MORTALITY AMONG VOLES (*MICROTUS AGRESTIS*) AT LAKE VYRNWY, MONTGOMERYSHIRE IN 1936–9

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[Plates 36 and 37]

CONTENTS

Lake Vyrnwy is a reservoir surrounded by many types of habitat including newly afforested areas suitable for field voles. Other areas form ecological barriers between these populations. The purpose of the present inquiry was to discover the causes of the periodic fluctuations in numbers which occur, often simultaneously, among such vole populations.

Several separate vole populations reached peak densities in 1937 and declined in 1938, in which year numbers were at a peak in most of the younger plantations. During the peak breeding season of 1937 there was an excessive juvenile mortality before August. The survival rate of the young then improved and the old animals became scarce, as they usually do at this time of year. All age groups ceased breeding in August 1937 and the survivors did not breed next spring. By contrast, populations which were at peak densities in 1938 continued breeding from May to October and the survivors bred again in 1939, though no recovery in numbers was brought about. Both in May 1937 and May 1938 high numbers were associated with unusually high body weights.

A sample population was studied by marking and recapturing the animals. Most spent their lives within an area of 10 to 15 yd. diameter. Both in September 1936 and 1937 there were about 300 young voles per acre. During 1938 survival was very poor from January onwards, particularly among the males.

During the time of their almost complete disappearance in 1938 or 1939 voles were not subjected to any known environmental conditions likely to have caused excessive mortality. The hypothesis is therefore advanced that death was primarily due to adverse conditions to which the parents were

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subjected in the previous breeding season. It is inferred (*a*) that the high juvenile mortality at that time was a symptom of severe intraspecific strife, (*b*) that intraspecific strife had deleterious effects, probably upon the hormone balance of the females, so that (*c*) their young suffered defects which reduced the longevity of those which survived the breeding season, and also (*d*) impaired their ability to produce a normal generation.

Peak numbers were reached simultaneously over wider areas than seems likely by chance alone. It is argued that this must have occurred through some interaction of the independent biological units with their common weather system. Competition for space, the process believed to control excessive increase, is shown to be a possible means through which environmental changes may cause further variations in mortality rates. A sufficiently variable physical environment should thus tend to eliminate differences in density between populations and so to effect a regional synchrony of their cycles.

It seems likely that periodic mortality in the North American snowshoe hare is also a delayed result of intraspecific strife. This extension of the hypothesis has implications which are at variance with some of the existing views about cycles in birds and mammals.

1. INTRODUCTION

The observations in the present paper were made during an inquiry into fluctuations in numbers of the field vole, *Microtus agrestis*. This species is one of a group of mammals and birds which fluctuate at fairly regular intervals between extremes of high and low population density. The periodicity in the vole and lemming (*Lemmus* spp., *Dicrostonyx* spp.) is about 4 years; certain animals in North America, including the snowshoe hare (*Lepus americanus*) and ruffed grouse (*Bonasa umbellus*) and their predators, have an approximately 10-year cycle. Elton (1942) describes the research which led to the present study and helped me plan it. In 1936 epidemic disease seemed a likely explanation of periodic decrease; accordingly, by the time war put an end to this work, some 2000 voles from Lake Vrynwy had been examined by Dr A. Q. Wells of the Sir William Dunn School of Pathology, Oxford. Vole tuberculosis was common (Wells 1946), but neither it nor any other infectious disease seemed to account for a widespread mortality in 1938 and again in 1939. Nor could the almost complete disappearance of voles be explained by peculiar conditions in the contemporary environment, for example, bad weather or absence of food. On the contrary, it appeared that the high death-rate was a result of conditions preceding the birth of these individuals. The most important cause of mortality seems to have been a form of mutual strife which had physiological effects transmissible to the next two generations. The present paper shows how this hypothesis was derived, and, though it is not verified, some progress has been made along these new lines of inquiry. The data, though much condensed, have been given in sufficient detail to permit a careful scrutiny. Certain conclusions from §§ 3 and 4 are applied in § 5 and Appendix 2, and the inferences of more general interest are developed in § 6.

Lake Vyrnwy, 140 miles from Oxford, is the nearest area which is big enough and known to be suitable for a study of vole cycles. Trace and trap-line indices for 1933–5 (mostly obtained by Mr A. D. Middleton, table 1) showed that voles declined in number before the New Year 1934 after high autumn numbers in 1933. Mortality in the spring before this main decline is discussed by Findlay & Middleton (1934). After April 1935 no visits were paid until September 1936, when voles were again abundant. In parts of the estate they died off once more in 1938; elsewhere they remained abundant until a year later.

Field work consisted of regular trapping, using local help, with visits from Oxford about every month, principally to study a marked population. Both methods gave information about numbers and growth-rates; the regular samples were examined by Dr Wells for disease and number of embryos, and the marking study explained some of the population processes. The main items of field work covered the following periods:

previous studies	Autumn 1932 to April 1935
study of one area (Glasgwm, figure 1):	
for relative abundance	Sept. 1936 to Aug. 1939
for absolute abundance	April 1937 to Aug. 1938
general survey of relative abundance	May 1938 to Aug. 1939

Animals trapped during the studies of relative abundance provided material for pathological examination.

Lake Vyrnwy is an artificial reservoir supplied from three valleys: Vyrnwy (18000 acres), Marchnant (1800 acres) and Cownwy (3200 acres). The estate belongs to Liverpool Corporation and includes 2100 additional acres below the drainage areas. New conifer plantations were made in most years up to 1936; figure 1 shows the distribution of the larger areas which were young enough to be good vole habitat in 1936–9. Ground vegetation varied from nearly pure stands of one of several species to complex communities of grasses, rushes and 'weeds'. These plants die after 6 to 10 years of tree growth and the habitats become unsuitable for voles. There were few voles outside the plantations (area *B*4, table 3; Appendix 1*a*), the main colonies thus being dispersed ecological units. Plates 36 and 37 explain these habitat conditions. The hills are typical rough grazing; plate 36 shows the vegetation 3 to 5 years after the exclusion of sheep (a ruined crofter's cottage is also seen), and plate 37 shows the dense stands of conifer eventually produced.

The first area studied was a small valley called Glasgwm, 1030 ft. above sea-level. Sitka and Norway spruce, planted in 1924–6, had mostly failed, and the southern half of Glasgwm was open and parklike in 1936–9. The chief grasses were *Molinia caerulea* (L.) Moench and *Deschampsia caespitosa* (L.) Beauv. with stretches of less tussocky types such as *Holcus* spp. The northern half of the valley was of a totally different character, most of it being a sphagnum bog. Surrounding areas had been successfully planted with conifers in 1924–6 and Glasgwm had become completely isolated from other vole habitats. This was the site of the marking study and also the source of all voles examined until May 1938. Field trips were less frequent after that, but a general survey of abundance (§ 2) was undertaken in the following areas (figure 1).

A. *Marchnant valley* (*including Glasgwm*). Most of the upper part of the valley was planted in 1920–9 except for hill tops over 1500 ft. which were grazed by sheep. Several separate patches of young trees had been replanted among older ones which had failed, but except for Glasgwm (about 35 acres) no areas were larger than 1 to 2 acres. The lower part, a small proportion of the whole valley, is grazed, cultivated or occupied by houses.

B. *Garth-bwlch* (352 *acres*). These young plantations, south-east of the lake, were about 2 miles from Glasgwm across the Vyrnwy River. The trees were planted in 1933 (*B*1, Grwn-oer, 46 acres), 1934 (*B*3, Tan-y-caeau, 77 acres) and 1936 (*B*2, Garth-bwlch house, 229 acres), the land having been grazed until the time of planting. The fields outside these plantations have been called area *B*4.

C. *Rhyd'r-yddan* (169 *acres*). This plantation, about 2 miles up the Cownwy valley, was separated from others by groups of scrub oak and birch, rough grazing or arable land. The site had been grazed until the winter of 1935.

D. *Allt Forgan*. A number of small plantations along the north-west arm of the lake were taken over from sheep or hay in 1933 or 1934. Although most were close together, near *D*1, these plantations were separate ecological units lying between points 981221 and 960243 and have been grouped for convenience only.

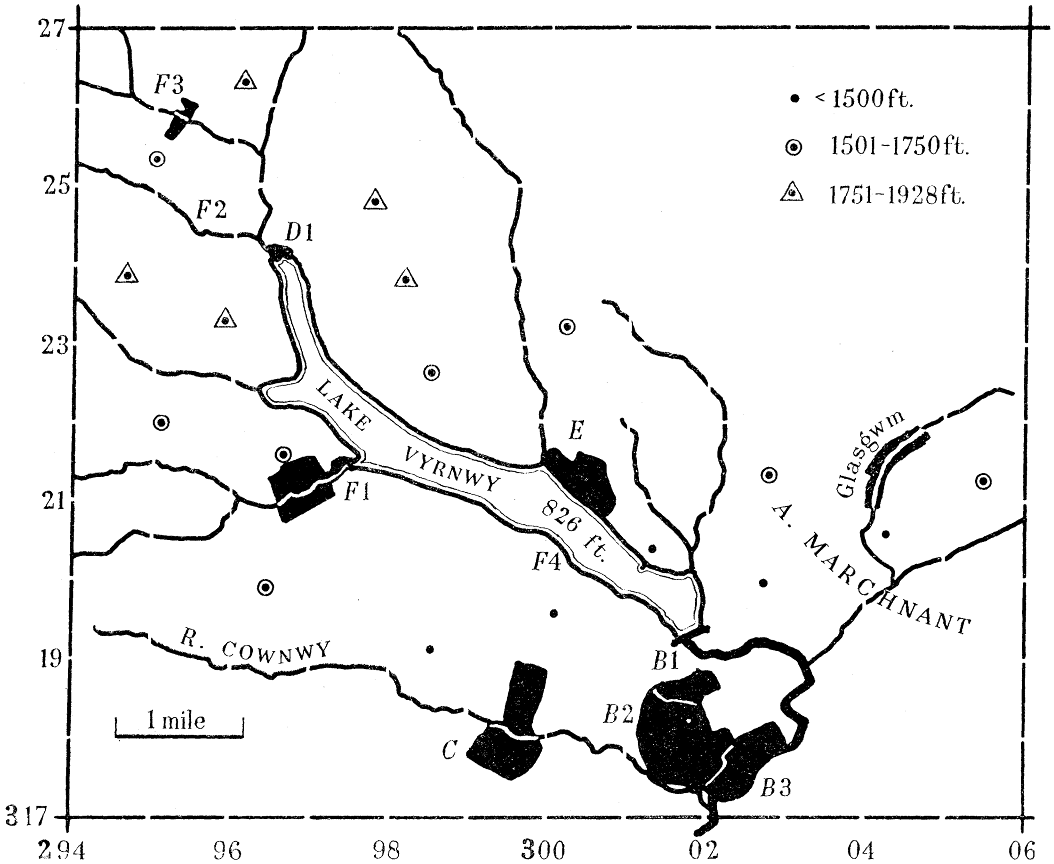

FIGURE 1. Distribution of the main vole habitats at Lake Vyrnwy. The smaller areas *F*2, *F*4 and most of those in groups *A* and *D* are not plotted (see text and table 3). The map is based on the 1947 edition of the 1 in. Ordnance Survey and shows the principal streams and hilltops and the kilometre divisions of the National Grid. (Example: 33/017192 is the full reference to the outlet of the lake.) The Marchnant and Cownwy waters are piped into the lake.

E. *Fron-gôch* (88 *acres*). Several hayfields on the north-east side of the lake were planted with trees in 1933.

F. *Miscellaneous areas*. Four areas planted in 1932–4 were completely isolated from all others. Welsh names have been avoided in the remainder of the text with the exception of the two most frequently needed. These are pronounced Glass-coom and Marchnant (ch as in 'loch').

2. GENERAL ABUNDANCE

From September 1936 to May 1938 surveys were made to see if results from intensive work on two small plots (§ 5) were representative of the rest of Glasgwm. As will be shown, a synchronous peak and decline did indeed occur all over this area. From May 1938 other populations were examined to see if that on Glasgwm was a fair sample from those on the estate as a whole. This was not so, some population trends being 1 year behind.

In order to obtain this type of information for a wide enough area the field methods had to be quick and simple. A supply of corpses was also needed. Known methods which fulfil these requirements are not precise, and the data so obtained cannot be assumed to vary in strict proportion to the density of the populations. Differences in seasonal activity, for example, affect the trapping results. However, the changes in population density most relevant to this inquiry were so great that their occurrence, if not their magnitude, could be established quite simply. The trace index and 5-day trap line were used as in previous studies (Elton 1942), and voles for pathological examination were trapped on a standard system which also gave a rough measure of abundance.

(*a*) *Miscellaneous methods and results*

Trace index. Two parallel lengths of Glasgwm were examined for the presence or absence of fresh droppings. Two series usually of fifty plots (2 × 0·5 yd.) were searched at 20 yd. intervals starting at the south of Glasgwm. Table 1 shows that most of the ground was occupied during both winters 1936–7 and 1937–8, with a decline to about 50 % in the intervening summer and to 2 % by May 1938.

TABLE 1. INDICES OF ABUNDANCE 1933–9

Numbers of voles and common shrews taken in 5 days in fifty break-back traps 5 yd. apart. Also percentages of sample areas in which fresh vole droppings were found.

Marchnant valley (0319)*

	1933							1934			1935
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Apr.	Aug.	Sept.	Apr.
no. of voles	38	35	42	71	29	13	6	3	2	.	2
no. of shrews	1	0	1	4	0	0	1	0	1	.	1
frequency of droppings (%)	30	.	.	71	.	.	.	4	.	1	0

Glasgwm (0421)

	1936		1937							1938			
	Sept.	Dec.	Mar.	Apr.	May	June	Aug.	Sept.	Nov.	Jan.	Apr.	May	Aug.
date of trapping	1–5	.	.	20–24	.	.	17–21	.	.	.	19–23	.	16–20
no. of voles	69	.	.	65	.	.	75	.	.	.	28	.	1
no. of shrews	6	.	.	3	.	.	4	.	.	.	1	.	2
frequency of droppings (%)	.	90	80	.	53	46	84	82	77	74	.	2	.

	Glasgwm		area *B*2 (0117)		
	1939		1938	1939	
	Apr.	Aug.	Sept.	Apr.	Aug.
date of trapping	18–22	15–19	6–10	25–29	8–12
no. of voles	0	3	34	3	3
no. of shrews	7	31	10	6	14

* This and similar National Grid references are to the south-west corner of the square which includes most of the area studied.

Five-day trap line. Twice yearly trapping was carried out with fifty break-backs set 5 yd. apart and visited daily for 5 days. This work was carried out first by Mr Hugh Jones then by Mr George Clark. The line was about 400 yd. north of the weekly trap lines described below, the marking area being half-way between. Table 1 shows that voles were abundant before April 1938, that they were becoming scarce at that time and had not recovered by

August 1939. A second trap line was started in the autumn of 1938 on area *B*2 at the time of peak abundance there. Numbers were about half those taken at the corresponding stage on Glasgwm. By April 1939 numbers had declined relatively farther than they had in the previous year on Glasgwm.

Weekly trap lines. Sixteen parallel lines about 120 yd. long and 25 yd. apart were marked out across the south end of Glasgwm. In most weeks one of these lines was trapped by Jones or Clark with twenty-five live traps set 3 to 5 yd. apart. After the area had been trapped once it was covered again on the intermediate ground; then alternately on and between the original lines. From October 1937 break-back traps were also used; they were placed where the live traps had been the time before. Live trapping was then done without prebaiting (i.e. without allowing an interval for the animals to become familiar with the unset traps) and is now known to be inefficient (Chitty & Kempson 1949). Indeed, the break-backs gave better catches even though the sites had already been live trapped. The range of success with the live traps was 15 to 30 animals per 100 traps in each month from November 1936 to December 1937. The rate then fell to 8 % in January and February 1938 and to 2 % in March when the scheme stopped. The monthly catches in the break-backs fell as follows between October and March: 41, 33, 26, 21, 15, 7 %. The trace index gave no evidence that the trapping itself was responsible for this fall in numbers. The full data are deposited in the Bureau of Animal Population.

From the evidence just given and also from that in § 5 it is clear that voles on Glasgwm declined abruptly in the late winter and spring of 1938. Up to that time, however, there was no information about other parts of the estate.

(*b*) *One-day trap lines*

In May 1938, thanks to Clark's remarkable initiative, a much wider survey of abundance was begun. Where possible he used a standard line of twenty-five break-back traps spaced 10 yd. apart; this gave a higher catch per trap than at the 5 yd. spacing previously used (Appendix 1*b*). Parallel lines 25 yd. apart were set on subsequent occasions. Traps were generally set after lunch and lifted next day before 10 a.m. By trapping at this intensity a negligible proportion of the total population was affected. Altogether 191 trap lines were set involving over 5000 trap-nights. Comparatively few lines were set during the summer, as this was the least profitable time for the epidemiological study for which these lines were also designed.

Not all lines could be set in an identical way nor were all areas large enough for a succession of parallel lines. Also, as reasonably large numbers of corpses were needed a high proportion of the traps had to be filled; hence in the areas of high abundance catches were disproportionately limited by the number of free traps. Corrections are also necessary where the standard line was not used, and there are insufficient data to do this accurately (Appendix 1*b*). Furthermore, the distribution of the lines had to be planned to fit in with Clark's work for the Corporation rather than with any ideal sampling arrangements. For these reasons it has seemed best to present the individual data (tables 2 and 3) rather than a statistical analysis.

Area A (*Marchnant*). As already shown, voles were scarce on Glasgwm in the spring of 938, and much time was spent finding out if similar scarcity prevailed in the rest of the valley. This proved to be so, and only one area was found where more than four voles were taken per standard line after May. As these areas had not been studied before, it is not known that all were suitable for high numbers at any time. This may have been true of area *A* 5, but the majority of habitats appeared to be favourable; and since body weights resembled those on Glasgwm (§ 3) it is probable that a similar decline in numbers was occurring everywhere. There was no recovery during 1939.

Area B. Within these plantations voles were trapped in some numbers, not only in May 1938 but on nearly all occasions up to the following spring. The highest catch was eighteen adults in May 1938 and the majority of lines yielded six to ten animals until April 1939. From then onwards not more than four voles were caught in most lines.

Area C. Numbers caught in 1938 were similar to those in area *B*. Only one strictly comparable line was trapped in the 2 years, but voles were fairly abundant in a series of parallel lines from June 1938 to early April 1939 and scarcer in three lines after this. One line yielded thirty voles in June 1938 compared with six a year later; another line, in which ten had been caught in September 1938, yielded one the next June. (This line was the sole exception to the practice of allowing a year before retrapping.)

TABLE 2. NO. OF VOLES CAUGHT IN SUCCESSIVE YEARS IN THE SAME ONE-DAY TRAP LINES

Spacing 10 yd., or 5 yd. where shown by italics.

	May					June					July			Aug.
areas *A* 1–6	1	1	4	.	.	2	3	3	6	6	1	1	3	6
no. of traps	50	34	*25*	.	.	25	25	25	25	25	25	*25*	25	25
no. of voles: 1938	9	7	8	.	.	3	8	3	3	4	2	2	2	1
1939	1	0	0	.	.	0	4	2	0	1	2	1	0	2
areas *B* 1–3	1	2	2	3	3	2	.	.	.	.	.	.	.	.
no. of traps	25	*25*	25	25	25	25	.	.	.	.	.	.	.	.
no. of voles: 1938	13	14	10	18	4	12	.	.	.	.	.	.	.	.
1939	2	3	1	8	2	2	.	.	.	.	.	.	.	.
area *E*														
no. of traps	25	25	.	.	.	50	.	.	.	.	.	.	.	25
no. of voles: 1938	3	5	.	.	.	7	.	.	.	.	.	.	.	2
1939	3	6	.	.	.	1	.	.	.	.	.	.	.	1

Area D. An average of 6·5 voles was taken per line in October to December 1938 but after this the average was less than two. One line caught thirty-two animals in fifty traps in June 1938 and only three in thirty traps the next year.

Area E. Results for this area are not easy to interpret. In the spring and summer of 1938 the capture rate was similar to that in the Marchnant valley and definitely lower than in the other areas. Later on, however, better catches were made in area *E*, suggesting that if there had been a decline in numbers it was not of comparable severity. Figures for three lines set in both seasons suggest about equal scarcity in the 2 years without the downward trend in the Marchnant valley between May 1937 and May 1938 and elsewhere between 1938 and 1939. There are not enough data to decide by the criterion of body weight (§ 3) whether these animals resembled those in the areas of high or low abundance.

Miscellaneous areas (*F*). Few lines could be set in any of these areas, but the following results were given by three standard lines which were trapped in June of both years: area *F* 1 (5:0), *F* 3 (17:7), *F* 4 (11:3). Together with the data in table 3 these differences leave no doubt that vole populations were higher in 1938 than in 1939.

TABLE 3. NUMBER OF VOLES CAUGHT IN ONE-DAY LINES TRAPPED IN ONE SEASON ONLY

Spacing of traps: 10 yd., or 5 yd. where shown by italics.
No. used: 25 except where shown by brackets and detailed in bottom line.

1938

area	square	May				June				July		Aug.		Sept.		Oct.			Nov.		Dec.			
*A*1	0421	.	.	.	.	(0)	(2)	*(1)*	*1*	1	.	*0*	(0)	.	.	0	.	.	0	.	.	.	.	.
*A*2	0420	.	.	.	.	3	3	4	1	0	.	0	.	3	.	.	.	.	.	.	0	.	.	.
*A*3	0419	0	12	1	2	0	.	.	.	.	.	.	.	.	.	0	0	*3*	.	.	1	.	.	.
*A*4	0520	.	.	.	.	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
*A*5	0521	.	.	.	.	0	0	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	.
*A*6	0320	*(1)*	2	3	3	3	.	.	.	1	(0)	0	.	.	.	.	.	.	.	.	.	.	.	.
*B*1	0118	2	9	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	10	.	.	.	.	.
*B*2	0117	.	.	.	.	(8)	.	.	.	.	.	.	.	5	.	10	.	.	.	.	14	*8*	2	5
*B*3	0217	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(8)	.	.	.	.	.	.	.	.
C	9918	.	.	.	.	.	.	.	.	.	.	.	.	10	12	.	.	.	.	.	9	13	*7*	3
D	9624	.	.	.	.	5	2	.	.	.	.	.	.	4	.	7	10	.	7	6	5	4	.	.
*F*1	9721	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	2	5	.	.
*F*2	9524	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.
*F*3	9525	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.
E	0021	.	.	.	.	3	0	.	.	.	.	.	.	3	6	.	.	.	.	.	7	5	.	.
*B*4*	0318	3	(2)	.	.	2	4	.	.	.	.	.	.	.	.	*3*	0	.	.	.	.	.	.	.

no. of traps used for catches shown in brackets

May	June	July	Aug.	Oct.
*A*6, *20* *B*4, 21	*A*1, 22, 50, *22* *B*2, 12	*A*6, 50	*A*1, 50	*B*3, 12

1939

area	square	Jan.				Feb.			Mar.			Apr.				May		June	July	Aug.
*A*1	0421	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*B*1	0118	.	.	.	.	10	.	.	10	10	6	6	*4*	4	1	7	.	.	2	.
*B*2	0117	6	7	10	8	3	7	9	6	8	3	3	0	.	.	*(3)*	4	.	.	.
C	9918	5	1	.	.	9	8	.	7	4	.	6	1	.	.	.	.	1	.	.
D	9624	0	3	0	.	1	0	5	.	.	.	3	.	.	.	0	.	.	.	.
*F*2	9524	.	.	.	.	.	.	.	15	.	.	.	.	.	.	(1)	.	.	.	3
E	0021	2	0	3	0	3	3	.	.	.	.	1	1	.	.	2	.	.	.	.

no. of traps used for catches shown in brackets

*B*2, *50*
*F*2, 12

* Hedgebanks outside plantations.

(*c*) *Shrews*

Common shrews (*Sorex araneus*) were scarce for most of the time, and other species of small mammals were very rarely taken. Shrews had become much more abundant by August 1939 at a time of universal scarcity of voles (table 1). Few occurred on the marking area. The full data are deposited; they show that this species did not have a parallel fluctuation, and that it was too scarce to have been a serious enemy of the vole.

(*d*) *Discussion*

This survey shows the striking contrast in 1938 between the low population densities in the Marchnant valley and the abundance in areas *B*, *C*, *D* and *F*; also that within each of these two divisions a number of populations, though completely isolated from one another, declined at about the same time. Where peak densities were passed 1 year later than on Glasgwm the areas had been enclosed for a shorter time. Before then trampling and grazing by sheep and cattle would have confined the voles chiefly to patches of rush (*Juncus effusus* L.) which is seldom grazed (Appendix 1*a*). Areas *C* and *B*2 were grazed almost until the spring of 1935 or 1936, and therefore the first vole cycles were completed in 3 or 4 years. The *B*1 and *B*3 areas were planted in 1933 or 1934, and voles therefore took 5 or 6 years to pass their peak. Voles in the former hayfields of area *E* had presumably built up and declined between 1933 and 1938, at least 1 year ahead of the contemporary population on *B*1. Voles in an area enclosed in 1932 probably decreased in 1939, though not necessarily for the first time (area *F*1). Another area, 25 miles south-west of Lake Vyrnwy, was enclosed in 1936 and voles reached their first peak in 1940 (Appendix 1*c*).

Glasgwm, by contrast, had supported voles since at least 1926, and other suitable areas in the Marchnant valley had also been fenced off about this time. The 1937 peak may therefore have been their third or fourth. In a new plantation the year in which voles reach a peak no doubt depends on many factors. The year of enclosure from grazing, type of vegetation, weather, initial vole numbers and amount of immigration may be expected to affect the rate of population growth. Therefore only by certain combinations of events would the first peak in a new area seem likely to coincide with a peak in an old one. It is therefore not specially remarkable that, with the exception of area *E*, peak densities in the new areas did not coincide with those in the older enclosures in the Marchnant valley. The problem, which was not answered by any facts discovered during this inquiry, is why peak densities should have been reached simultaneously in 1937 in all the old plantations, and in most of the younger ones in 1938 despite their different years of enclosure. This question is discussed theoretically in a later section.

3. BODY WEIGHTS AND REPRODUCTION

The main features of the seasonal changes in population structure of *Microtus* are known from Baker & Ranson (1933) and Brambell & Hall (1939). Overwintering populations consist largely of young of the previous breeding season whose body weight remains low until spring. There is then an increase in weight, the first young are born in April or May and breeding may continue until October. Baker & Ranson thought it probable that the young did not breed in their first year; but Brambell & Hall showed that some did and that an overwintering population included small parous females and males with shrunken testes. (Later on Ranson also found evidence that the young bred in their first season.)

Information about the Lake Vyrnwy populations of 1936–9 is available from 410 live voles sent to Oxford, 1587 caught mainly in break-back traps and 798 records of voles marked in the field. The most useful information is from the marked voles and less use need be made of the other data (which are deposited). Body weights have been grouped in 2 g intervals from 8·25 g upwards, as field measurements were to the nearest 0·5 g. Weights in the laboratory were read to the nearest 0·1 g; thus two animals weighing 20·2 and 20·3 g would have been recorded in the field as 20 and 20·5 g respectively. The common groupings for both field and laboratory readings are therefore 18·3 to 20·2 and 20·3 to 22·2 g. Animals sometimes lost weight in the live traps, but the present data agree closely with those from dead trapping.

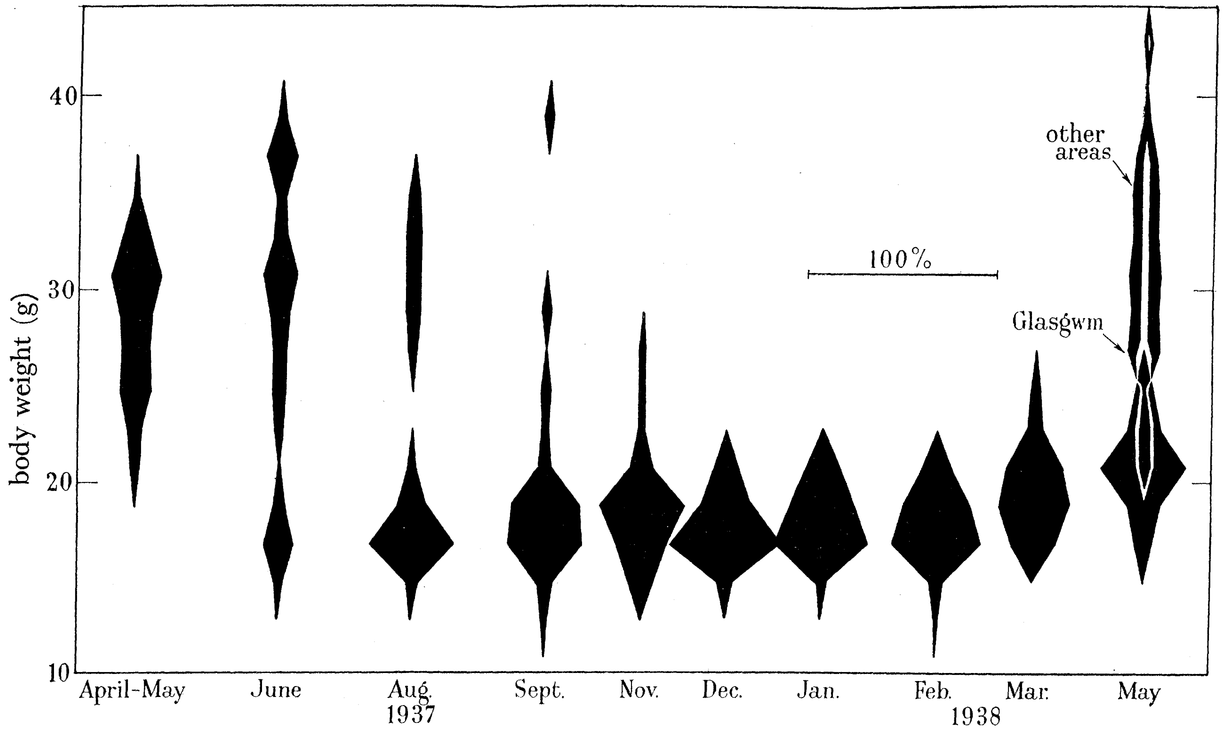

FIGURE 2. Distribution of male body weights > 12·2 g on the Glasgwm marking area; percentage of each sample in each 2 g group, calculated from table 4. The mean of the distribution for the other areas is in table 7 (range 20·3 to 44·2 g).

(*a*) *Body weight as a criterion of age*

One of the more difficult problems in small mammal studies is to distinguish between age groups. In a living population the best that can be done is to use data on body weight together with inferences from marked individuals. The following discussion shows the evidence for using 22·25 g as the critical weight for separating young from old animals and is an essential preliminary to the population analysis in § 5.

In March 1937 the males began to increase from their overwintering weights at 18 to 22 g and the weekly sample obtained alive on 27 March consisted of one male in each 2 g group from 16·3 to 32·2 g; five females were still below 22·3 g. Body weights of both

Table 4. Distribution of body weights of marked voles on Glasgwm

Figures in brackets show the number of adults previously marked in May and June respectively.

wt. group (g)	1937						1938				
	28 Apr.–5 May	21–26 June	10–12 Aug.*	28–30 Sept.	2–5 Nov.	3–5 Dec.	7–10 Jan.	19–22 Feb.	28–31 Mar.	5–7 May	8–10 June
					males						
38·3–40·2	.	1	.	1 (1, 0)	.	.	.	.	.	.	.
36·3–	.	5 (3)	1 (0, 1)	.	.	.	.	.	.	.	.
34·3–	1	2	2 (1, 0)	.	.	.	.	.	.	.	.
32·3–	8	2 (1)	3 (2, 0)	.	.	.	.	.	.	.	.
30·3–	14	6 (5)	3 (1, 0)	.	.	.	.	.	.	.	.
28·3–	10	3 (3)	3 (2, 0)	2 (2, 0)	.	.	.	.	.	.	.
26·3–	7	2 (1)	1 (1, 0)	.	1 (1, 0)	.	.	.	.	.	.
24·3–	9	2 (2)	.	2 (1, 0)	1	.	.	.	1	1	1
22·3–	3	1	.	1 (0, 1)	1 (1, 0)	.	.	.	2	2	.
20·3–	2	.	1	3	7	3	8	7	9	5	.
18·3–	.	2 (1)	6	17	25	6	15	15	11	2	.
16·3–	.	5	18	19	15	14	22	23	7	1	.
14·3–	.	1	3	4	7	1	1	3	.	.	.
12·3–	.	.	.	1	.	.	.	1	.	.	.
10·3–12·2	.	1	.	.	.	.	.	.	.	.	.
total	54	33	41	50	57	24	46	49	30	11	1
					females						
34·3–36·2	.	1 (1)	.	.	.	.	.	.	.	.	.
32·3–	.	2 (1)	.	.	.	.	.	.	.	.	.
30·3–	.	4 (3)	3 (0, 1)	.	.	.	.	.	.	.	.
28·3–	4	4 (1)	3 (2, 1)	3 (3, 0)	.	.	.	.	.	.	.
26·3–	2	5 (4)	9 (5, 1)	1	2	2 (0, 2)	1 (1, 0)	.	.	.	.
24·3–	7	7 (5)	7 (3, 2)	4 (3, 1)	1 (0, 1)	.	1 (0, 1)	.	.	.	.
22·3–	11	4 (3)	6 (3, 1)	5 (0, 2)	3	.	1	.	.	.	.
20·3–	20	1	1	3 (1, 0)	3 (1, 0)	1	5	3	1	.	.
18·3–	9	.	3	10 (1, 0)	10	2	4	6	2	1	.
16·3–	3	7	10	17	28	15	19	30	19	6	1
14·3–	.	4	6	3	8	2	2	7	6	10	3
12·3–	.	1	1	.	2	1	.	.	.	.	.
10·3–	.	.	.	1	.	.	.	.	.	.	.
8·3–10·2	.	.	1	.	.	.	.	.	.	.	.
total	56	41	50	47	57	23	33	46	28	17	4
TOTAL†	110	74 (34)	91 (20, 7)	97 (12, 4)	114 (3, 1)	47 (0, 2)	79 (1, 1)	95	58	28	5

* There were three unidentified ♀♀ $>24{\cdot}2$ g on each block in August; these have been counted as old adults. One young ♀ of 24·5 g was retaken and two new ones of 23·0 and 24·0 g are also likely to have been young.

† Numbers agree with those in table 12 except for a few missing records.

sexes increased during April, and at the beginning of May were as shown in table 4, many of these females being pregnant. Figure 2 shows the monthly weight distributions of males.

Few young are believed to have been weaned until June (see below); but by the fourth week weight distributions were clearly bimodal. Most animals over 22·2 g had been marked, and it is likely that unmarked ones over this weight were also adults. One unmarked male weighed only 23 g and may have been young; but since it died in the trap it is more likely to have been an old one that had lost weight. (One male weighing 19·5 g was 6 g less than in May.) It is possible that a few early young had already become pregnant; but it is more likely that the few unmarked females over 22·2 g were born in 1936. The lightest marked female weighed 23 g; those below this weight were probably all young.

In August the majority of both sexes over 22·2 g had either been marked in May or June, and only one of them was that season's young. The June-marked young, in fact, had almost all disappeared, as shown by the comparative number of recaptures in table 12. Thus out of forty-eight adults released in June twenty-five were retaken in August and fourteen in September; out of twenty-three young released in June only two were retaken in August; none in September. The two young recaptured in August weighed 24·5 g (♀) and 17·5 g (♂); another female, first recaptured in February, weighed 17 g. Since there is no reason to suppose that marking had affected their viability, the early young must have suffered a heavy mortality between June and August 1937.

The lowest weight of a marked adult male in August was 26 g, and unmarked males over 26 g are likely to have been adults too. It is equally likely that those below 22·3 g were young of the year since none carried rings from May or June. The grouping of the females is less distinct, and animals below 22·3 g form only 44 % of the catch compared with 68 % in the males. In addition to the single marked young of 24·5 g one animal weighing 23 g in August was still alive at the end of March 1938 and seems likely (see below) to have been young; another weighing 24 g has also been counted as young; it was last taken in May 1938. Six other females weighing 26·0 to 32·0 g have been classed as adults, but this decision may be wrong. For in a sample of thirty females trapped a week later three animals weighing 17·0 to 20·5 g had recently littered and might previously have weighed 7 to 10 g more.

TABLE 5. CHANGES IN BODY WEIGHT OF LIGHTEST VOLES MARKED IN AUGUST 1937

increase (g), Aug.-Sept.	0	0·5		1·0	1·5	2·0	2·5	3·0	3·5
body wt. (g) in Aug.	17	16·5	17	16	17·5	17	17	15	16
sex	♂	♀	♂	♀	♂	♀	♀	♀	♂

Voles which weighed 18 g or more when marked in August were within 1 g either way of the same weight in September; but nine lighter animals captured in both months had made the increases shown in table 5. One other female weighing 9·5 g in August was not recaptured until November when it weighed 21 g. These growing animals had presumably been weaned in late July or early August and no doubt there were other young animals not fairly represented in the catch.

From September onwards nearly all new males were in the lower weight groups, but there were a few unmarked females greater than 22·2 g which have been counted as young.

Animals of less than 22·3 g in September made little or no change in weight before March 1938, but some of the old, overwintered animals lost weight. These old ones died out naturally, or in disproportionate numbers in the traps, and the last of the animals born in 1936 were recorded in January 1938. If body weight had been the only criterion a few adults could not safely have been distinguished from young, i.e. they had decreased towards or below 22·3 g. However, the amount of overlap in weight was small and in most known cases the animals were dead when weighed. Table 6 shows the only marked adults whose weight approached that of the young, i.e. which weighed less than 26·3 g after June 1937.

TABLE 6. LOWEST BODY WEIGHTS OF OLD ADULT VOLES IN 1937–8

sex	May	June	Aug.	Sept.	Nov.	Dec.	Jan.
♂	28·5	34·0	31·0	26·0*	.	.	.
♂	31·0	36·5	35·5	29·5	23·0*	.	.
♂	—	32·5	—	24·0	.	.	.
♀	18·0	25·0	27·5	22·0*	.	.	.
♀	19·0	23·0	29·5	20·0*	.	.	.
♀	23·5	31·0	28·0	25·0	22·0	.	.
♀	—	25·5	24·0	23·5	25·5	28·0	26·0

* Died in a trap or tin.

TABLE 7. BODY WEIGHTS IN MAY (FEMALES CORRECTED FOR EMBRYOS. PEAK YEARS IN HEAVY TYPE)

	A (Marchnant)		other areas	
	1937	1938	**1938**	1939
males: no. of voles	62	53	51	26
mean wt. (g)	29·06	24·04	30·45	27·48
S.E. (±)	0·42	0·48	0·81	0·92
females: no. of voles	44	46*	34	21
mean wt. (g)	24·07	18·42	26·19	20·40
S.E. (±)	0·46	0·33	0·73	0·65

* Twenty-three of these animals were taken in live traps. Their weights have arbitrarily been increased by 2 g to correct for possible weight losses in the traps. Uncorrected distributions were as follows:

wt. group (g)	12·3–	14·3–	16·3–	18·3–	20·3–	22·3–
dead	1	4	10	5	3	.
live traps (miscellaneous)	.	.	2	1	2	1
live traps (table 4)	.	10	6	1	.	.

In March 1938 the mean weight of the males had increased by about 1 g since the previous month. Little further change had occurred by May and weights were significantly below those of 1937; the mean weight of the marked males was 29 g in May 1937 compared with 21 g in May 1938. There were also great differences among the females, but the contrast is exaggerated in table 4 because there were pregnancies in 1937 but none in 1938. Animals from the break-back traps are therefore used in the fuller analysis of both sexes below.

(*b*) *Body weight in relation to abundance*

The animals so far considered were a sample from areas where a decline occurred in 1938. At the same time voles elsewhere in the Marchnant valley were scarce and low in body weight. On most other areas, however, voles were much heavier at this time and were also very numerous. When, one year later, voles had become scarce on these other areas, body weights were correspondingly low (table 7). There are not enough data for comparisons between other months, but for May the following conclusions are statistically significant by the *t* test:

(*a*) in the Marchnant valley body weights were higher in May 1937 than May 1938 (difference: ♂♂, 5·02 ± 0·62; ♀♀, 5·65 ± 0·57);

(*b*) in other areas body weights were higher in May 1938 than May 1939 (difference: ♂♂, 2·97 ± 1·23; ♀♀, 5·79 ± 0·98);

(*c*) in May 1938 body weights were higher in other areas than in the Marchnant valley (figure 2) (difference: ♂♂, 6·41 ± 0·94; ♀♀, 7·77 ± 0·80).

It will be shown in a later paper that the significant feature of these comparisons is the unusually high body weight in the peak year. During the decline in numbers body weights are as a rule similar to those found during the early years of increase.

(*c*) *Reproduction*

Glasgwm. Visible pregnancies were found in the fourth week of April 1937 (table 8*a*), especially among the heavier animals (table 8*b*); but a sample from near the marking area (table 9; Appendix 1*d*) showed that comparatively few litters are likely to have been born before the middle of May, or weaned, therefore, until the end. 40 % of the females taken in early May were not visibly pregnant, and in another 40 % the embryos were not over 0·3 g each. One female would have littered within a day or two of capture on 4 May and one had already littered.

During June most of the heavier females were pregnant but there was no evidence of breeding among the young. In the third week of August three light and three heavier animals with vascular uteri had presumably just littered; but no animals were visibly pregnant. No samples were examined dead in September, but no growing young were taken alive (p. 517) and breeding seems to have ceased in August. This is 1 month earlier than could have been expected from Baker & Ranson's data for the neighbouring county in 1931–2.

In May 1938 there was no breeding on Glasgwm, but elsewhere in the Marchnant valley three out of eleven females were pregnant then and a higher proportion in June and July. (The pooled data for Marchnant include a non-pregnant female from Glasgwm in both these latter months.)

Other areas. Breeding was well established by early May 1938, and over half the heavier females were pregnant during June. Most heavy females were also pregnant in September and the latest was trapped on 26 October. During the decrease in May 1939 a smaller proportion of females was pregnant than in May 1938, though the difference is not statistically significant. The number of embryos per pregnant female was the same in May each year.

(*d*) *Summary*

1. On Glasgwm young males did not increase above 22·2 g in weight throughout 1937, whereas adult males seldom weighed less than 22·3 g after May. Young females weighed more than 22·2 g during pregnancy in August (516); the heavier females were otherwise old adults with a few further exceptions among the young in September and November.

2. Two groups of populations declined in different years. In each group body weights in May were unusually high in the peak year.

3. The peak breeding season ended in August 1937 on Glasgwm but continued into October 1938 on other areas. In May 1938 no females bred on Glasgwm but some were pregnant in nearby areas. During the decline elsewhere in 1939 the proportion pregnant was not greatly reduced. Thus a lowered fertility was not invariably associated with a decline in numbers.

TABLE 8. PROPORTION OF FEMALES PREGNANT AND THEIR AVERAGE NUMBER OF EMBRYOS

(*a*) All females > 10·2 g body weight

month	no.	% pregnant	av. no. of embryos per pregnancy	no.	% pregnant	av. no. of embryos per pregnancy
	Glasgwm					
1937–8: Apr.	25	40·0	3·3			
May	44	59·1	4·0			
June	38	34·2	4·5			
July	0	.	.			
Aug.	30	0	.			
Sept.	0	.	.			
Oct.–Mar.	76	0	.			
1938–9: Apr.	40	0	.			
May	12	0	.			
	Marchnant			other areas		
May	11	27·3	3·0	34	70·6	4·1
June	12	58·3	5·3	63	41·3	4·2
July	4	50·0	4·5	0	.	.
Aug.	1	0	.	0	.	.
Sept.	0	.	.	35	22·9	3·1
Oct.–Mar.	2	0	.	200	0·5	3·0
1939: Apr.	0	.	.	12	0	.
May	0	.	.	21	47·6	4·0
June	4	25·0	5·0	4	75·0	5·0
July	1	0	.	1	100	3·0
Aug.	1	100	5·0	2	50·0	3·0

(*b*) Females > 22·2 g body weight after correction for embryos*

	Glasgwm (1937)		other areas (1938)	
Apr.	14	71·4	0	.
May	32	75·0	28	75·0
June	18	72·2	38	52·6
Sept.	0	.	9	66·7

* This excludes the lighter adults in Apr.–May (there were no young in these samples), all the young taken in June on Glasgwm but not necessarily all young taken in other areas in June.

TABLE 9. STATE OF PREGNANCY, 29 APRIL TO 6 MAY 1937

total wt. of embryos and uterus (g)	< 1	1–	2–	3·0	8·0	total
condition: not visibly pregnant	.	.	.	.	.	17
3 embryos	5	.	.	1	.	6
4 embryos	9	2	3	.	1	15
5 embryos	3	.	1	.	.	4
6 embryos	1	.	.	.	.	1
already littered	.	.	.	.	.	1
total	18	2	4	1	1	44

4. Movements

In studying movements of small mammals the method of spacing the traps should generally differ from that used in determining abundance. Free movement is hampered in the conventional grid, and the apparent range will be some function of the distance between traps. Captures are also affected by the number of traps available (which may depend upon the abundance and activity of other species as well) and by the proportion of animals ranging partly outside the area. Any tendency to return to the original trap site reduces the chance of recapture elsewhere, a bias which is not necessarily overcome by closing the traps for an interval, for an animal living at a fixed site presumably tends to re-enter the nearest trap. Some workers have studied home ranges by continually re-trapping, in the hope that the limits of movement would eventually be measured. However, Blair (1942) found that the apparent home range of an individual deer-mouse might increase up to the 19th capture.

In choosing another experimental design it is first necessary to decide whether movements or numbers are the chief objects of study, or if both are important what modifications can be introduced. Two conditions seem essential for studying movements: freedom for all or some known fraction of the marked animals to move maximum distances and enough unoccupied traps when they get there.

From preliminary experiments of this type in April to May 1937 it seemed that 5 yd. was the average distance at which voles were at risk on either side of a trap line or around the outside of an area (figure 3). Two relatively small blocks were therefore chosen for a population study in the course of which more evidence was provided about movements. Results within block *E* (figure 3) are of no interest because of its small size; but within block *Q*, 85 % of recaptures were at the same place or at a single adjacent point 10 to 15 yd. away. (This statement is based on 119 recaptures of animals first caught at the inner sites only.) These observations conform with but are not valid evidence of naturally restricted movements. However, block *Q* was set in two sections, and animals released in the first were free to move 10 to 40 yd. before meeting another trap. Table 10 shows that in the 36 h after release few animals crossed even the 10 yd. gap between sections. This was also the case between one month and the next, and no more than three animals changed section from September to June; their movements were between adjacent rows only.

Recaptured voles had seldom missed more than two previous trappings. Three exceptions were: a male which was absent from August to May and two females absent from June to February or September to March. Each had been released in an outer row and was retaken there at an adjacent point. Because these animals were missed for so much longer than any others they had probably not been exposed to the risk of trapping in the interval. Yet they seem not to have moved far away, so perhaps their range of movement was contracted in the winter. The spacing of the traps, however, was slightly more variable in the spring.

The chief importance of these observations is in showing that movements were evidently restricted and without big seasonal differences; but in order to check the further conclusion that immigration and emigration were negligible the analyses in table 11 have been prepared. If there were at any time an increased amount of movement more new animals would be expected to appear in the twenty-four outer traps than inside the block. We may examine this point by comparing the proportions of marked and unmarked animals trapped in the outer and inner positions. In January, for example, 38 % of the animals in the outer lines were new (eleven out of twenty-nine) compared with 42 % new in the inner lines (fourteen out of thirty-three). In this case the tendency is in the opposite

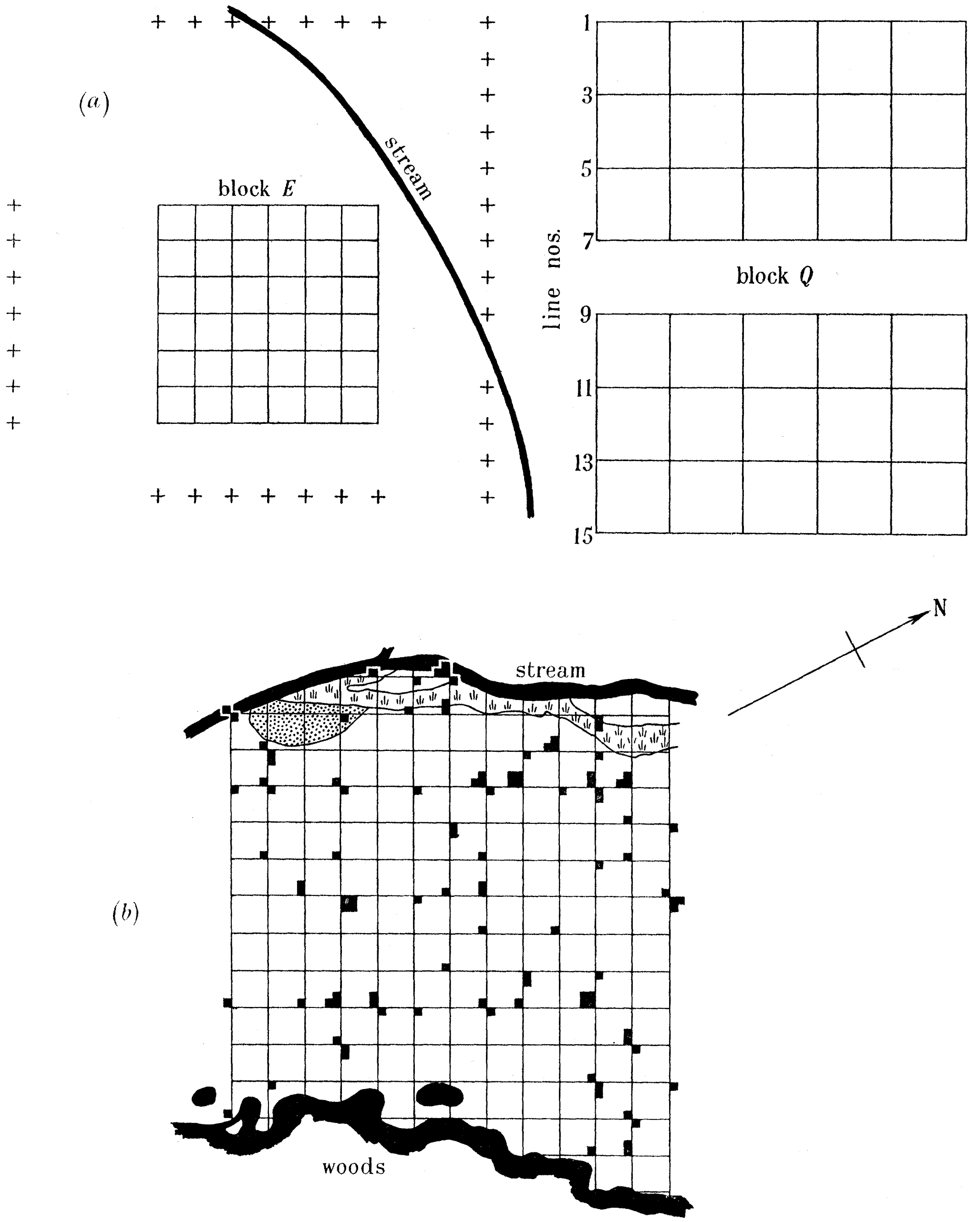

FIGURE 3. (*a*) Plan of the marking area showing block *E* and the two sections of block *Q* (lines 1 to 7 and 9 to 15). Plus signs show the distribution of traps during preliminary work on the dispersal of marked voles, in this case from block *E*. (*b*) Distribution of voles in an area from which almost the entire population was removed in break-back traps (Appendix 1*d*). Each small black square represents one animal, males to the upper left of the trap points, females to the lower right. In both (*a*) and (*b*) the smaller grids represent 5 yd. square.

direction from what might have been expected. Marginal immigration of new animals, however, might have been reduced by some chance redistribution of the marked animals. As a check we may examine marked animals only to see if those released in the outer lines were any less likely to be retaken next time. An example showing this trend was as follows. Fifty-nine voles were released in January, twenty-eight at the outer positions, thirty-one inside the block. In February ten were recaptured from those released from the outer traps (36 %) compared with fourteen from the rest of the sample (45 %). Even in this selected instance the difference is of no statistical significance, and the same is true of each pair of contingency tables from September 1937 to June 1938. Since most of the entries within each set of tables are of a similar magnitude it has seemed permissible to form the totals as shown. Clearly there is no evidence, of statistical significance, that voles from the outer lines tended to miss recapture. Presumably, therefore, they did not move off the area nor were crowded out of the traps by animals moving in. However,

Table 10. Movements within 36 hours between traps in two sections of block *Q*

	month ...	Aug.	Sept.	Nov.	Jan.	Feb.	Mar.	May
no. released in 1st section		(20)	24	29	27	49	33	(11)
no. retaken in 2nd section		(4)	0	1	0	1	5	(0)
frequency of distance moved:	10 yd.	3	.	1	.	.	3	.
	15 yd.	1	.	.	.	1	.	.
	20 yd.	.	.	.	.	.	1	.
	25 yd.	.	.	.	.	.	1	.

Notes. In August the first section was lines 1, 7, 9 and 15; before this the system varied in other ways. Lines 1 to 7 were set first in September, lines 9 to 15 in other months. In May animals from lines 9 and 11 were not released until trapping had finished in lines 1 to 7; brackets show animals released in lines 13 and 15. In June all animals were kept in tins until 48 h trapping had finished in lines 9 to 15.

Table 11. Comparative chances of recapture at 24 outer and 24 inner trap positions*

		(*a*) proportion of new voles			(*b*) proportion of recaptures		
			new voles			recaptures	
month	traps	total catch	no.	%	total released last time	no.	%
1937: Sept.	outer	25	16	64	23	7	30
	inner	30	19	63	23	11	48
Nov.	outer	30	18	60	24	10	42
	inner	31	15	48	29	14	48
Dec.	outer	14	6	43	19	8	42
	inner	14	5	36	10	4	40
1938: Jan.	outer	29	11	38	25	9	36
	inner	33	14	42	27	10	37
Feb.	outer	39	21	54	28	10	36
	inner	44	20	45	31	14	45
Mar.	outer	30	11	37	37	18	49
	inner	28	6	21	44	15	34
May	outer	14	1	7	28	9	32
	inner	14	2	14	28	11	39
June	outer	4	1	25	14	2	14
	inner	1	1	100	12	1	8
total	outer	185	85	46	198	73	37
	inner	195	82	42	204	80	39

* Totals agree with those for all ages in table 12 except that the January recaptures are from voles released in November (adjusted for accidental deaths in December) and the December recaptures are from those released in lines 9 to 15 in November.

there were slight discrepancies in the direction to be expected if movements were responsible for a very small error: (*a*) $\chi^2_c = 0{\cdot}44$, $p = 0{\cdot}7$ to $0{\cdot}5$; (*b*) $\chi^2_c = 0{\cdot}12$, $p = 0{\cdot}8$ to $0{\cdot}7$.

Direct attempts were also made to observe any dispersal outside the blocks. As they were 150 yd. north of the weekly trap lines (§ 2*a*), movements in that direction would probably have been discovered. Other traps were placed around the blocks, generally at distances of 100 to 150 yd., sometimes as close as 50 yd. Two marked animals were thus retaken, the first in March 1938 when a 20·5 g ♂ (released after confinement for 24 h) moved to a live trap 150 yd. away. After a further 24 h it was returned to its position in the block but next morning was again caught outside. The other vole was a ♀ 14·5 g taken in May 1938 in a break-back trap 150 yd. from the point of release the previous midday. This animal had spent the previous two nights in captivity.

One adult male moved 42 yd. from one block to the other between August and September; but during the winter the stream between the blocks generally prevented free passage. Only two other large moves were recorded, both by voles marked nearby in preliminary experiments in November 1936. They were retaken in May 1937, a male having moved 110 yd. and a female 70 yd.

It may be concluded that most voles were very local in their movements and the greatest distance across their home range could seldom have exceeded 10 to 15 yd. There was little obvious difference in activity according to season, and the number of movements greater than 10 yd. was so small that no analysis according to age or sex can be made.

It seems possible that trapping occasionally had some effect on the activity of the animal. The two exceptional moves of 150 yd. were made by animals just released, whereas none from previous occasions was retrapped outside the blocks and only one moved between them. Natural changes of position are to be expected, but the disturbance of trapping must evidently be considered in choosing an experimental design.

5. Population dynamics

(*a*) *Methods*

The methods so far described are inadequate to measure survival rates or absolute abundance. An attempt to measure these quantities was therefore made by trapping, marking, releasing and resampling. The field techniques employed were similar to those worked out for the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*) as described by Chitty (1937). Trap deaths among the wood mice had been almost eliminated by providing a nest box containing bedding and grain; but in the case of the bank vole nearly 20 % of the newly captured animals still died. Once the bank voles had been marked their mortality rate per recapture was only 2 %, and partly for this reason it was not suspected that succulent food might be needed in the traps. In the same way several field voles were lost at the start of the work at Lake Vyrnwy.

For trapping field voles a double-entranced trap was designed (Chitty 1938), though it is now known that the lack of success with more orthodox types was because so many tests were based on first-night captures only. Certain species of rodents tend to avoid unfamiliar objects; this form of behaviour is most strikingly shown by the brown rat (Chitty & Shorten 1946) and was later found to explain many of the difficulties of live-trapping other small mammals (Chitty & Kempson 1949).

A method of making nickel rings is described by Chitty (1937). These rings were carried on a U-shaped wire with an elastic band cross the open end of the U and were fitted round the vole's left hind-leg by means of pliers. A spring balance, accurate to 0·5 g, was also carried; the animal was placed in a small wire cage hooked on underneath.

Except where an isolated habitat is being studied the size of trapping area must be fairly large in relation to the animal's total range of movement (including that in the season of greatest activity). Blair (1941) recommends an area 10 to 20 times the size of the home range; but this is probably too small to minimize errors due to gains and losses of animals at the periphery. A trapping area about 40 times the size of the home range was thought desirable in the present study.

The problem of catching a high proportion of animals in an area was complicated in the case of the wood mouse and bank vole by the frequency with which the animals returned to traps which were reset in the same place. These immediate recaptures are undesirable for several reasons, particularly because of the diminishing chances of catching the other individuals in the remaining traps. A system of moving the traps on four successive days to positions 30 to 50 yd. away was successful in preventing multiple recaptures of the bank vole, though not of the wood mouse. In the case of the field vole this system was unsuited to the limited amount of time available on each trip. However, the same principle was adopted of making as few immediate recaptures as possible and leaving the area undisturbed for some weeks. What had not been suspected was that capture on one occasion would influence the probability of recapture even after this longer interval (see below).

Specific details of the Lake Vyrnwy study were as follows. The work was carried out between May 1937 and August 1938 on the blocks shown in figure 3. On block *E* seven rows of seven traps were spaced 5 yd. apart in the hope that all the individuals in this small area could be marked. On block *Q* eight rows of six traps were spaced 10 yd. apart. It was expected that there would be less error due to movements at the periphery of this larger area, but that other errors would be involved in finding numbers by calculation instead of enumeration. In practice it was impossible to catch all the animals on block *E*, and after November the inner twenty-five traps only (block *F*) could be managed. As there were also many accidental deaths the value of these results is limited.

On the day of arrival at about 2.30 p.m. traps were set in one of the blocks and left until 9 a.m. next day, when the voles were put in tins (except during May and June 1937) and the traps were reset. A second visit was paid in the afternoon. The traps were then lifted, made ready for setting elsewhere next morning and were visited in the afternoon and again in the morning of the fourth day. Block *E* was trapped at the same time as part of block *Q* which, after August, was trapped in two sections of four odd-numbered lines 1 to 7 and 9 to 15. From February onwards the intensity of trapping was increased, chiefly through clearing the traps more frequently. Weighing and marking was done either at the trap site or in a car, and after the final visit the animals were released where they had been caught.

It is likely that the efficiency of the traps improved slightly throughout the study or that voles were more easily trapped as the herbage died down; moreover, because of the growing numbers of marked animals (see below) the total catch does not reflect monthly trends.

The areas covered by traps were 30 × 30 sq.yd. on block *E* and 70 × 50 sq.yd. on block *Q*; but the area sampled probably extended another 5 yd. all round. This correction follows the practice of adding the mean dimension of the home range to those of the trapping block (Dice 1941). The assumption is that half the animals are drawn into the traps from a surrounding area equal in width to that of the home range. Voles in the present study evidently had a home range equivalent to one of about 10 yd. diameter (§ 4). The effective area of block *E* was thus about 1600 sq.yd. and of block *Q* about 1 acre.

TABLE 12. MARKING AND RECAPTURE RATES

Total catch shown by heavy type, accidental deaths by superscripts.

	block *Q*										
	1937						1938				
	May	June	Aug.	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	May	June
adults	**67**^{11}	19^{1}	9	6^{1}	3^{2}	0	1^{1}	.	.	.	.
	.	**28**^{2}	12	7^{1}	3^{2}	1^{1}	1^{1}	.	.	.	.
	.	.	**18**^{1}	5	3^{2}	1^{1}	1^{1}	.	.	.	.
	.	.	.	**8**^{2}	3^{2}	0	0	.	.	.	.
	.	.	.	.	**3**^{2}	0	0	.	.	.	.
	.	.	.	.	.	**1**^{1}	0	.	.	.	.
	.	.	.	.	.	.	**1**^{1}	.	.	.	.
young	.	**11**	1	0	0	0	0	1	1	1	0
	.	.	**30**^{1}	13	10^{1}	4	9	8	5	4	1
	.	.	.	**47**	21	6	12	17	7	4	0
	.	.	.	.	**58**^{3}	12^{3}	19^{1}	22	12	7	2
	.	.	.	.	.	**27**^{3}	13^{1}	10	7	4	1
	.	.	.	.	.	.	**61**^{2}	24	13	7	1
	.	.	.	.	.	.	.	**83**^{2}	33^{2}	18^{2}	2
	.	.	.	.	.	.	.	.	**58**^{2}	20^{1}	3
	.	.	.	.	.	.	.	.	.	**28**^{2}	3
	.	.	.	.	.	.	.	.	.	.	**5**
total	**67**^{11}	**39**^{2}	**48**^{2}	**55**^{2}	**61**^{5}	**28**^{4}	**62**^{3}	**83**^{2}	**58**^{2}	**28**^{2}	**5**

	block *E* 1937					block *F* 1938			
	May	June	Aug.	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.
adults	**44**^{7}	16^{2}	11	6^{4}	0	0	0	.	.
	.	**24**^{2}	13	7^{4}	1	1	1	.	.
	.	.	**20**	9^{4}	2	1	1	.	.
	.	.	.	**9**^{4}	1	1	1	.	.
	.	.	.	.	**2**	1	1	.	
	.	.	.	.	.	**1**	1	.	.
	.	.	.	.	.	.	**1**	.	.
young	.	**13**^{1}	1	0	0	0	0	0	0
	.	.	**23**^{1}	8	8^{1}	2^{1}	2	2	1
	.	.	.	**33**^{6}	14^{2}	3^{1}	2^{1}	3	1
	.	.	.	.	**51**^{7}	11^{4}	9	5	1
	.	.	.	.	.	**18**^{5}	5	3	0
	.	.	.	.	.	.	**16**^{1}	6	1
	.	.	.	.	.	.	.	**12**	1
	.	.	.	.	.	.	.	.	**5**
total	**44**^{7}	**37**^{3}	**43**^{1}	**42**^{10}	**53**^{7}	**19**^{5}	**17**^{1}	**12**	**5**

It was not possible to visit Lake Vyrnwy at equal intervals, but after August 1937 there were usually 4 to 6 weeks between visits (table 4). In December snow made trapping difficult on block *F* and impossible on one-half of block *Q*.

The main results of marking and recapture are given in table 12. Adults have been separated from young by the criteria discussed in § 3. Figures in bold type are total catches of animals, marked and unmarked; deaths in the traps or tins are shown by superscripts. Other figures are recaptures: horizontally from each sample released, vertically from all samples previously released. For instance: 83 animals were caught on block *Q* in February; two (unmarked) were accidentally killed. In March, May and June the numbers retaken from this sample were respectively 33, 18 and 2, with accidental deaths in both March and May. The composition of the February sample included 24 recaptures from those released in January and 10, 22, 17, 8 and 1 returns from earlier samples. Such figures (and their superscripts) do not represent individuals but totals of recaptures to which the same individuals may contribute more than once. This grouping by marks is essentially that of Dowdeswell, Fisher & Ford (1940), Fisher & Ford (1947) and Jackson (1948 and previous papers), except that columns are arranged differently.

(*b*) *Nature of the sample*

In estimating population parameters from the proportion of marked and unmarked animals it is generally assumed that sampling is random and that the death-rate is the same for all age groups. Sampling was not random on Glasgwm chiefly because animals were more readily captured after they had once entered a trap. Certain samples were thus biased in favour of older animals with a different expectation of life. These and other departures from ideal conditions occurred as follows:

(i) *Distribution of traps*

Traps were placed within about 1 yd. of stakes at the intersecting lines of the grid. Correct procedure would have been to allot trap positions at random within each square. Failure to do so may have contributed slightly to the tendency to recapture marked animals.

(ii) *Marginal errors*

There may have been slight changes in size of home range in the spring so that a greater area was sampled. It would have been preferable if part at least of the blocks had been bounded by natural barriers, but errors because of movements were probably small enough to be ignored (§ 4).

(iii) *Selective trapping*

There was little evidence except in March (table 14) that males and females were not equally at risk. Selection by weight can certainly be neglected from September onwards (table 4). Individuals with consistent peculiarities, however, may not have been sampled independently on successive occasions. Behaviour towards a trap is no doubt influenced by factors such as fear, curiosity, activity, memory, and the attractiveness of the bait. Therefore the use of the same technique of capture each time is not a random procedure. This was apparent from June to December 1937 because marked individuals were relatively more frequent in the first than in the second catch of the 24 h. This bias in the first subsample naturally affected the sample as a whole even if the second was taken at random. The total catch on block *Q* from June to December 1937 was distributed as follows (the full analysis is in Chitty & Kempson 1949):

	total no. of captures	marked recaptures no.	marked recaptures %
1st visit	119	64	54
2nd visit	112	34	30

$\chi^2_c = 12{\cdot}0$; D.F. $=1$; $p < 0{\cdot}001$.

Biased sampling continued during January, especially on the section that had not been trapped the previous month, but proof is no longer provided by χ^2 tests, perhaps because the second subsample was as biased as the first. The alternative evidence that there was selective trapping is obtained as follows. In the non-breeding season a given sample of marked animals should tend to form a constant proportion of later samples (provided certain assumptions are true). In the sampling on block Q the expectation of a constant proportion of marked animals is approximately fulfilled after February but not before. For example, 10 out of the 83 animals captured in February had been released in December. Clearly this proportion is little different from that found in March (7 out of 58) or in May (4 out of 28). In January, however, 13 out of 61 animals had been retaken from those released in December; other groups also formed a higher proportion of the January than of the February catch. The amount of this difference may be shown by the departure from unity of the fraction $\frac{61}{83} \times \frac{1+8+17+22+10}{0+9+12+19+13} = 0{\cdot}804$. Similar comparisons between months show that the ratios are consistently below unity at least until February. After February the animals at risk are less diluted by additions, and perhaps the errors are entirely those of random sampling. (The ratio between February and March is $<1{\cdot}0$, between March and May is $>1{\cdot}0$ and between February and May is unity.)

A series of numbers may now be obtained by the cumulative multiplication of these ratios as in Dowdeswell *et al.* (1940). Starting for convenience with 1·000 in September we obtain the following values (the February figure, for example, being 0·804 times that for January):

Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	May	June
1·000	0·623	0·432	0·348	0·280	0·220	0·262	0·226

$\underbrace{0{\cdot}280 \quad 0{\cdot}220 \quad 0{\cdot}262 \quad 0{\cdot}226}_{\text{av. } 0{\cdot}247}$

The last four values are similar, and about one-quarter that to be expected (1·000) in random sampling from a localized, non-breeding population. Undoubtedly the dilution of those originally at risk was largely because it was more difficult to capture unmarked animals. That this bias did not persist indefinitely may perhaps be because the unmarked animals became familiar with inefficient traps (Chitty & Kempson 1949). The voles therefore formed two groups: the marked and some unmarked ones being more readily trapped than the rest of the unmarked ones, the latter only learning to enter the traps as the work progressed. An analogy may be drawn to an insect population consisting partly of stages not sampled by the methods used for the adults.

(iv) *Induced mortality*

In May and June 1937 many animals died in the traps through lack of succulent food. Some of the later deaths occurred because so much fresh grass was provided that it was hard for the animals to get into the nest box (less space was occupied when apple was used eventually). Deaths appear to have occurred indiscriminately among marked and unmarked animals of similar ages, and there is no evidence that the chances of subsequent survival were affected by capture (Appendix 2).

The leg rings were fitted with great care and are most unlikely to have slipped off. These rings are believed, though without formal proof, not to have decreased the length of life of the animals; only three were retaken with swollen legs. Few if any others are likely to have been affected, since the voles were marked when already grown or as young which never reached full size (§ 3).

Older animals seem to have suffered a disproportionate trap mortality in the autumn (table 12). They would soon have reached the end of their natural life, but since they were not released the sample was biased in favour of the more viable animals. The error in this case is unimportant; but it may be that other less robust individuals tended to die in the traps. If so the rate of survival of the sample may have been better than that of the unmarked animals. Fortunately deaths were few during the important months on block *Q* and have been regarded as a negligible addition to the natural death-rate.

(v) *Natural mortality*

In calculating numbers or death-rates it may be necessary to assume either that mortality rates are constant (Fisher & Ford 1947) or independent of age (Jackson 1948). Neither of these assumptions could be made about the voles on Glasgwm, but luckily the more extreme differences between contemporary groups occurred before September 1937.

Age. The young marked in August seem to have been longer lived than some of those marked later. Table 12 shows that twenty-nine animals were released in August and forty-one recaptures were made between November and June 1938. In the same period sixty-seven recaptures were made from the forty-seven animals, of lower average age, which were released in September. The total recapture rate is 1·4 for both samples, although the older animals had been exposed to risk for an extra 7 weeks. Moreover, the September sample included thirteen August-marked animals and if these individuals are separated from the thirty-four new animals the contrast is greater. Table 13 compares recapture rates in this way between voles first caught in August and those captured and released under identical conditions each month. Periods for which the relative rate of recapture of August animals exceeds an arbitrary ratio of 1·5 are shown in heavy type. The odds against getting any one of these results by chance alone are not very great, and since none of the comparisons is independent the results of χ^2 tests may not be pooled. Therefore by familiar statistical tests these differences are of no significance. Nevertheless, it would be incorrect to dismiss the view that the survival rates did in fact differ and that by January there were relatively less survivors from the later samples. On block *E*, where the whole population declined more rapidly (tables 12 and 17), six out of eight August-marked voles were retaken in November compared with only eight out of the nineteen new animals also released in September. Other data are too scanty for analysis.

Sex. Table 14 shows that fewer males than females were recaptured from those released in March, the difference almost being statistically significant ($\chi^2_c = 3{\cdot}81, p \doteqdot 0{\cdot}05$). In addition, fewer males than females were recaptured from those released in February and May, the three results together suggesting a real trend from February onwards. Despite the loss of males the total catch in March still showed the slight preponderance of males typical of preceding months, for twelve out of seventeen newly captured animals were males. It is possible that marked males were lost through emigration and that the surplus of new males in March was due to immigration. The evidence, however, is largely against these explanations (§ 4), and an increase in both the activity and death-rate of the males is the more likely.

TABLE 13. RATES OF RECAPTURE OF ANIMALS CAUGHT IN AUGUST 1937 AND OF OTHERS RELEASED IN LATER MONTHS

Heavy type shows where the relative recapture rate (R^3) of August animals was 1·5 or greater.

month in which released	month in which first captured	no. released (1st figure) and no. recaptured								
		Aug.	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	May	June
Aug.	Aug.	29	13	10^{1}	4	9	8	5	4	1
Sept.	Aug.	.	13	6	2	6	8	4	2	0
	Sept.	.	34	15	4	6	9	3	2	0
	R^3	.	.	1·0	1·3	**2·6**	**2·3**	**3·5**	**2·6**	.
Nov.	Aug.	.	.	9	2	4	5	4	3	1
	Sept.–Nov.	.	.	46	10^{3}	15^{1}	17	8	4	1
	R^3	.	.	.	1·0	1·4	**1·5**	**2·6**	**3·8**	**5·1**
Dec.	Aug.	.	.	.	4	3	1	2	2	1
	Sept.–Dec.	.	.	.	20	10^{1}	9	5	2	0
	R^3	.	.	.	.	**1·5**	0·6	**2·0**	**5·0**	.
Jan.	Aug.	.	.	.	.	9	4	2	1	1
	Sept.–Jan.	.	.	.	.	50	20	11	6	0
	R^3	.	.	.	.	.	1·1	1·0	0·9	.
Feb.	Aug.	.	.	.	.	.	8	3	2	0
	Sept.–Feb.	.	.	.	.	.	72	29^{2}	15^{2}	2
	R^3	.	.	.	.	.	.	0·9	1·2	.
Mar.	Aug.	.	.	.	.	.	.	5	3	1
	Sept.–Mar.	.	.	.	.	.	.	50	16^{1}	2
	R^3	.	.	.	.	.	.	.	**1·9**	**5·0**
May	Aug.	.	.	.	.	.	.	.	4	1
	Sept.–May	.	.	.	.	.	.	.	21	2
	R^3	.	.	.	.	.	.	.	.	**2·6**

Superscripts show accidental deaths.

TABLE 14. NUMBER OF MALES AND FEMALES RELEASED IN ONE MONTH AND RETAKEN THE NEXT

month released	sex	no. released	no. retaken	month released	sex	no. released	no. retaken
Aug.	♂	17	8	Jan.	♂	32	13
	♀	12	5		♀	27	11
Sept.	♂	27	10	Feb.	♂	42	15
	♀	20	11		♀	39	18
Nov.	♂	28	5	Mar.*	♂	28	6
	♀	27	7		♀	28	14
Dec.	♂	15	8	May	♂	11	0
	♀	9	5		♀	15	3

* The 56 animals released included 13 out of 15 ♂♂ and all 18 ♀♀ recaptured from the February sample; 3 ♂♂ and 5 ♀♀ which missed capture in February; 12 new ♂♂ and 5 new ♀♀.

Areas. After January numbers diminished more rapidly in lines 1 to 7 than in lines 9 to 15. This is most simply seen from the total catch in the two sections (table 15). There were no obvious differences in habitat to account for the differential survival, and the only way in which treatment had differed was that lines 9 to 15 only had been trapped in December. It is improbable that this trapping had had any beneficial effects on survival in lines 9 to 15; moreover, on block F, which was also trapped in December, the rate of decrease was the fastest of all. These variations in death-rate were not explained by an unequal distribution of males. In fact, the only difference suggested is that in May 1937 voles may have been rather more crowded on block E than on block Q (see below); but there was no obvious difference between the two sections of block Q in population density during the breeding season.

TABLE 15. NUMBER OF VOLES TRAPPED IN THE TWO SECTIONS OF BLOCK Q (1937–8)

	Aug.	Sept.	Nov.	Jan.	Feb.	Mar.	May	June
lines 1 to 7	17^1	21	29^2	33^1	33^1	23	7	3
lines 9 to 15	13	26	29^1	28^1	50^1	35^2	21^2	2

Superscripts show accidental deaths.

(c) *Analysis*

The assumptions necessary for estimating population parameters by known methods were obviously not fulfilled. A complete analysis would require a rather extended discussion—the difficulties are obvious from the partial analysis in Appendix 2—and it will be simpler to suggest the material truth of the main deductions by using data which involve fewer assumptions.

(i) *Minimum survival rate*

Estimates of the survival rate (Appendix 2) can be supplemented by direct observation of the minimum survival rate. This quantity is the proportion of animals known to have been alive at one time out of those actually released the time before. An example is given in table 16 using data for the sample released in August. Trapping periods are numbered $0, 1, \ldots, T$. The symbols $01, 02, \ldots, 0T$ show animals captured in period 0 and recaptured for the first time in periods $1, 2, \ldots, T$. Similarly, $12, 13, \ldots, 1T$ show animals captured in period 1 and recaptured after being missed on zero to $T-2$ occasions. Of the twenty-nine animals released in August, thirteen were retrapped in September; seven missed this trapping but were retaken later ($02+03 \ldots 0T$). The minimum survival rate is therefore 20/29. The seven animals which missed capture in September were presumably survivors of others which were also missed but died before being retaken. The minimum survival rate will therefore be much below the true rate when many animals are missed and the death-rate is high. The minimum survival rate between September and November is $10/13 = 0{\cdot}769$ and cannot be obtained from figures in the bottom line of the table such as $17/20 = 0{\cdot}850$. (A bias of this nature accounts for at least part of the good survival reported by Hacker & Pearson (1946) for previously marked *Apodemus*.)

(ii) *Population changes*, 1936–8

Autumn 1936. Voles were frequently seen in the autumn and winter of 1936. Sixty-nine voles were taken in the 5-day trap line in the first week in September 1936, roughly the same as on 16 to 20 August 1937, and the trace index was similar in both winters (table 1). These observations suggest little difference in abundance between the two years. (The estimate for September 1937 is 300 voles per acre—see below.) Survival was undoubtedly better in the winter than it was in the spring and summer (table 17), unless numbers were very much higher in September 1936 than seems likely. Survival may also have been better than it was at the start of the winter 1937–8; if so these wild voles must have survived about as well as the laboratory voles studied by Leslie & Ranson (1940). If the rate of survival in the field were the same as that in the laboratory a young population of 300 at the end of September 1936 would have left 130 survivors at the beginning of May (figure 4) or approximately the number per acre actually observed. There seems, then, no reasonable doubt that population densities were at least as high in September 1936 as in September 1937. During the previous cycle it was considered that voles were about equally abundant in the autumn of the two years 1932 and 1933 (Findlay & Middleton 1934).

TABLE 16. MINIMUM SURVIVAL RATE OF ANIMALS MARKED IN AUGUST 1937

No. of voles released (heavy type) and recaptured after intervals shown in italics.

Aug.	Sept.	Nov.	Dec.	Jan.	all later periods	minimum nos. alive next period from each sample released	minimum survival rate
0	*1*	*2*	*3*	*4*	*T*		
0:**29**	*01*:13	*02*:4[1]	*03*:1	*04*:1	*0T*:1	20	0·69
.	*1*:**13**	*12*:6	*13*:1	*14*:2	*1T*:1	10	0·77
.	.	*2*:**9**	*23*:2	*24*:3	*2T*:2	7	0·78
.	.	.	*3*:**4**	*34*:3	*3T*:1	4	1·00
.	.	.	.	*4*:**9**	*4T*:6	6	0·67
		total individuals alive from original sample					
29	20	17[1]	14	14	.	.	.

[1] One animal accidentally killed.

May 1937. The best information about the breeding stock at the beginning of May is from the nearly complete trapping out of a nearby area (figure 3*b* and Appendix 1*d*), where there were 120 to 130 voles per acre. Table 12 shows that the numbers and proportions of animals marked on blocks *Q* and *E* are consistent with a similar abundance. This can also be seen from the following rough calculations: On block *Q* sixty-seven animals were caught in May, nine in June and seven later; on block *E* forty-four were caught in May, eight in June and five later. Since the survival rate was about 0·5 per period (table 17), these catches suggest that there were over 100 voles on block *Q* in May and well over half as many on block *E* which was about one-third the effective size.

June. Of the ninety-three adults released in May thirty-five were recaptured in June and at least two were missed until August. The minimum survival rate of 0·49 on block *E* (table 17) is probably close to the truth, as the traps were closely spaced and few animals seem to have missed recapture. The trace index (table 1) suggests little or no change in

TABLE 17. SURVIVAL DURING 1937–8

(*a*) Survival rates per period.

	May		June		Aug.		Sept.		Nov.*		Dec.*		Jan.		Feb.		Mar.		May		June
interval (weeks)		7·71		7·14		7·00		5·00		4·43		5·00		6·14		5·29		5·43		4·86	
ADULTS																					
block *Q*																					
nos. released	56		26		17		6		1		0		0		0		0		0		0
nos. alive next time	19		14		7		3		0		.		.		.		.		.		.
nos. included from later	0		2		2		0		.		.		.		.		.		.		.
min. survival rate		0·34		0·54		0·41		0·50		0		.						.			
block *E*																					
nos. released	37		22		20		5		2		1		1		0		0		0		0
nos. alive next time	18		13		10		1		1		1		0		.		.		.		.
nos. included from later	2		0		1		0		0		0		.		.		.		.		.
min. survival rate		0·49		0·59		0·50		0·20		0·50		1·0		0				.		.	
YOUNG																					
block *Q*																					
nos. released	.		11		29		47		28		24		59		81		56		26		5
nos. alive next time	.		2		20		33		21		19		31		37		20		3		0
nos. included from later	.		1		7		12		9		6		7		4		.		0		.
min. survival rate		.		0·182		0·690		0·702		0·750		0·792		0·525		0·457		0·357		0·115	
estimated survival rate (appendix 2)		.		.		0·772		0·727		1·0				(?>)0·544		0·601		0·464		.	
blocks *E-F*																					
nos. released	.		12		22		27		29		13		15		12		.		.		.
nos. alive next time	.		1		11		18		14		6		6		1		.		.		.
nos. included from later	.		0		3		4		3		1		0		.		.		.		.
min. survival rate		.		0·083		0·500		0·667		0·483		0·462		0·400		0·083		.			

(*b*) Weekly death-rates†.

	7·71	7·14	7·00	5·00	4·43	5·00	6·14	5·29	5·43	4·86
YOUNG ON BLOCK *Q*										
maximum observed	.	0·239	0·053	0·071	0·065	0·047	0·105	0·148	0·190	0·445
estimated	.	.	0·037	0·064	0		(?<)0·099	0·096	0·141	

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* Lines 9 to 15 only in block *Q*; 25 inner traps only in blocks *E* to *F* in calculating minimum survival rate.

† If P_t is the probability of survival over the interval of time t to $t+w$ weeks then the instantaneous death rate per week $= -\log_e P/w$.

numbers since May, which is consistent with the fact that less than half the sample consisted of young animals.

August. The minimum survival rate of the adults on block *E* was 0·59 for the interval; so that population density, after allowing for accidental deaths, should have been at least thirty animals per acre. By actual count only twenty adults are known to have been alive on block *Q*.

The young marked in June had almost completely disappeared, and even among males —where there is no reasonable doubt about the age groupings (§ 3)—there were only two young for every adult in the samples (table 4). Allowance must be made for inadequate sampling of the young, but the data suggest that numbers may have been little if any greater than in May. The trace index had, however, gone up.

September. The survival of the young marked in August was equal to or better than that of the adults, which were now very scarce. The presence of about 300 young per acre may be deduced by various methods (Appendix 2); but because of the doubtful validity of the premises the following evidence should also be considered. 187 individual young were counted on block *Q* between September 1937 and June 1938. Including those already marked in June and August 1937 the animals first appeared in the following months:

Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	May	June	total
47	37	12	26	42	17	4	2	187

The new animals added in each period were survivors of a larger number alive in September, and a rough estimate of the original population may be obtained by assuming some reasonable value for the rate of survival. A value of 0·9 per month, which is almost certainly too high, indicates that there were at least 240 voles in September; a value of 0·8 indicates 340. Refinements may be introduced to conform with the estimates given in table 17 and Appendix 2, but it is enough to know that 300 voles per acre is a fair statement of abundance at the end of the breeding season.

Winter and spring, 1937–8. In the 21 weeks between the trappings in September and February just over half the population died off; about 120 animals are estimated to have been left of which about two-thirds were caught (tables 12 and 19). Eleven weeks later, despite a greater trapping effort, only twenty-eight animals were taken; in June only five and in August none. During this last trapping not a single bait was disturbed. It is thus obvious that there was a difference in the mortality rates before and after February. From a more detailed analysis, however, it seems probable that the change occurred earlier (Appendix 2); and evidence from the estimated and observed minimum survival rates is that the death-rate accelerated rapidly from January onwards (table 17).

(iii) *Discussion*

The main facts about the population on block *Q* are as follows (figure 4). At the start of the winter 1936–7 there were about 300 animals; 120 to 130 were left by May 1937, and their death-rate probably increased from then onwards. Young born in May and June died rapidly and adults formed a fairly high proportion of the August population; numbers seemed little greater then than in the spring. (Table 1 and figure 4 show that the summer population of 1933 was also stationary.) The rate of juvenile survival now improved, and by September numbers were about what they had been a year before.

Severe mortality among the early young makes it likely that few if any had bred before August. Nearly all those marked in August were therefore first generation young. These females became pregnant (p. 516), and since few old breeders were left it must be assumed that a second generation entered the traps in September as well as more from the first. The second winter therefore started with a predominantly young population. Numbers remained high in the early winter, but between January and June almost the entire population disappeared. Body weights were low in the spring, and there was no breeding (§ 3).

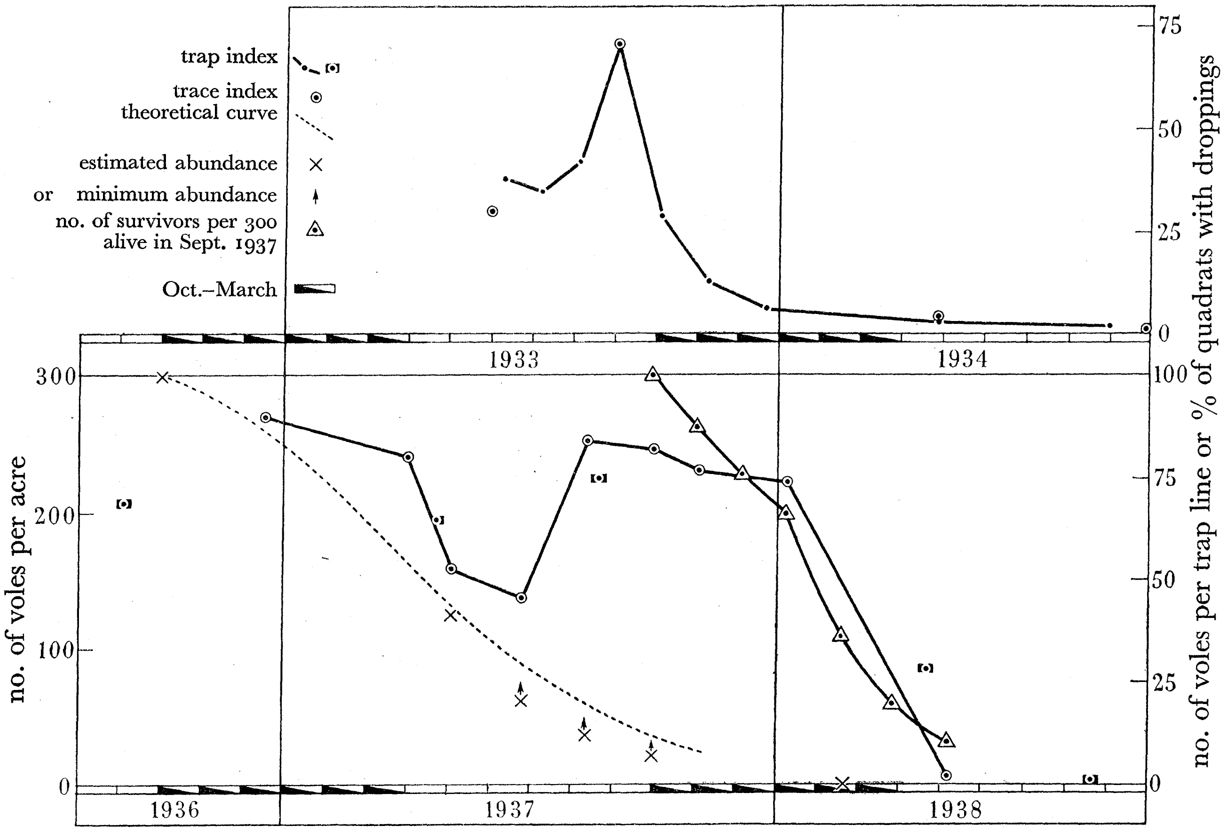

FIGURE 4. Changes in abundance of voles during two cycles. Data from table 1 for indices of abundance based on traces or number of voles taken in traps (lines join the points of the more complete index only). Estimates of the abundance of animals born in 1936 are respectively 300, 125, > 62, > 38, > 19 and 0 (from the text and best minimum survival rates in table 17). The broken curve shows the number of survivors to be expected from 300 animals if subject to the same death-rate as the laboratory voles studied by Leslie & Ranson (1940). The population curve for 1937–8 is obtained as described in Appendix 2.

Relatively more of the animals marked in August seem to have been alive from January onwards compared with those from the intervening samples. One generation only was marked in August but two were present by September, and this is the only important way in which the samples are known to have differed. We may be certain that both generations had a poor expectation of life; we may also suggest that the second tended to die off earlier than the first.

6. THE NATURE OF PERIODIC MORTALITY

The events of 1936–9 must now be interpreted to answer two questions: why the populations died off at all and whether those that disappeared simultaneously did so by chance alone. The latter question is dealt with separately, as it does not seem to be an essential part of these periodic phenomena for populations to be in phase. The attempt to answer the first question involves several preliminary difficulties. First it is necessary to define the mortality and to make a rather careful statement of the initial working hypothesis. Next, on the assumption that the observed mortalities were fair samples from a single class of such effects, various supposed causes can be eliminated. Finally, an explanation of the mortality is proposed; namely that the disappearance of two generations was a result of the stress to which a previous generation had been exposed.

(a) *Mortality*

A frequent difficulty in the search for invariant relationships is that one effect often seems to be produced by more than one cause. For example, there is no invariant relationship between the death of an individual and a single cause. But if the generic effect—death—is sufficiently well specified by symptoms—necrosis of the liver, gunshot wounds, etc.—then it will be less difficult to relate one effect to one cause. In the present instance the only known property of the mortality we are investigating is that it typically alternates with high abundance at fairly short and regular intervals. (The term 'periodic' used to describe these fluctuations should not be taken to imply mathematical regularity.) Unfortunately, we cannot test the regularity of events at Lake Vyrnwy because most of the areas had had no previous vole populations; also, because of the war and the complete change of habitat caused by the growth of the trees, few of the same areas were studied afterwards. We can only suppose, on the basis of a wider knowledge, that decrease in 1938 and 1939 was of the periodic type; there is certainly no evidence to the contrary. We also observe that certain changes in body weight were associated with the change from high to low abundance (§ 3), which suggests that the same population process was common to several areas. Before framing a general hypothesis, however, it is important to consider various mortality factors which may complicate the picture.

For example, if sheep had broken into a plantation and eaten enough grass the voles would have starved, migrated or become exposed to other risks. Or there might have been human interference or catastrophes such as flooding. Such accidents would no doubt have produced different effects from those resulting from the causes of periodic mortality; but if only the fact of decrease were known and its specific features had not been studied then accidents could not be eliminated as possible causes. Since the decrease has been defined as typically periodic these events would obviously destroy the 'standing causal conditions' implicit in the statement of every hypothesis relating cause and effect. Therefore, whatever the practical complications, no logical obstacles are raised when accidents occur. Other types of mortality, however, cannot be so readily discounted, for any increase in population density is likely to be accompanied by an increase in the rates of several mortality processes. The problem is to distinguish those which are merely contributory from those which are necessary and sufficient to account for periodic decrease. Let us suppose that a declining population is found to be heavily parasitized. It may be known that the parasites are capable of producing death, that the rate of infestation had increased as the population built up to a peak, and that during the decline some parasitized animals were found dead. It might be concluded that decrease in this case was a result of parasitism; in other instances diseases of various kinds might seem to explain why the populations died out. Dymond (1947) summarizes this viewpoint by saying: 'In the case of dense populations there appears to be a race between disease, emigration, and starvation as to which is to reduce the numbers....' It must be agreed that some of the more spectacular instances of abundance seem to have been terminated in these ways. However if any one of several causes is postulated as a sufficient explanation of periodic decrease some less obvious but more fundamental relationship may be overlooked. Therefore it may be more profitable to assume that despite their differences each instance is drawn from a single class of events. After examining sufficient instances we may then be able to eliminate all but one of several supposed causes. Even then it may still be impossible to prove that this single cause invariably produces the same effect, since clear causal relationships are unlikely to be observed among natural populations. Just as abundance may be terminated by accidents such as grazing or flooding, so various causes of mortality which are dependent upon population growth may mask, contribute to or entirely precede the effect of one supposedly common and sufficient cause. It is therefore necessary to define our working hypothesis in abstract terms, and the relationship we must postulate is between decrease, defined as typically periodic, and a single cause which will always produce it if no other process acts first.

If this single causal relationship existed at Lake Vyrnwy several possible reasons for the decrease can be eliminated. First, by comparing two or more populations we may rule out a group of mortality factors which were not common to all cases of decrease or which were sometimes present when the voles did not disappear.

Weather. At the time of decrease on Glasgwm voles were at a peak in nearby areas. No peculiarities of slope, vegetation or means of indirect action are known by which the same weather could have produced opposite effects on the body weight and fertility of the voles.

Disease. The only evidence of widespread disease was vole tuberculosis (Wells 1946). Voles were heavily infected on Glasgwm in 1938; but they had been as heavily infected in 1937. Moreover, voles disappeared in 1939 from areas where tuberculosis was rare. These findings will be published later, together with certain criticisms of the view that infectious disease is the primary cause of mortality among cyclic species.

Overcrowding, autumn 1937. There was little difference in initial density between the population which survived to breed on Glasgwm in 1937 and that which failed to breed there in 1938.

Qualitative food deficiency. There may have been a selective elimination of certain plant species. However, it is not known that any particular plants are essential to voles. Nor is a single deficiency disease likely to have been a common factor in plant communities as diverse as those at Lake Vyrnwy.

Next we may reject those explanations which were inadequate to explain the decrease on Glasgwm and by hypothesis elsewhere.

Predation. At the time of most rapid decrease there was little evidence of activity by hawks and owls (Appendix 1*e*). Moreover, the failure of reproduction could not have been caused by predators, though several species undoubtedly hastened the rate of decrease.

Migration. There was no evidence that voles migrated, nor were there any areas to which they might have gone.

Change in age structure. The overwintering population of 1937–8 consisted mainly of animals born in late summer; thus the age structure was not of the stationary type which Leslie & Ranson (1940) show would produce most rapid decrease. On the contrary the low age structure was similar to Leslie & Ranson's 'type A' from which the best survival would be expected.

No quantitative evidence was obtained about a number of other possible causes of death. Of several considered only the less improbable need be mentioned.

Starvation. The vegetation on Glasgwm was damaged in both winters 1936–7 and 1937–8. No areas, however, were devastated; indeed, from a distance of a few feet the effects on the vegetation were not always obvious. We may be reasonably sure, then, that there was no actual food shortage. We cannot dismiss the possibility that sufficient changes had been brought about to influence the behaviour of the animals; but such effects, if any, are likely to have been produced in both winters.

Environmental changes. Natural cover seemed adequate. The ground was somewhat contaminated with vole dung but not to an extent that seems likely to have produced toxic changes.

Season of birth. The majority of animals which overwintered on Glasgwm in 1937–8 were born late in the previous July or in August. The scarcity of young born earlier or later is thus one way in which this population was unusual, but no reason can be given for believing that birth at this time of year is a disadvantage.

Parasites. The study of parasites, other than *Toxoplasma* (Findlay & Middleton 1934), was judged irrelevant to this inquiry. None of the voles from Lake Vyrnwy died in the laboratory from parasitic infections of obvious importance.

There is no evidence, then, that decrease occurred because the contemporary environment was unusual. All possible causes have not, of course, been excluded, but earlier events now seem more significant. In one way at least 1937 was remarkable: despite a high birth-rate the population did not increase very much until August. In the two previous seasons, by contrast, the population must almost have realized its intrinsic rate of increase (Leslie & Ranson 1940), for numbers were low in April 1935, at least on areas adjacent to Glasgwm, and at a maximum in the autumn of 1936. Perhaps, therefore, the decline in the winter and spring of 1938 was a result of conditions among the stationary population of the previous summer. (Associated with these conditions in a way not yet understood was an unusually high body weight.)

The severe juvenile mortality in the early part of the breeding season suggests what may have been happening. The young may have died because they were not healthy; but if so this was probably not the whole truth. Later members of the generation survived better than their parents (table 17), and those brought into the laboratory in June and July lived at least as well (they did not, however, have a better survival rate). More probably the young in the field were killed by the adults, their selective removal being only the more obvious effect of intraspecific strife. If so, it is unlikely that only two age groups were involved, and probably there was fighting and mutual interference throughout the population. Most adults had died off by August, after which the young lived comparatively well until January. Two generations then disappeared without obvious reason.

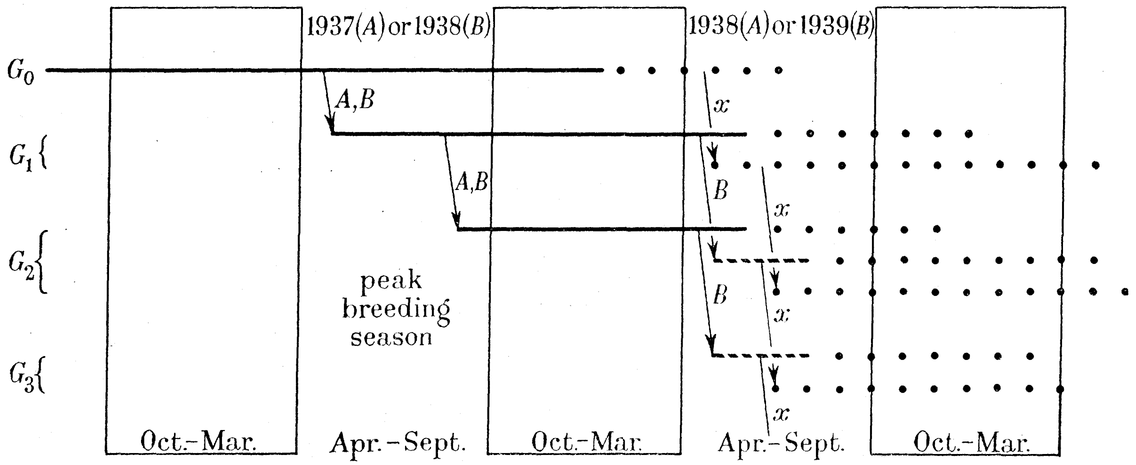

FIGURE 5. Scheme of probable relationships in time between generations (G_0 to G_3). Solid lines show the time during which some member of each generation was observed to be alive on the marking area or was inferred to be alive on other areas. Arrows marked *A* show the maternal origin of generations on the marking area; arrows marked *B* suggest the origin of the extra groups born on other areas (broken lines). Dotted lines and arrows marked *x* are a partial extension of the present data.

Let us now construct a diagram to show the relationships between these generations (figure 5). Horizontal lines show the length of time between the birth of the first member of a given generation and the death of its last survivor. Let G_0 represent the duration of life of the groups born on the marking area in 1936 and G_1 and G_2 represent the times lived by their descendants. The G_0 animals lived until January 1938 at least (table 12), and might have lived even longer if they had not been exposed to trap mortality. The longest known life among the G_1 generation was that of an animal marked in June 1937 and last retrapped in May 1938 (table 12). The first of the G_2 animals were marked in September 1937; they became virtually extinct by June 1938 and were probably less viable than the G_1 animals alive in the same period (table 13). This decrease in longevity is recorded in column *a* of the table of inferences below:

generation	(*a*) longevity	(*b*) fertility	(*c*) physiological condition
G_0	+	+	−
G_1	−	±	− −
G_2	− −	−	− − −

The reproductive rate of the G_0 animals was, as far as is known, entirely satisfactory. The G_1 animals gave rise to many young in August 1937, but failed to breed in the spring of 1938, and the G_2 generation did not breed at all. These observations are indicated in column *b* above. Now in order to account for this decrease in viability and reproductive performance it is necessary to postulate a delayed effect of some previous condition. It must be supposed, in fact, that the strife in the early part of the season, which was fatal for the young, had certain permanent effects upon the constitution of the G_0 animals. We cannot at present be more precise about this supposed condition than to imagine some disturbance of the hormone balance of the mother which in some manner affected the foetus (less probably the nestling). The inference that almost the entire population of adult females was physiologically affected through some intraspecific process thus differs from the observations of Calhoun (1949) on captive brown rats (*Rattus norvegicus*). Calhoun found that 'socially inhibited' brown rats were unsuccessful in rearing their young, but he records no ill effects among the dominants or their progeny. However, in a natural vole population, distributed as in figure 3*b*, for example, social relationships may be less clear-cut than those which Calhoun produced experimentally. Some of the G_1 voles in the overwintering population may have suffered in the summer from direct contact with the adults; but the majority seem to have been born in late July or August at a time when the older animals were getting scarce. Moreover, there was a good expectation of living for the next few months and the population was about to double its size. There is thus little evidence that conditions in the latter part of the breeding season could have been responsible for the eventual disappearance of the G_1 animals. Nor were they or the G_2 generation subjected to any greater crowding than that which had occurred in the previous autumn and winter. Now if there was indeed a progressive reduction in viability and fertility this may well have been a result of general constitutional defects. The sequence in column *c* above is therefore proposed, though clearly the process must come to an end within a certain time or within so many generations.

Next consider area *B* and others like it. The chief differences were that breeding continued through September instead of ceasing in August and was resumed in the spring of the decrease. Because of the later autumn breeding it seems likely that there were relatively more G_2 than G_1 animals in the overwintering population than there had been on the marking area, hence that they may have formed a higher proportion of those which survived until the spring. If this is true then both G_1 and G_2 generations were breeding at a fairly normal intensity (table 8). There is thus no agreement with the progressive decrease in fertility found on the marking area (column *b*), though the lowered expectation of life (column *a*) is amply confirmed. Also, since the young born in the spring of 1939 almost entirely failed to survive, there is reason to believe the inference from the last entry in column *c* that few of the G_2 animals could produce normal young.

All populations became practically extinct within 12 months of the start of the peak breeding seasons; but this may not always happen. The possibility of a more complicated pattern of decrease is shown by the dotted lines and additional arrows (x) in figure 5. If there were enough fertile survivors in the breeding season after the peak some recovery would be expected, followed by final decrease 12 months later. In general it seems likely that the rate of population decrease will vary a great deal, according to the expectation of life of the various generations and the relative numbers of each. Figure 5 thus extends the present data to include instances where the expectation of life is less drastically reduced, or is inherently greater as in some other species.

The steps which led to the mortalities of 1938 and 1939 may be summarized as follows: (1) strife during the breeding season resulted in (2) the early death of the young and physiological derangements among the adults. (3) The later progeny of these adults survived, but (4) were abnormal from birth and thus more susceptible to various mortality factors. (5) These constitutional defects, in a more severe form, were transmitted to the next generation.

At present these concepts can be stated but not explained. Physiological mechanisms have yet to be described whereby generations not directly exposed to stress may nevertheless suffer its consequences. It is not improbable, however, that such effects could be produced by the 'diseases of adaptation' of Selye. A useful account is given in the *Lancet* (Anon. 1951) of Selye's concept of the general adaptation syndrome, i.e. the non-specific morphological and physiological changes produced by various kinds of unfavourable conditions. Christian (1950), in a most important paper, has reviewed the evidence that symptoms found in certain natural populations are typical of disorders of this mechanism and has already concluded that they are responsible for periodic decrease in certain mammals. It has been known for some years that voles in captivity will fight to the death under some circumstances (Ranson 1934). More recently this aggressive behaviour has been studied at this Bureau by Mr J. R. Clarke, who has found certain morphological changes typical of a stressed condition. So far, however, there is no experimental evidence that the young of stressed females have a reduced longevity or fertility.

(*b*) *Synchrony*

If all properties of a fluctuation in numbers were accounted for by an intraspecific process, separate populations would fluctuate independently. In fact, there is a strong tendency for similar states of abundance to occur over larger areas than seems likely by pure chance. Exceptions are important in showing that no regular climatic cycle can be directly responsible for the mortality; but the tendency for separate units to be in phase must be due to some co-ordinating process.

It has been shown that some form of intraspecific strife seems to be the process controlling population density. We may reasonably suppose that the action of the factors capable of producing this control is 'governed by the density of the population controlled' (Nicholson 1933) or is 'density-dependent' (Smith 1935). Crombie (1944) has shown that the frequency of chance encounters between individuals has this property and that the resulting mortality rate in larvae of *Sitotroga cerealella* and *Rhizopertha dominica* increases in linear relationship to density. He has termed the process 'competition for space', having shown that the behaviour of the organisms was not caused by factors such as food shortage. Crombie also demonstrated a second type of competition for space. He found that irrespective of the number of larvae introduced into a wheat grain a constant number of adults emerged. The relationship between mortality rate and density was in this case curvilinear.

These experimental findings offer us a possible model of the type of competition among voles. It will be convenient to refer to their intraspecific strife as competition for space, though we know little about the factors involved and may suspect that the survival value is ultimately related to food supply. However, in a natural population it is unlikely that this competition is a function of an absolute amount of space. For example, voles seem to be much less tolerant of crowding at the height of the breeding season than they are in the autumn and winter. Similarly the amount of food and cover together with many other environmental factors are likely to modify intraspecific spatial relationships. Thus besides the likelihood that periodic mortality is accounted for by competition for space there may be further consequences if this process varies in response to environmental changes.

Let us examine these possibilities by considering two similar areas in one of which voles have reached the same abundance as that attained 12 months previously in the other. If the physical environment remained constant or if each season resembled that of the year before these populations would be expected to fluctuate one year out of phase. However, each breeding season will generally differ from the one before, and throughout each year there will be daily and seasonal changes in the environment. If such changes affect the severity of competition the expected tendency would be to favour the survival of individuals in the sparser population and thus to eliminate contemporary differences in numbers. In an unusually favourable season, for example, low populations might approach an exponential rate of increase, whereas those which were already abundant would not be able to increase as fast. Similarly, if each breeding female gained exclusive use of a territory then the number of established females per acre should be constant for all populations whose winter abundance had exceeded a certain threshold.

We may conclude that competition for space cannot by itself account for the tendency towards synchronous fluctuations. For this to be brought about it would be necessary for populations in different stages of abundance to experience marked changes in their relative rates of increase or survival. This could happen through density-dependent changes in the severity of competition for space. Such changes might be expected in response to changes in the environment, particularly those produced by weather. The extent to which fluctuations would be synchronized would thus depend upon the variability of the weather, the regional extent of the variations and the differences in initial density of the populations.

Other factors, such as predation, no doubt play an important part in producing a regional uniformity of abundance.

(*c*) *Implications*

If it is generally true that periodic decrease in voles is a result of intraspecific competition then certain extensions of the concept must be explored. The first is that periodic decrease in some other mammals is a result of intraspecific competition. This seems likely in the case of the snowshoe hare or 'rabbit' (*Lepus americanus*). The best evidence about the course of a decline is given by Green & Evans (1940). Their study began at the end of a period of increase, maximum numbers being found in the 1933 estimates of spring abundance. On 1 square mile of the area, however, the peak year was 1935, and it is possible that spring densities of population during 1933–5 were, in fact, rather similar over the rest of the 5 square miles. Whatever the truth of this it is certain that at least between 1935 and 1938 there was a rapid and continuous decline; also that this was largely because of an annually increasing death-rate among the young.

We must therefore account for the fact that although abundance (and presumably competition) was much reduced, yet the population continued to decline for at least three and possibly five consecutive years. Green & Evans were unable to account for this decrease in terms of the external environment, but found that the population was suffering from severe physiological derangements typified by low levels of blood-sugar and liver glycogen and known as 'shock disease' (Green & Larson 1938). Christian (1950) gives reasons for believing that shock disease may be a direct result of stress among crowded populations. However, the decrease for 3 to 5 years after peak numbers had been passed cannot be explained by the amount of overcrowding during the period of maximum juvenile mortality. It seems more likely that, as in the vole, the descendants of crowded animals were suffering from physiological derangements derived *in utero* from their parents. A progressive reduction in viability in each of the generations born during and after the period of peak numbers fits the observed facts well. On this assumption an acceleration in the total juvenile death-rate is an inevitable result of the dying out of the older, least affected breeders.

If it is true that intraspecific competition alone can account for periodic decrease in snowshoe hares we next have to explain why other species have a cycle of similar length, roughly in phase with that in the snowshoe hare. It will be sufficient to suggest the difficulty of explaining this by considering the cycle in ruffed grouse (*Bonasa umbellus*). There seem to be three ways in which synchronous cycles in hares and ruffed grouse might be explained. Both might be caused by some common factor; one might be dependent on the other; or the two cycles might be caused independently but be synchronized by weather. The hypothesis of some common cause of decrease is ruled out if it is true that intraspecific competition explains the cycle in the hare. It is, in any case, difficult to imagine any single factor except weather which might be capable of bringing about simultaneous decrease in both species; and it is virtually certain that the decrease itself is not caused by a cycle in weather or other climatic factors. Among other objections to such a view is the fact that decrease from peak numbers may occur in almost every year in some part of North America (Clarke 1936; H. Chitty 1950).

The disappearance of one species probably has some effect upon the other. Peak populations of hares may greatly damage the vegetation; hares and grouse have certain parasites in common (Green, Evans & Larsen 1943) and, as Lack (1951) has suggested, predators no doubt take a significant toll of grouse when the hares disappear. Nevertheless, it seems unlikely that there are enough hares to account for the grouse cycle in all areas where it occurs, nor is the hare always the first of the two populations to disappear (Clarke 1936). Moreover, there are certain population changes during a decline in ruffed grouse which are probably not caused by the disappearance of hares. Clarke (1936) reports a typically high proportion of old birds in declining populations, and King (1937) states, but without giving his data, that these older birds furnish the breeding stock responsible for the next recovery. In fact the decline in ruffed grouse, and also in bobwhite quail, *Colinus virginianus* (Errington 1945), is similar to that in the snowshoe hare in being spread out over several years after a period of fairly stationary numbers. The view that the ruffed grouse cycle is due to an intraspecific process is, of course, implicit in Errington's general conclusion (1946) that 'intraspecific self-limiting mechanisms basically determine the population levels...'. It is not impossible that these mechanisms may be essentially similar in both hare and grouse.

One of the difficulties about accepting such views on population control is to see why different species should have cycles of the same periodicity and be approximately in phase. The intrinsic rates of increase may well be different in the hare and ruffed grouse, and peak abundance is certainly not the same (Lack 1951). It would therefore be expected that their cycles would differ in length. Since this is apparently not so it must be supposed that periodicity is a function of some parameter of a rather similar magnitude in the two species. The mean time between generations, for example, might be similar in both species; but since the hypothetical common parameter is unlikely to be identical, we would expect the two cycles to differ slightly in periodicity, to coincide comparatively seldom and then by chance only. Why, then, do these supposedly independent cycles keep approximately in step? Apart from the interactions already discussed, the two species are exposed to certain common hazards of the physical environment. It is probably weather which, over quite large areas, keeps distinct populations of snowshoe hares approximately in phase, and it is not impossible that similarly powerful effects are produced upon other species. Moreover, a sufficiently strong action of the physical environment would reduce the effect of specific differences in population parameters. There is then one further difficulty. If weather has this powerful effect it would be expected that the length of the cycle would vary geographically in a species whose range included a wide variety of climatic conditions. There is no evidence that this is so, though no critical comparison has yet been made of the lengths of cycles, for example in Alaska and Nova Scotia.

We may summarize as follows the difficulties of extending to other species the concepts about vole cycles. If snowshoe hares die off periodically because of severe intraspecific competition then the cycle in ruffed grouse is likely to be independent. Given two independent cycles it would be expected that their periodicities would differ; but they apparently do not. If this can be accounted for by an overwhelming effect of weather then the length of a cycle should vary at the extremes of a species' range. No such differences have been described. The expectations from the hypothesis of intraspecific control of numbers are thus at variance with some of the current descriptions of cyclical phenomena, for example, that by Rowan (1950). The discrepancies, however, suggest additional ways in which the present hypothesis may be tested and modified.

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APPENDIX 1. SUPPLEMENTARY DATA

(*a*) *Voles outside the plantations.* Two comparisons were made of the relative numbers of voles inside and outside the plantations (see also area *B*4, table 3). Twenty-four traps were set in line 10 yd. apart, half inside the plantation, half in the sheep pasture. In a line which included a great deal of *Juncus effusus* three voles were taken in the pasture compared with eight in the plantation; in a line where there was short grass only none was taken compared with eight in the plantation.

(*b*) *Spacing of traps.* Relative efficiency of the 5 and 10 yd. spacing of traps was tested on three occasions. Twenty-five traps were set the same day in parallel lines 25 yd. apart. In these particular populations 14, 13 and 6 voles were taken at the 10 yd. spacing compared with 8, 7 and 4 at the 5 yd. spacing. At higher population densities there would presumably have been less difference in catch.

(*c*) *Numbers of voles in two other Welsh areas.* To the south of Lake Vyrnwy the Forestry Commission had enclosed a large area of similar country. I am indebted to Mr F. Davies, Forester of Dyfnant Forest, for having run a number of 1-day lines of twenty-five traps at 10 yd. spacing. His results showed that there was a very marked decrease in voles between 1938 and 1939. Four identical lines run in June yielded thirty-six voles in 1938 (6, 9, 10, 11) compared with none in 1939. The lines were about 1½ miles south of the Cownwy valley (square 9915 below figure 1) in plantations made in 1932–6, but all probably enclosed rather earlier. Dyfnant Forest adjoins the Cownwy River and area *C*.

Mr W. A. Cadman, then the Forestry Commission's District Officer at Machynlleth, kindly supplied me with extensive notes about voles on Hafren Forest, on the east slopes of Plinlimmon, 25 miles south-west of Lake Vyrnwy. This area was enclosed in 1936, but no abundance of voles was noted before the spring of 1939. Voles reached their first peak in 1940—when there was much damage to the trees—and decreased in 1941.

(*d*) *A direct count of numbers.* In April–May 1937 an attempt was made to determine numbers by trapping all the voles from an area by means of 158 break-backs. A natural boundary was formed by a deep stream along one side and a thick conifer plantation on the other; between them was an area about 60 yd. wide, mainly *Holcus* spp. with a patch of *Juncus effusus* by the stream. Traps were set every 5 yd. in grid formation for a length of 60 yd. (figure 3*b*). The area lay approximately opposite block *E*, the deep stream being about 25 yd. from and approximately parallel to line 15 of the marking area.

Traps were set on 29 April and visited twice daily until the morning of 6 May. After the morning visit of 4 May all traps were moved to new positions within a few feet of the first, and in the next 24 h the catch was higher than on any day since the first. The explanation may be either poor placing or setting of some of the original traps or the capture of animals which did not use or had learnt to avoid the old sites. The distribution of the catch is given in figure 3*b*. Nearly all the animals are likely to have been removed, though five were taken on the last morning:

April–May		29/30	30/1	1/2	2/2	3/4	4/5	5/6	total
no. of voles caught:	p.m.	15	10	6	4	4	9	0	
	a.m.	14	5	7	11	4	12	5	106

More males were taken than females, but there is no evidence that they had moved in at the two ends.

Numbers per acre may be estimated as follows: if it be assumed that the traps caught half the animals within 10 yd. of each end (§ 4), the area sampled was 4243 sq.yd. Alternatively, the lines at each end may be disregarded and the area trapped be taken to extend to within 2·5 yd. of them. If the two lines at each end are omitted the area is 2754 sq.yd.; if four lines are omitted the area is 1492 sq.yd. The numbers included within these three boundaries are 106, 76 and 37 voles, giving estimates of 121, 133 and 120 voles per acre.

(*e*) *Predators*. In 1936–9 Lake Vyrnwy supported a variety of predatory animals including buzzards (*Buteo buteo*), sparrow hawks (*Accipiter nisus*), little owls (*Athene noctua*), long-eared owls (*Asio otus*), stoats, weasels, polecats (*Mustela erminea*, *M. nivalis* and *M. putorius*), foxes (*Vulpes vulpes*) and the following birds whose pellets consisted chiefly of the remains of *M. agrestis*:

Kestrel (*Falco tinnunculus*). In September and December 1937 a kestrel was seen throughout the day on Glasgwm, though not more than two were seen in the air at once. From January 1938 they were seen much less often though they were present elsewhere, particularly in area *B*.

Short-eared owl (*Asio flammeus*). One was seen on Glasgwm at dusk on seven different days between 6 January and 30 March 1938. Two were reported to have been flushed here in January, and one may have been seen occasionally in area *B* in 1938.

Tawny owl (*Strix aluco*). As a rule not more than one was heard at dusk on Glasgwm during 1937–8, but on 19 February 1938 three were within earshot, one being very distant.

Barn owl (*Tyto alba*). This bird often roosted in derelict cottages among the plantations though few were heard on Glasgwm.

Ten fence posts were inspected for pellets on Glasgwm, though this scheme (Elton 1942, p. 192) was not started until January 1938. Many old pellets were found then (one included a vole ring), but only four new pellets had been produced by February, none by March, two by May and none thereafter during 1938–9.

APPENDIX 2. STATISTICAL ANALYSIS OF DATA FROM MARKING AND RECAPTURE

The results of marking and retrapping cannot be interpreted without a careful use of the facts in § 5 about the sampling procedure and characteristics of the animals. Results on block *E* cannot be used because immigration and emigration may not have been negligible, and old animals cannot be grouped with young because they had different death-rates, both natural and induced. Hence the present analysis is restricted to the fate of those young which were alive on block *Q* in August and September 1937 (table 12). Even among these animals there were differences in death-rates which affect the calculations. The most important are the apparently better survival of voles in the August sample, and of those in lines 9 to 15 which alone constituted the December sample. A big change in rate of survival half-way through the experiment makes it necessary, for certain purposes, to consider the data in two groups. Ideally we would wish to subdivide the data still further: into those for males and females, for the two sections and for smaller units of time. However, such procedure would mean a great loss of precision, and the individual estimates would not be as useful, given the present data, as the more general conclusions reached below. The non-random sampling of marked and unmarked animals complicates the estimates of total numbers before February but should have little effect upon the estimated rates of survival, probably none at all from November onwards. Accidental deaths among recaptured animals are ignored in calculating separately the survival rates for each period, an error which should not be serious.

While it is necessary to proceed with the analysis despite the obvious falsity of certain assumptions it is thought that enough precautions have been taken to derive a reasonable simplification of a complex natural event. Jackson's methods (1948) have been used with modifications, particularly in the weighting of the figures where procedure is based on that of Dowdeswell *et al.* (1940). Some acquaintance with these papers is necessary in order to follow the present analysis.

(*a*) *Probability of survival* may be estimated by comparing the numbers recaptured per animal released on two occasions; the assumption is that each sample is subject to the same death-rate after the release of the second sample. From table 12 it is seen that twenty-nine animals were released in August and that ten of them were recaptured in November, i.e. the recapture rate was $10/29 = 0{\cdot}345$. For the same trapping effort twenty-one animals were recaptured from the forty-seven released in September, a rate of $0{\cdot}447$. The ratio $0{\cdot}345/0{\cdot}447 = 0{\cdot}772$ estimates the survival rate during the 7 weeks between trappings in August and September. If there had been no deaths the expected ratio would be unity. Further estimates may be obtained from results in December, January, etc., the probability of survival P_t over the interval t to $t+w$ being estimated

$$P_t = \frac{47}{29}\left[\frac{10}{21}, \frac{4}{6}, \frac{9}{12}, \ldots\right].$$

It seems, however, that the two samples did not have the same expectation of life, and that after November (table 13) the relative recapture rates are not valid estimates of survival between August and September. The only available estimate is therefore the first one (0·772), later ratios being biased upwards.

Survival between September and November is estimated by

$$P_t = \frac{55}{47}\left[\frac{6}{12}, \frac{12}{19}, \frac{17}{22}, \frac{7}{12}, \frac{4}{7}, \frac{0}{2}\right].$$

These samples were drawn from two fairly comparable populations and should not be seriously affected by non-random sampling of older and more viable animals. A reasonable estimate of P_t is probably 0·727, obtained after summing all the numerators and denominators. Similarly for survival between November and December $P_t = 0{\cdot}773$. Unfortunately, the December sample was drawn only from the area with the higher survival rate, so that there should have been a greater probability of recapturing animals from this sample than from one representing the whole block. The estimate is therefore likely to be low. A less biased estimate should be obtainable from the data for lines 9 to 15 only:

Nov.	Dec.	Jan.	Feb.	Mar.	May	June
29^{1}	12^{3}	7	14	9	7	2
	27^{3}	13^{1}	10	7	4	1
		28^{1}	13	7	6	1

However, there is no evidence from these figures of any mortality between November and January. This result may be true for this section or merely a random error from subdividing already inadequate data; but returning now to the complete data we observe that between November and January

$$P_t = \frac{59}{55}\left[\frac{22}{24}, \frac{12}{13}, \frac{7}{7}, \frac{2}{1}\right] \doteqdot 1.$$

Yet the evidence from table 13 is that there had been mortality, at least among the animals first marked in September and November; if so, the observed recapture rate of the January sample is lower than expected. From a subdivision of these data it seems that the low recapture rate is not entirely explained by the excess of males (32♂♂, 27♀♀) or of animals from lines 1 to 7 (32 from lines 1 to 7, 27 from lines 9 to 15) though both these classes had higher death-rates. The fate of this sample must therefore be examined in more detail.

We may first see if there was evidence that trapping in January had weakened the unmarked voles and increased their subsequent death-rate. Conditions at the time were not obviously severe and there was no abnormal death-rate in the traps on block *Q*, but there was in fact a rather poor recovery of newly marked voles. This difference is not statistically significant, however, and there is no evidence from other months that it might have been expected. Indeed, the only other evidence—from the November sample—is in the other direction. These two extreme instances are given below, animals first marked in August being omitted in order to reduce any bias. The numbers recaptured include all individuals known to have been alive in the next month:

sample ...	November			January		
		alive next month			alive next month	
	released	no.	%	released	no.	%
previously marked	15	5	33	25	15	60
newly marked	31	15	48	25	10	40

These variations are presumably due to random errors of sampling.

The next task is to see if the marked animals themselves survived less readily than usual as a result of being trapped in January. To do this we can see if there were fewer recaptures from animals which were caught in January than from those which were missed. To find the number of marked animals which were missed in January we have the estimate from table 19 that the number of marked animals caught (36) was 0·45 of the marked total, i.e. that there were eighty marked animals of which forty-four were missed. From the original data the numbers of all animals recaptured may be compared as follows:

	Jan.	Feb.	Mar.	May	June	total alive in Feb.
released in January:						
newly marked	25	8	4	3	0	10
previously marked	34	16	9	4	1	21
missed in January:						
previously marked	44	17	9	6	1	19

From this there is no evidence that capture in January caused the death-rate to increase.

Having found no systematic errors in the data for this sample we may re-examine the conclusion that there was no death-rate between November and January. The number of new individuals added in each month was forty-seven in September, thirty-seven in

November and twelve in December. There were no accidental deaths among those recaptured from the September sample, but three new animals died in November and another three from this sample died in December. If we accept the estimate of survival between September and November then thirty-four marked animals were alive in November (out of the forty-seven previously released) and there can have been no deaths among them, or among the thirty-four released in November or the twelve released in December if eighty marked animals were alive in January. Even if eighty is a slight over-estimate of the marked population these calculations support the view that survival was very good up to January. Nevertheless, a slight random error seems probable in the recaptures from this month's sample; for it is hard to believe that a wild population could have suffered no mortality for over 2 months (see also Appendix 1*e*).

TABLE 18. DISTRIBUTION OF MARKED INDIVIDUALS ACCORDING TO THE INTERVAL SINCE THEIR PREVIOUS CAPTURE

	month of recapture ...	Sept.	Nov.	Dec.	Jan.	Feb.
month in which last captured:	Sept.	.	21	3	6	2
	Nov.	.	.	12^3	16^1	9
	Dec.	.	.	.	13^1	6
	Jan.	.	.	.	.	24
no. marked		.	21	15^3	35^2	41
no. unmarked*		47	37^3	12	26	42^2
total catch		47	58^3	27^3	61^2	83^2

	month of recapture ...	Jan.	Feb.	Mar.	May	June
month in which last captured:	Jan.	.	24	7	0	0
	Feb.	.	.	33^2	4^1	0
	Mar.	.	.	.	20^1	0
	May	.	.	.	.	3
no. marked		.	24	40^2	24^2	3
no. unmarked*		61^2	59^2	18	4	2
total catch		61^2	83^2	58^2	28^2	5

* Including those marked before the relevant period.

After January the survival rate decreased sharply, the estimates (table 17) being fairly reliable, as far as is known, except perhaps for that between January and February which may be too low, since adjacent estimates are negatively correlated.

In addition to these separate estimates a smoothed estimate of the rate of survival may be obtained (Leslie & Chitty 1951); the principle is that marked individuals are grouped according to the interval since their previous capture. It is assumed that the death-rate is constant and independent of age. Accordingly, the August sample must be excluded and the data must be considered in two periods within which the rate of survival was at least roughly constant. The data required for these calculations are given in table 18, superscripts denoting accidental deaths for which corrections have been made.

From these analyses the constant survival rates (P) and standard errors per period are estimated as follows:

Sept. to Jan. $P = 0{\cdot}874 \pm 0{\cdot}040$ (mean interval 4·81 weeks)
Jan. to May $P = 0{\cdot}544 \pm 0{\cdot}044$ (mean interval 5·62 weeks)

A slight error is introduced by the fact that the intervals between trappings were unequal. However, the order of magnitude of the change in death-rate is undoubtedly shown by comparing weekly death-rates based on the mean intervals within the two periods. From the formula in table 17 the increase in death-rate is found to be from about 0·028 to 0·108 per week.

(*b*) *Total numbers* in a non-breeding season should be obtainable from a modification of the 'Lincoln index' (Lincoln 1930); but unfortunately it was only from February onwards that the whole population seemed finally to be at risk to the traps (p. 527). Direct estimates of the February population, corrected for bias by the method of Chapman (1951) are:

$$N = (81+1)\left[\frac{58+1}{33+1}, \frac{28+1}{18+1}, \frac{5+1}{2+1}\right] = 142,\ 125,\ 164.$$

These estimates will be high if in fact some dilution was still occurring, but we may check this by using two of Jackson's methods which allow for it. Assuming mortality independent of age (which was probably true by February)

$$N = \frac{81\times 83}{24}\times\frac{13+7+1}{33+18+2} = 111.$$

We may also use Jackson's 're-recapture' method which does not make this assumption. Instead, the following relationship is assumed:

$$\frac{\text{marked animals recaptured}}{\text{total marked animals alive}} = \frac{\text{total catch}}{\text{total population}}.$$

The left-hand member may be estimated from recaptures in later months, as in the following set of data where x denotes a capture:

	distribution of captures			symbols
period	0	1	2	
3 animals, each	x	x	x	$\left.\begin{matrix} r_{012} \\ r_{02} \end{matrix}\right\} = k_{02}$
2 animals, each	x	.	x	
3 animals, each	x	x	.	r_{01}
total individuals	8	6	5	

In period 1 six marked animals were retaken. In period 2 three of these were again retaken out of a total of five from the original sample. The proportion $r_{012}/k_{02} = 3/5$ estimates the proportion of marked animals taken in period 1 and, by hypothesis, of the whole population at the time. If the catch of all animals is C_1 the population is estimated as $N_1 = C_1 \times 5/3$.

In columns 2 and 3 of table 19 the data for this analysis have been extracted from the original records; columns 4 and 5 are obtained from table 12 using all relevant data up to June 1938. For example, the figure 77 is obtained for February by summing all the entries $(1+1+0)+(5+4+1)+\ldots+(13+7+1)$. For method (*b*) the bottom row of twenty-one recaptures is omitted. If columns 2 and 4 are used (method *a*) the data are larger but not entirely independent of Jackson's previous method. If columns 3 and 5 are used (method *b*) the data are smaller but independent. These methods are invalidated if there is much re-immigration. Recaptures of the animal marked in June 1937 are therefore disregarded until after its inclusion in the February sample; for simplicity, no correction has been made for two other re-immigrants (p. 520). For February

$$\text{by method } (a) \quad N = 83\times 77/48 = 133$$
$$\text{by method } (b) \quad N = 83\times 56/37 = 126$$

Estimates may be made for each month by these two methods and the previous one and will be found to agree fairly well except in September for which month method (*a*) alone is valid. All these estimates are presumably subject to a slight upward bias which Chapman's correction is designed to remove.

Before February these estimates refer only to the population at risk. Each must therefore be corrected by factors worked out from table 12 as shown on p. 527. Thus for September the true population is about four times the uncorrected estimate of 69 by method (*a*), i.e. roughly 300 voles.

TABLE 19. PROPORTION OF MARKED ANIMALS RECAPTURED

month in which recaptured	no. of 're-recaptures'		total recaptures of all voles for same periods		proportion recaptured	
	(*a*)	(*b*)	(*a*)	(*b*)	(*a*)	(*b*)
Sept.	28	.	41	.	0·68	.
Nov.	40	19	77	31	0·52	0·61
Dec.	35	18	129	67	0·27	0·27
Jan.	50	39	111	89	0·45	0·44
Feb.	48	37	77	56	0·62	0·66
Mar.	42	26	52	32	0·81	0·81
May	10	7	10	7	1·00	1·00

Column headings (*a*) and (*b*) denote, respectively, the use of data by the full and independent 're-recapture' methods of Jackson (1948).

Other estimates may be derived by a different method. Assuming that there were about 120 voles in February, we may calculate, from the estimates of survival in table 17, how many there must have been in September. Again about 300 are indicated. (Calculations based on estimates of the March or May populations are similar but less reliable.)

Finally, by using the smoothed survival rates already obtained, we may make an estimate at least of relative numbers alive in each month. Assuming an original population of 300 in September the rate of 0·874 may be applied to obtain the numbers up to January and the rate of 0·544 to obtain the subsequent numbers. Results are as follows, mean intervals being used between September and January and January and May:

Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	May
300	262	230	200	109	59	32

The agreement with the previous estimates for February is satisfactory, but since the death-rate was probably accelerating (table 17) instead of being constant the smoothed rate tends to underestimate the February population. Probability of survival cannot be estimated for May to June, but the minimum survival rate of 0·115 (table 17) is no doubt close to the true value since trapping was very thorough. The minimum population is thus estimated as four animals. Five were actually caught, and it is not unlikely that they represented nearly all the survivors.

It must be emphasized that these figures apply to an imaginary population of 300 animals alive in September, and that numbers have not been estimated from the data themselves. The close agreement with other evidence, however, lends confidence to the belief that there were about 300 animals in September and that their rate of decrease was approximately as shown in figure 4.

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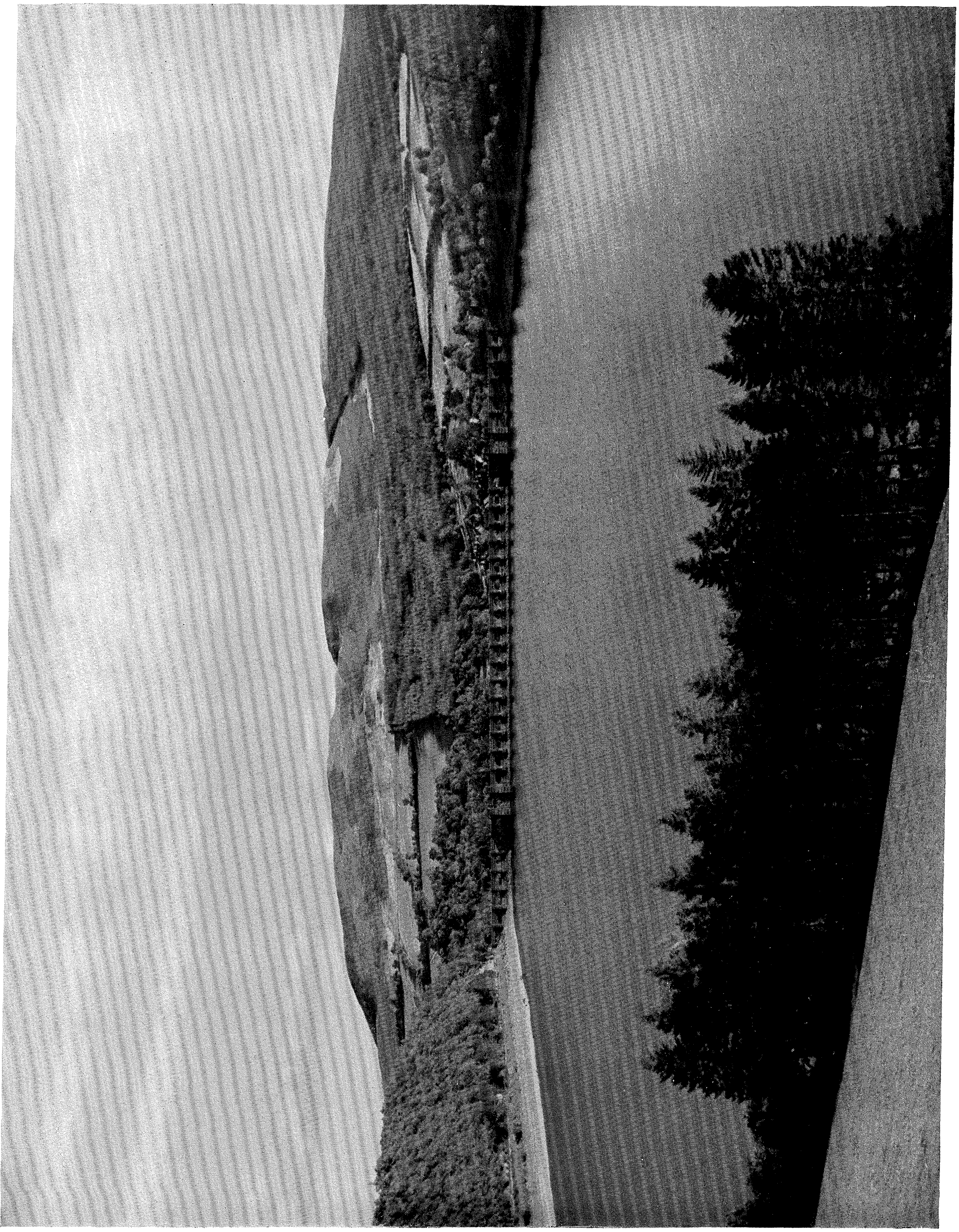
Above. Sitka spruce planted in 1936, photographed in January 1939; area *B*2 looking towards Garth-bwlch house. (Photo G. Clark.)

Below. Sitka spruce planted in 1934, photographed in February 1939; area *B*3 looking southeast. (Photo G. Clark.)

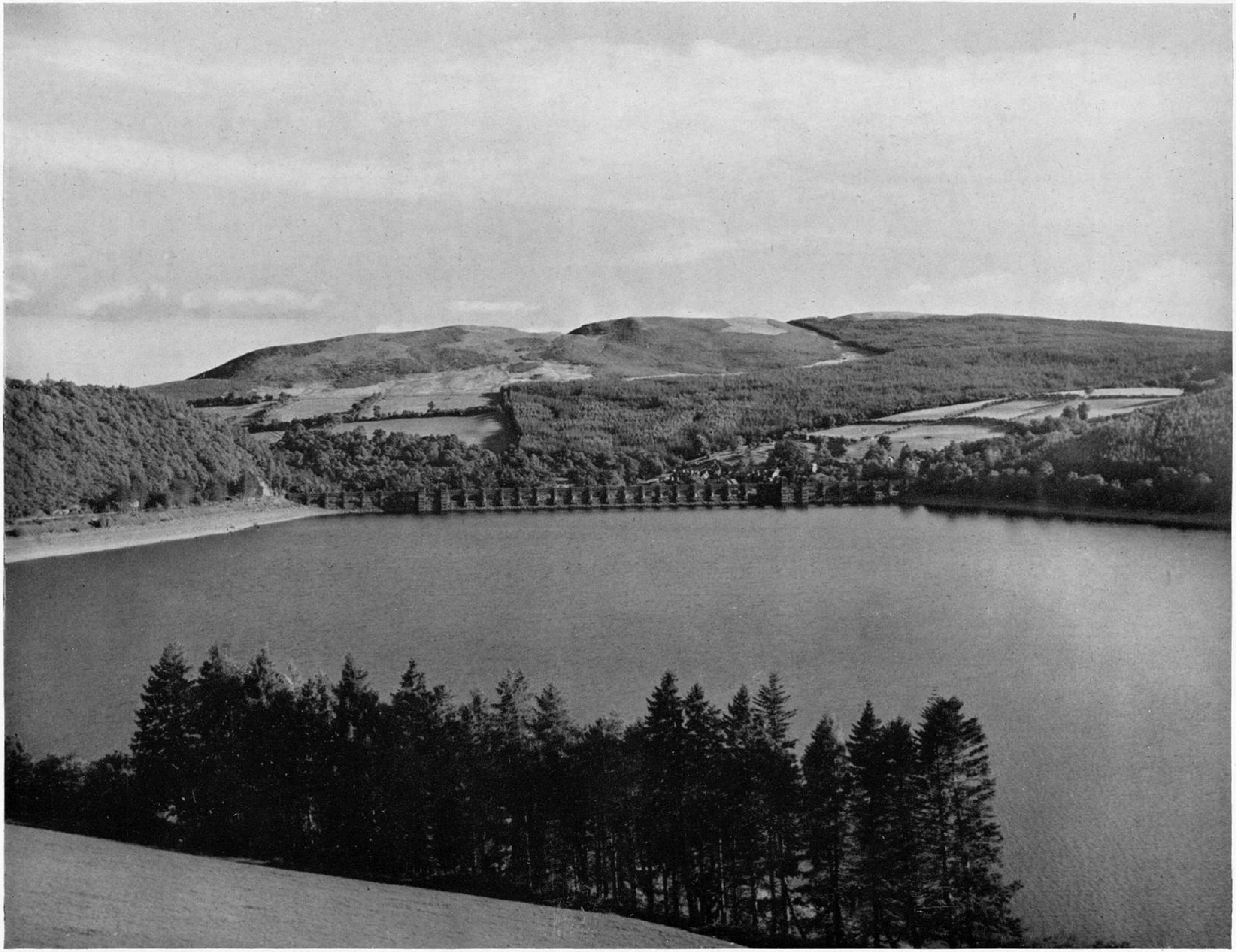
(*Facing p.* 552)



View from 015205 of Lake Vyrnwy dam and areas *B*1 and *B*2 beyond it; Sitka spruce planted in 1933 and 1936 and photographed in September 1949 when the areas were completely unsuitable for voles. This plantation would itself form an ecological barrier to voles in any new plantations on the surrounding land. The highest point in the photograph is 1304 ft. (Photo D. Chitty.)

Above. Sitka spruce planted in 1936, photographed in January 1939; area *B*2 looking towards Garth-bwlch house. (Photo G. Clark.)

Below. Sitka spruce planted in 1934, photographed in February 1939; area *B*3 looking southeast. (Photo G. Clark.)



View from 015205 of Lake Vyrnwy dam and areas *B*1 and *B*2 beyond it; Sitka spruce planted in 1933 and 1936 and photographed in September 1949 when the areas were completely unsuitable for voles. This plantation would itself form an ecological barrier to voles in any new plantations on the surrounding land. The highest point in the photograph is 1304 ft. (Photo D. Chitty.)