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A POPULATION STUDY OF FIELDMICE *APODEMUS SYLVATICUS* IN THE BURREN

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Abstract

This study entailed a comparison of two fieldmouse *Apodemus sylvaticus* populations in the karst country of the Burren, Co. Clare, using mark-recapture methods, from November 1976 to June 1977. The two populations inhabited respectively, a section of mature hazel *Corylus avellana* wood, and an adjacent area of open limestone pavement and grassland. Population densities in both areas pointed to the suitability of the Burren habitat for fieldmice; the density in the wood was considerably higher than in the open and surpassed that in all comparable estimates from previous Irish studies. In addition, mean body weights of mice in the wood were significantly higher than corresponding values for mice in the open throughout the study. An explanation of these disparities probably lies in the predominance of hazel in the wood, conditions apparently providing a particularly favourable habitat in terms of food and cover. There was evidence that the onset of breeding in the wood was more rapid, in males at least; survival there in spring and early summer was poorer than in the open.

Introduction

Most population studies of fieldmice *Apodemus sylvaticus*, including three of the five undertaken in Ireland (Fairley 1967*a*, Fairley and Comerton 1972, Fairley and Jones 1976), have been in woodland. The exceptions in Ireland have been on grassland (Fairley 1967*b*) and a recent investigation of dry-stone walls (Hynes and Fairley 1978). Trapping has, however, established that fieldmice are abundant in many other habitats (Fairley 1975). The purpose of the present study was to investigate one of these: the karst country of the Burren in the West of Ireland. The work entailed extensive grid-trapping in a small area fairly typical of the whole region. The site was chosen to include a plot of mature hazel *Corylus avellana* wood, widespread on the Burren, as well as an area of relatively open limestone. An opportunity was thus afforded to study and compare the mouse populations of two distinct, yet adjacent habitats.

The Study Area

The site chosen, an outline map of which is shown in Fig. 1, was part of a much larger tract of similar terrain which lay close to the University College, Galway,

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Field Station at Carron, Co. Clare (National Grid Reference R2899). It included a section of mature hazel wood adjacent to an exposed area, and sharply separated from it by a stone wall some 2m high. Smaller walls, in various stages of collapse, ran off from the main one. The whole area was grazed by cattle from time to time.

The open ground contained large amounts of limestone rock and stones, interspersed with grassland and scattered hazel bushes. There were, in addition, stretches of pavement, seamed with grykes, often colonised by moss and ferns. Hawthorn *Crataegus monogyna* and sloe *Prunus spinosa* bushes were both common, the former reaching maximum size on the margins of a small turlough (a seasonal lake—Praeger 1950) which was repeatedly flooded during the winter.

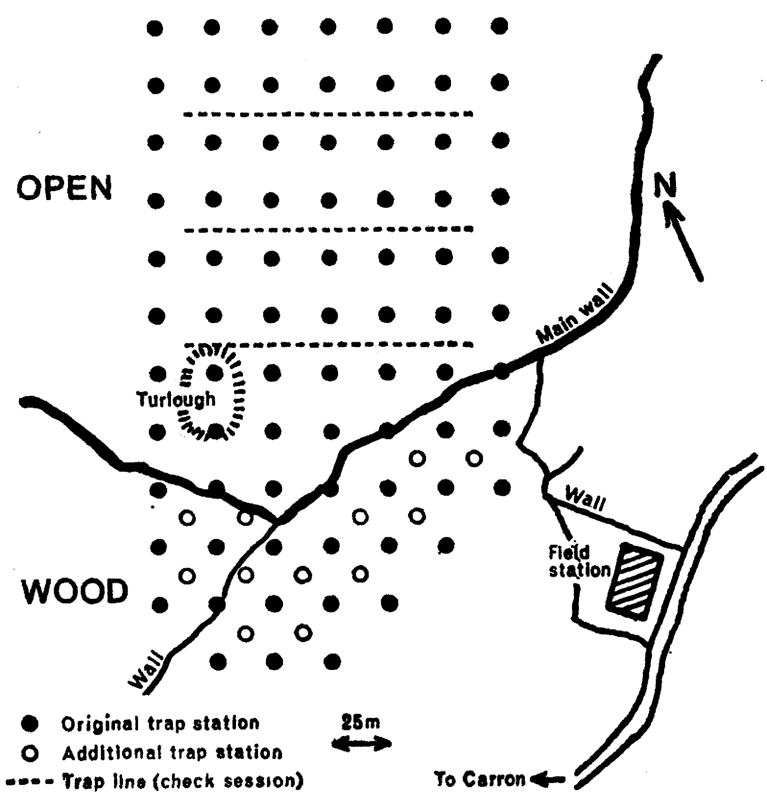

FIG. 1—Map of the study area and immediate surroundings. The trapping area south of the wall is mature hazelwood.

The hazel wood had a well-established ground flora of woodland plants. The moss layer, too, was rich, and several species were epiphytic. Hawthorn, sloe, bramble *Rubus* sp. and spindle *Euonymus europaeus* were all common. A more comprehensive flora list of both regions is given in the appendix. The canopy height within the hazel wood varied a great deal. Whilst some of it grew to around 4m, substantial areas remained stunted and much less dense. Consequently, in these latter areas the ground flora and moss layer were less well developed.

Seasonal cover differences were obvious, the undergrowth in the wood becoming particularly thick in May and June, the foliage of the hazel itself causing considerable cover increase in both areas at this time.

Fieldmice predators known to occur in the vicinity were foxes *Vulpes vulpes*, their droppings being found frequently, and kestrels *Falco tinnunculus*, which were seen three times during the study and in Ireland are the commonest and most widespread raptor (Sharrock 1977). One owl pellet was found, containing the remains of a fieldmouse, and was likely that of a short-eared owl *Asio flammeus*. The bird was probably a migrant, for the species is diurnal and none was seen.

Other mammals seen included hares *Lepus timidus*, several times in the open, a rabbit *Oryctolagus cuniculus* and pigmy shrews *Sorex minutus*, taken in the traps. The area supported a large avifauna, mostly of small passerine birds, though cuckoos *Cuculus canorus* were often heard in spring and summer. With the onset of spring, the richness of the resident fauna became apparent—frogs *Rana temporaria*, snails, slugs and, later, a remarkable variety of insect life.

Evidence of mouse activity was provided by the discarded shells of haws and hazelnuts eaten by them. The latter were sometimes found in the open area under rocks far from hazel bushes, implying transportation over some distance. Snail shells, especially of *Cepaea nemoralis*, were extremely common, often intact save for a small hole. Snails are known to be eaten by *A. sylvaticus*, the shell being bitten through away from the spire (Corbet and Southern 1977). Of course these might well have been taken by birds, or by frogs (Smith 1964). However as they were once found beneath a large rock together with haws and a hazel shell eaten by mice, it seems probable that the mice take them.

Methods

A grid of seventy-seven trap stations, enclosing a total area of 3.8ha, was laid out as shown in Fig. 1. The sides of the squares so formed measured 25m. Twenty stations lay in the wood and fifty-seven in the open. The former were marked with numbered plywood tags, painted red and attached to trees. Stations in the open were indicated by numbers painted on nearby rocks. Small 'DYMO' tape loops were often attached to branches to facilitate finding stations.

Trapping sessions of four nights each were undertaken every four or five weeks from November 1976 to June 1977. Initially, two Longworth live traps (Chitty and Kempson 1949) were placed at every point in the wood, but only one at each station in the open, for a much lower catch was expected there. Whole oats were used as bait and the traps were unbedded.

The catch was examined every morning. Each mouse was weighed to the nearest 0.5g in a polythene bag of known weight using a spring balance graduated in 1.0g. Occasionally, high winds made this impractical. Sex and reproductive condition were noted. Males were considered fecund if testes were descended, or obviously descending, and females if they had a perforate vagina, were lactating, or pregnant. The mice were marked by toe-clipping and ear-punching.

Personal observations on weather were noted.

During the third trapping session, an additional line of traps was laid in the wood, to check for possible sampling errors. Thirty traps, spaced approximately every 5m, were set in a line running roughly parallel and about 15m from the main wall. In order to explain further procedure it is necessary to anticipate the results. A total of 19 unmarked mice were captured in the wood on the third session, eight of these in the check-line. Marked mice numbered 54, with only 9 in the check-line. Significantly more new animals were, therefore, taken in the line (binomial test $d = 2.26$. $P < 0.05$). However, significance was only at the 5% level and running the check simultaneously with the existing system would have tended to accentuate any discrepancy. To investigate the situation more accurately a special check-session was run a fortnight later.

During this, twelve addtional points were sited in the wood, each at the centre of an existing grid square and marked by a stake with a red board attached for easy sighting.

Intensive trapping was then undertaken for four nights. Six traps were placed at the established wood points for the first two nights and transferred to the new points for the final two nights. Thus 6 out of 20 unmarked animals were caught at new points, and 8 out of 46 marked ones. While these figures are not, in fact, statistically significant ($d = 1.15$, $P > 0.10$), they were considered sufficient to justify retention of the new points, three traps being subsequently placed at all stations in the wood.

Three check-lines, shown in Fig. 1, were also laid in the open during the check session. There were ten traps, spaced approximately every 10m, in each. Of a total of 28 mice taken, only one was unmarked; additional points were therefore considered unnecessary in the open.

Results

Altogether 292 fieldmice (155 males, 135 females and two unsexed) were captured and recaptured. Four of these died in the traps (all on the first night on which they were taken), two by drowning at the same station. The latter was located in the depression of the turlough, overnight flooding proving fatal. The traps were placed thereafter a few metres away at a higher level. Other captures included slugs, a frog and 11 shrews.

Sometimes traps contained two or three mice. Of forty-two records of double-captures, twenty-three were male/female, sixteen male/male, and three female/female pairs. Assuming an equal sex-ratio, significantly fewer female/female captures were made. ($\chi^2 = 8.4$, $P < 0.50$). There were three triple captures: two male/male/female and one all female.

On a few occasions it was necessary to revisit the grid for other purposes after the trap-round. Altogether three mice were found, obviously having entered traps in daylight. On two occasions a mouse was seen abroad during the day.

The total number of captures, on each of the four nights for all sessions, were, respectively: 445, 481, 440, 417. There was clearly no increase in numbers related to the length of time the traps were down, as there would have been if many of the animals were either 'shy' or 'addicted' to them.

From the outset it was clear that there were differences between the fieldmouse populations in the open area and in the wood. It therefore seemed logical in most cases to separate the results accordingly. Mice caught in both sections (27 in all—less than 1 %) have naturally been included in both sets of results.

REPRODUCTION

The numbers of animals of both sexes caught on each session and the percentages fecund are given in Table 1. The testes of some males had descended in February; the first perforate female was taken in March. The only statistically significant difference in fecundity was on session four, when more males were mature in the wood ($d = 4.51, p < 0.01$) though there is a similar difference in session three which is nearly so.

TABLE 1—Numbers of male and female mice caught in the wood and in the open on each session and percentages fecund. Figures in parenthesis indicate percentages of females lactating.

Session number	Dates	Number of mice in wood		% fecund		Number of mice in open		% fecund	
		Male	Female	Male	Female	Male	Female	Male	Female
1	26–29 Nov	43	32	0	0	32	25	0	0
2	4–7 Jan	35	33	0	0	30	30	0	0
3	8–11 Feb	41	32	37	0	36	22	17	0
Check	24–27 Feb	33	33	52	0	17	11	59	0
4	25–28 Mar	43	30	81	0	40	23	33	4
5	26–29 Apr	27	34	100	38(21)	37	20	100	50(50)
6	21–24 May	31	26	100	73(73)	26	20	96	75(60)
7	18–22 June	27	21	100	95(95)	22	27	100	96(96)

WEIGHT

Day to day weights of individual mice fluctuated considerably, quite commonly by as much as 2g. Fluctuations of as great as 6g were recorded on rare occasions. Weights for each mouse on each session were therefore averaged. The main weights of mice of both sexes on each session, both in the wood and the open, are given in Table 2. Clearly, the results for the wood were nearly always higher than those in the open, and most of the differences were significant at 5 % level.

TABLE 2—Mean weights of mice in the open and in the wood on each session. S.E. indicates standard error. *P* is derived from a '*d*' or '*t*' test in each instance.

Session	1	2	3	4	5	6	7
MALES							
Wood	19.60	19.13	20.29	21.73	26.03	24.58	24.57
S.E.	0.33	0.31	0.36	0.50	0.52	0.49	0.44
Open	18.52	18.29	18.86	21.66	24.29	22.36	22.86
S.E.	0.38	0.32	0.39	0.44	0.51	0.62	0.58
P > or < 0.5	>	>	<	>	<	<	<
FEMALES							
Wood	18.41	17.38	17.79	17.96	19.12	18.58	20.55
S.E.	0.46	0.27	0.25	0.30	0.33	0.44	0.99
Open	17.37	16.34	16.52	16.85	19.10	17.34	21.15
S.E.	0.49	0.24	0.48	0.27	0.65	0.71	0.90
P > or > 0.5	>	<	<	<	>	>	>
COMBINED RESULTS							
P or 0.5	<	<	<	>	>	<	>

The weight distributions for both populations are given in Fig. 2. These give a fair reflection of the age structure. A gradual increase in weight was evident over the study, this being particularly marked, as usual (Evans 1942), at the onset of breeding. Maximum and minimum weights were 33.0g for a male and 6.5g for a female. Despite the widespread fecundity in the later sessions, very few juveniles were trapped—two in May and three more in June. Only one of these was taken in the wood, in June.

POPULATION

The size of the population was estimated by the methods of Leslie, Chitty and Chitty (1953) and Hayne (1949*b*). The latter has the advantage of producing an estimate solely from the data obtained on an individual trapping session. Results are given in Table 3, together with the numbers of marked and unmarked animals taken on each session. The estimates agree fairly well in most instances, though Hayne's method produced lower figures throughout. The maximum population was recorded in late November. This may represent the true maximum for the year, which normally occurs in autumn (Corbet and Southern 1977), but it is quite possible that the peak had already occurred somewhat earlier. After an initial sharp drop, which is by no means unusual (Evans 1942, Watts 1969, Crawley 1970), numbers declined slowly, trends being similar in both areas.

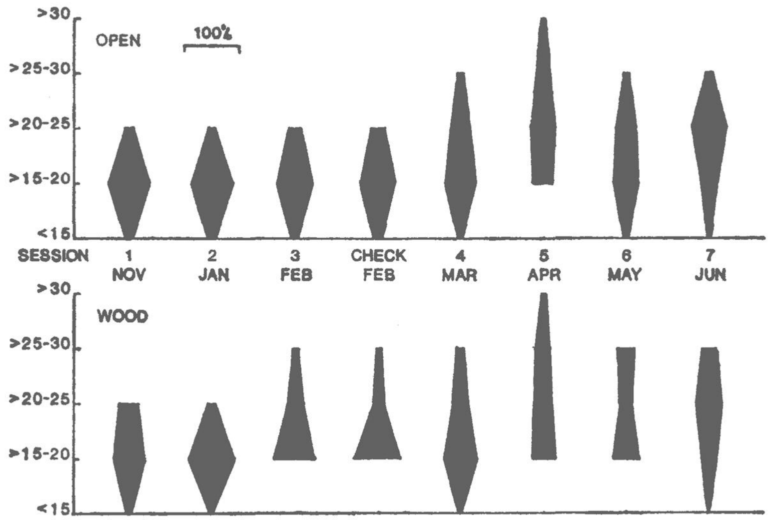

FIG.2 —The weight distribution, in g, of mice weighed on each session in the open and in the wood.

TABLE 3—Numbers of marked and unmarked mice taken on each session in the wood and in the open and estimates of total population by the methods of (1) Leslie, Chitty and Chitty (1953) and (2) Hayne (1949b).

	Session						
	1	2	3	4	5	6	7
WOOD							
Marked mice captured	—	43	54	60	46	48	40
Unmarked mice captured	76	26	19	13	15	9	8
Estimated population (1)	—	90.7	96.9	84.9	71.2	62.7	—
Estimated population (2)	114.5	83.7	80.9	74.7	64.4	53.9	42.5
OPEN							
Marked mice captured	—	36	41	54	53	43	43
Unmarked mice captured	57	25	17	9	4	3	6
Estimated population (1)	—	77.1	74.5	73.3	63.4	55.6	—
Estimated population (2)	115.6	75.4	72.3	65.9	57.9	43.6	47.5

To devise density estimates for both the wood and the open, a boundary strip, equal in width to half the corrected range length of the males (Stickel 1946), was added to each area. This compensated for the bias caused by movement of mice into and out of the grid, which would have overestimated population density. Boundary strips of 33.9m and 34.0m were added to the open and wood respectively. Thus the open area becomes 2.47ha (originally 0.72ha) and the wood 5.34ha (2.72ha). Peak densities were therefore 21.6/ha (8.8/acre) for the open and 46.3/ha (18.8/acre) for the wood. Uncorrected values are respectively 42.5/ha and 159.5/ha.

TABLE 4—Observed survival of mice caught on the first session to other sessions in the wood and in the open. A value of '*d*' greater than 1.96 indicates statistical significance at the 5% level.

	Session					
	2	3	4	5	6	7
WOOD						
Numbers surviving (out of 76)	55	45	33	23	17	11
% surviving	72	59	43	30	22	14
OPEN						
Numbers surviving (out of 57)	45	39	33	26	21	17
% surviving	79	68	58	46	37	29
d (binomial)	0.87	1.08	1.65	1.82	1.82	2.15

The observed survival of mice captured during the first session to the other sessions is traced in Table 4. Any of these individuals not recaught on a particular session, but recaught subsequently, is assumed to have been present in the former sessions. It is apparent that survival was rather better in the open than the wood and the figures for the final session are, in fact, statistically significant; those for sessions five and six are close to the 5% level of significance.

MOVEMENT

Table 5 shows the average distances moved on each session and is a good index of activity. It is almost impossible to attach statistical errors to such figures because of the irregular distributions from which they are derived. However, there was obviously a marked increase in the activity of both sexes by the fourth ession, corresponding approximately with the onset of breeding. There is also some indication of a further rise as the season progressed.

TABLE 5—Average observed distances moved by mice on each session in the wood and in the open. Mice occurring in both areas have been excluded. Results from the third session in the wood are invalid because of an extra line of traps (see text).

Session	1	2	3	4	5	6	7
WOOD							
Males	5.7	7.1	—	10.5	13.9	18.6	37.4
Females	2.1	2.2	—	14.2	10.4	18.3	19.3
OPEN							
Males	2.0	11.2	7.5	20.7	23.8	58.9	36.2
Females	0	12.4	7.9	19.1	17.7	16.1	26.5

Because of the inconsistency in the numbers of traps and trap spacing before and after the check session, only data from sessions four to seven have been used in estimating range lengths, and are therefore representative of the breeding season. Home range estimates are subject to criticism due to the obvious influence of trap spacing, size of trapping area, trapping periodicity and number of captures (Kikkawa 1964). Several methods have therefore been used to estimate range. Here the greatest distance observed between points of capture, the maximum observed range length, is used. The basic assumption made is that this distance constitutes the diameter of a circle, or the major axis of an ellipse, which is the animals' home range (Hayne 1949*a*). The actual areas (home ranges) have not been assessed, but inference may be gained from the data presented. All mice captured on two or more sessions from sessions four to seven have been included. Maximum distances moved were calculated for each mouse, and wood and open area results were separated, as were males and females.

A problem arises in comparing the figures for the two sections. The calculation of mean range length from such observations on a fixed trapping grid involves inherent errors, because of the irregular frequency distribution between the traps (Chitty 1937). Thus there is a higher probability of recording moves of medium distances than of short or long distances and values obtained from two different grids are neither accurate nor comparable. Watts (1970) has devised a method of computing correction factors for each grid which take into account layout, spacing and the total area available for movement. Such factors have been calculated here, and observed and corrected data are presented in Table 6. It is clear that the average for males in both

TABLE 6—Percentage distribution of observed and connected range lengths for all mice caught on two or more sessions from session four to session seven.

Range length in m	WOOD				OPEN			
	Observed		Corrected		Observed		Corrected	
	Males	Females	Males	Females	Males	Females	Males	Females
0–20	20	31	10	15	8	22	11	36
21–40	43	45	25	31	28	39	19	29
41–60	14	7	20	8	23	26	19	21
61–80	14	7	20	8	23	13	22	14
81–100	0	0	0	0	5	0	7	0
101–120	3	3	5	8	8	0	11	0
121–140	3	3	10	15	3	0	4	0
141–160	0	0	0	0	0	0	0	0
161–180	3	3	10	15	3	0	7	0
Mean range length	43.7	39.0	68.0	74.6	57.7	36.1	67.8	32.9

areas is virtually the same, 68.0m and 67.78m, wood and open respectively. For the females the average figure in the wood was 74.62m, compared to 32.86m in the open, the former estimate even exceeding those for males. Eliminating one possible marking mistake, this figure is only lowered to 57.27m. Nevertheless, the number of females moving long distances was small, and the correction factors have to be used with circumspection, the uncorrected figures being much the same in the two sections. There is, in fact, little valid statistical evidence for concluding a real difference.

HABITAT

A. sylvaticus requires cover in the form of trees, shrubs, herbs or rocks, though precise factors are somewhat more complex (Fairley 1975, Corbet and Southern 1971).

In the present study, the situation encountered was unusual in that there were two distinct habitat types—one heavily covered, the other relatively exposed. Presumably, therefore, different habitat factors were of significance within each area. Each region was thus subdivided into three categories—*A*, *B* and *C*—dependent basically on vegetation in the wood, and on terrain in the open. A greater number of categories would have introduced a high degree of subjectivity and weakened statistical treatment. The following classification was adopted:

Wood: *A* High canopy hazel
B Low canopy hazel
C Grazing areas; sparse hazel

Open: *A* Substantial rock cover, pavement and grykes
B Scattered rock, stones
C Open grassland; grass hummocks.

TABLE 7—Numbers of mice taken in different habitat types in the wood and in the open on each session. Figures in parentheses indicate the total numbers of traps in each habitat type. These numbers were greatly increased in the wood from session four onwards (see text). The two sets of results for 'Total' and 'Mean mice/trap' refer to the periods before and after the increase in traps respectively. In the wood: *A* = High canopy hazel, *B* = Low canopy hazel, *C* = Grazing areas, sparse hazel. In the open: *A* = Substantial rock cover, pavement and grykes, *B* = Scattered rock, stones, *C* = Open grassland, grass hummocks.

Session	1	2	3	4	5	6	7	Total	Mean mice/trap
WOOD									
Cover *A*	42(20)	43	33	47(45)	45	52	45	118/189	5.9/4.2
Cover *B*	23(12)	21	22	28(24)	19	17	18	66/82	5.5/3.4
Cover *C*	19(8)	13	6	22(27)	18	21	19	38/80	4.8/2.9
$P >$ or < 0.5	>	>	>	>	>	>	>	> <	
OPEN									
Cover *A*	10(9)	14	17	17	19	16	16	109	12.1
Cover *B*	29(27)	37	32	49	37	38	48	270	10.4
Cover *C*	17(21)	22	18	22	26	27	16	148	7.0
$P >$ or < 0.5	>	>	>	>	>	>	<	<	

Results are summarised in Table 7. While on only one individual session were results significant, the overall results from the open were significant, and also in the wood, from March onwards at least. There is a decided preference for cover; the only point where mice were never captured was an exposed one, at the edge of the depression of the small turlough.

WEATHER

The numbers of mice caught in prevailing weather conditions are given in Table 8. It is clear that maximum numbers were usually trapped on rainy nights, and numbers tended to be lower on clear or frosty nights.

TABLE 8—Numbers of mice caught on each day of each session together with the prevailing weather. *C* = clear; *F* = frost; *O* = overcast; *R* = rain.

Session	Number of captures and prevailing weather			
	Day 1	Day 2	Day 3	Day 4
1	*C*	*R*	*R*	O
	29	52	46	49
2	*R*	*F*	O	O
	62	45	55	53
3	*R*	*R*	*C*	*F*
	63	68	49	42
Check	0	0	0	0
	48	49	46	31
4	*R*	*R*	*F*	0
	79	81	58	58
5	*R*	*R*	*R*	0
	62	66	69	54
6	*C*	O	*C*	*C*
	48	63	65	64
7	O	O	O	*C*
	54	57	52	66

Discussion

This study was subject to the limitations of most trap-mark-recapture work on small mammals (Delaney 1974, Flowerdew 1976). These shortcomings have already been discussed with particular reference to an Irish population study of *A. sylvaticus* using similar techniques (Fairley and Comerton 1972).

The disproportionate number of female/female captures may be explained by the social interactions of *A. sylvaticus*. Both Garson (1975) and Randolph (1977) have noticed strong heterosexual pair-bonding in many fieldmice. Garson, in a series of observations on marked animals at feeding points, noted that a bonded female rarely fed with another. Thus male/female couples were the commonest.

Major differences clearly existed between the populations in the wood and in the open, essentially in terms of population density, survival, body weight and, apparently, in the onset of sexual maturity in males.

Surprisingly, precise comparison of the present population densities with others presents some difficulty. Corbet and Southern (1977) give densities up to 100/ha, though most figures in Britain rarely approach this, and it is uncertain to what extent it represents a fully-corrected figure. Comparable Irish studies in mixed woodland (Fairley and Comerton 1972, Fairley and Jones 1976) gave corrected peak densities of 22.1/ha and 7.2/ha and Fairley (1967*a*) obtained an uncorrected figure of 50.2/ha (about 31/ha uncorrected). The suitability of the Burren habitat for fieldmice is obvious and the peak density in the hazel can at least be considered high.

The two areas differed primarily in their vegetation, which probably explains all of the differences between the two populations. Vegetation could have influenced numbers directly, namely by providing cover and food. Cover was obviously locally important in this study. While fieldmice are widespread in Ireland, the availability of cover is of great significance and, even where they occur in grassland, they are markedly associated with even the lightest additional cover (Fairley 1967*b*). However, the differences between the wood and open were most likely due to relative availability of food in the two areas. In Britain tree seeds are the major food of fieldmice in autumn and winter and, to a lesser extent, in spring and summer (Watts 1968), when more arthropods are eaten. Since hazel was the predominant seed-producer at Carron, it is extremely probable that hazel nuts were of great significance as food to the mice, and the most obvious factor in allowing population increase to the high level observed.

Hazel seeds are relatively large and have a very high calorific value. Grodzinski and Sawicka-Kapusta (1970) found that, of the nineteen different European tree-seeds eaten by small mammals which they investigated, the kernels of hazel nuts had the highest calorific value. Moreover, these seeds were exceeded in size only by those of oak (*Quercus petraea* and *Q. robur*). Mr. Noel Kirby (Botany Department, University College, Galway) who is researching on hazel in the Carron area, informed us that the seed-fall during the autumn of 1976 was particularly good. During the winter of 1976–77 he conducted some seed-removal experiments in hazel-scrub near our study area. In these, cartons containing nuts, with and without kernels, were placed randomly on the hazel-wood floor and examined the following morning. In every instance there was extensive removal of nuts by mice (as evidenced by faeces) with a definite preference for nuts with kernels. In a typical pair of examples, nuts remaining with kernels were 8/393 and 3/290, whilst nuts without kernels numbered 54/100 and 191/214. The fact that so many nuts were removed and none eaten on the spot, suggests storage underground by fieldmice; the hoarding propensities of the species are well known. When smaller quantities of nuts were left down glued to boards, so that they could not be removed, they were almost invariably eaten overnight, the shells bearing the characteristic marks of having been opened by *A. sylvaticus* (East 1965).

In the light of the previous paragraph, it seems that the high population of *Apodemus* in the wood is best explained in terms of an exceptional abundance of nutritious food. It is well known that a good food supply can increase winter density (Hansson 1971, Flowerdew 1972, Louarn and Schmitt 1972). It might also explain why the mice in the wood were heavier than those in the open, and it is interesting in this context that Flowerdew (1972) was able to induce an increase in body weight in a population of fieldmice by supplying food in spring. It could, of course, be speculated that arthropods might have been of more importance than seed in early summer, but with the much greater biomass of vegetation in the wood, it would be quite reasonable to infer that there were more insects there too.

The only alternative explanation would have been a difference in population structure—in other words, the inclusion of a higher proportion of adults from the previous breeding season in the wood. If more growing juveniles had been present in the wood in autumn, a weight difference would indeed have resulted, but by spring such a disparity should have evened out. This was noted in females in the later sessions. However, many of the females were pregnant and greater variation in both areas is to have been expected. The mean weight of males remained significantly higher in the wood in spring and early summer when almost all of them in both areas were fully adult. The exclusion of the few juveniles does not alter this significance.

It has also been shown experimentally that additional food in spring may advance the start of the breeding season (Watts 1970), for there is some evidence of an earlier sexual maturity in the wood, in the males at least. The effects of a high autumn seed-fall on the breeding of *Apodemus sylvaticus* are not clearly understood. There is strong evidence that a good seed-crop in woodland may prolong the breeding season or allow it to continue through the winter (Smyth 1966, Hansson 1971, Louarn and Schmitt 1972), but this did not happen at Carron. On the other hand, some mice have come into breeding condition in January without abundant seed (Fairley and Comerton 1972).

An inconsistency in the obvious advantage of increased food supply is the evident better survival of the animals in the open. Watts (1969), in a broad study of the regulation of fieldmouse numbers, noted a frequent drop in survival of overwintering animals in spring and that this was slightly more marked following higher initial densities, which accords with the present findings. He speculated that this might be the result of increased strife within the population.

There can be little doubt that weather, especially rain, influenced the numbers of mice entering the traps. It has sometimes been shown that fieldmice are more active in wet and dark conditions (Brown 1956, Kikkawa 1964, Corbet and Southern 1977) and Sidorowicz (1960) states categorically that rain is the strongest factor influencing the activity of forest rodents. Nevertheless, an association between activity and weather is by no means always clear (e.g. Bergstedt 1965). It is worth noting that the unusual limestone terrain on which the present study was conducted could well have intensified any flushing-out effect rain might have on the mice in their holes.

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Appendix

The following is a list of plant species noted on the study area. The capitals after one or more species indicate where these plants were found: W in the wood, O in the open and WO in both.

ANGIOSPERMAE. RANUNCULACEAE: *Anemone nemorosa*, *Ranunculus ficaria* W, R. *acris*, *R bulbosis* O. CRUCIFERAE: *Cardamine praetensis* W, *C. hirsuta* WO. POLYGALACEAE: *Polygara vulgaris* O. VIOLACEAE: *Viola riviniana* WO. CARYOPHYLLACEAE: *Stellaria holostea* W, *Cerastium fontanum* WO. HYPERICACEAE: *Hypericum* sp. WO. GERANIACEAE: *Geranium lucidum*, *G. sanguinium* O, *G. robertianum* WO. OXALIDACEAE: *Oxalis acetosella* W. CELASTRACEAE: *Euonymus europaeus* WO. PAPILIONACEAE: *Lathyrus pratensis*, *Lotus corniculatus*, *Trifolium campestre*, *T. pratense*, *Vicia sepium* WO. ROSACEAE: *Alchemilla xanthochlora*, *Filipendula ulmaria*, *Fragaria vesca*, *Geum urbanum*, *Potentilla sterilis*, *Sorbus acuparia* W, *Dryas octopetala*, *Potentilla anserina*, *Saxifraga tridactylites* O, *Crataegus monogyna*, *Geum rivale*, *Potentilla erecta*, *Prunus spinosa*, *Rosa spinosissima*, *Rubus* sp. WO. UMBELLIFERAE: *Conopodium majus*, *Heracleum sphondylium* W. ARALIACEAE: *Hedera helix* WO. CAPRIFOLIACEAE: *Lonicera periclymenum* WO. RUBIACEAE: *Galium aparine* W, *G. saxatile*, *G. verum* WO. COMPOSITAE: *Arctium lappa*, *Taraxacum officinale* W, *Antennaria dioica*, *Centaurea nigra*, *Pilosella officinarum*, *Tussilago farfara* O. PRIMULACEAE: *Primula veris*, *P. veris* x *vulgaris*, *P. vulgaris* W. GENTIANACEAE: *Gentiana verna* O. SCROPHULARIACEAE: *Melampyrum pratense*, *Veronica chamaedrys* W, *Euphrasia nemorosa*, *Pedicularis sylvatica*, *Veronica officinalis* O. LABIATAE: *Glechoma hederacea* W, *Thymus drucei*, *Teucrium scorodonia* O, *Ajuga reptans* WO. PLANTAGINACEAE: *Plantago lanceolata* O. POLYGONACEAE: *Rumex acetosa* W. URTICACEAE: *Urtica dioica* W. CORYLACEAE: *Corylus avellana* WO. ORCHIDACEAE: *Listera ovata* W, *Dactylorhiza fuchsii*, *Orchis mascula* WO. LILIACEAE: *Endymion non-scriptus* W. ARACEAE: *Arum maculatum* W. CYPERACEAE: *Carex* sp. O. GRAMINAE: *Brachypodium sylvaticum*, *Poa trivialis* W, *Briza media*, *Cynosurus cristatus*, *Festuca rubra*, *Koeleria cristata*, *Lolium perenne*, *Sesleria caerulea* O, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Dactylis glomerata* WO.

PTERIDOPHYTA. POLYPODIACEAE: *Asplenium trichomanes*, *Ceterach officinarum*, *Phyllitis scolopendrium*, *Polypodium vulgare* O, *Polystichum* sp., *Pteridium aquilinium* WO.

BRYOPHYTA. MUSCI: *Acrocladium cuspidatum*, *Mnium undulatum*, *Rhytidiadelphis squarrosus*, *R. triquetris*, *Thuidium tamariscinum* W, *Breutelia chrysocoma* O, *Camptothecium sericeum*, *Ctenidium molluscum*, *Eurhynchium striatum*, *Neckera complanata*, *N. crispa*, *Thamnium alopecurum* WO. HEPATICAE: *Lophocolea bidentata* W, *Metzgeria furcata* WO.

LICHENES. *Peltigera* sp. O.