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THE NATURAL HISTORY OF THE HOUSE MOUSE

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A review is given of the biology of the house mouse *Mus musculus*, L. correlating laboratory findings with those from the field. Special reference is made to the isolated population on the island of Skokholm, Wales. Appendices give techniques for dealing with material collected when studying mice.

CONTENTS

INTRODUCTION

SCIENTIFIC study of British mammals dates from the end of the nineteenth century. The early work was summarized by Barrett-Hamilton and Hinton in their (unfinished) *History of British Mammals* which appeared in twenty-one parts between 1910 and 1921. Interest in the ecology of mammals was stimulated by the work of Charles Elton (particularly by his *Animal Ecology* in 1927, and *Animal Ecology and Evolution* in 1930). Especially relevant in the present context is the research on the economics and control of mice and rats undertaken by the Bureau of Animal Population in Oxford under Elton's Directorship during the 1939–1945 war (q.v. Chitty and Southern, 1954). This contributed to the approach of the "new naturalists" who combine the discipline and quantitative methods of the laboratory, with the complexity and uncertainty of field studies. This outlook is represented by Harrison Matthews's *British Mammals* (1952) in the New Naturalist series (together with monographs in the same series by other writers), and by the *Handbook of British Mammals* (1964) produced by the Mammal Society under the editorship of H. N. Southern.

This paper is intended as a contribution of the same outlook. Too often the natural history of any animal is taken to mean merely the ecological factors controlling its

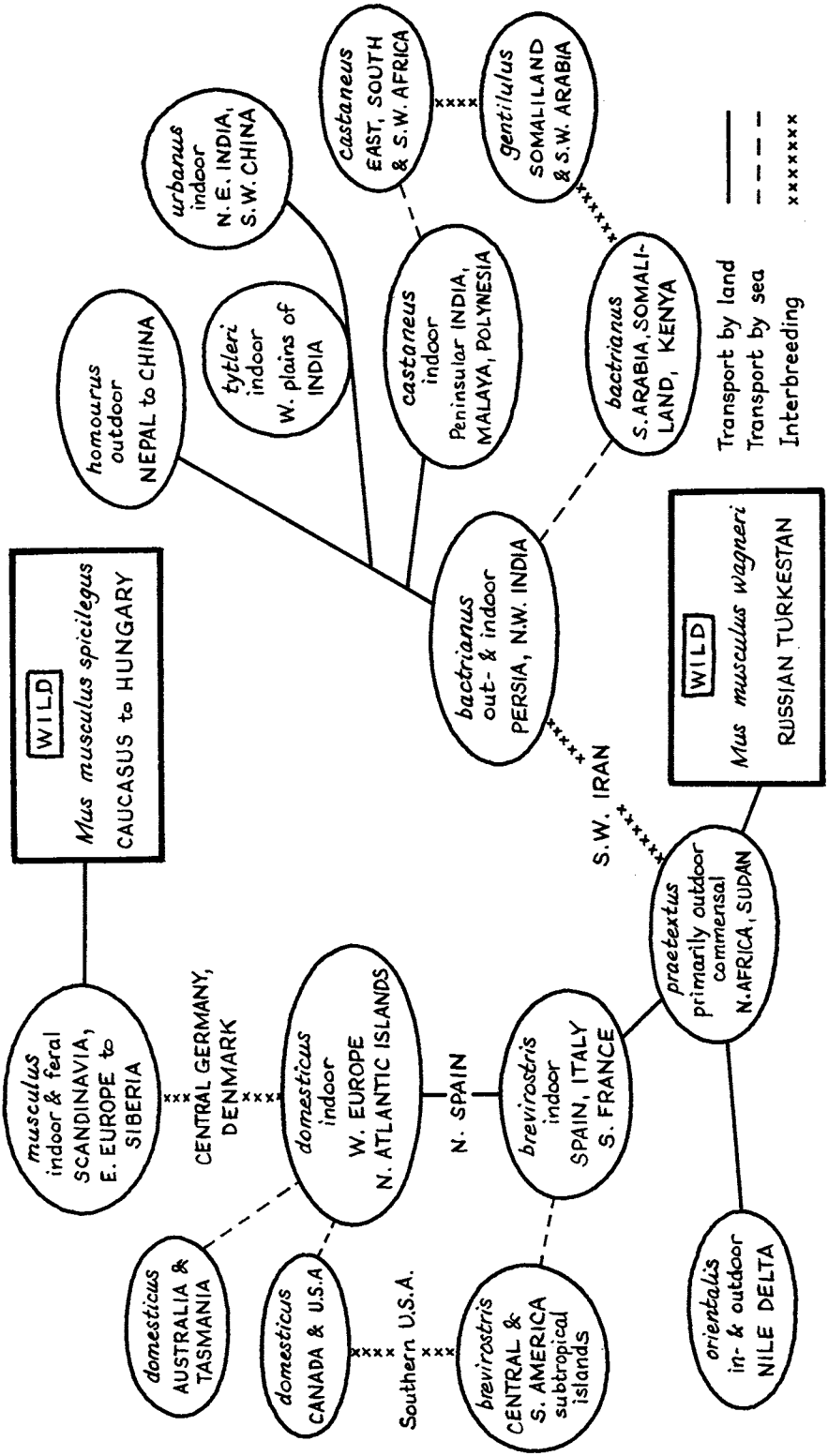

FIG. 1

Relationship between the sub-species of house mice derived from the wild-living *Mus musculus wagneri* and *M. musculus spicilegus* (after Matthews, 1952, based on Schwarz & Schwarz, 1943).

life-cycle. However, for a full understanding of population growth and decay, these factors have to be interpreted very widely, particularly with regard to the reactions of different animals to the same conditions (Anderson, 1970). For example, it is necessary to describe the characteristics and variations found in the mice themselves as well as in their environment, and to take into account the social structure of mouse communities at different times of the year. In a limited space it is not possible to do more than outline the main ecological themes, and leave the reader to follow up particular subjects. For this purpose I have given a large number of references, without claiming to have made anything like an exhaustive review of the literature. However, the reference list should serve as a complement to those in the large studies of the laboratory mouse on the one hand (Grüneberg, 1952; Green, 1966), and in the more general works on mammals on the other (e.g. Bourlière, 1955; Southern, 1964; Brink, 1967). Much of my work described herein was carried out in Pembrokeshire around the Dale Fort Field Centre, and on the island of Skokholm.

The origins and spread of mice

House mouse (*Mus musculus* L.) are commensal with man over virtually the whole of the tropical and temperate land masses of the world except part of tropical Africa. Fossil remains of the species are rare: the earliest record is from the early Pleistocene in the Crimea, where mice have been found associated with man (Anderson, pers. comm.). They occur also in the Middle Pleistocene of Hungary (230,000 years ago), and other members of the genus *Mus* have been described from Chinese Pleistocene deposits (Kurtén, 1968). These facts fit in with the conclusions of Schwarz and Schwarz (1943) based on a study of skulls and skins in museums. They suggested that *Mus musculus* originally lived on the borders of Persia and the U.S.S.R. and spread with man away from this savannah and steppe country. They recognized four wild sub-species, three of which (*M. musculus wagneri* Eversmann, *M. musculus spicilegus* Petenyi and *M. musculus manchu* Thomas) have given rise to commensal forms. The most important series has been derived from *M. musculus wagneri*, which lives in the dry area of central Asia east of the Volga (Fig. 1). From this region *wagneri* has spread, apparently with the practice of corn-growing: south and east, reaching from the Riu-Kiu islands and southern China to Malaya, Australia, Polynesia, India and East and South Africa; and westwards into North Africa and southern and western Europe. The mouse of southern Europe (*M. musculus brevirostris* Waterhouse) has been carried to the Latin American countries and the southern parts of the United States; the northern part of the United States and Canada has been colonized by the western European mouse, the dark-bellied *M. musculus domesticus* Rutty. A second centre of dispersal in southern Russia has produced the commensal *M. musculus musculus* from the wild *spicilegus* form. This light-bellied form occupies central Europe, extending into Denmark and Sweden. Although the different sub-species are apparently fully inter-fertile with each other in the laboratory (Zimmermann, 1949), they do not mix randomly in the wild. For example, there has been a narrow and apparently stable "hybrid" zone across southern Jutland in Denmark for at least 30 years (Degerbøl, 1935; Ursin, 1952; Selander, Hunt and Yang, 1969).

The earliest work involving the breeding of mice for scientific purposes seems to have been carried out by a Genevan pharmacist named Coladon who, before 1829,

bred large numbers of white and grey mice and obtained results in perfect agreement with Mendelian expectation at least 36 years before the publication of Mendel's researches on peas (Grüneberg, 1957). Later in the nineteenth century, many experimenters used mice to test the ideas of Francis Galton, who introduced statistical method into the study of heredity, and of whose *Hereditary Genius* (1869) Charles Darwin wrote: "I do not think I ever in all my life read anything more interesting and original."

After the rediscovery of Mendel's work in 1900, the results of such breeding became easier to interpret. The first inbred laboratory mice, as we know them today, were bred by C. C. Little in 1909, at the time a Harvard undergraduate. In the next few years, a large number of mouse strains were established, the founders being almost all mice obtained from dealers (Heston, 1949; Staats, 1966). These strains have provided the raw materials for a vast amount of genetical, pharmacological, cytological, behavioural, physiological, oncological and biochemical information, much of which could be applied to the "real-life" situation in nature to make the wild-living house mouse the best known mammalian species.

As well as the laboratory mouse industry, there is a large and flourishing mouse "fancy", which controls and organizes mouse shows in many places. The two main groups of fancy mice are "Self" (with coats of a single colour: black, fawn, silver, champagne, etc.) and "Marked" (dutch, tan, variegated, etc.).

The house mouse in Britain

From no good evidence, it is generally believed that house mice reached Britain in Roman times (e.g. Corbet, 1964). The species was known to classical Greek and Roman writers (Rolleston, 1868), but they do not mention it in their descriptions of Britain. However King Alfred knew the beast in the ninth century, and the writer of the Lambeth Homilies (1175) understood what he was about when he wrote: "When a man will bait his mouse-trap he binds thereupon the treacherous cheese and roasteth it so that it should smell sweetly; and through the sweet smell of the cheese, he entices many a mouse into the trap." The earliest Welsh record of the species appeared in 930 when Hywel Dda standardized the prices for cats: one penny for a new born kitten, twopence for an inexperienced youngster, but fourpence for a cat after it had caught a mouse. Good mousers were valued: the fine for killing any of the cats in the Chief's granary was either a ewe sheep and her lamb, or enough corn to cover the dead cat suspended by its tail and with its nose touching the floor.

A difficulty about most early records of "mice" is that the term tends to be applied to any small mouse-like rodent, and it is often impossible to recognize the species. Even commensalism may not be a guide, since the long-tailed field mouse (*Apodemus sylvaticus* (L.)) may be commensal with man in the absence of house mice (Berry, 1969*a*). Furthermore, archaeologists have a bad habit of ignoring any mouse remains they find when excavating, on the grounds that such animals burrow extensively and may be recent intrusions. When the term "mouse" is used without qualification in this paper, it should be taken to mean "house mouse".

THE CHARACTERISTICS OF THE HOUSE MOUSE

The house mouse is a member of the myomorph sub-order of the rodents, which includes the mice, voles, jerboas, etc. It belongs to the family Muridae (mice and

rats) which have three molars on each side in each jaw, each molar having a basic pattern of nine cusps. The voles (family Cricetidae) also have three molars, but these consist of several small columns joined to each other, the top being worn down to a flat platform. The field- and water-voles (*Microtus* and *Arvicola*), although not the bank-vole (*Clethrionomys*), have permanently rootless and, hence, continually growing molars.

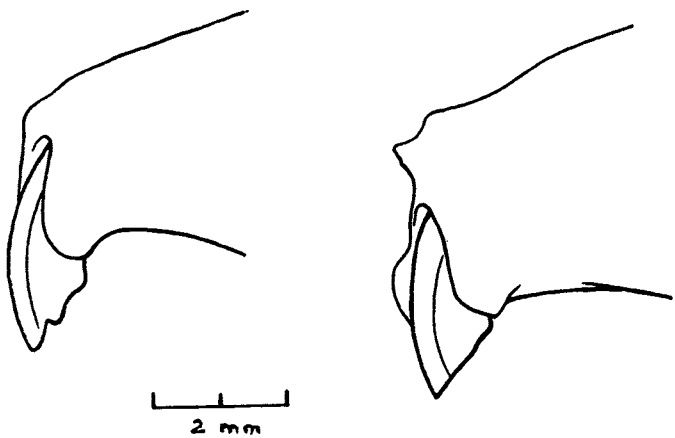

FIG. 2

Anterior parts of the skulls of *Apodemus sylvaticus* (right) and *Mus musculus* (left) to show the notch in the upper incisors of the latter which is the easiest way to distinguish the two species from their skulls.

The house mouse is closely related to the field mice (*Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior)). Adults of these species are much redder than the house mouse, but the colouring of the juveniles in all three species is virtually identical. However, field mice have much larger feet than house mice. The simplest way to distinguish the skulls of house from field mice is by a notch which is present in the upper incisors of the former only (Fig. 2). This notch apparently arises from the strength and peculiar mode of action of the large masseter muscle, which runs from the zygomatic arch to the lower edge of the mandible (Barrett-Hamilton and Hinton, 1910–1921). The other British murids are the two rat species (*Rattus rattus* (L.) and *R. norvegicus* (Berkenhout)) and the small harvest mouse (*Micromys minutus* (Pallas)).

Size

Mice vary in both absolute size and in bodily proportions in different environments. For example, the weight of mice caught in buildings used for storing meat (where the temperature is maintained at about —15°C) is about 15 per cent greater than that of mice caught in houses and shops (Laurie, 1946) (Table 1). Mice from corn ricks, where they are protected during the winter months from climatic extremes and from most predation (Southern and Laurie, 1946) are more like urban mice in size. On the other hand, mice caught on off-shore islands are often larger than cold store mice (Southern, 1938; Davis, 1957; Berry, 1964). The meaning of this last observation is not clear: under island circumstances the animals are exposed to much greater climatic variations than those living commensally (e.g. Berry,

Table 1. *External measurements, weight and litter sizes of some British and west European mouse populations (mature animals—over 12·5 gm.—only)*

Source and reference	Males					Females					
	No.	Head+ body (mm.)	Tail (mm.)	Hindfoot (mm.)	Weight (gm.)	No.	Head+ body (mm.)	Tail (mm.)	Hindfoot (mm.)	Weight (gm.)	Mean litter size
Reigate, southern England: Barrett-Hamilton and Hinton, 1910–1921 ..	20	79·0	77·6	17·7	15·6	20	77·6	77·5	17·8	15·5	5·7
Pembrokeshire, west Wales —corn ricks	113	88·8	74·8	17·1	17·9	135	92·1	76·9	16·8	18·9	7·3
Skokholm, west Wales: Berry, 1964; Batten and Berry, 1967	69	89·6	84·8	17·2	20·8	59	91·6	85·1	17·3	21·3	7·5
Cold Stores: Laurie, 1946	455	—	—	—	20·1	502	—	—	—	22·2*	6·4
Urban mice, Oxford district: Laurie, 1946	370	—	—	—	16·8	341	—	—	—	18·0*	5·1
Fife, east Scotland— corn ricks: Berry, 1964 ..	68	85·9	73·3	17·4	17·1	102	88·7	75·1	17·4	18·9	6·8
Isle of May: Berry, 1964 ..	43	88·1	71·5	17·8	18·7	44	88·9	73·3	17·8	20·4	6·7
St. Kilda Berry and Tricker, 1969 ..	3	83·0	79·7	17·3	—	8	85·2	82·2	17·7	—	6·9
Foula, Shetland: Berry and Tricker, 1969 ..	24	97·1	81·2	18·3	23·9	31	98·3	83·7	18·1	26·3	7·5
Faroes: Myggenaes: Degerbøl, 1942:	17	89·9	88·7	19·4	—	12	94·9	89·8	19·1	—	—
Heligoland: Zimmermann, 1949 ..	26	84·5	88·7	18·1	} Males and females combined						
Berlin: Zimmermann, 1949 ..	360	82·7	87·0	17·8							

* Including pregnant females; all other female weights omit pregnant animals

1968*a*), and any increase in size will decrease their body surface/volume ratio, and hence their rate of cooling. In fact, this increase of size when compared with mainland neighbours is probably due to a complex of factors, perhaps the most important being the removal of a need for small size to escape down holes from ground predators (Corbet, 1961; Berry, 1970). Rick and urban mice show a small increase in size when bred in the laboratory, but they still remain smaller than island mice. On average wild-caught female mice are slightly larger than male ones, and in this they differ from tame mice.

The length of the tail is the most sensitive indicator of the environmental temperature of the mouse during post-natal development—the higher the temperature, the faster the growth rate and the longer the adult tail (Harrison, Morton and Weiner, 1959). In fact the tail is a heat regulating organ (Harrison, 1958), and tail length will be expected to be less in mice living in cold regions. This is borne out by a cline in decreasing tail length that exists in the British Isles: the tail is the same length as the body in southern English mice, but is 20 per cent shorter in Scottish island mice. (For the methods and problems of measuring body and tail lengths, see Appendix 1.) However, in mice from the Faroe Islands the tail is relatively as long as in southern British mice (Berry, 1964). This implies that heat regulation is controlled by different mechanisms in British and Faroese mice (Barnett, 1965; Berry, 1969*b*).

Both over-all body-length and tail-length continue to increase slowly throughout the life of the mouse (albeit very slowly in mature individuals) (Dynowski, 1963). There is considerable variation in size and weight among like-aged individuals in a population, even among older adults (Crowcroft and Rowe, 1961; Dynowski, 1963). The length of the hind-foot attains almost its adult size at an early stage (2–3 months after birth) and therefore is in some ways a better indicator of the mean size of a sample than body length. However, it is difficult to make foot measurements sufficiently accurately to base critical distinctions upon small differences in mean values. Indeed all gross measurements are subject to such individual variation between measurers—quite apart from the variation in any wild-caught sample due to it being composed of individuals of different ages—that it is foolish to use them as more than indicative of the general size of the sample considered (Doutt, 1961; Jewell and Fullagar, 1966).

Delany (1964, 1965; Delany and Healy, 1964; etc.) has used "classical" measurements (body length, skull length, etc.) in combination with quantitative measures of coat colour variation (by comparing mouse skins with commercial colour charts) to characterize populations of *Apodemus sylvaticus*. He "corrected" the mean values of all characters in his sample for age (which meant the loss of some information) and then compared different samples in terms of these corrected values (cf. Berry, Evans and Sennitt, 1967; Berry, 1969*a*; Rees, 1969). Such sophistication is probably the limit to which traditional taxonomic traits can be used.

Coat colour

When the inheritance of albinism (in which there is a complete lack of coat colour) was worked out, it was assumed that there was a gene (*C*) which determined the production of coat colour, while homozygotes of an allelomorph (*c*) possessed no pigment. It is now realized that the normal coat colour (which contains a yellow pigment, phaeomelanin, and a black or brown one, eumelanin) is produced by

interactions between a large number of genes (Table 2). Most British mice are homozygous for genes determining a "dark-bellied agouti" phenotype (some excellent colour photographs of the effect of different genes on coat colour are given by Wallace, 1965). Occasionally small local populations are found where more esoteric colours exist (Barrett-Hamilton and Hinton, 1910–1921). For example, Brown (1965) described the mouse population of a granary on a Missouri farm. A third of the population had a pale-yellow coat (probably homozygous for the pink-eye gene, *p*; the frequency of this allelomorph would therefore be about 60 per cent). Subsequently cats were allowed into the granary, and all the light-coloured mice were quickly eliminated. A few pale juveniles were caught in the next few months, but the frequency of the *p* allelomorph had clearly been reduced to less than five per cent.

Table 2. *Main gene loci determining coat colour (following Searle, 1968; Deol, 1970)*

	Locus	No. of allelomorphs	Located on chromosome	Gene action	Appearance of common variants
A	Agouti	13	V	Follicular physiology, affecting the distribution of black and yellow pigments	Dark or light belly; black
B	Brown	4	VIII	Shape of pigment granules	Black
C	Colour	6	I	Activity of tyrosinase, and production of both black and yellow pigment	Albino
D	Dilute	5	II	Clumping of pigment granules	Lightening of colour
P	Pink-eye ..	7	I	Formation of black pigment	Pink-eye and yellowish fur
S, W, etc.	Spotting-genes .. (at least 10 loci)	2–8 at each locus	Various	Differentiation of melano-blasts *or* skin physiology	Spotting

The most common coat colour variant is one in which the belly is light (white or cream). This is commoner in the U.S.A. than in Britain (Dunn, Beasley and Tinker, 1960; Petras, 1967*a*), presumably reflecting the contribution of members of light-bellied sub-species to the colonization of North America (see above, and Nichols, 1944; Schwarz, 1945). Although most of the light belly colouration is probably due to the substitution of an allelomorph at the *A* gene locus (q.v. Grüneberg, 1952, pp. 37–38; Searle, 1968), Falconer (1947) showed that the "snow-belly" of a mouse caught in Virginia (Eaton and Schwarz, 1946) was due to multiple factors, rather than the allelomorph of *A*. The only British race of the house mouse ever to be accorded taxonomic differentiation, that of the lonely Atlantic island of Hirta in the St. Kilda group, was composed almost exclusively of light-bellied individuals (Clarke, 1914; Elton, 1936). This probably reflects its Norwegian origin (Berry, 1970), since the light-bellied *Mus musculus musculus* occurs in Scandinavia (O'Mahony, 1935; Schwarz and Schwarz, 1943).

However, most colour variation in British populations is restricted to redder or lighter hues of typical agouti pigmentation. The classical and extreme example of this is the light-coloured mouse population of the sand dunes of Bull Island in

Dublin Bay. This island appeared following the construction of a breakwater in the early nineteenth century. Jameson (1898) found that the house mouse population less than a century later ranged continuously in colour from the normal grey-brown to a light sandy hue. A similar colour spectrum persists to this day (O'Gorman and von Rizzori, pers. comm.). From Jameson's time, this population has been taken to be the result of natural selection for crypsis on the sandy background (e.g. Huxley, 1942). There is no direct evidence for this. A similar light-coloured (although variable) population of mice has been described living in buildings on the sandy Spurn Head in Yorkshire (Clegg, 1963).

Out-door living mice are often described (e.g. by Barrett-Hamilton and Hinton, 1910–1921) as being redder or "more tawny" than those living in buildings. Whilst this is probably true, the colour difference is not large and needs to be established by the comparison of series of skins taken from indoor and outdoor trapped mice (for the preparation of skins, see Appendix 2).

There are no differences in pelage colour between juvenile and adult house mice, such as occur in field mice.

Chromosomal complement

The house mouse has twenty pairs of rather similar sized, apparently telocentric chromosomes. The X and much shorter Y pair end to end at meiosis (Geyer-Duszyńska, 1963). Although variations in such a complement are not easy to identify, Searle, Berry and Beechey (1970) found that mice from the Pembrokeshire island of Skokholm had far fewer chiasmata than laboratory mice. In other words, cytogenetic differences can exist between apparently identical karyotypes.

Recently Gropp, Tettenborn and Lehmann (1969) have shown that a local race of mice from one of the Swiss valleys, described as *M. poschiavinus* Fatio in 1869 largely on the grounds of its dark coloration, has 26 chromosomes including seven pairs of metacentrics. These mice will breed with normal laboratory mice, although second and subsequent generations have lowered fertility due to the irregular disjunction of trivalents in meiosis in the hybrids. There is no doubt that this is an example of "Robertsonian variation", in which the seven metacentric chromosomes represent fourteen telocentric chromosomes joined end to end giving the same number of chromosome arms as previously, but with the loss of one centromere in each case. Reducing the number of centromeres allows more genetical variation to be "locked up" in the genotype. Although Robertsonian variation is apparently quite common in the common shrew (*Sorex araneus* (L.)) (Ford and Hamerton, 1970), this is the first time it has been reported in the house mouse.

Habitat

The most important habitats of mice in Britain are: buildings, corn-ricks, and free-living (feral). Although these offer very different conditions for the mice, the main differences in the organization of the animals seem to be those determined by the physical features of their environment. For example, the range of movement of free-living animals is very much greater than that of mice living in buildings, but this can be accounted for in terms of food gathering. This is also apparently the reason why mice living in buildings become isolated from the populations in other

buildings or in fields (Evans, 1949; Berry, 1964; Anderson, 1964; etc.) Hence these "building isolates" tend to become inbred and more genetically homogeneous than the freer ranging mice of the fields (Petras, 1967*b*; Berry, 1968*a*; Berry and Murphy, 1970). Although there is some movement into buildings at the beginning of winter, it is doubtful whether incoming animals can penetrate to any great extent into an existing territorially-organized community (Eibl-Eibesfeldt, 1950; Anderson, 1965; and see below).

Corn rick populations are intermediate in this respect: they are colonized by members of the field population immediately after their erection in the autumn and thereafter remain fairly isolated for the life of the rick (although see Rowe, Taylor and Chudley, 1963). There is a net movement into ricks for some time in the autumn, and a net movement out (particularly of young males—Southwick, 1958; Berry, 1963; Rowe, Taylor and Chudley, 1963) in the spring. Such rick populations double themselves every two months (Southern and Laurie, 1946) and show no decline in reproductive rate in the winter such as is found in mice from all other habitats (Laurie, 1946). A rick with a moderate to heavy infestation of mice when it is broken down for threshing in the spring (Southern and Laurie, 1946, record ricks with 2,000 mice) may have been colonized by about 100 mice (Berry, 1963).

In English arable land the house mouse is the third commonest small mammal, after the field mouse (*Apodemus sylvaticus*) and bank vole (*Clethrionomys glareolus*) (Southern and Laurie, 1946; Davis, 1955), although it is probably decreasing in numbers with the decline in threshing. Through the unfavourable winter period corn ricks formerly provided a reservoir of mice which was released into the fields at threshing time. Linduska (1942) found that the house mouse was the third commonest small mammal in winter shocks of maize in Michigan. House mice avoid open fields with little cover (Fenyuk, 1941; Justice, 1962; Newsome, 1969). Justice (1962) trapped mice in fields and farms in Arizona and concluded that "the most prominent feature of *Mus* populations is their instability. All of the habitats examined are subject to periodic catastrophic changes. Fields crops are harvested and the fields are plowed and irrigated, with crop rotation once or twice a year. Naturally and artificially irrigated pastures are subject to periodic inundation by water and cover destruction by grazing—the probability of gene exchange between isolates is thereby increased." Newsome (1969) described how mice colonize wheatfields in South Australia in the early summer each year from more permanent populations in reed-beds. He suggested that the "mice lived a largely opportunistic and prodigal existence in the wheatfield. Their numbers were controlled by the supply of colonists, the suitability of the soil for burrowing, and the food supply in that order."

Surprise is sometimes expressed about the existence of house mice living independently of man. For example, the extinction of the St. Kilda house mouse within 18 months of the human population being evacuated was attributed at the time to starvation due to its assumed obligate commensalism with man (Harrisson and Moy-Thomas, 1933). However, there are many descriptions of house mice living completely separate from human dwellings, even in north-west Europe where the species has been said to be almost exclusively commensal (Schwarz and Schwarz, 1943). For example, Darling (1938) wrote of his experiences on Lunga, one of the Treshnish Islands of the Inner Hebrides: "Within a few nights of our arrival, mice were coming into the tents and tackling the stores; and it was not long before they

were showing all the cheekiness of the house mouse and indulging in games. Trapping was essential as the stores were not rodent-proof, and in four months we caught 75 individuals. From the incidence of this trapping, it was obvious that there were always more coming in, so the total population must have been considerable. These mice showed no different features from type specimens, and it was interesting to note that after years of living as field mice, this island race was ready immediately to take up the traditional existence of house mice again." Other islands where house mice have a non-commensal existence are Skokholm (Berry, 1968*a*), the Isle of May (Southern, 1938), Foula in Shetland (Berry and Tricker, 1969), and many of the Faroes (Evans and Vevers, 1938; Degerbøl, 1942) (see also Elton 1934; Delany, 1961).

In buildings, mice may colonize any area where food is available. Infestation by rats keeps down mouse numbers to some extent, but situations where rats can live usually provide conditions for a large number of mice. The amount of food available for the mice can apparently be very little. For example, many coal mines were colonized by mice, which lived in and around the stables of the pit ponies. Even though a lot of pits no longer have ponies, yet the mice still survive, presumably eating scraps of food left by the miners (Elton, 1936; Clegg, 1965). Rubbish tips provide a favourable habitat for mice and their population dynamics seem to be similar to those of island populations: numbers build up from a minimum in the early spring to a peak in the autumn, with cold February weather providing the critical period for survival (Darlington, 1969). The most complete description of the ecology of mice in situations where they are a pest (i.e. inhabited buildings, warehouses, corn-ricks) is given by Southern (1954), summarizing much research carried out in the Bureau of Animal Population in Oxford between 1940 and 1945.

Reproduction and life-history

Female mice become sexually mature at around six weeks, although later under crowded or cold conditions (Crowcroft and Rowe, 1957, 1958; Barnett and Coleman, 1959). Indeed, females born in the wild in the autumn may not come into breeding condition until the following spring (Breakey, 1963). Males apparently attain puberty somewhat later than females, but they are less affected by environmental fluctuations. Breakey found some males with spermatozoa in testes and epididymides at all times of the year. There is no difference in breeding intensity throughout the year in commensal and rick mice (Laurie, 1946) but wild-living mice have a definite breeding season. In Britain this is approximately from April to September (Berry, 1968*a*). A little breeding occurs during the winter months, but few, if any, winter-born young survive.

The oestrus cycle varies from four to six days, oestrus itself (i.e. the period of willingness to mate) occupying less than a day of this period (Chipman and Fox, 1966). Fertilization is possible for about 10–12 hours after ovulation; the peak time of day for ovulation is 03.00; and most copulation takes place in laboratory mice between 22.00 and 01.00. Gestation lasts 19–21 days (Table 3), but implantation (which normally takes place five days after fertilization) may be delayed one to two weeks in suckling does. Parturition usually takes place during the night. It is followed immediately by a *post partum* oestrus, ovulation occurring 12–18 hours after birth of young.

Table 3. *Features in development*

Age	Crown-rump length (mm)	Av. weight (mg.)	
Prenatal (days from fertilization) (from Grüneberg, 1943, 1952)			Upper end of oviduct
Fertilization			Blastocysts settle in uterus
4			Implantation (may be delayed in suckling females)
5			
7			Somites begin to form
8		0·08	Embryo becomes C-shaped
9	1·9	1·47	Limb ridge; no outgrowth of tail
10	3·7	8·60	Large olfactory pit; short tail
11	5·9	32·9	Ring of pigment in eye; forefoot plate
12	7·5	76·2	Follicles of whiskers visible; segmentation only visible in tail
13	8·8	129·8	Pinna visible; anterior foot plate indented
14	10·5	228·8	Fingers appear on fore limbs
15	12·7	365·1	Fingers: and toes separate and divergent
16	15·0	592·6	Extensive wrinkling of skin
17	16·7	846·7	Whiskers erupt
18	19·8	1190	
19			BIRTH
Postnatal (days after birth)			
0–2			Hairless (except whiskers); eyes and ears shut
2–6			Skin pigmentation; ears become detached
8–10			Growth of baby fur complete
11–13			Incisors erupt
14			Eyes open
15–18			Very active; coat fully grown
18–20			Pinnae elongate.

The young weigh approximately one g. at birth. They are hairless and helpless. The rate of post-natal growth depends on the amount of milk available, and this in turn depends on litter size. Generally speaking, mice are close to 10 g. when they are weaned at the age of 3 weeks.

Litter size

In a female mouse, the number of ova shed is probably most closely determined by the size of the mother—the larger the female, the more ova are produced (Table 1). This correlation between maternal and litter sizes disappears in the large island races of mice. Presumably the number of young born in these circumstances is adaptive, and hence the result of natural selection (Lack, 1948; Batten and Berry, 1967). If fertilization occurs at all, virtually all the ova shed will be fertilized, but about 20 per cent fail to implant. Another 5–10 per cent of foetuses die between implantation and birth (Batten and Berry, 1967).

Litter size in laboratory mice increases for the first two or three litters of any female, and decreases in high parities. Ovulation rate increases for the first few litters but thereafter remains constant. In wild-living mice, mean litter size increases to a maximum in June and July, then decreases again (Fig. 3). This marked variation in litter size seems to be characteristic only of mice with a limited breeding season. (Exactly parallel changes were described by Baker, 1930, in British *Apodemus*.) The

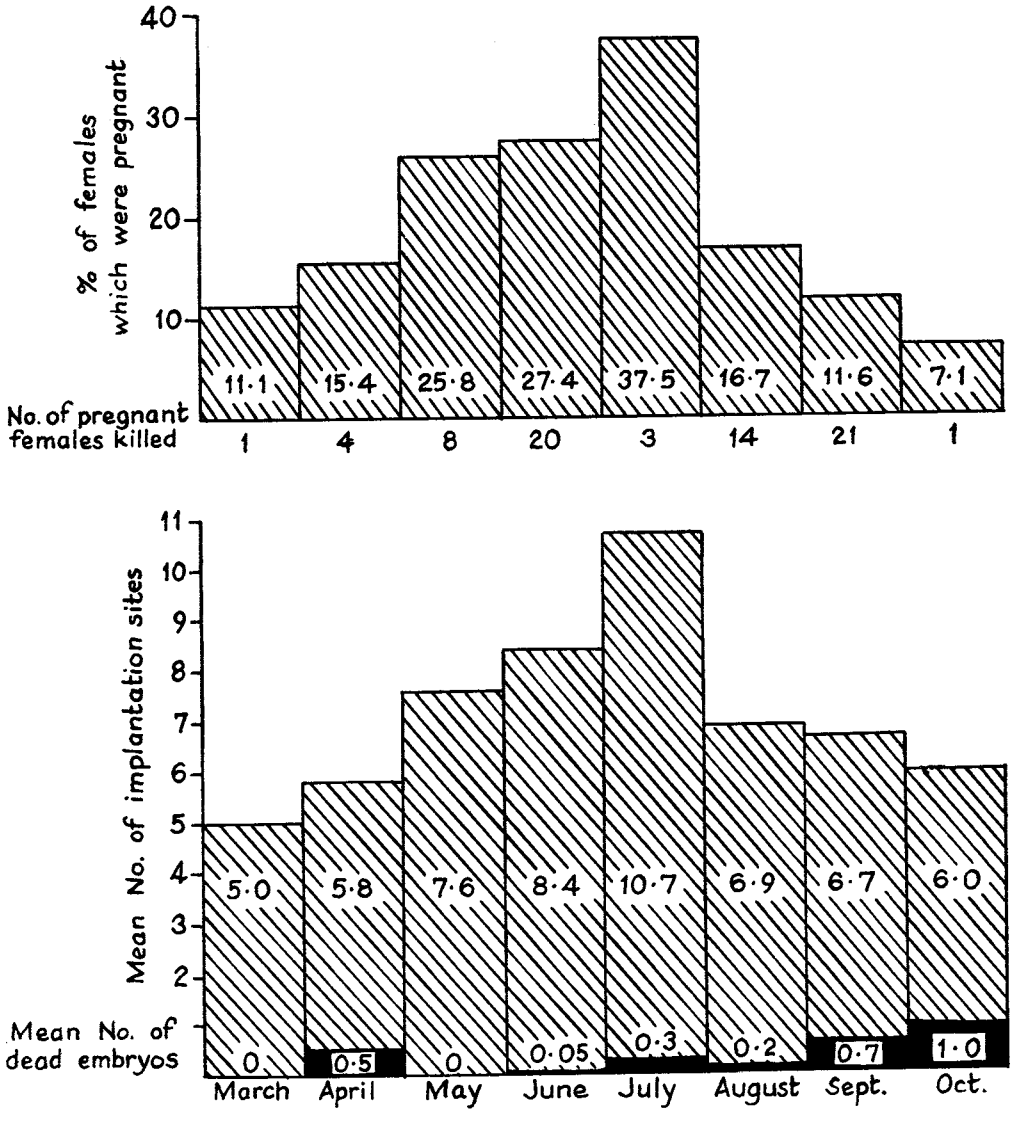

FIG. 3

Litter size and breeding intensity in mice on Skokholm (modified from Batten and Berry, 1967).

early increase may be attributable to similar causes to those operating in early parities of laboratory mice (Harkness and Moralee, 1956, have shown that collagen is not deposited in the uterus of non-breeding mice, and this may limit successful reproduction, until more collagen is synthesized), while the later decrease could be the consequence of an increasing number of young mice breeding for the first time. In her examination of the reproductive condition of mice from urban, warehouse, cold store and rick habitats Laurie (1946) concluded that "it does not appear as though there was any consistent increase or decrease in fertility at any particular time of the year". Skokholm mice bred in the laboratory have a virtually constant litter size throughout the year.

Population size

It is possible to make estimates of the numbers in a population of mice either by a mark-release-recapture technique or by a removal technique (see Appendix 4 for live-trapping; Appendix 5 for methods of marking; Appendix 6 for methods of calculating population size). In this way it is possible to determine the relationship between breeding and population increase.

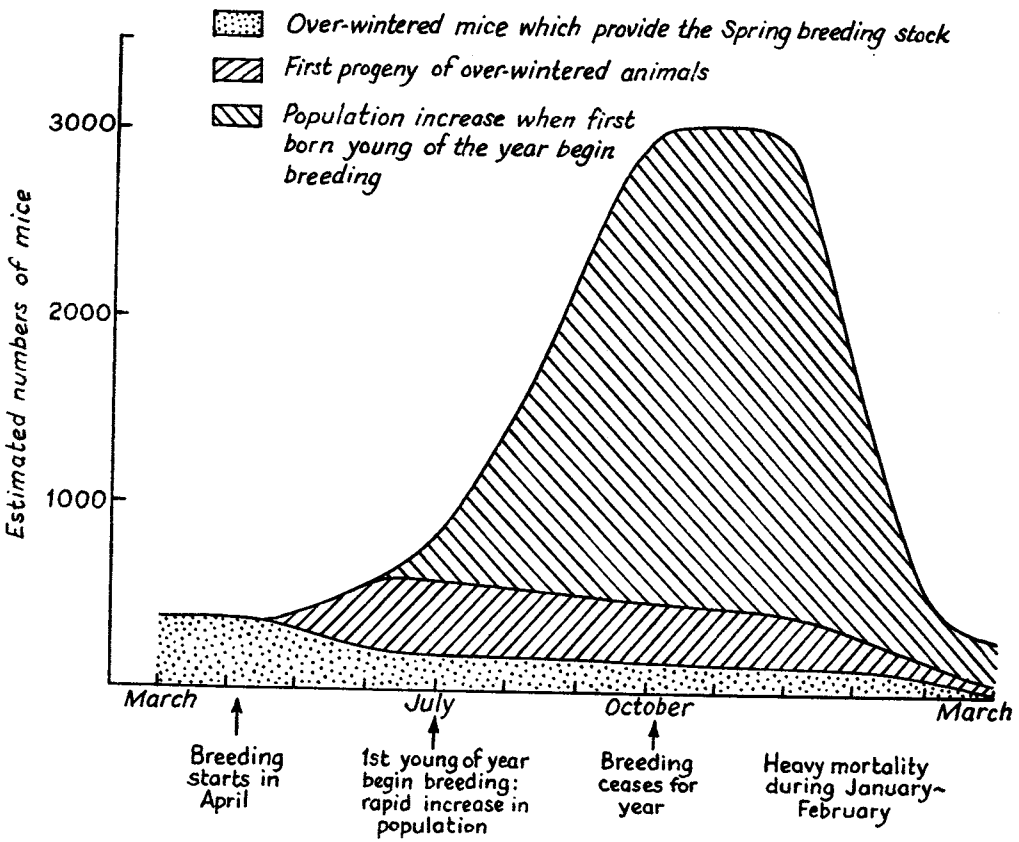

FIG. 4

Annual variation in the numbers of mice on Skokholm. The numbers refer to 1964–1965, but the cycle is similar in all years (from Berry, 1968*b*).

This has been done for the population on the small island of Skokholm (Fig. 4). There the ecological situation of the mice is not complicated either by competition with other small mammals (Berry and Tricker, 1969) or by heavy predation (Berry, 1968*a*, *b*). Now, assuming initially an equal sex ratio and enough movement to bring males and females together (both assumptions almost certainly correct), and making conservative estimates of a mean litter size of six young, eight weeks between successive litters from any pair (this means that pregnancy will be only detectable for two weeks in every eight for any given female—which accords with the mean observed pregnancy rate of 24 per cent), and mice producing their first litters at the age of 12 weeks, there will be an over 200-fold increase in population size during a 24-week

breeding season in which there is no mortality at any stage. Actual mortality statistics in different situations are set out in Tables 4 and 5.

Table 4. *Reproduction and mortality in two island populations*

	Brooks Island: Population failing to increase and subsequently becoming extinct (Lidicker, 1966)	Skokholm: Population increasing ten-fold (Berry, 1968*a*)
	%	%
Females failing to reproduce	60	15?
Post-implantation mortality	50	4
Loss of entire litters	55	21 (in laboratory)
Juvenile mortality	30	40+

Table 5. *Mortality and age in different habitats (after Varshavskii, 1949)*

	Approximate age-span (months)		Open country (steppe)		Urban (human dwellings)	
	Age	Length	% which survive	Av. % of deaths per month	% which survive	Av. % of deaths per month
Immature ..	0·5 to 2·5	2	35·2	32·4	80·8	9·6
Adult	2·5 to 14–15	*c.*12	14·7	7·1	15·8	7·0
Aged	14–15 to 20–21	6–7	78·1	3·4	75·0	3·9
Ancient	21 and above	6– *c.*9	4·0	13·4	22·2	*c.*10·8

Juvenile mortality

Over a number of years it has been found that the population on Skokholm increases slowly at the beginning of the breeding season, and only ten-fold over-all. This increase is probably typical of a normal house mouse population (Berry and Tricker, 1969). This means that there must be a net 60–70 per cent mortality in each litter, even assuming that over-wintered pairs only produce one litter each on average. Most of this mortality seems to take place between birth and weaning, but it is impossible to establish the precise causes of it in a widely distributed population such as the Skokholm one. Sadleir (1965) observed a similar population cycle in the American "field mouse", *Peromyscus maniculatus* (Wagner). He suggested that juvenile mortality was higher in the early months of the breeding season than at the end, due to the antagonism of the breeding adults. Brown (1953) studied population changes and mortality in a hay barn house mouse population, both in natural conditions and in large population cages in the laboratory. He found that "the most important factor related to survival of the young was the condition of the nest at and shortly after parturition. This nest condition was due largely to the amount of activity in the nest area by other mice" (cf. Southwick, 1955). Nest building was usually begun by females two or three days before parturition. The nests which provided the highest degree of juvenile survival were deep, covered nests with a small entrance at one side. Nests which were simple bowls with no cover yielded only half as many weanlings on average, whilst Brown found no young at all survived in his cages if the nest was merely a simple "platform" of nesting material.

The importance of the nest and its surroundings are emphasized by Crowcroft and Rowe (1957, 1958) who, contrary to the findings of most workers, reported a high survival rate of both infants and juveniles in large and relatively undisturbed mouse pens, even though the fecundity of the mature females decreased to nothing as the pens became more crowded. They concluded from "observations on wild mice kept under diverse conditions, that the deaths of unweaned mice are more likely to be caused by intraspecific strife when the nest-boxes are small with a single opening, than when they are large with a 'through' passage".

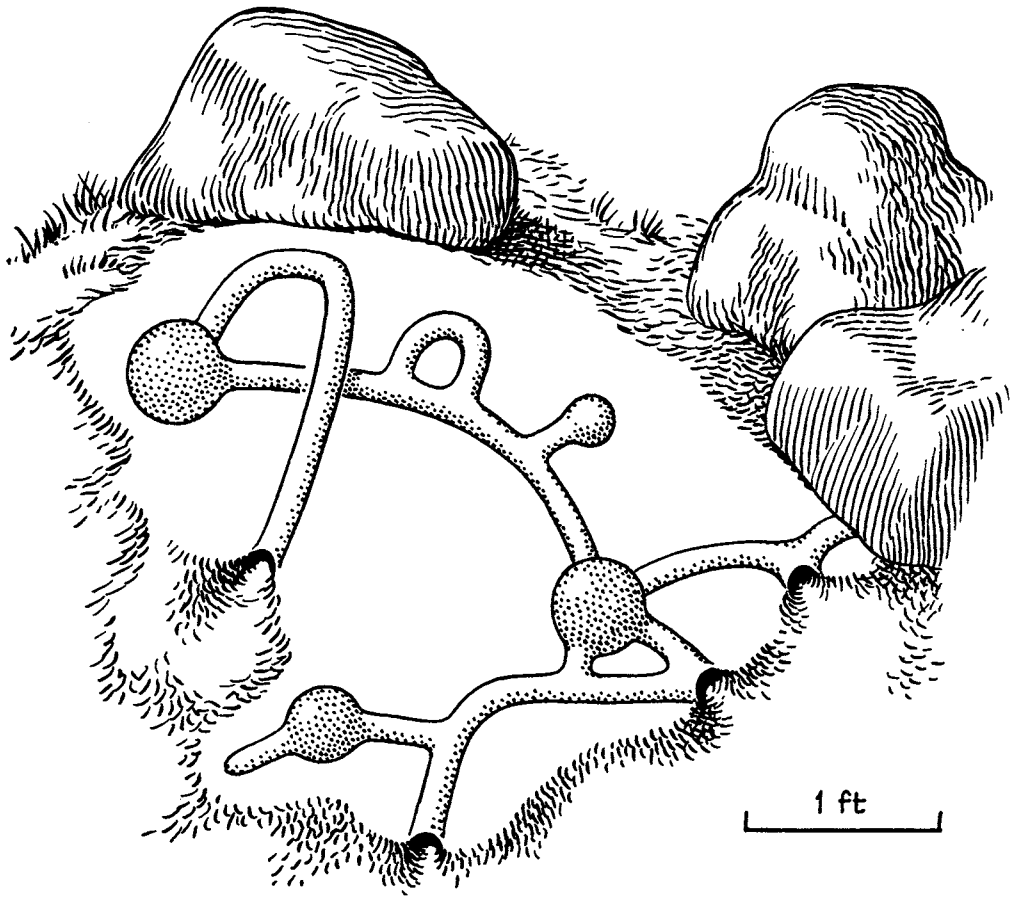

FIG. 5

Excavation of a typical mouse burrow in earth on Skokholm. The runway system was in a 30° grassy slope, with the actual runways up to about 9 in. below the surface (from Berry, 1968*a*).

(An infested corn rick contains a maze of branching mouse runs. Wild-living mice live in dry cracks in the rocks or in dry-stone walls. They may burrow extensively in soft earth or sand. Some burrows are short, with a tunnel about 1 in. in diameter stretching for a foot or more with one or more bends, ending in a circular chamber 6–7 in. in diameter lined with grass. However, most burrows have a fairly complex runway system, with several branches and chambers, and three or four exits (Fig. 5).)

All workers have found a decrease in the rate of population increase with increase

in population density. For example, Southwick (1958) found that the mouse populations of ricks increased twice as fast when the density was less than one mouse to two cubic metres than when it was more than 10 mice to two cubic metres (see also Rowe, Taylor and Cudley, 1964). Another aspect of disturbance is the fact that competition from other small mammals may so interfere with successful reproduction that isolated populations of mice may be unable to replace themselves and so become extinct. This has been shown for competition with voles (on an island in San Francisco Bay—Lidicker, 1966) and with field mice (on St. Kilda—Berry and Tricker, 1969). However simple intra- and inter-specific strife is not the only factor operating to determine survival before weaning. Genetical studies on the Skokholm population show that individuals with certain genotypes survive better than others during the summer. In other words, the mortality is to some extent selective and not random (see below).

Congenital malformations seem to be uncommon in wild mice. Batten and Berry (1967) reported only one abnormality (a two-headed embryo) out of over a thousand embryos examined. Goodlin (1965) and Chaganti, Madan and Ford (personal communication) found no chromosomal anomalies in about 1,200 foetal and newborn mice.

Adult mortality

All mice must die sometime. Russell (1966) concluded that the average life span of laboratory mice is about two years. Varshavskii (1949) aged wild mice by the amount of tooth wear. His oldest group (characterized by teeth falling out) is described as $2\frac{1}{2}$ to 3 years old. No mouse has been found to survive two winters on Skokholm. The animals which over-winter on Skokholm seem to be drawn from no particular age-class (Berry, 1968*a*). DeLong (1967) came to a similar conclusion, although expressed differently: "the survival rates of (resident) sub-adults and juveniles decreased constantly with an increase in population density, whereas adult survival decreased only slightly. Adults, however, showed markedly different survival rates depending upon the time when they entered the population. Over any time interval, individuals born during the population increase showed considerably lower survival rates as adults than those adults which were present in the population when breeding began. The effect of these changes was to increase the proportion of old individuals in the populations." In a mild winter on Skokholm, males survive better than females; in a severe one females come to outnumber the males.

The cause of death may be:

(i) *Disease*

Overtly pathological conditions are rarely found in wild mice. Most reports which refer to disease describe the situation during the decline of house mice "plagues". For example, pneumonia seems to have been an important cause of death in a plague in Kern County, California (Piper, 1928), and large numbers of mice dead from disease were reported during two Russian outbreaks (Fenyuk, 1934, 1941). Pearson (1963) described "large haemorrhagic patches of unknown aetiology" in the lungs when one of the populations he studied was decreasing in number in the winter. DeLong (1967), working in California, found mice carrying "an enteric streptococcus

in the spleen and liver", and apparently dying from septicaemia at a time when the population density decreased eight-fold in one month. However, these reports refer to the atypical situation of populations at high densities, and relate only to the immediate cause of death. In such situations there is considerable social and (probably) causally related endocrine stress, and this may be an important predisposing cause of death (Bashenina, 1963; Christian and Davis, 1964). Heavy infestations of endoparasites (helminthes in the liver; nematodes and tapeworms in the gut) cause some debilitation. Anderson, Dunn and Beasley (1964) found young mice in an island population "fatally parasitized" by larvae of bot-flies (*Cuterebra* sp.).

(ii) *Predation*

The clearest evidence of mortality is, of course, provided by predation. However, this is probably not an important factor in regulating house mouse populations, at least in western Europe. Most studies on the diet of birds of prey do not mention house mice as occurring in pellets. Mice live in nesting colonies of gulls, but Harris (1965) found only one house mouse (in the nest of a lesser black-backed gull) in an intensive study of the food of gulls on Skomer and Skokholm. Nevertheless over 20 per cent of the vertebrates in the diet of owls in the Ukraine and northern Caucasus are mice (Varshavskii, 1949); they form around 25 per cent of the prey of the barn owl (*Tyto alba*) in Washington, D.C., and Illinois, only 10 per cent in Pennsylvania and virtually nothing further north still in Michigan and Wisconsin (data summarized by Varshavskii, 1949). Evans (1949) records a barn owl roosting near an area of a high density mouse population and hunting over *c.* 165 acres, most of it potential mouse habitat. This bird ate at least 283 mice in a year (28 per cent of all its food items), many more individuals than any of its other prey species. Towards the end of the study when the house mouse population was decreasing, the proportion of mice in the owl's diet also fell. A recent study of barn owl diet in Britain (Glue, 1967, and unpublished) has shown that house mice composed, on average, only 1·4 per cent of their prey by weight, although they were found in 46 per cent of the pellets analysed (56/121, involving 32,353 vertebrate prey items). Most mice were found in samples from Ireland and the Isle of Man (7 per cent), and eastern England (3 per cent). This supplements earlier reports that mice provide 2·8 per cent of the diet of the barn owl in Worcestershire (Betts, 1936) and 7·8 per cent in Suffolk and Essex (Ticehurst, 1935). The weasel (*Mustela nivalis*) and to a lesser extent the stoat (*M. erminea*) are the only British mammals (except the domestic cat) which prey significantly on mice. Cats are not very efficient in controlling heavy infestations in buildings. Carnivores are an important factor in maintaining the fluctuations in abundance of microtine rodents (Pearson, 1966), but it is unlikely that they exercise as important an influence on the more nocturnal mice species.

(iii) *Climate and Starvation*

The size of the mouse population that survives the winter on Skokholm is dependent chiefly on the mean temperature in the early months of the year, the February temperature apparently being the most crucial (Table 6): 90 per cent of the population died during the winter of 1964–1965 when the mean February temperature was 1·9 °F. below average, whereas only about 40 per cent died in 1965–1966 when the February temperature was 1·7 °F. above average. The peak population

at the cessation of breeding in the autumn is thus correlated with the temperature in the preceding spring. The amounts of sunshine and rainfall appear irrelevant (Berry, 1968*a*). The only exception to this is that breeding may extend for a longer period if the autumn is warm and wet (DeLong, 1967). It is possible that successful colonization of a previously unexploited natural habitat may be dependent on a critical number of animals surviving the non-breeding period. For example, mice were almost certainly introduced to Skokholm in the late 1890s (Berry, 1964; Howells, 1968), and climatological records show a series of warm Februarys between 1896 and 1899.

Table 6. *Climate and fluctuations in Skokholm mouse population numbers (after Berry, 1968a)*

		Difference from mean temperature (°F)		
		January	February	March
1895	"The mice were originally shipped to Skokholm	−4·9	−10·0	−1·6
1896	. . . in the mid to late 1890s"	+0·5	+1·3	+2·3
1897		−3·7	+2·3	0·6
1898		+3·9	+1·5	−1·4
1899		+1·8	+1·5	+0·2
1907	"Mr. Jack Edwards rented the island in 1907 . . .	−0·6	−2·0	+1·0
1908	A few years later (the mice) were abundant and	−2·3	+2·3	−1·7
1909	caused an influx of owls in the winter"	+0·1	−0·9	−3·1
1910		−0·5	+1·2	−0·9
1913	"The lighthouse was rendered proof against the	+1·7	+0·4	+0·8
1914	entry of mice; whilst it was being built (in 1915)	−1·6	+2·9	+0·6
1915	a plague of these mice caused special precautions to be taken"	−0·3	−1·0	+1·4
1936	In 1938 . . . "Continues to increase, apparently	−0·5	−1·5	+1·9
1937	approaching a high peak of population after its	+1·7	+2·6	−2·9
1938	low numerical status 3 years ago"	+2·4	+0·6	+3·4
1947	"After human reoccupation, they were not observed till late in August"	−2·8	−11·8	−2·4
1948	"Very common throughout the year"	+2·7	+0·4	+7·5

Pearson (1963) surveyed five local mouse plagues in California. In every case the peak numbers were reached in the autumn. "There was no clear correlation between population eruption and rainfall", but "warm weather in the months preceding the usual beginning of reproduction in April causes the build-up of large populations . . . . the warm February–March–April period seems to be especially effective".

The relation between temperature and survival could be either causal or mediated through food availability. Adult mice require about 3·5 g. of dry food per day—about 20 per cent of their body weight. Although they are omnivorous, house mice seem to prefer insect to plant food (to a greater extent than field mice) (Berry and Tricker, 1969), and the former may become chronically short in the winter months. However, on small islands there is usually plenty of food on the beach, and on both Skokholm and Great Gull Island, Long Island, New York (Anderson, Dunn and Beasley, 1964; Anderson, 1965) the mice on the cliffs have a much higher winter survival rate than those living in the centre of the island (cf. Evans, 1942). More important, the mice that survive the winter do not lose any weight. Of course they may be short of some essential nutrient, but they do not show any obvious signs of food shortage.

Table 7. *Stomach content analyses: % of stomachs containing different foodstuffs (from Berry and Tricker, 1969)*

	FOULA July-August	SKOKHOLM		GOVERNMENT FLOUR STORES
		May	September	
Sample size	44	97	41	115
Plant fibres	59	99	98	93
Seed cases	27	—	—	—
Oil globules	6	—	—	—
Arthropod fragments	82	58	88	79
Larval remains	5	—	—	—
Spiders	5	—	—	—
Small feathers	14	—	—	—

Mice are not supposed to "avoid" the winter by hibernating, although reversible hypothermia is sometimes encountered (Fertig and Edmonds, 1969; see also Morris, 1968). (There is a strong tradition in the Faroe Islands of the North Atlantic that the mice hibernate. Degerbøl, 1942, tells of a man from one of the outlying islands who three times watched his dog scraping balls of matted grass out of some holes. Many mice—16 on one occasion—lay close together in these balls: "I took them into my hand, but they did not awake, and had they not been warm, I should have taken them to be dead.") However, wild-living (but not commensal) mice adapt in the physiological sense by reducing their metabolic rate with the onset of cold weather in the autumn. Because of the extent to which the cold tolerance of an individual can change, it is difficult to ascertain the key physiological characteristics of the animals which survive the winter. There is some evidence that mice with a high basal metabolic rate are more likely to survive than those with a low one (Berry, Jakobson and Moore, 1969). If this is so, it implies that the critical factor in survival is not food shortage but the scavenging necessary to get food.

Social and population structure

If a number of mice—either laboratory-bred or wild-caught—are put together, a considerable amount of fighting takes place until a social hierarchy is established. Several territorially-based hierarchies may be established if suitable cover is available (Anderson and Hill, 1965). The details of such social systems have inevitably had to be established using artificial colonies which it was possible to keep under observation. For example Crowcroft and Rowe (summarized in Crowcroft, 1966) spent hours watching mice in pens through holes in the floor of the first floor of a two-storey building. The following account is largely based on their observations (particularly Crowcroft and Rowe, 1963).

Social Relationships

When a mouse is released into a pen, it spends an hour or more exploring, making excursions of increasing length along the walls adjacent to the release point followed by tentative journeys into the centre of the area. Any object is sniffed at and explored. (Taste and smell are much more important to mice than sight. The eye

is sensitive merely to variation in light intensity, and hence change of pattern. According to Waugh, 1910, it cannot perceive form very clearly; only when he is thoroughly familiar with his immediate environment does the mouse take refuge.)

Mutual and immediate retreat is the invariable outcome of the first encounter of any two mice released at the same time, irrespective of sex. At subsequent encounters individual differences begin to appear: one mouse holds its ground and "freezes", and, when the other retreats, begins to make aggressive moves towards it. The reactions at these early encounters are often an indication of the social relationship which later develop. Smell forms an important part in the formation of relationships (Parkes and Bruce, 1961). This seems to be the reason why females prefer (apparently as a result of early learning) to mate with males of their own sub-species (Mainardi, 1963; Mainardi, Marsan and Pasquali, 1965).

A solitary mouse of either sex which has lived in the pen for 24 hours invariably rushes at and pursues a newly introduced mouse, apparently without any preliminary behaviour. After a few hours, it has usually established an amicable relationship with a mouse of the opposite sex. Similarly, two non-pregnant females do not persist in fighting. When two males are confined together, they fight savagely and persistently until one establishes dominance (the dominant is almost always the larger animal: Crowcroft and Rowe, 1961). Thereafter the dominant continues actively to seek and pursue the subordinate. When the dominant is active, the subordinate avoids it or remains within its nest box; when the dominant is inactive, the subordinate roams freely, although avoiding the dominant's nest. If a new mouse is introduced at this time its initial retreat from the subordinate produces an immediate response of dominant behaviour. When a number of males are introduced, one becomes a despotic dominant, and social hierarchies are set up among the subordinates.

Within a family group (of one male, several females, and young) there is normally no aggressive behaviour, but strange mice of either sex are attacked, even by quite young mice. Excitement is contagious if a stranger is introduced. Once the adult male or one of the breeding females detect the intruder, they search the room. When two residents meet, there is a momentary pause for identification by sniffing. If the stranger flees when approached, the retreat stimulates attack by the resident; if it freezes, sniffing is followed by a direct attack. Lactating females are particularly aggressive towards strangers, and, when excited, will attack any mouse that approaches the nest, including the resident male.

The young males leave the company of the females and young when they begin developing aggressive behaviour. They seek to monopolize other parts of the pen.

Territoriality

The aggressive behaviour of males suggest that its function is the setting up and defence of territories. Each territorial male spends most of its time within its own territory; tentative investigation of other areas ends after a sniff at the threshold of another male's nest box.

Fig. 6 shows the territories set up by 56 mice (28 ♂♂, 28 ♀♀) after several weeks in a pen 17 ft. in diameter (an area of 250 sq. ft.) with 14 nest boxes, abundant nesting material, food and water (Crowcroft, 1955). The boundaries of the territories were determined by observing the positions at which:

(i) the presence of a mouse elicited attack,

(ii) a chase was broken off by an attacker,

(iii) a retreating mouse turned, reared up, and drove its attacker away,
(iv) patrolling and "sentry" activities were seen. The male with the largest territory habitually sat on the roof of its nest box, peering about and sniffing, and when a mouse entered his territory, he hurled himself at the intruder in a violent attack.

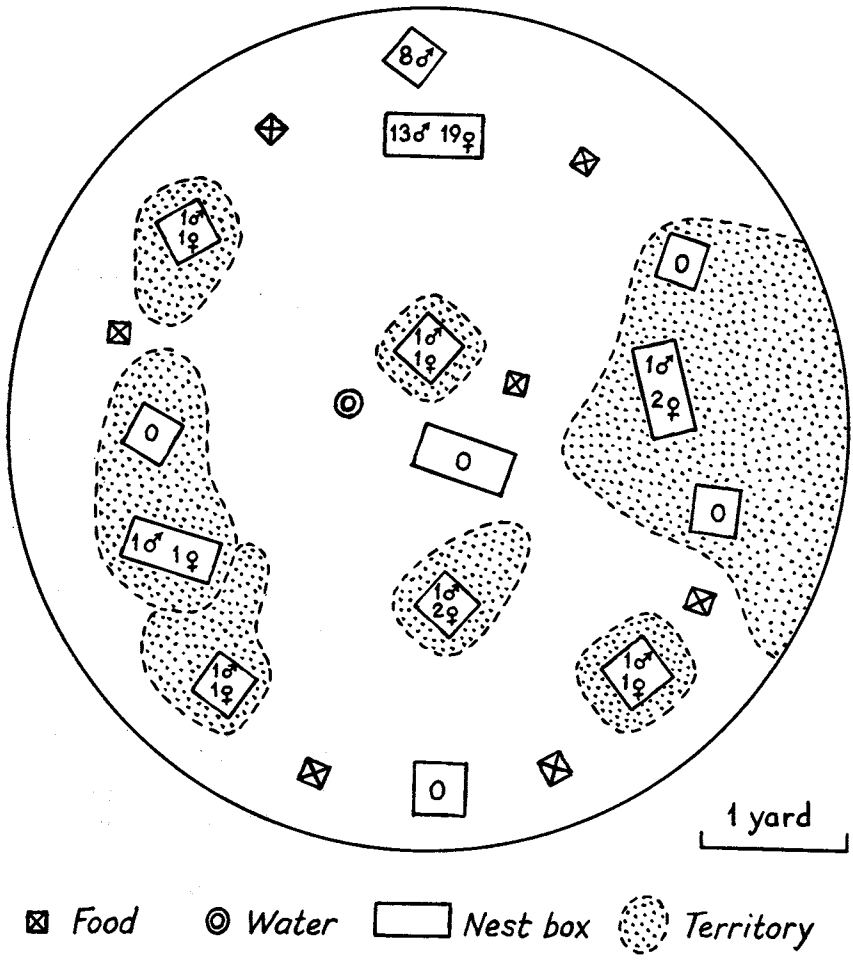

FIG. 6
Territories taken up by mice in an enclosure, supplied with 14 nest-boxes, abundant nesting material, food and water (after Crowcroft, 1955).

The nest box with eight males and no females contained the weak and down-trodden of the colony. They stayed together because none was allowed to remain in peace for long elsewhere. These mice were more active during the day when other mice rarely left their cover. In the nearby box with 32 mice, a dominance-subordination group was established in which one male completely tyrannized most of the others, and exerted an uneasy dominance over the rest. Of course under natural conditions such subordinate mice would move away from the established territories, and seek

to establish themselves elsewhere. Thiessen (1966) found that subordinate animals had heavier spleens than dominant animals, and were more active; Welch (1964) showed that the adrenals of subordinate mice contained more adrenalin than those of dominant animals. In other words there are physiological reasons leading to dispersion.

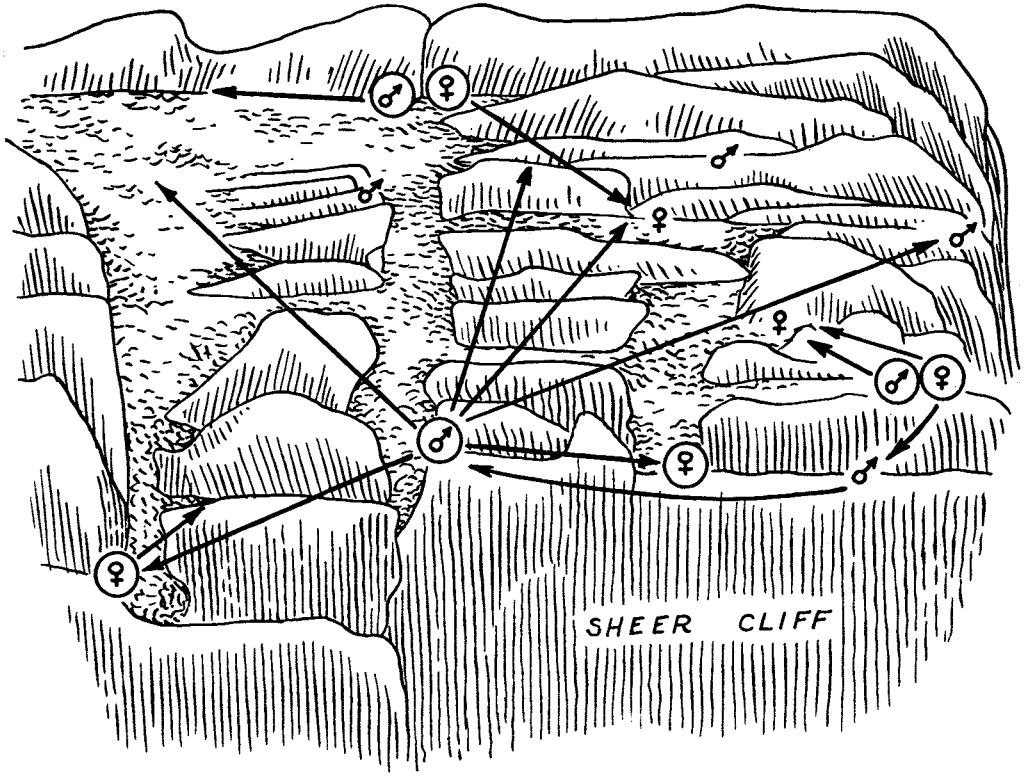

FIG. 7
Results from a grid with 40 traps on the Skokholm cliffs in July, where trapping was carried out for 8 consecutive nights. If a mouse was caught in the same trap for three or more nights indicated by ♂ or ♀, this was regarded as his "home" trap; movement from this point (in the sense of being caught in another trap) is shown as a line radiating from the "home" trap. Some mice were repeatedly trapped, and were presumably the resident animals; others were merely transients, or possibly residents of neighbouring territories (shown non- ringed).
The area shown is about 50 metres square.

Social structure under natural conditions

It is common when trapping wild-living mice, particularly when the density is fairly low, to catch one male and one or two females together in a local area or trap group, and to have only a small chance of catching other animals. The most likely other type of mouse to be caught is a young male, presumably without a territory since the probability of capturing him again in the same area is low (Fig. 7).

On Skokholm and Great Gull Island, the population in the spring is almost entirely confined to the periphery. As breeding proceeds, the interior of the islands are colonized by non-over-wintered animals. Virtually all of these fail to survive

the following winter; there is no reverse migration to the cliffs (Berry, 1968*a*). In other words the implication is of a territorially organized community, the colonizers being young animals driven off the parental territory. When a territory-holding mouse dies, presumably the most likely animal to take its place will be one of its own young. Naumov (1940) has described how a race of mice (*M. musculus hortulanus* Nordmann) in the Ukraine builds "hillocks" in which they store sufficient food for the winter. At the beginning of the winter each hillock is occupied by a pair of adults and their last litter of the season. Since the likelihood is that the adults will die during the winter, the probable result will be the taking over of the hillock and surrounding terrain by members of the family.

A striking confirmation of this rather conservative organization is provided by work of Dunn and Anderson on Great Gull Island (Anderson, Dunn and Beasley, 1964; Anderson, 1965). They released at one end of the island six male mice which were heterozygous for an allelomorph at the *T*-locus. Such heterozygotes transmit the recessive *t*-allelomorph in over 90 per cent of the sperm instead of the expected 50 per cent (Lewontin and Dunn, 1960; Yanagisawa, Dunn and Bennett, 1961). This means that *t*-allelomorphs will inevitably spread when introduced into a population, although the frequency they attain will be limited by the fact that most *t*-homozygotes die early in prenatal life. The allelomorph introduced on to Great Gull was a recessive lethal in this way.

Now Great Gull Island is only 18 acres in extent. Marked mice have been found to roam all over it. Yet although the introduced allelomorph reached a high frequency in the immediate area of its introduction within the first two breeding seasons, in the five years from the original release it spread rather slowly—much more slowly than would have occurred if the Great Gull population was behaving as a single interbreeding unit. Anderson (1965) has suggested that the tenancy of territories on the island tends to be passed on from the resident male to one of his own offspring from the last litter of each breeding season, in the same way as in the Ukrainian hillock mice. In intercommunicating population in cages in the laboratory, Reimer and Petras (1967) found that family groups were stable for a considerable time, even over several generations.

Home range

Estimates of the movement of mice have to be interpreted within the framework of this territorial organization (Hayne, 1949*b*). Burt (1943) has defined the "home range" of any animal as that area traversed in normal activities of food gathering, mating, and caring for young. Not surprisingly estimates of the home range of house mice have varied considerably. For example, Southern (1954) released wild-caught mice in a cellar containing a number of feeding points in which the food was mixed with a dye. By collecting droppings, it was possible to determine the area covered by the mice feeding at any point. The mean range of the mice was 50–60 sq. ft., more or less independent of the number of available food points. In contrast, Quadagno (1968) found by trapping that the home range of mice in the presence of voles (*Microtus californicus*) in fields in California was 1,316 sq. ft.; in the absence of voles it was 3,925 sq. ft. Mice studied by Lidicker (1966) on an island in San Francisco Bay where voles were present had a similar range—about 1,500 sq. ft. But home range of adult females in summer was only half this. On Great Gull Island, Anderson (pers. comm.) found that the mice wandered little from the splash zone

above the high water mark at the end of the winter, though they extended their ranges on to the vegetation area of the island during early spring.

Long movements (which may be described as dispersal rather than home-range movements) are undertaken mainly by juveniles of both sexes, and by sub-adult males (DeLong, 1967). On Skokholm there is considerably more long distance movement in the early spring (March–April) than in summer or autumn. It seems reasonable to associate this with the taking up of territories at the beginning of breeding. Movements of 400 yards in 2 or 3 nights are common, and several mice have been recorded travelling the maximum net distance possible on the island ($1\frac{1}{4}$ miles). A number of workers (e.g. Fenyuk, 1941; Rowe, Taylor and Chudley, 1963; DeLong, 1967) record considerable migration of mice into shelter with the onset of unfavourable weather in the autumn.

Activity

The general conclusion from laboratory studies is that mice exhibit periods of short-term activity (1–4 hours) related to feeding and stomach activity, and a longer-term activity related to the alternation of day and night (Southern, 1954). In the wild, mice begin to be caught in traps within the first two hours of darkness. It is rare for mice to be caught during the daytime.

Both excess food and light (e.g. moon-lit nights) reduce trapping success—presumably by restricting the activity of mice. If the early part of a night is light, few mice are caught until the moon is obscured; a smaller proportion of the total population can be caught in summer when there is plenty of food, than in winter (Tanton, 1969).

Age and genetical structure

In any population which does not have uniform reproductive and mortality rates throughout the year, the age structure will be continuously changing (for methods of determining age, see Appendix 7). This means that the variation present in any sample may be due to it being composed of individuals of different ages. However, a considerable amount of genetical variation exists in all populations where it has been looked for. For example Crowcroft and Rowe (1961) found that some males (bred from wild-caught individuals) were twice as heavy as others of the same age; Wallace (personal communication, quoted by Batten and Berry, 1967) found a sample of seven mice caught in Peru and bred in Cambridge to have been carrying one dominant and two recessive mutants, and one chromosomal deletion, all four being lethal or deleterious when homozygous; Dunn *et al.* (1964) bred mice from 30 localities and found mice heterozygous for one of the *t*-allelomorphs (v.s.) to be present in 17 of them. Over 36 biochemical variants have been described in laboratory mice (Arnason and Pantelouris, 1966; Pantelouris and Arnason, 1967; Selander, Hunt and Yang, 1969; Lush, 1970). These provide the most direct way of measuring the amount of variation present in a population. Selander (1970) has calculated that mouse populations are polymorphic at 28 per cent of their loci for electrophoretically-detectable protein variants (i.e. proteins differing in size or electrical charge), any individual being heterozygous in this respect at 8·5 per cent of his loci. This means that a mouse may be heterozygous at about 10,000 different loci (similar degrees of heterozygosity are found in man: Harris, 1966, 1969). Even

the Skokholm population, which would be expected to be poor in genetical variability owing to being founded by a small number of individuals only a comparatively short time ago, is apparently as variable as this (Berry, 1968*b*; Berry and Murphy, 1970).

Most studies on biochemical variation in mice have revealed a deficiency of heterozygotes (Petras, 1967*b*; cf. Philip, 1938). Virtually all such studies have been carried out on mice caught in buildings. The deficiency of heterozygotes has been interpreted to mean that these mice were drawn from small breeding units (of effective population size between 6 and 80) which are necessarily subject to a considerable amount of inbreeding (of an intensity calculated to be between 6 and 30 per cent). The results from Skokholm are therefore of particular import because no locus showed a deficiency of heteorozygotes, and two loci showed an *excess* of heterozygotes (Table 8) over expectation. The situation is interesting because a significant excess of heterozygotes *appeared* during the summer at one locus (diffuse/single haemoglobin), and *disappeared* at another one (pre-albumen esterase—2). This indicates that natural selection is acting in opposite directions (or *endocyclically*) during the juvenile and adult mortalities which preponderate during summer and winter, respectively. The corollary to this is that a large amount of heterozygosity enables the Skokholm mice to maintain a larger population size at all seasons than they could do if they were less genetically variable (Berry, 1970). The large amount of variation in the population has therefore arisen as an adaptation to stability and survival (Fig. 8). Mouse populations are not so uniform as cursory appearance and classical taxonomy would suggest.

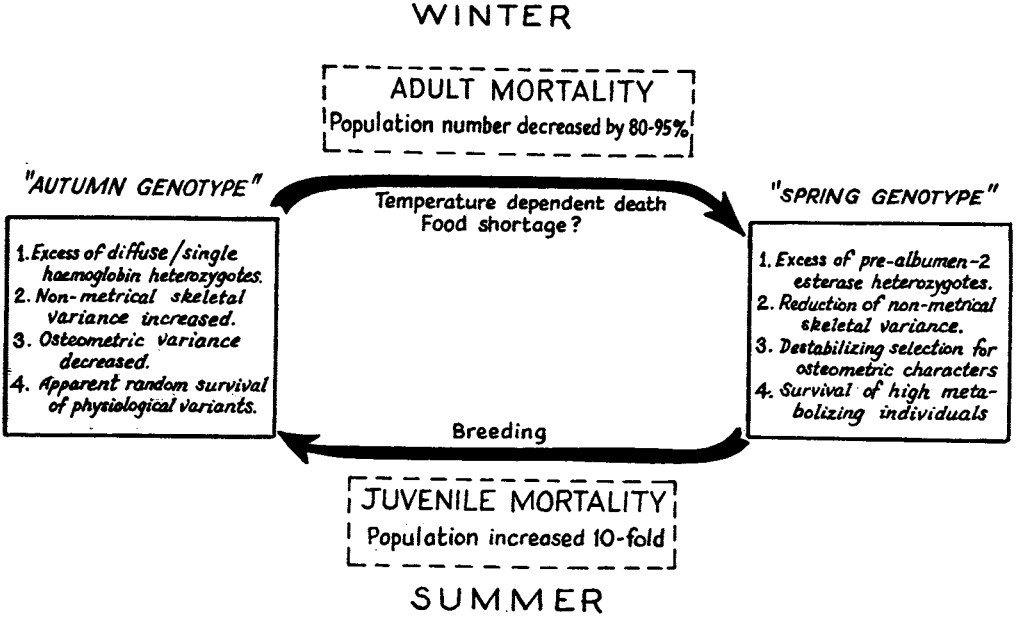

FIG. 8
Endocyclic selection in the Skokholm mouse population: selection acts differently during the winter mortality and summer breeding phases, so that the autumn and spring populations are genotypically dissimilar (from Berry, 1970).

Table 8. *Biochemical variation at five loci*

	Pembrokeshire corn rick			Skokholm					
				Spring, 1968			Autumn, 1968		
Number of animals	75			87			82		
Allelomorph	% frequency of allelomorph	Number of heterozygotes		% frequency of allelomorph	Number of heterozygotes		% frequency of allelomorph	Number of heterozygotes	
		Obs.	Exp.		Obs.	Exp.		Obs.	Exp.
Red cell									
Haemoglobin, diffuse	15·8	19	19·4	65·7	35	39	57·3	19	40
Peptidases, B, 1	100·0	0	0	100·0	0	0	96·3	6	6
C, 1	5·5	3	10	1·7	1	1	4·9	6	6
2	78·1	18	34	92·4	8	9	80·5	18	24
3	16·4	15	27	5·8	8	8	14·6	18	18
Serum									
Transferrin, A	1·3	2	2	2·3	4	4	1·2	2	2
Pre-albumen esterase 2, a	8·7	11	12	72·4	44	35	80·9	31	25
b	90·7	12	12	27·6	44	35	19·1	31	25
c	0·7	0	0	0	0	0	0	0	0

Economic importance

Mice are more of a nuisance than a danger. They may carry *Salmonella* organisms which can cause disease (food poisoning) and even death (e.g. Jones and Wright, 1936). They can harbour the causative agent of plague, *Bacillus pestis* (e.g. Cleland, 1918), but it is generally agreed that they play little part in its dissemination. Much the same applies to the other diseases usually associated with rats: typhus, leptospirosis, tularaemia, etc. (Southern, 1954; Davis, 1961). Outbreaks of ringworm (usually caused by *Achorion quinkeanum* in man) have been reported to coincide with mouse "plagues" (e.g. Place, 1917). It may be transmitted to man directly or *via* cats.

However, the main economic importance of mice is the damage they do to stored food, not the diseases they carry. Here the main loss they inflict is through damaging and contaminating food rather than in the actual weight of food consumed. For example, they make holes in sacks which may cause loss of their contents; they may nibble succulent foods for the sake of the water content; corn from an infested rick may contain a considerable amount of dried mouse faeces.

The total damage due to rodents cannot be calculated. Davis (1961) writes, "It is common knowledge that rats and mice damage food, crops and buildings, including public works such as sewers. Nevertheless, there are no reliable data, and astronomically high figures in terms of money are often quoted. We have no idea of the total rat and mouse population of the country, nor do we know to what extent it 'lives off the country' on natural foods and by scavenging. Even if we knew how many rats and mice there were, calculations based on how much grain an 'average rat' and an 'average mouse' eats would be unrealistic. . . . Apart from what rats and mice eat, we know from experience and experiment that the cost of cleaning and rebagging stored commodities that have been attacked by these pests, often exceeds the cost of the foodstuffs actually eaten. . . . "

Control

Mice can be trapped, poisoned or caught by a predator such as a cat. Poisoning is undoubtedly the most efficient means of control, and much research has been directed towards finding the forms of poisons most palatable to mice, and the best ways of making sure they eat toxic quantities. Since the early 1950s the anticoagulant poison warfarin has been used with considerable success against rodents. However, populations of both rats and mice which are resistant to killing by warfarin are becoming common (Lund, 1967; Drummond, 1970). The resistance is inherited as a single gene substitution in the rat, but multifactorially in the mouse. Attempts are now being made to find an alternative poison which could cause death in mice by interfering with thermoregulation, i.e. by inducing a fatal hypothermia (Davis, 1968).

Acknowledgements

The writing of this paper was suggested to me by Messrs. J. H. Barrett and J. H. Crothers. I should like to place on record my thanks to them for their help on numerous occasions, and especially to John Barrett and more recently David Emerson for their repeated assistance with the logistics of field-work on Skokholm. My thanks are also due to Professor Paul Anderson, Dr. Gillian Truslove, and Mr. John Gray for their comments on this paper and to Mr. A. J. Lee for making the drawings. Much

of my research has been financed by the Medical Research Council, and their support is gratefully acknowledged. Fig. 4 is reproduced by permission of West Wales Naturalists' Trust; Figs. 3 and 5 by permission of the editor of the *Journal of Animal Ecology*; and Fig. 8 by permission of the Zoological Society of London.

APPENDICES

Appendix 1. Making body measurements.

The measurements of the whole animal that are usually made are: length of head and body, of tail, of hind-foot, and sometimes of the ear. The hind foot (from heel to tip of the longest toe, excluding the claw) and ear (from notch to tip) can be measured easily and accurately. The main difficulties arise with the measurement of the head and body, and the tail. The problem is that the body is flexible and extensible. Furthermore the dividing point between body and tail is ordinarily understood to be the "base" of the latter where it emerges from the body, but in practice this point is difficult to define. Consequently series of measurements may not be consistent either when made by a single worker, or worse, by different workers (e.g. Doutt, 1961).

Jewell and Fullager (1966) compared five methods of measuring body and tail lengths and recommend the following (based on Corbet, in Southern, 1964):

Make sure the body is supple, then lay the animal fully extended on its back on a piece of paper, or better, on a soft wooden board. With a pencil, or by sticking in pins, mark the position of the tip of the nose, the base of the tail (by sliding the pencil or pin along the tail until it meets with resistance in the form of the pelvic girdle), and the tip of the tail (omitting the terminal hairs). Measure between the marks or pins to the nearest millimetre.

Appendix 2. Preparation of skins for study.

There are two methods of preparing skins, resulting in "carded" and "round" skins. "Carded" skins are easier to compare and store, and are now used and recommended by the British Museum (Natural History) (1968).

1. Select a piece of stiff, white card a little longer than the total length of the animal, and *c.* 60 mm. wide. Cut as shown in Fig. 9, simulating the degree of taper of the nose. The length of the shaped part should be 5–10 mm. longer than the head and body, and the width about a third of the length.
2. Make an incision (with fine scissors) between the hind legs, from the back of one knee, behind the anus to the other knee. This is the only cut to be make in the skin.
3. Loosen the skin around the incision, cutting through the rectum and urinogenital tract. Push one knee through the incision and cut through the muscle and bone as near to the ankle as possible. Repeat with the other leg.
4. Loosen the skin around the base of the tail. Grip the vertebrae with stout forceps, and, holding the skin at the extreme base of the tail with the fingers, pull to extract the vertebrae of the tail (This is the most tricky part of the whole operation: the tail may break, or the tail skin may become detached from the rest of the skin).
5. Peel the skin forwards, turning it inside out like a glove. Cut the forelegs in the same way as the hind; cut through the ears close to the skull; cut round inside the eyelids; sever the skin finally from the body by cutting across the front of the skull inside the lips.
6. Remove any flesh, fat or glandular tissue from the inside of the skin (the skin tears easily around the mammae in females).
7. The inside of the skin may show a pattern of black or grey markings, showing where the coat is about to moult. The pattern of dark areas may be sketched for dorsal and ventral views.
8. Rub powdered borax, or a mixture of powdered borax and arsenic, or a proprietary preservative soap, over the entire inner surface of the skin. The function of the borax is to arrest decomposition of the skin during drying; of the arsenic to poison any insects or other pests which may eat the skin.
9. Insert a wire or bamboo splint tapered to simulate the vertebrae into the tail, leaving about 1 cm. projecting.
10. Hold the card and inverted skin nose to nose and roll the skin on to the card. The skin should roll on without stretching. If it is too tight a fit, trim a thin strip from the card and try again.

11. Arrange the lips, eyes and ears symmetrically. Arrange the forelegs, one pointing upwards with palm showing, the other pointing backwards with the back showing. The forward one can be fastened down with a drop of rubber solution.
12. Attach hind feet with fuse wire to the ventral side of the card, one turned each way. Avoid splaying them sideways.
13. Arrange the tail symmetrically, making sure that the skin is dorsal side uppermost for the whole length.
14. Brush the fur with a stiff brush (such as a nail brush).
15. Write the collecting number on the card, and then leave flat for a day or two until the skin of the legs has hardened. Then write the rest of the details about the animal on the card (Fig. 9).

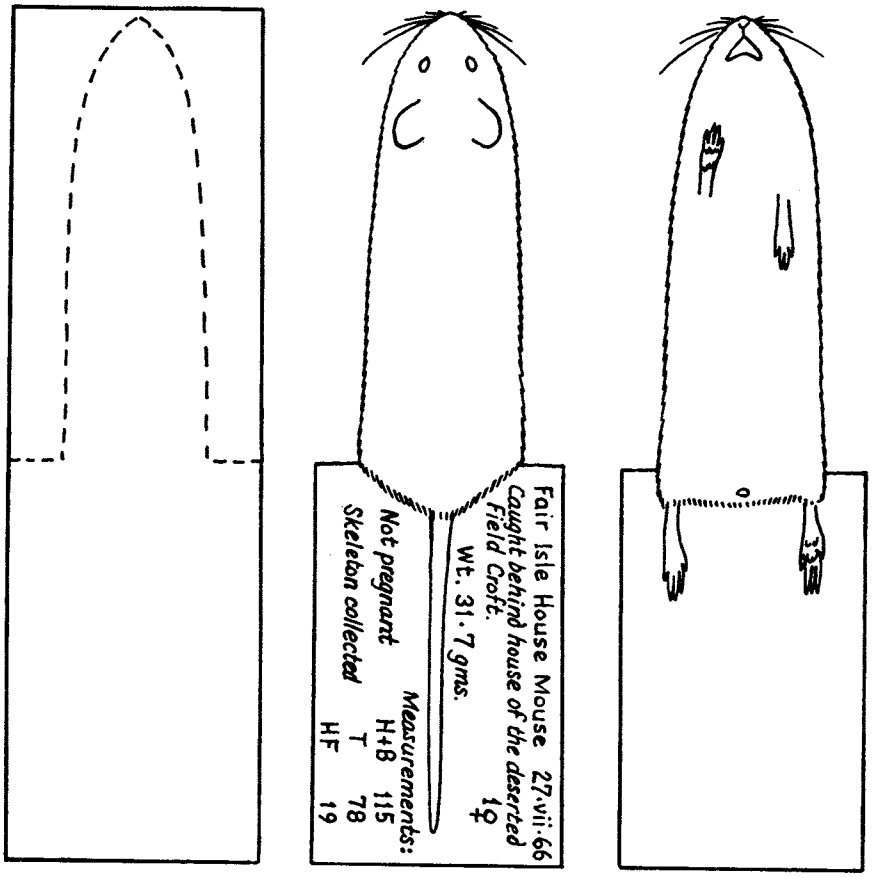

FIG. 9
Method of cutting card for preparing flat skins, and the appearance of the mounted skin.

APPENDIX 3. Chromosomal preparations.

The discovery in 1956 that excellent preparations of dividing cells with the chromosomes separated could be obtained easily by treatment of the cells with a hypotonic saline before fixation, stimulated the study of intra- and inter-population chromosomal differences (Meylan, 1970). Preparations of mitoses have to be made from cells grown in culture (a simple method using corneal cells has been developed by Fredga, 1964, q.v. Wallace, 1965). The most widely used technique for studying male meiotic chromosomes has been an air-drying method devised by Evans, Breckon and Ford (1964). Meredith (1969) has described a simpler and quicker method which has the advantages that it can be used under field conditions, and requires less equipment than the earlier ones.

It is this technique which is given here.

1. Remove testis and place in *freshly prepared* 7% sodium citrate. Remove tunica.

2. Transfer tubules to a large volume of fresh 1% citrate (about 20 times as much fluid as tissue) and tease out to ensure good penetration of hypotonic solution.
3. Transfer tubules to clean 1% citrate. The tubules should remain in hypotonic solution for *12 minutes* from the time of first washing.
4. Transfer tubules to a fixative of *c.* 80 mls. of 3:1 ethyl alcohol/acetic acid. Fixation takes about 15 minutes, but the tubules can be stored in the fixative for several weeks, preferably at 0–4 °C (the temperature of a domestic refrigerator).
5. Place the equivalent of about two inches of tubule in 0·5 ml. of 60% acetic acid in water in a small tube. The tubules quickly become transparent as the spermatogenic cells fall into suspension. Tap tube gently.
6. With a micro-pipette, put two drops of solution from the tube on to a warmed (60 °C) clean slide on a flat surface (such as a hot plate). Pick up the drops in the pipette and move to another spot on the slide. Repeat this four or five times. Repeat process with two more drops until the slide is covered with rings of cells.
7. Stain with two drops of 2% orcein in equal parts of glacial acetic and concentrated lactic acids; add coverslip and leave for 5 minutes.
   The slide is then ready to examine.

Appendix 4. Live trapping

A number of traps are marketed or can be made fairly simply. (A comparison of different break-back traps and their effectiveness has been made by Phillips and East, 1961.) The most commonly used live trap for mice in Britain is the Longworth small mammal trap, manufactured by the Longworth Scientific Instrument Company of Abingdon, Berkshire. This consists of two parts: a trap section and a nest box. The trap section consists of a trip-wire (the tension of which is easily adjustable) activating a door which falls by gravity into a closed position when released. Nesting material (hay or wood-wool, sometimes cotton-wool or paper), food (usually grain of some sort), and sometimes an attractant (such as peanut butter) can be put into the nest box.

Traps are best placed along mouse runs, i.e. parallel to a rock or wall.

One problem that arises with Longworth traps is getting the animal out of the trap without them escaping. With voles (which do not jump), it is possible to catch hold of the animal by putting the hand into the trap as it is opened (i.e. when the next box is separated from the trapping tunnel). Mice are much less easy to get hold of in this way. Some workers put the whole trap in a plastic bag, and open it therein. I use a large aluminium box (approximately 12 in. x 15 in. x 18 in. high) mounted on a pack frame. Traps can be opened in the box, and the mouse caught in the hand without danger of escape. Moreover the box can be used as a trap carrier (it will hold 55 traps) and as a wind shield when weighing mice in the field.

It is useful to wear a glove when handling wild mice. Even when picked up by the tail (if held by the tail, house mice, unlike field mice, cannot escape by shedding their tail skin) or the scruff of the neck some mice (especially young males) succeed in biting the handler. The problem is not so much the pain of the bite (although mice can easily break the skin), as the difficulty of overcoming the reflex action of opening the hand when bitten, and thus letting the mouse escape. Furthermore when catching mice at the time of threshing of corn-ricks (an activity which demands agility and fielding ability), it may be necessary to pick up three or four mice at once without opportunity to grasp them in such a way that they have difficulty in biting .

Direct observation of mice at night in the wild can be made with the use of a red light, to which the eyes of the animals are not sensitive (Southern, Watson and Chitty, 1946; Southern, 1964).

Appendix 5. Marking mice.

Mice may be temporarily marked with hair dye or by clipping a small area of fur. This is sufficient if the problem is merely to distinguish in a mark-release-recapture experiment between new and previously captured individuals. More information (e.g. of movement, survival of particular mice, etc.) can be gained by giving individual marks to mice. Ringing is not recommended: although it has been widely used for small mammals, rings may be lost if attached too loosely, or may become too tight, with the possible loss of the constricted limb (Fullager and Jewell, 1965). Ear-punching or toe-clipping, or a combination of the two, probably represent the most practical and least damaging ways of marking.

The large pinna of the mouse has at least 3 positions for marking. Using a punch, a hole or notch can be made. The most used ear punches are sold by poultry food dealers as "chicken toe punches". With a code of hole, notch or double notch, nine combinations can be recognized on each ear (Fig. 10). If the left ear is taken to represent tens and the right one units, a series of 99 can be used (or 2×99 if the sexes are kept separate). Except when ears become torn, the "number" given in this way remains unequivocal throughout the animal's life.

Although mice use their toes for grooming (Murray, 1961; Smyth, 1965), no harm comes to animals with one toe (i.e. the distal one or two joints) on any foot removed. House mice become infected extremely rarely indeed.

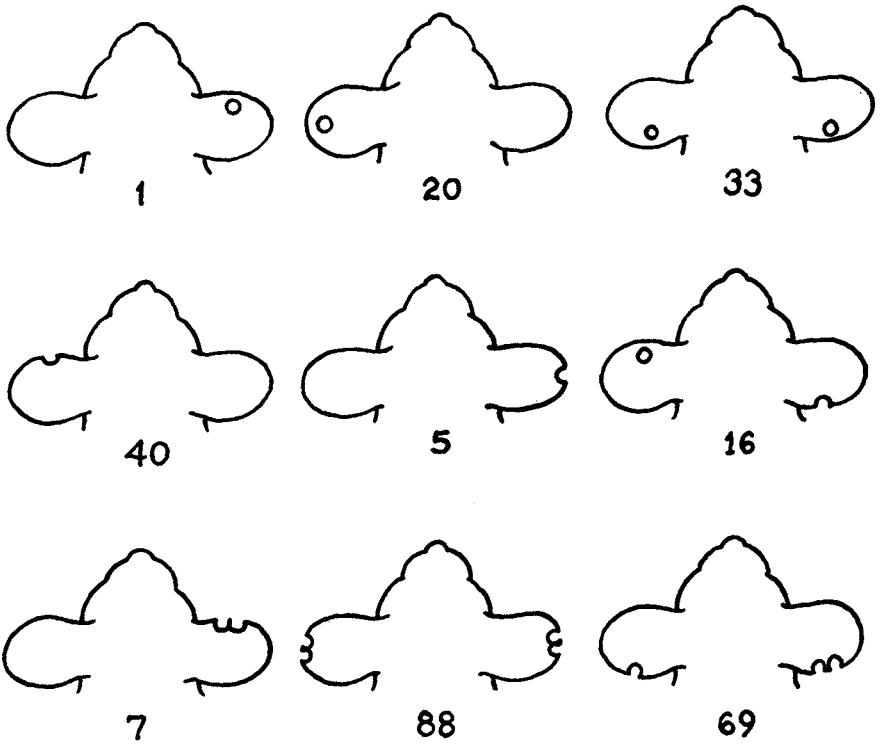

FIG. 10

Code for ear punching: units (1–9) on right ear; tens (10–90) on left ear.

APPENDIX 6. Estimating the size of mouse populations.

There are two inaccuracies inherent in virtually all estimates of mouse population size. Firstly, the calculated number of animals can only be the number of animals which are potentially trappable. During the summer catches of outdoor living animals tend to be small, and then there is a fairly sudden appearance of mature animals in the autumn. This seems to be due to a change in feeding habits (e.g. Tanton, 1965, 1969). In other words, summer trapping will tend to under-estimate the population size. A potentially more serious problem which affects both indoor and outdoor populations, is the higher probability of some individuals being captured than others, i.e. some individuals are "trap-prone", others are "trap-shy" (Young, Neess and Emlen, 1952). Crowcroft and Jeffers (1961) attribute most such differences to social strife. They found trap-proneness and trap-shyness to be absent in an all female population, but the same females showed different "trappabilities" when males were introduced into their pen. They suggest that there may be slight inherent differences in trappability since first generation offspring tended to have a similar amount of trap-proneness to their parents; there are well-documented behavioural differences between different inbred strains of laboratory mice (e.g. Calhoun,1956). However, the main effect

is that trap-shy animals tend to get caught later during the trapping period—but they are still caught. Crowcroft and Jeffers do not believe that trap-shyness causes much distortion in population estimates.

The other main inaccuracy in population size estimates derives from the heterogeneity of distribution and movement of mice. Simple recapture probabilities depend on a marked individual having an equal chance of being recaptured with all other members of the population. This is true, approximately, with insects, but with territorial animals such as mice, a mouse living near a trap will have a proportionately higher chance of being caught in that trap than a mouse living elsewhere or merely passing through the area. However house mice move sufficiently widely to give reasonable estimates of population size (Smith, 1968).

If the destruction of the population whose size is desired does not matter, a "trap-out" method can be used: trapping and removing animals from the area for a series of nights will produce a progressively lower catch (e.g. Southern, 1954). By plotting the number of animals caught each time against the accumulated total for all previous trappings, a line will be produced which can be extrapolated to give an estimate of the total population size (Hayne, 1949*a*, Zippin, 1958).

An alternative and less drastic way of estimating the number of animals in a given area is to count a fraction of the population and somehow relate it to the total. A modification of this "Lincoln Index" (q.v. elementary ecological texts) for use with small mammal populations has been devised by Hayne (1949*a*). The data are collected by trapping an area for 5–6 days; marking and releasing any individuals which are caught; and noting the number of marked animals recaught on any day. In essence the method bases a population estimate upon the increase in the proportion of marked individuals found in catches on succeeding days, as more animals become marked in the course of the experiment. The sort of results obtained in a mark-release-recapture experiment and the computation of population size are set out in Table 9.

Table 9. *Mark-release-recapture experiment on Skokholm in September 1965*

The data are from a grid of 8 lines of traps (a total of 196 traps) laid on a fairly isolated area of 16 acres ("the Neck") for six nights.

	Number of animals caught			Number of dead animals	Proportion of catch previously handled y	Total no. of mice previously handled x	ωxy	ωx^2
	Total ω	Caught for the first time	Previously handled (i.e. (marked)					
1st day	50	50	0	1	0	0	0	0
2nd day	63	29	34	0	0·540	49	1666·1	151,263
3rd day	55	9	46	2	0·836	78	3588·2	334,620
4th day	68	14	54	1	0·794	85	4589·9	491,300
5th day	75	12	63	1	0·840	98	6174·0	720,300
6th Day	80	8	72	2	0·900	109	7848·0	950,480

$$\text{Estimated population size} = \sum(\omega x^2) \Big/ \sum(\omega xy) = 2{,}647,963/23866{\cdot}2 = 110{\cdot}95$$

(*For theory of method, see Hayne*, 1949*a*.)

A source of inaccuracy in recapture data from an area which is not completely isolated, is that some animals will move into the trapping area and be caught, and others will move away and not be caught. The effect of this "edge effect" can be corrected for, but Southern's (1954) words of caution are probably more relevant: "There is no substitute for intensive observation of an animal's domestic habits in the field. Only the naturalist can detect, let alone measure, sources of error in population estimates."

Appendix 7. Ageing wild-caught mice.

The most common method of ageing wild-caught mice is on the basis of the amount of tooth wear. Lidicker (1966, and see Table 10) used the opportunity of following large numbers of marked mice in a field population throughout a large proportion of their life span. He found that no cranial, long bone, or body measurement, either alone or in combination, was as highly correlated with age

as molar tooth wear. Varshavskii (1949) produced a similar ageing guide. Breakey (1963) also used molar tooth wear to age wild-caught mice, but based his "calibration" on individuals raised in captivity. His older mice showed much less tooth wear than Lidicker's. "Any ageing system based entirely or partly on tooth wear must therefore be developed from the specific population being studied, or at least shown to be not different from some other previously studied population" (Lidicker, 1966).

Table 10. *Age and tooth wear (after Lidicker, 1966)*

Age-class (months)	Weight(g)	
0–1	less than 8·8	Teeth not all fully emerged. Mice of this age are only rarely trapped.
1–2	8·8–12·0	Initial lake development of cusps (i.e. separate cusps having common surface due to wear) but no wear on 3rd molar.
2–4	more than 12·0	Slight cusp wear, including 3rd molar.
4–6		3 lobes of anterior cusp of 1st molar distinctly connected, but lake thus developed still narrow.
6–8		3 lakes of first molar now broader and approach each other, particularly on the lingual side.
8–10		Cusps broadly worn and the 3 lakes of the first molar usually interconnected; enamel edges projecting, but rounded.
10–14		Interlake enamel still present, but lingual connections developing between lakes as well. Indentations in outer rim of enamel.
More than 14		Each molar composed almost or entirely of one large lake; outer rim approaches a smooth curve.

Berry and Truslove (1968) explored the possibility of using eye lens weight as an indicator of age in house mice, since this method has been used successfully in many larger mammals. They found the mean lens weight of laboratory mice at any age had such a large variance as to make it valueless for assigning an age to a wild-caught mouse. Moreover there appeared to be genetical differences between inbred strains in lens weight at a given age: indeed many Skokholm animals would have been classified as new-borns if they had been aged solely from the regression line of lens weight against age in laboratory mice.

It is not certain to what extent genetical differences can bedevil age determinations. For example, mice carrying the *sy* allelomorph may have molars almost completely worn down to the gums by the time they are five or six weeks old; there are marked differences between strains in the chance of agenesis of third molars, the time of ossification of skull sutures, and the rate of fusion of the epiphyses of the long bones . . . all characteristics which have been used or suggested as valuable for ageing purposes (Berry and Truslove,1968). Newsome (1969) aged mice on the basis of the regression of head and body length with age in captive mice, such that:

for males, $\log_e$ age in weeks $= -3{\cdot}859-(0{\cdot}086 -$ head and body length)

for females, $\log_e$ age in weeks $= -4{\cdot}075-(0{\cdot}090 -$ head and body length)

Although this may be legitimate when applied to a single population, the amount of heteorogeneity in size and growth rates in natural populations (Crowcroft and Rowe, 1961; Dynowski, 1963) renders it rather dangerous for general application.

A—C. *Leptopsylla segnis:*
- A. ♂: head, prothorax and fore coxa.
- B. ♂: hind end.
- C. ♀: hind end.

D—G. *Ctenophthalmus nobilis:*
- D. ♂: head.
- E. ♀: hind end.
- F. ♂ of *Ct. nobilis nobilis*: hind end, showing clasper.
- G. ♂ of *Ct. nobilis vulgaris*: clasper, to show difference from ssp. *nobilis*.

The typical subspecies occurs mainly in eastern Britain and Ireland, *vulgaris* is found mainly in western Britain and the islands.

H, I. *Nosopsyllus londiniensis*
- H. ♂: hind end.
- I. ♀: hind end.

FIG. 11

Fleas which may be ectoparasites on house mice (all redrawn from Smit, 1957*b*).

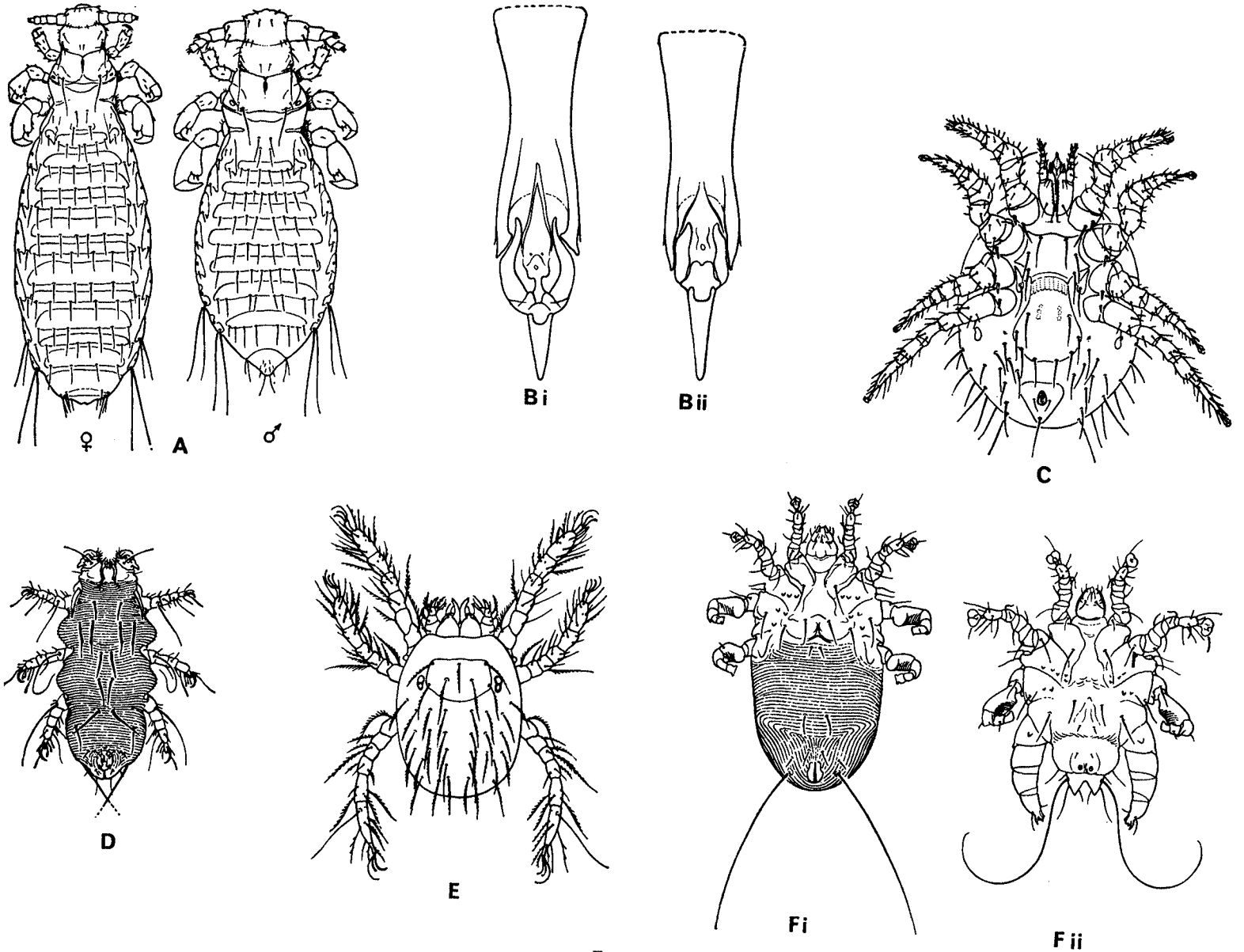

FIG. 12
Lice and mites which may occur on house mice.

Appendix 8. Husbandry

There are two problems in keeping wild mice which do not arise with laboratory mice.

Wild mice are much more agile and "jumpy" than normal tame mice. This means that they are liable to escape if the lid of their cage is removed unless either they are housed in a two-compartment cage in which each compartment can be shut off (such as the one designed by Jewell, 1964 and manufactured by E. K. Bowman, Ltd., Kentish Town, London, N.W.5), or the cage is put into a large container like a dusbin (see also: Evans, Smart and Stoddart, 1968).

The other difficulty is that wild-caught mice are very susceptible to disturbance: females in particular often react to disturbance by aborting or eating their young (e.g. Chipman and Fox, 1966). Cleaning and observation should be carried out as infrequently as practicable.

With these qualifications, wild mice can be reared under exactly the same conditions as tame mice (e.g. Philip, 1947; Grüneberg, 1952; Green, 1966; Tuffery, 1967), although they will probably fare better if housed in larger cages than normal laboratory mice for a few generations. Some workers believe that activity wheels help breeding (Lane-Petter, 1963). Wild-caught mice will retain their "wildness" for several generations unless either the young are subjected to a lot of handling, or newborn young are fostered on to lactating tame females. None of the infectious diseases which are so dangerous in a mouse colony have ever been reported as arising from wild mice, which means that wild mice can be introduced into the same room as other mice with little danger.

The offspring of wild and tame mice often show considerable hybrid vigour. However, some wild-caught mice do not breed when brought into captivity. Failure to breed is more common among females than males.

Appendix 9. Ectoparasites. (by R. S. George, of Duxford, Cambridge).

British mammals are, at times, hosts to a variety of ectoparasites:

Insecta	Siphonaptera	—fleas, which parasitize most of the land mammals and a majority of our birds.
	Diptera	—flies, some of which parasitize bats, birds, ponies or deer.
	Anoplura	—sucking lice, which are found on many species of mammals and most species of which are host-specific.
Arachnida	Acari	—mites, some of which parasitize mammals or birds, and —ticks, which are external parasites of terrestial vertebrates.

Of these the British house mouse is normally host to only three species of Siphonaptera, one Anopluran and four mites, though a considerable number of species of fleas and mites may occasionally live in the fur for a short while and thus are casual parasites on this host.

The fleas are:

Leptopsylla segnis (Schönherr) (Figs. 11A-C): a cosmopolitan flea on *Mus musculus*, though it has been known to feed on rats and recent records show it from *Apodemus sylvaticus* (Caernarvonshire, Gloucestershire, Leicestershire and Yorkshire), *Apodemus flavicollis* (Herefordshire, Leicestershire and Sussex) and *Clethrionomys glareolus* (Leicestershire). This flea has been reported sparingly from most parts of the British Isles (Smit, 1957*a*).

Ctenophthalmus nobilis (Rothschild) (Figs. 11D-G): an extremely common flea of small rodents and insectivores throughout the British Isles though it is more frequently found on field animals than those living in or near to buildings.

Nosopsyllus londiniensis (Rothschild) (Figs. 11-H,I): a mouse and rat flea of the Mediterranean area, approaching a cosmopolitan status (Smit, 1957*b*), though almost all the few British specimens have been taken in or near to ports.

Smit (1957*a*) suggests that *Ctenophthalmus nobilis* may occur only casually on the house mouse but as the flea is quite catholic in its attentions to our other small rodents and insectivores I consider more collecting will show there to be a closer relationship between it and house mice.

A. The louse *Polyplax spinulosa*, dorsal surfaces (redrawn from Ferris, 1923).
B. Differences between the ♂genitalia of (i) *Polyplax spinulosa* and (ii) *P. serrata* (redrawn from Ferris, 1923).
C-F. Mites
C. *Laelaps agilis*: ventral view of ♀ (redrawn from 'Baker, Evans, Gould, Hull and Keegan, 1956).
D. *Myobia musculi*: dorsal view of ♀ (redrawn from Baker *et al.*, 1956).
E. *Neotrombicula autumnalis*: dorsal view of the larva (redrawn from Evans *et al.*, 1961).
F. *Mycoptes musculinus*: (i) ventral view of ♀; (ii) ventral view of ♂ (redrawn from Baker *et al.*, 1956).

The only louse is *Polyplax serrata* (Burmeister) which is probably cosmopolitan though a shortage of records obscures the true picture. British specimens from house mice are known from the Forth and Shetland areas of Scotland and from London whilst a few others have been taken from white mice and *Apodemus sylvaticus*. There is no satisfactory illustration of the whole insect but Ferris (1923) illustrates *Polyplax spinulosa* (Burmeister) (Fig. 12A), an extremely closely related species, and the differences in the male genitalia are shown in Fig. 12B.

Only four species of mites are regularly associated with the house mouse though many others may occur as casual parasites and others may be taken from the fur about which there is insufficient evidence to establish a parasitic relationship.

Laelaps agilis C.L.K. (Fig. 12C) is common and has also been found on *Apodemus sylvaticus* and *A. flavicollis* (Evans, Sheals and Macfarlane, 1961).

Myobia musculi (Schrank) (Fig. 12D) is a very common parasite of the house mouse and may also be found on other rodents. When the infestation reaches a high level, as can occur on laboratory mice and rats, a dermatitis may develop on the head and neck of the host.

Neotrombicula autumnalis (Shaw) (Fig. 12E) parasitizes most mammals during its larval stage when it is known as the Harvest Mite or Bracken Bug (in Scotland as the Berry Bug). It tends to attach itself to the thinner parts of the skin and causes considerable irritation. After engorgement it drops from its host and goes through two developmental stages in the soil before becoming an adult feeding on arthropod eggs.

Mycoptes musculinus (Koch) (Fig. 12F) has been noticed particularly on laboratory mice and rats when it sometimes causes a mycoptic mange characterized by a thinning of the hair around the neck, shoulders and back.

There is such a shortage of records of ectoparasites from house mice that no opportunity to collect should be lost. It is difficult to make a complete extraction from the fur without killing the host but if this is unacceptable within the study being undertaken then the body should be anaesthetized in an envelope and the fur thoroughly searched over a sheet of clean paper. Each individual animal should be treated separately and its parasites put into individual tubes in which they should be stored in 10 per cent alcohol. Great care should be taken to avoid accidental transfer from one host to another by wrong tubing and this is especially important if field catches of different host species are being handled. It is possible to remove fleas from live hosts by holding the mouse over a piece of lint and blowing into the fur. The fleas will jump towards the operator, fall onto the lint, become entangled in its surface and may be collected at leisure. This method is useless for the other parasites.

Fuller instructions are given in George (1969).

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