UNIVERSITY OF LONDON

FACTORS AFFECTING THE POPULATION DYNAMICS OF THE SKOMER VOLE, CLETHRIONOMYS GLAREOLUS SKOMERENSIS

by

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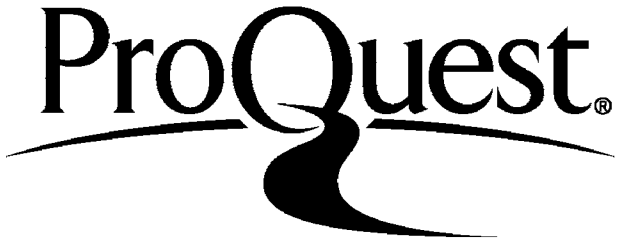

ABSTRACT.

This thesis describes a twelve year study of the Skomer vole (Clethrionomys glareolus skomerensis) which highlighted remarkable similarities between the voles' biology and that of other island rodents.

Capture-recapture trapping provided demographic data. The population fluctuated annually with a trough at the beginning and a peak at the end of the breeding season. There was no regular multi-annual population cycle. Densities between 58/ha and 475/ha were recorded.

Most young were produced by over-wintered animals; few animals bred in the year of birth. The numbers of adult males present during the breeding season varied little from year to year; the number of adult females was more variable. A removal experiment showed that interactions with adult females did not prevent the maturation of females in the year of birth. The dispersion of adult males and females was random.

Intrinsic population regulation was by reduced litter size, a shortened breeding season and delayed maturation of both sexes. Extrinsic factors appeared to influence the timing of the breeding season and the maturation of animals in the year of birth. Factors affecting the over-winter survival of females and the survival of young of both sexes during the breeding season were thought to be important in regulating the population.

The animals required dense cover and were closely associated with bracken (Pteridium aquilinum) and bluebells (Endymion non-scriptus). Dense grass under the bracken led to a reduced vole population.

The voles' diet consisted mainly of bracken, bluebells and grass; they ate little animal material. They had an annual fat cycle with a winter peak.

Predation may have exerted a local effect but probably did not regulate the population. There was no link between haemoparasitic infections and fluctuations of the vole population. Infections with pneumotropic viruses may have played a part in limiting the population of voles.

Format of the thesis.

(1). For the convenience of the reader some key definitions, several maps and the results of the measurements of the size of the population have been reproduced on a fold-out sheet at the end of the thesis so that they can be referred to constantly.

(2). Each topic in this thesis has been dealt with in a separate chapter, each chapter having an introduction, a section in which the methods are described and discussed in the light of published work, a section giving the results obtained, and a brief discussion of topics specifically relevant to that chapter.

(3). The results as a whole are discussed in a separate chapter in the light of published work on island populations of mammals and on the biology of Microtine rodents in general and on bank voles in particular.

(4) The pages are numbered at the bottom.

(5). The tables are numbered at the top right hand corner.

(6). The figures and plates are all numbered at the top right hand corner of the page.

(7). The pages on which the various topics in the discussion occur are listed in the index.

(8). A few topics have been dealt with in appendices where their treatment in the main body of the thesis would have unbalanced specific chapters.

(9). Several published papers which contain reports of material collected from Skomer by me during the course of this study are included at the end as additional appendices.

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INTRODUCTION

This thesis is an account of a study of various aspects of the population dynamics of the Skomer bank vole Clethrionomys glareolus skomerensis which has been carried out for three years full-time (1972, 1973 & 1975) and for ten years part time over the last thirteen years. The dates of the visits to the island are given in Table 1. Since the possiblities of visiting the island were limited an attempt was made to choose dates which would be biologically relevant but owing to the weather, the availability of research accommodation on the island, and the vagaries of the local boatmen it was not always possible to get to the island at the same time each year.

Table 1.

Dates of visits to Skomer.

1971	October	9 - 20	1976	August	4 - 9
1972	March	14 - 21	1977	August	3 - 8
	April	16 - 22			
	June	3 - 13	1978	August	2 - 7
	June 29 -	July 12			
	August	23 - 30	1979	August	3 - 8
	October	2 - 7			
			1980	August	4 - 9
1973	January	21 - 26			
	April	5 - 9	1981	May	25 - 30
	July	24 - 31		August	3 - 9
	August	2 - 15		Aug 26 -	Sept 4
	August	19 - 24		October	16 - 20
	September	2 - 6			
	September	17 - 23	1982	May	24 - 29
				August	5 - 10
1974	July	14 - 19		October	5 - 11
	October	5 - 11			
			1983	May	24 - 29
1975	March	1 - 8		August	1 - 5
	June	7 - 13		October	10 - 15
	July	19 - 31			
	August	2 - 6			
	September	9 - 13			

During the first two years of the study an experiment was undertaken to test the hypothesis that territorial behaviour by adult females might, by preventing younger animals from breeding, be regulating the size of the population. This experiment required intensive trapping of an area of about 1.5ha since both control and experimental areas were required. This had an effect on the trapping arrangements and, as a result, the data collected, whilst being suitable for answering the questions asked in the experiment, had not been collected in such a way that they could readily be used for other purposes. At the same time studies of the diet and of the body fat content of the voles were undertaken with the aim of determining whether food could be setting a limit on the size of the population and to provide an assessment of the physiological condition of the animals.

Only two visits to the island were made in 1974. In July a trapping programme was undertaken on my behalf by students from the Department of Zoology, Royal Holloway College London because I was, at that time, working abroad. On my return to this country in October I carried out a trapping programme on the island. Since 1975 studies on the longer term changes in the population have been undertaken, a part of the original grid being used as the study area. Between 1975 and 1980 it was not possible to make more than one visit to the island each year. A mark-recapture programme was carried out over five nights on each visit to provide an index of population parameters.

Since 1981, visits have been made to the island each year at the end of May, at the beginning of August and at the

beginning of October (that is to say at the beginning, middle and end of the vole's breeding season) five nights trapping being undertaken on the grid on each occasion. In 1977, 1978 and from 1980 onwards, blood samples have been collected from the animals as a part of a study of the role of disease in the population dynamics of wild rodents. The blood sera have been tested for antibodies to a range of viruses, and blood smears have been prepared for a study of blood parasites in the voles. A search for bacteria of the genus Salmonella was made between 1976 and 1978. Between 1975 and 1978 and since 1980 populations of bank voles on the mainland have been studied at the same time as the Skomer population (since 1980 these studies have been made on islands in inland waters) so that comparisons between the two sub-species can be made.

In 1981 a survey of the size and distribution of the population of the Skomer vole over the whole island was undertaken (Healing, Jewell, Jewell, Rowlands & Gipps, 1983). This was a repeat of a survey performed in 1960 (Fullagar, Jewell, Lockley & Rowlands, 1961, 1963) and was done to study long term changes in the size and distribution of the population of voles.

- o O o -

The genus Clethrionomys contains five species of voles found in Eurasia and North America and these are predominantly inhabitants of tundra or woodland. Only one species, C. glareolus, is found in Britain. This species is also found throughout Europe except in the tundra regions. It is found on

nine of the islands off the British coast and on four of these (including Skomer) it is the only member of the Microtinae present.

The bank vole (Clethrionomys glareolus) of mainland Britain and Europe is found chiefly in deciduous woodland, scrub, banks, dry stone walls and hedges (Kikkawa, 1964; Pollard & Relton, 1970; Flowerdew, 1977; Healing, 1980) and occasionally in thick grassland (Chitty & Phipps, 1966) and coniferous woodland (Birkhan, 1968). They have a decided preference for thick cover (Southern & Lowe, 1968) and their local distribution may change with changes in ground cover (Kikkawa, 1964).

Five sub-species of the bank vole have been described in the British isles: C.g.glareolus (mainland), C.g.caesarius (Jersey), C.g.alstoni (Mull), C.g.erica (Raasay) and C.g.skomerensis (Skomer)(Flowerdew,1977). It is thought that most if not all of these island populations may have resulted from accidental introductions by man rather than being relict populations that survived the last ice age (Corbet, 1961).

The first detailed mention of the Skomer vole was by Robert Drane (1898) who described a "very large variety of the bank vole ---- it cannot be the common field vole from which it differs widely in appearance, size and colour". Barrett-Hamilton (1903) believed that it was a survivor of an older fauna subsequently displaced from the rest of the British Isles by the bank vole and accorded it specific status (as Evotomys skomerensis). That it was a new type of bank vole was not definitely established until the publication of Miller's classification in 1912. There has been some argument as to

whether the Skomer vole can properly be accorded sub-specific status. Steven (1953), Godfrey (1958) and Alder (1972) all feel that it can whereas Corbet (1964) accords it "provisional sub-specific status", Bathgate (1978) calls it a race and Jewell (1966a) a micro-geographical race. This is not the place to unravel taxonomic complexities. Suffice it to say that I consider that the morphological evidence presented by Corbet (1964) and the genetical evidence presented by Hennig & Walker (1970), Alder (1972) and Bathgate (1978) justify considering it as a sub-species and I have therefore referred to it as Clethrionomys glareolus skomerensis (Cgs) throughout, the mainland bank vole being referred to as Clethrionomys glareolus glareolus (Cgg).

The Skomer vole is distinguished from the bank vole of mainland Britain and Europe and from other island sub-species by having a coat that is bright red above and cream on the belly. It is also larger (1/3 to 1/2 times heavier) a characteristic that it shares with other island sub-species, in particular those on Jersey and Raasay (Corbet, 1964). The main skeletal difference between the sub-species is that the posterior halves of the nasal bones are parallel sided in the Skomer vole but tapering in all the other sub-species (Corbet, 1964).

The breeding season of the Skomer vole is shorter than that of the bank vole on the mainland (Jewell, 1966a) and the animals rarely breed in the year of their birth (Coutts & Rowlands, 1969; Jewell, 1966a). The Skomer vole lives at densities much greater than those usually recorded for bank voles on the mainland (Jewell, 1966a).

The Skomer vole has been the subject of a number of studies. Phillips (1950) reported on surveys of its status performed in 1946 and 1947. More detailed studies were reported by Fullagar et al. (1961,1963), by Jewell (1965, 1966 a & b) and by Healing et al. (1983). The reproduction of the voles was studied by Coutts & Rowlands (1969) and studies have been made of hormonal control of the pubic symphysis of the voles (Zarrow & Wilson, 1963), on their social behaviour (Alder, 1972, 1975; Johnson, 1976), of their reproductive behaviour (Godfrey, 1958; Alder, Godfrey, McGill & Watt, 1981), of genetic variation (Bathgate, 1978), of Leptospira (Twigg & Cuerden, 1967; Twigg, Cuerden & Hughes, 1968), of heavy metals (Cameron, 1973), of virus infections (Kaplan, Healing, Evans, Healing & Prior, 1980), of enterobacteriaceae (Healing, Kaplan & Prior, 1980) and of blood parasites (Healing, 1981) in the voles. Where relevant these will be considered in relation to my work at various points in the discussion (Chapter 7.).

- o O o -

Skomer island lies off the coast of west Wales (Dyfed) to the south of St Brides bay (Latitude 51° 44' North; Longditude 5° 17' West: National grid reference: SM 725 095). It is an island of approximately 292 ha and lies about 1km offshore, being separated from the mainland by Jack sound (ca. 1/2 km wide) Midland island and Little sound (ca. 100m wide). Although the sounds are narrow the tide runs swiftly (exceeding 4 knots) and the island is effectively isolated from the mainland (Plates 1. & 2. & Fig 1.).

Plate 1.

Skomer island from the air.

(a) = Mainland; (b) = Jack sound; (c) = Midland island
(d) = Skomer; (e) = Farm; (f) = Approximate position
of the study area.

(Photograph: M.Alexander)

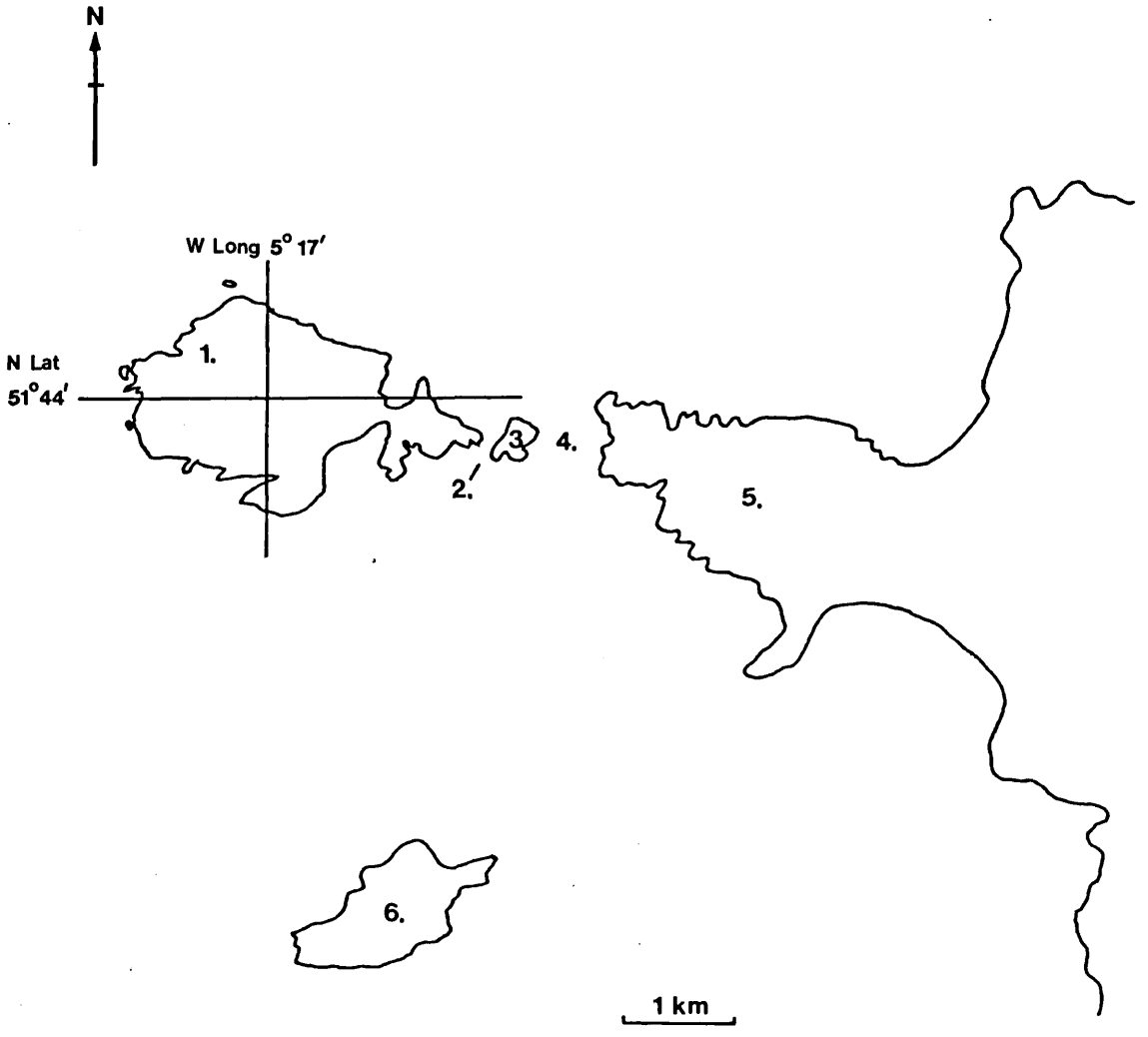
Plate 2.

Skomer island from Skokholm island.

(a) = Skomer; (b) = Little sound; (c) = Midland island;
(d) = Jack sound; (e) = Mainland.
(Photograph: T.D.Healing)

Fig 1.

Skomer and the adjacent islands.



1. Skomer island
2. Little sound
3. Midland island
4. Jack sound
5. Mainland
6. Skokholm island

Much of the southern part of Dyfed (including the nearby island of Skokholm (Fig.1.)) is composed of Old Red Sandstone but Skomer and the adjacent mainland are made largely of igneous rock types known as the Skomer volcanic series (Thomas, 1911). Parts are probably of Silurian age and the rocks are, in general, base rich (Ziegler et al. 1969).

The soils of the central part of the island (and some parts of the periphery) have been much affected by man. The island has probably been inhabited by man since the first century BC (Grimes,1950) and about half the area of the island has been used for cultivation at some time in the last two millenia. Ploughing has left the upper layers soft and structurally uniform and the depth of the topsoil varies from 30cm to more than 1m over much of the island. The surface layers are now acidic (pH 5 - 6) due largely to decomposing bracken. The soil has also been much affected by the activities of burrowing birds and mammals and by the deposition of dung particularly near the cliffs and, in recent years, in and near the rapidly expanding colonies of lesser black-backed gulls (Larus fuscus).

Skomer is visited by a wide variety of migratory birds and also provides the nesting ground for many species of seabirds and several species of predatory birds. Several of the seabird species affect the Skomer vole either by burrowing and thus providing tunnels for the voles to use (eg. the Manx shearwater, Puffinus puffinus and the Puffin, Fratercula arctica) or by altering the vegetation by the establishment of large breeding colonies and thus probably excluding the voles (eg. the lesser black-backed gull.).

The mammalian fauna of Skomer is impoverished with respect to that of mainland Britain. Apart from the Skomer vole, rabbits (Oryctolagus cuniculus), long-tailed field mice (Apodemus sylvaticus) and two species of shrew, the common shrew (Sorex araneus) and the pygmy shrew (Sorex minutus) comprise the land mammal community. No predatory mammals are found on Skomer.

Chapter 1.

STUDIES OF POPULATION PARAMETERS

INTRODUCTION

A capture-recapture programme was undertaken throughout the study to provide data on the demography of the population. The aims of the trapping programme changed during the course of the study. At first it was designed to meet the needs of an experiment to test the role of adult females in the dynamics of the population and this required both control and experimental areas. A large area had therefore to be trapped and this required special trapping arrangements. The data collected, whilst being suitable for answering the specific questions being asked in the experiment, were unsuitable for other purposes. Once the experiment was completed a more general population study was undertaken and only a part of the original grid was used. The method of trapping was standardised not only from visit to visit but to conform to the methods employed in concurrent studies of small rodents on the mainland (Kaplan et al. 1980; Healing, 1981 - see Appendices 6. & 7.).

For several years only one visit to the island each year was possible and so only an index of population processes could be kept, but during the last two years three visits have been made to the island each year, at the beginning, middle and end of the breeding season. Since 1976 the studies of the population have included studies of disease which have complemented similar studies on the mainland.

METHODS

(a) Study area.

The study area chosen for the present project lay to the

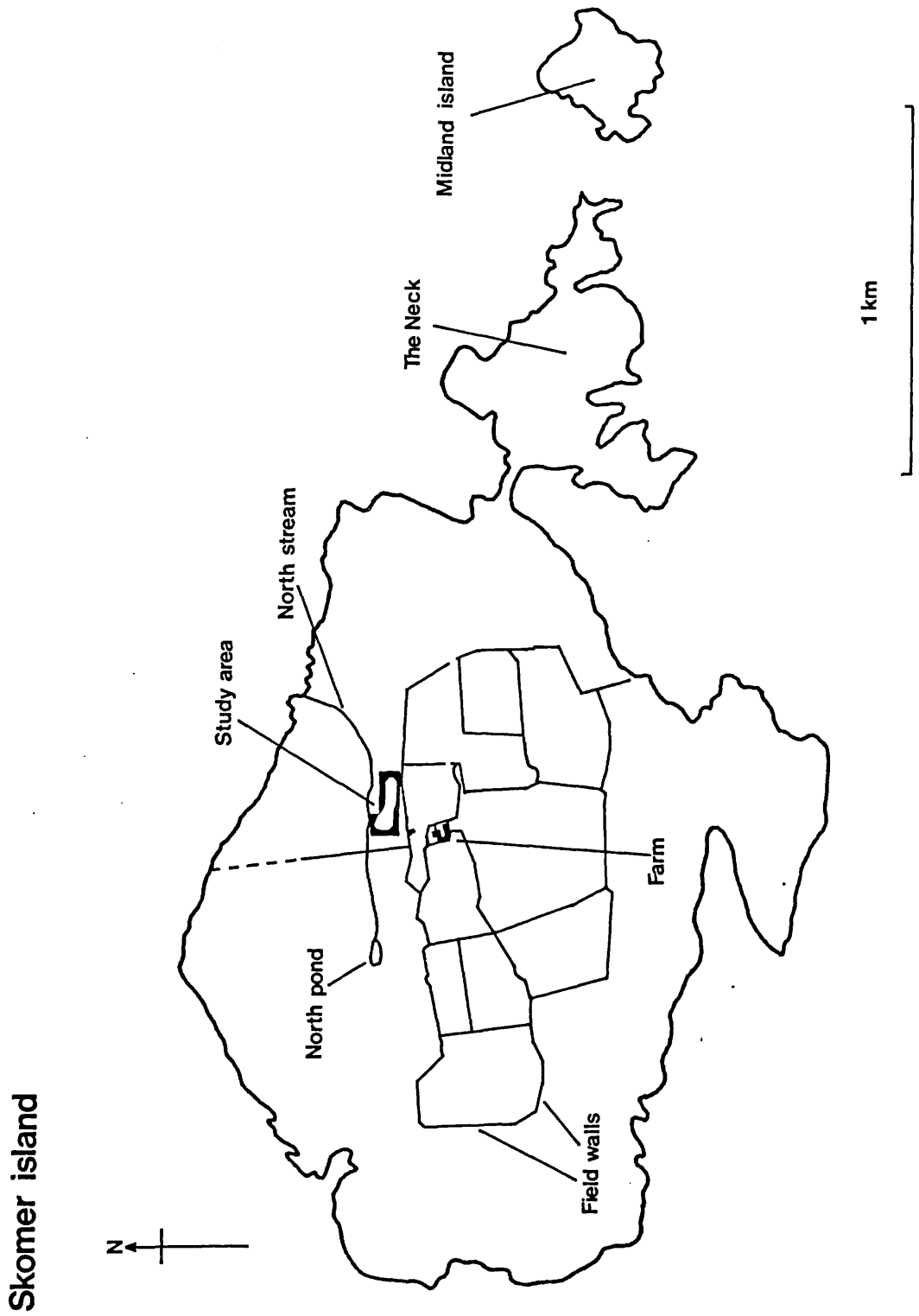
north-east of the farm and on the south side of the North-stream valley (Fig 2.). The area was largely covered by the association of bracken and bluebells which is dominant over about 60% of the surface of the island (Healing et al. 1983 and see Chapter 3.) and this type of vegetation, or others forming a suitable habitat for the voles, extended for some distance around the area (Fig 3.). The study area was bounded to the south by the remains of a dry stone wall, to the west by a path, and to the north by the North stream (Figs.2. & 4). It was chosen because it was known to support one of the densest concentrations of voles on the island (Fullagar et al. 1963).

Two trapping grids, each of 0.77 ha (including a five metre boundary strip) were located on the study area. The grids were adjacent and were so placed that their vegetation was as similar as was possible. This resulted in an 'L' shaped configuration (Fig 4.). The grids were initially laid out with an interstation distance of 20m (24 points per grid) but this was found to be too great a distance and to give too few points adequately to sample the population and an interstation distance of 10m, giving 77 points per grid, was adopted in 1972. In 1973 the grids were moved 20m to the east so as to reduce interference by members of the public using the footpath.

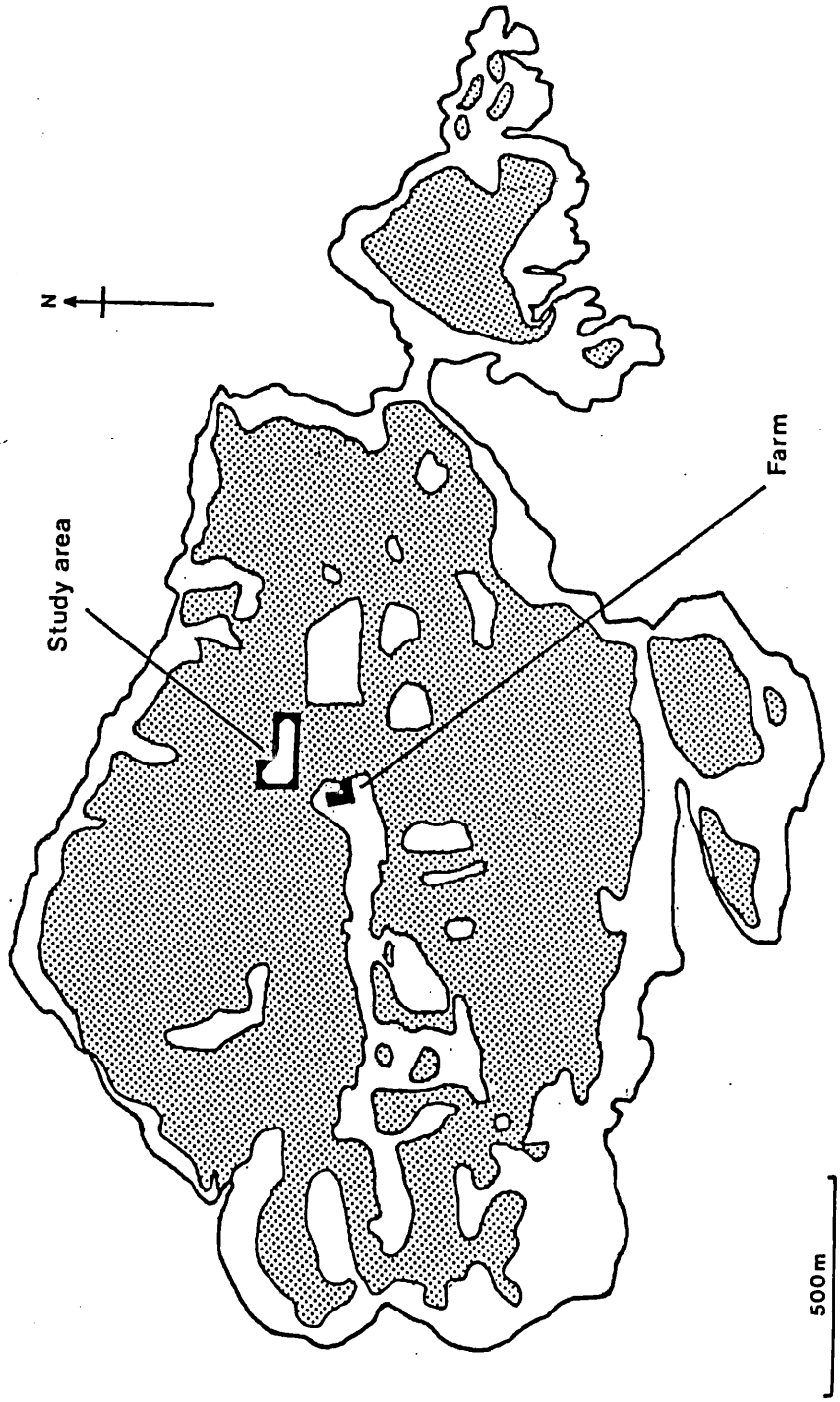
(b) Field methods.

The animals were caught in Longworth traps (Chitty & Kempson, 1949), hay or white felt (after 1981) being provided for bedding and whole oats for food. The food was replaced if an animal had been in the trap and the bedding if it became damp.

Fig 2.


Skomer island
Midland island
The Neck
1 km
North stream
Study area
Farm
North pond
Field walls
N

Skomer island ; extent of habitat suitable for voles (stippled)



Skomer island ; study area

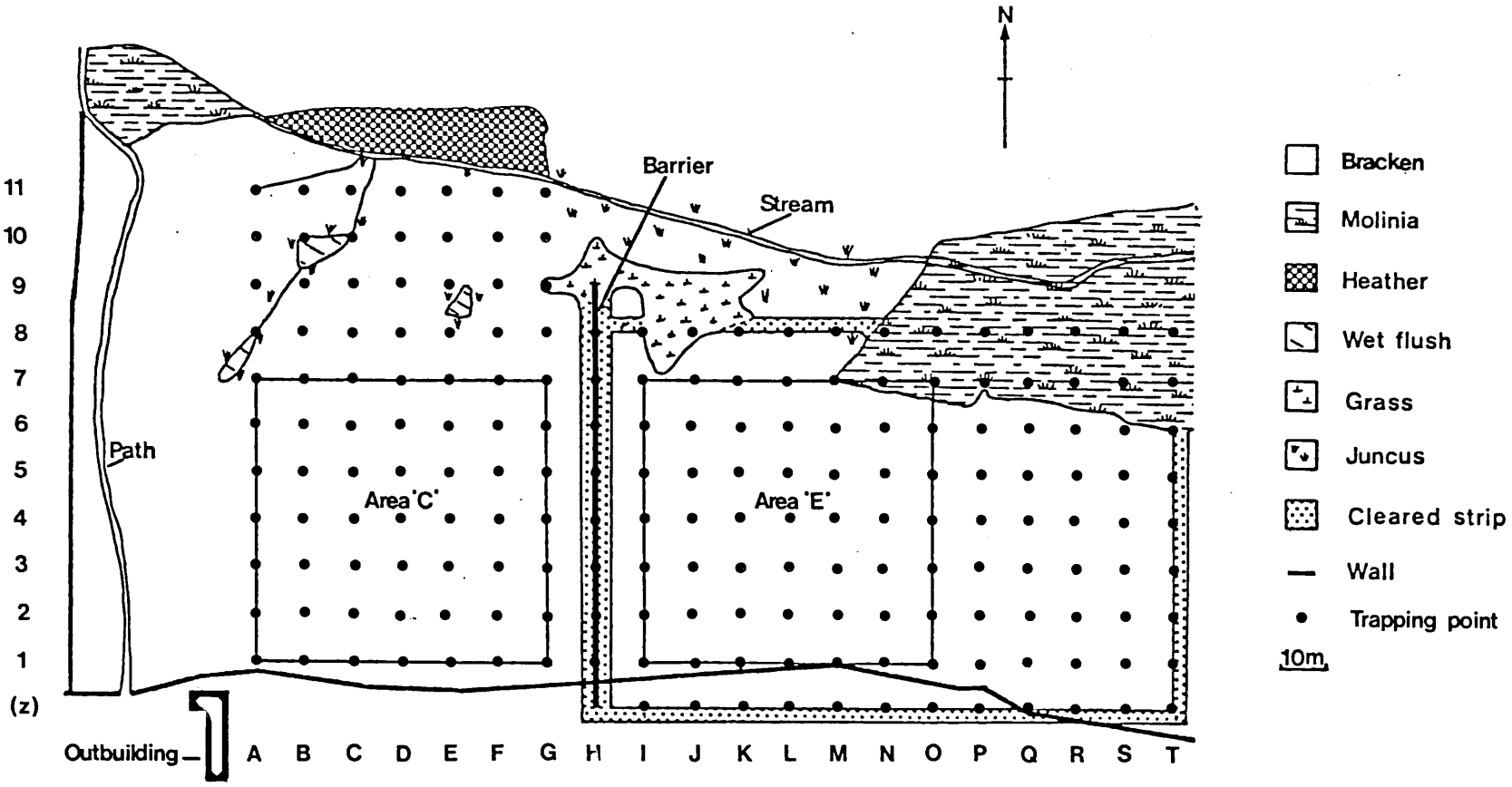
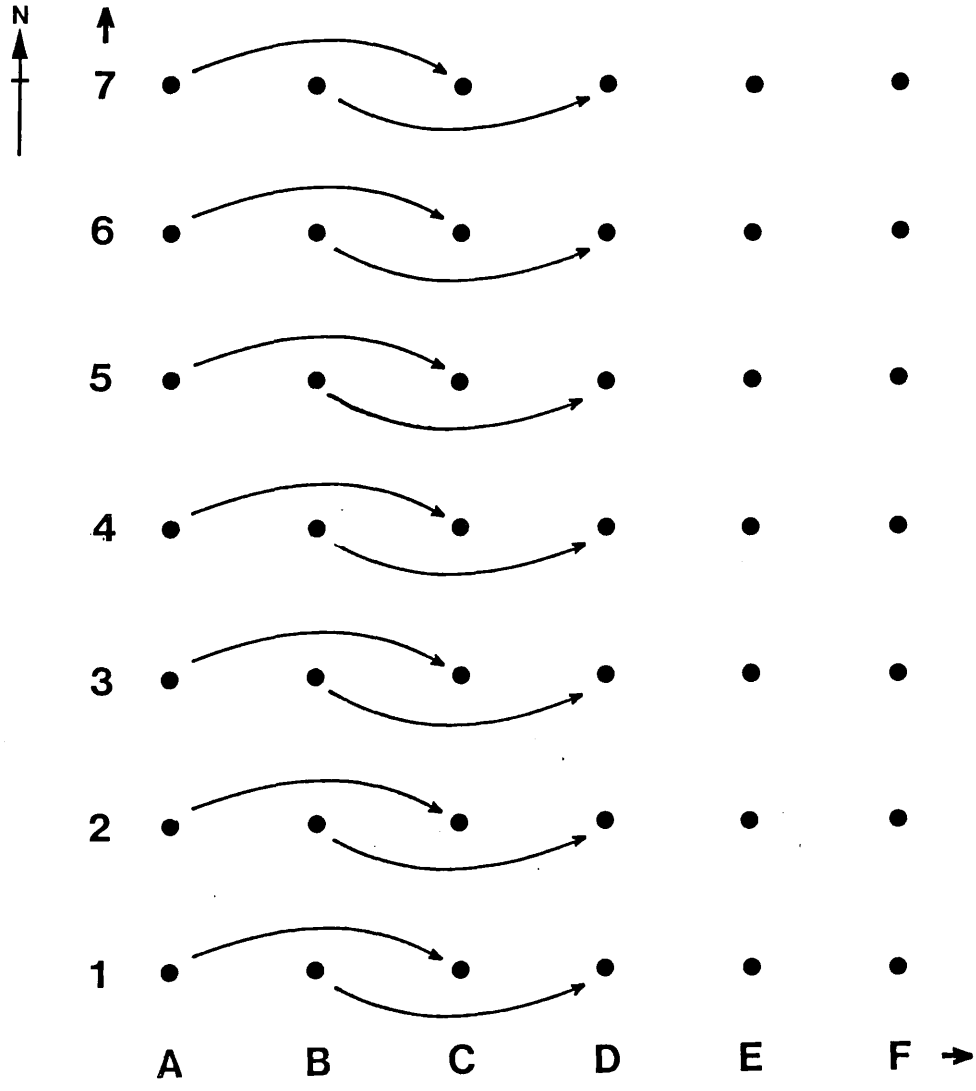


Fig 4.

The traps were checked before each trapping session to ensure that they were functioning properly and the treadles were adjusted so that a weight greater than six grams would set them off. This was done with the intention of reducing the mortality of shrews and of minimising the numbers of traps set off by the wind and by rabbits and shearwaters.That voles of less than six grams were unlikely to be caught had to be accepted. From 1976 onwards, when a survey of pathogens was being performed, the traps were sterilised by autoclaving before each visit to the island and the trap and animal carriers that were used were disinfected in a 1% solution of 'Tegodor' (Th. Goldschmidt Ag). In 1981 all the traps had a hole 12mm in diameter drilled into the side of the box. This was to allow shrews to escape and was done so as to meet the requirements of the Wildlife and Countryside Act, 1981. The holes were protected by galvanised iron washers to prevent rodents from damaging the traps.

The initial aim of the trapping programme was to capture as many animals as possible rather than simply to obtain an index of the size of the population. This was of particular importance for the removal experiment (Chapter 2.) when it was necessary to have most, if not all, of the female animals marked. For this reason varying numbers of traps (two to ten) were used at each point, the numbers being increased as the breeding season progressed. The size of the grids meant that it was not possible to trap the whole area at once (which would have required up to 1930 traps). A few of the north-south lines were therefore trapped and the traps moved to the next lines after one or two night's trapping ('Moving Line' trapping; Fig 5.). In 1975, with the removal experiment complete , the

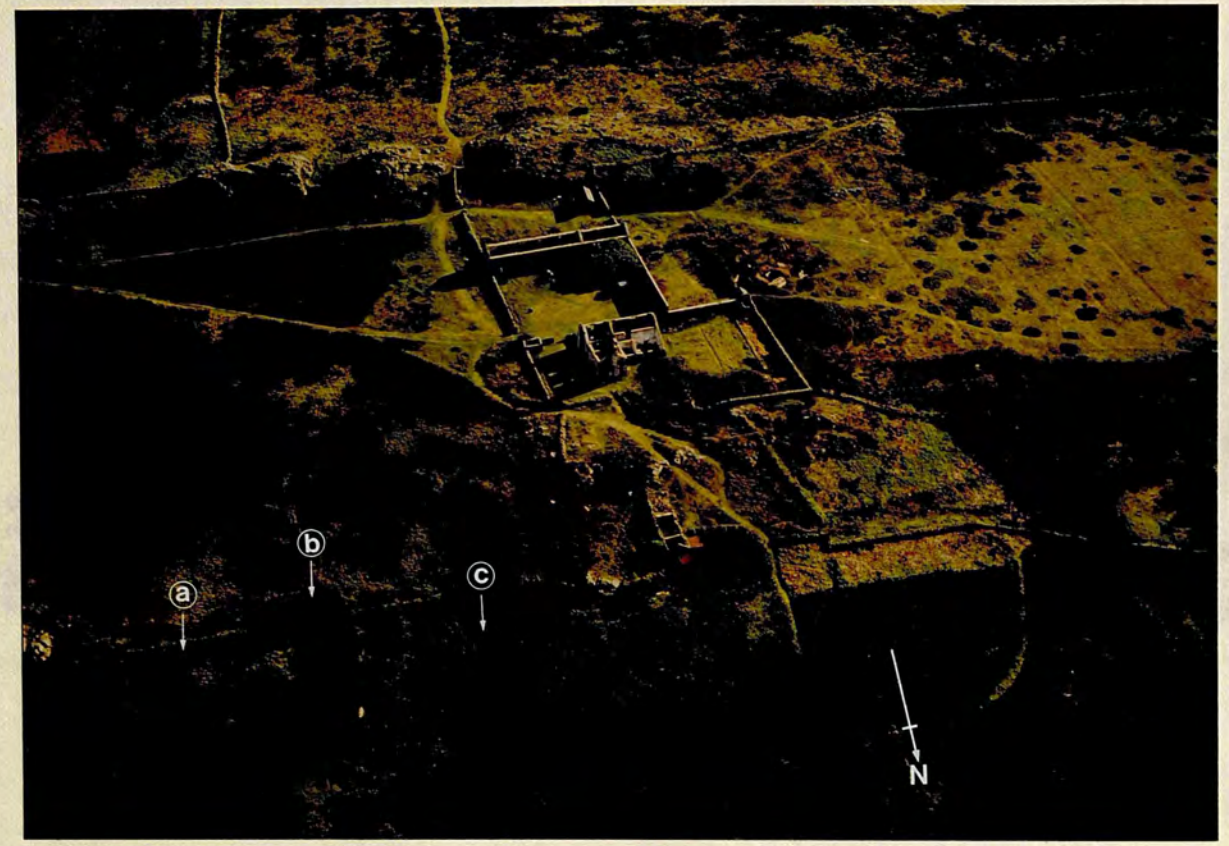
'Moving line' trapping



'Moving Line' method was abandoned and a portion of the control grid 60m x 60m was selected (area 'C'; Fig 4.;Plate 3.). This area, which was approximately the same as the Grid 'C' of Fullagar et al. (1963), was trapped for five consecutive nights on each visit to the island, two traps being used at each grid point. This change was made so that the trapping effort was consistent on each visit to the island and so as to bring the sampling method into line with that being employed in concurrent studies of small rodents on the mainland (Kaplan et al. 1980; Healing, 1981). During July 1975 ten nights trapping were performed, the traps being opened every other night. From August 1975 onwards the traps were open only at night, being closed during the morning trap round and opened in the evening. This practice was adopted because the extensive sampling procedures necessary for a study of pathogens in the voles then being undertaken meant that the trap rounds took many hours and two rounds a day were not possible. As an additional benefit, the risk that female voles might use the traps too readily as a source of food and might not therefore be able to feed their litters often enough was reduced, as was the mortality of shrews.

The animals were removed from the traps and weighed with a 'Pesola' spring balance graduated in one gram divisions from 0 - 50 grams (the accuracy of which was checked regularly with standard balance weights). The sex of the animals was determined and they were given individual marks by a system of toe and ear clipping (Fig 6.). In the first years of the study males and females were each given their own number series (thus there could be a male and a female with the same number) but

Plate 3.



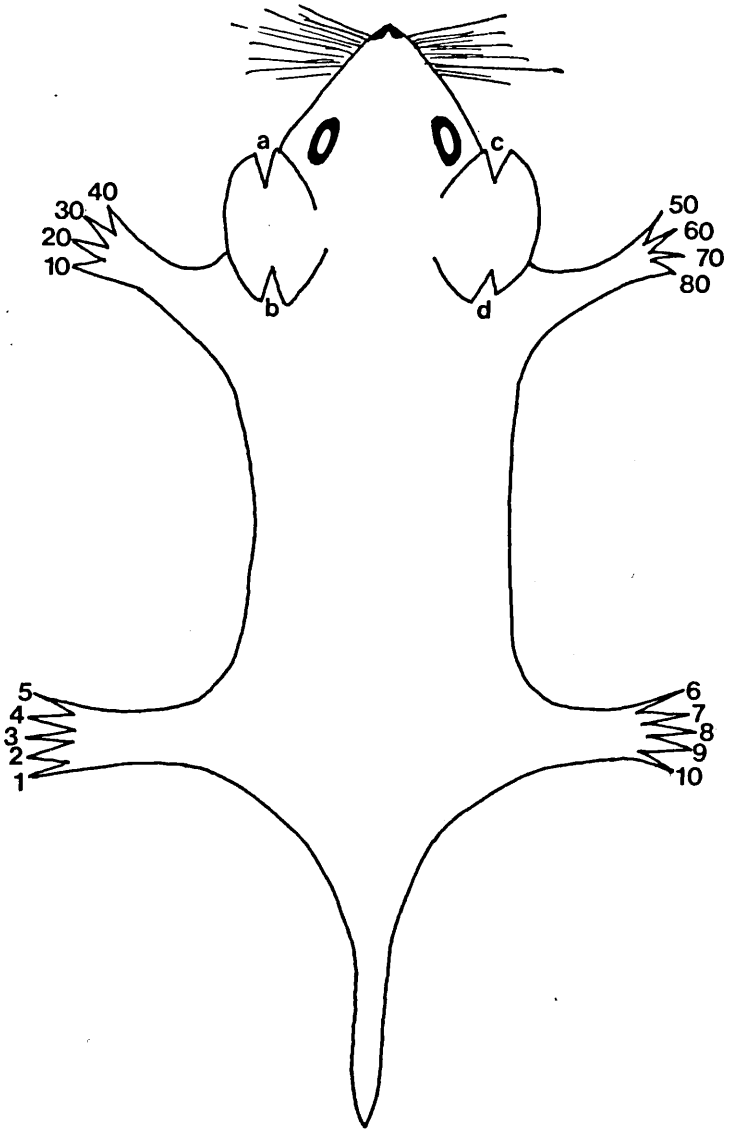
The farm and the study area from the air.

(a) = Area 'E'; (b) = Position of the barrier used in the removal experiment; (c) = Area 'C'. (The trap lines on the grid can clearly be seen).

(Photograph M.Alexander)

Fig 6.

Marking scheme



a - 100
b - 200
c - 300
d - 400
a b - 500
c d - 600
a c - 700
a d - 800
b c - 900
b d -1000

males (and occasionally females) sometimes sustained damage to their ears, possibly during mating or fights, that made the marks difficult to read and confusions arose. The adoption of a sequential numbering system in 1975 reduced the possibility of error. The relatively small distances moved by the voles (with respect to the study area as a whole) meant that an individual could often be identified with some certainty from its location on the grid. The animals were assigned to one of four age groups (Table 2.).

The criteria upon which the animals were judged to be sexually mature are listed below (Table 3.). Fulfillment of any of the appropriate criteria was sufficient for a female to be classed as an adult. Males were usually classed as adult on the basis of a combination of factors.

Table 2.

Age groups to which the animals were assigned and the criteria on which age was judged.

Juvenile	(J)	- recently weaned sexually immature animal (grey coat)
Immature	(I)	- sexually immature animal (brown coat)
Young adult	(YA)	- animal maturing sexually in the year of its birth
Adult	(A)	- animal born the previous year which was breeding or had bred

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Vaginal smears were taken from those females with patent vaginae with small swabs made by wrapping cotton wool around the end of toothpicks. The smears were air dried and subsequently stained with 0.1% watery methylene blue. They were

examined whilst still wet under a microscope at 100x magnification. The presence of blood and thick mucus in the smear indicated pregnancy (Bujalska, 1967).

Table 3.

Criteria upon which animals were judged to be sexually mature

Males	(1) Testes >1cm long (*) and scrotal or readily expressed into the scrotum. (2) Scrotal area rugose and blackened. (3) Scars or fresh wounds on rump and damage to eyes and ears.
Females	(1) Patent vagina or vaginal plug. (2) Nipples rugose and hair plucked from around nipples. (3) Milky mammae. (4) Palpable embryos. (5) Evidence of oestrus or pregnancy in vaginal smears.

(*) The testes of those adult males that were dissected during this project were all more than 1cm long.

(c) Habitat changes

From 1975 onwards vegetation surveys were carried out on the study area during August of each year. Quadrats one square metre in area were used and the percentage area covered by each plant species present was measured at each grid point on area 'C'. (For the details of the method see Chapter 3.). Fullagar et al.(1963) showed that the voles preferred areas of the island where there was less grass. So as to test this observation further the study area was sub-divided on the basis of the vegetation data into areas having a grass cover >50% or <50%. The density of the population in each of these areas was determined.

(d) Analysis of the data.

From 1975 onwards all the sampling was performed on part of the original control area (area 'C'; Fig 4.). For the sake of consistency only those data obtained on this area and a comparable area (area 'E'; Fig 4.) on the experimental side of the barrier have been used in the analyses of the data from 1971 - 1975 (unless otherwise stated).

(i) Number of animals alive.

Longworth traps (and other 'live' traps) do not sample the population at random and so the commonly used mark-recapture statistics cannot reliably be employed to estimate the size of populations if the data are collected by this means (Krebs, 1966). Instead the minimum number of animals known to be alive per hectare (MNA/ha) was calculated for each trapping session. These figures included those animals which were actually caught together with those that had been caught during previous trapping sessions, that were not caught during the trapping session in question, but which were caught subsequently and so could be added in retrospectively. The results are given as numbers per hectare rather than as numbers per fraction of a hectare so as to permit direct comparison with results obtained from those of my mainland study sites where the grids were of different areas. The results from a whole trapping session were treated as though the data were collected on a single occasion regardless of the length of that trapping session. Underestimation of the numbers present due to birth and immigration and overestimation due to deaths and emigration during the trapping session could not be calculated.

(ii) Survival.

The survival of animals born during 1971, 1972 and 1974 on

area 'C' was determined. The survival was calculated from October onwards treating all the animals as a single cohort. Samples were not always taken at the same time in each of the three years and when no value was available an estimate was used. The rate of loss of individuals between consecutive trapping periods was usually small and a uniform rate of loss per unit time was therefore assumed in the calculation of the estimates. The survival of animals captured between 1976 and 1983 was also determined but since no estimates were used the data were suitable for statistical analysis and were tested for statistical significance by the use of χ^2 with Yates' correction. Because only one visit was made to the island each year between 1976 and 1980 it was only possible to determine the survival on an annual basis. Several visits were made to the island in 1981, 1982 and 1983. The survival data were therefore more detailed and survival during the breeding season and between one breeding season and the next could be determined. The survival of males and females between subsequent trapping periods was tested using 2 x 2 contingency tables and calculating χ^2 with Yates' correction.

(iii) Relationship between the numbers of breeding females and the production of young.

Assessments of the relationship (if any) between the number of adult and/or young adult females present at certain stages of the breeding season and the number of young of both sexes known to be alive at that or at some later time were made by the use of linear regressions, the regressions being calculated following the methods described by Glantz (1981). The statistical significance (if any) of the results was

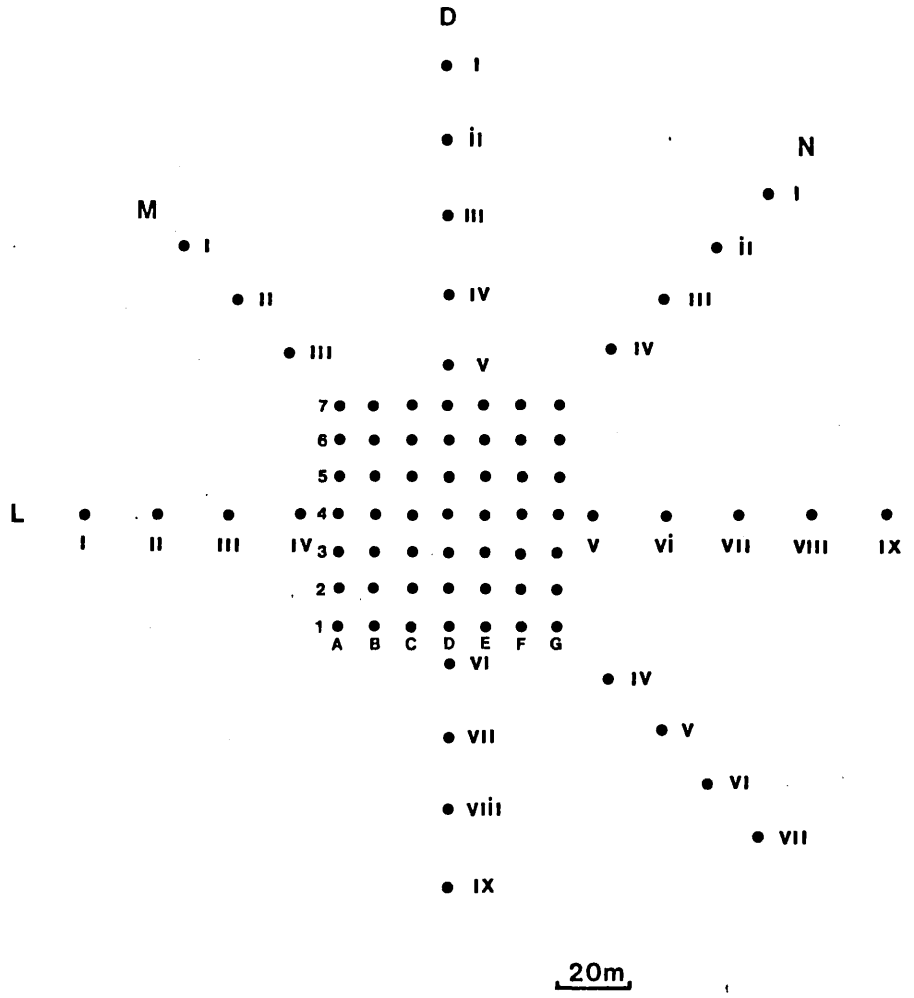
assessed by means of a 't' test.

(iv) Range of movement.

Live trapping is not a very effective method for the collection of data on the home ranges of small mammals because only one point in the home range is revealed at a time and because it has been shown that different age and sex classes react differently to traps (Kikkawa, 1964; Tanton, 1965; Brown, 1969). The size of the revealed range can also be affected by trap spacing, the size of the trapping grid, and the number of times an individual is caught (Kikkawa, 1964; Sanderson, 1966; Bonderup-Nielsen, 1983). Much effort has been devoted to finding methods to estimate the areas of home ranges (eg. Hayne, 1949; Stickel, 1954; Mazurkiewicz, 1971; Wierzbowska, 1972) but all these methods require several captures of the individual animal. The 'lifetime range' (Jewell, 1966b) of the animal may be calculated by accumulating data over several trapping periods and the area itself may be defined as the area enclosed by some geometric projection (eg. a polygon) enclosing most or all of the trap revealed points. The data obtained during the present study were difficult to analyse by such methods because the majority of the animals were caught few times during their lives.

Three different trapping regimes were followed during the period of the study. From 1971 to 1975 the whole grid was used but from 1976 to 1980 only area 'C' was trapped. In August 1982, in an attempt to detect longer movements, trap lines radiating out from area 'C' were established (Fig 7.). These lines were retrapped in October 1982 and throughout 1983. In addition, during the island-wide survey in 1981, animals caught

Arrangement of trapping points around area 'C' to detect long movements (1982 & 1983)



on that part of Line I. closest to the study area (Fig 8.) were individually marked. It was hoped that longer movements by the voles might thus be detected.

As a result of the use of the three different trapping regimes the data on range lengths were obtained from sampling areas of different sizes at different times throughout the study and it was necessary to analyse the data separately. In each case the averages of the maximum distances moved by the animals were used in the analyses. Four separate analyses were performed using data from animals caught at least twice:

(a) Lifetime ranges 1971 - 1973.

Data obtained after mid-August 1973 were not used because the removal experiment (Chapter 2.) might have distorted the results.

(b) Lifetime ranges 1976 - 1983 (August data only).

(c) Within trapping period ranges 1976 - 1983 (August data only).

(d) 'Long movements' experiment 1982 & 1983.

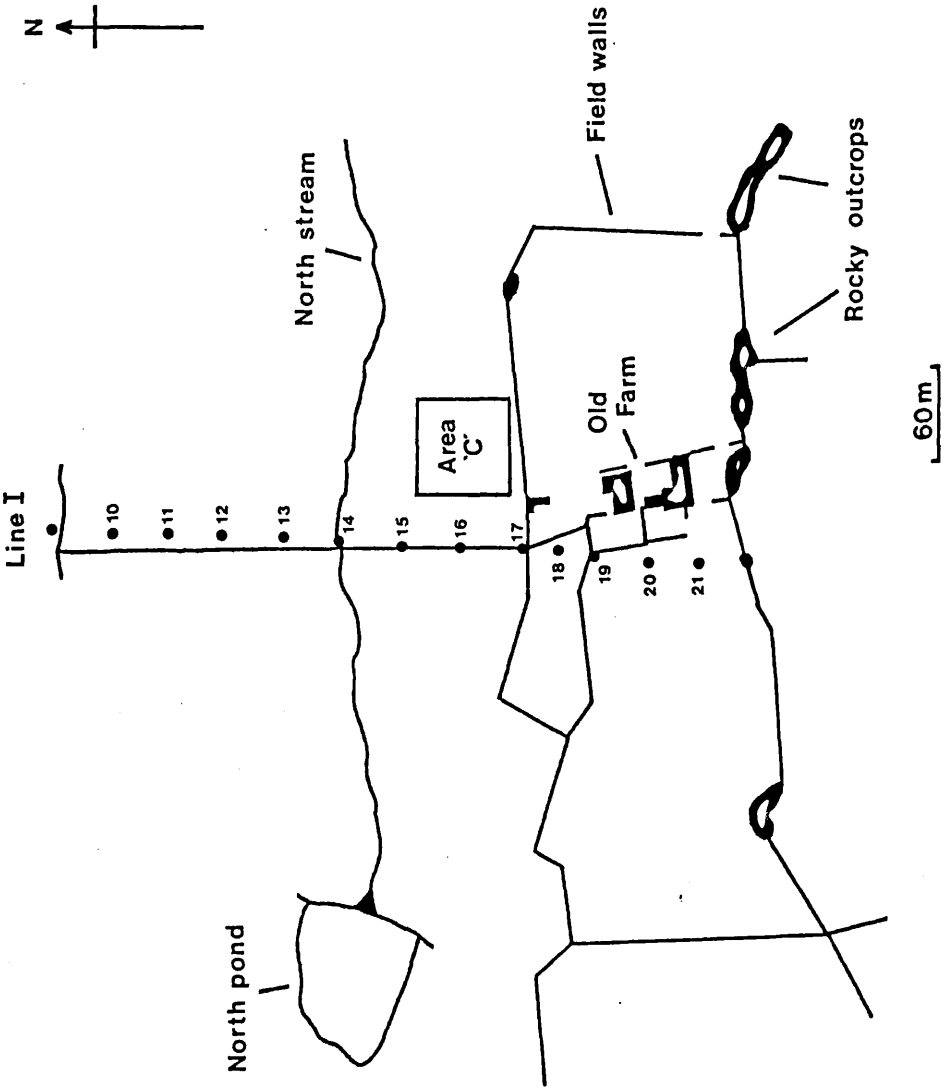
Statistical significance (if any) in the results obtained was determined by the use of the Mann-Whitney 'U' test (Siegel, 1956) (where the sample variances were approximately equal) or the two-sample t test (Ryan, Joiner & Ryan, 1980) (where the sample variances differed widely). The latter test has a value of $t = \bar{x}_1 - \bar{x}_2/s.d.$, the standard deviation (s.d.) being given by the formula

$s.d. = \sqrt{s_1^2/n_1 + s_2^2/n_2}$. This has approximately the Student t distribution with degrees of freedom given by the formula:

$$d.f = (s_1^2/n_1 + s_2^2/n_2)^2/(((s_1^2/n_1)^2/n_1-1) + ((s_2^2/n_2)^2/n_2-1))$$

Fig 8.

Central part of the island to show the position of area 'C' in relation to line I in the 1981 survey



(v) Dispersion.

The degree to which the dispersion of the voles differed from random was determined by calculating the ratio of the variance to the mean of the number of animals caught per trapping point (Blackman, 1942; Greig-Smith, 1983) where:

$$\text{Variance} = [\Sigma x^2 - ((\Sigma x)^2/n)]/n-1$$

$$\text{Mean} = \Sigma x/n$$

where x = number of captures at a trapping point and n = number of capture points (= number of observations).

This test makes use of the fact that the variance and mean of a Poisson distribution are equal. If the variance to mean ratio is less than one, a regular distribution is indicated, if greater than one, a contagious (clumped) distribution. The significance of any differences between this ratio and unity were tested by comparing the difference with its standard error by means of a 't' test where:

t = (observed - expected)/standard error

This value has n-1 degrees of freedom where n is the number of observations. The standard error (which depends only on the number of observations; Greig-Smith, 1983) is given by the formula $\sqrt{[2/n-1]}$ where n is the number of observations.

Interpretation of the results obtained by such analyses must be undertaken with caution because the patterns detected may be the result of the influence of the habitat on the distribution of the animals and not a direct reflection of behavioural interactions between the animals themselves.

(vi) Island wide-survey, 1981

The details of the methods employed in this survey and the greater part of the results have already been published

elsewhere (Healing et al. 1983 - Appendix 4.) but a few results obtained at that time and not previously published are included here. In particular the body weights of adult male and female voles in areas of habitat found to be more or less favoured by the voles were compared and the breeding condition of these animals noted.

(vii) Determination of the age of animals post-mortem

Several authors have determined the rate of formation and development of the roots of the molar teeth of bank voles and have used the information thus obtained to determine the age of the animals. Wasilewski (1952; cited by Hyvarimen & Heikura, 1971) stated that the teeth of bank voles do not develop roots until the animals are at least two months old and Lowe (1971) showed that the tooth roots of laboratory reared bank voles did not develop during the first six months of life but that, in field populations, root development occurred between 2 and 4.5 months of age depending on the season.

No use has been made of field material in studies of the determination of the age of Skomer voles but Al-Jumailly (1976), working with laboratory reared animals, found that the lateral grooves of the molars started to close at the base when the animals were 35 to 42 days old and that root formation started after 72 days.

When it was necessary to determine the age of animals post-mortem the methods described by Al-Jumailly (1976) were used. The skulls were boiled for about 10 mins in 1% NaOH and the teeth were then extracted, washed, dried, mounted on cards with the buccal (external) face upwards, covered with sellotape and examined under a dissecting microscope.

RESULTS

(i) Minimum numbers known to be alive

The minimum numbers of animals known to be alive per hectare (MNA/ha) on areas 'C' and 'E' have been plotted against time (Fig 9.). The greatest density of animals recorded during the project was 475/ha on area 'C' in October 1971 and the smallest was 86/ha on the same area in May 1983. The data from May 1983 must be treated with some caution however, since the vegetation was behindhand that year, the cover was very short, and a larger proportion of the animals known to be present were not caught than had been the case in the previous two years (Table 4.) (the difference between the numbers caught in May 1983 and those caught in May 1981 and 1982 is statistically significant (1981: $\chi^2=22.67$; df=1; $p<0.001$. 1982: $\chi^2=21.6$; df=1; $p<0.001$)).

Table 4.

Numbers of animals caught and known to be present but not caught (PNC) in May 1981 - 1983

Year	No.caught	No. PNC.
1981	69	7
1982	62	6
1983	21	21

The population of voles has fluctuated annually, the smallest numbers being found in April - May and the peak numbers in September - October (the beginning and end of the breeding season respectively). Few data are available for the late winter and early spring but, in 1973, the decline in

Minimum number of animals known to be alive per hectare (MNA/ha) on area 'E' (1971–1975) and area 'C' (1971–1983)

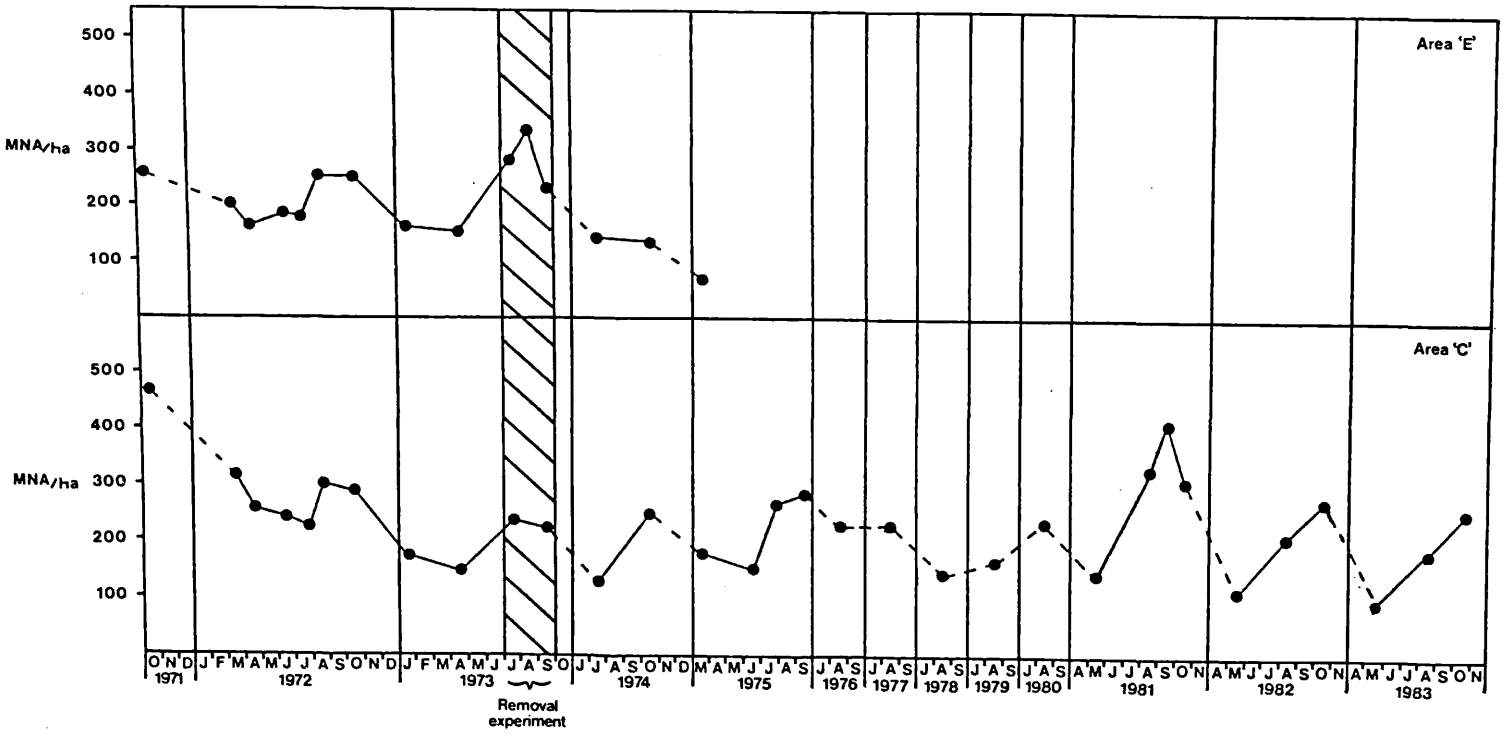


Fig 9.

numbers between January and April was small. It is possible therefore that the majority of the animals which are not recaptured disappear during the late autumn and early winter.

It is of interest to note that the numbers present in October 1981 - 1983 declined approximately in parallel with the decline in the size of the population in May of the respective years and that there was a decline in the size of the population between August and October in 1972 and between September and October in 1981.

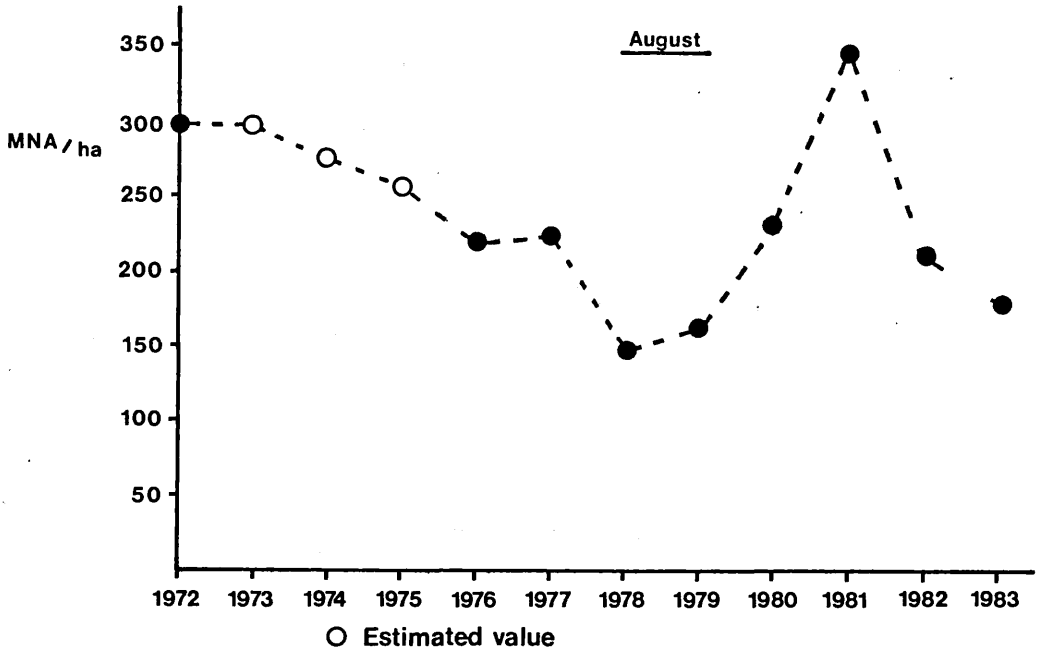
If the data for early August are considered (estimates being made for the size of the population in 1973, 1974 and 1975) (Fig 10.), there was a slow decline in numbers from 1972 to 1977, a more rapid decline from 1977 to 1978, a slight increase in 1979 followed by a fairly sharp increase to 1981 and a decline in the following years. The data for October 1971 to 1974 and 1981 to 1983 (Fig 10.) show evidence of a decline between 1971 and 1972 but the values for 1972 - 1974 and 1981 - 1983 show relatively little variation (the data from 1973 include the effects of the removal experiment).

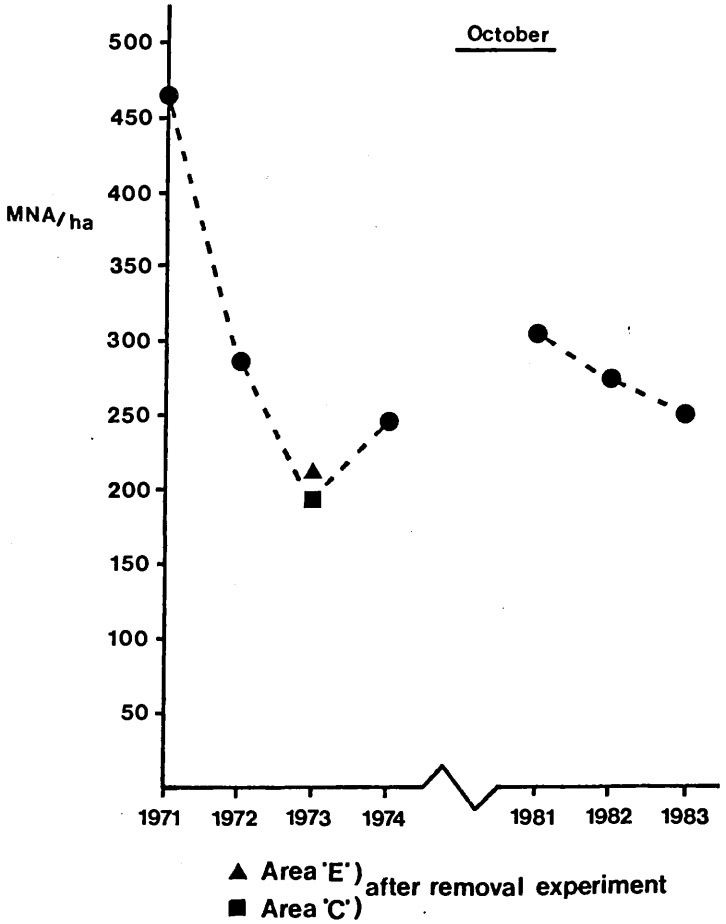
There is no evidence of regular two, three, four or five year cycles in the size of the population but the number of animals caught does show quite large changes both within years and over periods of several years.

The number of adult females present early in August (1976 - 1982) was almost directly proportional to the minimum number of animals known to be alive. By contrast the number of adult males present at the same time in each year remained almost constant (Fig 11.).

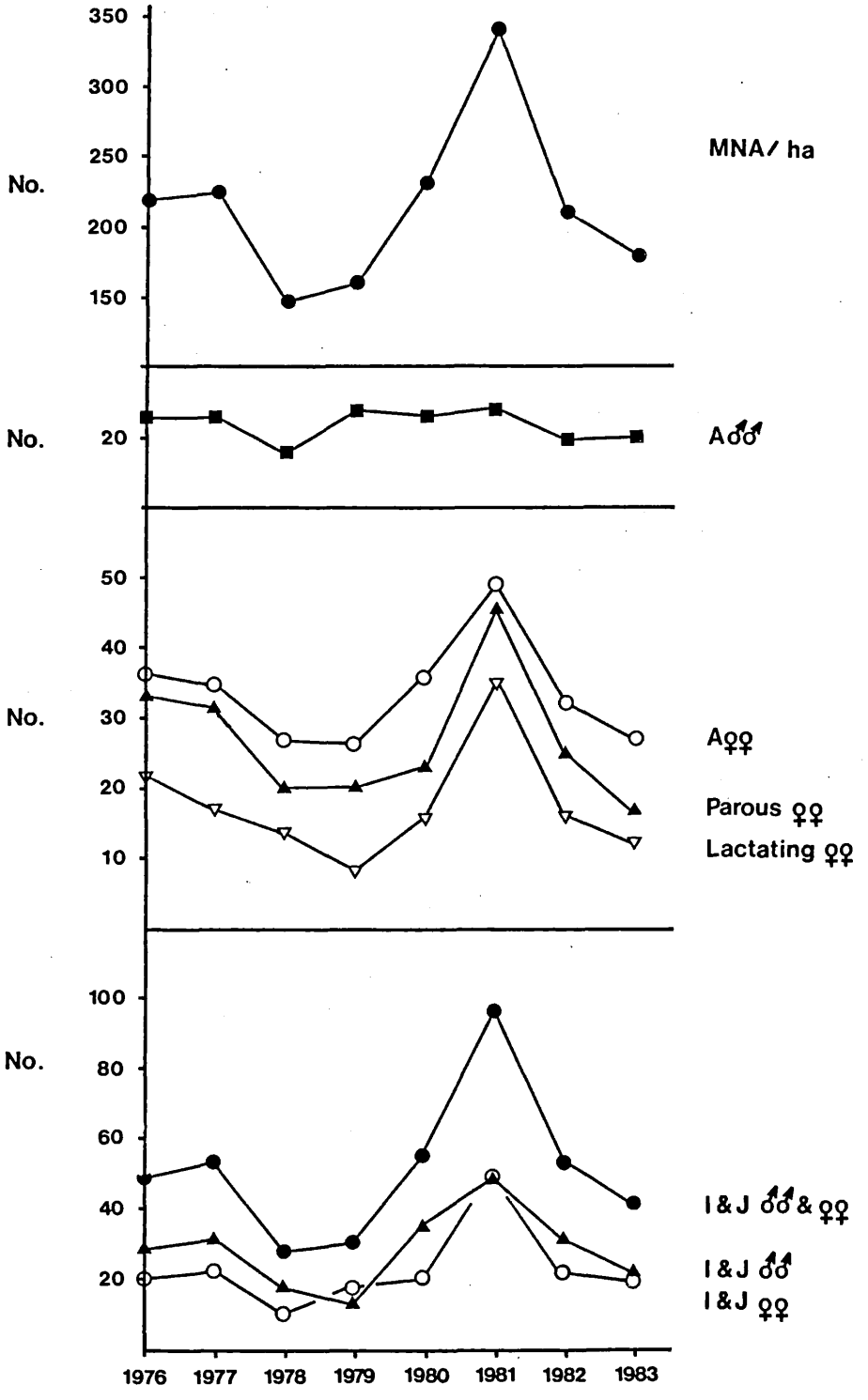
The number of nulliparous females varied from year to year

Minimum numbers of animals known to be alive per hectare (MNA/ ha) on area 'C' in August and October





Minimum numbers of animals known to be alive per hectare (MNA/ ha) and the size of the various sex and age classes on area 'C'; August 1-10, 1976 - 1983



the proportion of animals in this category varying approximately inversely to the size of the population (Fig 12). Not all of these nulliparous individuals were identified as young adults and a few were known to have been born in the previous year. The proportion of parous animals which were lactating during the first week in August varied approximately in proportion to the minimum number of animals known to be alive (Fig 12.).

Few males could, with certainty, be identified as having matured in the year of their birth. Some, whose weights were the same as the larger members of the immature age group, were found with testes which, when palpated, would move into the scrotum, but these testes were small (<1cm in length) and the animals were not scarred and could not positively be identified as part of the breeding population (see also section (v) of this chapter).

Although approximately the same numbers of adult females were caught at the beginning of the breeding seasons in 1981 and 1982 (May) variable numbers were caught later. Fewer adult females were caught in May 1983 than in the previous years, possibly for the reasons given above. The number of adult females caught in August of that year was greater than the number caught in May but was slightly smaller than the number caught in August the previous year. Not all the new adults caught in August of each year were young adults (Table 5.).

The numbers of adult males caught in May 1981 and May 1982 were almost the same, and they declined by approximately the same amount between May and August in both years. In both years seven new adult males were caught for the first time in August.

Proportions of adult females lactating and nulliparous, area 'C', 1976 - 1983 compared to the size of the population

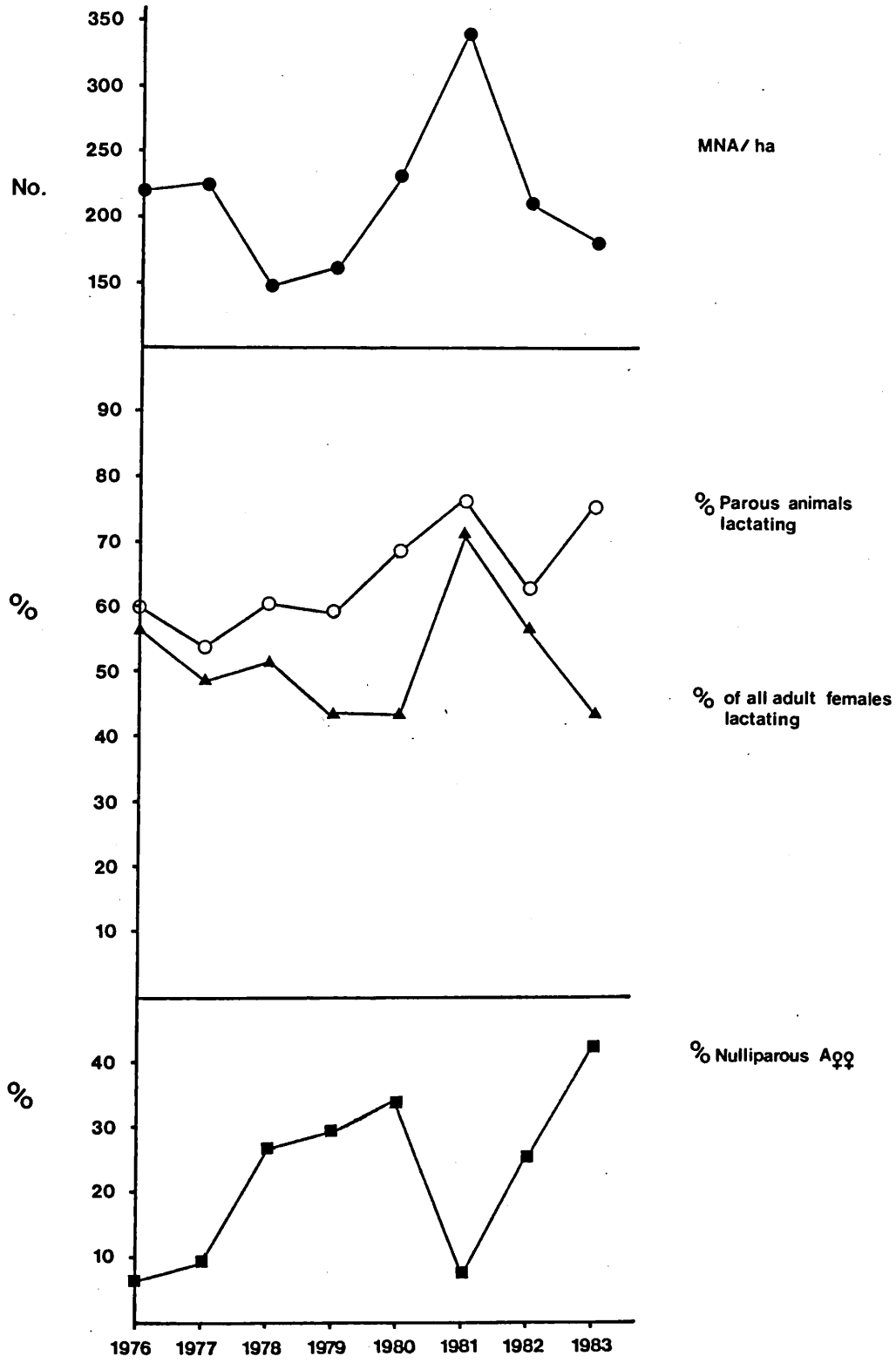


Table 5.

Numbers of adult females caught in May and August 1981, 1982 & 1983

	Number caught (A)	Number of young adults (B)	Number of new (over-wintered) adults (C)	(C) as a % of (A)	(B+C) as a % of (A)
May 1981	37	-	-	-	-
Aug 1981	49	3	12	24.5	30.6
May 1982	33	-	-	-	-
Aug 1982	32	6	3	9.4	28.1
May 1983	13	-	-	-	-
Aug 1983	28	9	7	25.0	57.1

Table 6.

Numbers of adult males caught in May and August 1981, 1982 & 1983

	Number caught (A)	Number new (B)	(B) as a % of (A)
May 1981	32	-	-
Aug 1982	23	7	30.4
May 1982	29	-	-
Aug 1982	21	7	33.3
May 1983	8	-	-
Aug 1983	20	9	45.0

These new animals were not young adults. In May 1983 fewer adult males were caught than in previous years possibly for reasons given above. The number caught in August of that year was almost the same as in the previous years (Table 6.).

Seventy-six percent of the new adult males and females caught in August 1981, 1982 and 1983 were caught at the edge of the trapping grid as compared to 46% of the new young animals (the 10m strip surrounding the outermost trapping points occupied 26.5% of the total area of the grid). Not all these new adults were necessarily immigrants. The trapping method employed did not involve a total catch and some of the animals could have been missed on earlier occasions.

In most years, in August, the catch of immature and juvenile males was greater than that of females of the same ages, the males usually comprising about 60% of the catch. In 1981, when the population reached a peak, there was a sharp increase in the numbers of both immature and juvenile males and females over the previous year, the greatest proportional increase being shown by the females. Only in August 1979 were more immature and juvenile females caught than males (Fig 11.).

(ii)Weights of animals.

The mean live weights of the animals at first capture in each trapping session are summarised for each month in Table 7. The values for each month (except January) contain data from more than one year and the data for each month were not necessarily taken at the same time in each month (see Table 1. and the fold-out endpaper). (Such a procedure is open to criticism on biological grounds but nevertheless I feel that the table presents a useful summary).

Those adult animals which survive from a previous year appear to overwinter at a relatively constant weight. The apparent decline in the weights of the adult male and female groups between January and April is probably due to the maturation of immature animals which enter the adult group at a lighter weight than the overwintered animals. The immature animals also lose weight at that time but whether this is due to a loss of condition or to the earlier maturation of heavier animals is not clear. The body weight of the adults rises rapidly in the late spring and early summer, reaching a peak in July and declining thereafter. Adult females are lighter than males from January until June but are, on average, heavier thereafter although this is probably a reflection of pregnancy. Females have a mean weight about 1gm lighter than males throughout the period of sexual immaturity.

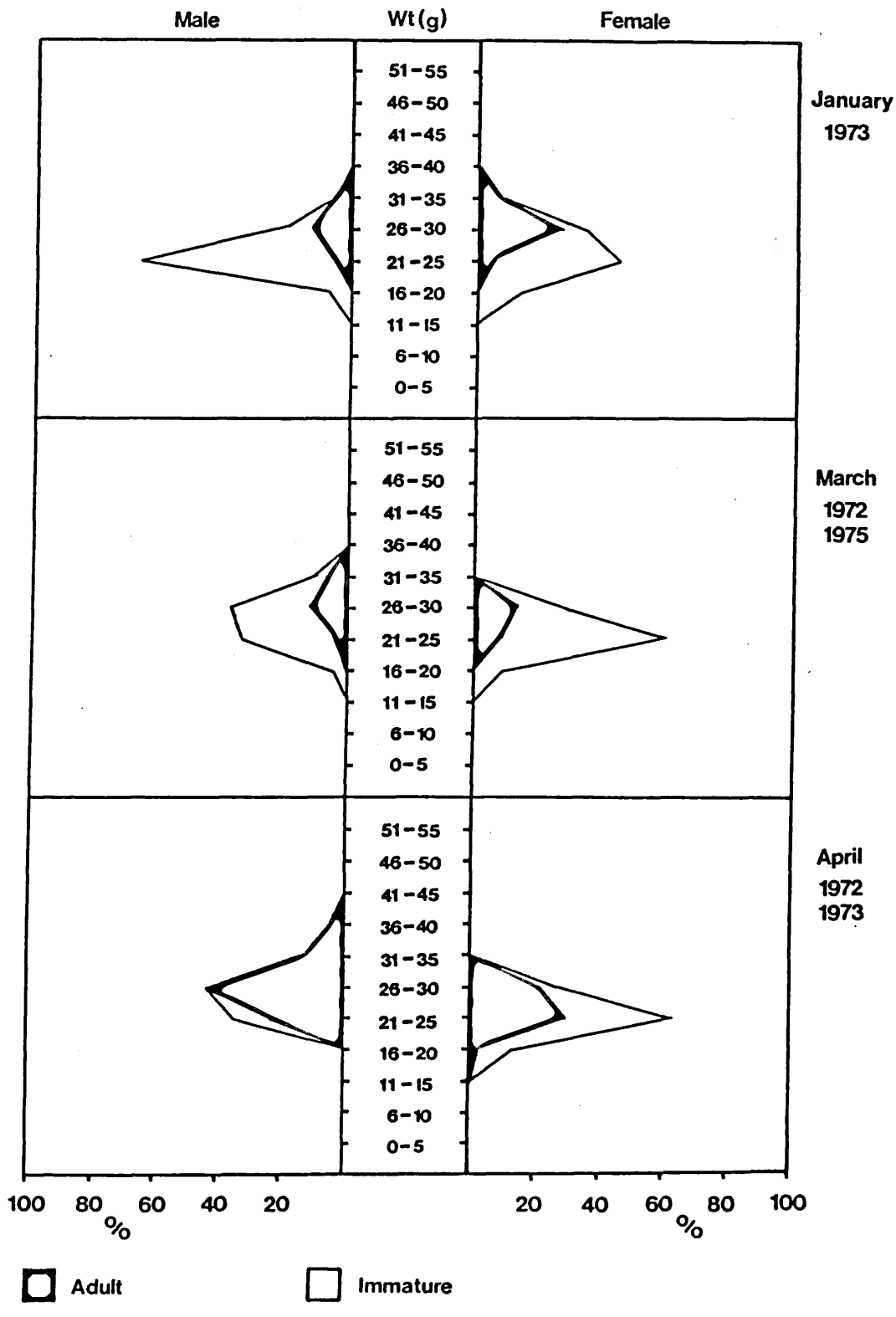
Table 7.

Mean body weight of Skomer voles for each month

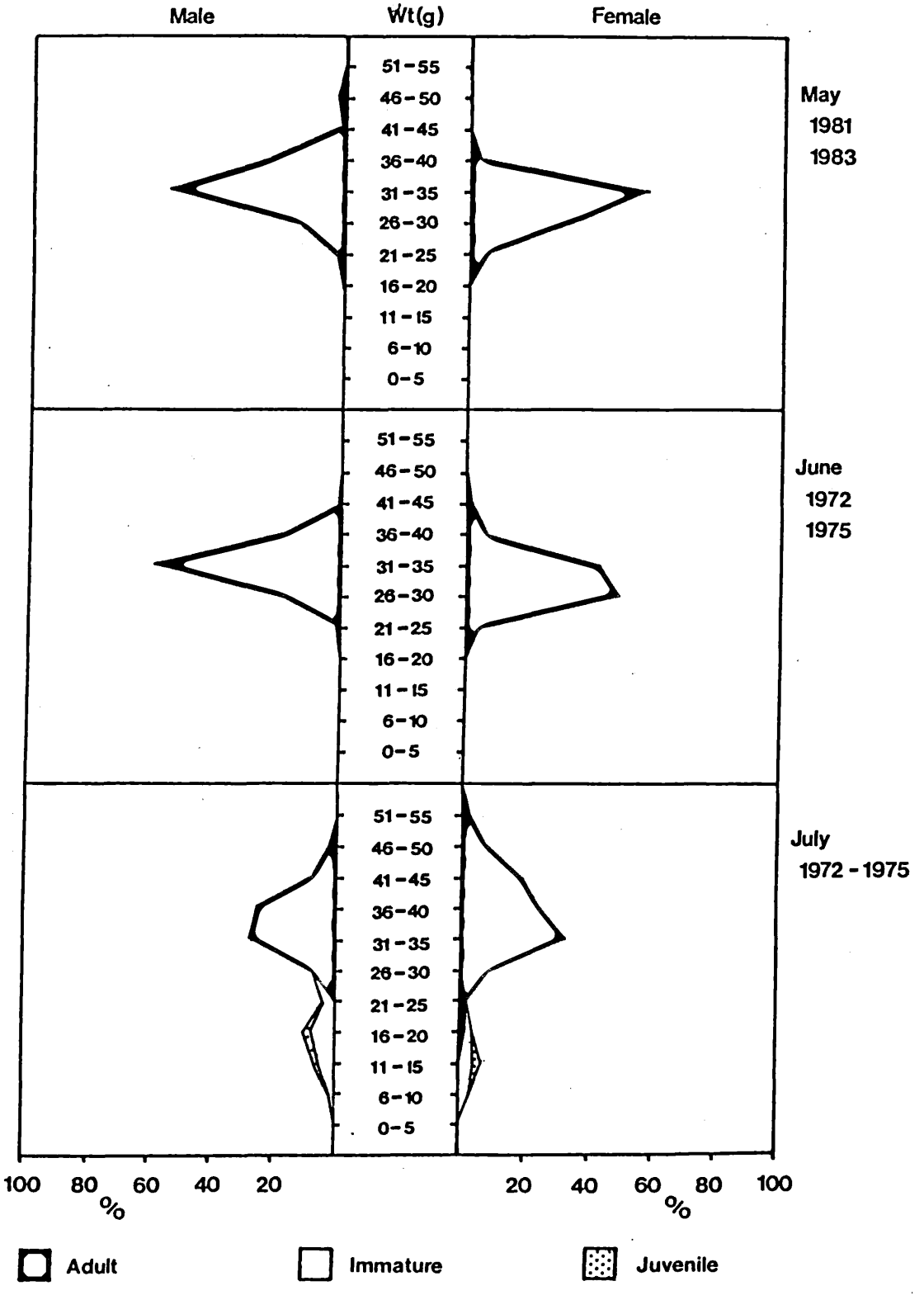
	Aσ	n	I+Jσ	n	A♀	n	I+J♀	n
Jan	28.2±2.7	17	23.1±2.0	55	28.3±2.6	22	22.0±2.4	35
Mar	28.2±3.1	40	25.8±2.7	138	26.7±2.8	32	23.4±2.4	116
Apr	27.8±3.8	109	23.7±1.5	15	24.7±2.7	53	22.3±2.1	48
May	34.5±3.4	30	-	-	31.2±2.7	29	-	-
Jun	33.2±3.3	139	-	-	30.8±3.3	124	-	-
Jul	35.6±4.6	203	16.2±4.2	61	36.9±5.8	230	11.5±2.8	16
Aug	32.4±3.8	330	17.9±4.3	474	33.2±5.9	464	16.9±4.0	377
Sep	32.8±3.7	87	22.0±3.0	195	33.7±3.8	90	20.9±3.3	179
Oct	30.3±3.0	109	22.5±3.4	393	31.2±3.2	181	21.8±2.8	326

The ranges of weights at first capture have also been plotted (Figs 13,14 & 15.). In these figures the weights have

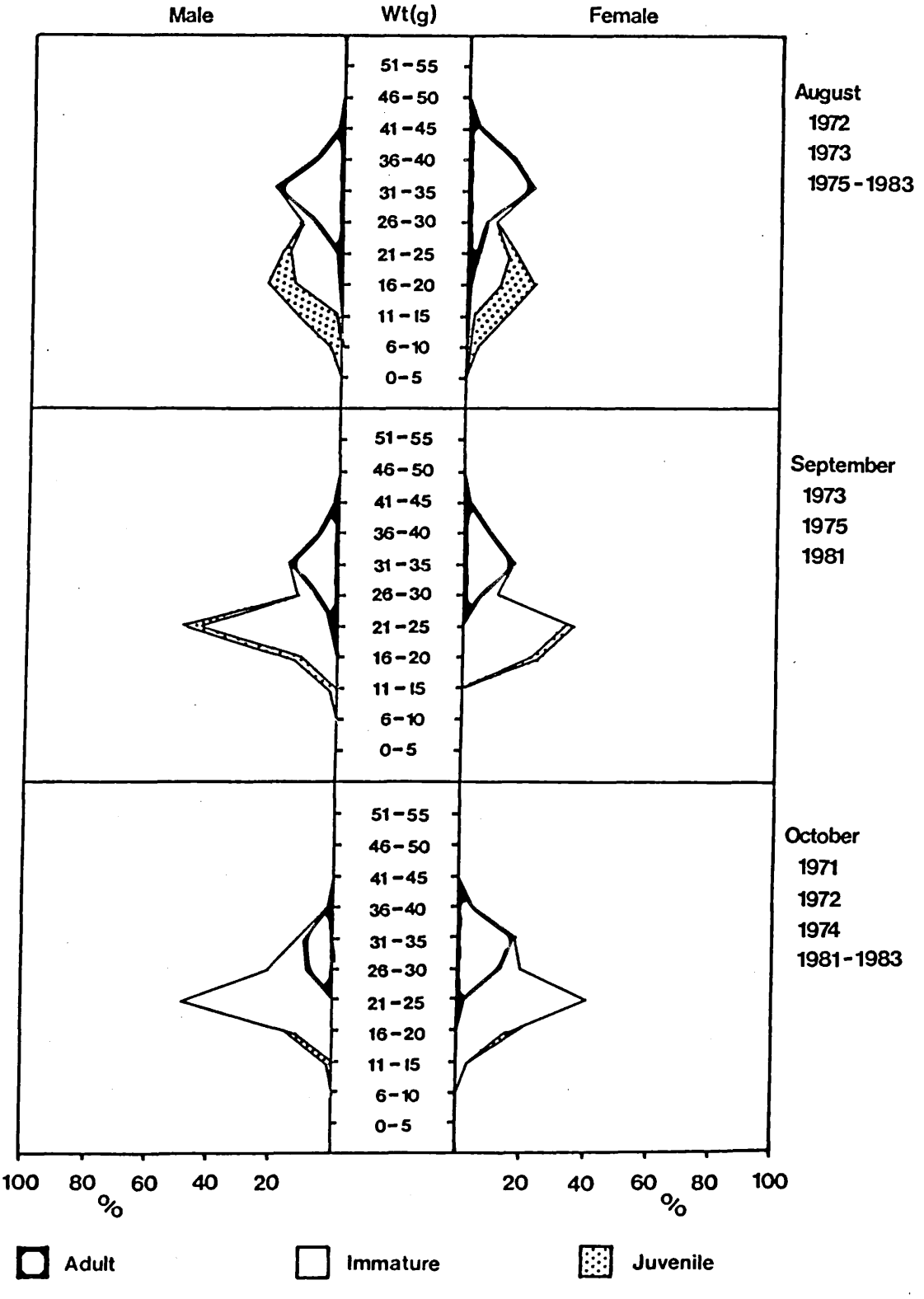
The proportional distribution of animals of each sex in 5g weight classes & by age within each weight class. (January – April)



The proportional distribution of animals of each sex in 5g weight classes & by age within each weight class. (May - July)



The proportional distribution of animals of each sex in 5g weight classes & by age within each weight class. (August-October)



been grouped into 5g groups and the proportion of each age and sex class falling within these groups plotted. This procedure avoids the problem of different sample sizes at different seasons (due to different trapping efforts), and gives a useful picture of the change in the weight structure of the population throughout the year.

(iii) Age structure of the population.

It was not possible to obtain data on the changing age structure of the population throughout any one year, but, using data obtained throughout the project it was possible to summarise such changes (Table 8. & Figs 13,14 & 15.).

Table 8.

Proportions of animals of each sex falling into the three age classes in each month.

Month	♂♂%			♀♀%		
	A	I	J	A	I	J
January	23.6	76.4	-	38.6	61.4	-
March	22.5	77.5	-	21.6	78.4	-
April	87.9	12.1	-	52.5	47.5	-
May	100.0	-	-	100.0	-	-
June	100.0	-	-	100.0	-	-
July	76.9	1.1	22.0	93.5	0.4	6.1
August	42.0	29.8	28.2	55.8	16.4	27.8
September	31.0	64.4	4.6	33.5	57.6	8.9
October	21.7	73.6	4.7	35.7	60.8	3.5

The proportion of animals which had bred the previous year declined throughout the winter. In the spring the males came into breeding condition slightly earlier than did the females but, in April, few immature animals were caught and, by the end

of May, all the animals were in breeding condition. The first young were caught at the beginning of July and the proportion of young animals increased rapidly as the breeding season progressed. By the middle of September few new animals were coming into the population. The last lactations ended in the first week in October. This basic pattern was maintained in those years when trapping was done throughout the breeding season but some variation in timing ocurred from year to year.

(iv) Survival.

The results of the calculations of the survival of the immature and juvenile animals alive in October 1971, 1972 and 1974 are summarised in Figure 16. The apparent differences in survival between males and females that are shown could not be tested statistically because estimates were used in the preparation of the figure.

Considerable variation occurred in the survival of animals first marked in August 1976 - 1980 (Table 9.). Considering only the summary values:

(a) the survival of both male and female animals first marked as adults was the same (χ^2=0.03).

(b) the survival of females first marked as immature or juvenile was better than that of males of the same age (χ^2=14.55;df=1;p<0.001).

(c) the survival of females with patent vaginae in the year of their birth was not significantly different either from those first marked as adult or from those first marked as immature or juvenile.

(d) the survival of all females marked in the year of their birth (eg. YA + I + J) was better than that of males of the

Percentage of immature and juvenile animals alive in October of the year of their birth (time T) surviving to T+1 month, T+2 months etc. (Data from October 1971, 1972, 1974. Area 'C')

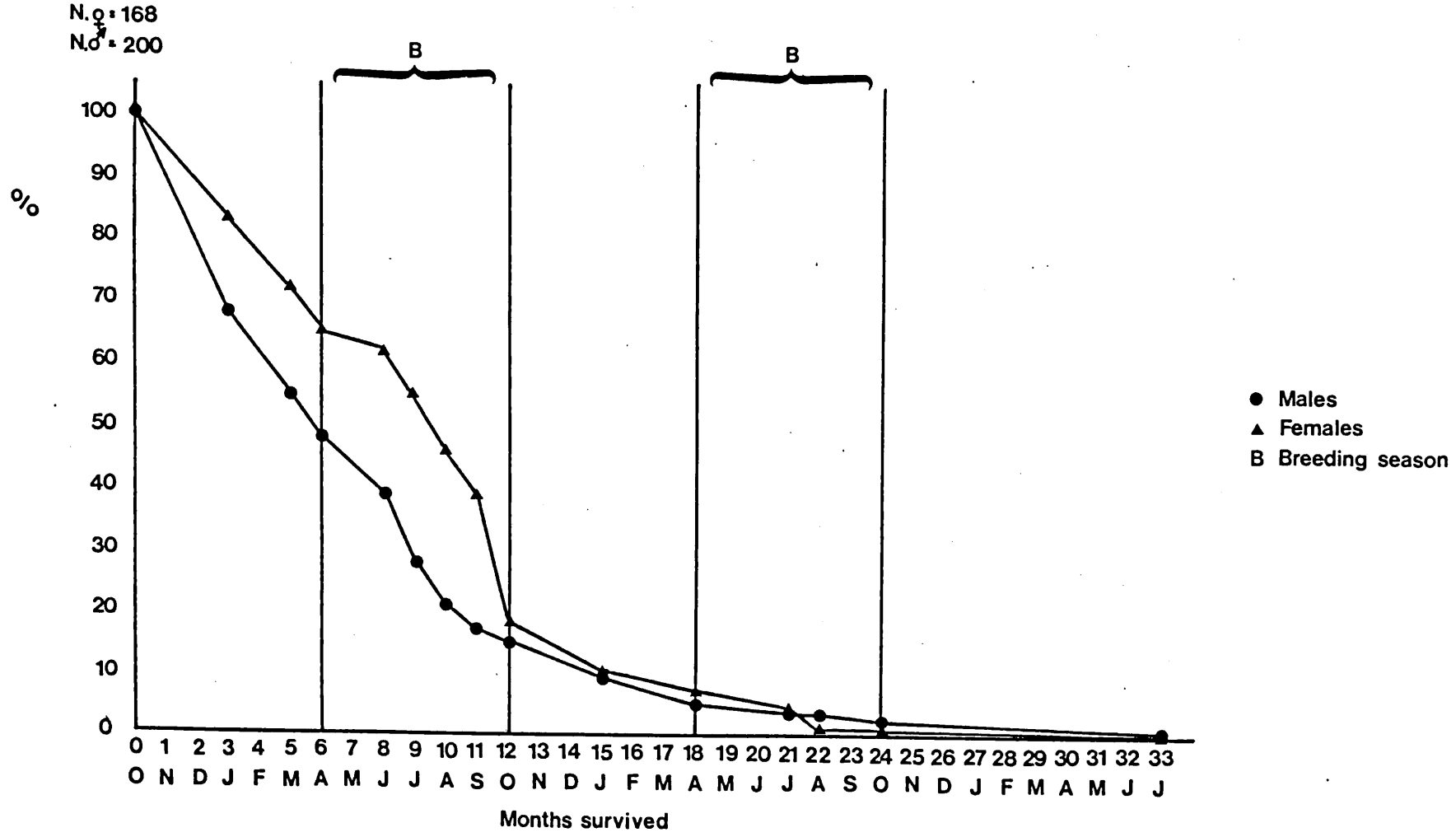


Fig 16.

Table 9.

Animals first marked in August 1976 to 1982 surviving until August of the year after that in which they were marked.

Year	Male A N	Male A S	Male A %S	Male I+J N	Male I+J S	Male I+J %S	Female A N	Female A S	Female A %S	Female YA N	Female YA S	Female YA %S	Female I+J N	Female I+J S	Female I+J %S
1976	18	2	11.1	31	9	29.0	19	2	10.5	6	1	16.7	21	9	42.9
1977	12	2	16.7	32	4	12.5	17	1	5.9	3	2	66.0	21	5	23 8
1978	14	3	21.4	19	5	26.3	15	2	13.3	6	1	16.7	9	3	33.3
1979	15	0	0.0	13	2	15.4	13	1	7.7	6	1	16.7	17	6	35.3
1980	21	3	14.3	35	6	17.1	18	4	22.2	8	0	0.0	20	13	65.0
1981	7	0	0.0	48	2	4.2	12	0	0.0	3	1	33.3	49	11	22.4
1982	7	0	0.0	31	5	16.1	3	0	0.0	6	1	16.7	22	6	27.3
ΣX	94	10	10.6	209	33	15.8	97	10	10.3	38	7	18.4	159	53	33.3

N	S	%S
197	60	30.5

N : Number marked
S : Number surviving

same age (χ^2=11.54;df=1;p<0.001).

(e) The numbers of immature males and females caught did not differ significantly.

The survival of those animals first caught in 1980, 1981 and 1982 has also been calculated (Figs 17., 18. & 19.). The overwinter survival of females first marked as immature or juvenile in August 1980 was significantly better than that of males of the same age (χ^2=4.5;df=1;p<0.05) but the survival of males and females of this age did not differ significantly during the subsequent breeding season. There was no difference in survival between males and females first marked as immature or juvenile in August 1981 except between May and August 1982 when the females survived better than the males (χ^2=7.58;df=1;p<0.01). The survival to October 1982 of females first marked as immature or juvenile in August of that year was significantly better than that of males of the same age (χ^2=3.88;df=1;p=0.005). Therefter there was no significant difference in survival betwen the two sexes in this age group. A much greater proportion of those young females marked in August 1980 survived to the following May than did those marked in August 1981 (65% and 22.4% respectively) but many more females were marked in 1981 and the same number (n=13) survived in both years.

There were no differences in survival between immature and juvenile animals first marked at the beginning of August 1981 and those first marked one month later in the same year or between immature and juvenile animals first marked in August or October 1982 (Figs 18. & 19.). It should be noted that a proportion of those animals marked in September (1981) or

Proportions of immature and juvenile animals marked in August surviving to the next breeding season (Area 'C', 1980–1983)

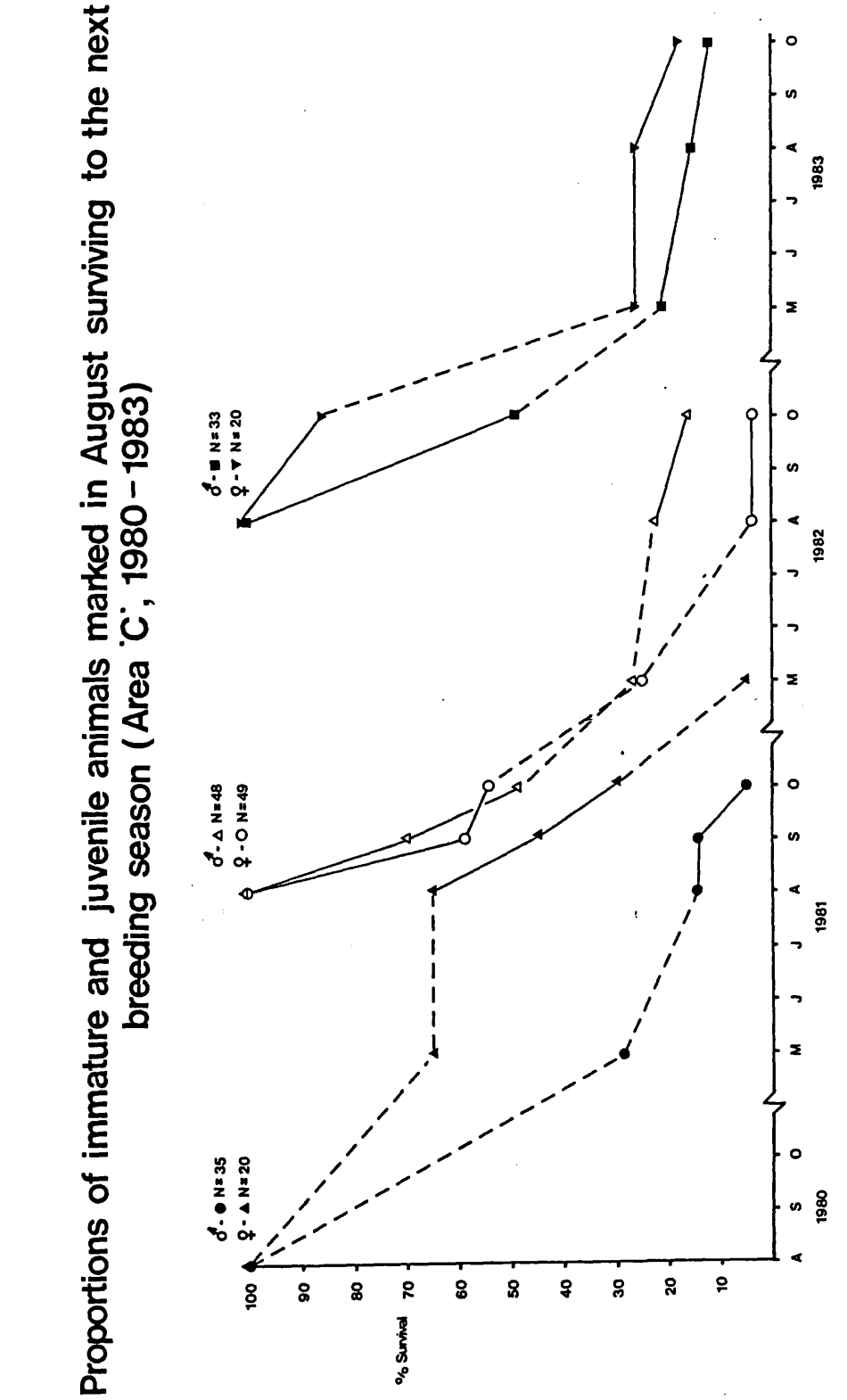
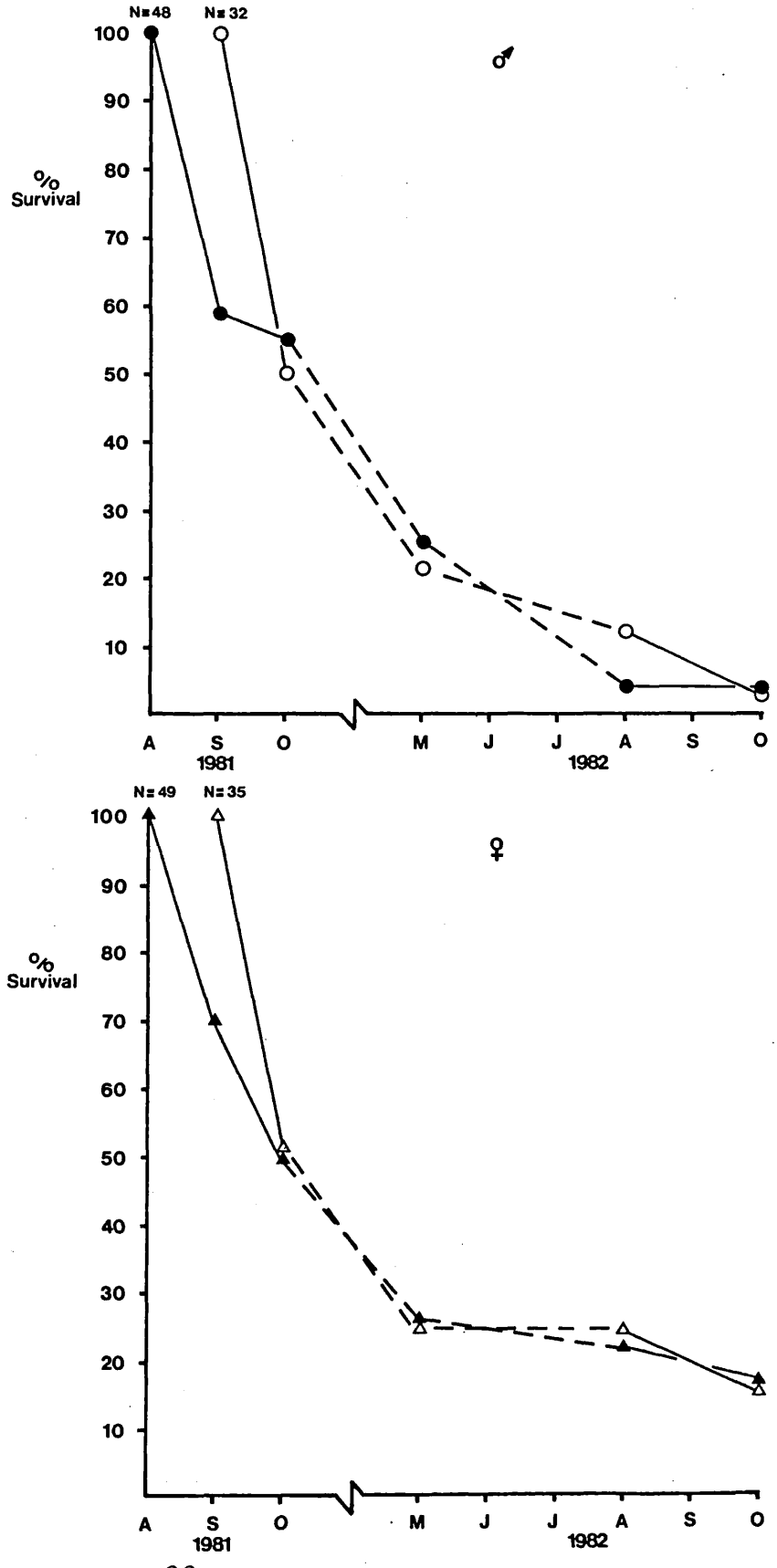
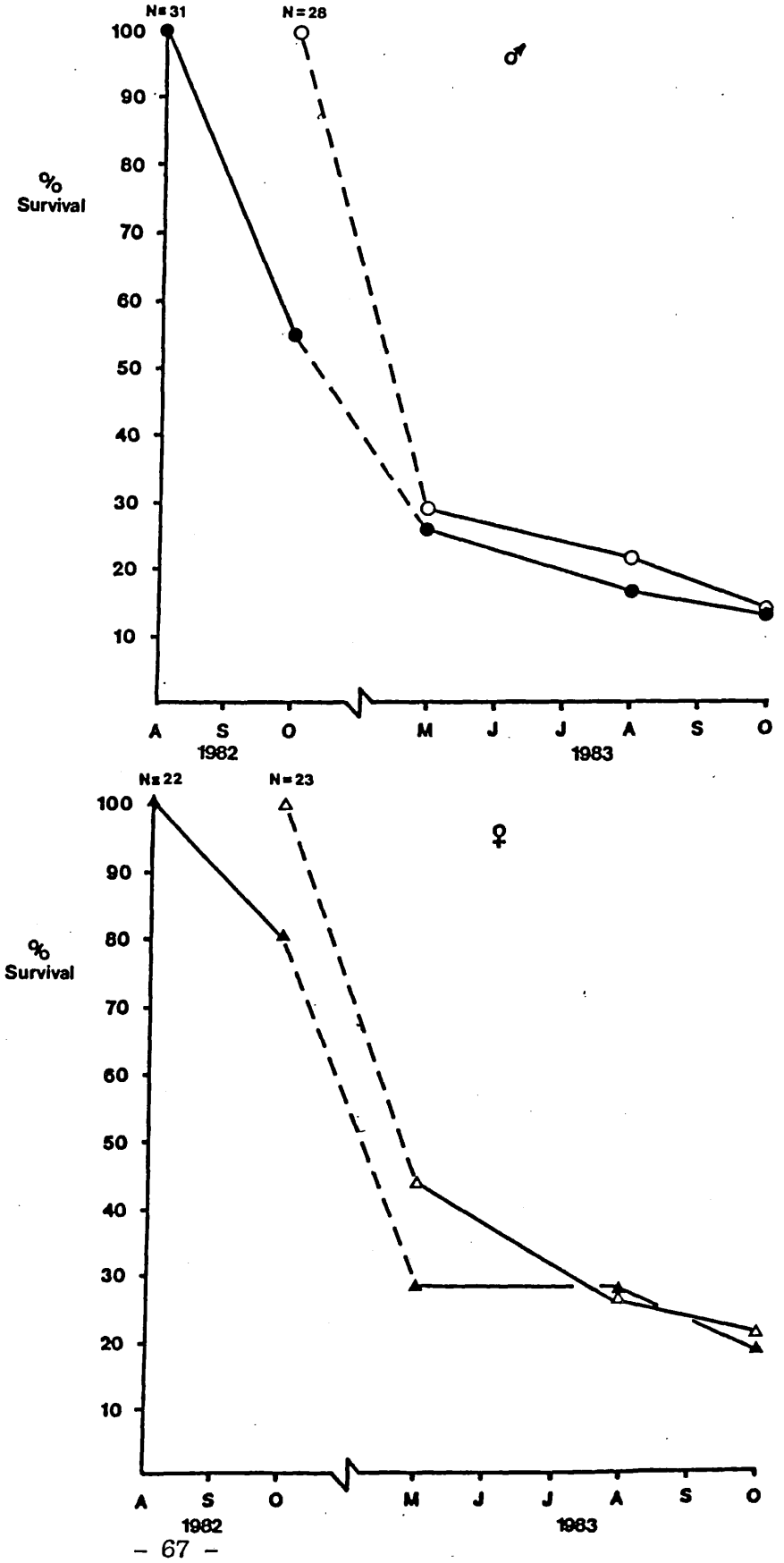


Fig 18.

Comparison of the survival of immature and juvenile males and females first marked in August and September 1981 (Area 'C')



Comparison of the survival of immature and juvenile males and females first marked in August and October 1982 (Area 'C')



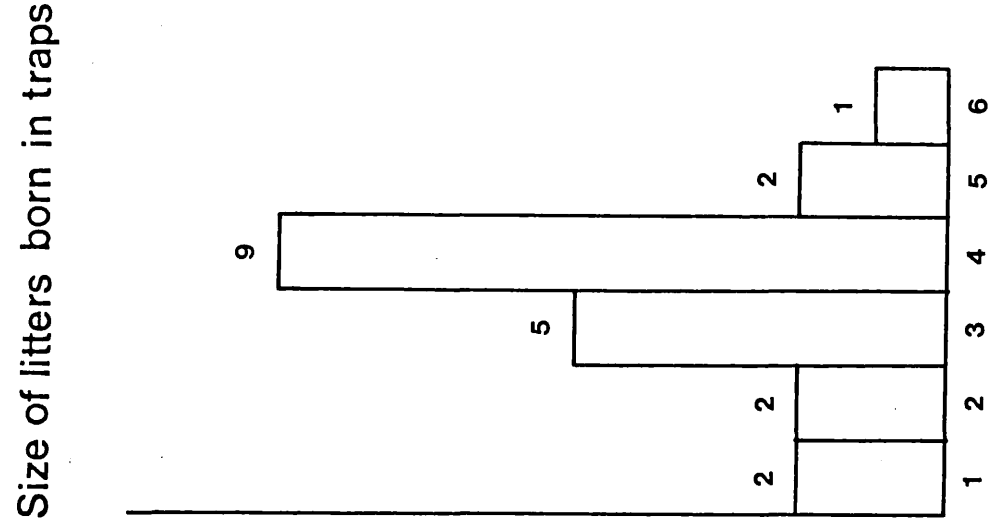
October (1982) were almost certainly present in August but were not caught at that time.

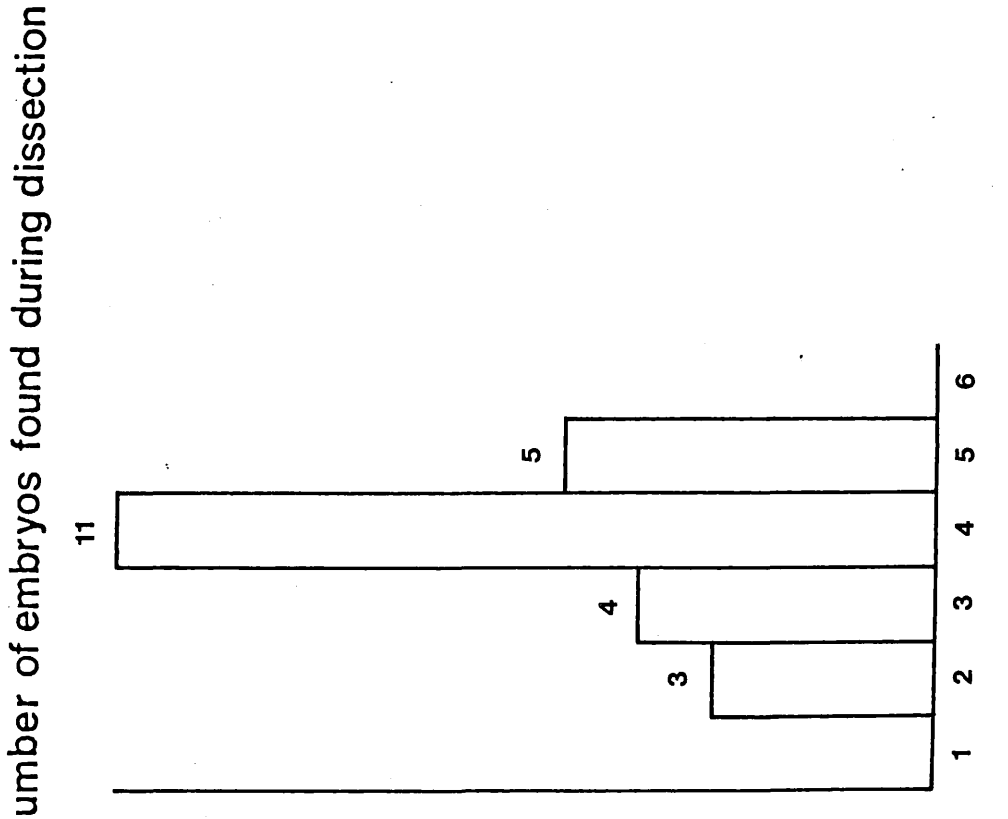
The Skomer vole is a longer lived animal than the bank vole on the mainland. At least 11% of both males and females were known to have survived for two years and six females were known to have bred three years running.

(v) Breeding.

Data on litter sizes were obtained during the dissection of the animals that were trapped for their stomach contents (Chapter 4.) and of animals which died in the traps. Twenty three of the 46 adult females that were dissected during the breeding season were obviously pregnant on gross examination (microscopical examinations were not performed). The number of embryos varied from two to five with a modal value of four (Fig 20.). The mean litter size found by dissection was 3.79 (±0.91). All the adult females that were examined during the breeding season had corpora lutea present; none was found in those examined outside the breeding season. Examination of the uteri for placental scars and comparisons of the number of corpora lutea with the number of embryos present suggested that resorption was a comparatively rare event, definite evidence being found in only two of the 46 females examined (4.3%).

Twenty-one animals had litters in the traps during the present study. The size of the litters varied from one to six with a modal value of four (Fig 20.) and a mean value of 3.48 (±1.22). Although this value is apparently smaller than that found by dissection the difference between the two values is not statistically significant (t=0.96,df=42). Considerable care was taken not to disturb these mothers more than was necessary.


(b) Size of litters born in traps
1
2
5
9
5
2
2
1 2 3 4 5 6


(a) Number of embryos found during dissection
11
5
4
3
1 2 3 4 5 6

They were not weighed or palpated under these conditions and so I could not determine whether they had completed parturition. (Only one of these mothers abandoned her litter in the trap).

Of the 87 embryos found, 48 were in the left horns of the uteri and 39 in the right (differences not statistically significant). Evidence of the transfer of an ovum from one horn of the uterus to the other was found in one animal.

Lactating individuals were first detected at the end of May and the beginning of June (1975,1981) although in other years none was detected at that time (1972,1982,1983), (Table 10.). By the end of July most of the adult females caught were parous. During the first ten days of August the percentage of adult females lactating varied from 41.7% (1979) to 74.5% (1981) and it remained at about 50% well into September. By the beginning of October less than 10% of the adult females were still lactating and these were at the end of lactation. By the third week in October no lactating females were caught (1974, 1981).

Only in 1972 was trapping carried out at the end of June and the beginning of July (Fig 21.). No lactating animals were caught at the beginning of June (up to the 13th; Table 10.). Between 29th June and 5th July about 10% of the adult females were lactating but between 5th and 12th this figure rose to over 90% (Fig 21.).

Four hundred and twenty-one adult females were caught in late July and early August during this study (Fig 22.). Of these, 98 (23.3%) weighed less than 30.0g (the lower quartile point - the modal weight of all the adults was 33.0g). Of the 98, thirty-eight were identified in the field as adult and 60

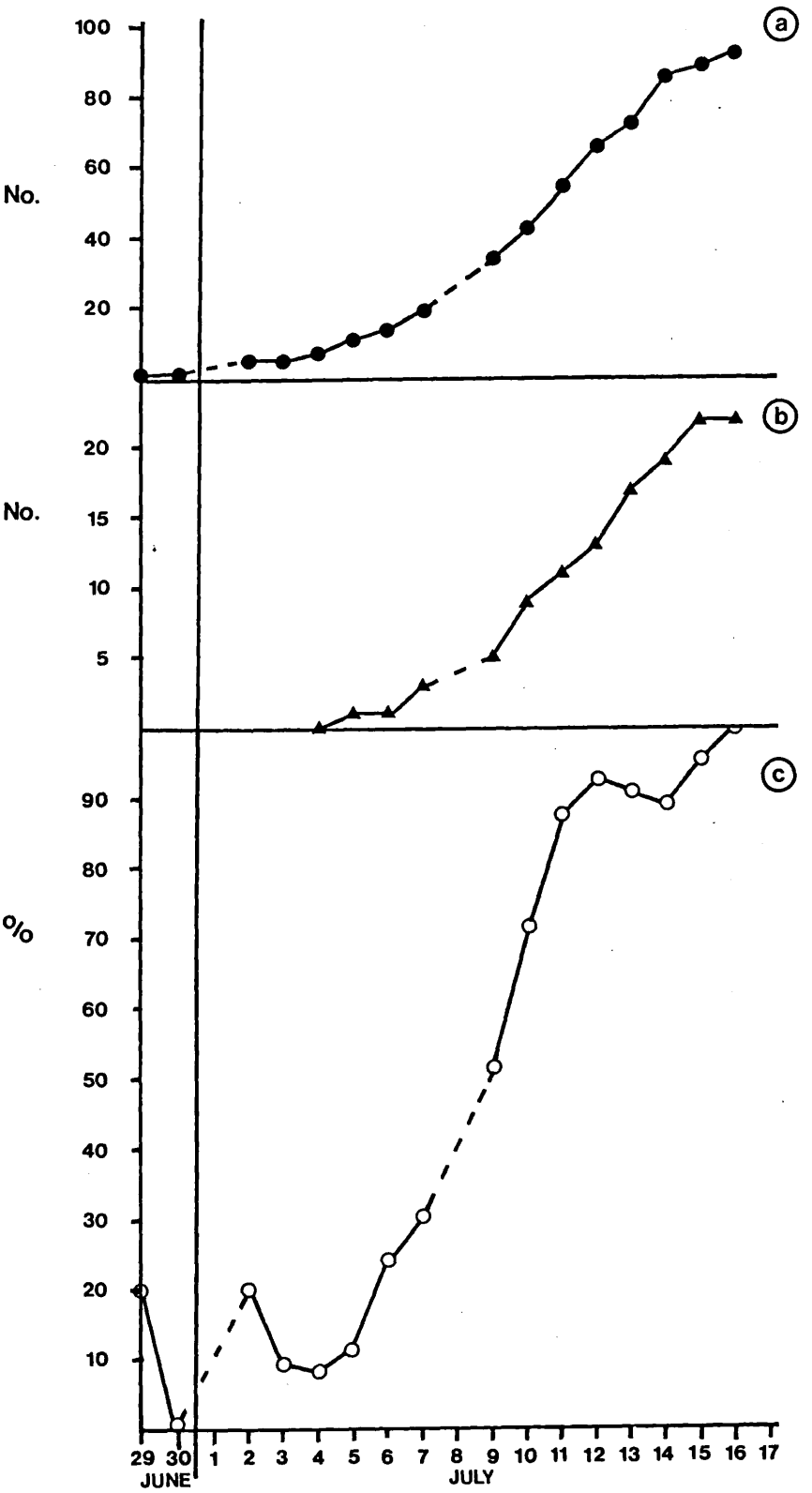
Table 10.

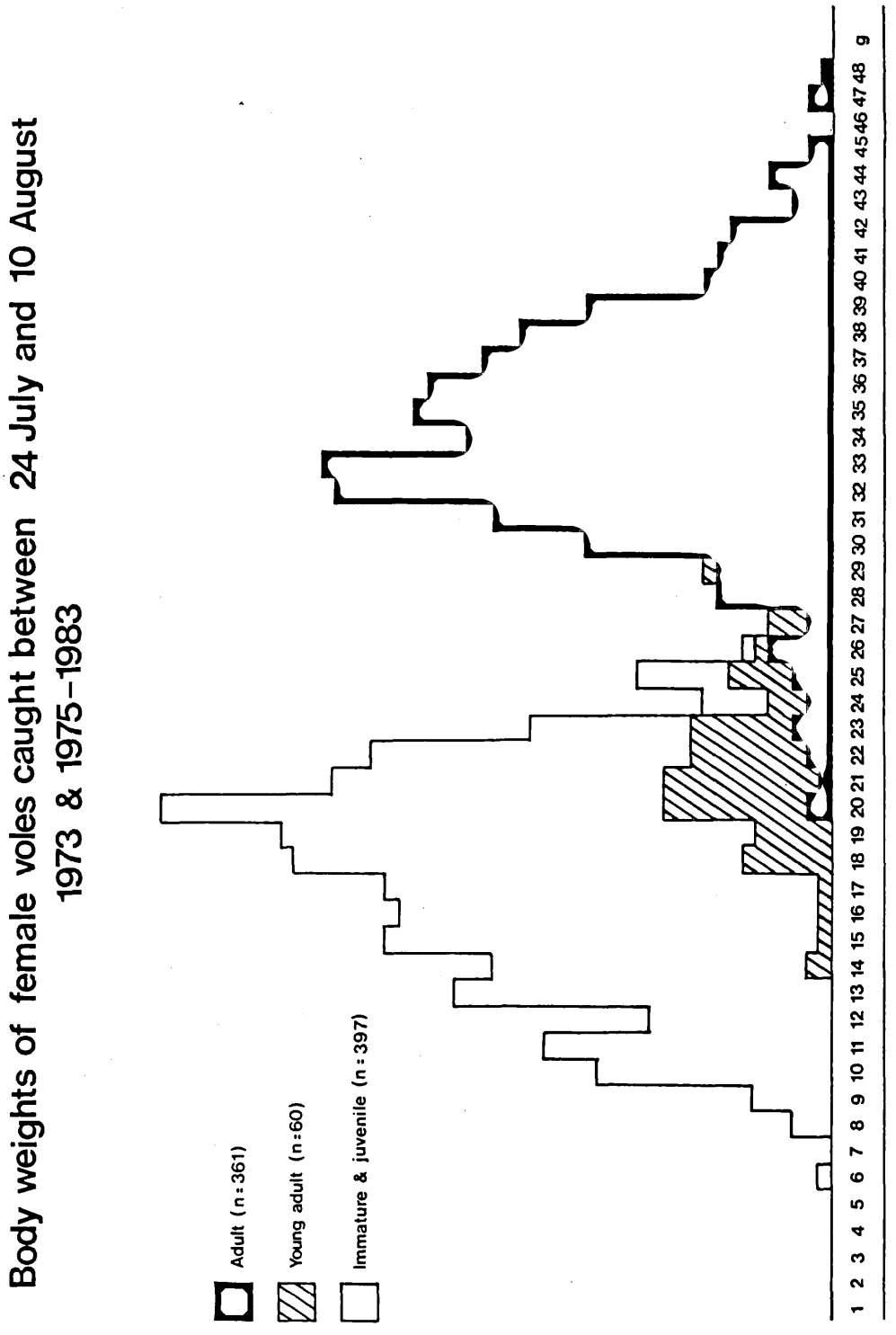
Proportions of adult female Skomer voles parous and lactating; April to October.

Month	Year	Dates	% Lactating	% Parous
April	1972	16-22	0	0
	1973	5-9	0	0
May	1981	26-30	2.7	2.7
	1982	24-28	0	0
	1983	24-28	0	0
June	1972	3-13	0	0
	1975	7-13	25.8	25.8
July	1973	24-31	72.1	85.2
	1974	14-19	64.3	64.3
	1975	19-31	50.0	73.6
August	1972	23-30	71.3	95.4
	1973	2-15	75.9	85.5
	1973	19-24	70.5	90.2
	1975	2-6	24.2	75.8
	1976	4-9	57.9	94.7
	1977	3-8	50.0	91.2
	1978	2-7	53.8	73.0
	1979	3-8	41.7	70.8
	1980	4-9	42.9	65.7
	1981	3-9	74.5	93.6
	1982	5-10	46.9	75.0
	1983	1-5	43.5	57.1
Sept	1973	17-23	35.5	96.7
	1975	9-13	55.9	85.3
	1981	1-3	34.1	87.8
Oct	1971	9-20	3.4*	96.5
	1972	3-7	13.5	100.0
	1974	18-28	0	94.2
	1981	16-20	0	100
	1982	5-11	9.7	93.5
	1983	10-15	5.0	100

* No lactating individuals were detected after 12th October

July 1972 ; (a) cumulative total of lactating females caught
(b) cumulative total of juveniles caught
(c) proportion of adult females caught each day which were lactating




Body weights of female voles caught between 24 July and 10 August
1973 & 1975–1983
Adult (n:361)
Young adult (n:60)
Immature & juvenile (n:397)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 g

as young adult.The young adults ranged in weight from 14.0g to 29.0g (modal weight 21.0g) and the adults from 20.0g to 29.0g (modal weight 28.5g). Twenty of the adults were parous at the time of sampling. Those animals identified as young adult had a different appearance to the adults. Their coats were paler and sleeker. In several instances they still had grey juvenile coats.

Of thirty seven young adult females first seen late in July or early in August in 1972, 1973, 1981, 1982 and 1983, twenty five were still alive in mid-September (1973) or early October (1972, 1981, 1982 and 1983) and of these, twelve (48%), were identified as immature at that time. Three young adult females were caught early in August of 1981. Two were recaptured during the island-wide survey in late August and early September 1981 when both were identified as immature; they were also recaptured in October and again identified as immature. Of the six young adults first seen in August 1982, four were recaptured in October 1982 when all were identified as adults. Eight young adult females were caught in August 1983. Seven were recaptured in October and of those three were identified as immature and the rest as adult at that time. The adults displayed clear evidence of recent lactation.

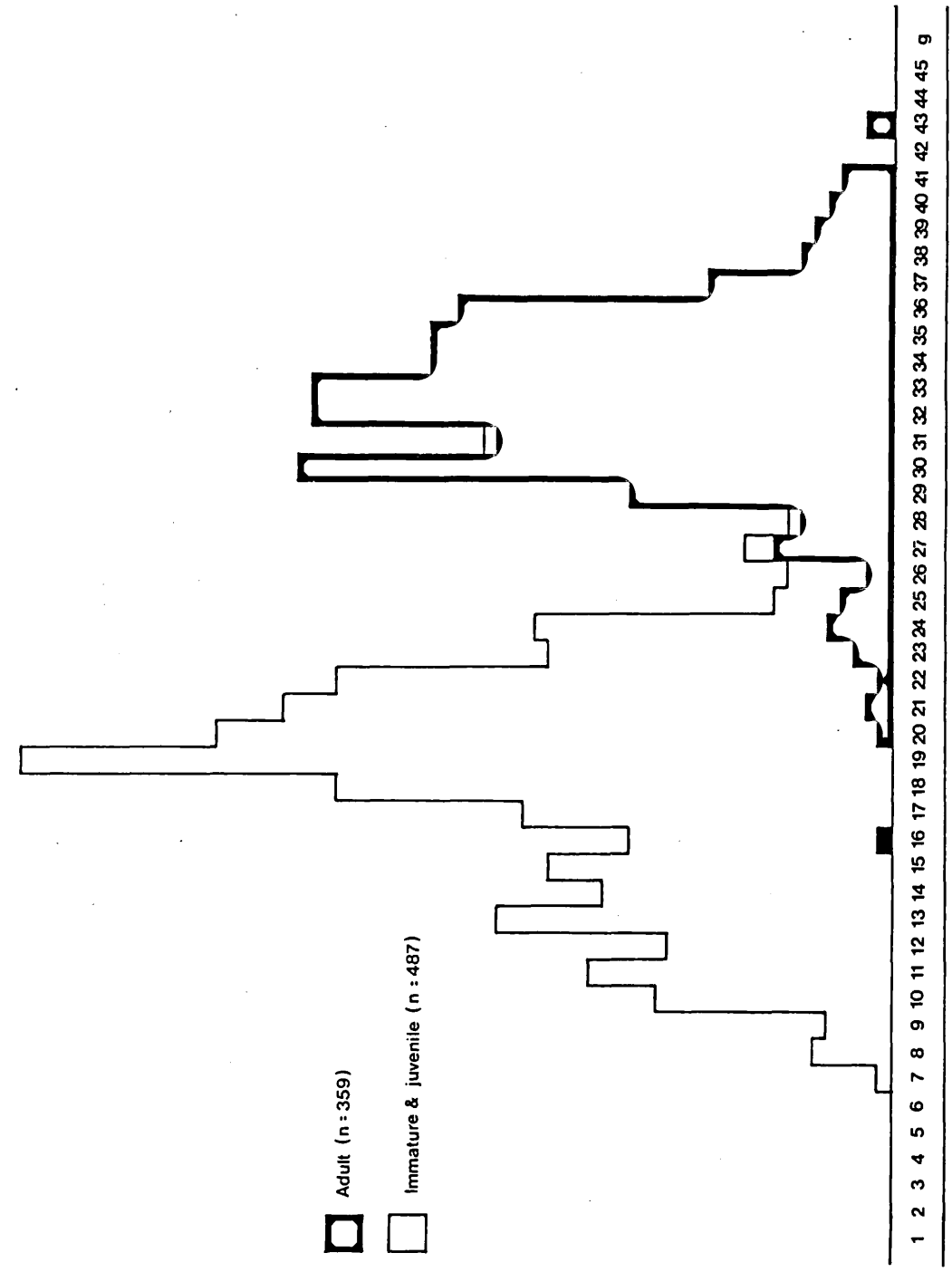
A single female Skomer vole tentatively identified in the field as a young adult (weight:25.0g) was found dead in a trap on area 'C' on 9/8/1982. Dissection revealed that the animal was pregnant, four embryos (seven to ten days post implantation) being found. The skull of this animal was kept and the molar teeth extracted and prepared for examination following the method proposed by Al-Jumailly (1976) (see

Methods). This confirmed that, on the basis of the criteria established by Al-Jumailly (1976) the animal was less than three months old.

Fewer data were available concerning the maturation of male Skomer voles in the year of their birth. A plot of the weights of those adult males first caught in July and August 1973 & 1975 - 1983 (Fig 23.) showed that 28 adult animals (8.5%) had weights less than the lower quartile point (28.0g). These animals had testes which, when palpated, would move into the scrotum but which were small (<1cm long) by comparison with those of the bulk of the adult male population. Few of them had any scars or fresh wounds and those which did rarely had more than one or two. The weights of the immature and juvenile animals are given for comparison.

Comparisons of the numbers of adult females and of the numbers of overwintered adult females present in August 1976 - 1983 with the number of young animals known to be alive at that time showed strong positive correlations (Fig 24. (a) and (b)). suggesting that the production of young per adult up to the middle of the breeding season varied little from year to year. The number of young adults present at that time showed no correlation with the number of young (Fig 24.(c)). Comparisons were made between the numbers of adult females present in May 1981 - 1983 and the number of young animals known to be alive in August or in October of those years and betwen the number of adult females known to be alive in August 1981 - 1983 with the number of young known to be alive in October of those years but the samples were very small (n=3) and the results were not satistically significant. It is also worth noting that the

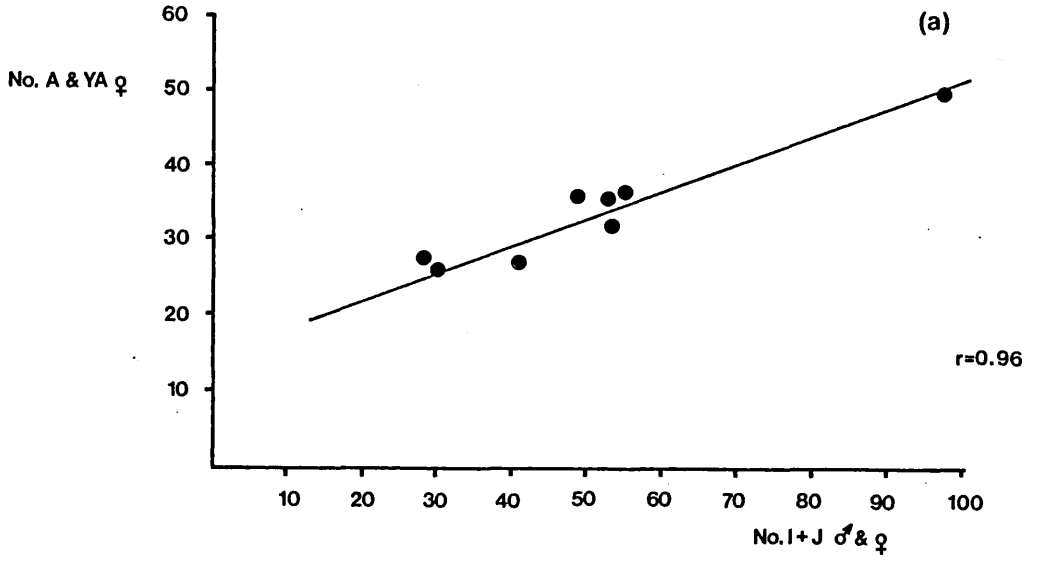
Body weights of male voles caught between 24 July and 10 August 1973 & 1975-1983

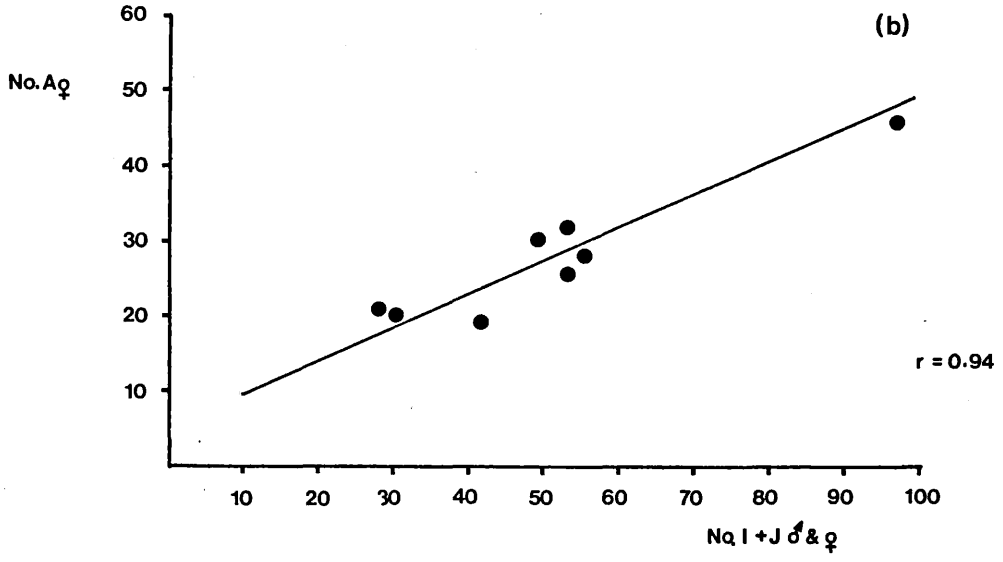


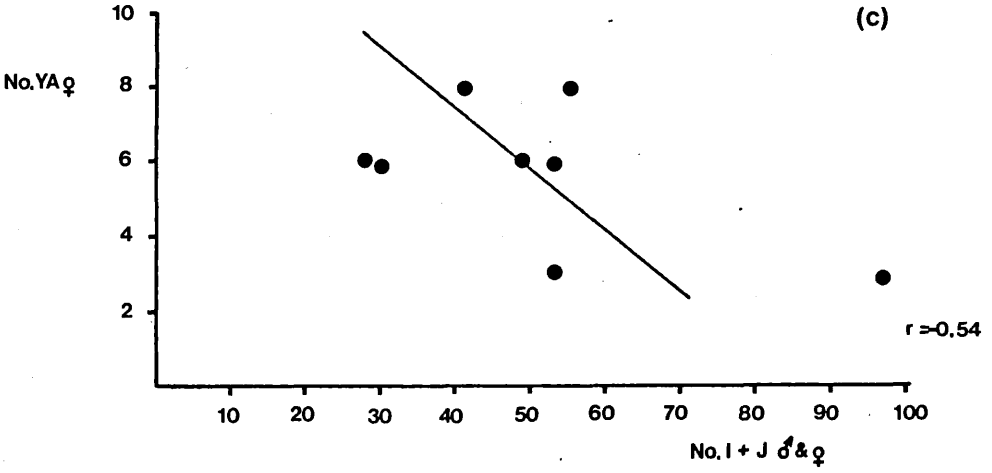
Number of adult females vs number of young; August 1976-1983

Fig 24.

(a) All A♀ vs I & J ♂ & ♀
(b) A♀ (less YA) vs I & J ♂ & ♀
(c) YA♀ vs I & J ♂ & ♀







October samples were taken at a time of year at which breeding had ceased. Data from 1972 and 1981 (Fig 9.) showed that there could be a decline in numbers between September and October and so the results of the comparisons with the October data could have been confused by mortality factors.

(vi) Range lengths.

(a) Lifetime ranges 1971 - 1973.

Males: 30.11m ± 25.4 (n = 405)

Females: 25.25m ± 25.1 (n = 416)

These values are significantly different ($p<0.001$).

(b) Lifetime ranges 1976 - 1983.

Males: 25.64m ± 15.1 (n = 138)

Females: 17.80m ± 12.2 (n = 142)

These values are significantly different ($p<0.001$).

(c) Within trapping-period ranges 1976 - 1983

Males: 14.07m ± 10.5 (n = 196)

Females: 8.98m ± 7.0 (n = 260)

These values are significantly different ($p<0.001$).

(d) "Long-movements" ranges 1982 & 1983

Males: 43.50m ± 31.9 (n = 36)

Females: 19.80m ± 20.3 (n = 32)

These values are significantly different ($p<0.001$).

The ranges of males were therefore always significantly larger than those of the females. The range sizes revealed by the different methods differed quite markedly. Comparison of the results obtained between 1971 and 1973 with the lifetime ranges obtained between 1976 and 1981 showed that those of both males and females were significantly different (Males: $t=3.12$; $df=442.8$; $p<0.005$. Females: $t=4.81$; $df=534.3$; $p<0.001$).

The within trapping-period ranges found between 1976 and 1981 were significantly smaller than the lifetime ranges obtained between 1971 and 1973 (Males: t=10.73; df=519.1 p<0.001. Females: t=10.9; df=442.4; p<0.001), than the lifetime ranges obtained between 1976 and 1981 (Males: t=7.32; df=191.4; p<0.001. Females: t=6.91; df=161.1; p<0.001) and than the "long movements" ranges (Males: t=5.87; df=36.4; p,0.001. Females: t=3.21; df=31.5;p<0.005).

Comparisons of the lifetime ranges (1971 - 1973) with the "long movements" ranges (1982 & 1983) showed no significant differences either for males (t=-1.78; df=44.0) or for females (t=1.7; df=45.3) and comparison of the lifetime ranges (1976 - 1981) with the "long movements" ranges showed a significant difference between those of males (t=3.2; df=42.4; p<0.005) but not between those of the females (t=0.81; df=38.1).

The greatest recorded movement by a male was 193m and by a female was 175m (1971 - 1973 sampling period).

None of the animals marked on Line I during the island wide survey of 1981 (Fig 7.) was subsequently caught on the grid.

(vii) Dispersion.

No consistent pattern of dispersion of adults or immatures and juveniles of either sex was found for any particular time of year. The distribution of adult males was never significantly uniform and that of adult females was only significantly uniform in July and September 1975 and in October 1972. The distribution of adult males and females was significantly clumped in May and June in most but not all years when measurements were taken at that time. Immature and

Table 11.

Dispersion: values of the variance to mean ratio for the numbers of captures of the various age groups per trapping point.

Date		A ♂♂	A ♀♀	I+J ♂♂	I+J ♀♀
Jan	1973	0.950	1.047	1.136	1.308"
Mar	1972	1.106	1.413*	1.699"	1.114
	1975	0.941	0.958	0.950	0.986
Apr	1972	2.100"	0.861	-	-
	1973	0.934	1.157	-	-
May	1981	1.264	1.453*	-	-
	1982	1.549**	0.939	-	-
	1983	1.425*	1.378*	-	-
June	1972	1.806"	1.479*	-	-
	1975	1.949""	1.000	-	-
July	1972	1.041	0.948	-	-
	1973	0.886	1.025	1.169	1.167
	1974	1.064	1.050	-	-
	1975	0.875	0.595*	0.659	1.245
Aug	1972	0.886	1.081	1.312"	1.159
	1976	1.265	0.740	1.050	1.398*
	1977	1.403*	0.788	1.171	0.705
	1978	1.400*	1.308	1.264	1.281
	1979	1.023	1.039	1.064	1.167
	1980	0.847	0.955	1.083	1.212
	1981	0.800	0.890	0.934	0.803
	1982	0.994	0.693	1.196	1.094
	1983	1.208	0.838	0.948	1.264
Sept	1973	0.963	0.908	0.991	0.974
	1975	0.917	0.543*	1.261	0.795
	1981	1.039	0.834	1.203	0.773
Oct	1971	0.970	0.665	1.651	1.143
	1972	0.979	0.810*	1.037	0.691
	1974	1.112	0.921	1.166	1.333"
	1981	0.972	0.913	0.692	0.974
	1982	1.021	0.693	0.932	1.181
	1983	1.264	0.912	0.635"	0.836

* p<0.05 ** p<0.01 " p<0.005 "" p<0.001

juvenile males were significantly clumped in March and August 1972; in October 1983 they were uniformly distributed. Immature and juvenile females were significantly clumped in January 1973, October 1974 and August 1976. (Table 11).

(viii). Habitat changes and their effect on the size of the population of the voles.

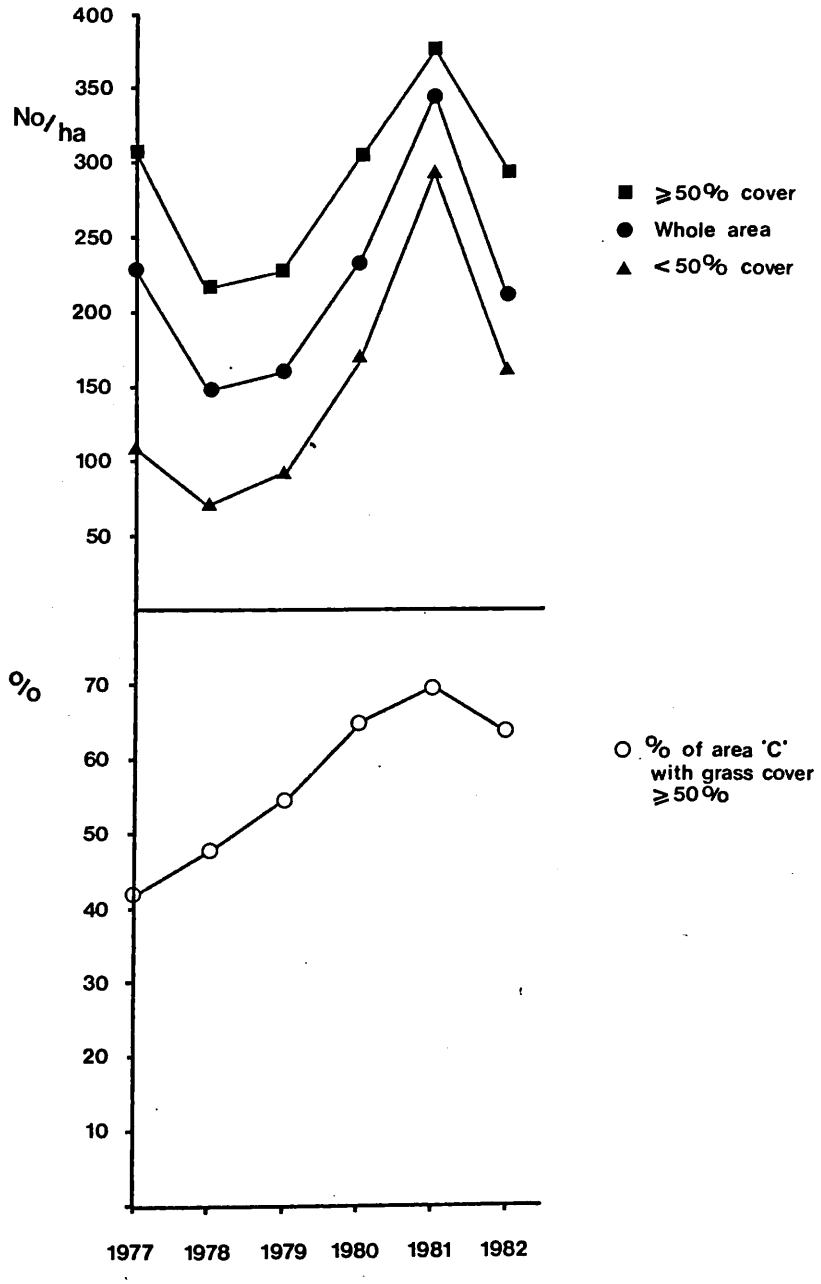
In 1975 no quadrat placed on sub-area 'A' revealed a grass cover greater than 30%. In 1976 only 12 quadrats were measured, these being placed at grid points selected at random and again none revealed a grass cover greater than 30%. Measurements made from 1977 onwards showed that an increasing proportion of the grid was being covered by an increasingly dense cover of grasses, the predominant species being Holcus lanatus. This proportion declined slightly in 1982 (Fig 25.). Data obtained in August 1983 have not been included. In this month very little grass was found on the study area due to the very dry conditions which affected the island in July and August. Only 53% of the grid had any detectable grass cover. Less than 12% of the grid had a grass cover exceeding 50%, the grass was very short, and no animal was caught in that area.

In the other years the numbers of voles caught per point and the minimum numbers known to be alive per hectare were consistently greater in the area where the cover of grass did not exceed 50% but the numbers fluctuated in a similar way in both areas (Fig 25.).

(ix) Island-wide survey 1981: body weights in different habitat types

The body weights of adult males and females were found to be significantly lower both on those parts of the lines which

MNA/ha on parts of area 'C' with a grass cover <50% or ≥ 50% & over the whole area. Proportion of the area with a grass cover ≥ 50%.



ran through habitats less favourable to the voles and on grid 'A' which also lay in an area of less suitable habitat as compared to those parts of the lines in favourable habitats and grid 'C' (Tables 12.& 13.).

Table 12.

Body weights of adult male and female voles caught in favourable and unfavourable habitats on the trapping lines during the island-wide survey, 1981.

Adult males	Good habitat	30.3 ± 3.7	n = 18
	Poor habitat	26.3 ± 1.9	n = 6
	(t = 2.52; df = 22; p<0.02)		
Adult females	Good habitat	33.8 ± 4.1	n = 32
	Poor habitat	30.5 ± 5.1	n = 15
	(t = 2.38; df = 45; p<0.05)		

Table 13.

Body weights of adult male and female voles caught on grids 'A' & 'C' during the island wide survey, 1981

Adult males	Grid 'C'	34.2 ± 3.36	n = 27
	Grid 'A'	30.0 ± 3.32	n = 8
	(t = 3.10; df = 33; p<0.005)		
Adult females	Grid 'C'	34.8 ± 3.48	n = 45
	Grid 'A'	37.0	n = 1

Six young adult females and five males which were possibly young adults were caught in the "good" habitat types and one male and five females of that age in the "poor" habitat types. Inclusion of these animals in the results given in Table 12. removed the statistical significance.

The male:female ratios of the adult animals on grids 'C' and 'A' were 0.6 : 1 and 8.0 : 1 respectively (or 2.0 : 1 on the latter if young adults are included).

The adult males found on grid 'C' were not only heavier, but they all had large scrotal testes. The testes of the adult males on grid 'A' were nearly all noticeably smaller and were wholly or partially retracted into the body. Too few adult females were caught on grid 'A' for comparisons to be made between the two grids. The males and females caught on the lines did not, for the most part, show such obvious differences in sexual condition.

The results given in this chapter will be discussed in the main discussion (Chapter 7.).

Chapter 2.

REMOVAL EXPERIMENT

INTRODUCTION

Females of several species in the genus Clethrionomys appear to establish discrete ranges (eg. C.rufocanus (Kalela,1957; Viitala, 1977), C. rutilus (Koshkina et al. 1972; Koshkina & Korotkov, 1975; cited by Wiger, 1982) C.gapperi (Perrin, 1979b) and C.glareolus (Bujalska, 1970, 1973).

A population of C.glareolus on an island of about 4ha in the Mazurian lakes region of Poland was the subject of intensive study for a number of years (Bujalska & Ryskowski, 1966; Gliwicz, Andrzejewski, Bujalska & Petrusewicz, 1968; Bujalska, Andrzejewski & Petrusewicz, 1968; Bujalska & Gliwicz, 1968; Petrusewicz, Andrzejewski, Bujalska & Gliwicz, 1968; Bujalska, 1970; Gliwicz, 1970; Petrusewicz, Bujalska, Andrzejewski & Gliwicz, 1971; Bujalska & Gliwicz, 1972; Bock, 1972; Bujalska, 1973; Bujalska, 1975; Andrzejewski, 1975). The distribution of adult (breeding) females was found to be uniform over the island (Bujalska, 1970, 1973) and the number of breeding females remained almost constant throughout the breeding season (Bujalska, 1973, 1975). The theory that the females were territorial was advanced and, in an experiment devised to test this hypothesis, 27.6% of the breeding females were removed from the island. It was found that not only were they replaced by a similar number of females from the (much larger) pool of potential breeders, but also that estimates of the production of young suggested that there was no difference from previous years (Bujalska, 1973, 1975).

It was known that Skomer voles rarely breed in the year of

their birth (Coutts & Rowlands, 1969; Jewell, 1966a). Although preliminary studies in 1972 showed that the number of breeding females declined steadily throughout the breeding season, the possibility remained that territorial behaviour by the breeding females might be preventing the maturation of young animals. To test this hypothesis a removal experiment was undertaken.

METHODS

The removal of animals from the whole island (as had been done by Bujalska (1970,1973)) was clearly impractical and so an attempt was made to create an isolated area (in effect an island) on the study area. One half of the study area was separated from the other by means of a barrier. This was made from corrugated iron sheets which were nailed to wooden fence posts with 3" roofing nails and buried to a depth of about 1/2m in the soil (Fig 26.). Care was taken to ensure that the joins between the iron sheets had no gaps in them. The barrier was 90m long and overlapped the study area by 10m at each end (Fig 4.). The experimental area was further isolated by cutting the vegetation on the remaining sides to ground level in a strip 3m wide (Plates 4. & 5.) except in the area of Molinia in the North stream valley (Fig 4.) which was not touched so as to avoid long term damage to this rather sensitive part of the island's flora.

Trapping was performed on both sides of the barrier until no new adult females were detected and the majority of the immature and juvenile females had apparently been marked (July 24th - August 14th). The removal was carried out between August 19th and 24th. Fifty-two adult females had been caught on the experimental area in July/August. Forty-eight were recaptured

Barrier

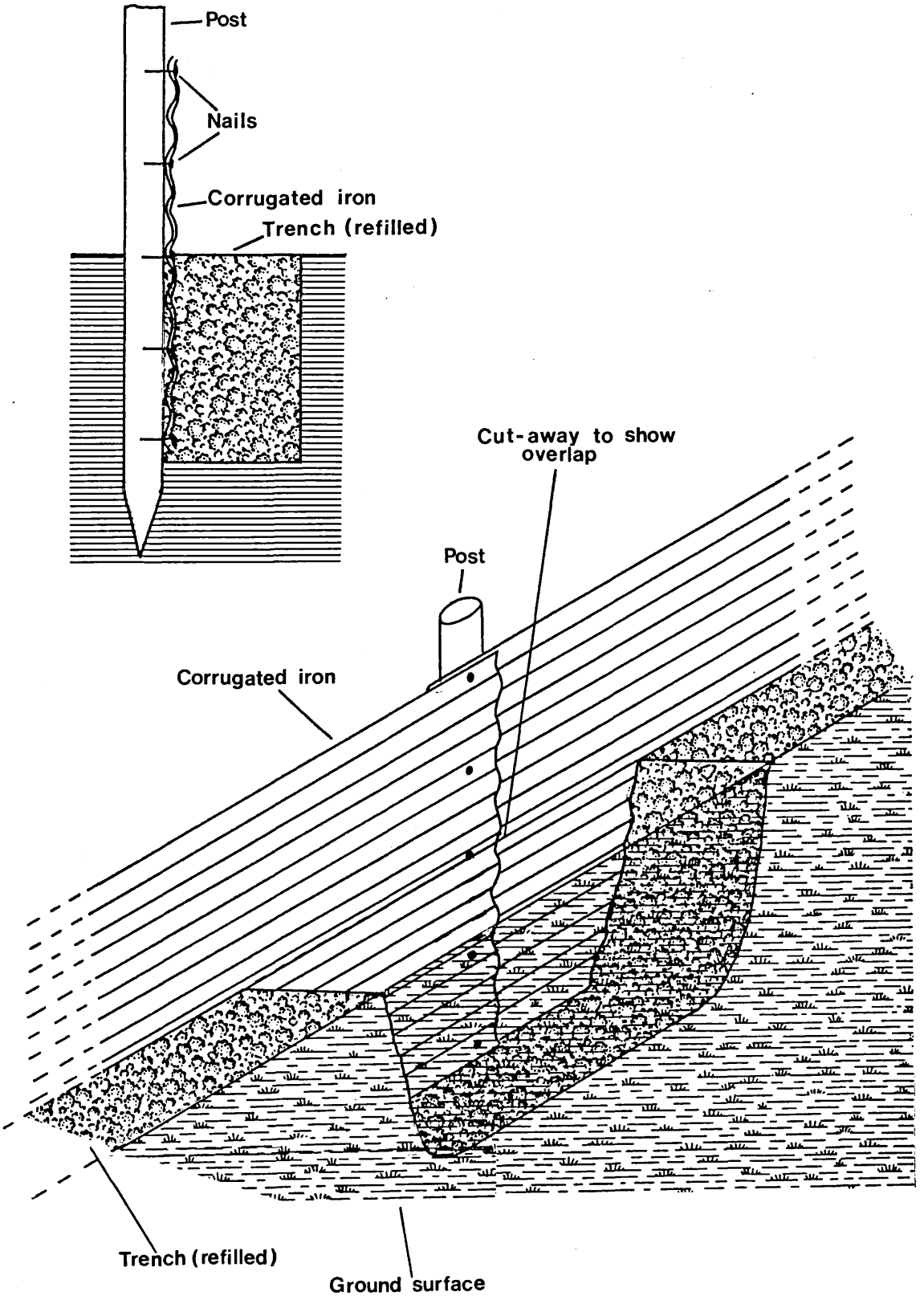

Post
Nails
Corrugated iron
Trench (refilled)
Cut-away to show overlap
Post
Corrugated iron
Trench (refilled)
Ground surface

Plate 4.

Removal experiment. The study area seen from the north.

(a) = Cleared strip; (b) = Experimental area; (c) = Barrier;
(d) = Control area; (e) = Farm.

(Photograph: T.D.Healing)

Plate 5.

Removal experiment. The barrier seen from the south.

(a) = Control area; (b) = Cleared strip (3m wide);
(c) = Experimental area.

(Photograph: T.D.Healing)

at the time of the removal and 46 were removed to the Neck (Fig 2.) where they were released (the other two escaped during handling and were not recaptured).

Trapping was carried out around the outer edge of the experimental area early in September (3rd - 6th) to increase the isolation of the area. The control and experimental areas were trapped from September 17th - 22nd to detect the results of the experiment.

RESULTS

Of the 56 adult females on the control grid 27 were caught again in September (48.2% of the July/August total). Only three adult females were caught on the experimental grid in September and two of these were animals which had escaped during the removal. The third was new and had the appearance (and body weight) of an older animal and may have been an immigrant. None of the 65 immature and juvenile females that was present on the experimental area at the time of the removal had matured to replace the adults.

The survival of the adult males was apparently slightly worse on the control than on the experimental grid (44% Control: 54.3% Experimental). That of immature and juvenile males first caught in July/August was better on the experimental side than on the control (61.9% Experimental : 53.9% Control) and that of immature and juvenile females first caught in July/August was similar on both sides of the barrier (56.9% Experimental : 53.6% Control). None of these differences was statistically significant.

Approximately equal numbers of adult males either gained or lost weight between July/August and mid-September on the

control area but on the experimental grid one animal gained weight and 16 lost weight. The modal value for this weight loss was only one gram and such changes in weight were often detected from day to day but the difference between the two areas was marked and was statistically significant (χ^2=6.39; df=1; p<Ø.Ø5) (Table 14.). No such comparison was possible for the adult females and no significant differences in changes of weight by immature and juvenile males or females were detected on either area.

Table 14.

Gains and losses of weight by adult male Skomer voles between July/August and mid-September 1973

	Number of animals	Number gaining weight	Number loosing weight	Number not changing weight
Control	15	7	6	2
Experimental	19	1	16	2

DISCUSSION

The experimental area was effectively isolated by the barrier and by clearing the vegetation and trapping around the area. A few animals were caught on both sides of the barrier during the trapping in July/August 1973, indicating that it was not a complete bar to the movement of the voles but since it only went 1/2m into the soil and some of the rabbit burrows went down 1m or more this was not surprising.

No animals were detected as having crossed the barrier during the removal experiment. Only one new adult female vole

was found on the experimental area in September, no new adult males, and only two new immature females and nine new immature males (as compared to one new adult female, two new adult males, 36 new immature females and 36 new immature males on the control area). The attempts made to isolate the experimental area were therefore effective.

The date of the removal experiment was chosen so as to ensure that there would be an adequate number of females as potential replacements for the removed adults. The rather short breeding season of the Skomer vole dictated the time at which the experiment could be performed but also meant that it was performed rather near the end of the breeding season.

Chapter 3.

VEGETATION

INTRODUCTION

The first detailed survey of the flora of Skomer was undertaken shortly after the second world war (Buxton & Lockley, 1950). Those authors pointed out that the island exhibited a considerable diversity of plant habitats and that it was difficult to describe discrete ecological communities due to the lack of a dominant plant species over considerable areas. As a guide they divided the vegetation into eleven major categories (Table 15.).

Table 15.

The vegetation categories proposed by Buxton & Lockley (1950).

(A) Inland.	(i)	Bracken areas
	(ii)	Inland pasture
	(iii)	Dry turf
	(iv)	Heath
	(v)	Rock outcrops
	(vi)	Ponds and streams
	(vii)	Bogs
	(viii)	Human habitation
(B) Maritime.	(ix)	Exposed cliffs (S.& W. facing)
	(x)	Less exposed cliffs (N.& E. facing)
	(xi)	Steep sea cliffs

Fullagar et al.(1963) showed that the Skomer vole was confined largely to areas with bracken cover. They performed a brief survey of the vegetation by eye and divided the island's habitats into three categories (High, Medium and Low density) on the basis of the density of the populations of voles found in them (Table 16.).

Table 16.

Vegetation categories of Fullagar et al.(1963).

Category	Description
High Density	Tall bracken with little understory except sorrel and dead bluebell leaves and stems.
Medium density	Shorter bracken, ragwort, woodsage, dense grass cover (especially Yorkshire fog)
Low density	The remaining habitat types.

During the survey of 1981 (Healing et al.1983. Appendix 4.) a vegetation survey similar to that of Fullagar et al.(1963) was undertaken and a map of the vegetation was compiled by eye from a ground survey of the island. The vegetation was divided into nine categories which are defined in Table 17. (after Healing et al.1983) which also shows the correspondence between the categories used in the survey of 1981 and the habitat types of Fullagar et al.(1963). Several transects were walked, the limits of each category determined roughly by reference to the topographical features, and the area of each determined as a proportion of the total (292 ha).

The study area used for the present project was in an area described by Fullagar et al.(1963) as being covered by "High density" habitat, that is to say by a dense growth of bracken with little undercover except sorrel. Part of the grid used during the early years of the study extended into marshy areas containing plant species not met with on the rest of the area (Fig 4.).

An extensive survey of the vegetation on the the study

area was undertaken in 1973. In subsequent years only the vegetation on area 'C' was sampled.

Table 17.

Vegetation types used in the 1981 Skomer survey with the dominant plant species in each. (After Healing et al. 1983).

Vegetation categories (1981)	Habitat types (1960)	Flora
Bracken/ sorrel	High density	Tall bracken (Pteridium aquilinum) dense bluebell (Endymion non-scriptus, sorrel (Rumex spp.)
Bracken/ grass	Medium density	Medium to tall extensive bracken, some bluebell, Yorkshire fog (Holcus lanatus)
Patchy bracken	Low density	Mainly Yorkshire fog, patches of bracken.
Heather		Heather (Calluna vulgaris) and heaths (Erica spp)
Yorkshire fog		Mainly Yorkshire fog, some Poa spp., Festuca spp., clumps of ragwort (Senecio jacobea)
Clifftop/ rocky outcrop		Sea campion (Silene maritima), mixed grasses (mainly Festuca spp., thrift (Armeria maritima) lichens, bare rock.
Rabbit lawn		Mixed grasses, well grazed,short.
Moor grass/ rushes		Tussocks of purple moor grass (Molinia caerulea) clumps of rushes (Juncus spp.).
Bramble/ mixed cover		Clumps of bramble (Rubus spp.) Umbelliferae and thistles (Cirsium spp.)

METHODS

From 1973 onwards quadrats $1m^2$ were used to sample the vegetation near each trapping point. The regular use of the grid meant that paths were trampled through the bracken following the north-south lines (Plate 3.). To avoid these and

to ensure that their influence was minimised the quadrat was always placed at least 1m due east of the paths at the trapping point. The plant species present in each quadrat were noted and the percentage cover of each recorded. Because the quadrats were placed at or near the points on a regular grid the sampling was not random. This limited the choice of mathematical methods by which the vegetation could be described. The Czekanowski cluster analysis (Czekanowski, 1913 - cited by Goldsmith & Harrison, 1976) was therefore used. This is a coefficient of similarity in which the contribution of each species is weighted by a measure of its abundance. This coefficient is:

$$C = 2W/A+B$$

where A & B are the quantities of all the species found in each of the two quadrats to be compared and W is the sum of the lesser values for the species common to the two stands.

The percentage cover for the common plant species on area 'C' was determined in August of each of the years 1976 - 1983 for each of those quadrats in which the species occurred (except 1976 when only 12 randomly selected quadrats were examined). The percentage cover data were also used to study changes in the grass cover on area 'C' (Chapter 1.).

RESULTS

Thirty plant species were found on the study area (Table 18.) but the majority of them were confined to the marshy areas around the North stream (Fig 4.) and many of these were species characteristic of wet areas. The vegetation in the bracken areas further from the stream contained relatively few species

by comparison with the study area as a whole.

Table 18.

Plant species found on the study area.

Pteridium aquilinum +	Bracken
Ranunculus repens *	Creeping buttercup
Silene dioica +	Red campion
Cerastium holosteoides *	Chickweed
Stellaria sp.*	Stitchwort
Trifolium sp.*	Clover
Lotus pedunculatus *	Trefoil
Lotus corniculatus *	Birdsfoot trefoil
Rubus ulmifolius	Bramble
Epilobium palustre *	Marsh willow-herb
Hydrocotyle vulgaris *	Pennywort
Rumex acetosa +	Sorrel
Urtica dioica +	Nettle
Anagallis tenella *	Bog pimpernel
Digitalis purpurea	Foxglove
Glechoma hederacea +	Ground ivy
Galeopsis tetrahit *	Common hemp nettle
Teucrium scorodonia +	Wood sage
Galium palustre *	Marsh bedstraw
Senecio jacobea	Ragwort
Cirsium vulgare	Spear thistle
Cirsium palustre	Marsh thistle
Cirsium arvense	Creeping thistle
Endymion non-scriptus +	Bluebell
Juncus effusus *	Soft rush
Juncus acutiflorus *	Sharp-flowered rush
Molinia caerulea *	Purple moor grass
Festuca sp.	Fescue
Poa sp.	Meadow grass
Holcus lanatus +	Yorkshire fog

+ = Common
* = Largely confined to the wetter areas around the North stream

Some minor variations occurred from year to year in the results of the Czekanowski analysis but it was possible to collate the results from each year and this indicated that there were three vegetational groupings which could be

characterised by the presence of certain plant species (Table 19.).

Table 19.

Key plant species in associations on area 'C' (1973 - 1979, August only).

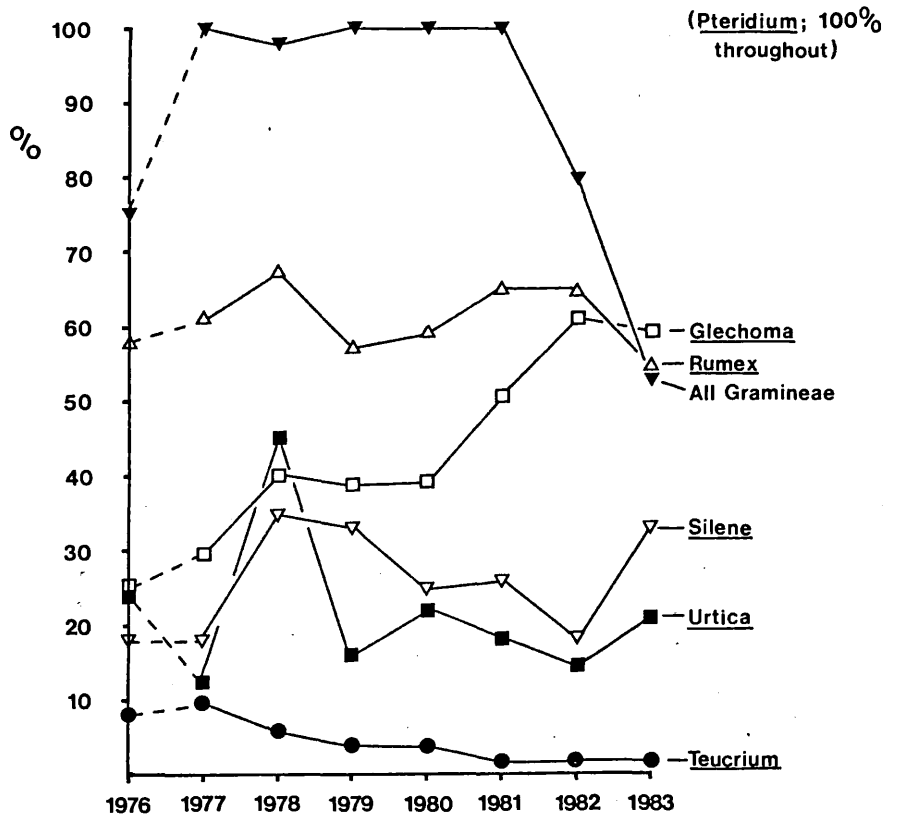
(1)	Pteridium aquilinum Endymion non-scriptus All Gramineae Rumex spp.
(2)	Silene dioica Glechoma hederacea Urtica dioica
(3)	Teucrium scorodonia Cirsium spp. Rubus ulmifolius Digitalis purpurea

Other plant species were present in these associations (eg. Pteridium was found in all of them in varying quantities) but the species listed in Table 19. were the key species on which the analysis divided the associations.

Pteridium, and Endymion were found at each grid point in every year of the study. The proportion of the points at which the other common species were found in August each year is shown in Figure 27. Cirsium was found mostly to the east of the grid where the bracken cover was sparse and Teucrium, Rubus and Digitalis to the south of the grid along a wall.

The proportions of the surface of the island which were found to be covered by the different vegetation categories during the vegetation survey of 1981 are given in Table 20. (after Healing et al. 1983). These results were difficult to

Proportion of quadrats in which the most common plant species occurred on area 'C', August 1976 - 1983



Twelve quadrats were sampled in 1976 and 49 in the other years

compare directly with those of Fullagar et al.(1963) but suggested that, although there appeared to have been a reduction in the Bracken/sorrel category there had been little change in any of the others.

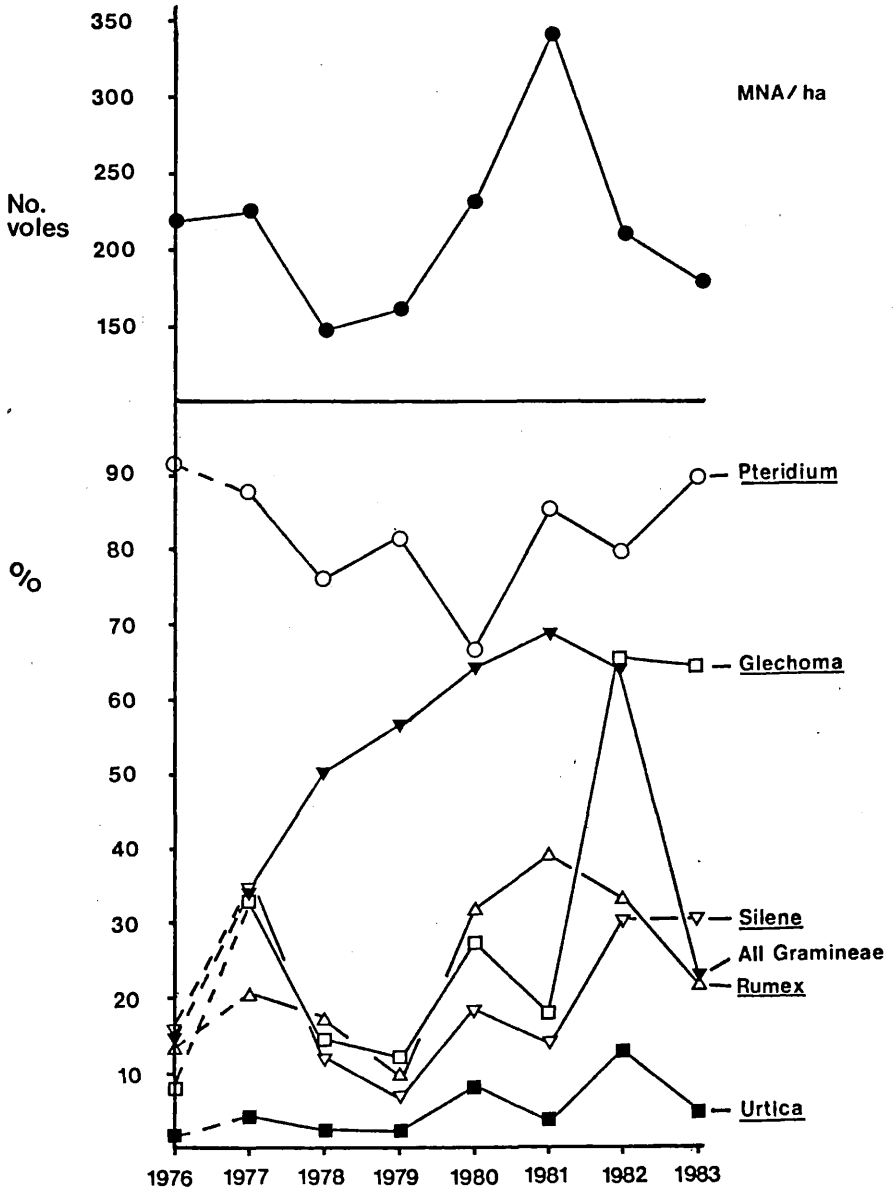
Table 20.

Percentage of the area of the island covered by the different vegetation categories in 1960 and 1981.

Vegetation categories	1960		1981	
Bracken/sorrel	22	41	15.0	36
Bracken/grass	19		21.0	
Patchy bracken		59	24.8	64
Heather			8.1	
Yorkshire fog			8.9	
Clifftop/rocky outcrop			9.7	
Rabbit lawn			10.1	
Moor grass/rushes			0.6	
Bramble/mixed cover			1.8	

Analysis of the mean percentage cover value in August (1976 - 1983) for those grid points at which the most common plant species occurred (Fig 28.) (excluding Endymion which had a mean percentage cover of 73.4% (May 1981 - 1983)) showed that the cover of these species varied from year to year. The cover of Pteridium remained high between 1976 and 1983 whereas that of all the grasses increased in every year except 1982 and 1983. The other common species fluctuated, most having the lowest percentage cover in 1979 (in which year the population of voles was also at its lowest). Changes in the percentage cover of Silene, Urtica and Glechoma followed very similar patterns over the years.The changes in the percentage cover of

Mean percentage cover values for the common plant species on area 'C' at those grid points at which they occurred, August 1976 - 1983 (MNA/ ha for comparison)



Rumex followed a curve approximately paralleling that of the minimum number of voles known to be alive.

DISCUSSION

The results of the vegetation survey in 1981 showed that bracken (in association with various other plant species) dominated the island's vegetation, covering some 60% of the surface of the island. Comparison with the results obtained by Fullagar et al. (1963) showed that the vegetation communities were rather stable.

Pteridium, Endymion and the Gramineae dominated the vegetation on the study area. The proportion of the grid occupied by the other species present fluctuated from year to year but only Glechoma showed an overall tendency to occupy an increased area. This plant is characteristic of grassy swards that are well established and well grazed (by rabbits) and this spread probably reflects increasing activity by rabbits on the area.

The generally close parallel in the changes in the percentage cover of Silene, Glechoma and Urtica supports the results of the cluster analysis which grouped them together. They seem to occupy rather similar niches.

It would be rash to suggest that a direct cause and effect relationship is indicated by the parallel fluctuations in the numbers of voles present in August and the percentage cover of Rumex spp. that occurred between 1976 and 1983. However, Rumex is a plant species particularly found where the vole population is at its densest and the changes in the cover of Rumex may be a reflection of some other physical factor affecting the

population. It is also of interest to note that the percentage cover of most of the other common plant species on the study area was at its lowest at the same time as was the population of voles.

The data from 1983 were difficult to analyse. Not only was the spring later than in the two preceding years but the summer was exceptionally dry and very little grass grew under the bracken in the areas where the latter was dense. Whether this was simply a reflection of prevailing weather conditions or if it represented a step in longer term changes already underway is not known.

Chapter 4.

THE DIET OF THE SKOMER VOLE

INTRODUCTION

Three lines of investigation have been followed in studies of the diet of herbivorous mammals. Two of these, (a) the sampling of vegetation before and after the animals have fed (eg. Cowlishaw & Alder, 1960) and (b) observations on the use made of plant species both in the field and in the laboratory (eg. Hunter, 1954), are of particular value in studies of the diet of large herbivores such as sheep and cattle although laboratory tests (choice or cafeteria tests) have been used to study food selection by rodents (Chitty, 1954; Miller, 1954; Pinowski & Drozdz, 1975). The third method, the identification of plant remains in gut contents or faeces (eg. Stewart, 1967; Watts, 1968; Hansson, 1970; Milner & Gwynne, 1974; Drozdz, 1975; Flowerdew & Gardner, 1978), relies on the fact that the epidermal layer of plants is resistant to digestion in the gut and on the fact that the fine structure of plant epidermes, whilst varying betweenplant genera, is remarkably consistent within the genera.

During the present study samples of stomach contents were taken from voles trapped between 1972 and 1975 from ten sites around the study area and the diet of these animals determined.

METHODS

(a) Preparation of a reference collection of plant epidermes.

A reference collection of slides of the epidermes of the plants found in the habitats occupied by the voles was prepared. Material from the abaxial and adaxial surfaces of leaves, from petals, and from the surfaces of stems, roots,

bulbs and seeds was used and the epidermal material was prepared by one of three methods:

(i) Boiling in 50% nitric acid.

This method was successful with the tougher grasses but tended to disintegrate the softer plants.

(ii) Nail varnish/Cellulose acetate.

Nail varnish or cellulose acetate (2% solution in acetone with 0.7% crystal violet) painted onto the surface of the plant, allowed to dry, and then peeled off produced reasonable reproductions of the topography of the epidermes. The results were both coarsened and slightly distorted however and this method was only used when no other would work.

(iii) Scraping with a scalpel under glycerol.

Pieces of plant tissue were placed flat on microscope slides with the desired epidermis next to the glass. A drop of glycerol was put on the tissue and the unwanted material gently scraped away with a curved 'Swann Morton' scalpel blade (No.10 or No.15). This method proved to be the most successful and was used for the majority of the preparations.

After preparation the epidermal specimens were mounted in glycerol on microscope slides, covered with coverslips of the appropriate size and the edges of the coverslips sealed with rubber solution (Dunlop). Such preparations last for many years.

The epidermes were photographed using a camera attached to a Watson 'System 70' microscope at 100x magnification and prints of the photographs were prepared at a standard enlargement so as to preserve the relative proportions of the features of the epidermes of the various species (Plates 6, 7.

& 8.).

(b) Capture of animals.

The animals used during this study were captured in 'Selfset' breakback mousetraps baited with peanut butter. Up to 50 traps were used and these were examined in the evening and the early morning. Ten sites around the main study area were used for the collection of the animals. These were selected as having a vegetation cover as similar as possible to that of the main study area.

Breakback traps are suitable for catching rodents for studies of their diet by analysis of gut contents because they kill the animals before they can eat too much bait. The use of a bait such as cheese (Watts,1968) or peanut butter (present study) which is readily recognisable in the stomach ensures that there is no confusion between the bait and the diet.

(c) Treatment of stomach contents.

Several authors (eg. Watts, 1968; Hansson, 1970) have recommended that the contents of the caecum be used for the analysis of the diet of rodents because the epidermal material is often partially separated from the underlying material by the time it reaches this organ. Tests performed during the present study showed that the caecal contents still needed to be cleared and so the stomach contents were used so as to reduce the risk that very fragile tissues might be damaged beyond recognition during the digestive process.

The contents of the stomachs were removed from the voles as soon as possible after capture and stored in a mixture of 70% ethanol/10% glycerol which preserves without distorting (Pantin, 1946).

Plate 6.

Epidermes of the common food plants (x100).

(a) Bracken.

(b) Bluebell leaf (adaxial surface).

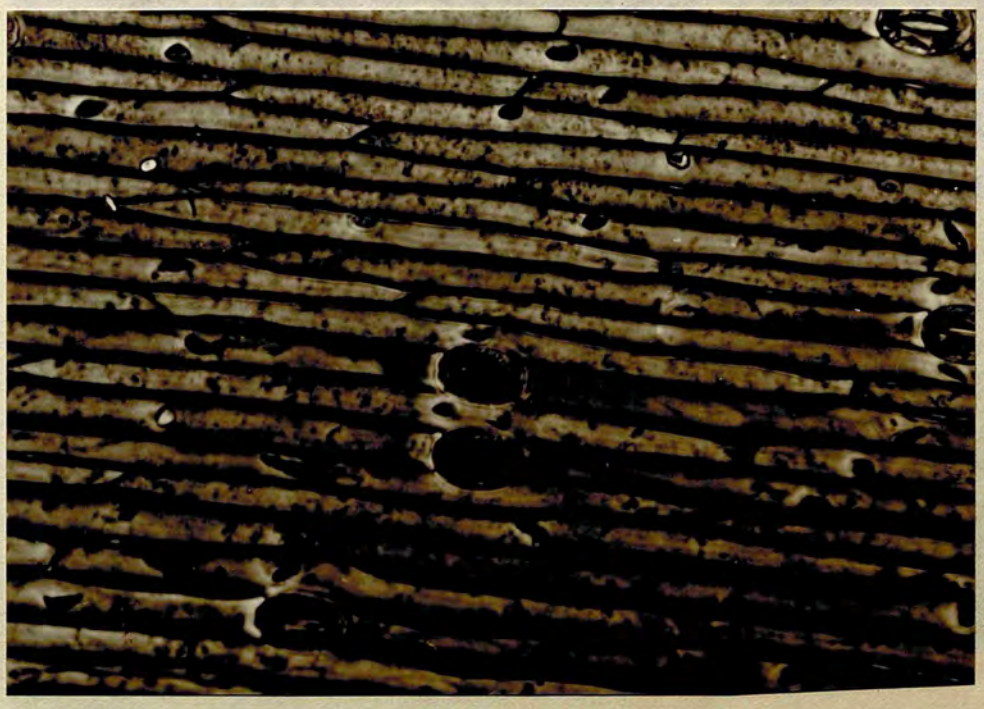
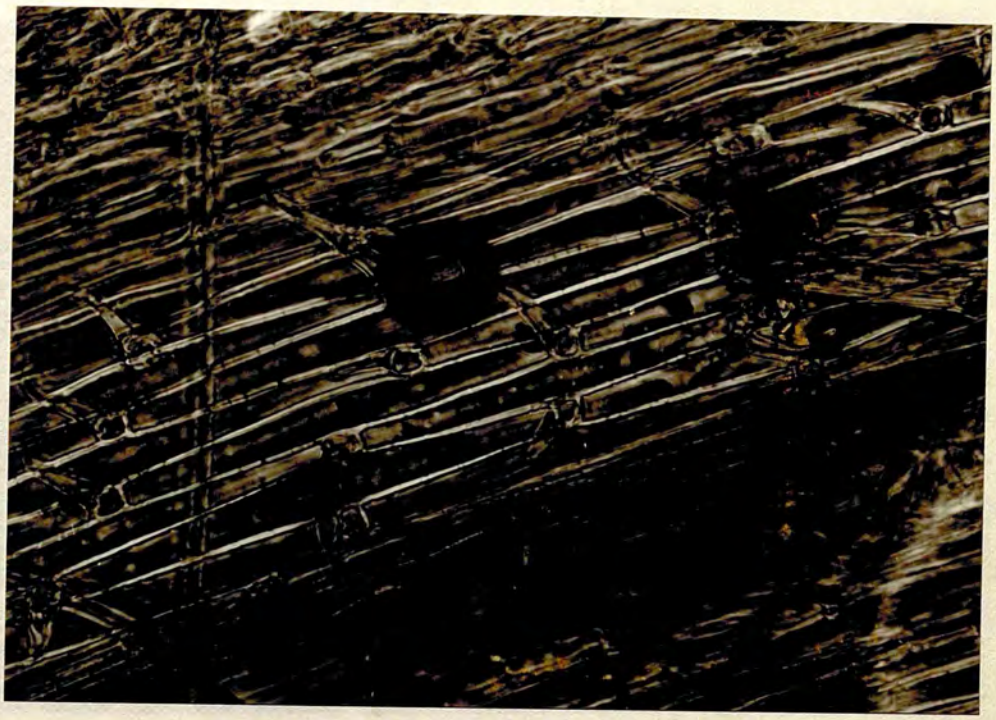


Plate 7.

Epidermes of the common food plants (x100).

(a) Fescue grass.



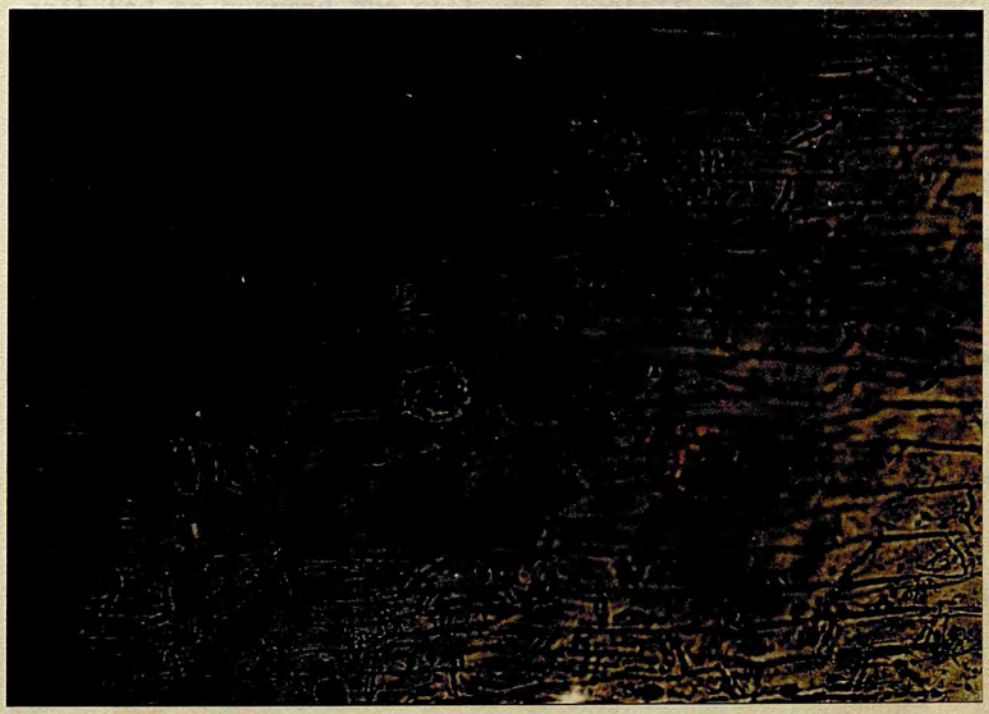
(b) Creeping buttercup.

Plate 8.

Epidermes of the leaf (a) (abaxial surface) and bulb (b) of the bluebell (x100).

(a)

(b)



The epidermal fragments in the stomachs were rarely identifiable without treatment due to the large amounts of adhering tissue. Several methods were tried in an attempt to remove this tissue including boiling in 50% nitric acid (Stewart, 1967) and boiling in a solution of 60 parts of 50% chromic acid: 40 parts nitric acid diluted 1:2 with distilled water (Dunnet, Harvie & Smit, 1973) but these methods were found to destroy both fragile plant tissue and all animal tissue including chitin. The method finally adopted was to clear the tissues with a solution of sodium hypochlorite, a modification of the method proposed by Evans (1973).

The stomach contents in preservative were agitated violently to ensure that they were well mixed. Sub-samples were placed in 10ml centrifuge tubes and centrifuged for 5 minutes at 1000 rpm. This compacted the tissues and allowed the preservative to be poured off without loss of the sample. Five ml. of distilled water were then added to each tube, the tubes agitated to suspend the contents, centrifuged as before and the water poured off. Each tube was then half filled with distilled water, agitated to suspend the contents and a few drops of a concentrated solution of sodium hypochlorite added. The tubes were allowed to stand for one hour (or longer if the contents had not bleached completely) and a 10% solution of hydroxylamine hydrochloride (a reducing agent) was then added drop by drop until evolution of chlorine ceased. The tissues were then washed twice with centrifugation as before and stored in 70% ethanol/ 10% glycerol for future examination.

Evans (1973) suggested that a stain be used on bleached plant tissues so as to highlight the fine structure but this

was found to be unnecessary because even if the tissues underlying the epidermis were not totally removed they were rendered transparent and, since their structure was rather ill defined, the pattern of the epidermis showed up well. A disadvantage of preparing the plant tissues by this method was that the bleaching action made it virtually impossible to distinguish between live and dead plant material. The fact that animal remains and fragile epidermes were not destroyed was felt to outweigh this disadvantage.

The separation of the gut contents into several sub-samples on the basis of particle size by the use of fine mesh sieves has been recommended by some authors (eg. Flowerdew & Gardner, 1978) but such treatment was not deemed necessary during the present study because the voles chewed their food into pieces of rather uniform size.

(d) Determination of plant species present.

The tubes containing the cleared stomach contents were agitated to suspend their contents and to ensure thorough mixing. Drops of the suspension were immediately put onto microscope slides with Pasteur pipettes and covered with 40mm coverslips. Each slide was then scanned at 100x magnification, 50 fields being examined on each slide. Tests showed that this number of fields provided a repeatable sample and that, provided the tubes were well agitated, only one slide need be scanned. Plant material seen in each of the 50 fields was identified by reference to the collection of photographs of plant epidermes.

(e) Analysis of diet.

The analysis of the diet was performed following the

method proposed by Evans (1973):

(i) The percentage composition of the items in each stomach was determined and graded on a scale of relative importance. The scale was:

4 : item composed >75% of the total composition

3 : item composed 51-75% of the total composition

2 : item composed 20-50% Øf the total composition

1 : item composed <20% of the total composition

The median value for the relative importance of each dietary item was calculated for each month.

(ii) The percentage of the total number of stomachs examined which contained each item was determined for each monthly sample. The two values were then multiplied together to give a 'Utilisation Index' (UI) for each food species at the time of sampling.

The UI values were grouped into four seasons: winter(Dec,Jan,Feb), spring,(Mar,Apr,May), summer(Jun,Jul,Aug) and autumn(Sept,Oct,Nov). To permit the direct comparison of the values for each season the total UI for each season was calculated and each UI within this total expressed as a percentage. This index contains information both on what proportion of animals were eating a particular item and how much was eaten in proportion to the other species present in the diet. It is not therefore a simple measure of percentage occurrence but also contains a quantitative component. There are many sources of error in quantitative estimates of different components in studies of the diet of herbivorous mammals (Watts, 1968; Hansson, 197Ø). An index such as that used during this study is not absolutely quantitative and

indeed care must be taken that the results are not imbued with an aura of spurious accuracy but it does provide information on changes in the diet from season to season and it does reduce bias due to the preferences of individuals.

There is always a risk in studies of the diet of herbivorous mammals that the tougher items will be overestimated in the analysis of the diet. The differential digestibility of dietary items can be tested both in vitro (Evans, 1973) and, in vivo, by feeding animals diets containing known proportions of different plant species (eg. Dunnet et al. 1973) but owing to lack of time it was not possible to perform such experiments during the present study.

(f). Bluebell bulbs.

One of the largest potential sources of food for the voles during the winter is bluebell bulbs. To determine the approximate numbers and weight of bluebell bulbs available, ten quadrats each of 1/16 square metre area on and immediately around area 'C', were dug over and the bulbs extracted, counted, oven dried to constant weight at 60°C and their dry weight determined. Captive Skomer voles were given fresh bulbs to see if they would eat them.

RESULTS

A total of 236 samples was examined, 27 from the winter, 42 from the spring, 109 from the summer and 58 from the autumn. The results were grouped under four headings; Major items, Gramineae, Minor plant items and Other (for a list of the individual items in these groups see Figure 29). Bracken, bluebells, bluebell seeds and fescue grasses were the most common items in the diet of the voles. Bracken was most common

Table 21.

Plant species: order in the diet and commonness on the study area

Plant species	Order in diet	Commonness on the ground
	(rank order, 1 = most common)	
Pteridium aquilinum	1	1
Endymion non-scriptus	2	2
Festuca spp.	3	11
Ranunculus spp.	4	+
Cirsium spp.	5	9
Holcus lanatus	6	3
Trifolium spp.	7	12
Teucrium scorodonia	8	10
Rumex spp.	9	4
Dactylis glomerata	10	x
Molinia caerulea	11	8
Poa spp.	12	6
Stellaria holostea	13	+
Carex spp.	14	x
Urtica dioica	15	5
Achillea millefolium	16	x
Lolium perenne	17	x
Glechoma hederacea	18	7
Taraxacum officionale	19	x
Arrhenatherium elatius	20	x
Cynosurus cristatus	21	x

+ = uncommon; confined to wetter part of study area.
x = plant species not found on the study area. The order in the diet is based on the UI values over the whole year. The commonness on the ground incorporates data on the frequency and mean cover of the plant species

in the summer and autumn, bluebell seeds in the autumn and winter, the other parts of bluebells in the winter, spring and summer and grasses (particularly Fescues) in the spring. The remaining dietary items were individually present only in small amounts and only comprised a large proportion of the diet of

the voles in the spring (Figs 29. & 30.).

The proportions of the plant species found in the diet were compared with the results obtained during the extensive survey of the vegetation on the study area undertaken in August 1973 to see if there was any evidence of an active selection or rejection of certain items by the voles (Table 21.).

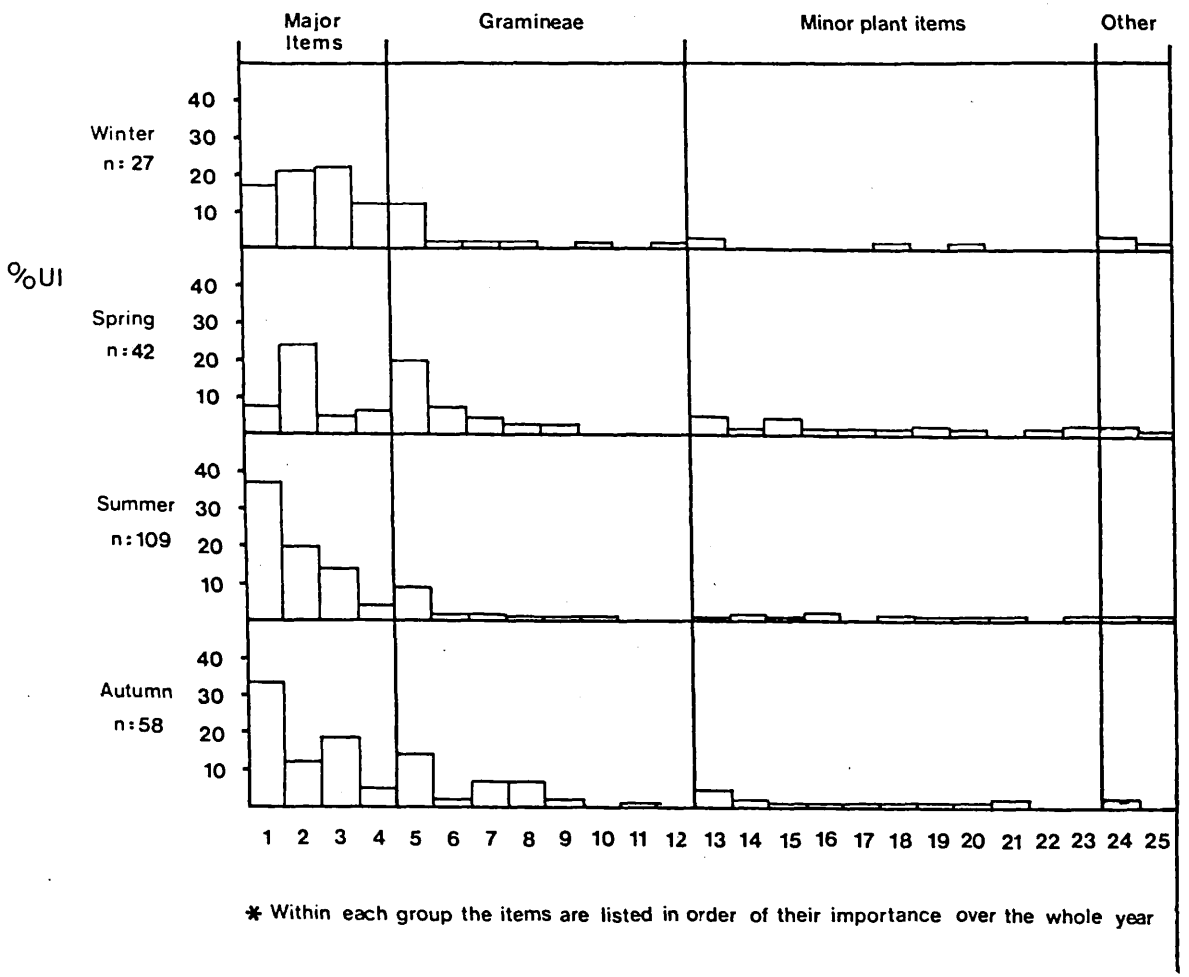
Not all the plant species found in the diet were also present on the study area (for instance Ranunculus spp. which were quite common in the diet were not found there) but of those which were, Pteridium and Endymion were common both in the diet and on the ground. Festuca was more common in the diet than on the study area while conversely Holcus, Rumex, Urtica and Glechoma were more common on the ground than in the diet. Silene dioica which was quite common on the study area was not apparently eaten by the voles.

The numbers and dry weights of the bluebell bulbs dug up from the 1/16 square metre quadrats indicated that there was a large potential source of energy for the voles if they ate the bulbs (Table 20.) and indeed, when bulbs were given to the captive voles they were found to eat at least part of them.

DISCUSSION

The samples for this study were collected from ten different sites around the main study area. The greatest part of the diet of the voles consisted of those plant species which were most common on the ground. Although in general the vegetation differed little from site to site and from that on the study area some site effects showed up amongst the results. For instance the Ranunculaceae were important in the winter

Skomer vole ; items in the diet

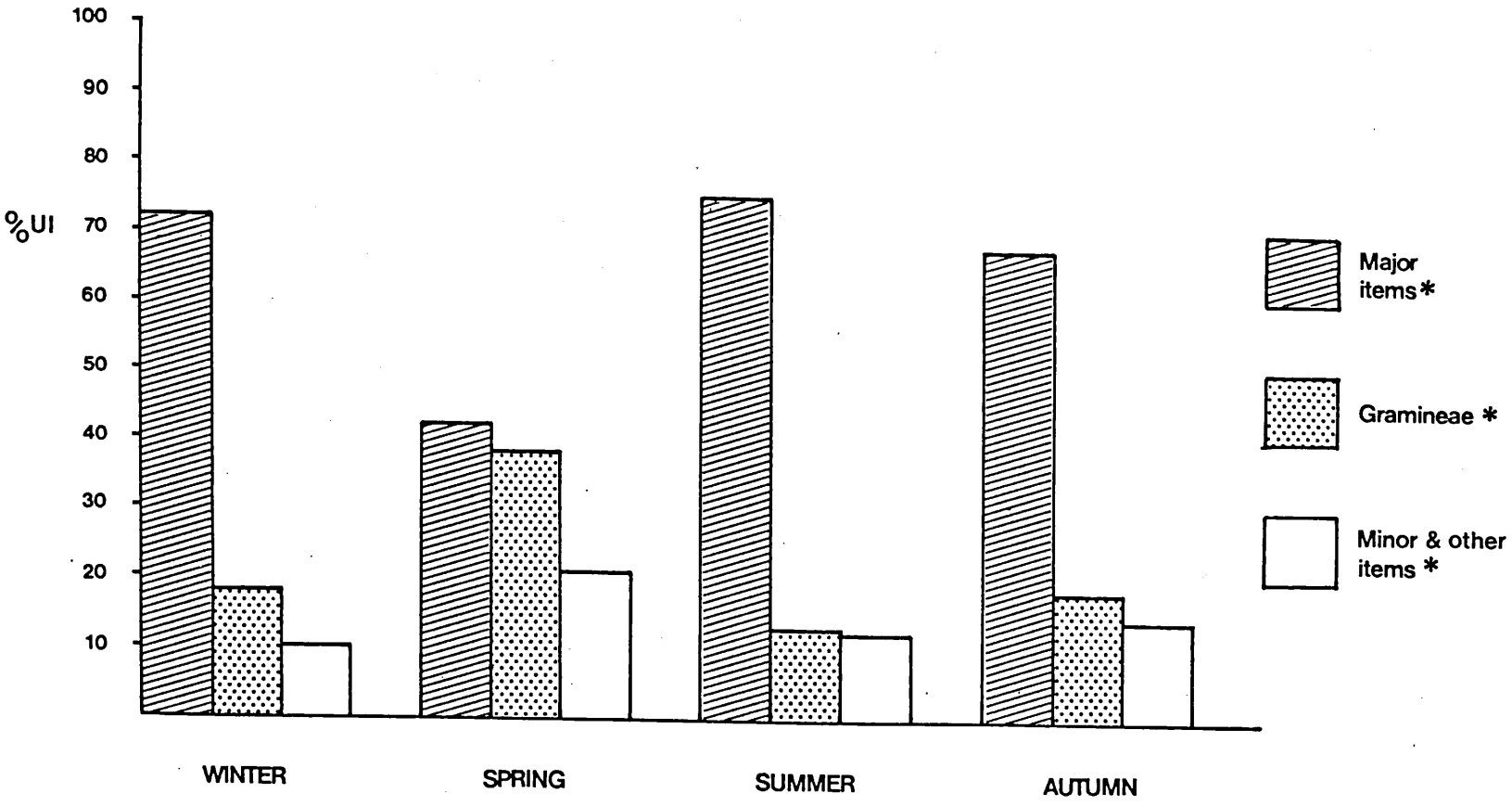


* Within each group the items are listed in order of their importance over the whole year

Food items	
1. Pteridium aquilinum	Major* items
2. Endymion non-scriptus (green parts, bulbs)	
3 Seeds (mostly E. non-scriptus)	
4. Ranunculus spp.	
5. Festuca spp.	Gramineae*
6. Holcus lanatus	
7. Dactylis glomerata	
8. Molinia caerulea	
9. Poa spp.	
10. Lolium perenne	
11. Arrhenatherum elatius	
12. Cynosurus cristatus	
13. Cirsium spp.	Minor* plant items
14 Trifolium spp.	
15. Teucrium scorodonia	
16. Rumex spp.	
17. Stellaria holostea	
18 Carex spp.	
19. Urtica dioica	
20. Achillea millefolium	
21. Glechoma hederacea	
22. Taraxacum officinale	
23. Pollen	
24. Arthropoda	Other*
25. Fungi	

Fig 29.

Skomer vole; seasonal changes in the diet



* For the plant species in these categories see Fig 29.

Fig 30.

Table 22.

Numbers of bluebell bulbs per 1/16 square metre, dry weights and an estimate of numbers and dry weights per hectare.

Sample No	No.bulbs	Dry wt (g)	Wt (g)/m^2
1	30	23.0	368.0
2	48	55.4	886.4
3	12	12.4	198.4
4	24	25.2	403.2
5	45	59.1	945.6
6	77	38.1	609.6
7	41	43.1	689.6
8	35	45.5	728.0
9	45	26.2	419.2
10	46	47.7	763.2
$\bar{x}$ =	40.3	37.6	601.1

601.1 g/m^2 ~ 6011 kg/ha

sample (taken in January 1973) but this sample was collected from a part of the island where plants of this order were more common than usual. Similarly the predominance of Festuca spp. in the spring sample was due largely to the commonness of this grass in the sample from April 1973 which was taken from an area where this species was particularly plentiful. Sorrels were not as common outside the study area as on it. It was hoped that grouping the data by seasons would tend to overcome or at least reduce these effects.

The vegetation on the study area lacks some species found elsewhere so the ranking data obtained from the results of the survey of August 1973 (Table 21.) must be treated with caution

but, despite this caveat, the fescue grasses and the Ranunculaceae appeared to be selected actively by the voles. They certainly formed a much greater proportion of the diet than they did of the vegetation community even outside the study area. Because the samples were collected at different times of year within the seasonal groupings and because they were all taken from different areas it was not possible to compare the results statistically.

The use of bluebell bulbs as a source of food by the voles could not be determined precisely and any such use would probably have been under-estimated both because the epidermis of the bulb is difficult to distinguish from that of the leaves (Plates 6. & 8.) when examining fragments made up of only a few cells and because the volume of the bulb is large compared to the surface area. The internal material of the bulb has a poorly defined structure indistinguishable from the mesophyll of other plant species and would not have been recorded. Many chewed bluebell bulbs were seen on the island but the areas of disturbed earth around these bulbs and the size of the tooth marks on the bulbs suggested that they were being eaten or at any rate dug up by rabbits and not by voles or mice. No bulb that had definitely been chewed by small rodents was found on the surface but the voles may have used them as a food source during the winter and they might either not have been seen or might have been eaten in underground tunnels. Bulbs are certainly a valuable potential source of food for rodents (Meese, 1971).

The voles are apparently fond of bluebell flowers, especially those which are not quite yet out. Well chewed

pieces of flowers were often found in rodent runs under the bluebell leaves during the spring. No absolute evidence that these remnants were the result of the activities of the voles was adduced but the frequency with which such remains were found (2 - 3 piles per square metre) over the whole study area and the rarity of mice in the capture results from that area suggest that the voles were responsible. These remnants were always in obvious small mammal runs under otherwise undisturbed bluebell leaves which suggests that rabbits were not involved.

Phillips (1950) reported that a Skomer vole just released from a trap was observed to eat roots of celendine (Ranunculus ficaria), dead bracken stems and leaves of ground ivy (in October). He also reported that others observed early in 1947 ate the leaves of ground ivy and the tips of bluebell leaves. On several occasions during the present study voles which had just been released from traps were observed to eat bracken fronds (both live and dead) and sorrel leaves (during August).

Chapter 5.

THE ANNUAL FAT CYCLE OF THE SKOMER VOLE.

INTRODUCTION

The majority of the workers who have studied the body fat content of small rodents have used the Soxhlet extraction method or some variation on this process to extract the fat from the tissues. This method, which involves refluxing the tissues with solvents in a special extractor, is satisfactory in that it extracts fats very efficiently but it is rather slow and many of the the solvents used are highly flammable and readily form explosive mixtures with air. In order to avoid these problems a chloroform/methanol-water partition method was used during the present study (Folch, Ascoli, Lees, Meath & LeBaron, 1951; Bligh & Dyer, 1959; Radin, 1969). This method extracts fats with the same efficiency as the Soxhlet method (Atkinson, Fowler, Garton & Lough,1972). The technique adopted during the present study was essentially that proposed by Atkinson et al. (1972) but the method described by those authors was designed for the routine testing of the fat content of food materials and had to be modified to suit small sample sizes and to take account of the presence of hair.

Skomer voles were trapped from 1972 to 1975 for studies on their diet (Chapter 4.). The fat content of the carcasses was analysed with a view to determining if an annual fat cycle occurred and if such a cycle could be correlated with any of the other population parameters being measured.

METHODS

(a) Capture of animals.

The animals were caught in 'Selfset' breakback traps

baited with peanut butter (Chapter 4.).

(b) Preparation of tissues for analysis.

The animals were dissected as soon as possible after capture and the intestines and any uteri containing embryos removed, any fat deposits attached to these organs being returned to the carcass. The intestines were removed from the animals for two reasons. The stomachs had been opened to remove their contents for the identification of items of diet (Chapter 4.). To have left the gut in place would have caused contamination and autodigestion of the surrounding tissues even when the carcasses were frozen. Secondly, the fat content of the items in the gut might have varied from individual to individual and it proved difficult completely to clear the guts of their contents. Uteri with embryos were removed because the ranges of numbers and sizes of embryos encountered would have made different and unquantifiable differences to the results for the different adult females. The bodies were frozen to -20° C at which temperature they were stored.

The carcasses were then freeze dried. This was done because it is much easier to homogenise dry tissue than wet and because the extraction process used required a fixed proportion of water to the other components and the amount added would have had to be varied depending on the water content of the tissues; lyophilisation effectively reduced this to zero. Freeze drying was chosen during the present study rather than drying in a hot oven as has been done by some other workers (eg. Sealander, 1951; Hayward, 1965; Sawicka-Kapusta, 1968) to reduce the risk of loosing the more volatile elements of the lipids by evaporation.

The lyophilised carcasses were homogenised in a 'Moulinex' rotating blade homogeniser which was cleaned with chloroform between each process. Not all homogenisers are suitable for this work because they can contaminate the sample with oil (Radin, 1969). The one used during the present study had the shaft protected by plastic washers which prevented this from occurring.

(c) Extraction of fat from tissues.

The extraction process described by Atkinson et al.(1972) involved the use of specially made tubes in which the samples were shaken with a mixture of chloroform, water and methanol in the proportions 1.0:0.9:1.0, some glass beads being added to aid mixing. The tubes were fitted with a cap with a central hole which was plugged with a silicone rubber sealant. Separation of the solvents after extraction was achieved by centrifuging the tube (cap outwards) at 1000rpm for about five minutes. Sub-samples of the chloroform layers were then removed from the inverted tubes via the silicone plug by means of specially modified syringes fitted with fine injection needles. The sub-samples were dispensed onto tared evaporating trays, the chloroform removed by evaporation and the fat content of the sub-samples determined gravimetrically.

During the present study, flat bottomed 40ml 'Pyrex' tubes were used in place of the specially made round bottomed tubes suggested by the original authors. These had the advantage of being available 'off the shelf' and observations of the shaking process at low speeds in both round bottomed and flat bottomed tubes showed that the flat bottom caused a greater swirl and thus promoted a more thorough mixing. Glass beads were added to

the tubes to aid mixing. 'Analar' grade chloroform and methanol, and glass distilled water, were added to the weighed tissue samples in the tubes in the proportion 1.0:1.0:0.9 using 'Zipette' automatic pipettes (Jencons). The tubes were tightly capped and shaken on a 'Rotatest' orbital shaker for one hour. This time, which was longer than that suggested in the original description of the process, was adopted to ensure complete extraction. The tubes were then centrifuged for five minutes at 1000rpm to separate the two fractions. This separated the chloroform and the methanol/water layers efficiently, the remaining solid tissues collecting at the fluid interface.

The removal of the chloroform layer into a syringe via a silicone plug (cf. Atkinson et al. 1972) was not possible during this study because fine injection needles readily blocked if hair was present. Very coarse wide bore needles had to be used and it did not prove to be possible to make a cap for the tubes that was rigid enough to resist centrifugation yet pliable enough to allow the passage of a wide needle without at the same time spilling an appreciable portion of the sample. The tubes were therefore centrifuged cap inwards but this meant that the chloroform layer was under the methanol/water layer. The latter was removed by the use of a filter pump and the plunger of the syringe was depressed as the needle was passed through the remaining layers of unwanted material. This effectively prevented the contamination of the chloroform, any contaminant being readily visible as a milky suspension on those occasions when contamination did occur. Any hair remaining in the chloroform layer was prevented from entering the syringe by interposing a 'Millipore' filter holder

between the syringe and the needle, discs of 'Whatman's No.1' filter paper being used as the filter (Fig 31.). The centrifugation effectively removed any methanol/water adhering to the hair remaining in the chloroform.

Atkinson et al. (1972) used specially modified syringes to remove a measured sub-sample of the chloroform for evaporation. During the present study the greater part of the chloroform layer was removed from the tubes by the use of 10ml 'Repette' syringes (Jencons) (Fig 31.) and measured volumes were dispensed onto previously tared glass petri dishes, the filter and needle being removed from the syringe prior to the dispensing of the samples. The glass dishes were then placed on a hot plate at 30°C in a fume hood. This temperature was chosen so as to reduce evaporative loss of the more volatile lipid fractions. The chloroform was allowed to evaporate and the weight of the extracted fat determined. The fat content of the original tissue was determined using the formula:

$$\text{Total fat} = \frac{(\text{wt of fat in aliquot}) \times (\text{vol of chloroform used})}{\text{volume of aliquot}}$$

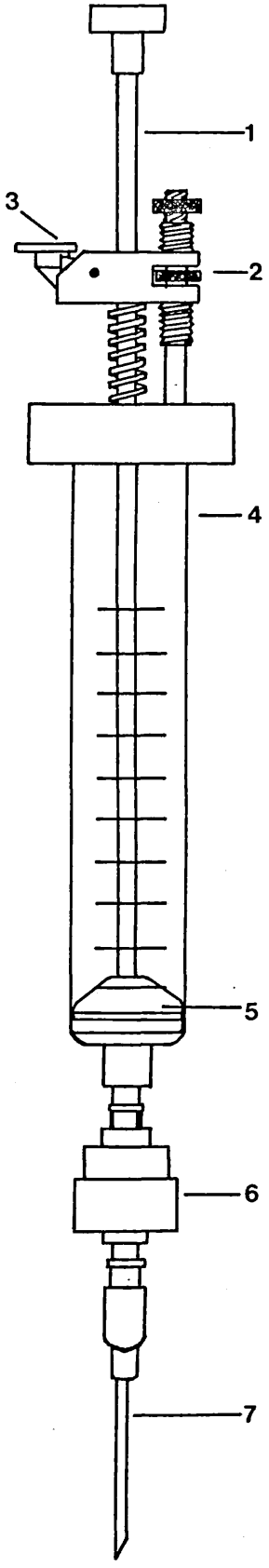
The results were expressed as a percentage by weight of the original tissue sample.

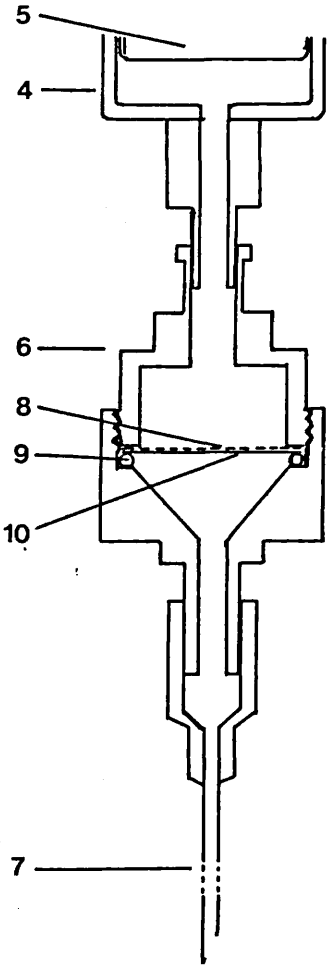
The results are given by seasons: winter (Dec,Jan,Feb), spring (Mar,Apr,May), summer (Jun,Jul,Aug) and autumn (Sep,Oct,Nov).

A few of the intestines and uteri containing embryos that were removed from the animals were processed to determine their fat content, the contents being first removed from the guts.

All the glassware used was washed in 'Pyroneg' detergent (Gallasea), rinsed with three changes of tap water and three changes of demineralised water and dried in a drying oven. The

Fat extraction: 'Repette' syringe, filter and needle





syringes, filters, glass beads and needles were all washed with three changes of fresh chloroform. The paper filters were washed with three changes of chloroform before use.

This method proved to be more demanding of the operator's time than the Soxhlet type of extraction but many more extractions could be performed each day and so the total time involved was reduced.

RESULTS

A total of 237 carcasses was analysed, 29 from the winter, 38 from the spring, 140 from the summer and 30 from the autumn. The peak fat content was found in those carcasses collected during the winter (Table 23.), and this was significantly greater than that found in carcasses collected during the rest of the year ($t=6.64$; $df=235$; $p<0.001$).

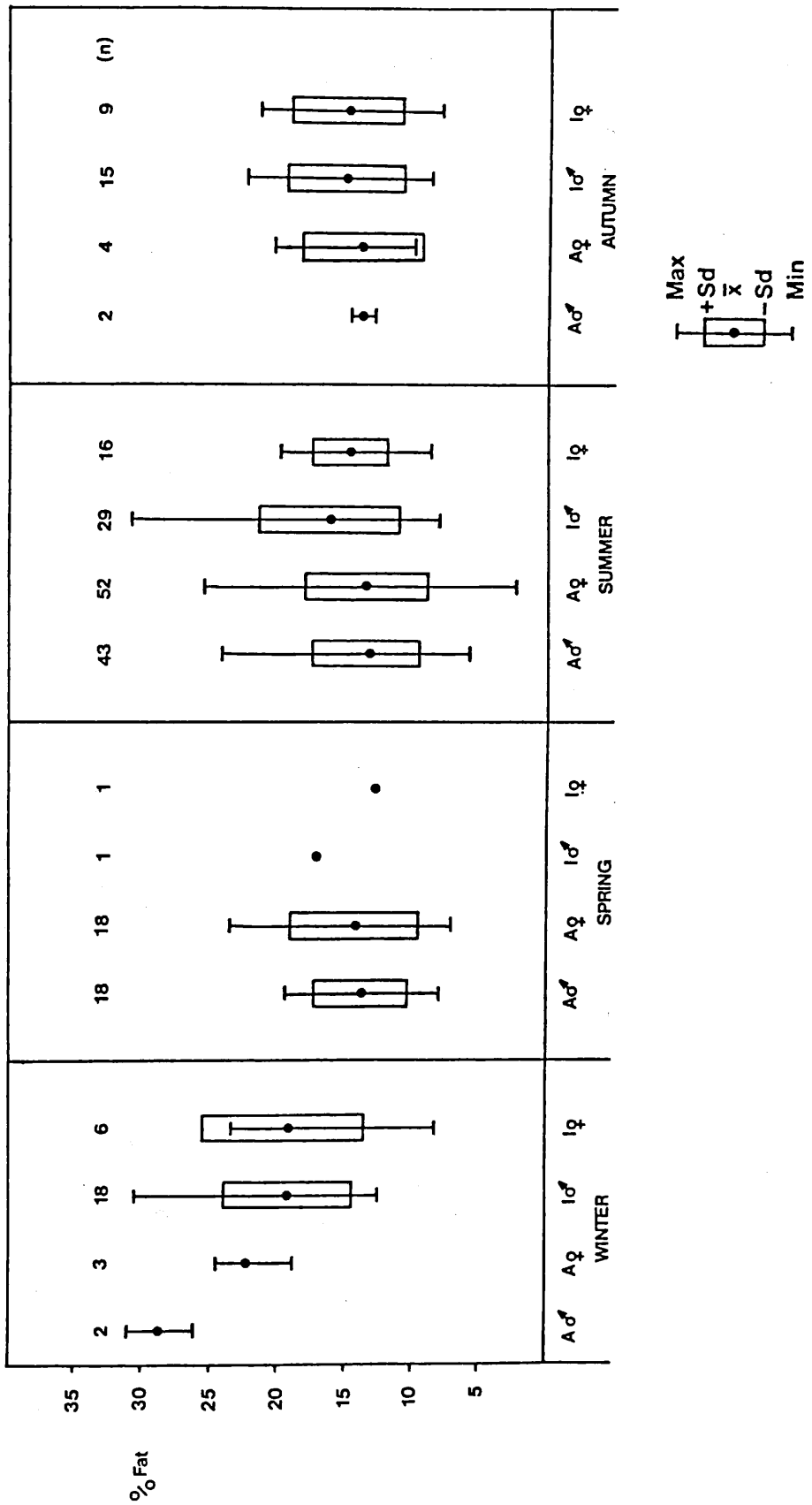
Table 23.

Skomer voles: body fat content as a percentage of dry weight. All animals 1972 - 1975

Season	Mean fat content(%)±SD	n
Winter	20.1±5.3	29
Spring	14.0±4.2	38
Summer	14.1±4.5	140
Autumn	14.7±4.2	30

Figure 32. shows the percentage fat content (dry weight) of the different age and sex classes for the four seasons. All the groups had a greater fat content during the winter than during the other seasons (although very few adult males and females were caught during the winter). The range of variation of the samples was greatest during the summer.

Skomer voles; body fat content as a percentage of dry weight



The fat content of non-pregnant but lactating adult females was smaller than that of adult females which were not lactating (Table 24.) but this difference was of minimal statistical significance ($t=1.82$; $df=31$; $p<0.1$)

Table 24.

Body fat content of different classes of breeding female Skomer voles June-September, 1972 - 1975.

	N.	Mean fat content ± SD
(a) Pregnant females	20	14.94 ± 4.72
(b) Females not demonstrably pregnant	25	12.64 ± 4.09
(c) Females pregnant but not lactating	11	14.91 ± 5.13
(d) Lactating females (not demonstrably pregnant)	8	10.86 ± 4.49

Table 25.

Fat content (% dry weight) of intestines and of uteri with embryos removed from Skomer voles in August 1975).

Age and sex	Intestines Fat content(% dry wt)	Uteri + embryos Fat content(%dry wt)
Adult males	8.6±1.4 (n=6)	
Adult females	10.3±0.8 (n=8)	10.4±0.7 (n=3)
Young males	8.8±3.1 (n=9)	
Young females	8.3±2.0 (n=5)	

The average fat content of the intestines removed from the animals caught during August 1975 was lower than that of the

carcasses from which they were taken ($t=5.33$; $df=50$; $p<0.001$). Those from adult males and from immature and juvenile males and females were all very similar but although those from adult females apparently had a greater fat content than the others (Table 25.) this difference was not statistically significant.

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The results obtained during this study are discussed in the main discussion (Chapter 7.).

Chapter 6.

PARASITES AND DISEASE ORGANISMS.

INTRODUCTION & METHODS.

Before this study was undertaken little work had been done on the parasites and diseases of the Skomer vole. The only studies were those of Twigg, Cuerden & Hughes (1966) and Twigg & Cuerden (1967) who reported that bacteria of the genus Leptospira, present in up to 20% of bank voles on the mainland, were absent from Skomer voles. The ecto- and endoparasites of the voles and the other micro-organisms had been entirely neglected.

The role that parasites and disease organisms may play in the dynamics of populations of wild animals has been the subject of speculation amongst ecologists but remarkably few field data are available on the subject. Between 1976 and 1979 studies of the carriage of viruses and blood parasites by small British rodents were undertaken by myself and several other workers (Kaplan et al. 1980; Healing, 1981. Appendices 6. & 7.). Samples were taken from the voles on area 'C' as part of these studies.

Blood samples were taken from the tails of the animals and prepared for serological study by the method described by Healing (1978) (Appendix 5.). The sera were subsequently tested in the laboratory (at the Department of Microbiology, Reading University) for antibodies to nine viruses by the Complement Fixation and Haemagglutination Inhibition methods (for details of these methods see Grist, Bell, Follet & Urquhart, 1979). The viruses studied were Orthopox viruses (Ectromelia (Mouse pox) being used as the type virus), Mouse adenovirus, Sendai

(parainfluenza virus 1), Pneumonia Virus of Mice (PVM), Louping ill, Lymphocytic choriomeningitis virus (LCM), Reovirus III, Encephalomyocarditis virus (EMC) and Theiler's mouse encephalomyelitis (GDVII). These viruses were chosen either because their existence in populations of wild rodents had already been reported or because they were known to be common infections of laboratory colonies of rodents.

Because population studies were being made on the rodents only rather small blood samples (ca. 0.1ml) could be taken. This meant that it was not possible to test each one against the whole battery of antigens. Instead different samples were tested against two or three different antigens, the whole range of antigens being covered in the course of the analyses. The size of the samples also meant that it was rarely possible to titrate them against the antigens. The initial tests were performed at a nominal dilution of 1:10 and then tests were made at serial twofold dilutions as far as the size of the samples permitted.

Blood smears were made, air dried, fixed in absolute methanol, stained for 1h in Giemsa stain diluted 1:10 in buffered water (pH 7.0) and then rinsed briefly in two changes of buffered water (Cruikshank, Duguid, Marmion & Swain, 1975b). The smears were examined at magnifications of 100x and 1200x to detect parasites, 50 fields being examined at each magnification.

A search was made at the same time for bacteria of the genus Salmonella. Samples of faeces were collected directly from the animals in 2ml vials each containing 1ml Selenite broth (Lab M.) and maintained at ambient temperature. When

returned to the laboratory the samples were analysed by the methods described by Healing et al. 1980 (Appendix 8.).

A small collection of ectoparasites from the voles was made in August 1982. Fleas were identified following the methods and characteristics described by Smit (1957) and the other ectoparasites according to details given by Chandler & Read (1961).

RESULTS.

(a) Viruses

One hundred and fourteen blood serum samples were obtained from Skomer voles in 1977 and 1978. The results of the tests against the various antigens are given below, the results obtained in analyses of sera from bank voles on the mainland being given for comparison (Table 26.).

Table 26.

Percentage of serum samples with antibodies to the nine viruses from Skomer voles (Cgs) and mainland bank voles (Cgg).

Virus	Cgs		Cgg	
	No +ve	% +ve	No +ve	% +ve
Ectro	2/18	11.1	0/9	0.0
M.adeno	0/4	0.0	0/5	0.0
Sendai	28/33	84.8	6/15	40.0
PVM	26/67	41.8	36/88	40.9
L.ill	0/23	0.0	1/21	4.8
LCM	4/10	40.0	0/8	0.0
Reo III	4/72	5.6	1/15	6.7
EMC	0/13	0.0	2/5	40.0
GDVII	11/46	23.9	0/8	0.0

Evidence of infection with Orthopox viruses, LCM and GDVII was therefore found on Skomer but not on the mainland but the

numbers of samples were small. Louping ill was not found on Skomer but that virus is very localised in its distribution in the UK being confined largely to the north of England and the south-west of Scotland. Large numbers of samples were tested for evidence of infection with pneumotropic viruses. Infection with Sendai virus was apparently particularly prevalent on Skomer whereas the proportion of animals that had sera positive against PVM was approximately the same on Skomer as on the mainland over the period of the study. However the majority of the positive results from Skomer were obtained in 1978 (Table 27.) in which year the number of voles caught in August was much smaller than in the previous year (149 : 226, see Chapter 2.).

Table 27.

Percentage of Skomer and mainland bank voles with antibody to PVM

	1977	1978
C.g.skomerensis	7%	67%
C.g.glareolus	37%	42%

The decline in numbers of voles between the two samples on Skomer was therefore apparently accompanied by an epizootic outbreak of PVM although there is no evidence to suggest that this was responsible for the decline.

(b) Blood parasites.

Three hundred and thirty four blood smears were taken from Skomer voles in the first week in August 1977 - 1980. Four

Table 28.

Percentage of Skomer voles (Cgs) and mainland bank voles (Cgg) infected with the four genera of haemoparasites (after Healing, 1981).

Parasite	% Cgs infected	% Cgg infected
Babesia	0.0	12.7
Hepatozoon	45.8	32.8
Trypanosoma	14.1	11.1
Grahamella	16.2	8.3

Table 29.

Percentage of adult (A) and of immature + juvenile (I + J) voles infected with the various parasitic genera (after Healing, 1981).

Parasite	Age group	% Cgs infected	% Cgg infected
Babesia	A	0.0	14.0
	I+J	0.0	10.3
Hepatozoon	A	71.6 *	33.6
	I+J	21.2	31.4
Trypanosoma	A	6.0 *	6.8 *
	I+J	23.8	19.2
Grahamella	A	21.3 +	9.9
	I+J	9.9	5.1

* - significant difference, $p<0.001$
+ - significant difference, $p<0.01$

genera of parasites had been found in the blood of bank voles on the mainland and three of these, Hepatozoon (Coccidiida), Trypanosoma (Zoomastigophora), and Grahamella (Bartonellaceae) were found in the blood of Skomer voles. A fourth genus, Babesia (Haemosporidea), which was present in about 12% of mainland bank voles, was not found in the voles examined on Skomer. Just over 60% of the Skomer voles examined were infected with at least one parasitic genus. The proportion of animals infected with the different genera is given in Table 28., with data from the mainland for comparison.

Comparison of infections in the adult and immature + juvenile age groups showed some significant differences (Table 29.).

(c) Enterobacteria.

Sixty eight faecal samples were collected from Skomer voles. Salmonella was not found in any of them. The only enterobacteria isolated were Hafnia alvei and Citrobacter freundii, both normal non-pathogenic inhabitants of the mammalian gut.

(d) Ectoparasites.

Specimens of four species of fleas (Rhadinopsylla (Actenopthalmus) pentacantha, Hystrichopsylla talpae talpae, Amalaraeus penicilliger mustela and Ctenopthalmus nobilis) were found on the voles during this study as were specimens of the bracken-bug Trombicula autumnalis and of ticks Ixodes sp. The prevalence of T.autumnalis approaches 100% in some years and the infestations can be extremely heavy. The parasites tend to congregate around the anus, the scrotum or vagina, in the ears and on any wounds.

DISCUSSION.

The pathogenicity of the various viruses studied for the voles is not known. Their effect on the laboratory mouse (Mus musculus) has however been quite well documented. In this host species Ectromelia, which is found as a latent infection in many laboratory stocks, may be activated by stress and cause death due to hepatic lesions and pancreatic necrosis (Andrewes, Pereira & Wildy, 1978). Extensive serological cross reaction occurs within the orthopox virus group (Cruikshank, Duguid, Marmion & Swain, 1975a) and the positive results obtained during analysis of sera from the Skomer voles indicates no more than that they have sustained infections with a member of this group of viruses. Both Sendai virus (Andrewes et al. 1978) and PVM (Tennant, Parker & Ward, 1966) may be maintained as inapparent infections in laboratory mice but their virulence can be enhanced by serial passage from mouse to mouse and they can cause fatal pneumonias. These may be bronchial (Sendai) or interstitial (PVM)(Carthew & Sparrow, 1980).

Lymphocytic choriomeningitis probably causes inapparent infections in wild house mice (Andrewes et al. 1978) but can cause death in adult laboratory mice due to an overactive immune response (Hotchin, 1962). Reovirus III has been isolated from both wild (Hartley, Rowe & Huebner, 1961) and laboratory (Cook, 1963) strains of house mice. In the latter symptoms appear mainly in newborn animals and may include jaundice and stunted growth (Andrewes et al. 1978). Infections with the enterovirus GDVII are probably inapparent in wild house mice but fatal involvement of the central nervous system has occurred following experimental infections of laboratory

animals (Andrewes et al. 1978).

Data also exist concerning the effect of some of these pathogens on hamsters which, being members of the Cricetidae, may be immunologicaly more similar to the Skomer vole than are house mice. Sendai virus can cause a fatal pneumonia in Chinese hamsters (Andrewes et al. 1978); PVM can cause lung lesions in Syrian hamsters infected experimentally (although serial inter-hamster transmission does not readily occur) (Andrewes et al. 1978); LCM produces an apparently symptomless infection but with a viraemia of long duration (Andrewes et al. 1978); Reo III may cause obstructive hydrocephalus (Kilham & Margolis, 1969); and the effect of GDVII is unknown.

The effect that the blood parasites found during this study may have on wild voles is not known. Wiger (1979b) considered that these organisms do not play a role as mortality factors in populations of bank voles but Mansfield (1977) has pointed out that normally non-pathogenic trypanosomes can produce a fatal disease if the host's immune mechanisms are seriously impaired. Their effect may be indirect; haemoprotozoa can exert an immunodepressive effect (eg. Plasmodium falciparum: Williamson & Greenwood, 1978; Cox, 1975) or can stimulate a non-specific resistance (eg. Trypanosoma brucei, Alexander & Phillips, 1978).

The absense of Salmonella from the faecal samples collected from Skomer voles parallels the results obtained from mainland Britain during the same study (Healing et al. 1980; Appendix 8.) and agrees with the results obtained by Taylor (1968) and by Jones & Twigg (1976). In both of these studies infections with Salmonella were found to be rare in small wild

rodents. The only enterobacteria identified in the samples from Skomer voles were common non-pathogenic inhabitants of the mammalian gut. That a wider range of the normal bacterial flora of the mammalian gut was not found during this survey was due to the selective nature of the analyses used. That some were found was due to the fact that the media are highly but not absolutely selective.

The precise effect exerted on the hosts by the ectoparasites found during this study is not known but must be presumed to be deleterious, firstly because the nutrient losses incurred by the host when they feed upon it must, at the least, face it with a requirement to increase its food intake, and secondly because they are known to act as disease vectors (Chandler & Read, 1961; Andrewes et al. 1978).

Chapter 7.

DISCUSSION

Populations of small rodents often follow a pattern of changes in numbers with a periodicity of three, four or five years (Krebs & Myers, 1974). These are called cycles, a term which, when used in this context, implies that the fluctuations follow a regular pattern. Populations of the bank vole tend to be cyclical towards the northern part of their range (eg. in Fennoscandia: Kaikusalo, 1972; Koshkina (1966 - cited by Krebs & Myers, 1974); Larsson & Hansson, 1977; Hornfeldt, 1978; Wiger, 1979a) but non-cyclical in the British isles and mainland Europe (Bergstedt, 1965; Hansson, 1971b, 1979; Alibhai, 1976; Southern,1979).

Island populations of rodents tend to be rather stable. Lidicker (1973) studied a population of Microtus californicus for thirteen years on Brooks island (California) following the accidental introduction of this species to the island (Lidicker & Anderson, 1962). During the first two years following its establishment the population fluctuated unevenly but it then settled down into a regular pattern characterised by annual peaks of abundance at the end of the breeding season and an alternating (two year) pattern of "high" and "low" winter densities. This population was much more stable than a population of the same species on the nearby mainland (Lidicker, 1975).

A population of bank voles on Crab Apple island in north-eastern Poland was found to follow a two year cycle. At the beginning of the breeding season in each year the number of individuals in the population was remarkably constant (ca. 16/ha) and the numbers rose to a peak of about 50/ha in "low"

density years and of about 100/ha in "high" density years (Petrusewicz et al. 1971; Bujalska, 1970, 1973; Gliwicz, 1975).

Tamarin (1977b) simultaneously studied a population of Microtus breweri on Muskeget island (Massachusetts) and a population of M.pennsylvanicus (its ecological counterpart) on the nearby mainland. The density of the island population fluctuated little over a four year period whereas the mainland population followed a three to four year cycle.

Sullivan (1977) found evidence to suggest that populations of deermice (Peromyscus maniculatus) on islands off British Columbia were rather stable but he only trapped the populations for two years.

Berry (1968, 1970) and Berry & Murphy (1970), who studied a population of house mice (Mus musculus) on Skokholm island near to Skomer, found a wide range of variation in the size of the population in the summer but the size of the winter population was less variable. There was also evidence of a two year cycle of abundance. The ecology of this population was of considerable interest. The mice overwintered in dry stone walls, around buildings and on cliffs and only expanded into the rest of the island during the summer. A large part of the island was therefore available during the breeding season to absorb the excess production of young.

The numbers of Skomer voles were found to fluctuate annually, the numbers being at their lowest at the beginning and at their highest at the end of the breeding season, but no evidence of a regular two, three, four or five year cycle in numbers was found. The numbers present in the first week in August showed an apparent peak in 1973, declined to a trough in

1978, rose to another peak in 1981 and declined in the next two years. It is not clear whether this oscillation in numbers was truly evidence of a rather long term cyclical change or not but the decline between 1973 and 1978 took five years and the increase between 1978 and 1981 took three years. This suggests a irregularity incompatible with the concept of a cycle as defined at the beginning of this discussion. The August values obtained between 1976 and 1980 can only be treated as an index and must be used with caution since it cannot be assumed that the duration and magnitude of breeding events preceeding and following the measurements were the same in each year or that the trapability of the voles did not alter. Although the population of the Skomer vole is not as stable as some of the populations of island rodents mentioned above (quite large variations in the numbers of the voles having been noted both within and between years) nevertheless the absence of catastrophic declines or eruptive increases in the size of the population is, in my opinion, evidence that the population is basically stable.

The densities achieved by island or enclosed populations of rodents are frequently much greater than those reached by unconfined populations of the same species. Krebs, Keller & Tamarin (1969) found that whereas open populations of Microtus pennsylvanicus reached densities of 88 - 100/ha confined populations achieved densities of 250/ha and similarly that an open population of M.ochrogaster reached densities of 25/ha as compared to 88/ha in enclosed populations. Sullivan (1977) reported densities of 19/ha in open populations of Peromyscus maniculatus as compared to up to 43/ha in confined populations.

Gipps (1977) and Gipps & Jewell (1979) found that the density of an enclosed population of C.glareolus (supplied with abundant food) reached 3127/Ha. Some enclosed populations reach quite remarkable densities. For instance Lidicker (1976) recorded densities exceeding 50,000/Ha in enclosed populations of house mice (Mus musculus). Such exceptional densities are usually only achieved when food and water are supplied ad libitum.

The maximum densities recorded for bank voles on the mainland and in Europe vary from 50/ha (Raiska-Jurgiel, 1976) to 247/ha (Newson, 1963). The normal field densities are around 50/ha (French, Stoddart & Bobek, 1975). Very high densities (up to 752/ha) were recorded in fenland in Cambridgeshire where flooding created temporary islands which were used as refuges by the animals (S.G.Hall - personal communication).

The densities reached by island populations of bank voles tend to fall within the range given for mainland populations but are generally higher than the usual field densities. Petrusewicz et al. (1971) and Gliwicz (1975) reported densities of up to 100/ha on an island in Poland and densities of up to 135/ha have been recorded on a small island (0.37ha) in a lake near Reading in the British Isles (T.D.Healing - unpublished results). The Skomer vole reaches exceptionally high densities for this species. Jewell (1966a) reported densities of up to 250/ha and a peak density of 475/ha was recorded during the present project. The lowest density recorded on area 'C' during this project was 74/ha (May 1983) although lower densities, similar to normal field densities on the mainland, have been recorded in habitats less favourable for the voles (eg. 51/ha

in August 1960; Fullagar et al. 1963: 58/ha in August 1980; Healing et al. 1983). It is interesting to note that whilst the densities recorded in the same area of less favourable habitat in different surveys twenty years apart were very similar, the same authors reported very different densities in an area of more favourable habitat (259/ha and 355/ha respectively). It is possible that the voles rapidly achieve the maximum possible density in the less favourable habitat but that the carrying capacity is not reached in the more favourable habitat.

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The importance of dispersal in the regulation of populations of small rodents was first shown by studies on populations in artificial enclosures. Clarke(1955), Louch (1956), van Wijngaarden (1960), Houlihan (1963), and Lidicker (1979) showed that populations of various species of Microtus achieved densities many times greater than normal when dispersal was frustrated. However these studies were not really representative of the natural situation because the enclosures were small and food was supplied. Krebs, Keller & Tamarin (1969) enclosed populations of Microtus ochrogaster and M.pennsylvannicus in large (2ha) enclosures to which no extra food was added and which apparently did not exclude predators. The population inside built up to very high levels, the habitat was overgrazed, and the population declined due to food shortage. Dispersal appeared to have been the only parameter altered by fencing the population. (This experiment was carried out over quite a short period. It is possible that the wide fluctuations seen may have paralleled those described by Lidicker (1973) for a population of rodents on an island off the Californian coast in the years immediately following their

accidental introduction to the island. Unfortunately nothing is known about the long-term stability of artificially enclosed populations of rodents).

Lidicker (1975) in his general discussion of the demography of small mammals used the term "dispersal sink" to describe areas of unfilled suitable, marginal, or even unsuitable habitat which could provide a refuge, if only a temporary one, for the disperser. In addition he defined two kinds of dispersal, saturation dispersal and pre-saturation dispersal, the former being the movement of individuals away from a population living at or near its carrying capacity and the latter being movement from populations that are still in their growth phase. Animals which disperse from saturated populations tend to be surplus individuals, social outcasts, juveniles and the old or ill and thus they have a poor chance of survival whereas pre-saturation dispersers may well be in good condition and survive in their new habitat.

Krebs (1978) noted that the highest rates of dispersal in cyclical populations of Microtus spp. occurred during the increase phase of the population cycle (eg. pre-saturation dispersal) and was the result of spacing behaviour and agonistic interactions. Hestbeck (1982) has suggested that, at low densities, dispersal is possible and spacing behaviour limits the population through emigration but that as densities rise the neighbouring populations effectively "fence" the population thus limiting emigration. Thereafter population regulation is achieved by resource exhaustion. Thus, as Krebs (1978) has pointed out, the result is that dispersal in cyclical populations is favoured for a short time when

population densities are low and rising but is disadvantageous when populations are high and all habitats are occupied.

Dispersing Microtus townsendii were found to attain sexual maturity at a lighter weight than did residents and a high proportion of the dispersers were juvenile and "sub-adult" (Beacham, 1981). Dispersing members of this species were also found to be subordinate to control animals in neutral arena bouts (Krebs, 1978) suggesting that vacant areas may be colonised by subordinate and not by dominant animals.

Tamarin (1978) argued that a dispersal sink is necessary if population cycles are to occur and he developed a model which showed that the degree of cycling was related to the degree of dispersal. He based this on observations of an island population of Microtus breweri which did not cycle whereas a population of M.pennsylvannicus on the nearby mainland apparently did so (Tamarin,1978). He suggested (Tamarin, 1978) that the island population, with no dispersal sink and with too little predation to produce an adequate loss was under K-selection (MacArthur & Wilson, 1967; Pianka, 1970) the carrying capacity being the limiting factor whereas, on the mainland with dispersal sinks available, r-selection operated, the inherent rate of increase being the limiting factor.

Keith & Tamarin (1981) performed a removal experiment on Muskeget island (Massachusetts) and the nearby mainland. Animals which moved into the denuded areas were assumed to be dispersers. In essence, those animals which dispersed on the mainland were found to be heterogeneous (in body weight, age, and certain genetic loci) with respect to those that did not move whereas those on the island were homogeneous. On the

mainland therefore there appeared to be a class of animals predisposed to disperse whereas, on the island, dispersers were drawn from every group in the population. Since the island had no adequate dispersal sink those which dispersed during the experiment were assumed to be predisposed to disperse under normal circumstances but were frustrated by a 'social fence' effect (Hestbeck, 1982).

Both Tamarin (1978) and Keith & Tamarin (1981) were working with species which are normally cyclical (at least M.pennsylvanicus is). The role of dispersal in the regulation of populations of non-cyclical rodent species is less clear if only because it has been less studied. Dispersal undoubtedly occurs in populations of these species but whether pre-saturation or saturation dispersal is most important is not known. Krebs (1978) has suggested that aggressive behaviour in cyclical populations of rodents is genetically controlled and does not operate at low densities when it is unnecessary, whereas aggressive behaviour in non-cyclical populations is phenotypically controlled by hormone levels and experience. If so, saturation dispersal would probably be more common in non-cyclical populations than in cyclical ones.

Populations of rodents on islands tend both to achieve high densities and to be rather stable. Dispersal sinks are often reduced or absent and the 'social fence' effect is probably important at least on the larger islands. Andrzejewski & Wroclawek (1961) argued that dispersing individuals were in poorer physical condition than residents and Metzgar (1967) that they were more at risk from predators. If spatial dispersal is limited or absent the predation and disease

pressures may well fall most heavily on those animals which would otherwise have dispersed and would, as Tamarin (1978) has suggested, act as the equivalent of a dispersal sink.

Some evidence exists to suggest that island dwelling rodents are less aggressive than those found on the mainland or at least that they are more tolerant of contact with other members of the population. Halpin & Sullivan (1978) found that island populations of deermice (Peromyscus maniculatus) were less aggressive than mice from the nearby mainland and Tamarin (1978) found that Microtus breweri is less aggressive than its mainland counterpart M.pennsylvannicus.

Skomer voles are unusually docile (for this species) when handled in the field and rarely attempt to bite or to flee. Alder (1972) has suggested that such behaviour has a strong selective advantage in a situation where ground living predators are absent and the only predation is by birds. Under such circumstances to stay still rather than rush away conspicuously would be a great advantage. Interestingly this type of behaviour is lost if Skomer vole young are fostered by mainland bank vole mothers and the young of these C.g.skomerensis young do not regain the trait. C.g.glareolus young fostered by C.g.skomerensis mothers do not become tame. This behaviour apparently contains both a phenotypic and a learnt element (Alder, 1972). Skomer voles maintained in laboratory colonies also lose this trait over several generations. Alder (1972) reported its loss within five generations and third generation Skomer voles in the animal house at Reading University are markedly less docile than the wild caught animals (T.D.Healing - unpublished observations).

Ashworth (1973 - cited by Johnson, 1976) reported that male Skomer voles were less aggressive than mainland bank voles in laboratory test situations and that the latter were less tolerant of other voles and tended to flee when attacked. Johnson (1976) has suggested that mainland voles may come into contact with other voles less often than do Skomer voles and cites studies of urinary behaviour to support this hypothesis. The markedly greater incidence of wounding found on Skomer voles as compared to bank voles on the mainland supports the suggestion of more frequent contact between individuals.

Few data are available concerning the possible role of dispersal in the population dynamics of the Skomer vole. Resident animals apparently become attached to their home site from an early age. The great majority of the animals which were recaptured on consecutive visits to the island during the last few years were caught close to the point at which they were first caught (within 30m).

My study and that of Fullagar et al. (1963) have shown that certain parts of the island are apparently less suitable than others for occupation by the voles and indeed that about 40% of the island's area is avoided by them. The population therefore has available areas which could act as dispersal sinks. The results of the survey of 1981 in which few voles were found in those areas at a time at which the population (on area 'C') was large suggest that these areas are not so used. Those few adult voles found in such areas towards the end of the breeding season in 1981 were significantly lighter in weight than those in more favourable areas and, in some parts of the island, were showing signs of sexual regression absent

from animals in more favoured areas. Whether these animals were residents responding to a less favourable food supply or subordinate animals which had dispersed into these areas is not known.

When trapping was undertaken in 1971, 1972 & 1973, on an area which would permit movements of up to 225m to be detected, 72.5% of the movements of males and 93.5% of the movements of females that were detected during the trapping periods were of less than 40m and only 9.7% of the movements of males and 6.4% of the movements of females exceeded 60m. A few long movements (in excess of 100m) were detected during this programme and by the trapping programme designed to detect such movements which was undertaken in 1982 and 1983. Area 'C' lies in an extensive area of habitat suitable for the voles. Animals attempting to disperse would have to penetrate a "social fence" and indeed would have to move considerable distances to find a potential dispersal sink. The arrangement of the grid to detect long movements, whilst extending the area trapped quite considerably, nevertheless did not reach into any areas of poor habitat and so animals that had dispersed might not have been detected by this trapping programme.

The fate of those animals which disappear from populations usually remains a mystery. The role of predation and disease is considered later in this discussion. Whether dispersal is involved on Skomer is not known but the data gathered during this project tend to agree with the results of Sullivan (1977), Tamarin (1977a) and Crowell (1983) all of whom stated that the tendency to dispersal in island populations was much less than in open populations. In addition the stability of the Skomer

population suggests that dispersal may not be important in its dynamics (cf. Tamarin; 1977a, 1978).

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Jewell (1966b) defined home range as "the area over which an animal normally travels in pursuit of its routine activities". A portion of the range (or even the whole) may be maintained by the animal for its exclusive use and is actively defended. This area is termed the animal's territory.

The role of spacing behaviour in the dynamics of animal populations has been the subject of intensive debate. Watson & Moss (1970) provided an extensive review of the literature on the subject then available and concluded that behaviour is frequently a major factor limiting populations of vertebrates. They also pointed out however that behaviour could only be said to limit a population provided that the effects of extrinsic factors (such as space or food) could be eliminated and provided that social interaction could be shown to prevent breeding by animals otherwise physiologically capable of doing so.

Recent studies of Microtine rodents have led to the suggestion that female voles are territorial at certain times of the year thus safeguarding resources so as to ensure the successful rearing of their offspring. Such behaviour has been described for Microtus spp. (Boonstra, 1977b, 1978; Redfield, Taitt & Krebs, 1978; Jannett, 1980; Madison, 1980; Taitt & Krebs, 1982) and for Clethrionomys spp. (Koshkina, 1957; Koshkina et al. 1972 (- both papers cited by Wiger, 1982), Kalela, 1957; Bujalska, 1970, 1973; Viitala, 1977; Perrin, 1979b).

Bujalska (1970, 1973) found that the number of adult females in an island population of C.glareolus varied little despite wide fluctuations in the number of immature females and in the population density as a whole. The dispersion of these adult females over the island was uniform. Viitala (1977) showed that overt aggression played an insignificant part in the territorial behaviour of C.rufocanus the territories being maintained by the avoidance of conspecifics rather than by actual fighting. Similarly, females of C.rutilus and C.gapperi have been shown to establish discrete ranges (Perrin, 1979b; Wiger, 1982)

Male Microtus spp. appear to be aggressive but non-territorial, competing for access to oestrous females (Boonstra, 1977b; Madison, 1980). Groups of male Clethrionomys rutilus utilised common home ranges, each individual holding a territory within the common area. Increases in the number of adult males led to increases in the size of the common range and to decreases in the size of the territories (Koshkina et al., 1972; Koshkina & Korotkov, 1975 - cited by Wiger, 1982). Group formation and territorial behaviour is similar in C.rufocanus (Viitala, 1977)

Interactions between mature males of the genus Clethrionomys appear to be aggressive, at least during the breeding season (Viitala, 1977) with the heavier males being dominant (Grant, 1970). Adult females tended to dominate adult males (Bujalska & Gliwicz, 1972; Mihok, 1976; Viitala, 1977) and older females tended to be dominant over lighter ones (Mihok, 1976).

The numbers of adult female Skomer voles present in the

middle of the breeding season varied from year to year in proportion to the total number of animals present (presumably a reflection of the breeding activity of the females) and the dispersion of these animals was generally random . Variable numbers of animals matured in the year of their birth and apparently bred successfully (although this number was always small by comparison with the number of adult animals present which had been born the previous year) and the results of the removal experiment indicate that, at least towards the end of their breeding season, the adult females present are not preventing the other females from breeding. In addition the dispersion of the animals did not differ significantly from random. The female Skomer voles caught on the study area did not therefore appear to have adopted the territorial habit shown by other Microtine species but nothing is known of their behaviour in less favourable habitats on the island.

The adult males are certainly aggressive towards each other during the breeding season and almost always have many fresh wounds at that time. Adult male bank voles on the mainland commonly have fresh wounds on the rump and tail and on the ears and face. The extent of wounding on adult male Skomer voles is much heavier than on mainland males especially on the head. Their ears are sometimes reduced to stumps, their lips damaged and, not infrequently, the animals are unilaterally blinded by bites to the eyes. Very few wounds were found on adult females or on immature animals of either sex and no fresh wounds on adult males outside the breeding season.

The number of adult males present on area 'C' in the middle of the breeding season varied little between 1976 and

1983 despite wide variations in the number of animals in the population and in the number of immature males present. The numbers present at the beginning of the breeding seasons of 1981 and 1982 were almost the same (the numbers caught at the beginning of the breeding season in 1983 were lower, but some trapping problems were encountered at that time; see Chapter 2.). This does suggest that the males were territorial although their dispersion did not differ significantly from random. It is possible that the trap spacing used to sample the population was not adequate to detect the true spacing of the animals and that habitat effects were being detected.

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The range lengths detected during this project were markedly affected by the sampling method employed. Those obtained during the lifetimes of the animals between 1976 and 1981 were significantly larger than those obtained within the trapping periods (August only) and those obtained on the larger sampling areas were larger than those obtained on area 'C' alone. Regardless of the sampling method employed, the ranges of males were always larger than those of females sampled in the same way.

If the range lengths found are adjusted by adding half the distance between trapping points to each end of the line (the extended range length; Stickel, 1954) then the mean home range lengths obtained vary from 24.01m (within trapping periods, 1976 - 1981) to 53.5m ("long movements") for males and from 19.02m to 29.8m for females with average lengths of 38.3m for males (43.1m if the within-period ranges are excluded) and 28.0m (30.9m) for females. These results compare well with those of Jewell (1966b) who gave range diameters of 30 - 40 yds

(27.7 - 36.9m) for Skomer voles. The reported ranges of movements of bank voles in woodland vary from about 20m (Kikkawa, 1964) to about 75m (Brown, 1956) but are usually around 53m for males and 43m for females (Brown, 1966). The average ranges of movement of Skomer voles therefore fall within the normal range for bank voles but are slightly smaller than the average, possibly reflecting the greater density of the population.

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The individuals in a population of C.glareolus may be assigned to various cohorts depending on when they were born. These may be defined as follows:

K_0 - the spring breeding population of overwintered individuals. These animals are often larger than animals born later in the year particularly in peak populations (Krebs & Myers, 1974). This cohort often consists largely of animals born near the end of the previous breeding season, especially in sub-arctic populations (Newson, 1963; Crawley, 1970; Wiger, 1979a). This is not invariable however and earlier born young may be included (Petrusewicz, Bujalska, Andrezejewski & Gliwicz, 1971; Gliwicz, 1975).

K_1 - animals of this cohort are born early in the breeding season, usually before mid-July, and the majority die by autumn of the same year. This cohort often forms the bulk of the breeders in any one year.

K_2 - animals born in the middle of the breeding season (usually mid-July to mid-August). Overwinter survival of members of this cohort is usually better than that of members of K_1.

K_3 - animals born from the middle to the end of the breeding season. This cohort often forms the bulk of the $K_\emptyset$ cohort in the following year.

The K_1 cohort of the Skomer vole is usually small and may be very small indeed. The bulk of the annual production of young falls within the K_2 cohort and the K_3 is intermediate in size betwen the other two. There is no apparent difference in survival between individuals of cohorts (K_1 + K_2) and K_3 but, because the K_2 is the largest, the greater part of the $K_\emptyset$ in the next year is derived from this cohort.

Several strategies are employed by island populations of rodents to limit their reproductive output. These include a behavioural limitation on the number of breeding females, reduced litter size, delayed maturation of females and a shortened breeding season.

Bujalska (1970, 1973) reported that the number of breeding females present in an island population of bank voles in Poland varied little from year to year and indicated that this was the result of territorial behaviour by the adult females. The data obtained during the present project indicate that territorial behaviour by adult females is not important in the demography of the Skomer vole. However the sub-population studied was not confined and Gliwicz (1980) states that such behaviour is not found in unconfined populations of bank voles (although Boonstra (1977b) and Madison (1980) have suggested that it may be important in unconfined populations of Microtus spp.).

Smaller litter size is not a strategy employed by all island dwelling rodents. Tamarin (1977c) reported that the size of the litters of an island population of Microtus breweri was

smaller than those of nearby mainland populations of M.pennsylvanicus but Bujalska (1970, 1973) found no significant reduction in the size of the litters of an island population of C.glareolus and Jewell (1966a) reported that some island populations of A.sylvaticus had litter sizes greater than those found on the mainland.

The Skomer vole has smaller litters than does the bank vole on the mainland. Brambell & Rowlands (1936) reported a mean litter size of 4.18 for mainland bank voles and Zejda (1962) one of 3.95 whereas Jewell (1966) recorded a size of 3.71 (n=14) and Coutts & Rowlands (1969) of 3.77 (n=90) for the litters of the Skomer vole. The litter size of 3.79 (n=23) obtained from pregnant females which were dissected during the present project did not differ significantly from these values. The size of litters found in the traps during this project was apparently smaller (3.48) but this may have come about because some animals had not completed parturition. Little sign of intra-uterine loss was detected during this project but Coutts & Rowlands (1969) who made a more detailed examination reported pre-natal losses of one or more embryos in up to 69% of the animals that they examined and the smaller litters found in the traps during this project may in part be a reflection of pre-natal loss.

Delay in the maturation of females has been reported for a range of island populations of rodents (Jewell (1966a) - for the Skomer vole; Bujalska (1970,1973) - for C.glareolus; Gliwicz (1973) - for Proechimys semispinosus and Tamarin (1977c) - for Microtus breweri).

Fullagar et al. (1963) caught 88 adult female Skomer voles

during early September 1960. Thirty six palpable pregnancies were detected and approximately half of these (17) were in animals which were tentatively identified as being primiparous. Of the adults 50% were reported as being nulliparous. These figures suggested that a large proportion of the animals were breeding in the year of their birth.

More detailed studies, which included histological examinations,were reported by Coutts & Rowlands (1969). These authors identified some of the adult females that they examined as having matured in the year of their birth (mainly on the basis of body weight) and suggested that some at least of these females produced litters by the end of the breeding season but that the proportion was probably much smaller than that suggested by Fullagar et al. (1963).

Coutts & Rowlands (1969) noted that, at the beginning of the breeding season, female Skomer voles ovulate several times in quick succession without conception. They also noted evidence of such a rapid series of ovulations in the ovaries of early born females maturing in the year of their birth. Westlin (1983) and Westlin & Nyholm (1982) reported that a series of sterile matings were required before C.glareolus could breed successfully and Andersson & Gustafsson (1982) reported that, in bank voles, mating activates two neuroendocrine reflex mechanisms which separately induce ovulation and the development of luteal function. Bank voles are induced ovulators (Clarke, Clulow & Grieg, 1970). Westlin (1983) and J.Clarke (personal communication) are of the opinion that, to breed successfully, bank voles require two or three sterile matings which induce ovulation and provide corpora lutea and

that the products of these corpora lutea prime the reproductive tract and enable it to accept fertilised ova. In addition, Westlin & Nyholm (1982) and Westlin (1983) have shown that fertility in bank voles is related to age, the older the female, the higher the fertility.

The results of my study indicate that a few early born female Skomer voles are able to mature and breed in the course of the breeding season; that is to say are able to undergo a series of sterile matings and a sufficient number of potentially fertile matings to overcome any inherently lower fertility due to their age. Some other young females have patent vaginae at the beginning of August (although whilst this is evidence of sexual development it is not absolute evidence of involvement in mating since the vagina of bank voles perforates spontaneously (J.Clarke - personal communication)) but fail to become pregnant and rapidly go out of breeding condition (by the end of that month). The cutoff point between maturation or failure to mature in the year of birth therefore appears to operate early in August (a suggestion supported by the results of the removal experiment). What then is the possible nature of this cut-off mechanism? Is it the same mechanism that limits the duration of the breeding season as a whole?

The breeding of island living rodents is typically confined to a set breeding season whereas rodent populations on the mainland often breed outside the normal breeding season (Jewell,1966a; Lidicker,1975). Populations of A.sylvaticus found on islands around the British isles have been shown to have shorter breeding seasons than populations on the mainland

(Jewell,1966a; Berry,1968; Bishop & Delany,1963). Lidicker (1973) noted that the individuals in a newly founded island population of Microtus californicus gradually delayed their reproduction for up to three months by comparison to populations on the nearby mainland. Tamarin (1977c) found that an island population of M.breweri never bred during the winter unlike a population of M.pennsylvanicus on the nearby mainland and Redfield (1976) found evidence to suggest that seasonal breeding occurred in island populations of Peromyscus maniculatus.

The breeding season of the Skomer vole is generally shorter than that of bank vole on the mainland although that of the latter can be variable in duration (Flowerdew, 1977). Usually the breeding season of bank voles begins in April and ends by September/October but it can continue into or throughout the winter (Baker,1930; Brambell & Rowlands,1963; Newson,1963; Jewell,1966a). Jewell (1966a) reported that the first pregnancies occurred in Skomer voles during May and that the first juveniles joined the trappable part of the population late in June. Coutts & Rowlands (1969) detected a few pregnant animals early in April but the majority of the pregnancies they found occurred from May (55% of females pregnant) onwards. They reported that the proportion of females which were pregnant rose to above 90% in June and remained at that level throughout July and August before falling to 70% in September and below 20% early in October. The majority of pregnancies they detected early (April) and late (September and October) were pre-implantation stages and they suggested that breeding came to an end due to the failure of blastocysts to implant. They reported that young were produced between the beginning of May and the

end of August. They gave the mean gestation period as 22 days (19 days + 3 days delay in implantation in concurrently lactating females).

The data on lactation obtained during the present project show that the majority of young are produced between the end of June and the end of August. The data from October indicate that the timing of the end of the breeding season varies little from year to year but the data from May and June suggest that events at the beginning of the breeding season may be more variable. What is not clear from these data is whether the breeding season starts at different times in each year or if it starts at the same time in each year but the actual production of young is delayed in some years. What is apparent is that there is a variable period in May and June when few young are produced.

Population density can affect the length of the breeding season of small rodents. Corbet (1964) noted reduced breeding in June and July in a population of bank voles at a time when the population density was high and Bergstedt (1965) found a slight extension of the breeding season of bank voles in Sweden in years when the population density was low. Both Chitty (1952) and Krebs & Myers (1974) noted that the breeding seasons of rodents may be shortened at peak population densities and lengthened at times of population expansion.

The population on the study area in 1972 (June: 240/ha) was much greater than in 1975 (June: 150/ha), 1981 (May: 145/ha), 1982 (May: 115/ha) or 1983 (May: 74/ha). Lactating individuals were detected at the end of May (1981) but not at the same time in 1982 or 1983. In 1972 no lactating individuals

had been caught up to the middle of June and the majority of the first lactations did not occur until mid July. In 1975 by contrast more than 25% of the females caught by mid-June were lactating. No lactating females were therefore recorded at the end of May or the beginning of June in the years with the highest and lowest recorded population densities for that time of year. Delay in the beginning of the production of young Skomer voles does not seem therefore to be solely a response to high population density and consideration must be given to the effects of environmental factors.

The effects of photoperiod, nutrition, temperature and rainfall on breeding have all been examined for several species of rodents. Whilst each factor and combinations of each factor can be tested experimentally it is less easy to separate their effects in the field and it is generally considered that they interact, some having a greater influence than others (Sadleir,1969; Clarke,1981). Of the external cues photoperiod is probably the most important (Clarke,1981; Clarke, Baker, Craven, Feito, Mansard, Petts, Stewart & Wong, 1981). Decreasing photoperiod has been shown to reduce reproductive activity in Microtus spp. (Baker & Ranson, 1936a; Clarke & Kennedy, 1967) and increasing photoperiod has been shown to have the opposite effect (Clarke et al. 1981; Lecyk, 1962).

Relatively little is known about the effect of photoperiod on the breeding of C.glareolus but Clarke & Grieg (1971) reported that increasing daylength affected breeding in this species and Clarke et al. (1981) found that the testes and seminal vesicles of male bank voles kept under summer light conditions were significantly heavier than those of animals

kept under winter light regimes.

Nutrition can modify the effects of photoperiod. The availibility of additional food, whether natural or artificial, can extend the length of the breeding season of rodents (Zejda, 1962; Smyth, 1966; Watts, 1970; Andrzejewski, 1975; Hansen & Batzli, 1979; Taitt, 1981) and can enhance survival and growth rates in the population and increase its density (Cole & Batzli, 1978) although Krebs & Delong (1965) were unable to alter reproductive activity in M.californicus by supplementary feeding. Supplying additional food (laboratory diet) at the rate of 20kg/ha/week to a population of rodents on an island in a lake near Reading resulted in an extension of the breeding season in 1982 by about one month, and the breeding season in 1983 started about six weeks earlier than that on a control island without additional food (T.D.Healing, unpublished observations).

The effects of food on reproduction are not necessarily due to its function as a source of vitamins, minerals, protein and metabolisable energy. A considerable body of evidence now exists to suggest that chemicals in their food may be important in the initiation or inhibition of reproduction in mammals (Bennetts, Underwood & Shier, 1946; Allen & Kitts, 1961; Adler, 1962; Allison & Kitts, 1964; Pinter & Negus, 1965; Negus & Berger, 1977). Substances which can initiate reproduction in rodents have been isolated from newly sprouted plants (Sanders, Gardner, Berger & Negus, 1981; Berger, Negus, Sanders & Gardner, 1981) and substances which can inhibit reproduction both from newly sprouted plants and, more commonly and in greater concentrations, from senescing plants (Berger, Sanders,

Gardner & Negus, 1977. - these authors pointed out that the closer were the plants to senescence, the more abundant were these inhibitory substances and suggested that these compounds could act as cues signalling a reduction in food quality thus leading to the end of the breeding season).

Baker & Ranson (1932b) found that reducing the ambient temperature for M.agrestis kept on a summer food and light regime reduced the output of young and found that the fecundity of females was more affected than that of males. Clarke et al. (1981) found that constant ambient temperature had no effect on the gonadal activity of M.agrestis or C.glareolus but that ambient temperature had a marked effect on the gonadal development of male (but not of female) A.sylvaticus. Baker (1930) found no correlation between winter temperature and winter breeding in A.sylvaticus and C.glareolus and Hamilton (1941) similarly failed to find any such correlation for M.pennsylvanicus. Zejda (1962) found a reduction of winter breeding of C.glareolus in Czechoslovakia during periods of extreme cold. Ashby, (1967) reported that C.glareolus and A.sylvaticus bred later in years when the summer temperature stayed high well into the late summer and autumn. In years with cooler summers breeding ended earlier. He suggested that this effect was mediated through the food supply which was better when the weather was warmer but he also noted that rainfall might be involved since warmer summers were usually also drier.

Several studies of the effect of rainfall on the reproduction of rodents have been made but the majority of these have involved desert living or tropical rodents (Chew & Butterworth, 1964; Sadleir, 1969; Reynolds & Turkowski, 1972).

The authors of the majority of these studies concluded that the effects of rainfall were indirect and generally affected the food of the animals.

Of the various external cues operating on the reproduction of herbivores photoperiod and nutrition appear to act directly and temperature and rainfall appear to act indirectly, usually exerting their effects by altering food quantity or quality. Some indication of the effects of external cues on the breeding of Skomer voles can be deduced from laboratory studies. Laboratory colonies can be induced to breed throughout the year when maintained under conditions of more than 15h daylight, a temperature of more than 20°C and food and water ad libitum (T.D.Healing - unpublished observations) so presumably some or all of these factors play a part in the field; of these several factors only photoperiod is seasonally constant. The timing of the end of the breeding season of the Skomer vole seems to vary little from year to year and so may be under the control of photoperiod but events at the beginning of the season seem to be more variable and it is possible that the effects of photoperiod may be modified by a nutritional cue. Further work is needed to study this problem in more detail.

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Both the quantity and quality of food have been associated with fluctuations in the size of populations of vertebrates. Lack (1954) examined the possible role in vertebrate population regulation of a wide range of density dependent and independent factors and concluded firstly that vertebrate population regulation was density dependent and, secondly, that food was the most important factor limiting the size of such

populations. Watson & Moss (1970), whilst arguing the case for a behavioural theory of population regulation, conceded that such an explanation was only tenable provided that, among other factors, food could be proved not to be a limiting resource. Alterations in food availability can affect populations either by altering reproductive success (see above) or by altering survival. Information on the role of changes in food supply in altering the survival of individuals has been derived from experiments in which supplementary food was given to populations but the results of these experiments were equivocal. Bendell (1959) and Fordham (1971) both noted an increase in survival of juvenile Peromyscus maniculatus in populations with additional food. Flowerdew (1972) found an enhanced overwinter survival of A.sylvaticus when he provided extra food as did Cole & Batzli (1978) with a population of Microtus ochrogaster. By contrast Krebs & Delong (1965) were unable to alter survival in a population of Microtus californicus by increasing the food supply and Flowerdew (1973) and Adrzejewski (1975) reported similar results with populations of Clethrionomys glareolus.

Increases in the size of populations of rodents following the supply of additional food have been reported by several authors (eg. Bendell (1959 - for Peromyscus leucopus noveboracensis); Smith (1971 - for P.polionotus); Fordham (1971 - for P.maniculatus); Andrzejewski (1975 - for Clethrionomys glareolus); Taitt (1980 - for P.maniculatus) and Taitt & Krebs (1981 - for M.townsendii). Krebs & Delong (1965) however did not obtain an increase in the size of a population of Microtus californicus when they supplied additional food and Flowerdew

(1971, 1976) was unable to affect the dynamics of a population of C.glareolus by winter feeding. Several authors (eg. Flowerdew, 1976; Taitt, 1981) noted increased immigration into areas in which additional food was supplied. Slobodkin et al. (1967) suggested that animals whose diet consists mainly of the leaves stems and roots of plants (which they called "vegetation") are not food limited whereas those which mainly consume seeds, fruits and nuts ("plant products") are, and Smith (1971) suggested that the results obtained by Krebs & Delong (1965) as compared to his own were the result of their having worked with a "vegetation" consumer rather than a "plant product" consumer as he did.

Many workers have studied the diet of the bank vole in various habitats in Britain and Europe. The findings of the most detailed studies are summarised in Table 30. The authors quoted in this table used different methods to analyse the results of their studies and so no attempt has been made to present their data in quantitative form. Instead the relative importance of the various items in the diet has been indicated. Where the author has indicated that an item has seasonal importance this has been shown in the table.

The results of these studies indicate that the bank vole is largely granivorous and herbivorous preferring seeds, the leaves of herbs and woody plants, fungi, fruits and berries. This granivorous habit was confirmed by Drozdz (1967) in a series of cafeteria tests in the laboratory. The voles were also shown to eat animal (invertebrate) material in most of the studies. Dead leaves were apparently important to the voles in the winter but at no time of the year did they eat much grass,

Table 30.

Summary of the major studies of the diet of the bank vole..

A = Major dietary item
B = Common dietary item
C = Occasional dietary item
sp = Spring; s = Summer; a = Autumn
w = Winter

Source	Country	Habitat type	Seeds	Herbs	Fruit/berries	Tree leaves	Dead leaves	Grass	Fungi	Animal	Woody stems	Flowers	Ferns	Roots	Moss	Bark
Miller 1954	UK	Mixed broad-leaved woodland	A	C	C	B			C	B				C		
Drozdz 1967	Poland	Beech forest	B			B			C			C		C		
Watts 1968	UK	Mixed broad-leaved woodland	B	C		A	C		B	C			C			
Hansson 1971 (a)	Sweden	Many different types	B (a w)	B	C (a)			B	B (a)	B (s)	B		C	C	B	
Zemanek 1972	Poland	Oak & Hornbeam forest	B (sp a w)	B	C (a)	C		C	C	C						C
Gebczynska 1976	Poland	Oak & Hornbeam forest	B (w)	B		B				B (s)						
Larsson & Hansson 1977	Sweden	Re-afforested area	B	B				C	B							C
Flowerdew & Gardner 1978	UK	Ash woodland	A (w)	B (sp s)	B (a)	B (sp s)	C			C	C					
Hansson 1979	Sweden	Mixed forest	B	B	B			C	B							C

bark, roots, flowers, lichens or moss.

Bank voles normally live in scrub or woodland. Many of the plant species normally eaten by them are not available on Skomer and the island animals have adapted their diet accordingly. However this does not wholly reflect the availability of different plant species. It was found that bracken and bluebell were among the most common items on the ground and were also the most common items in the diet but some other very common plant species were largely ignored (Table 19., Chapter 4.). Some of the preferred food items of the mainland bank vole are not available to the Skomer voles (eg. tree leaves, fruits and nuts). Skomer voles ate little animal material or fungi (the larger fungi being present in profusion only during the autumn, mainly in the open areas). Grasses were more important to Skomer voles than to bank voles on the mainland.

The diet of the Skomer voles became more catholic during the spring. It is possible that, at that time, plant species which are unpalatable later in the year may be palatable when they are newly sprouted and also that seeds distributed during the previous year succeed in sprouting in the spring in those areas where the plants in question would not normally be found. In this way a wider range of species than normal would be made available to the animals at that time of year.

The ability of the voles to eat bracken without apparent ill effect is of considerable interest. That bank voles will eat this plant has been reported before (Watts,1968) but the amount eaten was small (ca. 1% of the diet).Hansson (1971a) reported the eating of small amounts of 'ferns' by this

species.

Bracken (Pteridium aquilinum) is a plant which is both toxic and carcinogenic to mammals. Bracken poisoning in horses and pigs causes thiamine deficiency due to large quantities of thiaminase in the plant. In ruminants bracken causes a depression of bone marrow activity with pancytopenia and it can cause retinal atrophy in sheep (Blood, Henderson & Radostits, 1979).

Bracken has been implicated in the aetiology of Bovine Enzootic Haematuria, a world-wide disease characterised by chronic haemorrhage from neoplasms in the mucosa of the urinary bladder (Pamukcu, Goksoy & Price, 1967; Pamukcu, Price & Bryan, 1976) and has been linked with tumours of the bladder in sheep (Harbutt & Leaver, 1969). Alimentary carcinomas of cattle, which are rare in lowland areas of Britain, are much more common in upland areas and a strong correlation between the eating of bracken and the development of such carcinomas has been established (Jarrett, 1980). The strong possibility exists that there is an interaction between carcinogenic agents in the bracken and a normally benign papilloma virus causing the virus to produce malignant changes (Jarrett, Murphy, O'Neil & Laird, 1978; Jarrett, 1980; Jarrett , McNeill, Laird, O'Neil, Murphy, Campo & Moar, 1980).

In the laboratory, mice fed bracken develop a high incidence of lymphatic leukaemia, urinary bladder and intestinal cancers, the majority of the animals developing tumours six to nine months after the beginning of the experiments (Pamukcu, Erturk & Bryan, 1977). Rats fed bracken in the laboratory develop intestinal and urinary bladder

tumours (Pamukcu & Price, 1969; Sumi, Hirono, Hosaka, Ueno & Miyakawa, 1981) and bracken has also been shown to cause cancers in guinea pigs (Jarrett, McNeill, Grimshaw, Silman & McIntyre, 1978).

Phytochemical analyses (undertaken following the methods described by Harborne, 1973) have shown that, in terms of the content of the main carcinogenic agent (Quercetin), bracken from Skomer does not differ significantly from bracken from mainland sites (T.D.Healing - unpublished observations). No obvious signs of neoplasia were detected during the dissection of the voles used for analysis of body fat content (although no special search for such signs was being undertaken at that time) and the Skomer vole is an unusually long lived bank vole (Chapter 2.). It is possible that bank voles in general and the Skomer vole in particular have evolved a method of detoxifying the harmful substances in bracken but further work is needed.

More detailed work on the selection of various parts of their food plants and upon the ages of the plants preferred by the voles is needed before the role of food in the population dynamics of the voles can properly be understood. The possible role of chemical cues in the food and their effect on breeding has already been discussed and this topic warrents further investigation. Taitt (1981) has suggested that, in north-temperate regions, "granivorous rodents have low winter weights and cease breeding as a proximate response to food availability". (It is of interest to note that in the feeding experiment mentioned earlier which was undertaken in 1982 & 1983 on islands in lakes near Reading the animals on the experimental island in March 1983 had mean weights

approximately 4g greater than those on the control - T.D.Healing, unpublished observations). It would therefore be of great interest to undertake a supplementary feeding experiment on Skomer to see if the duration of the breeding season or the survival or density of the voles could be altered. Such experiments should be undertaken both in areas which are favoured and in areas less favoured by the voles. If the hypothesis advanced by Slobodkin et al. (1967) is correct then one might expect that the Skomer vole, which is largely a "vegetation" consumer, might not have its population regulated by food availability.

One tactic which is used by island populations to maximise the space available to them is the use of marginal habitats. These may be areas of vegetation types which would, on the mainland be preferentially occupied by other species but which, in the absence of competition, become available to the population. Southern (1979) and Williamson (1981) have suggested that on those islands around the British coast on which C.glareolus is found and from which Microtus agrestis is absent, the former species has expanded its range so as to fill the niche of the latter. Certainly under normal circumstances C.glareolus is at a selective disadvantage to M.agrestis in grassland and M.agrestis to C.glareolus in woodland (Grant, 1972). Although the results reported by Fullagar et al. (1963), Healing et al. (1983) and the results of this study go some way to support the concept of a niche shift by the Skomer vole, the voles are apparently reluctant to use the grassy areas extensively. Healing et al. (1983) reported that whilst about 34% of the surface area of the island was covered by grassland

habitat only 9% of the voles caught were found in that habitat type and indeed that the voles had a strong and statistically significant negative correlation with that habitat type. (This was apparently not due to an active avoidance of A.sylvaticus since the mice were not strongly associated with this habitat type). Nevertheless the voles do occupy areas where there is an extensive cover of grass provided that there is an adequate cover of bracken as well (Healing et al. 1983; present study). The particular need of the voles seems to be for a greater degree of physical cover than the grasses alone can provide. Healing et al. (1983) reported a strong positive association of high densities of voles not only with dense bracken but also with areas where dense cover was provided by brambles, umbelliferae and thistles.

The diet of the Skomer voles has shown a shift towards that of M.agrestis and they eat more grass than do bank voles on the mainland (Watts, 1968). Skomer voles have a high incidence of the "complex" molar condition (an extra ridge on the third upper molar) as do bank voles on other small islands. Southern (1979) has suggested that the persistence and high incidence of such a condition in island populations is a response to the greater than normal proportion of tough grasses in the diet. The degree to which the Skomer vole can shift to occupy the niche normally occupied by M.agrestis may in part be limited by the fact that their teeth develop roots (unlike those of M.agrestis) and a diet consisting wholly of grass would rapidly wear out their teeth.

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Annual fat cycles have been described for several species

of rodents. Two main types of cycles are found, namely cycles with a winter peak and a summer low, and cycles with a low during the breeding season but no marked peak at other times of the year. The former type is found in rodents from temperate regions and the latter tend to occur in rodents living in tropical and sub-tropical regions.

The cause of seasonal fluctuations in the body fat content of small rodents has been suggested by various authors as being environmental stress (Sealander,1951); food supply (Connell,1959 - cited by Golley,1962; Sawicka-Kapusta,1968); physiological status and age of the animals (Jameson & Mead, 1964); and changing population density (Hsia-wu-ping & Sun-chung-lu,1963).

The occurrence of a winter peak of fat content in rodents from temperate regions has generally been ascribed primarily to the physiological demands of winter when ambient temperatures are low and food may be scarce, and most investigators have suggested that a high fat content in winter provides both increased insulation and a ready, if short term, supply of metabolic energy (eg. Sealander, 1951 - for Peromyscus leucopus; Hayward, 1965 - for P.maniculatus; Sawicka-Kapusta, 1968 - for A.flavicollis; Fleherty, Krause & Stinnett, 1973 - for P.maniculatus, R.megalotis and S.hispidus; Kolodziej-Banach, 1976 - for M.agrestis; Tamarin, 1977b - for M.breweri). However, only a relatively small part of the fat reserves of most small rodents consists of brown fat (R.J.Berry, personal communication). Overwinter increases in the fat content of such animals may therefore provide a reserve of energy to cover periods when the diet is barely adequate rather than a rapidly

mobilised reserve to cover periods of food deprivation.

Not all species of rodents from temperate regions exhibit a winter peak of fat content. Neither Pucek (1973) nor Sawicka-Kapusta (1974), in independent studies, could find detailed evidence of a fat cycle in C.glareolus in Poland and Perrin (1979a) reported two peaks of fat content, one in the winter and one in the summer, in rodents of this species. Evans (1973) found an autumn peak and a spring low in the body fat content of M.agrestis from near Oxford (UK). Alibhai (1976) reported a seasonal trend in the fat content of C.glareolus at one site near Oxford (UK) with a large winter peak and a minor summer peak and declines during the spring and autumn but a nearby population showed no such seasonality. In the latter population the fat content of the animals was high in the winter and spring and low in the summer and autumn. He was unable to find any correlation between body fat content and the availability of the two major components of the diet of the animals (green plant material and seed endosperm).

The occurrence of a summer (or breeding season) low in body fat content in some rodent species has been ascribed to the pressures of breeding since breeding activity greatly increases the energy requirements of rodents. Kaczmarski (1966 - for C.glareolus) and Migula (1969 - for M.arvalis) both reported a greatly increased intake of food during lactation and Trojan & Wojciechowska (1967) found that the metabolic rate of M.arvalis rises sharply after parturition and remains at a high rate throughout lactation. Indeed Migula (1969) showed that the energy demands of a lactating M.arvalis are three times greater than those of a non-breeder. It might be expected

that these energy demands would result in a lowered body fat content as reserves are drawn on to meet the animals needs. This certainly seems to occur in rodents from tropical and sub-tropical regions. Field (1975) found that body fat levels in Lemniscomys striatus and Praomys natalensis in Uganda were negatively correlated with reproductive activity, Caldwell & Connel (1968) reported lowered fat reserves in Peromyscus polionotus in S.Carolina during the breeding season, Fehrenbacher & Fleharty (1976) detected marked decreases in lipid levels in the pocket gophers Geomys bursarius and Pappogeomys castanops during the peak reproductive period and Judd, Herrera & Wagner (1978) reported decreased lipid levels during the breeding season of Peromyscus leucopus in Texas.

Lipid levels in rodents from temperate regions are not necessarily correlated with breeding however. Fleharty et al. (1973) found no correlation between lipid depletion and breeding in P.maniculatus, R.megalotis and S.hispidus in Kansas.

Environmental factors can affect the body fat content of rodents both directly, as the animals react to changes in weather conditions, and indirectly, by altering the quality or availability of food. Hayward (1965) measured the body fat content of six geographic races of Peromyscus and showed that the majority of the races had a greater fat content in the winter than in the summer. An exception was P.maniculatus sonorensis from high altitude desert in Nevada. This author pointed out that although the winter is extremely cold in that area, desert animals tend to store fat during hot arid conditions (Bodenheimer, 1952; Wright, 1954; both cited by

Hayward, 1965). Field (1975) found that seasonal changes in the body fat content of Lemniscomys striatus and Praomys natalensis in Uganda were positively correlated with rainfall.

The range of individual body fat content of Skomer voles was found to be large irrespective of the season, a finding common to many studies of the body fat content of small rodents. Sawicka-Kapusta (1968) found that the fat content of individual A.flavicollis could vary from 5% to 30% of dry weight and Pucek (1973) reported variations from 1.5% to 19% of dry weight in the body fat content of C.glareolus in Poland.

The peak fat content found in Skomer voles during this study occurred in the winter (January) although sampling was only undertaken in one year (1973) (the results for the other seasons contained data from more than one year). This finding parallels those of Sealander (1951 - for Peromyscus leucopus noveboracensis), Hayward (1965 - for P.maniculatus) Sawicka-Kapusta (1968 - for Apodemus flavicollis) and Tamarin (1977b - for Microtus breweri) but conflicts with the results obtained for C.glareolus by Pucek (1973) and Sawicka-Kapusta (1974) both of whom found that the minimum fat content in this species occurred in the winter. The occurrence of a winter peak suggests that they may be reacting to the harsher conditions experienced during that season. The mean fat content of all animals varied little over the rest of the year but the range of variation was greatest during the summer months.

Lactating female Skomer voles were not significantly less fat than breeding animals which were not concurrently lactating and pregnant, non-lactating animals did not have a significantly different fat content from non-pregnant animals

or from adult males. Lactation does not therefore appear to make a heavier demand on the fat reserves of the females than does the production of young *in utero.*

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Parasites may be divided into macro-parasites (worms and arthropods) and microparasites (viruses, chlamydia, mycoplasma, rickettsia, bacteria and protozoa). The former tend to be characterised by low levels of infection and a poor immune response by the host leading to repeated infections, the latter by a good immune response by the host and a long duration of immunity following infection. The former tend therefore to exert a chronic and debilitating effect and the latter an acute effect.

The way in which parasites affect populations ultimately depends on the way that they affect individual hosts. Their effects can fall anywhere along a continuum from a benign (symptomless) infection, via clinical illness which may lead to reduced growth or reproductive output, to the death of the individual. Parasites may affect or be affected by many of the attributes of the host including its social status (Jenkins, Watson & Miller, 1963), its genetic background (Wakelin, 1978), its plane of nutrition (Anderson, 1979), the way in which it is stressed (Anderson & May, 1981) and its previous disease history (Macfarlane Burnet & White, 1972). In turn the outcome of a host parasite interaction can be affected by factors stemming from the parasite including its genetic makeup (Basch, 1975), its ability to resist or avoid the defensive responses of the host (Bloom, 1979), the number of parasites present (Anderson & May, 1978) and the presence of other parasitic

species which may interact directly (Holmes, 1961) or indirectly (Cypess, Lubiniecki & Hammon, 1973; Cox, 1975) with the parasite. Ultimately the most important factor is the degree to which host and parasite have adapted to each other over time by the evolution of a greater resistance to the parasite by the host and a reduction of pathogenicity of the parasite (Holmes, 1982).

At the population level the impact of parasites on host populations may be even more complicated. Parasitised animals may have a reduced ability to compete for food or mates (Jenkins et al. 1963; Anderson, 1979) or may be more at risk from predators (Holmes & Bethel, 1972; Anderson, 1979). Population biologists have tended to take an apocalyptic view of disease and to think of it only in epidemic terms (and the literature contains many examples of the dramatic effect of such phenomena (eg; Vaughan & Vaughan, 1969; Vizoso, 1969)) but such events are probably relatively rare and the interactions between hosts and parasites tend to be relatively stable. Anderson (1979) has pointed out that parasites can be envisaged as agents which depress populations from the equilibrium levels they might otherwise have achieved and that they are likely to play a role analagous to that of predators or resource limitation in constraining the growth of animal populations.

A large body of published work now exists detailing mathematical models which attempt to define the possible role of disease in animal population dynamics (eg. Anderson, 1978, 1979; Anderson & May, 1978, 1979). Unfortunately the state of theoretical knowledge is now far in advance of our knowledge of what occurs in natural populations. The majority of studies of

disease in wild populations have provided information on the types of parasites present in the animals and often some idea of their prevalence but few have provided information on the role of disease in the dynamics of field populations of animals and particularly of vertebrates (cf. Elton, Ford, Baker & Gardner, 1931; Chitty, 1952; Baker, Chitty & Phipps, 1963; Young, 1970).

Wiger (1979b) considered that blood parasites did not play a role as mortality factors in small rodent populations but Mansfield (1977) pointed out that normally nonpathogenic trypanosomes can cause a fatal disease if the host's immune mechanisms are impaired and evidence exists to show that some members of haemoparasitic genera found in small British rodents are capable of causing an immunodepression under laboratory conditions (Cox, 1975). Several authors (eg. Krampitz & Baumler,1978; Wiger, 1979b) reported seasonal fluctuations in the prevalence of blood parasite infections in small wild rodents but Healing (1981 - Appendix 7.) was unable to find any such evidence.

Very little is known about the role naturally occurring virus infections may play in the population dynamics of rodents. Elton, Davis & Findlay, (1935) studied virus infections in Microtus agrestis but their results were inconclusive. Kaplan et al. (1980 - Appendix 6.) found evidence of a wide range of different viruses in small British field rodents and were able to associate some population declines with epizootic outbreaks of virus infections (although without being able to assign a cause and effect relationship). One of these populations was that on the study area on Skomer used for

this project.

The survival of female Skomer voles tended to be better than that of males. The effect of the sex of an individual on its survival has been the subject of some controversy. Some evidence exists that male mammals may have a greater susceptibility to infectious disease than females. The survival of male and female gnotobiotic laboratory mice is the same whereas normal male mice survive less well than females (Mimms, 1977). Nicol, Bilbey, Charles, Cordingley & Vernon-Roberts, (1964) and Nicol, Vernon-Roberts & Quantock (1965) showed that oestrogen is a most effective stimulant of the reticulo-endothelial system and suggested that the increased secretion of oestrogens in the female associated with pregnancy could confer a particularly strong protection at a time when the female might otherwise be unduly susceptible to infection. Gomwalk (1981) however reported that whilst the susceptibility of laboratory mice to infection with Mount Elgon bat virus was not reduced by the artificial administration of oestrogens it was increased by the administration of androgens.

The exact role of disease in the dynamics of the population of the Skomer vole remains unknown but since a fairly large proportion of the annual losses of animals cannot readily be accounted for, further research is justified.

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Some authors consider that predation plays an essential part in the cyclical behaviour of some populations of rodents. Pearson (1964, 1966, 1971); Ryskowski, Goszczynski & Truskowski (1973) and Goszcynski (1977) concluded that predation both prolonged and deepened the low phase in cyclical populations.

Pitelka (1973 - cited by Erlinge, Goransson, Hansson, Hogstedt, Liberg, von Schantz & Sylven, 1983) found that heavy avian predation began the cyclic decline of a population of lemmings and Krebs (1979) suggested that low predation was the probable explanation for the non-cyclicity in Microtus townsendii.

By contrast Ryskowski, Wagner, Goszczynski & Truskowski (1971) found heavy predation on non-cyclic rodent populations, Boonstra (1977a) concluded that predation was not necessary to initiate or maintain a decline in a population of M.townsendii and Erlinge et al. (1983) concluded that predation was the primary cause of the lack of cyclicity in the population of M.agrestis that they studied. They noted that the important pre-requisites for predation to play such a role included a good supply of alternative prey species so as to maintain a high and constant predator population density, the availability of rodents for most of the year, and a heterogeneous environment influencing dispersal and the availability of rodents.

Taitt, Gipps, Krebs & Dundjerski (1981) found indications that the relative predation impact in spring determines whether the population is cyclical or not.

There is a general tendency for the numbers of predatory birds to change as a response to the availability of prey (Phelan & Robertson, 1978). The number of predatory birds breeding on Skomer has varied little over the last ten years suggesting that the availability of prey and also that the predation pressure are relatively constant. Small numbers of predatory birds do visit the island during the day throughout the summer but the only dramatic change in the numbers of birds

of prey seen on Skomer is the autumnal influx of buzzards which appears to occur in response to the large amount of carrion available at that time. Since the bracken is, at that time, being destroyed by the wind, and since the population of voles tends to be high at that time, the population is possibly more at risk from predators than earlier in the year. The data obtained in 1973 and 1981 showed a decline in the numbers of voles between early September and mid-October. This may have been the result of increased predation.

Short-eared owls are almost certainly the most important predators of Skomer voles throughout the year with the other common predatory birds possibly exerting a seasonal effect.The number of pairs of short-eared owls found on Skomer varies little from year to year and has not risen above five during the last ten years. These birds are territorial and, although they can make heavy inroads into a population of rodents (Witherby, Jourdain, Ticehurst & Tucker, 1938), their effects on the population of the Skomer vole are presumably limited by their own behaviour. Understanding of the precise effect that short-eared owls have on the population of voles is further limited by a lack of knowledge of the breeding success of the birds on the island. The size of the clutches of the short-eared owl varies depending on the availability of food (Witherby et al. 1938). Attempts are made not to disturb the nests of the birds that breed on Skomer and since the young owls remain in the nest only for a few days after hatching, thereafter dispersing into the surrounding vegetation (Mikkola, 1983), regular visits to the nests would be necessary if hatching and fledging success was to be determined. Since the

size of the clutches that the owls produce each year is not known the pressure exerted by the parents in their search for food cannot be calculated.

These owls probably exert the maximum pressure on their prey during May and early June when they are feeding their young (the majority of which hatch in May). They may therefore exert an increased pressure on the voles at a time of year when the numbers of voles are at their lowest and before the vegetation has grown sufficiently to give adequate cover. If this is so it is to the advantage of the voles to delay the production of young until the bracken is tall enough to hide them from predators. It is interesting to speculate that if young voles were produced earlier the owls might be able to take smaller territories, more might then be able to nest, and the predation pressure on the population of voles would then increase. Buxton & Lockley (1950) reported that three young short-eared owls were killed by gulls as soon as they left the nest and the gulls may therefore limit the area that the owls can occupy successfully and hence set a limit on the population resident on the island.

Both Fullagar (1964) and Healing & Quarmby (unpublished observations) have attempted to assess the effect that predation may have upon the population of voles. Fullagar (1964) suggested that the three most important predatory bird species (buzzard, kestrel & short-eared owl) might take up to 100 voles daily during the autumn and that this could, over a period of six weeks, account for the loss of up to 25% of the population that had been present in early September. This was based largely on the premise that the buzzards were feeding

mainly on voles at that time. However, this species is known to feed largely upon carrion in the autumn (M.Alexander; personal communication) and so this estimate may well be too high. Healing & Quarmby (unpublished observations) suggested that the predators might take between 15 and 30 voles per day; that is to say between 5475 and 10,950 per year but they obtained no data on the diet of kestrels during their survey and this species apparently takes quite large numbers of voles. On the basis of these estimates it appears that up to 20% of the voles born each year are lost to predators.

Further estimates based on data collected from 1980 to 1983 suggest that between 25% and 35% of the animals born survive from one year to form the breeding population in the next. Clearly such estimates may be wildly innaccurate. They take no account of the fluctuations in the size of the population from year to year and also assume that events on the study area accurately reflect events over the island as a whole. Even so the fate of about 50% of the annual production of young cannot be accounted for by predation or survival.

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What conclusions can be drawn from this study as to the mechanisms by which the population of the Skomer vole is regulated? Extrinsic factors undoubtedly play a part in the timing of the initiation and ending of the breeding season and in preventing the maturation of animals in the year of their birth but such factors must work by operating on intrinsic (inherited) mechanisms. Intrinsic regulation is effected by reduced litter size, a shortened breeding season and delayed

maturation of both sexes, mechanisms common to the majority of island dwelling rodent species.

Dispersal may play some part in the dynamics of the population since potential dispersal sinks are available but small numbers of animals were found in such areas during the survey of 1981 (which was undertaken at a time of high population density on area 'C') and this suggests that, in common with many other island rodent species, the Skomer vole does not rely on dispersal as a method of population regulation. (It is conceivable that predators could be removing any animal which disperses to areas where the cover is inadequate (the majority of the potential dispersal sinks) but the major predators of the voles hold territories covering areas of good habitat for voles (where they may act as the equivalent of dispersal sinks) and there is no evidence of heavy predator activity in less suitable habitats).

Certain statements may be made concerning breeding activity on area 'C':

(1) There is no apparent behavioural limit to the numbers of adult females found on the area during the breeding season. Therefore:-

(2) The production of young in any one year depends on

(a) The rate of loss of adult females throughout the breeding season (includes death and emigration).

(b) Immigration of adult females from other areas.

(c) The duration of the breeding season.

(d) Breeding success (includes factors such as litter size, number of pregnancies, loss of animals in utero).

(e) The number of young which mature and breed in the year of their birth.

(f) The numbers of females which have survived the winter.

To consider these factors may be considered seperately and in more detail:

(2a) The rate of loss of adult females during the breeding season varies little from year to year but losses when the numbers are low are more significant in terms of the proportion of the production than when the numbers of adult females are large. What proportion of the losses are due to death and what are due to emigration is not known.

(2b) The rate of immigration of adult females onto the area is not known. Previously unknown adult females which are almost certainly overwintered individuals are caught throughout the breeding season but these may be previously trap-shy residents.

(2c) The duration of the breeding season varies little from year to year. "Fine tuning" may occur at the ends but probably has little effect on the total production since the bulk of the young are produced in July and August (ie. in the middle of the season.

(2d) Breeding success apparently varies little from year to year, at least in the first half of the breeding season. At the height of the breeding season (August) the number of young caught depends on the number of adult females present.

The proportion of the young lost in-utero is not known. The proportion of animals which had resorbed one or more embryos which was detected during the present study was small but Coutts & Rowlands (1969), in a much more detailed survey, found losses of at least one embryo in up to 60% of the animals

that they examined. Certainly the litters found in trap during the present survey were smaller than those found *in utero* (but see Chapter 2.).

(2e) Few animals mature and breed in the year of their birth and their contribution to the total production of young is small (Appendix 1.).

(2f) The bulk of the annual production of young is by animals which have survived the winter. It follows therefore that whatever affects the overwinter survival of the females plays a major role in determining the size of the population.

An additional factor which must be taken into account when the size of the population at any time in (and particularly at the end of) the breeding season is considered is the survival of young animals. Estimates of the potential production of young on area 'C' (Appendix 1.) suggest figures of 752 (1981), 511 (1982) and 446 (1983) (although such estimates must be viewed as speculative and potentially inaccurate). The actual numbers caught in October of those years were 112 (1981), 92 (1982) and 93 (1983) respectively. The proportion of animals present in October which were not caught is not known. In May 1982, 12.3% of the animals known to be alive were previously unmarked and in May 1983 the figure was 9.5% but these may have been immigrants. The potential production of young is probably rarely achieved due to losses *in utero* and pre- and post-weaning.

No field evidence of the rates of infant mortality of Skomer voles is available but Alder (1972) found that, in laboratory colonies, infant mortality was significantly greater in the litters of Skomer voles than in those of mainland bank

voles, up to 30% of the litters being lost completely and up to 50% of them losing at least one pup. Certainly young voles are extremely vulnerable during the first three weeks of life. Popov (1960 - cited by Buchalczyk, 1964) reported that, under field conditions, 11.7% of young voles die in the first 10 days of life and that 15.6% die between 15 to 18 days.

The decline in numbers between September and October that occurred in 1972 and 1981 can largely be accounted for by losses of adults at the end of the breeding season but some young were lost also.

A far greater understanding of the factors affecting the numbers of females present at the beginning of the breeding season and the survival of young during the breeding season, and of the mechanism preventing the maturation of animals in the year of their birth is needed before the mechanisms regulating the population of the Skomer vole are to be understood.

The larger size and greater longevity of the Skomer vole as compared to the mainland bank vole, the relative stability of the population, and the apparent reduction in dispersal all suggest that the Skomer vole may be more K-selected than its mainland conterpart. Skomer voles do not fulfill all the attributes of K- selection listed by Pianka (1970) however. In particular their survival characteristics (with a heavy loss of individuals early in life) and their rapid growth rates are more characteristic of r- selected individuals. In general they appear to have moved further towards the K- end of the r - K continuum than have bank voles on the mainland.

The work reported here is the most detailed long-term

study which has yet been made on a population of C.glareolus on the British offshore islands and is one of the longest term studies yet reported on any island population of rodents. The work has suggested several mechanisms which may play a part in the regulation of the population of the voles and has highlighted areas in which future research may usefully be undertaken. Comparisons of the results obtained with those of other studies of island, enclosed or unrestricted populations of bank voles have shed light on the similarities and differences between such populations and the Skomer population. The results have also been compared with those obtained in studies of island populations of several different species of rodents both of the Cricetidae and Muridae and this has highlighted the remarkable similarity between the population dynamics of these island dwelling species and those of the Skomer vole. Clearly some aspect of the island habitat is capable of modifying widely divergent rodent lifestyles and of forcing them into a single mould.

SUMMARY.

(1) A study area was established on a part of Skomer island known to support a large population of voles.

(2) Two trapping grids were laid out adjacent to each other. Initially they had trapping points 20m apart but for the substantial part of the study they were 10m apart. The two grids were used as experimental and control grids for an experiment designed to test the hypothesis that female territorial behaviour was preventing the maturation of females in the year of their birth.

(3) The grids were separated from each other by a sheet iron barrier and partially isolated from their surroundings by cutting the vegetation.

(4) Trapping was carried out for one year (1972) to establish basic population parameters.

(5) The adult females were removed from the experimental area in August 1973.

(6) Retrapping undertaken in September 1973 revealed that no young females had matured to replace the animals that were removed thus disproving the hypothesis.

(7) The barrier was removed and a part of the original control area, 0.49Ha in area, was used as a study area for the rest of the project.

(8) Thirty-five trapping programmes were undertaken between October 1971 and October 1983.

(9) Between 1976 and 1980 only one visit was made to the island each year (in the first week in August).

(10) The population of voles on the study area was found to show an annual cycle with a trough in May and a peak in

September.

(11) The population was relatively stable over the period of the study but did show a slow oscillation. Too few data are available for this to be defined as a cycle.

(12) The number of adult females present during the first week in August 1976-1983 varied in proportion to the size of the population. The number of adult males remained almost constant.

(13) The body weights of adult voles reached a peak in July and declined thereafter. Females were lighter than males throughout most of their lives, only being heavier when they were breeding.

(14) Females generally survived better than males. The survival of males and females of cohorts from different years varied. (Here cohort means all the young produced in one breeding season). In some cohorts male survival was significantly poorer than that of females at the end of the breeding season in the year of their birth, in others it was significantly poorer during the subsequent breeding season.

(15) The litters of the voles were smaller than those of mainland bank voles.

(16) The majority of the young were produced in July and August.

(17) The timing of the beginning of the breeding season varied slightly from year to year but that of the the end seemed to be remarkably consistent.

(18) A few very early born females were found to have litters in the year of their birth. A few, born slightly later, matured for a brief period of time but failed to be impregnated and rapidly went out of breeding condition. The majority of females

did not mature in the year of their birth.

(19) Very few males were thought to have matured in the year of their birth.

(20) Few retrapped voles had moved distances greater than 30m. The ranges of the animals were slightly smaller than those of bank voles on the mainland.

(21) The dispersion of both adult male and adult female voles did not differ significantly from random.

(22) The populations of voles in areas with an extensive grass cover were smaller than in areas where there was little grass but only a dense bracken cover, but the dynamics of the populations did not appear to differ betwen the two types of habitat.

(23) Animals living in marginal habitats at the end of the breeding season were found to be lighter in weight than those animals in favoured habitats and, in some areas, to be partially regressed sexually.

(24) Animals were collected by snap trapping at several sites around the main study area for studies of their diet and body fat content.

(25) The voles were found to eat mainly bracken and bluebells and some grasses. Several of the common plant species in the areas in which they lived were rarely consumed.

(26) The body fat content of the animals was at its maximum during the winter and varied most widely during the summer.

(27) The predation pressure on the population could not be measured precisely but was thought to vary little from year to year.

(28) Estimates of the annual production of animals suggested

that predation was not controlling the size of the population as a whole (although it might exert a local effect).

(29) Studies of disease in the population were started in 1977 and have permitted an assessment of the role of disease in population regulation.

(30) The results obtained were compared with published literature on island populations of rodents. The Skomer vole was found to fit the general pattern especially in regard to:

(a) The stability of the population.

(b) The high densities achieved.

(c) The relative unimportance of dispersal as a mechanism of population regulation.

(d) Reduced range size.

(e) Shortened breeding season.

(f) Reduced litter size.

(g) Delayed maturation of both sexes.

(31) The females were non- territorial. This contrasts markedly with the results obtained by other workers in other studies of the biology of Microtine rodents.

(32) The overwinter survival of females and the survival of young during the breeding season are considered to be of particular importance in regulating the size of the population.

APPENDIX 1.

Estimate of the annual production of young by the adult and young adult females on area 'C'.

Table 31.

Estimates of the production of young on area 'C' by adult and young adult females, August values, 1976 - 1983.

Year	No. A♀♀	No. YA♀♀	No. Young from adults (Estimated)	No. young from young adults (Estimated)	% from young adults
1976	36	6	541	30	5.25
1977	35	3	526	15	2.77
1978	27	6	406	30	6.88
1979	26	6	391	30	7.12
1980	36	8	541	40	6.88
1981	49	3	737	15	1.99
1982	32	6	481	30	5.87
1983	27	8	406	40	8.97

(1) Mean gestation period = 22 days (Coutts & Rowlands, 1969).

(2) Mean litter size:

(i) 3.71 (Jewell, 1966)

(ii) 3.77 (Coutts & Rowlands, 1969)

(iii) 3.79 (this study)

Average mean litter size = 3.76

(3) The majority of pregnancies occur between mid June and mid August, a period of about 90 days. This would allow time for a maximum of four litters per animal given that the animals have a post-partem oestrus (Coutts & Rowlands, 1969).

(4) The young adults mature at the end of July and could manage a maximum of two litters by the end of the breeding season.

(5) Young adult bank voles tend to have a lower fertility than overwintered animals (Westlin, 1982).

(6) Not all the young adults breed successfully in the year of their birth.

(7) The average size of the litters of young adults is therefore probably smaller than those of the adults. An estimate of 2.5 is used here.

APPENDIX 2.

Estimation of annual production of young voles on Skomer

(a) Estimate of size of population:

(i) 21548 (Fullagar et al. 1961)

(ii) 21161 (Healing et al. 1983)

Mean estimate = 21354

(b) Proportion of adult females:

(i) 25.4% (Fullagar et al. 1963)

(ii) 27.5% (Healing et al. 1983)

Mean proportion = 26.5%

Therefore number of adult females = 5659

(c) Approximately 17% of the adult females caught in August are young adults (= 962 animals)

Therefore of the adults present, 4697 are overwintered animals.

(d) Mean litter size = 3.76 (for adults - see Appendix 1.).

= 2.5 (for young adults - see Appendix 1.).

(e) Maximum of 4 litters for adults and 2 for young adults (see Appendix 1.).

(f) The estimated production of young in this period is therefore:-

(4697 x 4 x 3.76) + (962 x 2 x 2.5)

~ 70643 + 4810

= 75453

(g) Some animals have litters earlier and later than normal in the breeding season. If 10% of the adults have one more litter then an additional 1766 animals would be produced giving an annual production of 77219 young.

APPENDIX 3.

Predation on Skomer voles.

There being no predatory mammals on Skomer, the only predators on Skomer voles are birds. Seventeen species of predatory birds have been recorded on the island during the last ten years but the majority of these were occasional visitors. Four species, the buzzard (Buteo buteo), the short-eared owl (Asio flammeus), the little owl (Athene noctua) and the kestrel (Falco tinnunculus) were common. All of these predatory bird species are known to prey largely on small mammals (Witherby et al. 1938) and are therefore potential predators on the voles.

Of these four species only the buzzards and short-eared owls have bred on the island throughout the study. Kestrels have not bred there since 1975 and the little owl has bred there since 1977. The number of pairs of buzzards breeding on the island has varied from three to six over the last ten years and the number of pairs of short-eared owls from two to five (Table 32.). Little is known about the breeding success of these birds because attempts are made not to disturb them and their nests are not visited.

Table 32.

The number of pairs of buzzards and short-eared owls breeding on Skomer, 1970 - 1983

	'70	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83
Buzzard	4	4	4	5	5	3	4	4	4	6	5	5	5	3
Short-eared owl	4	5	3-4	1-3	2	2	3	3	4	5	5	2	4	3

The majority of the short-eared owls on Skomer nest in the stream valleys, usually two or three pairs in the north valley and one or two pairs in the south. The study area used during this project has, throughout this study, fallen within the territory of one of these pairs. The buzzards all nest on cliff ledges around the edges of the island and of the three pairs of little owls that have nested on the island during the last five years, one pair nested near the Wick, one to the west of the farm, and one at the west side of the Neck (see Island Map: Fig 2. and the fold-out endpaper).

The number of short-eared owls is at a peak just before the breeding season (March/April), the breeders being supplemented by two or three additional birds (which may be prospecting for nest sites). Throughout May and June the number of birds (eg. the breeding population) remains stable.

The number of little owls on the island (two pairs) varies little throughout the year. A few kestrels (two or three birds each day) are present on the island in March and April but none is seen in May, June or July. Thereafter a few birds (up to three) are present each day.

The number of buzzards present on the island rises sharply at the end of September, up to 30 birds having been seen on some days. The majority of these birds are apparently attracted to the island by the large amount of carrion (rabbit carcasses and dead shearwaters) that is available at that time.

Only one barn owl has been resident on the island during this project (and then only over winter and not during the last four years) so, although members of this species do feed largely upon voles when they are on the island, their overall

impact is probably small.

Both ravens (Corvus corax) and carrion crows (Corvus carone) are found on Skomer, the numbers fluctuating throughout the year being at their highest (up to 150 ravens and 30 crows) in the autumn when the amount of carrion is greatest. Although both species have been reported as taking small rodents they are mainly scavangers and are unlikely to cause serious damage to the population of voles.

Large numbers of gulls nest on Skomer and some species of these, notably the lesser black-backed gull (Larus fuscus) and the greater black-backed gull (Larus marinus) are potential predators on Skomer voles. However the gulls have not been observed to search actively for prey among the bracken and neither Fullagar (1964) nor Healing & Quarmby (unpublished observations) found evidence of vole remains in their castings and Harris (1965) who examined a large number of stomachs and pellets from herring gulls (Larus argentatus) and greater and lesser black-backed gulls from Skomer and Skokholm found very little mammal material. Only one Skomer vole was found in a sample of 200 feeds taken from lesser black-backed gull chicks during a recent survey (M.Alexander - personal communication). Gulls are not therefore thought to be significant predators of Skomer voles.

Several surveys of the diet of the predatory birds on Skomer have been made. Phillips (1947) examined pellets from Buzzards and Barn owls (Table 33.).

Fullagar (1964) collected pellets from buzzards, kestrels and short-eared owls following the winter of 1960 - 1961. A summary of his results is given in Table 34. This author

reported that the buzzards were observed to prey on rabbits but the pellets he examined did not contain identifiable rabbit remains.

Table 33.

The number of Skomer voles in pellets of buzzards and barn owls collected on Skomer in 1947. (After Phillips, 1947).

Species of predator	No. of pellets	Approx No.voles
Buzzard	9	1
Barn owl	60	86

Table 34.

Number of voles in pellets collected from the roosts of predatory birds on Skomer, winter 1960 - 1961. (After Fullagar, 1964).

Sp of predator	No. pellets examined	Approx no. voles eaten	Voles as approx % of diet
Buzzard	68	9	13
Kestrel	73	33	45
Short-eared owl	180	143	53

The detailed results of the analysis of material from short-eared owls are given below (Table 36.).

Davis & Saunders (1965) found that, in 1960, buzzards on Skomer were taking several species of prey, puffins (Fratercula arctica) and rabbits being the most important during the buzzard's breeding season. Few small mammals were taken.

Table 35.

Skomer vole as a percentage of dietary items. (Healing & Quarmby, unpublished observations).

Sp.of predator	Cgs%	No. prey items identified
Buzzard	8.1	37
Little owl	12.0	33
Short-eared owl	16.7	24
Barn owl	38.0	489

Table 36.

Analysis of pellets from short-eared owls, May 1983. The results of similar analyses obtained by Fullagar (1963) are given for comparison.

Prey species	Number of prey items identified. (a) Fullagar (1964) (180 pellets)	(b) This study (51 pellets)
C.glareolus	143	42
A.sylvaticus	66	4
O.cuniculus	14	20*
M.musculus	20	-
Bird spp.	11	4
M.agrestis	4	1
S.araneus	2	4
S.minutus	2	1
Beetle spp.	6	23+
Bufo vulgaris	1	-

* Only parts of rabbits (usually limb bones) were found in any one pellet. The majority of the bones were from young rabbits (small bones with non-fused epiphyses).
+ Mostly Geotrupes sp.

Phillips & Worden (1950) and Clevedon-Brown & Twigg (1971) reported that Skomer voles, woodmice and common shrews comprised the greater part of the diet of barn owls on Skomer. Plant (1975) found that Skomer voles made up 51.4% of the diet of the barn owl of the basis of his examination of 46 pellets.

A survey of the diet of some of the avian predators on Skomer was undertaken in 1975 with the assistance of Miss V.S.Quarmby, a student from Royal Holloway College, London. (Table 35.).

Glue (1977) found that Skomer voles comprised 44% of the weight of the prey eaten by short-eared owls on the island when he analysed a sample of pellets collected from near the study area used during this study.

Analysis of 51 pellets from short-eared owls collected from around the study area in May 1983 revealed the remains of 42 bank voles (Table 36.).

APPENDIX 4.

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Populations of the Bank vole (*Clethrionomys glareolus*) and Long-tailed field mouse (*Apodemus sylvaticus*) on Skomer island, Dyfed

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(With 5 figures in the text)

The methods used to study the populations of the Bank vole and Long-tailed field mouse on Skomer Island in 1981 are described. The survey was a repeat of one performed in 1960 and the methods used were almost identical.

The distribution of both species of rodent over the island was studied using trap lines and was found to be similar in both surveys.

The vegetation of the island was divided into nine categories and the habitat preferences of both rodent species assessed. These have remained distinct and, as in the previous survey, the voles were found to be most strongly associated with areas of deep bracken with little undercover and the mice with open areas such as cliff tops and rocky outcrops.

A crude survey of the distribution of the nine vegetation categories was undertaken, a vegetation map was prepared, and the area of each category was estimated. Two trapping grids were established in vegetation categories favoured by the voles. The data from these grids were used in conjunction with the vegetation map to estimate the population of voles over the whole island. Insufficient data were available for such an estimate to be made of the size of the population of mice.

Contents

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Introduction

In 1960 a survey was made of the size and distribution of the populations of the Skomer vole (*Clethrionomys glareolus*) and the Long-tailed field mouse (*Apodemus sylvaticus*) on Skomer Island, Pembrokeshire (Fullager, Jewell, Lockley & Rowlands, 1963). This survey contributed to the study of what Southern (1979) termed "Microdistribution" that is to say the local distribution of animals with respect to different habitats; the voles being associated particularly with bracken, and the mice with open areas. It was the first survey of its kind and we considered that, after 20 years, it would be valuable to repeat it in such a way that the results would be directly comparable with those of 1960. Many points of interest attach to the survey. Not only is there a dearth of information on long-term changes in the population density of small mammals in general, but, because the Skomer vole is a race of the Bank vole peculiar to the island, its status is of concern for the conservation policies for the island. Several aspects of the ecology of Skomer have altered over the past two decades; the distribution of bracken (*Pteridium aquilinum*) has changed and attempts have been made to control its spread by swiping and by the application of herbicides. The number of nesting Lesser black-backed gulls (*Larus fuscus*) has increased sharply (M. Alexander, pers. comm. the density of the population of rabbits (*Oryctolagus cuniculus*) has fluctuated widely, due largely to periodic outbreaks of myxomatosis (S. B. Evans, pers. comm.) and the island has not been grazed by sheep since 1964 (S. B. Evans, pers. comm.). All these factors could have affected the distribution and abundance of the populations of small mammals on the island.

The Skomer vole is a distinctive island race of *C. glareolus* that has been exploited for comparative taxonomic, genetic, physiological and behavioural studies (Corbet, 1964; Godfrey, 1958; Coutts & Rowlands, 1969; Alder, Godfrey, McGill & Watt, 1981). These studies have thrown light on the Bank vole's evolutionary response to particular ecological circumstances, which have been further investigated by Jewell (1966*a,b*) and Healing (unpublished data). The Skomer field mouse has contributed to analogous comparative studies on *Apodemus* (Fullagar, 1964; Jewell & Fullager, 1965). These isolated populations of rodents have also provided reference material in studies of the incidence and the possible role of disease in the dynamics of rodent populations (Twigg, Cuerden & Hughes, 1968; Kaplan, Healing, Evans, Healing & Prior, 1980; Healing, Kaplan & Prior, 1980; Healing, 1981). Studies of disease in Skomer voles are continuing and will draw upon the results of the survey.

A general account of the position, climate, topography and vegetation of Skomer is given in Buxton & Lockley (1950) and is briefly summarized by Fullager *et al.* (1963). The weather during the present survey was warm and sunny with a few light showers and mist, and there was no moon at night. The weather during the survey in 1960 was more mixed with some wet and windy days, and the nights were moonlit.

Methods

Period of study

Intensive trapping was carried out between 26 August and 4 September 1981. The methods used during the survey of 1960 were followed unless otherwise stated. They are described briefly here; for the full details see Fullagar *et al.* (1963).

Traps

A total of 400 Longworth traps were used to permit all procedures carried out in 1960 to be repeated in a shorter period. The traps were set ready stocked with whole oats and hay without pre-baiting.

Examination of captured animals

A record was made of the species, sex, body weight, and of the condition of the external genitalia and mammary glands of each animal. The animals were marked by fur clipping (short-term) or by toe clipping (long-term). Each animal was assigned to one of three age classes; Adult (breeding animals); immature (non-breeders in adult coat) and juvenile (animals in first grey coat) (Fullager *et al.*, 1963). Pregnancy was diagnosed by palpation.

Line trapping

Seven lines of traps were set down as nearly as possible in the same places as in 1960 (lines I, IIa, IIb, III, IV, V and VI) (Fig. 1). The numbers of traps at a point (usually four but sometimes six and the number of points on each line were also the same as in 1960, as was the timing of the periods of trapping, giving a daytime and an overnight catch at each point.

Grid trapping

Two grids ("A" and "C") were set out and trapped in approximately the same places that had been used in 1960. For Grid "A" the procedure followed in 1960 was repeated almost exactly; the grid was of 6×6 squares each with sides of 9·14 m; two traps were set in each square over a succession of five days. These were placed in one corner of the square and were moved clockwise from corner to corner every morning. The only change of procedure was to examine the traps in the evening as well as the morning instead of only once every 24 h in the morning. This procedure was followed so as to ensure that lactating females were not kept too long from their litters, and to minimize mortality of shrews. Procedures of Grid "C" were more complex. This grid has been the standard study site of one of us (TDH) since 1971 and is permanently set out, with marking canes, as a grid of 7×7 points with an interstation distance of 10 m (instead of 25 squares with 10 yd sides as in 1960). On this grid two traps were set at the grid intersections over a succession of three days (as opposed to three traps in the corners of the square over four days, the traps being moved every 24 h in 1960). The traps were examined in the morning and evening. The number of "trap days" (1 trap laid for 24 h was the same on grid "A" during both surveys (360). The number on grid "C" was 300 in 1961 and 294 in 1981.

Analysis of grid trapping data

Longworth traps (and other "live" traps) do not sample at random and so the commonly used mark-recapture statistics cannot reliably be employed to estimate the size of populations if the data are collected by this means (Krebs, 1966). The minimum number of animals known to be alive per hectare was determined for each trapping grid. The data from grids "A" and "C" were used to estimate the total population of voles on the island. The island was divided into the three habitat types of Fullagar *et al.* (1963) (Table I). Grid "A" lay in a "medium density" area and Grid "C" in a "high density" area. The data from these grids were used to estimate the population density in the habitat types. In 1960 an arbitrary figure of 12·3 voles/ha (=5 voles/acre) was assumed for "low density" areas. An estimate was used because no grid trapping was done in a "low density" area and the figure of 5 voles/acre was chosen as a conservative estimate. This convention was followed during the analysis of the data obtained during the present survey. The area of each habitat type was calculated and the population in each determined.

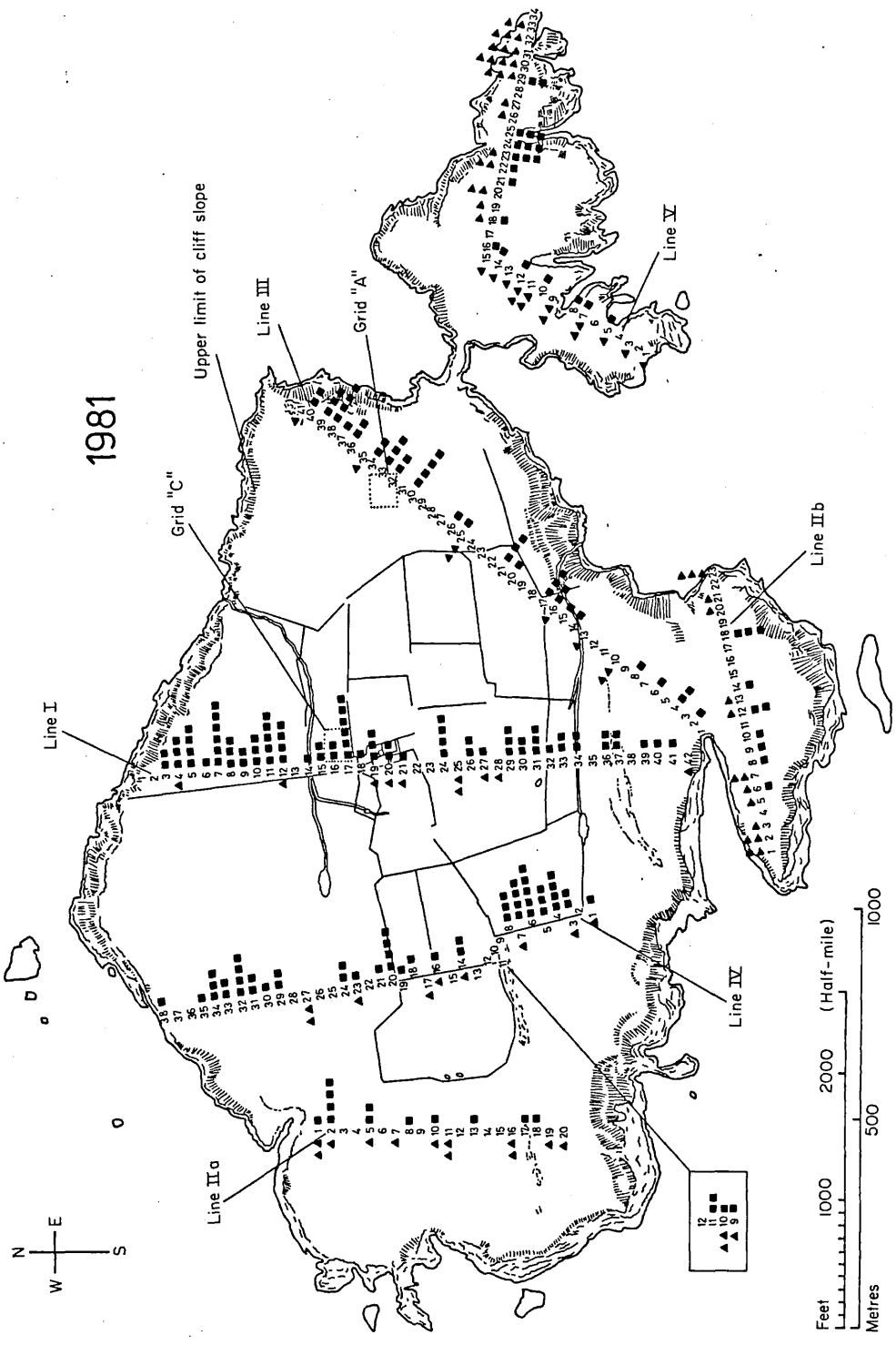

FIG. 1. Map of Skomer Island showing the position of the trap lines and of Grids "A" and "C" the numbers along each line are the trapping points. The catch (first trapping only) at each point in 1981 is shown by symbols, each symbol representing one animal. The National Grid reference for the old farmhouse at the centre of the island is SM 727 096. The rocky cliffs and cliff slopes are indicated by hatching. ■ = *Clethrionomys glareolus*: ▲ = *Apodemus sylvaticus*.

The ratios between the different sex and age classes in 1960 and 1981 were compared using 2×2 contingency tables and calculating χ^2 with Yates correction.

Vegetation

A map of the vegetation was compiled by eye from a ground survey of the island. The vegetation was divided into nine categories (defined in Table I). Several transects were walked, the limits of each category determined approximately by reference to topographical features and the area of each determined as a proportion of the total (292 ha). Also shown in Table I is the correspondence between the categories used in the 1981 survey and the habitat types of Fullagar *et al.* (1963) which were based on the numbers of voles detected in those areas.

The vegetation at each trapping station on each line was also ascribed to one of the nine vegetation categories. Those that could not be ascribed unambiguously were omitted from further analysis. The total number of traps set and the total numbers of voles and mice caught in each category were determined and a habitat use index I was calculated. This was defined as the proportion of the total number of voles or mice caught in a particular vegetation category divided by the proportion of the total number of traps set in that category. The χ^2 1-sample test was used to compare the numbers found in each vegetation category with the numbers expected from an even distribution of animals throughout all nine vegetation categories.

Results

The difference between the numbers of voles caught on the lines in 1960 and 1981 was small (230 and 217 respectively) but many fewer field mice were caught during the present

TABLE I

Vegetation categories used in the 1981 Skomer survey with the dominant plant species in each

Vegetation categories (1981)	Habitat types (1960)	Flora
Bracken/sorrel	"High density"	Tall bracken (*Pteridium aquilinum*), dense bluebell (*Endymion non-scriptus*), sorrels (*Rumex* spp.).
Bracken/grass	"Medium density"	Medium to tall extensive bracken, some bluebell, Yorkshire fog (*Holcus lanatus*).
Patchy bracken	"Low density"	Mainly Yorkshire fog, patches of bracken.
Heather		Heather (*Calluna vulgaris*), heaths (*Erica* spp.).
Yorkshire fog		Mainly Yorkshire fog, some *Poa* spp., *Festuca* spp. clumps of ragwort (*Senecio jacobea*).
Clifftop/Rocky outcrop		Sea campion (*Silene maritima*), mixed grasses (mainly *Festuca* spp.), thrift (*Armeria maritima*) lichens, bare rock.
Rabbit lawn		Mixed grasses; well grazed, short.
Moor grass/rushes		Tussocks of Purple Moor Grass (*Molinia caerulea*), clumps of rushes (*Juncus* spp.).
Bramble/mixed cover		Clumps of bramble (*Rubus* spp.), Umbelliferae, and thistles (*Cirsium* spp.).

survey (99 as compared with 220 in 1960). The distribution of captures of voles and mice along the lines was similar in both surveys (Figs 1, 2), but some minor differences may be noted. In the present survey, voles were caught at points set in heather, as on Line IV, points 31–34 and Line I, point 7. They were also more readily caught on The Neck, at the eastern end of the island (Line V).

To test whether a single trapping for 24 h gave a repeatable record of distribution, traps were set again on Line III, after an interval of 6 days (Fig. 3). The distribution was similar and this was confirmed by trapping again on short sections at the ends of Lines I and IV. The number of animals caught in the second trapping on Line III was greater than in the first (Fig. 3). Although more field mice were caught in the second trapping the total (16) was still very low compared with the single trapping of 1960 (43).

Similar numbers of mice were caught on both grids during both surveys and similar numbers of voles on Grid "A". More voles were caught on Grid "C" during the present survey (Table II). The number of "trap days" was the same on Grid "A" in both surveys and thus the results can be compared directly. Slightly fewer "trap days" were employed on Grid "C" in 1981 but the number of voles caught per trap day was greater (Table II). The combined results from the grids and lines (Table III) show that more voles were caught in 1981 and that this was due largely to an increased capture of immature males ($\chi^2 = 11{\cdot}7$, d.f. $= 1$, $P < 0{\cdot}001$). More adult female voles were caught in 1981 and fewer adult males ($\chi^2 = 5{\cdot}6$, d.f. $= 1$ $P < 0{\cdot}05$). Many fewer mice were caught in 1981 the difference being mainly due to a very much smaller catch of immature males ($\chi^2 = 29{\cdot}2$, d.f. $= 1$, $P < 0{\cdot}001$). The proportion of palpably pregnant female voles was almost the same in 1960 and 1981 but a greater proportion of the female mice were pregnant in 1981 ($\chi^2 = 10{\cdot}5$, d.f. $= 1$, $P < 0{\cdot}01$).

The population of voles over the whole island was estimated as 21,161 (Table IV). The 1960 survey gave a figure of 21,548 animals. No grid trapping was done in the areas most favoured by the mice and so it was not possible to estimate the population of mice on the island.

The data on body weights of the voles and mice showed no differences in both the ranges and the modal weights of the different age categories from the data obtained in 1960 (Fullagar *et al.*, 1963).

The results of the vegetation survey (Fig. 4 and Table V) suggested that there had been a reduction in the bracken/sorrel category (equivalent to the "High Density" habitat type of Fullagar *et al.*, 1963) but little change in any of the others.

Comparison of the proportions of the traps set in the different vegetation categories with the proportion of the island covered by these categories (Table VI) suggests that the lines were providing a representative sample.

The animals were not evenly distributed between the different vegetation categories (Table VI and Fig. 5). Significantly more voles than expected were found in Bracken/sorrel ($\chi^2 = 59{\cdot}2$, d.f. $= 1$, $P < 0{\cdot}001$), Bracken/grass ($\chi^2 = 9{\cdot}1$ d.f. $= 1$, $P < 0{\cdot}01$) and in Bramble/mixed cover ($\chi^2 = 9{\cdot}1$, d.f. $= 1$, $P < 0{\cdot}01$). Conversely, fewer than expected were caught in areas of Patchy bracken ($\chi^2 = 17{\cdot}9$, d.f. $= 1$, $P < 0{\cdot}001$), Yorkshire fog ($\chi^2 = 14{\cdot}2$, d.f. $= 1$, $P < 0{\cdot}001$), Cliff top/Rocky outcrop ($\chi^2 = 27{\cdot}4$, d.f. $= 1$, $P < 0{\cdot}001$) and Rabbit lawn ($\chi^2 = 6{\cdot}4$, d.f. $= 1$, $P < 0{\cdot}02$). Only in the vegetation category Clifftop/rocky outcrop were mice found significantly more than expected ($\chi^2 = 54{\cdot}9$, d.f. $= 1$, $P < 0{\cdot}001$); they were caught less than expected in Bracken/sorrel and Bracken/grass ($\chi^2 = 7{\cdot}4$, d.f. $= 1$, $P < 0{\cdot}01$; $\chi^2 = 6{\cdot}5$, d.f. $= 1$, $P < 0{\cdot}02$, respectively).

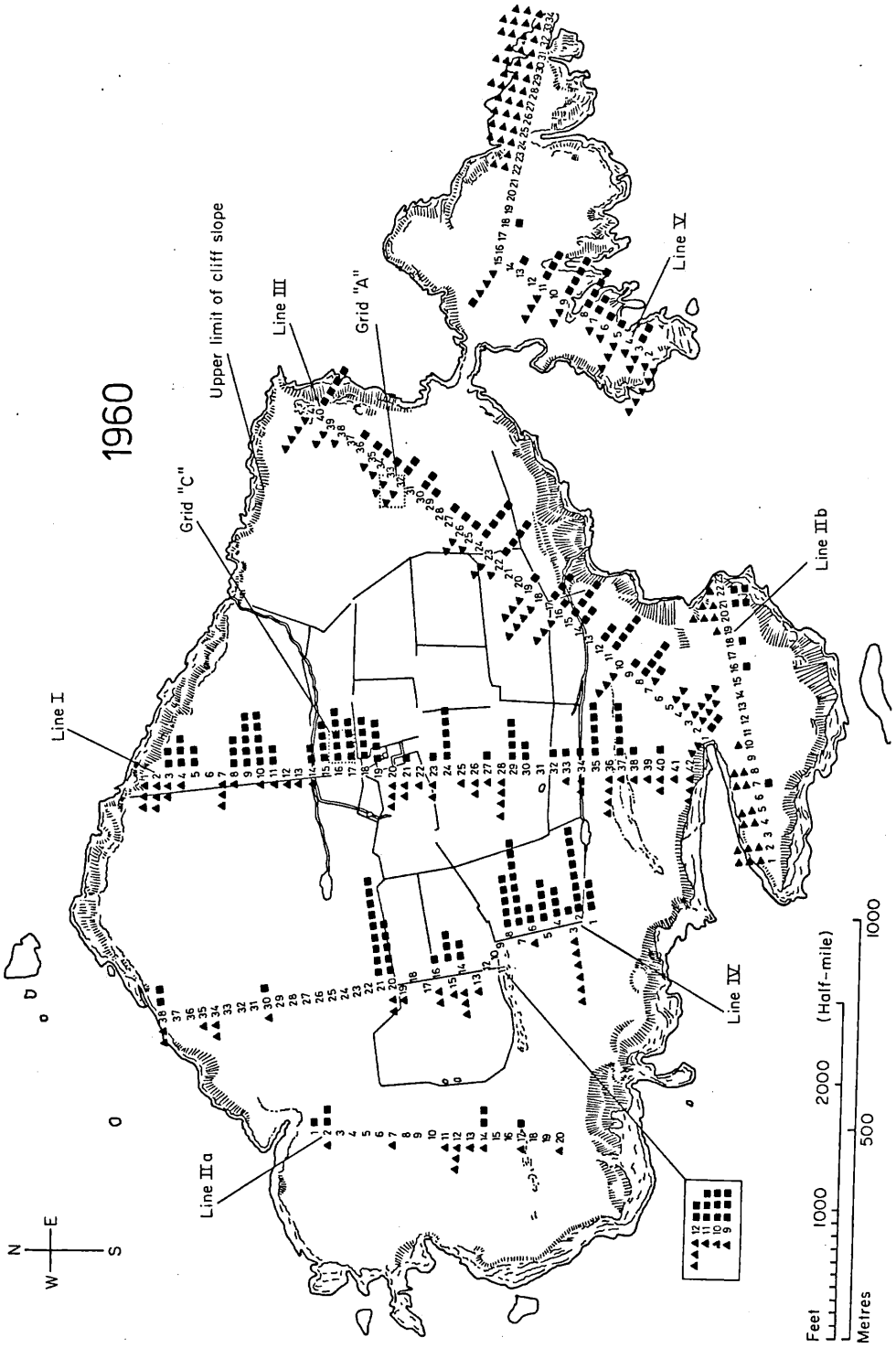

FIG. 2. The results of the survey in 1960 for comparison with Figure 1. ■ = *Clethrionomys glareolus*: ▲ = *Apodemus sylvaticus*.

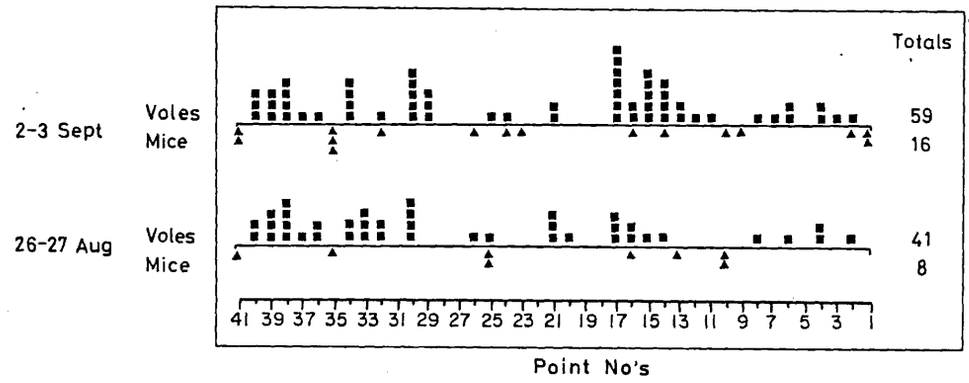

FIG. 3. Repeat trapping of Line III. Catches at the first (26–27 August) and second (2–3 September) trapping. ■ = *Clethrionomys glareolus:* ▲ = *Apodemus sylvaticus.*

TABLE II

Number of voles and mice caught, numbers/hectare and numbers per trap day on Grids "A" and "C" in 1960 and 1981

Species			Number caught	Number/ hectare	Number of trap days	Numbers/ trap day
Voles:						
	Grid "A"	1960	21	51	360	0·06
		1981	24	58	360	0·07
	Grid "C"	1960	78	259	300	0·26
		1981	174	355	294	0·59
Mice:						
	Grid "A"	1960	20	49	360	0·06
		1981	17	41	360	0·05
	Grid "C"	1960	5	10	300	0·01
		1981	3	6	294	0·01

Some animals were caught on both lines and grids and the various totals in the text and Tables II and III therefore do not necessarily tally.

Discussion

Approximately the same numbers of voles were caught on the trap lines in 1981 as in 1960. Since the same trapping effort was applied during both surveys this suggests that populations of similar size were being sampled. The repeat trapping on Line III and at the ends of Lines I and IV gave similar results to the first sample except that more animals were caught. This could be expected if the first trapping has a pre-baiting effect. The estimates of the size of the population of voles on Skomer were almost the same in 1960 and 1981.

TABLE III

Total numbers of voles and mice of different sex and age classes caught in 1960 and 1981 (grids and lines)

	Voles				Mice			
	1960		1981		1960		1981	
Males:								
Adult	83		62		77		68	
Immature and juvenile	82		132		71		8	
Total		165		194		148		76
Females:								
All adult	87		112		55		37	
Pregnant	(32)		(54)		(17)		(25)	
Immature and juvenile	90		101		18		6	
Total		177		213		73		43
Grand totals		342		407		221		119

TABLE IV

Numbers of voles in different habitat types in 1960 and 1981

Habitat type	Area (ha)	Percentage of island's surface area	Density of voles/ha	Number in habitat type
1960				
"High density"	64	22	259	16576
"Medium density"	56	19	51	2856
"Low density"	172	59	12·3	2116
				$N=$ 21548
1981				
"High density"	43	15	355	15265
"Medium density"	62	21	58	3596
"Low density"	187	64	12·3	2300
				$N=$ 21161

It seems, therefore, that the several kinds of interference with the environment that occurred in the period between the two surveys and that are mentioned in the Introduction have not affected the voles adversely. This is reassuring from the point of view of their conservation. However, information from two widely separated points in time does not permit the conclusion that the population is stable at a relatively high density. Trapping carried out on Grid "C", in the first week in August from 1977 onwards (T.D.H.—unpublished data) revealed vole densities of 224/ha in 1977, declining to 145/ha in 1978 and to 122/ha in 1979, and rising to 218/ha in 1980 and 318/ha in 1981. Whether these fluctuations follow a regular cycle over the years is not known.

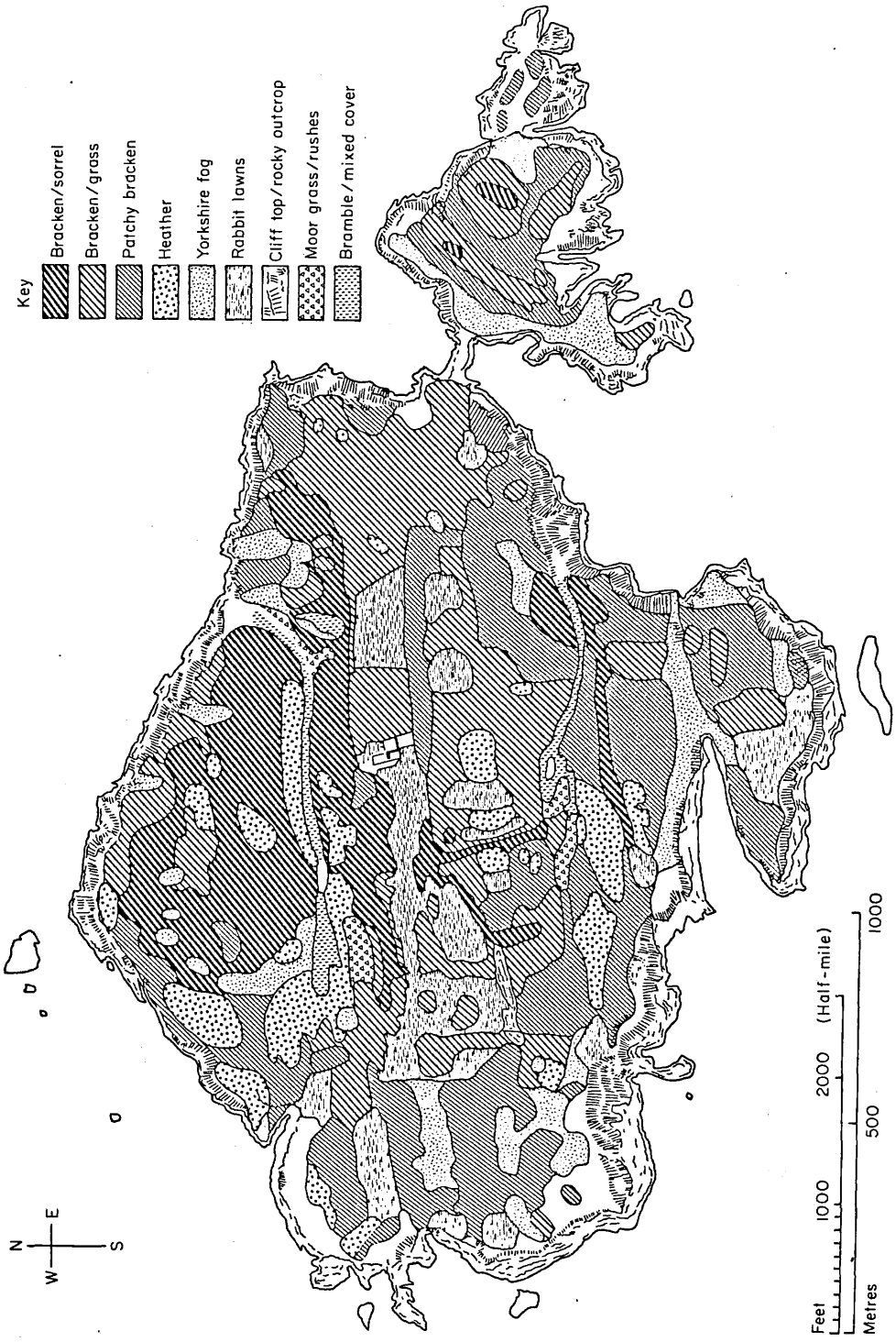

FIG. 4. Map prepared from the data collected during the vegetation survey (1981), showing the approximate boundaries of the nine vegetation categories.

TABLE V

Percentage of area of island covered by the different vegetation categories in 1960 and 1981

Vegetation categories	1960		1981	
Bracken/sorrel	22	41	15·0	36
Bracken/grass	19		21·0	
Patchy bracken		59	24·8	64
Heather			8·1	
Yorkshire fog			8·9	
Clifftop/rocky outcrop			9·7	
Rabbit lawn			10·1	
Moor grass/rushes			0·6	
Bramble/mixed cover			1·8	

TABLE VI

The area of the island covered by each vegetation category and the percentages of traps set and of voles and mice caught in each category (Trap Lines only. For category descriptions see table 1)

Vegetation category	Bracken sorrel	Bracken grass	Patchy bracken	Heather	Yorks. fog	Clifftop rocky outcrop	Rabbit lawn	Purple moor grass	Bramble mixed cover
Area (%) of island covered	15·0	21·0	24·7	8·1	8·9	9·7	10·2	0·5	1·9
Percentage of traps set	14·4	27·2	15·6	5·0	12·6	12·6	6·9	2·2	3·5
Percentage of voles caught	33·2	36·6	4·9	7·3	3·9	0·5	2·4	3·9	7·3
Percentage of mice caught	4·4	15·4	13·2	5·5	7·7	38·4	9·9	0	5·5

Not all the points were used in this analysis.

The mice of Skomer are of no less interest than the voles as a distinctive island race (Jewell, 1966*a*) although they have received less attention. Grid trapping was not performed in those areas particularly favoured by the mice and so the density of the population could not be calculated but such a sampling method can be of limited value in assessing the density of populations of field mice. These animals, which forage over much greater distances than voles, (Fullagar, 1964; Jewell, 1966*b*) can be attracted to baited traps from an extensive area and the results thus obtained may therefore overestimate the size of the population. Fewer mice were caught in 1981 than in 1960 but our survey of the vegetation showed that this was not due to loss of their preferred habitat (that which is bracken-free).

The habitat preferences of the Skomer voles and mice have remained distinct, the voles being closely associated with areas of dense bracken and the mice with areas of open or sparse

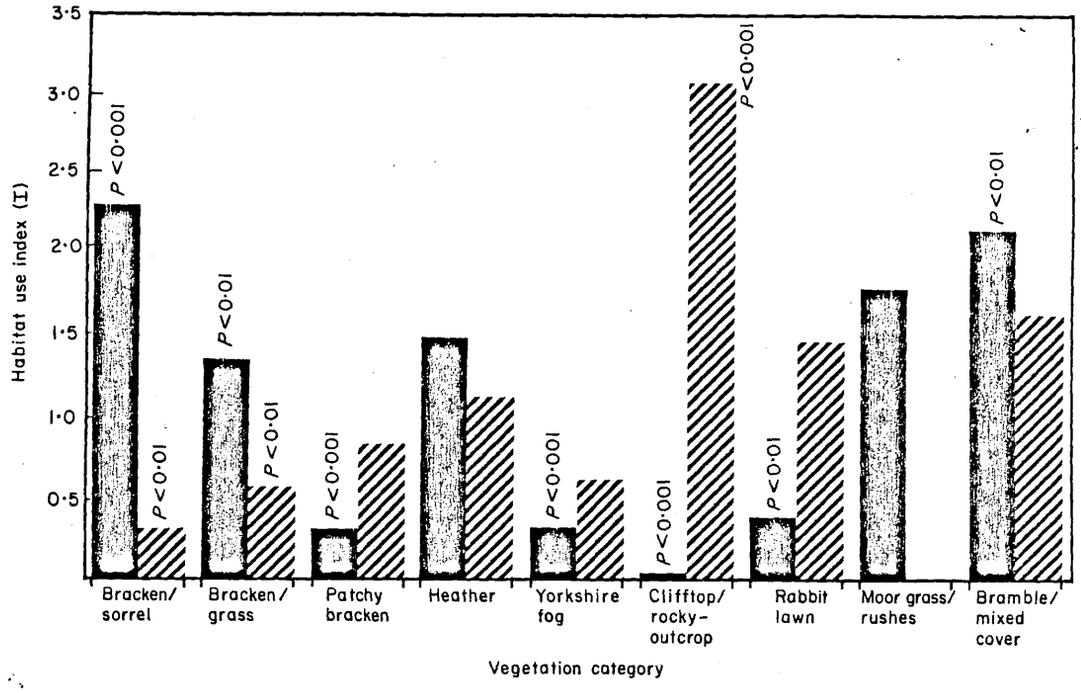

FIG. 5. Use of the different vegetation categories by the voles and mice. Values greater than 1 indicate a positive association and vice-versa. The probability values at the top of some of the columns indicate a statistically significant positive or negative association between the relevant species of rodent and that vegetation category. ■ = *Clethrionomys glareolus;* ▨ = *Apodemus sylvaticus.*

vegetation. In addition, in the present survey, high densities of voles were found in some areas of heather although the results from all the lines showed no significant association of the animals with the type of habitat. The heather areas are made up of three layers; the surface flowering layer, a middle tangle of woody stems which supports a layer of dead flowers and leaves, and a lower open space above the peaty ground. It was in this lowest layer that the traps were set on this occasion.

The influence of cover on the habitat preferences of *Clethrionomys* and *Apodemus* are well known (Fullagar *et al.*, 1963) but the specific factors contributing to the separation of the two species on Skomer are not clear. In a survey of published data on choice of habitat by small rodents, Fleming (1979) concludes that the important cues appear to be associated with food or foraging areas and/or shelter. Smal & Fairley (1982), in their study in Ireland found a highly significant correlation between the numbers of voles and mice captured and the nearness of shelter, the correlation being higher for voles than mice. The Skomer vole prefers areas where there is a dense cover of bracken with little vegetation (except bluebells) growing under it. Fewer voles are found in those areas where there is an extensive mat of grasses (particularly Yorkshire Fog) under the bracken. Conversely the mice tend to avoid those areas preferred by the voles and are strongly associated with the cliff-top type of vegetation. The selection of habitat by both species may be a result, in part, of dietary preferences. Recent studies (T.D.H.—unpublished data) have shown that bracken and bluebells

form up to 70% of the diet of the Skomer voles and that they eat little grass. The greatest density of voles is found in those areas where their preferred food items are most common. The diet of the mice on Skomer has not been studied but Watts (1968) showed that, in Wytham Wood, near Oxford long-tailed field mice eat quite large amounts of animal material and one of us (P.A.J.—unpublished observations) has noted that field mice on St Kilda gnaw the carcases of dead sheep. The greatest densities of mice are found in areas where seabirds are common and the mice may be scavenging from them.

Summary

This survey of the size and distribution of the populations of the Skomer vole and field mouse was a repeat of one performed in 1960 and the methods employed were almost identical in both surveys.

Trapping was carried out on Skomer Island, Dyfed between 26 August and 4 September 1981. Four-hundred Longworth traps were used.

Two hundred and seventeen voles and 99 mice were caught on five lines of traps ranging over all parts of the island, the positions of each trapping point being the same as in 1960. Similar numbers of voles were caught in 1960 (230) but many more mice (220). The distributions of captures along the lines was similar in both surveys but there were minor differences. In the present survey voles were caught in areas of heather and on the Neck at the eastern end of the island.

To test whether a single trapping for 24 h gave a repeatable record of distribution parts of some lines were trapped again. Forty-nine animals were caught in the first trapping and 75 in the second, but the distribution of captures was the same on both occasions.

Two trapping grids were used. These were in the same places as the grids used in 1960. The size of one of the grids (Grid "A") and the trapping regime was the same in both surveys but the other grid (Grid "C") was 42% larger in 1981 and 23 more traps were used. Three days were spent trapping this grid during the 1981 survey (four in 1960) and the total trapping effort (294 trap days) was slightly smaller than in 1960 (300 trap days). Similar numbers of mice were caught on both grids during both surveys and similar numbers of voles on Grid "A'. More voles were caught on Grid "C" in the present survey.

The combined results from the grids and lines showed that more voles were caught in 1981 than in 1960 (407 and 342 respectively) due mainly to increase in the number of immature males caught (132 : 82). More adult female voles were caught in 1981 than in 1960 (112 : 87) and fewer adult males (62 : 83). Fewer mice were caught in 1981 than in 1960 (119 : 221) due to a much smaller catch of immature males (8 in 1981 and 71 in 1960). Fifty-four pregnant voles were caught in 1981 as opposed to 32 in 1960. Twenty-five pregnant mice were caught in 1981 and 17 in 1960.

The population of voles over the whole island was estimated as 21,161 as compared to 21,536 in 1960. In neither survey was it possible to estimate the population of mice because grid trapping was not done in their preferred habitat.

A crude survey of the vegetation was performed by eye and a map prepared. Comparison of the results of this survey with those obtained in 1960 showed little change but the area of the bracken/sorrel category (equivalent to the high density category of Fullagar *et al.*, 1963) appeared to be smaller.

The report of the 1960 survey noted that the voles were associated with drier more sheltered areas, especially those with a deep bracken cover with a sparse understory, and that few mice were caught there; that both fewer voles and more mice were captured in areas where the bracken cover was less and there was an undercover of grass; and that the mice were most numerous in exposed sites, especially cliff slopes and rocky outcrops. These results were confirmed by the present survey.

We thank the West Wales Naturalists Trust and the Nature Conservancy Council for permission to carry out the survey and for providing accommodation on the island; the British Ecological Society, the Mammal Society and St John's College, Cambridge for financial support; Mr S. B. Evans of the Nature Conservancy Council, the Warden of Skomer, Mike Alexander and his wife Rosanne for their help; Dr P. Cox, and Henry and John Russell for assistance with the field work; and the Departments of Zoology of University College, London and Royal Holloway College, London for the loan of traps.

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APPENDIX 5.

Reprinted from *J. Zool., Lond.* (1978) **185**, 273–277

A method for the collection of small volumes of whole blood in the field and their preparation for serological studies

During a study of the carriage of viruses by wild British rodents it has become necessary to collect samples of blood serum for complement fixation and haemagglutination inhibition tests. Since a dynamic study of the populations is being made, individuals cannot be removed from the population and samples must therefore be taken in the field. In order to minimize the risk of killing animals these samples must be small (*ca.* 0·05 ml) and a technique has therefore been devised to collect and transport the serum and to obtain the maximum return from small samples. Disposable polypropylene tips (10–200 µl size) for "Oxford" micropipettes are used. The fine end of the tip is heat sealed, the tip is sterilized and 0·05 ml sterile phosphate buffered saline put into the tip using a tuberculin syringe with a 21G × 1½" injection needle, care being taken that no air is trapped under the buffer. The

level reached by the buffer in the tube is then marked with a fine felt-tipped pen and the tip put into a 2 ml flat bottomed blood sample tube for storage and transport (Fig. 1).

The blood sample from the animal is put into the tip and centrifuged for *ca.* 3 min at 1500–2000 rev/min. This is best done in a centrifuge with a 6/12 V motor since this can be run off a car battery but a hand centrifuge is adequate. The tip (in its tube) is then placed in a Dewar flask containing liquid nitrogen or dry ice.

In the laboratory, the level reached by the blood and buffer in the tip is marked and the increase in level noted. Previous calibration makes it possible to determine the volume of blood taken and hence the dilution of the serum. While the serum is still frozen the end of the tip containing the red cells is cut off at the interface of the serum and red cells. A stainless

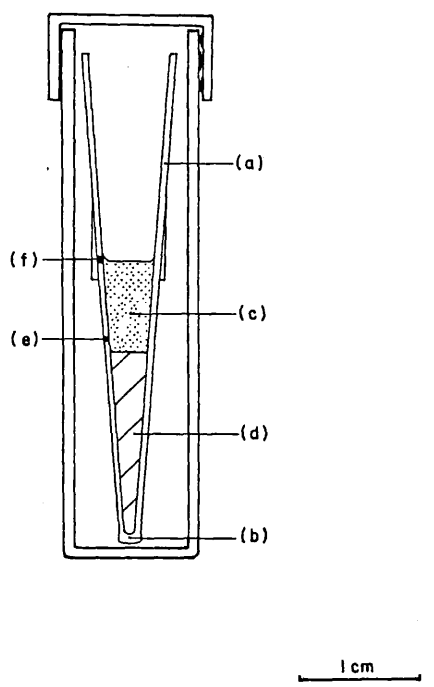


FIG. 1.

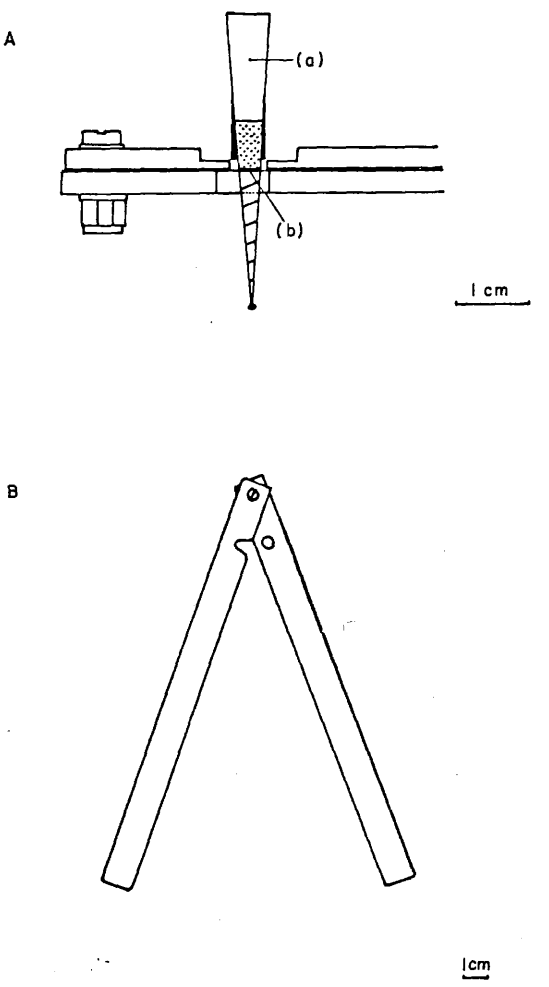


FIG. 2.

FIG. 1. A screw-capped plastic tube containing a filled "Oxford" tip. (a) "Oxford" tip; (b) sealed end; (c) serum and buffer; (d) red blood cells; (e) initial buffer level; (f) final level.

FIG. 2. (A) Tube cutter in cross-section. (a) "Oxford" tip; (b) cut at interface of serum and red cells; (B) tube cutter.

steel cutter suitable for this job is shown in Fig. 2 (this works with a shearing action). The presence of the buffer and the consequent dilution of the serum minimizes losses due to mechanical damage during cutting. The cutter must be carefully cleaned after each tip is cut. The red cell fraction may be used for isolating parasites or other pathogens.

The tip is then placed in an extractor, the serum is allowed to thaw and is then spun out of the tip into a 2 ml tube at *ca.* 1500 rev/min in a bench centrifuge. The extractor (Fig. 3) consists of the tip of a 5 ml or a 10 ml graduated pipette, cut down to a length of approx. 5 cm. A cork collar is cut from 8 mm thick cork using a No. 6 cork borer and hollowed using a No. 3 cork borer; this centralizes the pipette tip and prevents it being forced into the 2 ml tube in which the sample is collected. The whole system is put in a 15 ml centrifuge tube with cotton wool at the bottom to absorb the pressure of centrifugation.

This technique has proved very successful and allows samples as small as 0·01 ml (whole blood) to be used.

I would like to thank Professor C. Kaplan, Miss N. Evans, and Mrs A. Prior for their advice and Mr H. J. Bolton for his help and skill in making a centrifuge and in devising and making the tube cutter. The work was supported by the Agricultural Research Council.

T. D. HEALING, Department of Microbiology, The University of Reading.

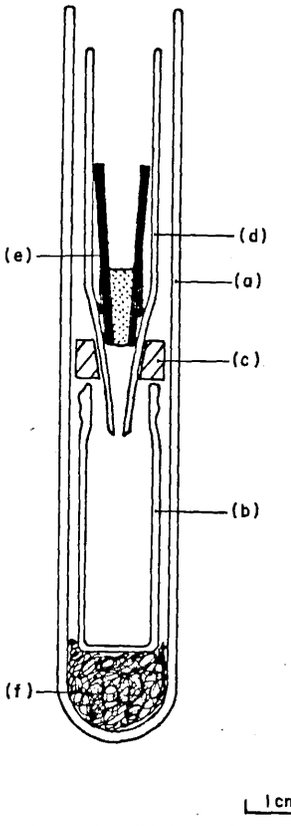
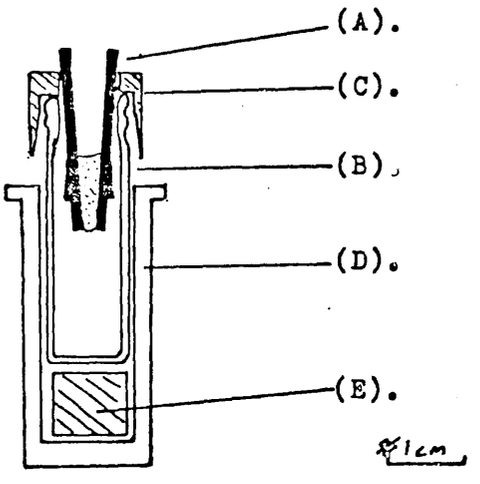


FIG. 3. Serum extractor. (a) 15 ml centrifuge tube; (b) 2 ml glass tube; (c) cork washer; (d) tip of graduated pipette; (e) "Oxford" tip, with the end cut off and containing serum; (f) cotton wool.

A method for the collection of small volumes of whole blood in the field and their preparation for serological studies: Addendum.

A modified serum extractor, suitable for both field and laboratory use, and which eliminates the need for large numbers of the type of extractors described in the main text, is illustrated below.

The cut tip (A) is supported in the neck of the collecting tube (B) by an aluminium collar (C). The tube is supported in the centrifuge bucket (D) by an aluminium block (E) which is removable



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APPENDIX 6.

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Evidence of infection by viruses in small British field rodents

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SUMMARY

Four populations of small wild British rodents were studied by capture–re-capture methods over a period of three years. Samples of blood were taken from these animals and tested for antibodies to nine viruses. Animals were removed from another 11 sites around the UK, and immunosuppressed. Samples of tissue from these animals were tested for the presence of viruses by passage in laboratory mice and serum samples from some of them were tested for antibody to the nine viruses. Indications were found of the possible influence of epizootic outbreaks of certain diseases on animal populations.

INTRODUCTION

The role of communicable disease in the control of wild animal populations is not clear. Elton, Davis & Findlay (1935) undertook an investigation of virus infections in voles (*Microtus agrestis*) but were unable to report positively on their findings after several years. In the forty years that have elapsed since their pioneering work, the sensitivity of virological and serological methods has been greatly increased. We thought it opportune, therefore, to reopen the investigation, since although much epidemiological work has been done on animal reservoirs and carriage of individual viruses of public health importance, the role of infection in the population dynamics of natural wild populations has been neglected.

In addition, because of reports from Central Europe of the presence of rabies-like viruses in field rodents (Sodja, Lim & Matouch, 1971; Schneider, 1972) we took the opportunity to test neural tissues of British field rodents for the presence of neurotropic viruses including rabies and rabies-like viruses.

METHODS

Rodent species studied

The species studied were the Woodmouse (*Apodemus sylvaticus*), the Bank Vole (*Clethrionomys glareolus*), the Skomer Vole (*Clethrionomys glareolus Skomerensis*)

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Table 1. *Sites visited once only during the project*

Banchory, Kincardineshire	July	1977
Tregaron, Dyfed	May	1978
Marlborough, Wilts.	May	1977
Thatcham, Berks.	March	1978
Woodley, Berks.	—	1977 (various dates)
Bagnor, Berks.	July	1977
Alton, Hants.	February	1978
Rye, Sussex	March	1978
Babraham, Cambs.	May	1978
Coxtie Green, Essex	May	1978
Sheffield, Yorks.	April	1978

and the Short-tailed Field Vole (*Microtus agrestis*). A few examples were obtained of Yellow-necked mice (*Apodemus flavicollis*).

Study areas

Four areas were studied throughout the project, Laurieston, Kirkcudbrightshire; Llanerchyrfa, Powys; Oakfield, Berkshire; and Skomer Island, Dyfed. In addition, a site at Alice Holt, Hampshire was studied for one year (1976) and eleven other sites (the subsites) (Table 1) were visited once only during the project.

Field work

Squared trapping grids of 0·49 Ha with 10 m interstation distances were established at the four main sites and visited at approximately six-weekly intervals, except for Skomer which was visited once a year. The animals were caught in Longworth traps (Chitty & Kempson, 1949), hay being provided for bedding and oats for food. After capture the animals were removed from the traps, identified, weighed, sexed, and assigned to an age class – they were individually marked by means of toe clipping. Samples of blood were taken for the detection of antibodies. The blood samples were taken from the tail, ethyl chloride being used to stimulate a reactive hyperaemia. The blood was then prepared for serological study by the method described by Healing (1978). In order to prevent the transmission of pathogens from one study area to another, the traps were autoclaved before each trapping session and the trap and animal carriers were washed in a 5 % solution of 'Tegodor' (Th. Goldschmidt Ag. Essen).

The rodent populations were calculated using Jolly's stochastic population model (Jolly, 1965). These results will be published elsewhere (Healing & Kaplan, in preparation).

Any animals found dead in the traps and animals caught during the single visits to the subsites were brought back to the laboratory for analysis.

Antibodies

The blood samples were analysed for antibodies to the various viruses by Complement Fixation (CF) and Haemagglutination Inhibition (HAI). Micro-methods were employed using 'Microtiter' mechanical diluting apparatus and

Table 2. *Viruses studied with the provenance of the antigens and antisera*

Ectromelia (Mouse pox) virus (Professor K. R. Dumbell, St Mary's Hospital Medical School, London W2).
Mouse adenovirus (Professor J. van der Veen, University of Nijmegen, Netherlands).
Sendai virus (Parainfluenza virus 1) (University of Reading).
Pneumonia virus of mice (PVM) (Central Veterinary Laboratories, Weybridge, Surrey, England).
Louping ill virus (Mordun Institute, Edinburgh).
Lymphocytic choriomeningitis virus (LCM) (Virus Reference Laboratory, Central Public Health Laboratories, Colindale, London NW9).
Reovirus III (Department of Pathology, Royal Berkshire Hospital, Reading, England).
Encephalomyocarditis virus (EMC) (Dr F. Brown, Animal Virus Research Institute, Pirbright).
Theiler's mouse encephalomyelitis virus (GD VII) (Dr R. Shope, Department of Epidemiology, Yale University, New Haven Commune, USA).

'Microtiter' 96-well plastic plates (Flow Laboratories Ltd). For each antibody investigated a single batch of antigen was used. Antigen potencies were checked regularly.

Removed animals

Sixty-eight animals removed from the subsites were brought back to the laboratory and treated with ACTH as an immunosuppressant. Ten doses, each of 5 i.u., were given intramuscularly over a period of 14 days. The ACTH used was Synacthen Depot (CIBA Laboratories). In view of the small numbers of animals that could be obtained at any time, it was not possible to run controls. Animals which died following this treatment were dissected aseptically and 10% (w/v) suspensions of brain, lung, and spleen tissues were prepared in phosphate buffered saline using TenBroeck grinders. Similar suspensions were prepared from tissue taken from animals that died in the traps. Penicillin, streptomycin, and fungizone were added to these suspensions and they were then passaged in suckling mice by intracerebral inoculation. Mice that died following this procedure were dissected aseptically, tissue suspensions prepared as above and further passage undertaken.

Passage animals that did not die were killed by exsanguination three weeks after inoculation and their blood tested for antibodies to the various viruses. Immunosuppressed animals that did not die were killed by exsanguination at the end of the treatment and their blood tested for antibodies.

Viruses studied

The viruses studied are listed in Table 2, with the provenance of the antisera and antigens used.

RESULTS

Blood samples from the field

Four hundred and thirty-six blood samples were taken at Laurieston, Llanerchyrfa, Oakfield and Skomer and tested for antibodies to the viruses (Table 2).

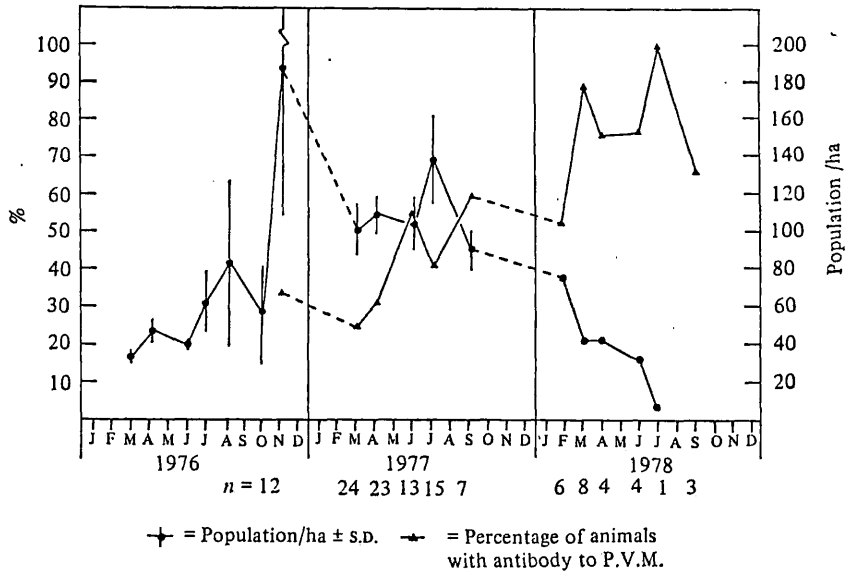

Fig. 1. Percentage of *Apodemus sylvaticus* at Oakfield with antibody to pneumonia virus of mice, related to calculated population size. *n*, Number of blood samples tested.

Some of these samples were very small and were only tested for antibody to PVM. Antibody to this virus cross-reacts slightly with Sendai virus and vice versa; some of the PVM positives may, therefore, have been due to antibody to Sendai virus. In the larger samples and the bloods from the animals that were immunosuppressed but did not die it was possible to distinguish clearly between these two infectious viruses.

Rodent populations and virus antibodies

Only for PVM and the two species, *Apodemus sylvaticus* and *Clethrionomys glareolus* from Oakfield, was there enough information to allow the percentage of individuals with antibody to the virus to be plotted against the populations (Figs. 1 and 2). The population data are drawn from Healing & Kaplan (in preparation). The PVM antibody data from Oakfield and from Skomer were examined for differences in occurrence of antibody to this virus between the two sexes (Table 3).

Removed animals

Fifty-two per cent of the animals treated with ACTH died during the treatment and dissection revealed gross pathological changes of the lungs consistent with pneumonia. Eighty-one animals were found dead in the traps and showed similar changes in the lungs on dissection. The suspensions made from the lungs of these animals were shown to be free of bacteria (before the addition of antibiotics). Of the animals brought in from the sub-sites, 22 which did not die during immuno-

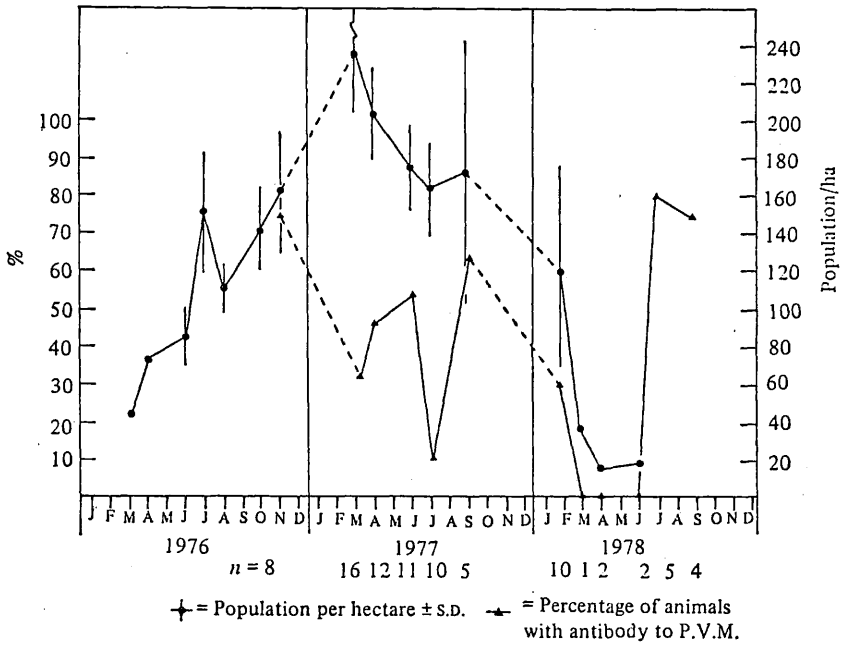

Fig. 2. Percentage of *Clethrionomys glareolus* at Oakfield with antibody to pneumonia virus of mice, related to calculated population size. *n*, Number of blood samples tested.

Table 3. *Antibody found in animal house stock after inoculation with tissue extracts from field rodents*

Tissue extract	Antibody in recipient mice
Spleen, A.f.*	LCM
Spleen, M.A.†	Reovirus III
Kidney, C.g.‡	Reovirus III; GDVII (at 2nd passage)
? A.s.§	GDVII (at 3rd passage)

* *Apodemus flavicollis*, Oakfield.
† *Microtus agrestis*, Alice Holt.
‡ *Clethrionomys glareolus*, Oakfield.
§ *Apodemus sylvaticus*, Thatcham.

suppression, were subsequently killed by exsanguination and their blood tested for antibodies to the various viruses by CF and HAI (Table 4).

Animal passage of tissue suspensions

Two hundred and sixty-nine tissue suspensions were prepared from field material and injected into suckling mice. The intracerebral route was used for all suspensions other than lung, which were inoculated intranasally. Twenty tissue suspensions were prepared from the 26 mice that died following inoculation and passaged again. In total, 5400 mice were used for passage. The sucklings were killed by exsanguination 21 days after inoculation and the bloods from each litter inoculated with a single suspension were pooled and CF and HAI tests performed. In total, 448

Table 4. *Serum samples with antibody*

	Oakfield		Laurieston		Llanerchyrfa		Skomer	Subsites			Total			
	As	Cg	As	Cg	As	Ma	CgS	As	Cg	Ma	As	Cg*	Ma	All†
Ectro	—	0/1	1/11	0/3	0/9	7/20	2/18	1/8	0/5	—	2/28	0/9	7/20	11/75
M. Adeno	1/4	0/1	—	—	—	—	0/4	0/7	0/4	0/2	1/11	0/5	0/2	1/22
Sendai	6/13	3/7	1/1	0/1	0/1	1/2	28/33	6/8	3/7	2/2	13/23	6/15	3/4	50/75
PVM	48/108	30/78	1/9	1/1	1/3	2/10	28/67	8/9	5/9	2/3	58/129	36/88	4/13	126/297
L. Ill	0/7	0/3	1/42	1/13	—	0/2	0/23	0/8	0/5	0/1	1/57	1/21	0/3	2/104
LCM	0/4	0/2	—	0/1	0/1	1/2	4/10	2/8	0/5	—	2/13	0/8	1/2	7/33
REO III	0/11	0/5	0/3	0/2	0/1	0/2	4/72	0/8	1/8	—	0/23	1/15	0/2	5/112
EMC	1/4	0/1	—	—	—	0/1	0/13	0/7	2/4	1/2	1/11	2/5	1/3	4/32
GD VII	1/5	0/2	—	0/1	—	0/1	11/46	0/6	0/5	0/2	1/11	0/8	0/3	12/68

–, Not tested; As, *Apodemus sylvaticus*; Cg, *Clethrionomys glareolus*; CgS, *Clethrionomys glareolus Skomerensis*; Ma, *Microtus agrestis*. * Excluding CgS. † Including CgS.

blood samples were tested. Antibodies to PVM and Sendai virus were present in many of these bloods but were also present in the animal house controls. A few positive reactions to other viruses were obtained (Table 3).

Rabies virus. No animal inoculated intracerebrally with suspension of neural tissue showed any signs of neurotropic infection.

Ectromelia virus. The orthopox viruses cross-react quite extensively; the positive results for the presence of complement-fixing antibody can thus only be taken as indicating the presence of antibody to one or more orthopox viruses in the blood of the animals studied.

Ectromelia itself is a highly contagious and often fatal infection which frequently occurs in laboratory mice. It can be carried in latent form by individual mice and activated by stress (Andrewes, Pereira & Wildy, 1978).

Antibody to pox viruses was demonstrated in Skomer voles but not in the (rather small) group of mainland bank voles. Such antibody was also found in a small number of woodmice and a rather large number of short-tailed voles. Although 7/13 short-tailed voles from Llanerchyrfa were positive for pox-virus antibody, none of the nine woodmice examined was (Table 4).

Murine adenovirus. Like the pox viruses, the adenoviruses cross react, and any field results can only be considered as indicating the presence of adenoviruses in the wild animals. In laboratory stocks, murine adenovirus can fatally infect both suckling mice and adults, or cause inapparent infections (Andrewes *et al.* 1978). Antibody to adenovirus was found only in one woodmouse (from Oakfield) but the groups examined were small.

Sendai virus (*Parainfluenza type* I). Antibodies to Sendai virus were present in a large proportion of the animals examined. The slight cross reaction of Sendai with PVM has already been mentioned, but in all the positive sera (Table 4) it was possible to distinguish between the two by testing against both viruses; the titre against Sendai virus was always higher.

Pneumonia virus of mice. The results of tests for antibodies to PVM must be treated with caution owing to the possibility of cross reaction with Sendai virus. A large proportion of the samples were indeed tested for both, but in the case of the smaller samples it was only possible to test for PVM. These small samples were, however, mostly diluted 1/10 and cross-reactions occurred only occasionally at this dilution.

The presence of antibody to both PVM and Sendai virus in the animal-house stock at Reading University rendered abortive much of the passage work undertaken.

Louping ill virus. Smith, Varma & McMahon (1964) found louping ill in woodmice in Ayrshire. The present study demonstrated the presence of antibodies to louping ill in one woodmouse and one bank vole at the Kirkcudbrightshire site. Samples taken elsewhere in the United Kingdom (Table 4) were negative.

Lymphocytic choriomeningitis virus. Although house mice (*Mus musculus*) are probably the principal natural reservoir of LCM (Lehmann-Grube, 1971) a number of other rodent species have been implicated. According to Lehmann-Grube (1971) several authors have tested a number of species of small mammals both for the

virus itself and for antibody in their sera. Of 24 named species only 6 species of rodent were positive. The rodents were *Mus musculus*, *Microtus arvalis*, *Clethrionomys glareolus*, *Apodemus sylvaticus*, *A. flavicollis*, and *A. microps*. We examined a small sample of rodents for antibody to LCM and positive results were only obtained from Skomer (the Skomer vole), Llanerchyrfa (*M. agrestis*), Babraham (*A. sylvaticus*) and Rye (*A. sylvaticus*). A patchy distribution of LCM is not uncommon (Lehmann-Grube, 1971).

Reovirus III. Reoviruses cross react and cannot be distinguished by CFT. During the present study antibodies to Reovirus were found in one bank vole (from Essex) and in four Skomer voles.

EMC virus. Antibody to EMC virus was found in all three species studies on the mainland but not in the few Skomer voles tested. Andrewes *et al.* (1978) suggested that infection in wild rodents is probably inapparent, but its role in wild populations is not known.

GD VII. Antibody reacting with GD VII was detected in a single woodmouse at Oakfield and in several Skomer voles. In laboratory mice, infection with this virus usually causes inapparent intestinal infection (Andrewes *et al.* 1978).

DISCUSSION

Sodja *et al.* (1971) and Schneider (1972) have reported an isolation rate for rabies-like viruses from European field rodents of between 2% and 3%. Steck (1972) who has also isolated such viruses believed he could not exclude the possibility of a laboratory contamination. We were particularly careful to prepare all tissues for intracerebral inoculation in a class-3 safety cabinet which was sterilized frequently by exposure to formaldehyde and water vapour. Our failure to isolate rabies virus probably indicates its absence from the populations we investigated.

Although some of the groups in which particular antibodies were found were rather small, the results are nevertheless interesting since to the best of our knowledge no other survey has been made in the United Kingdom which covers so wide a geographical range. Antibody to all nine of the viruses used as test antigens was found in the blood of wild rodents. Each species of rodent studied lacked antibody to one or more of the viruses. Although the number of animals was usually small this may not have been a significant factor, since antibody to other viruses was found in equally small groups of animals. Assuming the presence of antibody to indicate a previous infection, woodmice were infected by the largest number of viruses (8/9), followed by Skomer voles (6/9), and mainland bank voles and short-tailed voles (5/9).

Some of the viruses in which we were interested are able to cause severe epizooties in mice (*Mus musculus*) housed in animal houses, e.g. ectromelia. The proportion of wild rodents with antibody to this virus was small except in *Microtus*, where 35% of the animals tested had antibody. All of these *Microtus* were caught at Llanerchyrfa, Powys during 1977 and 1978 when the population was small (Healing & Kaplan, in preparation). The coincidence of a relatively high incidence

Table 5. *Percentage of male and female animals with antibody to PVM*

		Males			Females		
Species	Date	No. tested	No. +ve	% +ve	No. tested	No. +ve	% +ve
Cg*	1977	24	8	33	30	12	40
	1978	14	5	36	10	5	50
CgS†	1977	13	0	0	15	2	13
	1978	20	14	70	19	12	63
As‡	1977	51	18	35	31	11	35
	1978	20	15	75	6	4	67

* *Clethrionomys glareolus*. Oakfield. All of 1977 and 1978 data.
† *Clethrionomys glareolus Skomerensis*. Skomer. August 1977 and 1978.
‡ *Apodemus sylvaticus*. Oakfield. All of 1977 and 1978 data.

of antibody to ectromelia virus and a small population may be significant of a recently antecedent epizooty of mousepox, but there is, of course, no way of confirming such a speculation.

The problem of cross-reacting antibodies has already been mentioned. The number of sera tested for antibodies to both PVM and Sendai virus was large and the results indicate that infections by both viruses were common in the populations studied as well as at the sub-sites sampled occasionally. The percentage of animals at Oakfield with antibodies to PVM was plotted against time for two rodent species (Figs. 1 and 2). For *Apodemus sylvaticus* there was an approximately inverse relationship between the population size and the percentage of animals with circulating antibody; for *Clethrionomys glareolus* the relationship was more direct. The results for 1978, when the rodent populations were low, are based on rather few animals and are difficult to interpret with certainty but suggest (Fig. 1 and Table 5) that there was an epizootic outbreak of PVM in the population of woodmice at Oakfield coinciding with a decline in the population. The data for the bank voles (Fig. 2 and Table 5) are less easy to interpret. Either there was no epizooty of PVM in this species or else bank voles are more susceptible than woodmice to respiratory infection and succumb more readily, which might explain reports (e.g. Ashby, 1967) that bank voles are particularly prone to death in trap. The results in Table 5 also suggest that there may have been an epizooty of PVM in the population of voles on Skomer Island in 1978. The population, which is rather stable (T. D. Healing, unpublished data), has been sampled in early August for several years and averaged $236{\cdot}5 \pm 14{\cdot}1$ animals per hectare from 1975 to 1977 inclusive. The numbers declined to 168·7/Ha in 1978 (population calculated using the capture–recapture model proposed by Hayne, 1949). Unfortunately no data on circulating antibodies are available for 1975 and 1976.

When rodents brought in from the field were immunosuppressed 52 % died with severe pneumonia. Animals that were immunosuppressed but survived were subsequently killed by exsanguination; they had no gross post-mortem signs of lung involvement. Tests on tissue suspensions made from the lungs of those animals that did die showed that the aetiology of the pneumonia was not bacterial.

The immunosuppressant was therefore either activating a latent infection, making apparent an inapparent infection, or turning a chronic infection into an acute infection. Of these three alternatives the last is less likely than the others, since the animals showed no signs of being in poor condition before treatment; their coats were sleek, their eyes clear, and their appetite good. In addition, obviously ill animals are rarely captured in small-mammal traps which have to be searched for actively; any animal that is unfit is unlikely to move far. We conclude, therefore, that the infections activated were either latent or previously inapparent. There is little chance that the animals contracted the infections in the animal house despite the existence of both PVM and Sendai virus there. It was not possible to run controls, but not all the immunosuppressed animals died of pneumonia and not all the surviving animals had antibody to PVM and/or Sendai virus.

The presence of latent or inapparent viral infections in wild rodent populations could be important in the control of such populations, particularly if the infections could be activated by stress. This is a topic we hope to study experimentally in managed populations.

Our thanks are due to Sir M. Milne-Watson, Mr J. Houston, The Economic Forestry Group, The West Wales Naturalists Trust Ltd, and the Forestry Commission for permission to trap at Oakfield, Laurieston, Llanerchyrfa, Skomer and Alice Holt respectively; the owners of the sub-sites; Mr F. Edwards for help with computing the population data, and the Agricultural Research Council who funded the project.

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APPENDIX 7.

Parasitology (1981), **83**, 179–189
With 4 figures in the text

Infections with blood parasites in the small British rodents *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*

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SUMMARY

Three populations of small wild British rodents were studied by capture–recapture methods over a period of 3 years, a fourth group was studied for 1 year and a fifth was sampled annually for 4 years. Blood smears were taken from 3 species of rodents: the woodmouse *Apodemus sylvaticus*, the bank vole *Clethrionomys glareolus* (and an island sub-species *C.g. skomerensis*) and the short-tailed vole *Microtus agrestis*. The smears were examined microscopically. Four genera of haemoparasites *Babesia*, *Hepatozoon*, *Trypanosoma* and *Grahamella* were detected. *Babesia* was absent from *C.g. skomerensis*, *Hepatozoon* was rarely found in *A. sylvaticus* and *M. agrestis* and *Trypanosoma* was rare in *A. sylvaticus*. More males were infected than females but the difference was only statistically significant for the infection with *Hepatozoon* in adult *C.g. skomerensis*. Infections with *Babesia* and *Hepatozoon* were more prevalent in adult animals and infections with *Trypanosoma* were more prevalent in younger individuals. Only in *C.g. skomerensis* was there a significant difference between age classes in the prevalence of infection with *Grahamella* – there being more adults infected. Concurrent infections were detected, *Hepatozoon* being the parasite most commonly involved. The prevalence of infections was found to be approximately proportional to the number of animals known to be alive, regardless of the season.

INTRODUCTION

The small wild rodents of the British Isles have been the subject of intensive study but relatively little work has been done on their haemoparasites. The most detailed surveys have been those of Coles (1914), Elton, Ford, Baker & Gardner (1931) and Young (1970). Less extensive studies have been performed by Ring (1959) and by Baker, Chitty & Phipps (1963), and useful reviews of the protozoan parasites have been published by Cox (1970) and by Baker (1974). Few studies have been made of the seasonal and annual variation in the prevalence of blood parasites in small rodents, the main ones being by Young (1970), Krampitz & Baumler (1978) (in Bavaria; for *Babesia* only) and Wiger (1979) (in northern Norway). A study of viral infections in small wild British rodents (Kaplan, Healing, Evans, Healing & Prior, 1980) made possible a concomitant survey of blood parasites.

STUDY AREAS AND METHODS

Three study areas were used throughout the project, Laurieston in Kircudbrightshire (National Grid Reference: NX 678 649), Llanerchyrfa in Powys (N.G.R: SN 836 557) and Oakfield in Berkshire (N.G.R: SU 673 664). A site at Alice Holt, Hampshire (N.G.R: SU 805 425) was used during the first year of the project and Skomer Island, Dyfed (N.G.R: SM 727 096) was visited annually. The study sites at Laurieston and Llanerchyrfa were in grassy upland areas that had recently been planted with Norway spruce (*Picea abies*), Oakfield was covered by mixed broadleaved woodland and Alice Holt was an area of grassland with some young (approximately 10-year-old) beech trees (*Fagus sylvatica*). The Skomer site was in an area of bracken (*Pteridium aquilinum*) with bluebells (*Endymion non-scriptus*) and some grass.

Woodmice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareolus*), and short-tailed voles (*Microtus agrestis*) were caught at all the mainland sites except Alice Holt where only *M. agrestis* was present. Skomer voles (*Clethrionomys glareolus skomerensis*) and *A. sylvaticus* were caught on Skomer Island. The animals were caught in Longworth traps laid out on chequer board grids of 0·49 Ha with 10 m interstation distances. Each grid on the mainland was trapped for 5 successive nights at intervals of approximately 6 weeks; Skomer was visited early in August each year, the grid being trapped for 5 successive nights on each visit. The animals were marked individually by toe clipping and their reproductive age determined. Two age groups were defined, immature or pre-breeding animals and adult or breeding animals. The immature age group included newly weaned animals in their first grey coat and animals which had moulted into the adult coat but which showed no sign of sexual maturity. Those males whose testes were scrotal and those females which showed patent vaginae and/or evidence of pregnancy (by palpation or from the results of vaginal smears) and parturition (milky mammae and plucked hair around the teats) comprised the adult group. This group also included animals which were known to have bred but which had gone out of breeding condition at the end of the breeding season.

Blood samples were taken from the tails of the animals and thin smears were prepared and air dried. The smears were fixed in absolute methanol, stained for 1 h in Giemsa stain diluted 1/10 in buffered water (pH 7·0) and then rinsed briefly in 2 changes of buffered water (Cruikshank, Duguid, Marmion & Swain, 1975). The smears were scanned at magnifications of 100× and 1200× with a Leitz microscope to detect parasites, 50 fields being examined at each magnification. Chi-squared tests were performed on the original data to establish statistical significance, if any, in the differences detected. Probabilities of 5% or less were regarded as significant. No attempt was made to calculate the size of the rodent populations using statistical methods because the method of sampling was not random (Krebs, 1966). Instead, the minimum number of each species alive/hectare at each site and time was determined.

RESULTS

A total of 501 samples was obtained from *A. sylvaticus*, 508 from *C. glareolus*, 321 from *M. agrestis* and 345 from *C.g. skomerensis*. Since several samples were obtained from some animals over a period of time, only the first record of a parasitic genus in the individual animal was used in the analyses. Three genera of haemoprotozoa were detected; *Babesia*, *Hepatozoon* and *Trypanosoma*. *Grahamella*, a member of the Bartonellaceae, was also found. All 4 genera of parasites were found in the 3 mainland host species studies whilst *Babesia* was not detected on Skomer Island (Table 1). Less than 20 % of *A. sylvaticus*, 33·8 % of *M. agrestis*, 51·1 % of *C. glareolus* and 60·8 % of *C.g. skomerensis* had detectable infections. The prevalences of the individual parasitic genera were also lowest in *A. sylvaticus* (with the exception of the infection with *Grahamella*, fewer *C. glareolus* being infected with this genus) and highest in *C.g. skomerensis*. There was a range of prevalence of infections for each host species and each parasitic genus at the different sites (Table 2).

The data were examined to establish whether any relationship existed between the reproductive age of the host and the proportion of individuals infected with the different parasitic genera (Table 3). Statistically significant differences in the numbers of infected individuals of the different age classes were demonstrated for several of the hosts and parasites. *Babesia* was more common in adult *A. sylvaticus* and *M. agrestis* than in immature individuals. *Trypanosoma* was found in immature rather than adult animals. *Hepatozoon* was more common in adult *C.g. skomerensis* than in immature animals but there were no significant differences in mainland *C. glareolus*. Only in *C.g. skomerensis* was there a statistically significant difference between age classes in infections with *Grahamella*, with a greater proportion of adults being infected.

Tests were also made within the age groups to detect differences between males and females but these were not statistically significant, except for infection with *Hepatozoon* in adult *C.g. skomerensis* where 86·3 % of males and 52·7 % of females were infected ($P < 0{\cdot}001$; χ^2 test on original data). When the data on adult and immature host animals were combined and males compared with females, although a larger proportion of the males was infected with each parasitic genus, the differences were not statistically significant. A total of 138 concurrent infections, 126 double infections and 12 triple infections were detected. The majority of the concurrent infections occurred in *C.g. skomerensis* (49·3 %) and in *C. glareolus* (36·2 %). Of the rest, 11·6 % occurred in *M. agrestis* and 2·9 % in *A. sylvaticus*. *Hepatozoon* was the parasitic genus most commonly involved in concurrent infections (71·7 %) followed by *Grahamella* (62·3 %), *Trypanosoma* (46·4 %) and *Babesia* (44·3 %). The associations between the various parasitic genera in concurrent infections were determined (Table 4).

In order to detect seasonal changes in the prevalence of new infections, the numbers of such infections with each parasitic genus detected on each visit to a trapping site and the minimum numbers of animals known to be alive/hectare were plotted against time for *A. sylvaticus* and *C. glareolus* from Oakfield, for *M. agrestis* from Llanerchyrfa and for *A. sylvaticus* from Laurieston (Figs 1–4). For each species at each site the numbers of new infections detected were approximately

Table 1. *Percentage infection with various parasitic genera*

Host species	No. of samples tested	Percentage of total infected	Percentage of individuals infected with			
			Babesia	*Hepatozoon*	*Trypanosoma*	*Grahamella*
Apodemus sylvaticus	494	18·5	6·8	0·4	1·0	10·5
Clethrionomys glareolus	448	51·1	12·7	32·8	11·1	8·3
C.g. skomerensis	334	60·8	0·0	45·8	14·1	16·2
Microtus agrestis	311	33·8	13·5	1·3	10·3	15·4

Table 2. *Percentage infection with parasitic genera at different sites*

Host species and site	No. of samples tested	Percentage infected	Percentage infected with			
			Babesia	*Hepatozoon*	*Trypanosoma*	*Grahamella*
Apodemus sylvaticus						
Laurieston	140	15·0	2·1	0·7	2·9	10·7
Llanerchyrfa	38	7·9	2·6	0·0	0·0	5·3
Oakfield	300	22·3	10·0	0·3	0·3	18·3
Skomer Island	16	0·0	0·0	0·0	0·0	0·0
Clethrionomys glareolus						
Laurieston	73	45·2	9·6	28·8	9·6	1·4
Oakfield	375	52·3	13·3	33·6	11·5	9·6
C.g. skomerensis	334	60·8	0·0	45·8	14·1	16·2
Microtus agrestis						
Laurieston	49	38·8	4·1	0·0	12·2	22·4
Llanerchyrfa	154	33·8	10·3	1·9	14·3	17·5
Alice Holt	108	31·5	22·2	0·9	3·7	9·3

Table 3. *Percentage of adult and immature animals infected with the various parasitic genera*

	Apodemus sylvaticus		*Clethrionomys glareolus*		*C.g. skomerensis*		*Microtus agrestis*	
Babesia								
Adult	9·5	$P < 0{\cdot}05$†	14·0		0·0		18·6	$P < 0{\cdot}01$†
Immature	3·9		10·3		0·0		7·2	
Hepatozoon								
Adult	—		33·6		71·6	$P < 0{\cdot}001$†	1·2	
Immature	1·0*		31·4		21·2		1·4*	
Trypanosoma								
Adult	0·7		6·8	$P < 0{\cdot}001$†	6·0	$P < 0{\cdot}001$†	7·0	$P < 0{\cdot}05$†
Immature	1·5*		19·2		23·8		14·4	
Grahamella								
Adult	9·5		9·9		21·3	$P < 0{\cdot}01$	13·4	
Immature	12·7		5·1		9·9		18·0	

* Positive sample very small.
† χ^2 tests performed on original data.

Table 4. *Concurrent infections: percentage of infections with parasite 'A' associated with parasite 'B'*

'A'	'B'	Including Skomer Island data	Excluding Skomer Island data
Babesia	*Hepatozoon*	45·7	45·7
	Trypanosoma	17·1	17·1
	Grahamella	37·1	37·1
Hepatozoon	*Babesia*	18·4	36·4
	Trypanosoma	33·3	34·1
	Grahamella	48·3	29·5
Trypanosoma	*Babesia*	10·9	16·7
	Hepatozoon	52·7	41·7
	Grahamella	36·4	41·7
Grahamella	*Babesia*	17·3	31·7
	Hepatozoon	56·0	31·7
	Trypanosoma	26·7	36·6

proportional to the numbers of animals known to be alive whether these numbers fluctuated annually or over a longer period. No epizootic outbreaks were detected during the present study.

DISCUSSION

Small prevalence of infection by certain genera of haemoparasites of, or indeed the total absence of these parasitic genera from, populations of the small rodent species involved in the present study have been noted previously (Elton *et al.* 1931; Ring, 1959; Baker *et al.* 1963; Young, 1970; Krampitz & Baumler, 1978; Wiger, 1979).

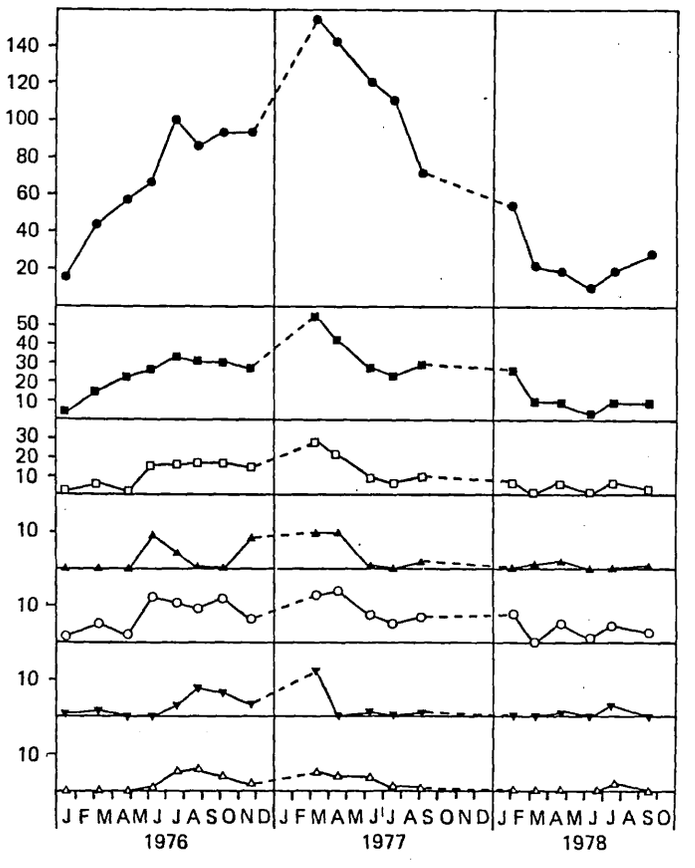

Fig. 1. *Clethrionomys glareolus*: Oakfield. Minimum number alive/hectare and the numbers of new infections with the various parasitic genera detected on each visit to the trapping site. ●, Minimum no. alive/hectare; ■, no. of animals sampled; □, total no. of animals with new infections; ▲, no. of new infections with *Babesia*; ○, no. of new infections with *Hepatozoon*; ▼, no. of new infections with *Trypanosoma*; △, no. of new infections with *Grahamella*.

The host animals were divided into 2 age classes on the basis of their reproductive age. The term 'reproductive age' is used here for 2 reasons. Firstly, the samples were taken at intervals of 6 weeks or more which meant that it was difficult to assign an accurate temporal age to the animals – especially since a total count of the animals was not attempted and an animal could have been present on a study grid but not caught during one or more visits. Secondly, in the rodent species studied, animals engaged in reproduction may have been of different temporal age. Thus, those animals forming the population at the beginning of the breeding season would have been born the previous year and could have been nearly 1 year old. It is possible for animals born early in the breeding season to mature and breed at the age of 2 or 3 months and this may have applied to my sample. This would not have applied on Skomer Island because Skomer voles rarely, if ever, breed in the year of their birth (Jewell, 1966; T. D. Healing, unpublished observations). Parasites of the genus *Babesia* infect a wide variety of

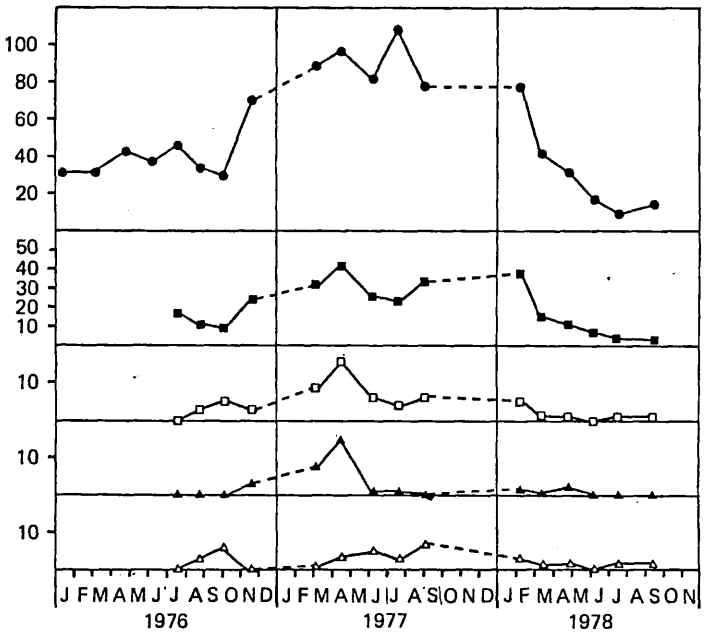

Fig. 2. *Apodemus sylvaticus*: Oakfield. Minimum number alive/hectare and the numbers of new infections with the various parasitic genera detected on each visit to the trapping site. ●, Minimum no. alive/hectare; ■, no. of animals sampled; □, total no. of animals with new infections; ▲, no. of new infections with *Babesia*; △, no. of new infections with *Grahamella*.

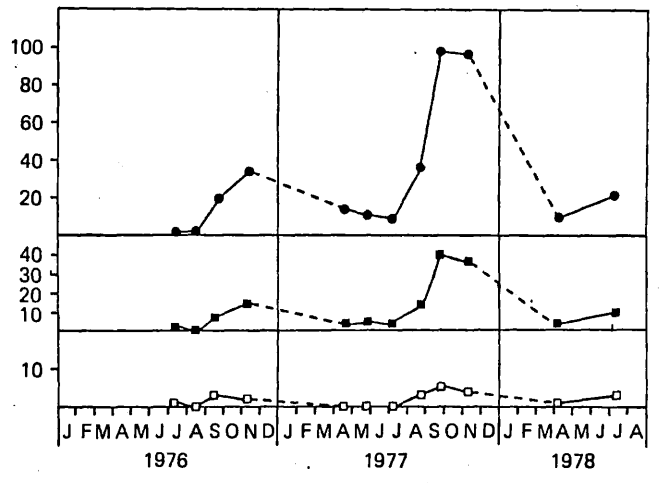

Fig. 3. *Apodemus sylvaticus*: Laurieston. Minimum number alive/hectare and the numbers of new infections with the various parasitic genera detected on each visit to the trapping site. ●, Minimum no. alive/hectare; ■, no. of animals sampled; □, total no. of animals with new infections (mostly *Grahamella*).

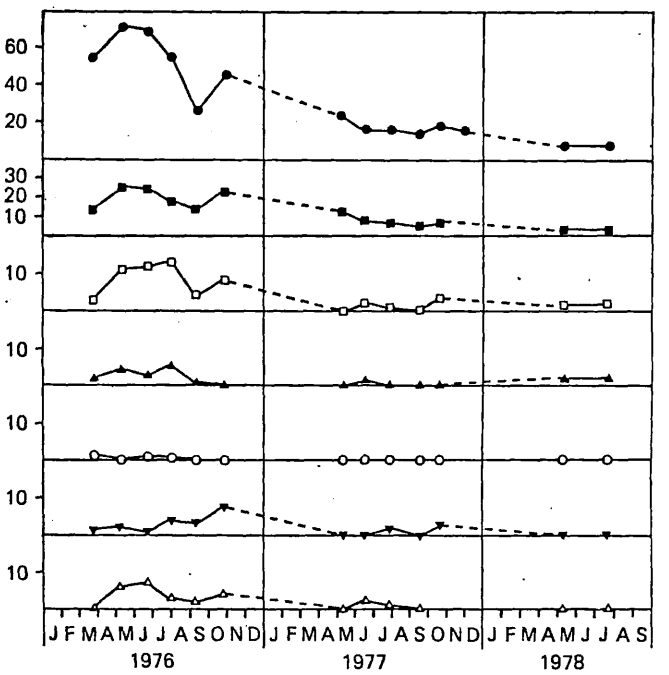

Fig. 4. *Microtus agrestis*: Llanerchyrfa. Minimum number alive/hectare and the numbers of new infections with the various parasitic genera detected on each visit to the trapping site. ●, Minimum no. alive/hectare; ■, no. of animals sampled; □, total no. of animals with new infections; ▲, no. of new infections with *Babesia*; ○, no. of new infections with *Hepatozoon*; ▼, no. of new infections with *Trypanosoma*; △, no. of new infections with *Grahamella*.

hosts. Cox (1970) considered that one species, *B. microti*, is common to *A. sylvaticus*, *C. glareolus* and *M. agrestis*. In general, young animals tend to be more susceptible than older individuals to *Babesia* spp. (Zwart & Brocklesby, 1979). The results of the present study appear to be in conflict with this observation but it is possible that antibodies obtained from the mother may have protected very young animals. Krampitz & Baumler (1978) reported that the prevalence of infection with *Babesia* in *M. agrestis* was greater in heavier (i.e. older) animals. They also reported that infections with *Babesia* were 3 times more prevalent in males than in females and were absent from pregnant females.

A. sylvaticus and *M. agrestis* were rarely infected with *Hepatozoon*. This may have been due to a reluctance by the vector to feed on these hosts or to an innate species resistance on the part of the hosts. It is not clear why the data from *C.g. skomerensis* should show such a bias towards infection in the adult males whereas the data from *C. glareolus* caught at mainland sites did not. However, the samples from Skomer Island were all obtained at the same date in each year whereas those from the mainland were obtained throughout the year. This difference may therefore be the reflexion of a seasonal effect (due possibly to an upsurge in the vector population) but not enough data are available.

The trypanosomes of the small rodent species captured during the present study are extremely host specific (Cox, 1970). Their classification needs revision (Cox,

1970) but they most closely resemble *T. musculi* (F. E. G. Cox, personal communication). The reproduction of *T. musculi* in the blood of rodents is gradually reduced by a reproduction-inhibiting antibody and ultimately the immune response eliminates the parasites from the blood (Mansfield, 1977) although they may persist and reproduce in small numbers in the internal organs (Wilson, Viens, Targett & Edwards, 1973). The vectors of *T. musculi* are probably fleas (Hoare, 1972). Whether the trypanosomes of the rodent species studied during the present project are also transmitted by fleas is not known. Molyneux (1969) was unable to find intracellular forms of *T. musculi*-like trypanosomes in the mid-gut cells of fleas (*Nosopsyllus fasciatus*) fed on infected *C. glareolus* and *M. agrestis*. *N. fasciatus* is not the only flea found on these host species, however, (Handbook of British Mammals, 1977) and may not have been the normal vector of their trypanosomes. If the trypanosomes detected during the present study behave in a way similar to *T. musculi* then early exposure to fleas in the nest, combined with an early and possibly permanent elimination of the parasites from the blood, would tend to confine this parasite to younger animals, but such an explanation must be regarded as speculative. Wiger (1979) found that the majority of infections with *Trypanosoma* that he detected were in rodents weighing 15–20 g, that is to say the older part of my immature group. Antibody acquired from the mother may protect younger animals. Innate species resistance to *Trypanosoma* may explain the rarity of infection with this parasite in *A. sylvaticus*.

Several parasitic genera comprise the Bartonellaceae but the only one found as patent infections in wild rodents during the present study was *Grahamella*. Patent infections with two other members of the group, *Haemobartonella* and *Eperythrozoon*, have been reported in the rodent species caught during the present study but they are rare (Young, 1970) and were not positively identified during this project. There is very little information on the immunological response of the hosts to *Grahamella* (Weinman & Kreier, 1977).

The relationship between the sex of the host and the prevalence of parasitic infections is not well understood. Nicol, Bilbey, Charles, Cordingley & Vernon-Roberts (1964) and Nichol, Vernon-Roberts & Quantock (1965) showed that oestrogen is a most effective stimulant of the reticulo–endothelial system and suggested that, whilst oestrogen is the principal natural stimulant of the body's defences in both male and female humans, the increased secretion of oestrogens in the female associated with the oestrous cycle and with pregnancy confers a particularly strong protection. The existence of such a mechanism in rodents would help to explain the sex differences found during the present study. The reason for the lack of statistical significance in the results from the mainland populations in the present study is not clear. It cannot be explained by the inclusion of data from the whole year because tests performed on the data from the breeding season alone (not tabulated) were also without statistical significance.

The paucity of concurrent infections in *A. sylvaticus* and *M. agrestis* (Table 4) can be explained by the rarity of infection with some of the parasitic genera in these host species. Concurrent infections in small rodents have been reported previously (Coles, 1914; Young, 1970).

What role parasitic infections may have played in the rodent populations studied is not known and indeed the whole role of disease in the dynamics of animal

populations has been the subject of much speculation (for example, Lack, 1954; Anderson, 1978). The degree to which an organism is pathogenic to its host depends on many factors including the nutritional status of the host, the degree to which the host is stressed and the presence or absence of other potentially pathogenic organisms.

The degree to which the parasitic genera studied during the present project were pathogenic to their hosts is not known. Wiger (1979) considered that these organisms do not play a role as mortality factors in populations of small rodents of the same species as those caught during the present study, but Mansfield (1977) has pointed out that normally non-pathogenic trypanosomes can produce a fatal disease if the hosts' immune mechanisms are seriously impaired. The effect of apparently non-pathogenic organisms may be indirect rather than direct; recent work has shown that the effect of a pathogen can be greatly modified by the presence of other parasitic species and that such an effect may be synergistic or antagonistic (Cox & Young, 1969; D'Alessandro, 1970; Salaman, Wedderburn & Bruce-Chwatt, 1969; Cox & Wedderburn, 1972; Carter, Chesterman, Rowson, Salaman & Wedderburn, 1970; Morrow, Kisuule, Pike & Smith, 1970). An organism may be pathogenic in one population of a host species but not in another simply because a second organism is present in one population and not in the other. A much more detailed knowledge of the role of pathogenic organisms in the dynamics of naturally occurring populations of wild animals is required if we are to understand fully the means by which such populations are controlled.

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APPENDIX 8.

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A note on some Enterobacteriaceae from the faeces of small wild British mammals

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(*Received* 1 *April* 1980)

SUMMARY

Over a four-year period 878 samples of faeces were collected from five species of small wild rodents and two species of shrews at sites in England, Scotland and Wales. A search was made for *Salmonella* in these samples but no isolations of this genus were made. Several other genera of Enterobacteriaceae were identified.

INTRODUCTION

Jones & Twigg (1976) searched for *Salmonella* in 16 species of wild mammals. Samples were obtained from 1269 animals but isolations of *Salmonella* were made from only eight house mice (*Mus musculus*) and seven of these were known to have been in contact with cattle artificially infected with *Salmonella*. These authors therefore concluded that infections with *Salmonella* in wild mammals in Britain were extremely rare. Gibson (1961 (cited in Jones & Twigg, 1976)) found a small incidence (0·6 %) of infections with *Salmonella* in rats (*Rattus norvegicus*) and Taylor (1968) suggested that infections with *Salmonella* are rare in house mice that are not in contact with infected man or domestic animals.

A survey of the carriage of viruses by small wild British rodents performed between 1975 and 1979 (Kaplan *et al.* 1980) made possible a concomitant search for *Salmonella*.

METHODS

The samples were obtained from several sites in the United Kingdom (Table 1). Seven small mammal species were sampled (Table 2).

Laurieston, Llanerchyrfa and Oakfield were visited at intervals of approximately 6 weeks from 1975 to 1979. Alice Holt was trapped at intervals of 6 weeks during the first half of 1976 and Skomer was visited annually in August. The remaining sites were each visited once only during 1977 and 1978. Few samples were obtained from these sites which were grouped together as the 'subsites'.

The animals were captured in Longworth traps. To prevent dissemination of infection the traps were sterilized by autoclaving between each trapping session and the trap carriers were washed in 5 % solution of Tegodor (Th. Goldschmidt Ag). Detailed descriptions of the study areas and trapping methods will be published elsewhere (Healing & Kaplan, in preparation).

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Table 1. *Sampling sites in the United Kingdom*

1	Laurieston, Kirkcudbrightshire	7	Rye, E. Sussex
2	Llanerchyrfa, Powys	8	Avington, Hampshire
3	Oakfield, Berkshire	9	Sheffield, Yorkshire
4	Alice Holt, Hampshire	10	Tregaron, Dyfed
5	Skomer Island, Dyfed	11	Babraham, Cambridgeshire
6	Thatcham, Berkshire	12	Coxtie Green, Essex

Table 2. *Small mammal species sampled*

Woodmouse	*Apodemus sylvaticus*
Yellow-necked mouse	*A. flavicollis*
Bank vole	*Clethrionomys glareolus*
Skomer vole	*C. glareolus skomerensis*
Short-tailed vole	*Microtus agrestis*
Red squirrel	*Sciurus vulgaris*
Common shrew	*Sorex araneus*
Pygmy shrew	*S. minutus*

Table 3. *Numbers of samples of faeces*

	Laurie-ston	Llaner-chyrfa	Oak-field	Alice Holt	Skomer	Subsites	Total
Apodemus sylvaticus	48	22	207	—	5	19	301
A. flavicollis	—	—	3	—	—	—	3
Clethrionomys glareolus	20	4	191	—	—	6	221
C. g. skomerensis	—	—	—	—	68	—	68
Microtus agrestis	25	71	16	72	—	5	189
Sciurus vulgaris	1	—	—	—	—	—	1
Sorex araneus	14	31	37	—	7	5	94
S. minutus	—	1	—	—	—	—	1
Total (rodents)	94	97	417	72	73	30	783
Total (shrews)	14	32	37	—	7	5	95

Table 4. *Enterobacteriaceae from faecal samples*

	As	*Cg*	*Cgs*	*Ma*	*Sv*	*Sa*	*Sm*	Total (rodents)	Total (shrews)	Total
Hafnia alvei	5	7	3	2	1	13	1	18	14	32
Citrobacter freundii	1	1	1	—	—	1	—	3	1	4
Proteus vulgaris	1	—	—	—	—	—	—	1	—	1
P. mirabilis	1	—	—	—	—	—	—	1	—	1
Escherichia coli	2	1	—	—	—	—	—	3	—	3
Yersinia enterocolitica	1	—	—	—	—	—	—	1	—	1
Klebsiella rhinoschleromatis	—	—	—	—	—	1	—	0	1	1
Total	11	9	4	2	1	15	1	27	16	43

As, Apodemus sylvaticus; Cg, Clethrionomys glareolus; Cgs, C. glareolus skomcrensis; Ma, Microtus agrestis; Sv, Sciurus vulgaris; Sa, S. araneus; Sm, S. minutus.

When animals defaecated while being handled, the faecal pellets were collected in 2 ml vials, which each contained 1 ml Selenite broth (Lab M). The samples were kept at ambient temperature. When returned to the laboratory the tubes of broth were incubated for 24 h at 37 °C and then subcultured on DCLS agar (Lab M). These cultures were incubated at 37 °C and examined after 24 h, and again after 48 h if no bacterial growth had occurred by the first examination. Bacterial colonies having the appearance expected of non-lactose fermenting bacteria growing on this medium were then subcultured on modified brilliant green agar and XLD agar (Lab M) and incubated for 24 h at 37 °C. Any samples that were not eliminated by these means were tested biochemically using the API 20-E system. Those few which were provisionally identified as *Salmonella* by this system were subjected to more tests by the Veterinary Investigation Centre, Coley Park, Reading.

RESULTS

The number of faecal samples obtained from the different mammal species and the different sites are listed in Table 3. Of the samples, 835 were eliminated on the basis of their growth characters on the three agars: 313 samples were tested on modified brilliant green and XLD agar and of these 270 had growth characters indicative of common Enterobacteriaceae other than recognized pathogens such as *Salmonella* and *Shigella*. Some of these results are given in Table 4.

DISCUSSION

The results obtained during the present study support the conclusion of Jones & Twigg (1976) that infections with *Salmonella* in populations of small wild mammals are very rare and that such mammals are unlikely to constitute an important reservoir of infection for domestic animals. The bacteria other than *Salmonella* identified by the API 20-E system are almost all common inhabitants of the mammalian gut. The only isolate of particular interest is *Yersinia enterocolitica*, which has been associated with a number of different human illnesses. Its effect on wild mice is not known.

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Fig 33.

opulation graph.

of animals known to be alive per hectare.
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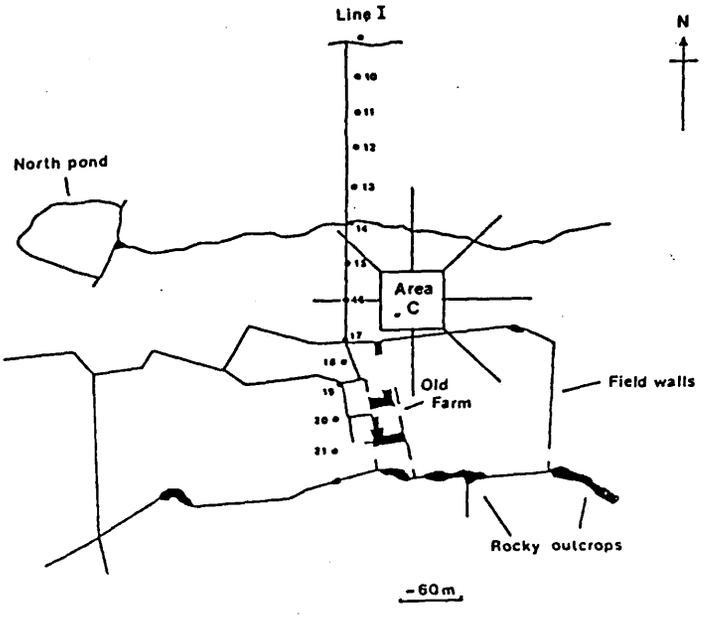
(c) Area 'C' and the radiating trap lines.



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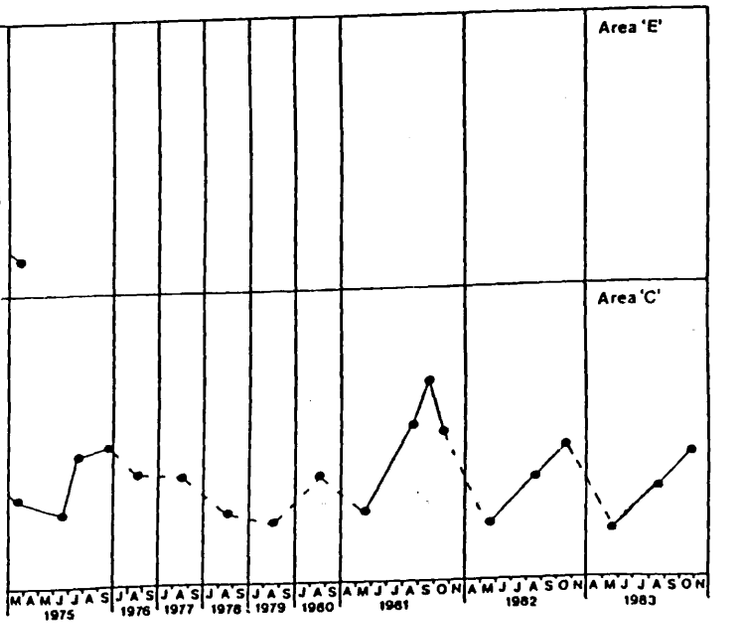

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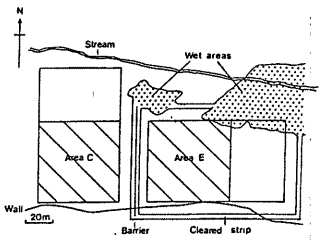
Endpaper. Definitions, maps, population graph.

Definitions

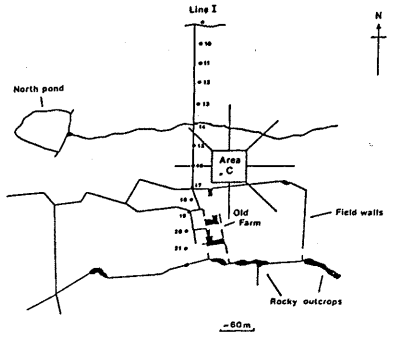
(1) MNA/ha - Minimum number of animals known to be alive per hectare.
(2) Juvenile (J) - Recently weaned sexually immature animal (grey coat).
(3) Immature (I) - Sexually immature animal (brown coat).
(4) Young adult (YA) - Animal maturing sexually in the year of its birth.
(5) Adult (A) - Animal born the previous year which is breeding or has bred.

(a) Skomer island (1), Farm (2), Study area (3), Neck (4), Little sound (5), Midland island (6), Jack sound (7), Mainland (8).

(b) Study area (for the removal experiment).



(c) Area 'C' and the radiating trap lines.



(d) Population graph (MNA/ha), 1971 - 1983.