Road and those in Douglas Road.

The distributions of *Arion hortensis* (Fig. 25) and *Milax gracilis* (Fig. 26) are most interesting. At the lower or east end of Douglas Road, Moreton End Lane and Moreton Place the numbers are high, decreasing as one proceeds up the slope until (at No. 20 Douglas Road and No. 17 Moreton End Lane) the numbers become large again. There is a distinct band across the roads where the numbers are low. The similarity in distribution of these two species again suggests some connexion between their ecology.

As a contrast there seems to be a belt of high numbers of *Milax sowerbyi* (Fig. 27) running from No. 9 Douglas Road across to No. 16 Douglas Road across to No. 9 Moreton End Lane and No. 5 Moreton Place. In addition high numbers of this species occur in certain Luton Road gardens.

The distribution of *Arion subfuscus* (Fig. 28) reveals no such bands of abundance, but it is much commoner in the Moreton End Lane and Moreton Place gardens than in the Douglas Road gardens and still less are found in the Luton Road gardens. This grouping follows the age of the gardens, the Luton Road ones being the oldest, followed by those in Douglas Road, while those in Moreton End Lane and Moreton Place are the most recent. As regards its almost complete absence in the gardens on the east side of Luton Road, one is tempted to recall the map (Pl. 20) showing the distribution of this species in Taylor's volume of slugs (1907, p. 208). In this *subfuscus* is shown as being absent from the following counties: Buckinghamshire, Bedfordshire, Hertfordshire, Huntingdonshire, Cambridgeshire, Norfolk and Essex. (It is as well to recall that this 'absence' is based on collectors' records. It is quite possible that more extensive sampling at the most favourable season of the year would reveal this species' presence, though not abundance, throughout these eastern counties.)

It can be suggested that since the year of publication of this map, the distribution of *subfuscus* has advanced eastwards and that this species is now well established on the west side of the Luton Road which runs roughly north and south through Harpenden. *A. subfuscus* occurred in 165 out of the 167 samples taken throughout 1942 in gardens on the west side of this road, but not once in the three samples taken in gardens on the east side of the road. In 1943 the comparative figures are *subfuscus* present in 162 out of 164 samples taken on the west side, but only in two out of 17 samples taken on the east side. Emphasis is laid on 15 of these 17 samples having been taken in May and June when *subfuscus* was at its peak of numbers in the gardens on the west side.

Another perhaps more reasonable suggestion to account for its absence from the eastern counties

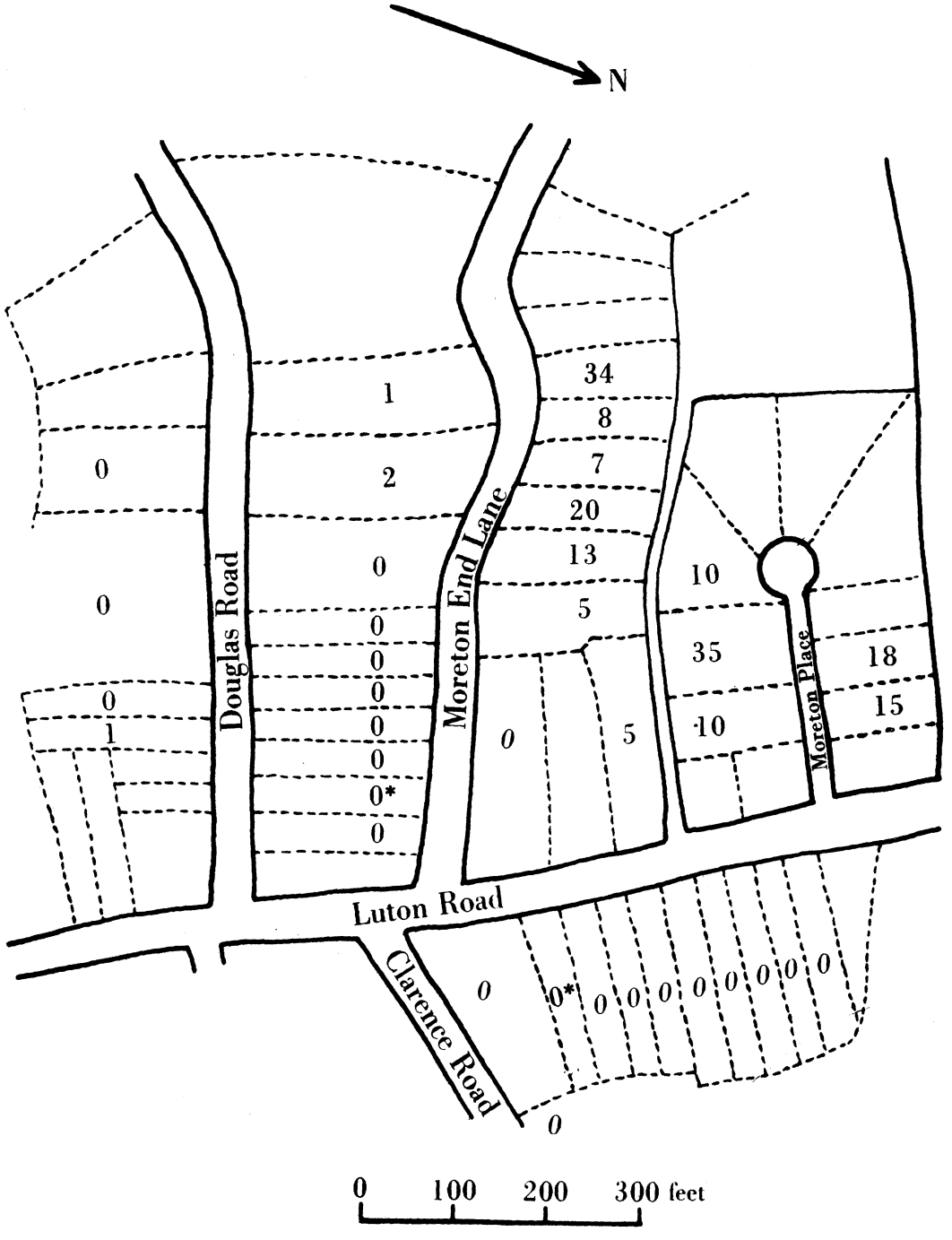


Fig. 24. Numbers of *Arion ater* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

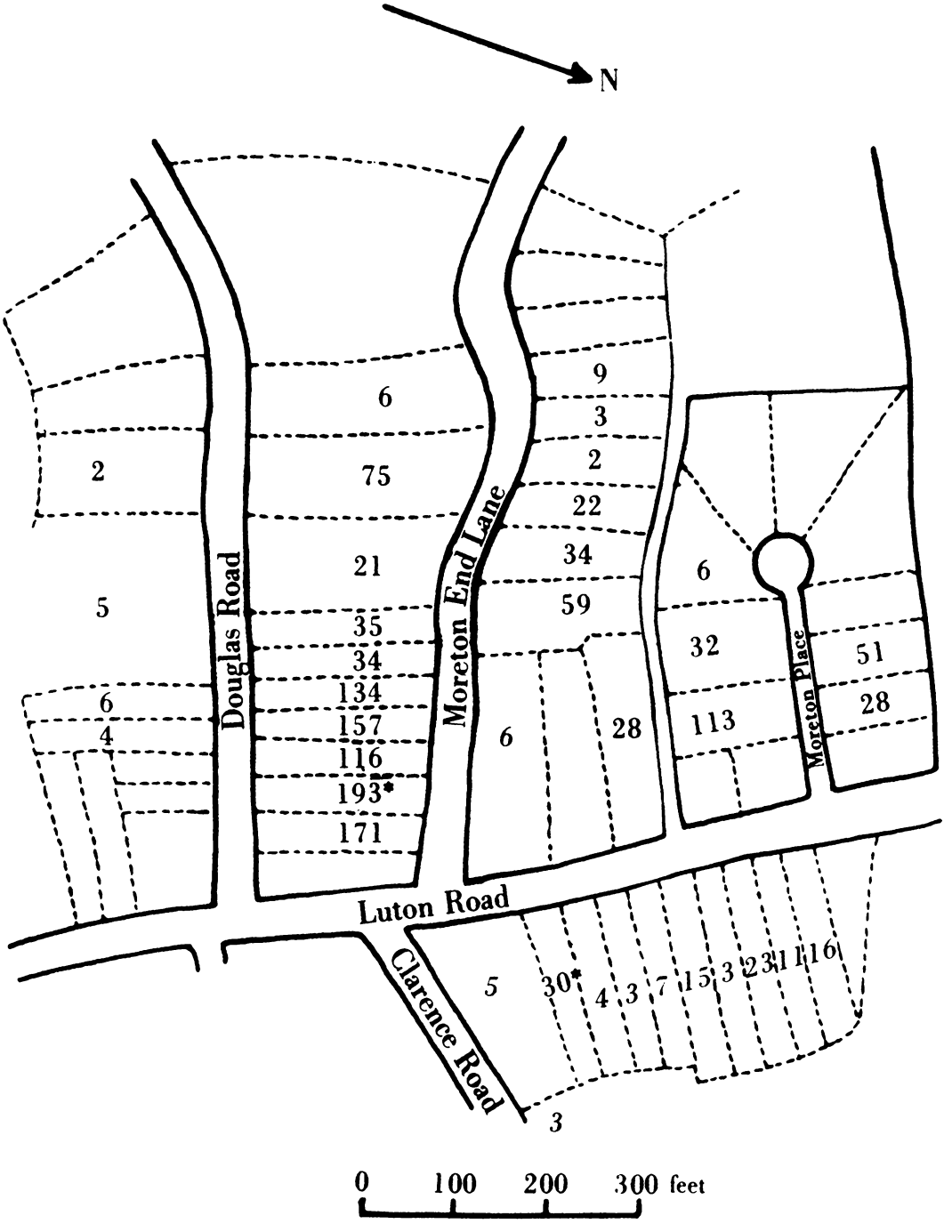


Fig. 25. Numbers of *Arion hortensis* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

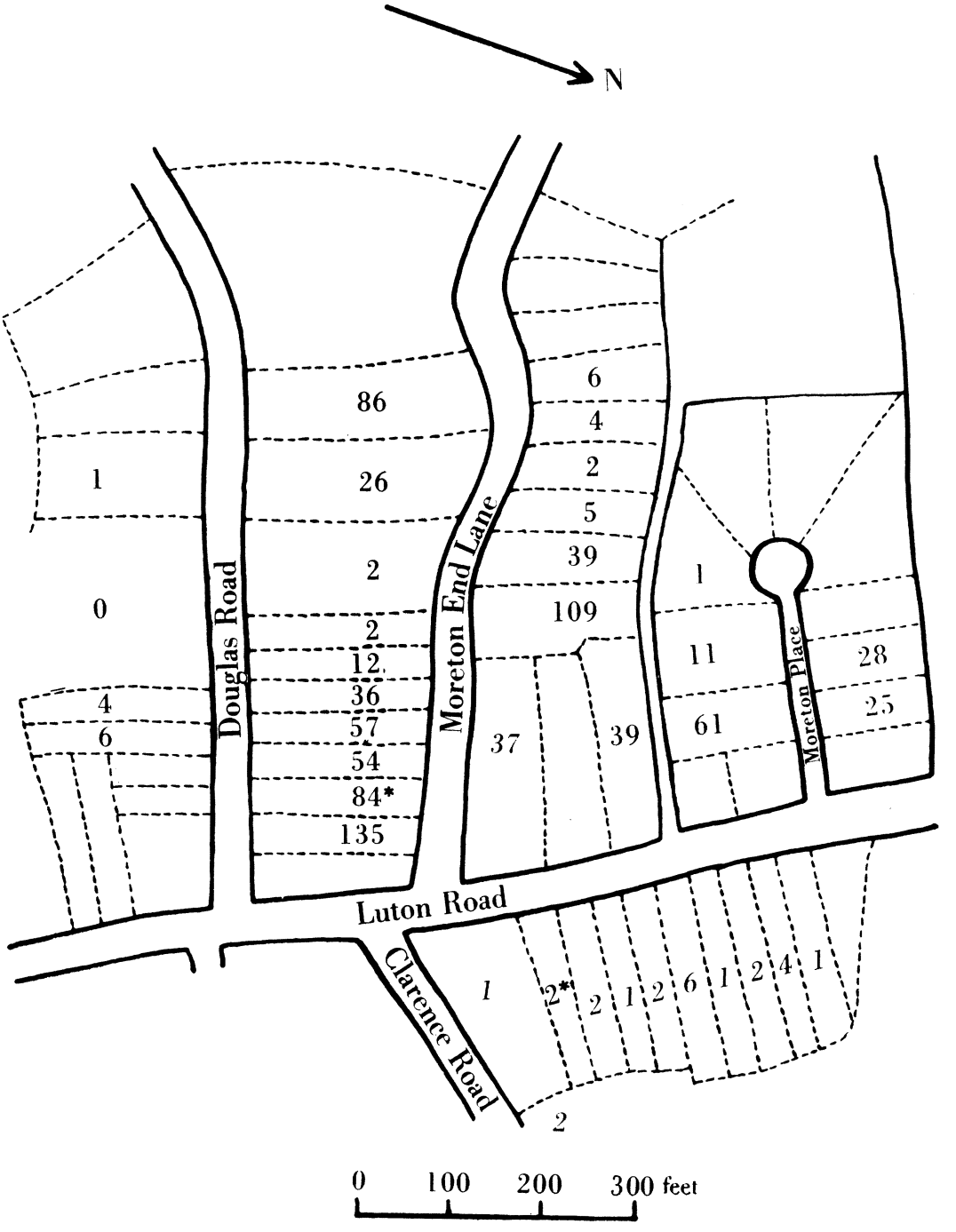


Fig. 26. Numbers of *Milax gracilis* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

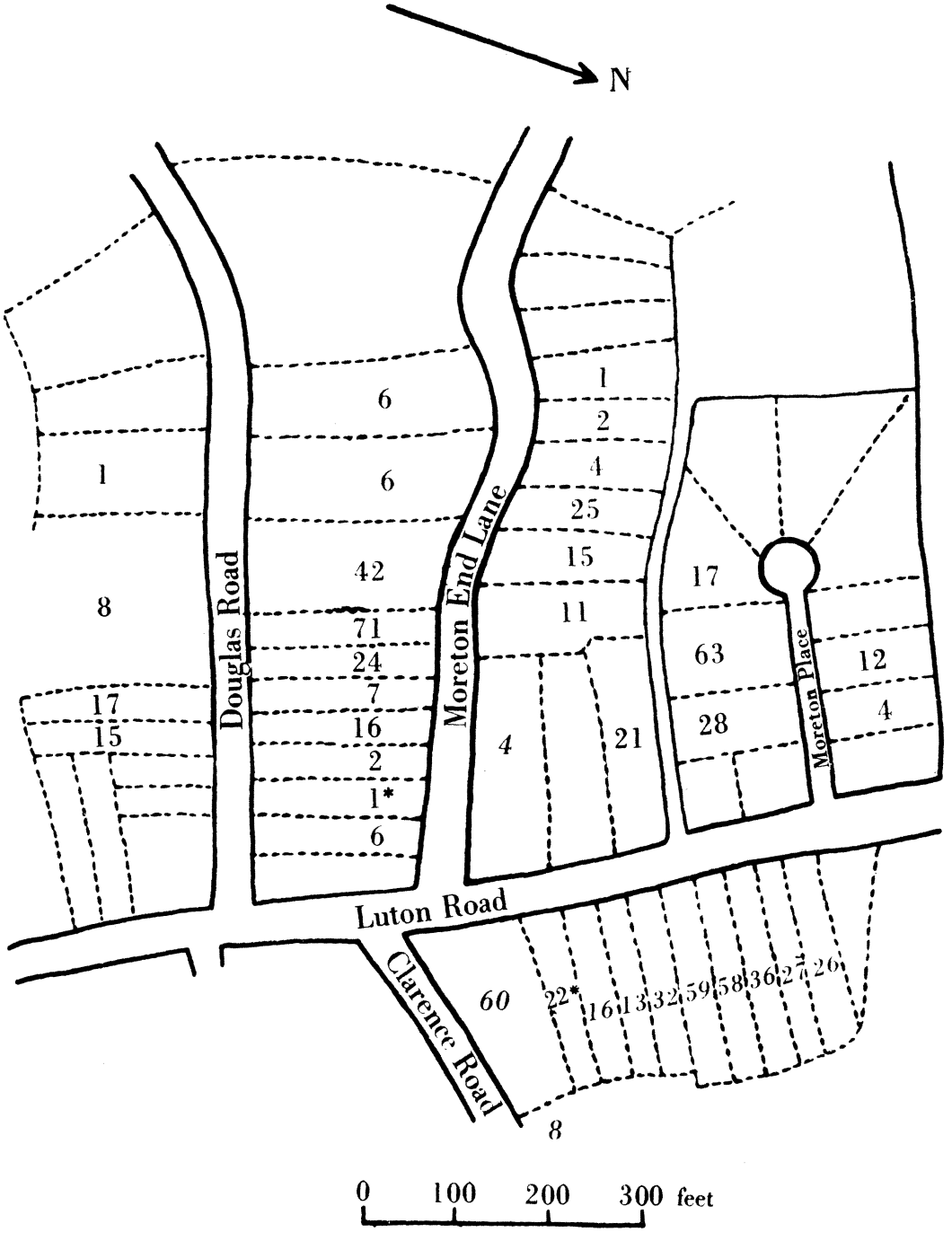


Fig. 27. Numbers of *Milax sowerbyi* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

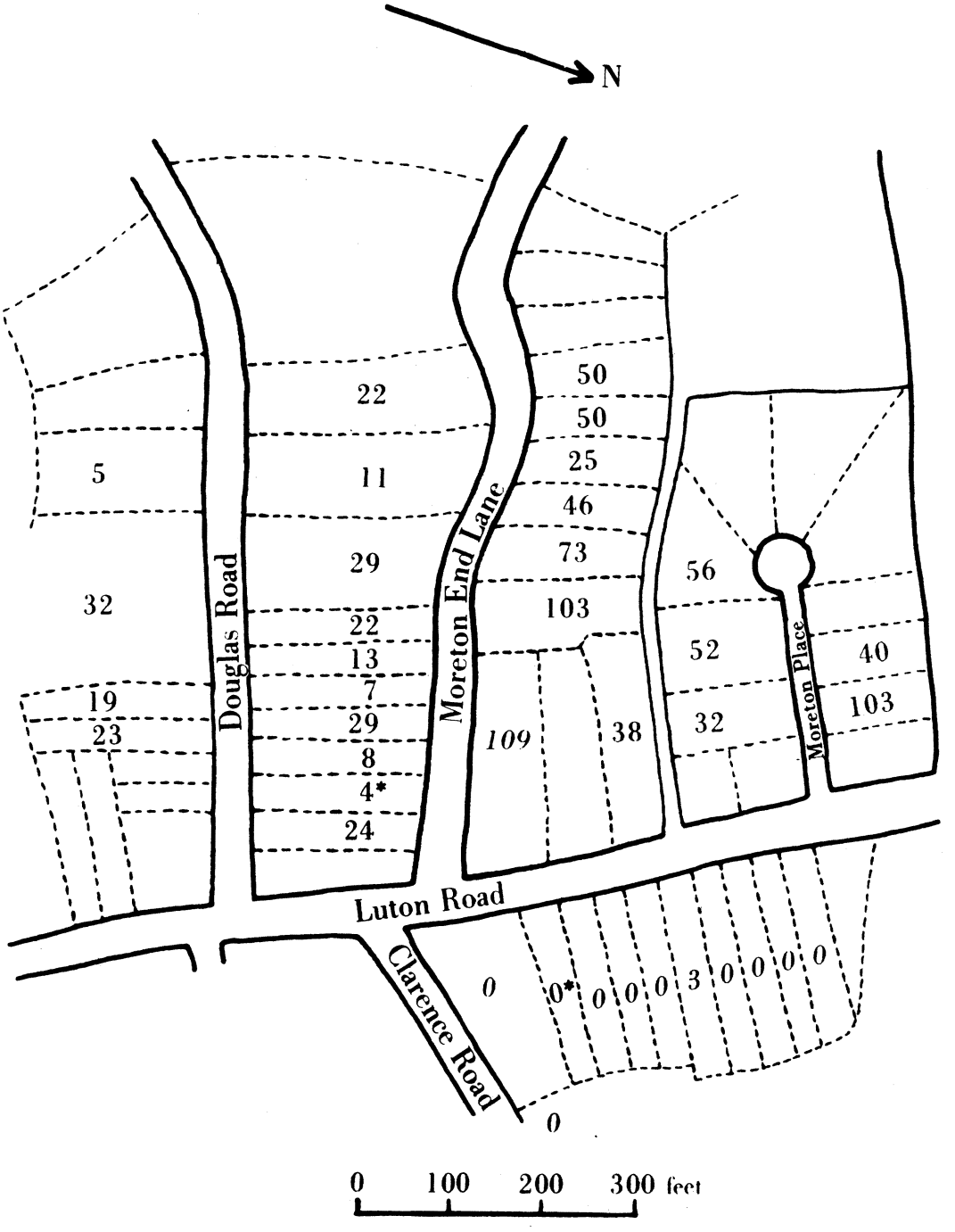


Fig. 28. Numbers of *Arion subfuscus* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

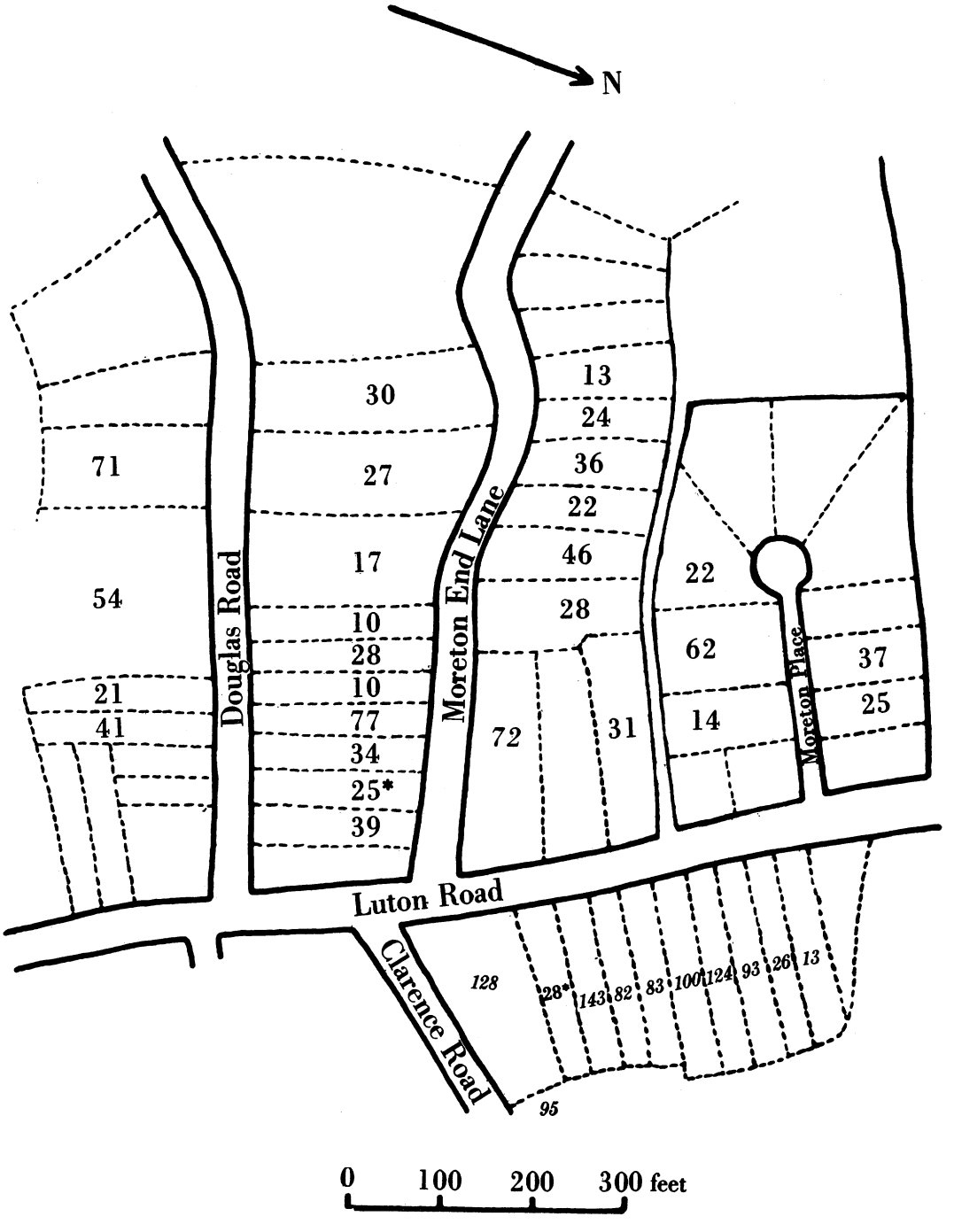


Fig. 29. Numbers of *Agriolimax reticulatus* per sample in the Moreton End district of Harpenden during April (figures asterisked), May, and June (figures in italics), 1943.

may be found in the fact that this species reaches its peak of activity and mating in the summer. It has already been stated that it is surprising to find the peak of any slug during what is normally warm dry weather. It may be that the summer in the eastern counties is too dry for successful annual replenishment of the species, i.e. by mating, oviposition and hatching, whereas in the rest of the country there is usually enough moisture in spite of the temperature being at its highest. There is evidence (Part 1, Fig. 6) that a real drought in the height of summer does reduce activity in this species.

The distribution of *Agriolimax reticulatus* (Fig. 29) was found to be as expected, i.e. it occurred everywhere and there were no obvious differences in any garden or sets of gardens.

Limax maximus seems to occur in small numbers in many gardens, but in two gardens (Nos. 74 and 76 Luton Road) exceptionally high numbers for this species were found.

The gradients shown in the numbers of *Arion hortensis* and *Milax gracilis*, as well as the ridge in abundance of *M. sowerbyi*, may indicate that the soil and underlying formation is a factor influencing the abundance of these species.

Another possible explanation of the distributions of the slug species may be revealed when the moisture retention properties of the soil in the various gardens have been examined. Also spectroscopic examination of the soils may reveal some striking differences, for example in the presence or quantities of some of the rarer elements, sufficiently clear cut to be associated with these observed distributions of the slug species.

The importance of discovering the explanation becomes apparent as soon as control measures are envisaged.

12. TIME OF NOCTURNAL ACTIVITY

It is well known that slugs are largely nocturnal in their habits, but that under special circumstances they do become active to some extent during the daytime. It is obvious that, for such a study as this, involving the observation and collection of active slugs, as well as for the interpretation of baiting and trapping experiments, it is essential to have more exact information regarding their periods of activity. It has, for example, already been pointed out (Part 1, § 4) that collecting should be done at an hour when all the species are fully active. In order to do this it is necessary to have partial answers at least to such questions as the following: does each species become active at the same time and is the duration of its activity period the same, do the young and old of a species behave in the same manner, is the period of activity dependent chiefly on the duration of the night, i.e. longer on the long winter nights than on the short summer ones, and controlled by the times of sunrise and sunset, and does the whole slug population automatically become active (atmospheric and soil conditions permitting) each day as the light fails or are the slugs active only when in need of food, etc.? If the latter were true, it would indicate that a much greater proportion of the population could be expected to be active on any suitable night during the winter and summer months when favourable nights are relatively more infrequent than on similar nights during the spring and autumn when the chances of a sequence of nights favourable to slug activity are correspondingly much greater. This implication, if proven, would be of the utmost importance in any attempt to estimate population figures from activity numbers.

The first definite indication that species of slugs might have different times of nocturnal activity in relation to the season of the year was obtained in the early baiting experiments (Barnes & Weil, 1942). The proportion caught on the baits before and after midnight varied, fewer before midnight in the spring than in the early autumn. This gave rise to the suggestion that different species of slugs had different times of nocturnal activity and that different species predominated in the garden at different seasons of the year. This latter has subsequently been proved. The slugs attracted per hour throughout one night (30–31 August 1941) to heaps of three baits (bran only, bran mixed with powdered metaldehyde and powdered metaldehyde alone) were counted after removal. Fig. 2 (loc cit.), in which these numbers are shown, clearly indicates that on this particular August night (sunset 18.58 hr. G.M.T.) slugs began to be active between 18.30 and 19.30 hr., that the greatest numbers were active (i.e. attracted to the baits) between 19.30 and 20.30 and that after this the numbers fell off rapidly until 5.30 hr. the next morning. Unfortunately the slugs were not identified specifically until September 1941, so these facts can only be taken to refer to slugs as a group. But from our more recent work on seasonal activity it can be safely judged that large numbers of *Agriolimax reticulatus* would have been active that night.

In 1942 an attempt was made to get exact data on the numbers of the different slugs species active throughout the night during June. Accordingly ten replicated heaps of bran only were placed at different points in the back garden of No. 5 Moreton End Lane at 12.00 hr. on 13 June. The numbers of slugs seen at these heaps at various times throughout the next 48 hr. were recorded. The slugs were allowed to remain on the heaps and were not removed. The figures are given in Table 24.

It will be seen that the duration of the activity periods of the various species is not the same, different species being active for longer or shorter periods and some starting earlier, others later. Their times of activity on these two successive nights were surprisingly similar, although there were more of each species, except *Arion hortensis* and *Milax*

sowerbyi, active on the second night. Thus, for example, appreciable numbers of *hortensis* were active each day both before sunset and after sunrise as well as throughout each night, whereas the other species had shorter periods of activity. In fact, the bulk of the slug fauna active up to sunset and from dawn onwards consisted of this species. Likewise, there is evidence that *Agriolimax reticulatus* reaches its peak of activity before midnight, *Arion subfuscus* at about midnight and *Milax gracilis* after midnight. Taken as a group it would appear that the majority of the slugs were active by 2 hr. after sunset and remained so until 2 hr. before sunrise.

It remains to be proved whether these times of activity of the different species remain relatively constant throughout the seasons of the year and also whether or not these actual times, in relation to sunrise and sunset, are the same during the long winter nights.

By observation the impression had been gained that slugs do not come out so soon after sunset in the middle of winter as they do in the height of summer. But the only numerical evidence that it has been possible to obtain is given in Table 25.

When the bran baits were put in position on 27 December the weather was mild and the sky overcast, but very soon after the sky cleared and the temperature fell from about 41°F. at 15·15 hr. to about 37°F. at 19·15 and about 32°F. in patches at 21.15 hr. The night of 2–3 January was favourable for slug activity, but it was not found possible to continue the observations throughout the night. So that, although there was no appreciable slug activity on these two occasions until the third hourly count after sunset (compared with the one at sunset or the first one after during June, see Table 24), it would not be wise to conclude that this was proof that slugs become active later in relation to sunset in the winter than in the summer. Further evidence must be obtained.

But it seems clear that for the present, if the method of collecting after dark all visibly active slugs is adopted as a sampling method, such collections should be made not earlier than 2 hr. after sunset nor later than 2 hr. before dawn at least during June, nor earlier than 3 hr. after sunset in December. Otherwise the relative numbers of *Arion hortensis* would be too high in proportion to the other species and also the numbers of all species at such an early or late hour would give an unnecessarily inaccurate idea of the total numbers active on that particular night.

These times of activity are also most important when a comparison is made of different sampling methods. For example, the times of activity must influence the proportion of the various species found on any baits or traps that are examined the next morning, since there is a much longer period each night (at least in June) during which *Arion hortensis* can be attracted to, or by chance come within the range of attraction of, the bait than, for example, *A. subfuscus*. Consequently, results might tend to show that *hortensis* was more attracted to the bait or caught by the traps than *subfuscus*, although in reality a higher percentage of the available *subfuscus* might have been attracted or caught.

On six occasions during 1942 half-hour collections were made around sunset in the back garden of No. 5 Moreton End Lane and once at dawn. No electric torch was used in these collections, otherwise they were carried out in the same manner as the after-dark collections. Full details are given in Table 26. In the evening collections the bulk of the slugs of all species were quite small and this was in great contrast to the normal nightly collections, although small slugs were collected after dark but not in such overwhelming proportions. The second outstanding feature is the steady decrease from May to December in the total number as well as those of the individual species. It seems unlikely that this decrease is purely fortuitous. The diminution of *hortensis* (virtually all immature or 'babies') is most striking, especially when considered in relation to the seasonal activity curves of this species obtained by collecting after dark. The decrease may be linked up with the rate of breeding.

13. RESTRICTION OF ACTIVITY BY VARIOUS WEATHER CONDITIONS

In such an observational and essentially field study as this, there have been many opportunities of seeing how slugs behave under various weather conditions. The more one sees, the more obvious it becomes that no single factor or even simple combination of factors is ever at work. It is the result of these complex combinations, or the weather conditions changing, that the numbers of active slugs vary from time to time.

In this section examples will be given of the numbers of slugs found active under various conditions. These examples are for convenience grouped under the most obvious prevailing factor, such as cold, drought, falling rain, warmth and wind. But it must be appreciated that in each case a host of other physical factors is at work, sometimes dependent on the prime factor involved, at others quite independent. For this reason it is impossible to state specifically the exact cause of every sudden increase or decrease in the numbers of slugs active in the field.

Under laboratory conditions the effect of particular and simple combinations of factors can be disentangled. But it seems that it would be usually well-nigh impossible to apply these results out in the garden, because in the first place the various combinations in the field are so very complex and there is no instrument available by which the weather as such can be measured. Secondly, there is little uniformity

Table 24. *Number of slugs seen at, but not removed from, baits of bran only on* (*a*) 13–14 *June and* (*b*) 14–15 *June* 1942 (*sunset* 20.15 *hr.: sunrise* 3.45 *hr.*). *The baits were placed in position in the back garden of No.* 5 *Moreton End Lane at* 12.00 *hr. on* 13 *June*

Species		Hour (G.M.T.) 13.15	16.15	19.15	20.15	21.15	22.15	23.10	00.50	1.45	2.45	3.45	4.45	5.45	7.45	10.45	Total seen
Arion ater	(*a*)	0	0	1	1	5	8	—	—	4	5	2	0	0	0	0	26
	(*b*)	—	0	0	0	1	5	8	4	4	2	2	2	2	0	—	30
A. circumscriptus	(*a*)	0	0	0	0	0	3	—	—	1	1	1	1	0	0	0	7
	(*b*)	—	0	0	0	1	4	5	3	2	1	0	0	0	0	—	16
A. hortensis	(*a*)	8	7	13	28	36	43	—	—	44	51	43	52	20	5	2	352
	(*b*)	—	3	13	23	30	34	41	38	37	29	23	37	22	13	—	343
A. subfuscus	(*a*)	1	0	0	1	16	37	—	—	59	38	15	8	4	2	0	181
	(*b*)	—	0	0	2	24	31	40	43	33	25	5	3	3	0	—	209
Milax gracilis	(*a*)	0	0	0	1	12	19	—	—	22	19	2	1	0	0	1	77
	(*b*)	—	0	0	4	8	11	14	17	17	8	4	1	1	0	—	85
M. sowerbyi	(*a*)	0	0	0	0	0	3	—	—	9	3	0	0	0	0	0	15
	(*b*)	—	0	0	0	2	1	3	4	3	2	0	0	0	0	—	15
Agriolimax reticulatus	(*a*)	1	1	0	2	5	10	—	—	13	7	5	3	1	0	0	48
	(*b*)	—	0	0	0	8	20	21	16	13	6	4	4	2	0	—	94
Total	(*a*)	10	8	14	33	74	123	—	—	152	124	68	65	25	7	3	706
	(*b*)	—	3	13	29	74	106	132	125	109	73	38	47	30	13	—	792

Table 25. *Number of slugs seen at, but not removed from, baits of bran only on* (*a*) 27 *December* 1943 (*sunset* 15.57 *hr.*) *and* (*b*) 2–3 *January* 1944 (*sunset* 16.03 *hr.*). *The baits were placed in position in the front garden of No.* 5 *Moreton End Lane at* 12.00 *hr. on* 27 *December and the same baits were used on* 2–3 *January*

Species		Hour (G.M.T.) 13.15	14.15	15.15	16.15	17.15	18.15	19.15	20.15	21.15	22.15	23.15	00.15	1·15	8·15	Total seen
Arion ater	(*a*)	0	0	0	0	0	0	0	1	1	1	—	—	—	—	3
	(*b*)	—	—	0	0	0	0	0	0	0	0	1	2	1	0	4
A. circumscriptus	(*a*)	0	0	0	0	0	0	0	0	0	0	—	—	—	—	0
	(*b*)	—	—	0	0	0	0	0	0	1	2	1	0	0	0	4
A. hortensis	(*a*)	1	1	1	1	0	10	10	7	12	10	—	—	—	—	53
	(*b*)	—	—	0	0	2	12	23	26	30	24	18	21	21	5	182
A. subfuscus	(*a*)	0	0	0	0	1	7	12	10	7	5	—	—	—	—	42
	(*b*)	—	—	0	0	2	15	18	26	30	21	18	17	14	0	161
Milax gracilis	(*a*)	1	0	0	2	4	9	11	6	9	9	—	—	—	—	51
	(*b*)	—	—	0	1	3	9	7	8	9	12	16	16	19	3	103
M. sowerbyi	(*a*)	0	0	0	0	0	0	0	0	0	0	—	—	—	—	0
	(*b*)	—	—	0	0	0	0	0	0	0	0	0	0	1	0	1
Agriolimax reticulatus	(*a*)	0	0	0	0	2	9	11	10	5	4	—	—	—	—	41
	(*b*)	—	—	0	0	1	11	17	20	21	17	12	14	15	0	128
Total	(*a*)	2	1	1	3	7	35	44	34	34	29	—	—	—	—	190
	(*b*)	—	—	0	1	8	47	65	80	91	76	66	70	71	8	583

Table 26. *Numbers of slugs collected during twilight at sunset and at dawn, No. 5 Moreton End Lane, 1942*

Date	Time of collection (30 min.)	*Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax maximus*	Total
				At sunset						
22 May	19.30–20.00	5	1	249	6	58	0	7	0	326
25 May	19.25–19.55	1	1	208	7	14	0	6	0	237
5 June	20.00–20.30	1	0	74	11	19	1	16	1	123
23 Aug.	18.45–19.15	0	0	49	0	10	0	1	0	60
29 Sept.	17.30–18.00	0	0	18	0	7	0	3	0	28
22 Dec.	15.45–16.15	0	0	0	0	0	0	1	0	1
				At sunrise						
7 June	4.15– 4.45	1	3	81	6	5	0	11	0	107

Note. Sunset: 22 May, 19.54 hr.; 25 May, 19.58 hr.; 5 June, 20.11 hr.; 23 Aug., 19·08 hr.; 29 Sept., 17.44 hr.; 22 Dec., 15.54 hr. Sunrise: 7 June, 3.45 hr.

of conditions outside, particularly in gardens and on allotments. Even in fields the lack of uniformity of such conditions is obvious if one considers microclimates and, after all, it is probably these that account for slugs being active or not.

(*a*) *Activity during cold spells and immediately afterwards*

There is no slug activity when it is actually freezing. During periods when the day and evening temperatures are moderate and there are frosts each early morning, full activity goes on during roughly the first half of the night but ceases during the latter half. Thus, 289 slugs (comprising the normal number of each species for this season of the year) were collected between 21.00–21.30 hr. of 20 February 1943, although the minimum grass tem perature early that day had been 26·6° F. and early on the next morning it was 25·6° F. These temperatures were not recorded actually in the garden involved, but there were certainly appreciable frosts.* The evening of 6 March 1943 was quite similar. In the early morning the temperature had fallen to 29·3° F. and the following morning 20·4° F. was recorded, but slugs of all species were fully active on the evening of the 6th, 288 slugs being collected between 20.35–21.05 hr.

It has also been observed frequently that some slugs may still be found active in the more sheltered parts of a garden even when a frost is already settling in the more exposed parts of the same garden. But all activity ceases as soon as the frost becomes general.

After short periods of cold weather, the slugs quickly resume full activity. Thus, after the cold spell, 26–31 December inclusive at the end of 1941, there was full activity on the evening of 2 January 1942. After prolonged periods of cold, the speed of resumption of full activity is equally striking. In 1942 there was an unusually severe and prolonged cold period from 6 January until 14 March inclusive during which the minimum grass temperature was above 32° F. on only four nights (25 and 26 January, 4 and 12 March). On 2 January, just before this cold spell started, 181 slugs were collected in half an hour. On 14 and 15 March, immediately after it had ended, 182 and 187 slugs respectively were collected per half hour. The numbers of the various species comprising these samples were:

	Arion ater	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax maximus*	Total
2 Jan.	5	4	84	14	37	4	32	1	181
14 Mar.	3	0	99	20	35	4	20	1	182
15 Mar.	2	2	106	19	28	6	24	0	187

Similar results were obtained in other gardens (see Appendix 2). It is thus obvious that after even such a prolonged period of unusual cold the same numbers of slugs are active as before. This proves conclusively that one cannot depend on cold winters in England destroying slugs. It also indicates that slugs can take up positions where fairly intense and certainly prolonged cold does not reach them sufficiently to decimate their numbers.

During this cold spell a few observations were made to see what effect a slight thaw had on slug activity. Thus, on 24 January, when the minimum night temperature was a fraction of a degree above freezing, a half-hour collection was made between 20.20 and 20.50 hr. It was not freezing at this time

* All the collections of slugs referred to in this section were done in the back garden of No. 5 Moreton End Lane and all the temperatures are those recorded at Rothamsted Experimental Station. Specific analyses of the slug captures are given in Appendix 1.

but snow was covering all the ground except for small patches round plants and there was none on the rubbish heap. 31 slugs (3 baby *Arion ater*, 9 *A. subfuscus* and 19 *Agriolimax reticulatus*) were found, of these all except two or three (*reticulatus*) were found on the rubbish heap, which was largely composed of the autumnal leaves. Again, the following night when it was freezing (21.20–21.50 hr.) except on the rubbish heap, no slugs could be found except one *Arion hortensis* and two *Agriolimax reticulatus* which were on the rubbish heap. On 4 March, with the minimum temperature again a fraction of a degree above freezing, 32 slugs (10 *Arion hortensis*, 6 *A. subfuscus*, 1 *Milax gracilis* and 15 *Agriolimax reticulatus*) were collected. Similarly, on 11 and 13 March, 60 and 56 slugs respectively were collected in half-hour periods. This was followed by the full numbers being active again on 14 March as already stated.

More information on the activity of the various species during cold spells has already been given in the sections dealing with the abundance and seasonal activity. One cannot help gaining the impression that the species may be arranged roughly in the order of their apparent resistance to cold. The most resistant, to all weather changes considered together, appears to be *Agriolimax reticulatus* followed by *Arion subfuscus*, *A. ater* and *Milax sowerbyi* come next, while *M. gracilis* and *Arion hortensis* appear to be most susceptible.

The return of the species to activity after severe cold probably depends to some extent on the depth under leaves and in the soil at which the different species take cover. Thus *reticulatus* seems to take up comparatively superficial positions and so would be able to resume activity almost immediately a thaw set in. On the other hand, *gracilis* goes definitely into the underlying soil, so temporary thaws at the surface of the ground would not necessarily penetrate the soil down to where *gracilis* was taking cover and the thaw would have to be more prolonged to enable full activity of this species to be resumed.

For this reason it is not wise to be too dogmatic in stating that the different species have different susceptibilities to cold. Only laboratory experiments could decide this. Carrick (1942), after experimenting with *reticulatus*, comes to the conclusion that 'normal extremes of weather in Britain are not usually lethal to *A. agrestis* [*A. reticulatus*], but they do serve to inhibit adult activity and reproduction'.

(*b*) *Activity in periods without rain and soon after*

The activity of slugs has been reduced during rainless periods at certain periods of the year, but at others it seems to have been almost unaffected. The recovery rate after such periods also seems to have changed with the season of the year.

The following examples taken from after-dark sampling in the back garden of No. 5 Moreton End Lane illustrate this. The full analyses of the numbers of the individual species are to be found in Appendix 1.

1. On 21 and 23 February 1943, 6 and 8 days after 0·014 in. of rain on 15 February, 210 and 127 slugs were collected in 30 min. compared with 289 on 20 February, which was 5 days after any rain. There was 0·018 in. of rain at about 16.00 hr. on 25 February and the same evening between 21.20 and 21.50 hr. 261 slugs were collected. This small amount of rain apparently was sufficient to enable full activity to be resumed on this night.

2. On 6 March 1943 288 slugs were collected although it was 9 days since any rain had fallen, but on 8 March (11 days since any rain) only 133 were collected. However, on 6 March dew had fallen by the time the collection was started at 20.35 hr. and the surface was quite moist, whereas on 8 March no dew had fallen by the time of collecting (20.20 hr.) and the surface was dry. On both occasions the water content of the soil was high.

3. On 24 April 1942, the fifteenth day since any rain (0·214 in., 9 April), only 56 slugs were collected and on 7 May, the twenty-eighth day since rain, only 83 slugs were collected. Previous to this drought period 230 slugs were collected in a sample on 12 April. One day after the drought was broken, by 0·548 in. rain on 10 May, 258 slugs were collected. In this case apparently full activity was resumed the night after the drought was broken.

4. On 4 June 1942 (5 days after 0·135 in. rain on 29 May) 243 slugs were collected. On 30 June (18 days since 0·175 in. rain on 12 June) only 103 slugs were found. In this case the recovery to normal numbers being active was not immediate as in the two previous cases (in February and April). Rain fell on 3 days (0·012 in. on 3 July; 0·029 in. on 4 July and 0·019 in. on 6 July), but only 140 slugs were collected on the evening of 6 July. Again, after further rain (0·148 in. on 7 July; 0·160 in. on 9 July; and 0·270 in. on 10 July), 193 slugs were collected on the evening of 10 July. By 27 July nearly 1·5 in. rain had fallen (on 8 days) and the numbers of slugs collected on 27 July was 212, thus practically reaching the number (243) collected before the rainless period in June.

The following deductions seem justifiable from these data. During the earlier part of the year when there is plenty of moisture in the soil, following the winter rains and snow, a very slight amount of rain (e.g. Example 1) is sufficient to cause full activity to be resumed after a rainless period. In addition, at this season of the year, the breaking of a drought is followed by an immediate resumption of full activity (e.g. Examples 1 and 3). Even heavy dew during a rainless period early in the year enables full activity

to be resumed (e.g. Example 2). Later, in the summer when the water content of the soil is lower, full slug activity is not resumed immediately rain has fallen (e.g. Example 4).

It would appear that slug activity depends ultimately on there being a film of moisture over the places where they are going to be active. If this is absent, activity is curtailed, even although there may be plenty of moisture in the soil. This has been frequently demonstrated by the fact that on nights when concrete paths are dry but the soil on either side is moist, the slugs are active on the soil but not on the path. But immediately the surface of the path becomes moist by slight rain many slugs can be seen moving across it and feeding on anything, such as dead leaves, which they can find upon it. Again, even when there is plenty of surface moisture, the slugs cannot be active unless the moisture reaches them wherever they happen to be.

(c) *Activity while rain is falling*

When heavy rain is actually falling the number of slugs found active has been reduced. The following example is given of half-hour collections made in the same garden on successive nights when apparently the only difference in conditions was that on one night rain was actually falling heavily all the time the collection was being made and on the next there was no rain.

Table 27. *Comparison of the numbers of slugs active* (A) *during heavy rain*, (B) *no rain falling* (*No.* 10 *Douglas Road*)

	A 5 Oct. 42	B 6 Oct. 42
Arion hortensis	45	268
A. subfuscus	7	5
Milax gracilis	23	73
M. sowerbyi	1	12
Agriolimax reticulatus	24	79
Total	100	437

On the other hand, when slight gentle rain is falling there seems to be no appreciable reduction in the numbers of active slugs. And usually immediately after rain has ceased falling an increase in numbers is obvious.

(d) *Activity during hot spells*

Carrick (1942) found that *Agriolimax reticulatus* was only slightly active under laboratory conditions at 77° F., although it could exist at 86° F.

In the present study no temperatures approaching these were encountered, as the night temperatures have always been lower. But during the summer of 1942 reduced activity of the slugs occurred during June and July. In addition to the normal decrease in the numbers of certain species which are active at this time of the year, it is considered that this lack of activity was partly due to unfavourable conditions concerning moisture rather than to the summer temperatures prevailing at that time. No evidence has been obtained that heat, as such, is responsible for immobilizing slugs in the field and in fact conditions for such a possibility to occur must be extremely unlikely to obtain in this country.

It is concluded that any diminution of slug activity in this country during hot weather is not due to the actual temperature, but to increased evaporation causing drought conditions to obtain on the surface and in the surface layers of the soil.

(e) *Activity in heavy wind*

It has been observed that on windy nights fewer slugs are active than usual. Often wind results in a reduction in temperature and what is more important a drying out of the surface layers of the soil. On the other hand, the wind may be definitely moisture-bearing and it is then that the true effect of wind on the activity of slugs is observable. Table 28 gives the results of sampling on a damp windy night and on a still night in December. The wind was very strong, but of course there were plenty of places, e.g. behind bricks, perennial plants, etc. where its full force could not have been felt. Observation showed that few slugs were active in exposed places and most of the slugs collected were found in sheltered sites. This would account for the comparatively large numbers of slugs to be found in gardens during heavy damp winds. On the other hand, the full effect of wind would be seen in exposed fields.

Table 28. *Comparison of the numbers of slugs active* (A) *on a damp windy night*, (B) *on a damp still night*

	A 5 Dec. 42	B 6 Dec. 42
Arion ater	2	2
A. circumscriptus	0	1
A. hortensis	102	183
A. subfuscus	13	13
Milax gracilis	32	95
M. sowerbyi	5	7
Agriolimax reticulatus	22	28
Total	176	329

14. SUMMARY

Section 8. Observations of slugs feeding in gardens indicate that very little of their food consists of plant material grown for human consumption or pleasure. In places where one crop only is grown, e.g. potato patches in the autumn, the damage would be higher owing to the absence of alternative food.

Section 9. Mating of *Agriolimax reticulatus* and *Arion subfuscus* takes place out in the open on the surface of the ground after dark, the peaks being soon

after the peaks of seasonal activity; the former species also mates to some extent throughout the year, whereas in the latter species mating is restricted to July–October. *Arion hortensis* and *ater* usually require some shelter, e.g. dead leaves, under which to mate, while it is presumed that the *Milax* species usually mate underground or under cover.

Section 10. By weighing the slugs species by species en masse as collected and then calculating the weight per 100 individuals, regular changes in weight throughout the year have been found. This method has been found to be as satisfactory for assessing seasonal changes in weight as the half-hour method of collecting slugs is for measuring seasonal changes in activity numbers. The slugs are heaviest soon after the greatest numbers are found active and at the time when the peak of mating occurs.

Section 11. The distribution of the species varies from garden to garden. *Arion hortensis* and *Milax gracilis* are most abundant in the gardens at the bottom of an old river bed slope and decrease steadily until their lowest numbers occur half-way up it. *Milax sowerbyi* has a ridge of abundance across the slope. *Arion subfuscus* is almost completely absent on the east side of the valley. Two particular gardens form the focal point of abundance of *Limax maximus*, and *Arion ater* is more abundant in gardens of recent origin in close proximity to coarse grass areas than in old well-established gardens. These distributions have persisted month by month throughout 2 years.

Section 12. There is some evidence that each species has its own regular curve of nightly activity, providing of course weather conditions are suitable. In the summer activity appears to be more closely adjusted to the time of sunset than in the winter. Immature specimens of *Arion hortensis* preponderated in steadily decreasing numbers in twilight collections made from May to December.

Section 13. All species are fully active at about 40° F., but some activity continues until almost freezing point; below this there is no activity. Some species, e.g. *Milax gracilis*, resume activity after cold spells later than others, e.g. *Agriolimax reticulatus*, perhaps owing to their deeper penetration of the soil.

Lack of surface moisture seems to be one of the factors limiting activity. Slug activity in rainless periods is reduced more at some periods of the year than at others. Rainless periods in the spring have less effect on limiting activity than summer droughts. This is probably due to the different water contents of the soil at these seasons. Activity is reduced while heavy rain is actually falling and also in heavy wind.

The optimum conditions for slug activity may be summarized thus: a warm still night with plenty of surface moisture either in the shape of recent rain or dew.

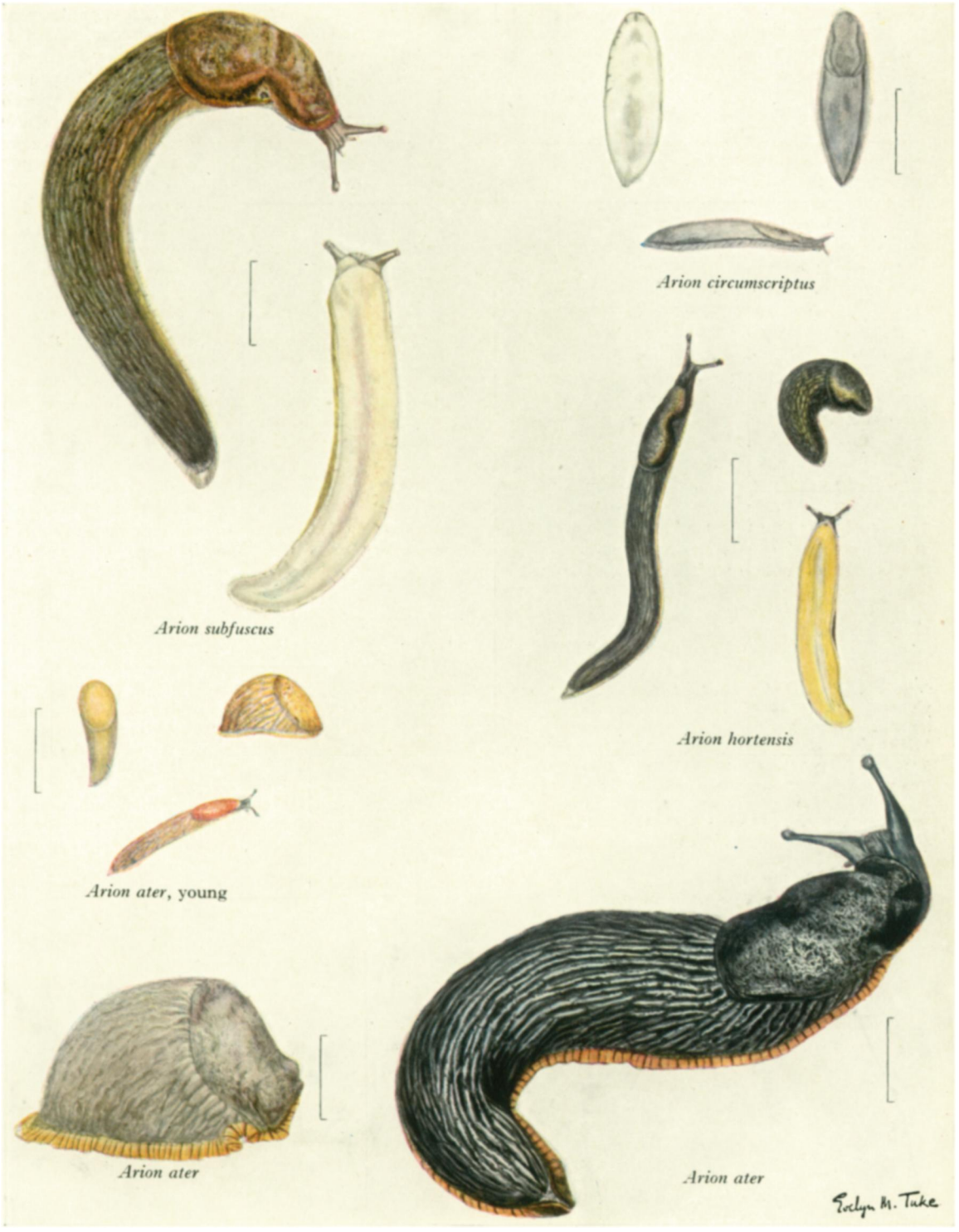
EXPLANATION OF PLATES 3–5

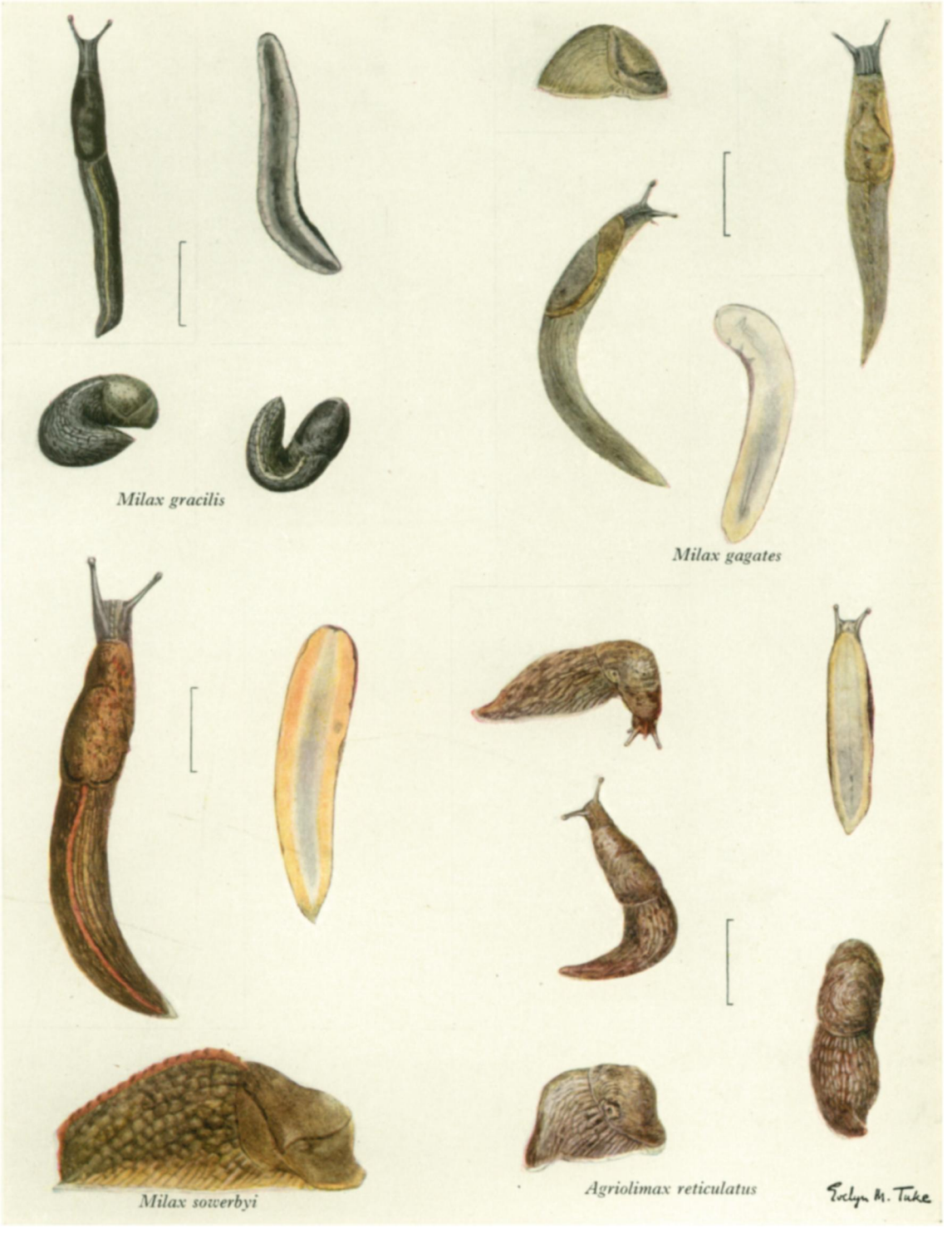
Miss Evelyn M. Tuke, Lecturer in Biology, Goldsmiths' College, University of London, has most generously painted eight of the common species of slugs found during this study at Harpenden. They include most of those of economic importance found in this country. In order to be able to compare the three species of *Milax* (see Part 1, § 2), Miss Tuke also painted some specimens, unfortunately not full grown, of *M. gagates* which Mr D. C. Thomas sent us from Devon.

Owing to the generosity of Messrs H. R. Napp, Ltd., the manufacturers of metaldehyde, to whom we express our grateful thanks for having shown their interest in scientific research in this most practical way, it has been possible to reproduce these paintings as three coloured plates. They are intended to supplement the key for the identification of the species (Part 1, pp. 144–5) and illustrate the characters used in their recognition. It is scarcely necessary to state that it is not claimed that the colours portray the extent of variation that occurs in slugs throughout the country, but they are faithful representations of the species as found by us most commonly in Harpenden. The length of each scale represents 1 cm.

ERRATUM, PART 1

P. 141, § 2, para. 2: *for* (? *carvanae* Poll.) (p. 145)
read (? *caruanae* Poll.) (p. 175)





APPENDIX 1. *Collections of active slugs in the back garden of No. 5 Moreton End Lane, Harpenden, after dark, 1941–3*

(In 1941 the collections made on 16 Oct., 9 and 10 Dec. lasted 60 min., while that on 23 Dec. went on for 45 min. The figures of the number of slugs obtained on these dates have been adjusted so as to be comparable with all the other entries, i.e. 30 min. collections.)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min.									
		Arion ater	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
1941: Sept.	—	1	0	0	24	12	3	155	0	0	195
16 Oct.	—	0	0	30	7	30	2	44	0	1	114
10 Nov.	—	0	0	40	9	26	3	53	0	0	131
11 Nov.	—	1	0	34	25	32	4	37	0	0	133
9 Dec.	—	2	2	44	11	11	2	34	0	1	107
10 Dec.	23.20–00.20	2	0	44	16	22	2	24	0	0	110
22 Dec.	20.30–21.00	6	3	64	6	21	5	30	0	0	135
23 Dec.	21.25–22.10	7	3	52	6	14	2	23	0	0	107
1942: 2 Jan.	20.15–20.45	5	4	84	14	37	4	32	0	1	181
24 Jan.	20.20–20.50	3	0	0	9	0	0	19	0	0	31
4 Mar.	18.45–19.15	0	0	10	6	1	0	15	0	0	32
11 Mar.	19.45–20.15	5	0	34	4	2	0	15	0	0	60
13 Mar.	20.25–20.55	0	1	42	4	4	1	4	0	0	56
14 Mar.	21.15–21.45	3	0	99	20	35	4	20	0	1	182
15 Mar.	19.30–20.00	2	2	106	19	28	6	24	0	0	187
29 Mar.	22.10–22.40	3	0	103	20	23	4	23	0	0	176
12 Apr.	19.55–20.25	5	0	86	47	34	7	51	0	0	230
13 Apr.	3.00– 3.30	1	0	84	26	12	0	11	0	1	135
24 Apr.	20.45–21.15	0	0	18	12	4	1	21	0	0	56
7 May	21.30–22.00	0	0	15	20	22	4	22	0	0	83
11 May	21.05–21.35	2	0	83	58	71	4	39	0	1	258
24 May	21.40–22.10	9	2	101	65	47	5	51	0	1	281
4 June	22.05–22.35	6	2	34	66	63	7	61	0	4	243
30 June	22.15–22.45	3	1	2	34	33	2	28	0	0	103
6 July	22.15–22.45	4	3	9	31	63	7	23	0	0	140
10 July	22.20–22.50	1	1	27	43	65	4	52	0	0	193
27 July	21.45–22.15	2	0	35	58	39	8	69	0	1	212
2 Aug.	21.40–22.10	5	0	61	73	67	9	91	0	2	308
4 Aug.	21.35–22.05	0	0	113	48	73	18	75	0	0	327
14 Aug.	22.35–23.05	5	0	76	62	87	21	103	0	0	354
21 Aug.	22.10–22.40	1	0	61	45	58	22	117	0	0	304
23 Aug.	21.00–21.30	1	0	83	26	86	12	105	0	0	313
31 Aug.	21.20–21.50	1	0	93	37	74	30	131	0	0	366
20 Sept.	20.35–21.05	1	0	84	26	79	22	138	0	1	351
28 Sept.	22.00–22.30	1	0	135	18	82	14	78	0	1	329
29 Sept.	21.10–21.40	0	1	141	19	97	9	67	0	0	334
30 Sept.	20.45–21.15	3	1	239	25	125	16	83	0	0	492
11 Oct.	20.50–21.20	1	1	165	26	86	23	81	0	0	383
17 Oct.	19.15–19.45	1	0	177	17	139	16	63	0	0	413
25 Oct.	19.15–19.45	0	2	208	15	54	10	67	0	0	356
28 Oct.	21.20–21.50	1	0	190	18	92	11	39	0	0	351
3 Nov.	19.10–19.40	3	0	215	24	99	8	33	0	0	382
15 Nov.	19.15–19.45	0	2	168	17	81	7	40	0	0	315
25 Nov.	19.05–19.35	1	0	131	9	80	5	34	0	0	260
25 Nov.	22.00–22.30	0	1	135	9	89	5	25	0	0	264
5 Dec.	21.30–22.00	2	0	102	13	32	5	22	0	0	176
6 Dec.	20.05–20.35	2	1	183	13	95	7	28	0	0	329
12 Dec.	19.15–19.45	1	0	201	10	54	5	38	0	0	309
13 Dec.	17.30–18.00	1	2	221	32	83	11	38	0	0	388
21 Dec.	18.15–18.45	2	2	229	20	78	8	43	0	0	382
1943: 12 Jan.	21.50–22.20	1	1	151	14	70	14	25	0	0	276
16 Jan.	19.30–20.00	2	1	131	28	45	2	29	0	0	238
19 Jan.	21.15–21.45	3	0	122	20	78	5	21	0	0	249

APPENDIX 1 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
21 Jan.	20.20–20.50	0	2	118	10	73	5	25	0	0	233
28 Jan.	19.15–19.45	0	7	192	32	48	7	46	0	0	332
2 Feb.	19.45–20.15	1	0	128	45	36	2	28	0	0	240
20 Feb.	21.00–21.30	5	2	130	29	84	7	32	0	0	289
21 Feb.	19.30–20.00	5	1	96	18	45	5	40	0	0	210
23 Feb.	20.50–21.20	2	1	65	13	19	0	26	0	1	127
25 Feb.	21.20–21.50	1	1	144	29	64	0	21	0	1	261
6 Mar.	20.35–21.05	3	1	123	42	78	10	29	0	2	288
8 Mar.	20.20–20.50	1	0	72	23	10	4	23	0	0	133
18 Mar.	19.30–20.00	2	2	32	10	25	3	24	0	0	98
23 Mar.	20.30–21.00	3	2	78	29	48	11	24	0	0	195
29 Mar.	20.30–21.00	9	0	198	26	89	7	39	0	2	370
9 Apr.	20.45–21.15	4	3	119	47	89	7	36	0	0	305
13 Apr.	21.15–21.45	6	1	80	38	76	10	24	0	0	235
18 Apr.	21.30–22.00	3	0	17	30	34	3	12	0	1	100
23 Apr.	22.05–22.35	3	0	75	47	107	8	23	0	1	264
27 Apr.	21.40–22.10	5	0	115	87	102	11	28	0	0	348
5 May	22.05–22.35	3	1	67	81	87	8	28	0	1	276
13 May	21.45–22.15	3	1	62	84	102	15	28	0	1	296
22 May	21.30–22.00	3	1	43	108	109	9	28	0	1	302
26 May	22.15–22.45	6	1	101	112	155	15	22	0	0	412
30 May	22.20–22.50	9	0	21	129	91	8	34	0	2	294
6 June	22.30–23.00	1	1	60	99	110	8	21	0	0	300
13 June	22.20–22.50	5	0	14	112	84	14	62	0	1	292
21 June	22.45–23.15	2	0	8	106	84	12	87	0	1	300
24 June	22.35–23.05	3	0	6	101	59	4	75	0	5	253
28 June	22.45–23.15	4	0	2	71	55	6	59	0	1	198
3 July	22.30–23.00	1	1	1	42	26	7	74	0	1	153
11 July	22.30–23.00	2	2	4	88	79	5	87	0	2	269
16 July	22.30–23.00	1	0	6	61	42	7	98	0	0	215
20 July	22.15–22.45	0	0	3	41	42	9	53	0	2	150
24 July	23.00–23.30	3	1	28	71	101	17	125	0	0	346
1 Aug.	22.05–22.35	1	0	23	55	141	8	66	0	0	294
4 Aug.	21.50–22.20	1	0	17	35	81	15	119	0	1	269
7 Aug.	21.45–22.15	0	0	36	34	122	17	96	0	0	305
26 Aug.	21.10–21.40	0	0	46	28	129	17	79	0	0	299
28 Aug.	22.00–22.30	0	0	49	17	117	17	69	0	2	271
4 Sept.	21.35–22.05	0	0	60	27	73	16	47	0	0	223
10 Sept.	21.30–22.00	3	1	75	19	119	19	64	0	1	301
16 Sept.	21.35–22.05	0	0	73	27	166	27	62	0	0	355
21 Sept.	21.35–22.05	0	1	91	9	101	13	43	0	1	259
28 Sept.	21.45–22.15	0	0	140	16	293	25	29	0	0	503
5 Oct.	20.45–21.15	4	1	101	15	279	25	46	0	0	471
10 Oct.	21.00–21.30	0	2	137	9	371	17	34	0	0	570
10 Oct.	22.00–22.30	1	1	142	7	337	5	24	0	0	517
17 Oct.	19.10–19.40	0	6	210	8	237	14	30	0	2	507
23 Oct.	20.45–21.15	0	4	165	10	238	16	39	0	0	472
28 Oct.	20.15–20.45	2	1	203	8	275	15	55	0	0	559
2 Nov.	20.30–21.00	2	1	161	7	260	14	22	0	0	467
10 Nov.	19.15–19.45	0	0	122	12	101	12	49	0	0	296
21 Nov.	20.05–20.35	2	2	111	8	95	7	30	0	0	255
28 Nov.	19.25–19.55	1	1	105	9	124	9	24	0	0	273
7 Dec.	22.00–22.30	3	0	61	6	80	0	12	0	0	162
18 Dec.	22.15–22.45	0	0	96	8	129	2	19	0	0	254
25 Dec.	21.05–21.35	2	3	101	18	84	4	29	0	1	242

APPENDIX 2. *Collections of active slugs in other Harpenden gardens after dark*, 1942–3

(The gardens are arranged in alphabetical order of the roads; in addition the gardens on each side of the roads are kept together. The gardens are back gardens unless otherwise stated.)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
		2 Clarence Road, north side									
1942: 6 Apr.	20.30–21.00	0	0	28	0	0	1	34	0	0	63
1943: 8 June	21.50–22.20	0	1	5	0	1	60	128	4	2	201
		4 Clarence Road									
9 June	22.20–22.50	0	0	3	0	2	8	95	0	3	111
		10 Clarence Road									
8 June	22.30–23.00	0	0	46	0	11	14	88	0	0	159
		7 Douglas Road, south side									
28 May	21.35–22.05	1	0	4	23	6	15	41	0	3	93
9 Oct.	20.40–21.10	0	0	37	4	9	7	43	0	1	101
		9 Douglas Road									
15 May	21.15–21.45	0	0	6	19	4	17	21	0	0	67
9 Oct.	21.20–21.50	0	0	67	2	25	13	99	0	0	206
		11 Douglas Road									
27 May	21.35–22.05	0	0	5	32	0	8	54	0	0	99
		13 Douglas Road									
28 May	22.15–22.45	0	0	2	5	1	1	71	0	0	80
		4 Douglas Road, north side									
11 May	21.45–22.15	0	17	171	24	135	6	39	0	0	392
12 Oct.	20.50–21.20	0	0	189	1	253	4	46	0	0	493
		6 Douglas Road									
28 Apr.	21.30–22.00	0	8	193	4	84	1	25	0	0	315
12 July	22.20–22.50	0	0	53	5	56	0	84	0	0	198
14 Sept.	22.50–23.20	0	0	195	2	57	3	52	0	0	309
		8 Douglas Road									
9 May	22.10–22.40	0	2	116	8	54	2	34	0	0	216
		10 Douglas Road									
1942: 8 Apr.	20.30–21.00	0	0	146	6	39	0	33	0	0	224
27 Apr.	20.50–21.20	0	0	4	1	2	5	25	0	0	37
19 May	21.30–22.00	0	1	99	7	44	4	34	0	0	189
16 July	22.10–22.40	1	0	45	17	23	2	69	0	0	157
10 Aug.	21.50–22.20	0	0	187	12	45	7	127	0	0	378
24 Sept.	20.10–20.40	0	0	234	12	55	11	146	0	0	458
5 Oct.	20.15–20.45	0	0	45	7	23	1	24	0	0	100
6 Oct.	20.15–20.45	0	0	268	5	73	12	79	0	0	437
25 Nov.	20.15–20.45	0	0	307	4	77	5	76	0	0	469
8 Dec.	19.00–19.30	0	0	305	5	97	4	64	0	0	475
1943: 13 Jan.	21.45–22.15	0	0	128	6	20	1	45	0	0	200
16 Jan.	20.15–20.45	0	0	219	8	25	1	52	0	0	305
28 Jan.	20.20–20.50	0	1	315	13	67	5	60	0	0	461
23 Feb.	19.20–19.50	0	0	114	2	22	0	59	0	0	197
24 Mar.	19.45–20.15	0	0	110	6	35	13	44	0	0	208
27 Apr.	21.00–21.30	0	1	192	36	85	4	48	0	1	367
26 May	21.35–22.05	0	1	157	29	57	16	77	0	0	337

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
				10 Douglas Road (*continued*)							
1943; 24 June	21.55–22.25	0	0	32	24	13	3	145	0	0	217
24 July	22.15–22.45	1	0	78	11	22	2	138	0	0	252
26 Aug.	22.10–22.40	0	0	152	7	45	8	98	0	0	310
28 Sept.	22.30–23.00	0	0	247	2	110	13	82	0	0	454
28 Oct.	19.30–20.00	0	0	225	2	87	6	33	0	0	353
27 Nov.	20.20–20.50	0	0	147	2	11	7	59	0	0	226
				12 Douglas Road							
10 May	22.15–22.45	0	1	134	7	36	7	10	0	0	195
				14 Douglas Road							
7 May	21.05–21.35	0	1	34	13	12	24	28	0	0	112
8 Oct.	20.45–21.15	0	0	130	1	36	31	87	0	0	285
				16 Douglas Road							
6 May	22.10–22.40	0	0	35	22	2	71	10	0	0	140
12 July	22.55–23.25	0	0	22	25	7	33	55	0	0	142
27 Aug.	22.30–23.00	0	0	51	6	31	100	65	0	0	253
1 Oct.	22.00–22.30	0	0	146	4	30	86	42	0	0	308
				18 Douglas Road							
11 May	21.10–21.40	0	0	21	29	2	42	17	0	1	112
13 Oct.	20.45–21.15	0	0	36	1	5	32	50	0	0	124
				20 Douglas Road							
10 May	21.30–22.00	2	1	75	11	26	6	27	0	1	149
				22 Douglas Road							
6 May	21.30–22.00	1	0	6	22	86	6	30	0	0	151
8 Oct.	21.25–21.55	0	1	70	2	205	8	68	0	0	354
				Luton Road, west side, Moreton End School							
21 June	22.10–22.40	1	2	6	109	37	4	72	0	1	232
13 Sept.	21.35–22.05	0	0	62	44	78	12	104	0	0	300
				Luton Road, Vane Lodge							
1942: 8 Apr.	21.10–21.40	3	0	120	5	12	1	13	0	0	154
27 Apr.	21.30–22.00	8	0	30	9	17	3	20	0	0	87
19 May	22.15–22.45	5	0	76	18	48	8	20	0	0	175
16 July	22.45–23.15	6	0	10	35	9	3	50	0	0	113
10 Aug.	22.30–23.00	9	0	81	35	22	23	159	0	0	329
24 Sept.	20.50–21.20	2	0	86	13	27	28	111	0	0	267
6 Oct.	20.55–21.25	1	0	127	9	45	23	84	0	0	289
26 Nov.	19.05–19.35	3	0	151	7	61	6	42	0	0	270
9 Dec.	20.35–21.05	4	0	130	13	56	7	33	0	0	243
1943: 29 May	22.15–22.45	5	0	28	38	39	21	31	0	0	162
				60 Luton Road, east side							
28 Apr.	20.55–21.25	0	1	30	0	2	22	28	0	0	83
12 Sept.	22.15–22.45	0	0	58	0	2	43	78	0	0	181
				62 Luton Road							
9 June	21.45–22.15	0	0	4	0	2	16	143	0	3	168
				64 Luton Road							
17 June	21.55–22.25	0	0	3	0	1	13	82	0	5	104
				66 Luton Road							
17 June	22.30–23.00	0	0	7	0	2	32	83	0	1	125
				68 Luton Road							
15 June	21.50 22.20	0	0	15	3	6	59	100	0	0	183

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
				70 Luton Road							
1943: 20 June	22.10–22.40	0	0	3	0	1	58	124	0	1	187
				72 Luton Road							
19 June	21.55–22.25	0	0	23	0	2	34	93	0	2	154
				74 Luton Road							
19 June	22.30–23.00	0	0	11	0	4	27	26	1	13	82
				76 Luton Road							
15 June	22.30–23.00	0	0	16	0	1	26	13	3	23	82
				5 Moreton End Lane, back garden							
See Appendix 1											
				7 Moreton End Lane, back garden							
1942: 2 Jan.	20.45–21.15	5	4	57	13	35	4	41	0	0	159
13 Mar.	21.10–21.40	2	1	32	5	9	0	16	0	0	65
12 Apr.	20.30–21.00	6	1	45	18	18	1	63	0	0	152
13 Apr.	3.30– 4.00	2	2	66	12	15	2	26	0	0	125
25 Apr.	20.30–21.00	2	1	30	21	11	3	78	0	0	146
11 May	21.45–22.15	9	4	65	27	48	8	95	0	7	263
4 June	22.40–23.10	6	3	13	38	23	4	93	0	1	181
12 July	22.10–22.40	3	1	8	30	21	2	52	0	1	118
28 July	22.10–22.40	2	0	13	29	17	5	73	0	0	139
7 Aug.	22.15–22.45	7	0	10	23	19	5	109	0	2	175
21 Sept.	20.05–20.35	4	0	50	22	79	20	126	0	0	301
12 Oct.	20.55–21.25	8	0	56	18	73	18	95	0	4	272
3 Nov.	20.20–20.50	3	0	105	5	58	13	44	0	0	228
6 Dec.	20.40–21.10	3	0	164	10	56	7	39	0	0	279
1943: 18 Jan.	18.45–19.15	3	0	55	16	17	0	63	0	1	155
31 Jan.	19.30–20.00	9	0	83	26	41	1	64	0	0	224
25 Feb.	20.05–20.35	7	0	72	20	45	11	71	0	0	226
24 Mar.	20.30–21.00	12	2	82	15	61	11	45	0	2	230
24 Apr.	20.45–21.15	5	0	54	31	31	7	52	0	1	181
25 May	21.30–22.00	13	1	34	73	39	15	46	0	1	222
27 June	22.00–22.30	3	0	5	39	27	0	145	0	1	220
23 July	21.55–22.25	11	0	3	37	25	3	145	0	2	226
27 Aug.	21.10–21.40	6	0	6	11	13	11	54	0	0	101
27 Sept.	22.00–22.30	0	0	38	1	39	6	42	0	1	127
25 Oct.	19.15–19.45	0	0	65	2	102	7	38	0	0	214
28 Nov.	18.30–19.00	2	1	44	8	66	2	36	0	0	159
				9 Moreton End Lane, back garden							
1942: 4 Jan.	18.30–19.00	34	6	25	23	5	10	45	0	2	150
14 Mar.	19.50–20.20	18	0	25	20	2	2	28	0	0	95
26 Apr.	20.50–21.20	8	0	2	17	0	9	46	0	0	82
12 May	22.00–22.30	24	1	12	33	6	13	68	0	1	158
12 July	22.40–23.10	6	0	0	27	1	14	12	0	3	63
11 Aug.	22.10–22.40	8	0	7	38	3	34	44	0	0	134
21 Sept.	20.50–21.20	6	0	20	29	13	100	112	0	0	280
1 Oct.	21.15–21.45	3	1	56	12	34	83	74	0	3	266
14 Oct.	20.55–21.25	5	1	64	13	37	91	75	0	1	287
4 Nov.	20.40–21.10	6	1	82	19	10	14	49	0	0	181
20 Nov.	22.20–22.50	5	0	95	13	40	26	28	0	0	207
6 Dec.	21.20–21.50	8	1	109	12	33	33	32	0	0	228
1943: 17 Jan.	19.15–19.45	10	0	54	6	9	4	22	0	0	105
29 Jan.	19.05–19.35	25	1	56	15	12	13	45	0	0	169
22 Feb.	19.25–19.55	6	0	18	4	5	4	34	0	0	71
19 Mar.	21.15–21.45	13	0	16	9	9	5	22	0	1	75

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
		9 Moreton End Lane, back garden (*continued*)									
1943: 3 Apr.	20.10–20.40	19	4	60	25	14	31	26	0	1	180
8 May	21.05–21.35	20	0	22	46	5	25	22	0	4	144
6 June	22.10–22.40	17	1	5	47	3	21	50	0	2	146
10 July	22.00–22.30	14	0	0	32	0	18	110	0	0	174
5 Aug.	21.50–22.20	7	0	3	34	3	25	118	0	1	191
8 Sept.	21.30–22.00	7	0	2	16	7	36	97	0	0	165
7 Oct.	21.45–22.15	3	0	82	7	33	38	74	0	2	239
4 Nov.	19.25–19.55	2	0	81	3	40	27	37	0	0	190
26 Dec.	18.20–18.50	4	1	47	3	44	15	25	0	1	140
		11 Moreton End Lane, back garden									
1942: 7 Apr.	20.10–20.40	10	0	12	24	5	3	92	0	0	146
26 Apr.	21.30–22.00	4	0	0	12	0	1	50	0	0	67
13 May	21.40–22.10	5	1	6	39	7	0	67	0	0	125
13 July	22.15–22.45	3	0	1	44	1	0	12	0	0	61
11 Aug.	22.40–23.10	1	0	0	63	1	12	90	0	0	167
23 Sept.	21.45–22.15	3	0	1	36	11	19	165	0	0	235
30 Sept.	21.30–22.00	1	0	14	19	21	38	106	0	1	200
15 Oct.	20.50–21.20	6	0	11	39	17	19	94	0	0	186
5 Nov.	21.00–21.30	0	2	48	18	26	20	45	0	0	159
7 Dec.	21.00–21.30	1	0	37	24	32	20	43	0	0	157
1943: 18 Jan.	19.25–19.55	1	0	12	29	3	3	21	0	0	69
31 Jan.	18.55–19.25	2	0	33	55	15	11	38	0	0	154
25 Feb.	20.45–21.15	0	1	10	18	14	4	22	0	0	69
30 Mar.	21.00–21.30	1	0	7	12	5	4	18	0	0	47
25 Apr.	20.50–21.20	6	0	4	26	14	7	14	0	1	72
25 May	22.05–22.35	7	0	2	25	2	4	36	0	0	76
27 June	22.40–23.10	6	0	0	48	0	6	163	0	1	224
23 July	22.35–23.05	3	0	1	41	2	3	73	0	2	125
27 Aug.	21.45–22.15	2	0	2	24	5	15	61	0	0	109
1 Oct.	21.15–21.45	0	0	5	18	20	34	74	0	1	152
25 Oct.	20.25–20.55	2	0	21	10	20	17	75	0	1	146
28 Nov.	22.05–22.35	3	0	15	2	8	5	19	0	0	52
		13 Moreton End Lane, back garden									
1942: 18 Mar.	20.55–21.25	13	0	9	26	7	0	74	0	0	129
13 Apr.	20.10–20.40	10	0	6	33	3	0	65	0	0	117
13 May	21.05–21.35	11	2	3	25	4	0	42	0	0	87
12 June	22.45–23.15	18	0	2	56	2	0	26	0	0	104
15 July	22.45–23.15	4	0	0	31	0	0	27	0	0	62
12 Aug.	22.55–23.25	17	0	0	34	0	0	47	0	1	99
22 Sept.	21.00–21.30	13	0	0	21	1	0	81	0	0	116
15 Oct.	20.10–20.40	12	0	9	19	5	0	56	0	0	101
6 Nov.	18.50–19.20	14	0	19	15	6	2	53	0	0	109
7 Dec.	20.25–20.55	2	0	22	20	21	1	46	0	0	112
1943: 13 May	21.10–21.40	8	0	3	50	4	2	24	0	0	91
18 Oct.	20.35–21.05	4	0	17	2	20	1	36	0	0	80
		15 Moreton End Lane, back garden									
1942: 4 Jan.	19.10–19.40	66	7	3	20	9	2	45	0	0	152
14 Mar.	20.30–21.00	28	0	4	20	4	0	39	0	1	96
13 Apr.	20.45–21.15	21	0	2	24	3	0	77	0	1	128
12 May	21.25–21.55	35	0	2	23	4	0	39	0	1	104
12 June	22.10–22.40	13	0	1	54	0	0	53	0	2	123
15 July	22.10–22.40	12	0	0	33	0	0	31	0	0	76
12 Aug.	22.20–22.50	23	0	0	55	1	0	45	0	5	129
22 Sept.	22.20–22.50	30	0	1	39	0	0	58	0	2	130
14 Oct.	20.15–20.45	37	0	4	19	6	1	50	0	3	120
6 Nov.	19.25–19.55	40	0	18	27	2	0	42	0	1	130
7 Dec.	19.15–19.45	13	1	22	32	14	0	34	0	0	116
22 Dec.	20.30–21.00	37	1	22	27	2	0	12	0	0	101

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min. *Arion ater*	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
		15 Moreton End Lane, back garden (*continued*)									
1943: 17 Jan.	21.00–21.30	32	1	12	31	11	0	52	0	0	139
29 Jan.	19.40–20.10	67	2	28	40	9	2	58	0	3	209
22 Feb.	20.25–20.55	10	0	4	8	4	0	22	0	0	48
19 Mar.	20.20–20.50	36	0	3	26	1	0	39	0	2	107
3 Apr.	20.45–21.15	69	1	16	62	5	2	40	0	1	196
8 May	21.40–22.10	34	1	9	50	6	1	13	0	5	119
6 June	21.35–22.05	102	2	3	110	4	0	19	0	1	241
10 July	22.35–23.05	34	0	0	58	0	0	15	0	3	110
5 Aug.	22.30–23.00	20	0	0	43	0	1	55	0	1	120
8 Sept.	22.05–22.35	13	0	1	20	0	1	87	0	0	122
7 Oct.	22.40–23.10	8	0	13	16	6	0	40	0	0	83
11 Nov.	20.30–21.00	17	2	23	28	6	3	41	0	0	120
26 Dec.	19.00–19.30	20	0	27	31	10	1	41	0	0	130
		17 Moreton End Lane, back garden									
1942: 22 Oct.	20.20–20.50	5	0	35	14	9	0	59	0	2	124
7 Nov.	18.55–19.25	3	0	51	9	2	0	45	0	1	111
		19 Moreton End Lane, back garden									
20 Oct.	20.15–20.45	7	0	30	15	17	0	38	0	0	107
22 Oct.	19.15–19.45	7	0	30	11	48	1	60	0	0	157
		21 Moreton End Lane, back garden									
29 Oct.	19.15–19.45	1	3	123	5	38	3	92	0	0	265
7 Nov.	20.15–20.45	1	0	87	10	21	3	73	0	0	195
9 Dec.	19.15–19.45	0	0	80	5	31	1	54	0	0	171
1943: 18 Oct.	19.10–19.40	0	0	107	6	39	0	61	0	0	213
		29 Moreton End Lane, back garden									
15 Oct.	20.30–21.00	0	0	46	5	3	22	37	0	0	113
		33 Moreton End Lane, back garden									
16 Oct.	20.30–21.00	4	0	60	18	42	17	82	0	0	223
		37 Moreton End Lane, back and front gardens									
6 Oct.	22.00–22.30	1	0	12	0	13	4	15	0	1	46
12 Oct.	21.45–22.15	0	0	5	2	27	5	14	0	0	53
		41 Moreton End Lane, back and front gardens									
14 Oct.	21.10–21.40	0	0	4	1	3	4	8	0	0	20
		47 Moreton End Lane, back garden									
15 Oct.	21.10–21.40	2	2	33	0	4	0	18	0	0	59
		5 Moreton End Lane, front garden									
1942: 9 Apr.	21.15–21.45	3	4	87	31	27	2	32	0	0	186
21 July	22.15–22.45	1	2	20	29	21	2	67	0	0	142
7 Aug.	22.50–23.20	1	3	46	20	65	5	72	0	0	212
28 Sept.	20.30–21.00	0	0	88	11	52	4	67	0	0	222
16 Oct.	20.45–21.15	0	0	114	16	97	2	60	0	0	289
15 Nov.	18.40–19.10	5	5	84	9	70	5	57	0	0	235
13 Dec.	19.25–19.55	4	5	121	18	82	1	57	0	0	288
		7 Moreton End Lane, front garden									
10 Apr.	20.10–20.40	6	3	87	23	30	2	51	0	0	202
21 July	22.50–23.20	2	1	3	25	0	0	44	0	1	76
8 Aug.	21.40–22.10	4	0	14	35	13	1	86	0	0	153
28 Sept.	21.10–21.40	3	0	35	12	23	3	56	0	0	132
17 Oct.	20.30–21.00	6	0	43	13	24	7	60	1	1	155
13 Dec.	20.25–20.55	4	0	68	12	21	13	44	0	0	162
		9 Moreton End Lane, front garden									
13 Oct.	19.20–19.50	0	0	6	6	5	10	90	0	0	117
14 Dec.	19.15–19.45	0	0	43	4	9	3	43	0	0	102

APPENDIX 2 (*continued*)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min.									
		Arion ater	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
		11 Moreton End Lane, front garden									
1942: 10 Apr.	20.45–21.15	2	0	56	5	8	0	67	0	2	140
22 July	22.30–23.00	0	0	1	16	0	0	17	0	0	34
8 Aug.	22.10–22.40	2	0	10	16	3	0	57	0	0	88
19 Oct.	19.20–19.50	3	0	23	13	7	7	109	0	0	162
14 Dec.	20.45–21.15	0	0	104	7	17	0	33	0	0	161
		13 Moreton End Lane, front garden									
11 Apr.	19.55–20.25	14	0	11	18	7	0	72	0	0	122
23 July	23.00–23.30	2	0	0	29	2	0	60	0	0	93
13 Aug.	22.00–22.30	2	0	2	15	0	0	92	0	0	111
19 Oct.	20.20–20.50	8	1	4	12	10	2	80	0	1	118
15 Dec.	19.10–19.40	6	0	32	15	10	2	38	0	0	103
		15 Moreton End Lane, front garden									
11 Apr.	20.30–21.00	29	4	21	19	8	0	67	0	0	148
23 July	22.20–22.50	4	0	0	31	1	0	43	0	0	79
13 Aug.	21.25–21.55	2	0	0	27	0	0	74	0	0	103
18 Oct.	20.20–20.50	12	0	6	10	13	1	62	0	0	104
15 Dec.	20.30–21.00	16	2	23	12	14	0	36	0	0	103
		3 Moreton Place, south side									
1943: 1 May	21.05–21.35	10	0	113	32	61	28	14	0	2	260
		5 Moreton Place									
12 May	22.00–22.30	35	0	32	52	11	63	62	0	4	259
6 Oct.	22.40–23.10	8	0	88	6	57	71	85	0	0	315
		7 Moreton Place									
12 May	21.25–21.55	10	0	6	56	1	17	22	0	2	114
		4 Moreton Place, north side									
29 May	21.35–22.05	15	2	28	103	25	4	25	1	6	209
		6 Moreton Place									
1 May	21.50–22.20	18	7	51	40	28	12	37	0	1	194
5 Oct.	21.30–22.00	1	0	80	6	53	40	58	0	0	238
		43 Ox Lane, north side									
13 July	22.10–22.40	0	0	1	0	0	1	21	0	0	23
11 Oct.	21.20–21.50	0	1	138	0	45	1	12	0	0	197
		47 Ox Lane									
13 July	22.50–23.20	0	0	1	4	1	0	14	0	0	20
11 Oct.	22.30–23.00	0	0	58	0	28	2	22	0	0	110
		Langdale, Salisbury Avenue									
1942: 14 Apr.	21.00–21.30	1	1	28	1	12	0	46	0	0	89
		23 Station Road									
4 Apr.	21.05–21.35	0	0	110	0	3	0	6	0	0	119
19 July	22.10–22.40	0	0	15	0	0	0	10	0	1	26
		Brookfield, Townsend Lane									
3 Jan.	23.00–23.30	4	6	28	1	3	0	11	0	0	53
3 Apr.	23.34–29.00	0	0	53	2	4	0	14	0	0	73
25 Apr.	22.30–23.00	0	0	5	2	2	0	17	0	0	26
14 May	22.20–22.50	6	1	34	13	0	0	36	0	1	91
11 July	22.30–23.00	0	1	3	12	0	0	27	0	0	43
9 Aug.	22.30–23.00	0	0	2	8	0	0	61	0	0	71
26 Sept.	22.15–22.45	0	0	11	1	0	0	37	0	1	50
16 Oct.	23.00–23.30	1	0	61	0	3	1	30	0	0	96
26 Nov.	22.30–23.00	0	1	82	0	4	0	15	0	0	102
12 Dec.	00.05–00.35	0	1	84	1	3	0	19	0	0	108

APPENDIX 3. *Collections of active slugs in places other than gardens after dark*, 1942

(The collection made on 15 Mar. at Crouch Hall lasted 60 min., the figures for this collection have been adjusted so as to be comparable with all the other entries, i.e. 30 min. collections.)

Date	Time of collection G.M.T.	No. of slugs obtained in 30 min.									
		Arion ater	*Arion circumscriptus*	*Arion hortensis*	*Arion subfuscus*	*Milax gracilis*	*Milax sowerbyi*	*Agriolimax reticulatus*	*Limax flavus*	*Limax maximus*	Total
Vegetable patch at 22 Douglas Road											
16 Mar.	21.15–21.45	0	0	51	2	36	0	7	0	0	96
Vegetable patch at 24 Douglas Road											
19 Dec.	20.40–21.10	0	0	196	1	144	1	27	0	0	369
20 Dec.	21.05–21.35	0	0	175	2	66	1	25	0	0	269
21 Dec.	20.20–20.50	2	0	302	0	130	2	19	0	0	455
Vegetable patch at Director's House, West Common											
17 Mar.	21.10–21.40	0	5	105	0	29	0	9	0	0	148
Vegetable patch at 14 The Pleasance											
30 Mar.	20.30–21.00	0	0	66	5	193	5	44	0	0	313
30 Mar.	21.30–22.00	0	0	41	4	142	0	18	0	0	205
28 Apr.	20.45–21.15	0	0	0	1	5	0	5	0	0	11
15 May	21.15–21.45	0	1	34	11	173	1	33	0	0	253
22 May	21.45–22.15	0	0	50	4	253	1	19	0	0	327
Crouch Hall, Redbourn (collections made by J. W. Weil)											
15 Mar.	19.30–20.30	1	0	33	1	0	0	18	0	0	53
18 Mar.	19.15–19.45	1	0	75	0	0	0	33	0	2	111
12 Apr.	—	2	0	18	0	0	0	57	0	0	77
Potato patch at 5 Moreton End Lane											
9 June	22.10–22.25	0	0	3	6	8	0	3	0	0	20*
28 July	21.30–22.00	0	0	25	11	39	0	13	0	0	88
4 Sept.	22.45–23.15	0	1	48	18	130	12	43	0	0	252
6 Sept.	22.00–22.30	0	0	28	4	71	6	13	0	0	122
13 Oct.	20.30–21.00	1	3	44	8	33	2	32	0	0	123
20 Oct.	20.50–21.20	0	1	37	4	57	1	6	0	0	106
8 Dec.	22.00–22.30	0	0	56	12	102	10	41	0	1	222
Allotment 1											
17 Mar.	20.35–21.05	0	6	51	0	12	0	161	0	0	230
Allotment 2											
31 Mar.	20.00–20.30	3	0	24	0	2	0	185	0	0	214
Allotment 3											
31 Mar.	20.35–21.05	0	0	57	0	18	0	73	0	0	148
Field: Harpenden potato club, pre-planting											
7 Apr.	21.00–21.30	0	0	1	1	0	0	40	0	0	42
Glasshouse											
2 Apr.	21.40–22.10	0	0	1	0	2	0	11	0	0	14

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* Abandoned after 15 minutes