

The population ecology of house mice (*Mus domesticus*) on the Isle of May, Scotland

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(With 10 figures in the text)

The colonizing ability, catholic habitat utilization and wide distribution of house mice (*Mus domesticus*, Ruddy) are indicators of their ecological resilience. Numerous studies have been made of commensal, caged and free-living mouse populations though few have assessed the relative importance of physiological and genetical components of adaptability in a simple ecosystem. This paper reports such findings, derived from live-trapping which formed part of an inter-disciplinary study of adaptability in a feral population of house mice living on a small Scottish island (57 ha).

The population size ranged from 450–3250 animals. A high proportion of mice showed home-range tenacity, though 15–20% shifted their range during winter. This ‘churning’ of the population is consistent with the island population forming an effectively panmictic unit rather than fragmented demes. The breeding season, survival of individuals and change in population size related to patterns of gross climatic variation (temperature and rainfall) so that rates of reproduction and survival were lowest in cold, wet conditions. Thermoregulatory adjustment of the mice to lowered ambient temperatures and its contribution to overwinter survival are discussed. Genetical monomorphism of May Island mice is discussed in relation to their biological performance compared with other populations, especially that of the ecologically comparable Skokholm Island (Wales).

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Introduction

The resourcefulness of house mice is evident from their global distribution and the broad range of habitats which they occupy including buildings, agricultural land, coastal regions, grasslands, salt marshes, deserts, frozen meat stores and coal mines. Field studies of populations living in such diverse environments have generated an extensive literature on house mouse biology (Berry, 1981; Sage, 1981, for reviews), a common theme being the resilience and adaptability of populations to

environmental challenge. Island populations are particularly valuable subjects for study owing to the biological simplicity of the habitat compared with that of large mainland land-masses. They provide opportunity to increase our understanding of wild populations at an inter-disciplinary level, e.g. ecophysiological and genetical, a level not easily analysable in more complex ecosystems. A study of this nature on the house mice of Skokholm Island was carried out by R. J. Berry and colleagues between 1960 and 1970 (Berry, 1978, for review). An important finding from this work was that the size of the population which survived the winter was dependent on the mean temperature in the early months of the year, particularly February. The relationship between thermoregulatory performance and survival was investigated in Skokholm mice by M. E. Jakobson between 1967 and 1969 (Jakobson, 1971; Jakobson & Moore, 1971) and on the Isle of May, Fife, Scotland, by the present author from 1970 to 1973 (Triggs, 1977). This paper describes the biology of the Isle of May mice and compares the findings with those from other populations, especially Skokholm. Although the Isle of May lies nearly 800 km north of the latter, it is broadly similar in the environment it provides for the mice: house mice are the only small mammals present, the population is genetically isolated, there are no resident predators and the islands are approximately of the same size (Southern, 1938; Berry, 1964).

Natural history of the Isle of May

The Isle of May is 1.6 km long and 0.5 km wide; it lies on a NW/SE axis (Fig. 1). Eggeling (1960) has given a comprehensive description of its human and natural history. It is grassy and treeless with many outcrops of exposed rock. Geologically it is composed of a medium-grained dolerite which has weathered to a reddish-brown crust where exposed. The peaty soil is poor in quality and shallow in most places.

Rabbits (*Oryctolagus cuniculus* L.) thrive on the island and have been present since at least the 13th century. In addition to mice and rabbits, one other burrowing vertebrate species is present, namely the puffin (*Fratercula arctica* L.) which nests on the island during the summer. The population totalled about 3000 pairs in 1972 (Eggeling, 1974) and has recently risen substantially, in part because of immigration (Harris, 1977). Herring gulls (*Larus argentatus* L.) and lesser black-backed gulls (*Larus fuscus* L.) also nest extensively though recent control measures have reduced their numbers substantially (Harris & Galbraith, 1983).

The earliest record of the house mouse is in an undated letter from light-keeper James Agnew, quoted by Muir (1885): 'We have no rats but legions of mice'; a plague was noted by visiting ornithologists in 1907. During the 17th and 18th centuries a tiny village existed at the southern end of the island and before that there was a small priory. Mice may have been introduced at any time during human occupation, possibly more than once.

Methods

Data were gathered from mark-release-recapture studies using Longworth small mammal traps. Captured mice were sexed and weighed and females were examined for evidence of pregnancy. Individually marked mice were released close to their point of capture.

Two complementary trapping schedules were used: (1) 'saturation' trapping of particular study areas to assess accurately local density, home range and survival; and (2) 'round-the-island' trapping to provide data on distribution and an approximate estimate of total population size. 'Round-the-island' censuses were performed with 185 traps in 37 groups for 5 consecutive nights during autumn, early winter, mid-winter and

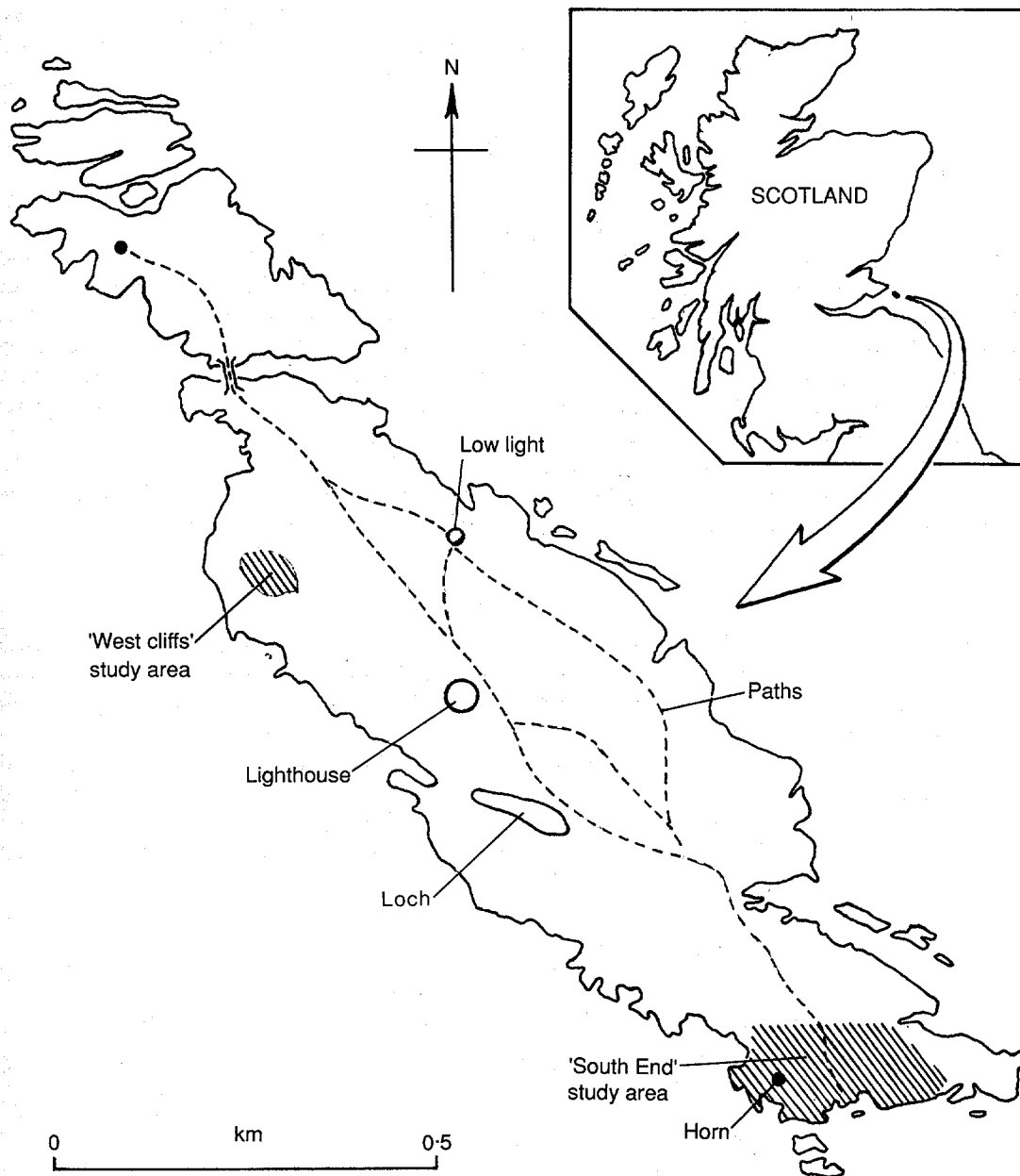


FIG. 1. The Isle of May.

spring of 1970–71 and 1971–72, and in autumn 1972 and spring 1973 (Table I). The traps were set 10–20 m apart and in the same position each time. 'Saturation' trapping employed a single grid of traps set 5–10 m apart, again for 5 nights. Four censuses were performed each winter on the 'South End' study area (Fig. 1). The trapping was carried out immediately before or after the 'round-the-island' censuses. A population

estimate from each census was calculated using Hayne's method (Hayne, 1949). Estimates of numbers from 'saturation' trapping were used in conjunction with those from 'round-the-island' trapping to compute total island population size (see Berry, 1968, for method).

Results

Population size and change

The total number of mice on the island was estimated on 10 occasions between autumn 1970 and spring 1973; the population size ranged from 450–3250 mice (Table I; Fig. 2). Numbers of mice were low in spring and rose to a peak at the end of the year. The population size was low at the start of the study during autumn 1970 and remained low throughout the 1970–71 winter. Subsequently the numbers increased dramatically in the summer of 1971. The September 1971 estimate was 2.5 times greater than that for the preceding April. No similar increase occurred during summer 1972; indeed, the September 1972 estimate was lower than that of April 1972. A population decline occurred each year between mid-winter and spring, that of 1972 being the greatest.

Changes in the numbers of mice inhabiting the 'South End' study area mirrored those of the island as a whole. The density fluctuated between 58 and 140 mice per hectare (Fig. 3).

Breeding season

Pregnant mice were identified by abdominal enlargement and palpation of young. The incidence of breeding (Fig. 4) is expressed as the proportion of females pregnant relative to the number of adult females, i.e. those over 18 g, this being a weight which conservatively separated juveniles from reproductively mature mice.

There was little reproduction during the winter months. The incidence of pregnancy increased during spring and rose to a peak in midsummer, that of August 1971 being the highest observed (and preceding the largest population size recorded during the study). Breeding began earlier during spring 1971 than in the two subsequent years. Mice were already pregnant in February, and

TABLE I
Population size estimates, Sept. 1970–April 1973

Island census start date	Number of mice handled	Estimate, to nearest 50
15 Sep. 1970	51	450
26 Nov. 1970	241	1600
7 Feb. 1971	181	1150
26 Apr. 1971	157	1100
23 Sep. 1971	296	2500
17 Nov. 1971	420	3200
27 Jan. 1972	458	3250
24 Apr. 1972	313	2100
26 Sep. 1972	277	1800
28 Apr. 1973	320	2100

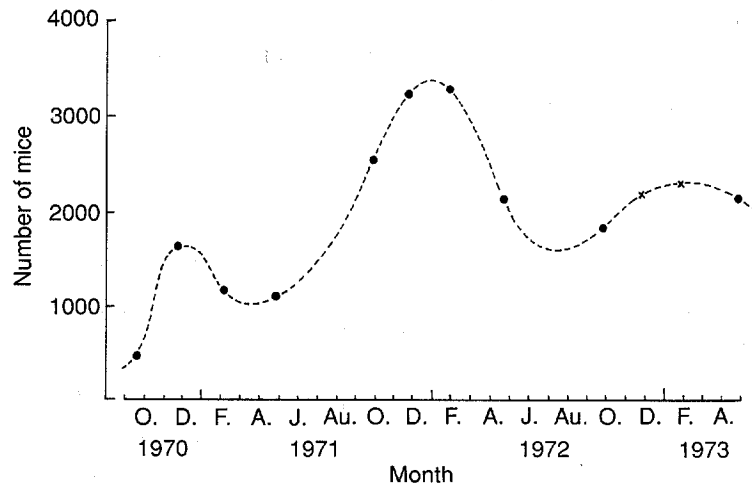


FIG. 2. Change in total population size, 1970-73. (x=interpolation from study area censuses).

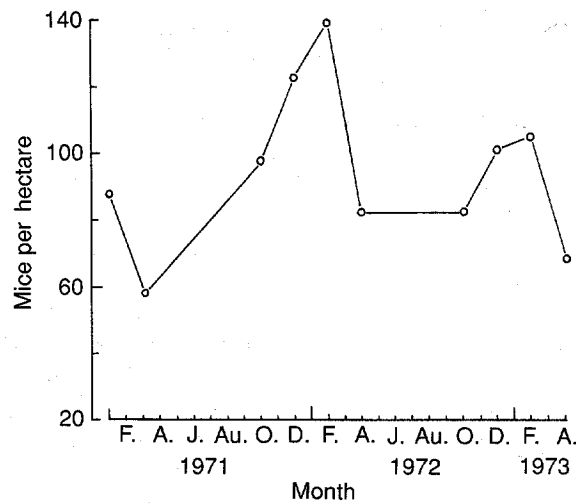


FIG. 3. Density of mice on the 'South End' study area expressed as number of animals handled per hectare during each five-day census.

by March/April 1971 three censuses showed 30-40% pregnant females. In 1972, no pregnant mice were found in February, and five censuses in March/April showed only 2-15% incidence; in spring 1973 no pregnant animals were found until mid-April. The 1971 breeding season not only began earlier but lasted longer than in 1972: in October 1971, 25-40% of adult females were pregnant, compared with only 6% in October 1972.

The seasonal breeding pattern influenced the population weight distribution. During autumn the distribution was bimodal, separating late-born young of the year from mature, larger

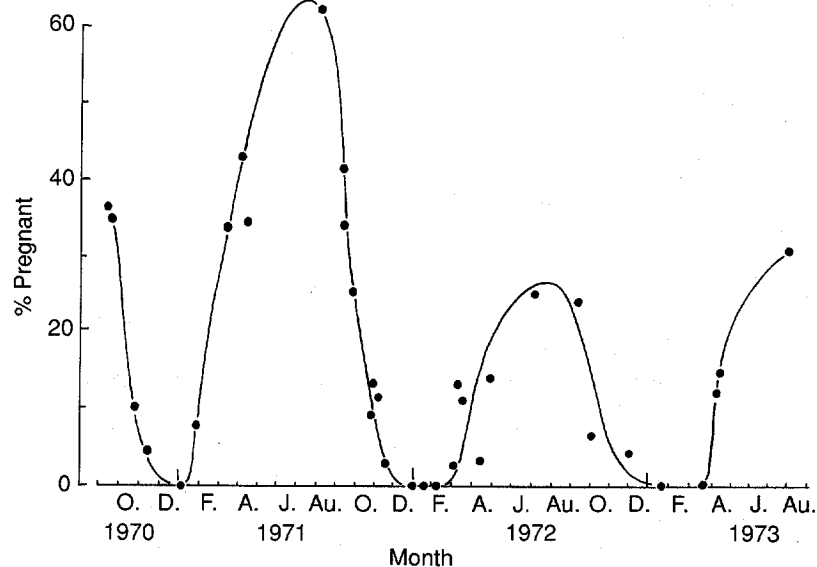


FIG. 4. Percentage incidence of pregnancy in adult female mice, 1970-73.

individuals. In spring the distribution was unimodal for both sexes, the modal classes being 20-22 g for males and 16-18 g for females.

Survival

Lack of recapture of a marked mouse was provisionally equated with death. The accuracy of this classification depends on mouse trappability being high and on home range being relatively stable. Evidence for home-range stability is presented later in the paper. Trappability is impossible to assess in the field. However, an estimate of the accuracy of equating absence with death was gained from the proportion of mice initially classed as 'dead' which reappeared in a later trapping period. Of 1103 mice marked during autumn 1971 and 1972, 304 were not recaptured two months later and were classed as 'dead'; 53 (17%) of these were caught subsequently. In practice, misclassification was reduced inasmuch as the data were corrected for those mice caught subsequently. Overall, about 5% error remains in the classification of mortality for any particular sample.

Overwinter survival in cohorts of sub-adult mice (<18.0 g) newly handled in autumn was monitored by repeated 'saturation' trapping in study areas. Data for 1970-71 come from the 'West Cliffs' study site (Fig. 1); for 1971-73 the 'South End' study area was used. Overwinter survival (Table II) was lowest during 1971-72: for combined sexes 34% survived from October to April compared with 46% over 1970-71 and 57% over 1972-73. Survival between October and December, and between December and February of the 1971-72 and 1972-73 winters varied from 69-96%. By contrast, survival between February and April was much lower, from 48-78%. Overwinter survival in older mice (using weight as an indicator of age) was lower than in younger mice (Fig. 5).

TABLE II

(a) *Percentage survival from October to April, i.e. overwinter, of summer-born mice (sample sizes in parentheses)*

	1970-71	1971-72	1972-73
Males	48 (21)	29 (113)	55 (75)
Females	45 (20)	38 (134)	59 (66)

(b) *Percentage survival every two months from October to April of summer-born mice*

	1971-72		1972-73	
	Male	Female	Male	Female
Oct.-Dec.	78	69	88	76
Dec.-Feb.	78	86	85	96
Feb.-Apr.	48	64	73	78

Life-tables have been constructed for newly-weaned cohorts of mice marked during September/October 1971 and November/early December 1971, respectively (Table III). For both cohorts the life expectancy of females was approximately 20% greater than that of males. In the September/October group, the survival rate for both sexes remained high during the autumn and early winter, dropping in midwinter to 66% in females and 50% in males. The overwintered males continued to suffer high mortality during the following breeding season, and only one individual of the cohort remained alive during July 1972. By contrast, females suffered less summer mortality: 20 out of 44 animals survived from spring to late summer during 1972. Indeed, seven survived well into their second winter, the last being handled during January/February 1973. The pattern of survival in the later-weaned females was similar to that of the females of the earlier group. The later-weaned males, however, fared better overwinter than the earlier-weaned males and a small number of them lived on into autumn 1971.

Taking the study as a whole, only four mice (all females) were known to have survived two winters. They were in poor condition and were unlikely to have bred subsequently. Individual mice consistently showed significant weight increase through winter (Table IV). Growth of juvenile females during winter was lower than that of males (Fig. 6); most remained within the 14-18 g range, well below the 20-24 g range of reproductively mature adult females.

Distribution, home range and movement

Distribution

Mice were present in all island areas including two islets at the northern end which are isolated at high tide. Comparison of the average number of mice caught per trap site in different regions on each census showed that fewer mice inhabited the grassy, central areas than the rocky, more peripheral parts of the island. The central areas represent marginal habitat which is occupied

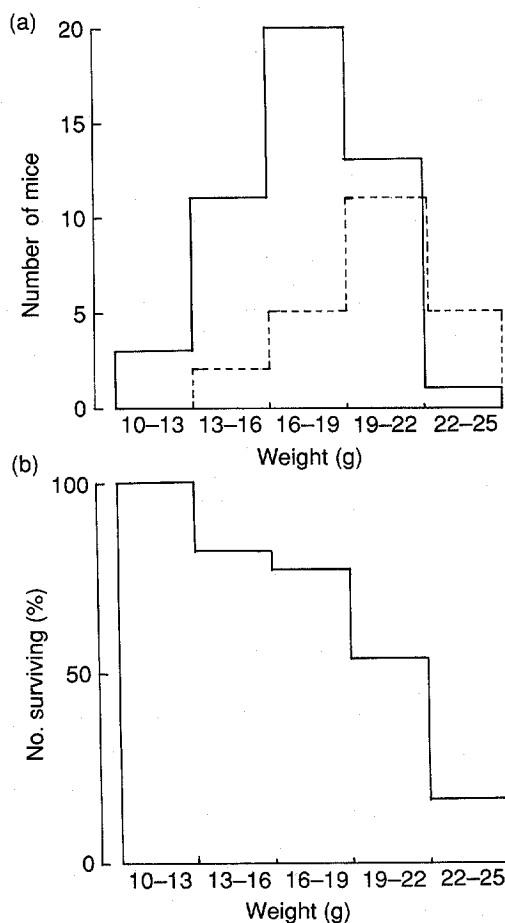


FIG. 5. (a) Weight histograms for 72 male mice weighed during October 1971, grouped on the basis of their survival or non-survival to December 1971 (---) or spring 1972 (—). (b) Percentage of each weight class shown in Fig. 5a which survived to spring 1972.

mainly when the island population is at high density. Mice live around the lighthouse buildings, but at densities no higher than in other areas.

No formal investigation was made of any association between mice and rabbits, gulls and puffins. However, mouse numbers were not noticeably elevated or reduced in areas where the other species were abundant. Predation by gulls is probably low (Harris, 1965). Mice may benefit from the burrowing activities of rabbits and puffins; they frequently headed directly for burrows on release from traps. Indeed, several excavated mouse tunnels with nest chambers led directly from rabbit burrows.

Home range

Release-recapture data allowed the distribution of individual mice to be mapped. Observations

TABLE III

Life-tables for two cohorts of house mice on May Island (from time when animals entered the trappable population: autumn 1971)

Month	Males				Females			
	Obs. nos.	No. of survivors per 1000	Prob. of survival	Life expectancy (weeks)	Obs. nos.	No. of survivors per 1000	Prob. of survival	Life expectancy (weeks)
Sep.-Oct.	87	1000	0.828	20.4	107	1000	0.729	25.4
Nov.-Dec.	72	828	0.777	15.2	78	729	0.859	24.7
Jan.-Feb.	56	644	0.500	9.7	67	626	0.657	19.4
Mar.-Apr.	28	322	0.214	6.5	44	411	0.682	18.8
May-Jun.	6 ^a	169	0.174	5.7	30 ^a	280	0.667	16.9
Jul.-Aug.	1	12	0.000	4.3	20	187	0.500	14.6
Sep.-Oct.	0	0	0.000	0.0	10	94	0.700	16.3
Nov.-Dec.					7	66	1.000	12.9
Jan.-Feb.					7	66	0.000	4.3
Mar.-Apr.					0	0	0.000	0.0
Nov.-Dec.	74	1000	0.797	19.5	74	1000	0.878	26.7
Jan.-Feb.	59	797	0.695	14.8	65	878	0.708	21.2
Mar.-Apr.	41	554	0.439	10.8	46	622	0.696	19.6
May-Jun.	18 ^a	243	0.444	10.5	32 ^a	432	0.688	17.7
Jul.-Aug.	8	108	0.500	9.7	22	297	0.545	15.2
Sep.-Oct.	4	54	0.250	6.5	12	162	0.750	15.8
Nov.-Dec.	1	14	0.000	4.3	9	122	0.667	11.0
Jan.-Feb.	0	0	0.000	0.0	6	81	0.167	5.7
Mar.-Apr.					1	14	0.000	4.3
May-Jun.					0	0	0.000	0.0

^a Calculated value, assuming constant mortality between April and July

are presented for 54 male mice trapped in one part of the 'South End' study area over eight nights during the 1971 early winter census (Fig. 7). Mice caught on four or more nights have their capture positions outlined; those caught on three or fewer nights are denoted 'm'. The location of mice was consistent enough to allow traps to be set in a particular locality for the capture of specific animals for physiological tests. Although resident mice had localized areas of surface activity, the large degree of overlap between areas suggests that they did not maintain exclusive ranges. Home-range data for female mice provide a similar picture to that for males, i.e. a partially overlapping mosaic of ranges indicative that they have preferred, though not necessarily exclusive, areas of surface activity.

Comparison of male and female ranges frequently showed close overlap between small groups or even pairs of mice. Whilst it would be tempting to identify these aggregations as breeding or family units, caution must be exercised in making deductions on social structure solely from limited capture-point data. For example, data presented in Fig. 7 illustrate that many males maintain discrete ranges of surface activity. However, this is contradicted by observations which show that mice with apparently discrete ranges often nested communally (Triggs, 1977).

Individual ranges were about 100-400 m² with variation seemingly dependent on natural topography and landmarks. For example, males 1, 2 and 14 (Fig. 7) remained in close proximity to a wall; mice 6 and 10 were localized on top of a hillock separated from mice 5, 7 and 13 by rock

TABLE IV
Body weight change (g) in individual mice over two-monthly intervals during winter 1972-73

Two-monthly interval	n	Mean initial weight	Mean change in body weight (\pm S.E.)	Paired <i>t</i> -test (mean change vs. zero) (<i>P</i>)
Males				
Oct. 72-Dec. 72	26	15.66	$+3.32 \pm 0.34$	<0.001
Dec. 72-Feb. 73	29	18.09	$+1.42 \pm 0.25$	<0.001
Feb. 73-Apr. 73	24	18.11	$+1.33 \pm 0.21$	<0.001
Females				
Oct. 72-Dec. 72	17	15.14	$+2.59 \pm 0.46$	<0.001
Dec. 72-Feb. 73	17	16.58	$+0.74 \pm 0.25$	<0.01
Feb. 73-Apr. 73	9	16.06	$+0.62 \pm 0.25$	<0.05

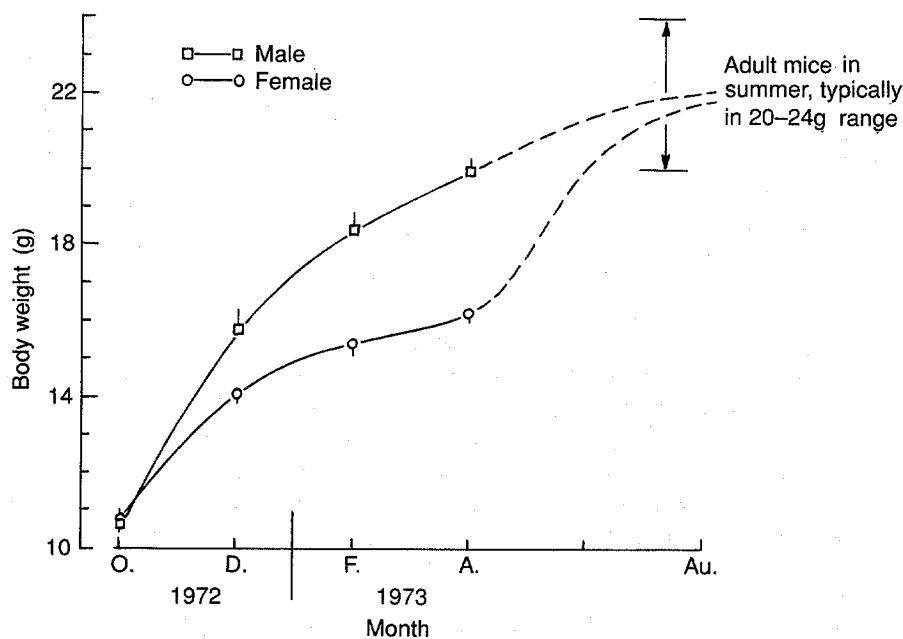


FIG. 6. Change in mean body weight \pm S.E. (g) of a cohort of 16 male mice and a cohort of 21 female mice first handled as juveniles in October 1972 on the 'South End' study area.

outcrops. Mice 3, 16 and 17 inhabited barren, grassy slopes exposed to predominantly south-westerly winds. Animals living in open, featureless areas tended to have larger ranges than those living in varied habitats with plenty of cover: such variation precludes rigid specification of home-range characteristics.

Movement

'Saturation' trapping was performed on a part of the 'South End' study area during November 1971 and March 1972. Thirteen males were caught in both censuses on four or more nights. They have been taken as representative of resident mice whose ranges can be compared between early winter and spring (Fig. 8). The ranges of all of them were relatively stable. Most individuals were caught at one or two trap positions which were common to both periods. Three mice showed no area of overlap between censuses but the new locations were only 20–30 m from the old. There seemed to be greater mobility and an enlarged range during spring: six of the 13 mice were caught in a greater number of different traps than in winter; only one was caught in fewer.

Change of home range in winter was investigated more widely by examining the capture positions of 162 mice caught in both the autumn 1971 and winter 1971 censuses. Those trapped at a particular or adjacent trap location during both censuses were classed as 'stable'. Of the mice that survived the winter, the majority—86% (62/72) of males and 83% (75/90) of females—remained in the area occupied during autumn 1971. Of those which changed area, 22 moved between 10 and 60 m; only three had moved the edge of their range by more than 60 m.

Discussion

Home-range data presented in Figs 7 and 8 show that individual mice maintained substantial site tenacity, the population being structured into a relatively stable mosaic of overlapping ranges. A similar pattern was seen on Skokholm (Berry & Jakobson, 1974). None the less, 15% of the overwintered population moved from their autumn location so that there is considerable genetical 'churning'. Similarly, Berry & Jakobson (1974) note that a minimum of 20% of the breeding females on Skokholm breed at a site different from where they were born. Both populations can be regarded as effectively panmictic units, in marked contrast with the tight demes of population size 4–6 for mice living in buildings (Anderson, 1965; DeFries & McClearn, 1972; Berry, 1986, for review).

The population density varied from about 20–150 mice per hectare. This compares with a maximum of 60/ha on Skokholm (Berry & Jakobson, 1975), 3/ha in New Zealand forest (Fitzgerald, Karl & Moller, 1981), 53/ha on open grassland in Maryland, USA (Stickel, 1979) and 875/ha in plague populations in southern Australia (Newsome & Crowcroft, 1971).

The population showed a seven-fold variation in size during the study. The numbers were low in spring and increased during the breeding season to a mid-winter peak. **Breeding showed marked seasonality, being absent or at very low intensity during winter.** Similar observations have been documented for other feral populations, for example in California (Breakey, 1963; DeLong, 1967) and South Australia (Newsome, 1969). **On Skokholm the change in mouse population size resembled that on May Island but the range of fluctuation was greater (12-fold over a 10-year period) and the population peak occurred in October/November rather than January/February, followed by a steady decline between November and spring (Berry, 1968).**

For May Island mice there is a strong association between the spring population size and the change in mouse numbers between spring and autumn. Figure 9 shows this relationship using data from both the study reported here and subsequent work carried out during 1982–88 (Berry *et al.*, 1991) in which the hybridization of May mice with, and the spread of alleles from, a small number of house mice introduced from Eday Island (Orkney group) was monitored. The correlation between log population change and the population size (as numbers handled) is significant

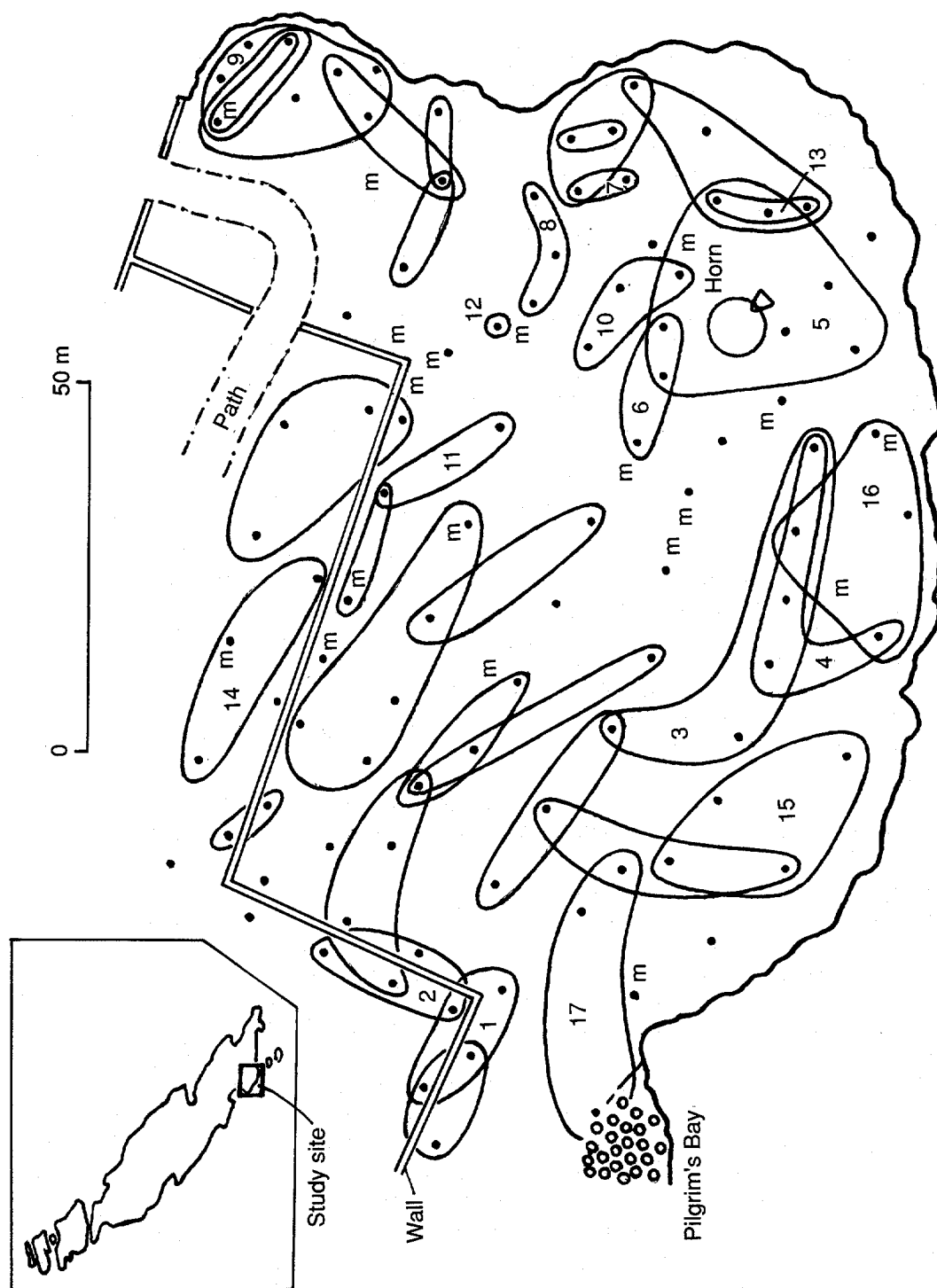


FIG. 7. Distribution of male mice caught on part of the 'South End' study area (location shown inset) during November 1971. Numbers identify individual mice; see text for further details.

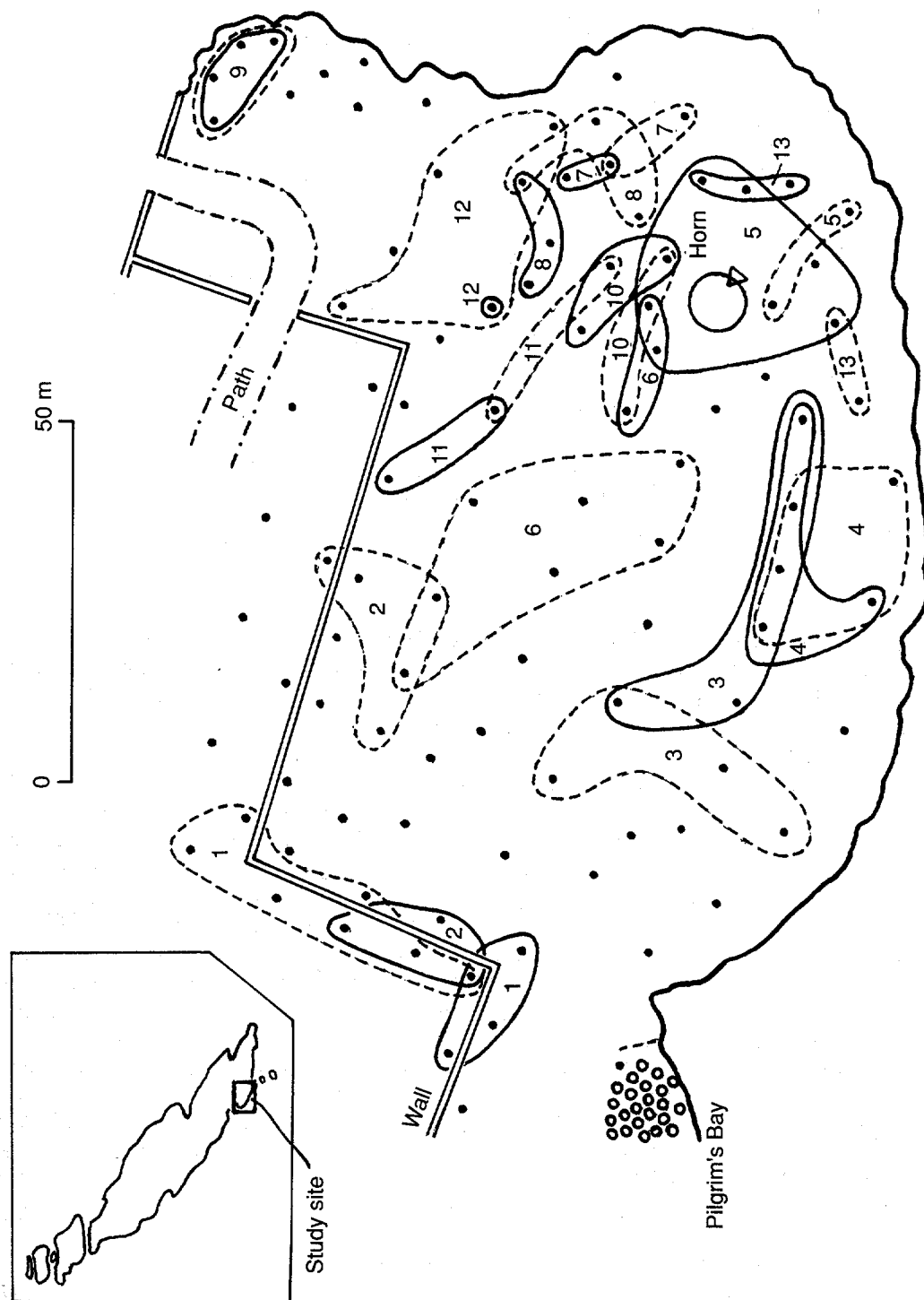


FIG. 8. Ranges of 13 male mice (numbered as in Fig. 7) caught in both November 1971 (—) and March 1972 (---) on the 'South End' study area.

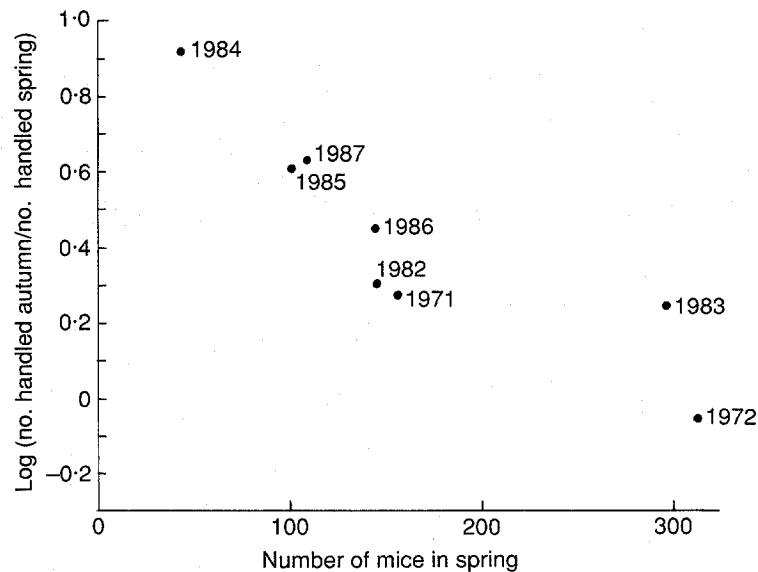


FIG. 9. Log change of population size between spring and autumn plotted against population size (as numbers handled) for 1971-72 and 1982-87.

($r = -0.89$, $P < 0.01$) and indicative of underlying, though unidentified, density-dependent regulatory factors. Possible factors could include social repression of reproduction at higher densities (Lidicker, 1976) and food availability or quality (DeLong, 1967; Newsome, 1970; Bomford & Redhead, 1987).

Overall, the change in population numbers depends on the interaction between factors which influence births, deaths, immigration and emigration. The latter two obviously play no normal part in changing the numbers of mice in an isolated island population. Furthermore, predation losses of May Island mice are presumed to be small, given the lack of resident predators. There were no obvious signs of widespread disease, though a small percentage of animals had livers with parasitic cysts, and berry bugs (*Neotrombicula autumnalis*) were commonly seen infesting the anal-genital region of mice during late summer. Bellamy *et al.* (1973) recorded infertility and uterine oedema in a number of bug-infested adult female mice on Skokholm. In contrast, the present study provides evidence that climate has an important influence on rates of natality and mortality. Climatological data were collected from the May Island lighthouse records (rainfall) and from St. Andrews meteorological station (mean air temperature) located on the Fife coast and about 25 km north-east of the island. Differences from the long-term (1940-71) monthly means for temperature and rainfall are given in Fig. 10. Five facts emerge from these data:

1. Mid-winter 1970-71 was mild with average rainfall.
2. Summer 1971 was warm relative to 1972.
3. Mid-winter 1971-72 was cold and wet.
4. Summer 1972 was colder than average and relatively dry.
5. Mid-winter 1972-73 was mild and exceptionally dry.

Table II shows that mortality over each two-month period between October and April was

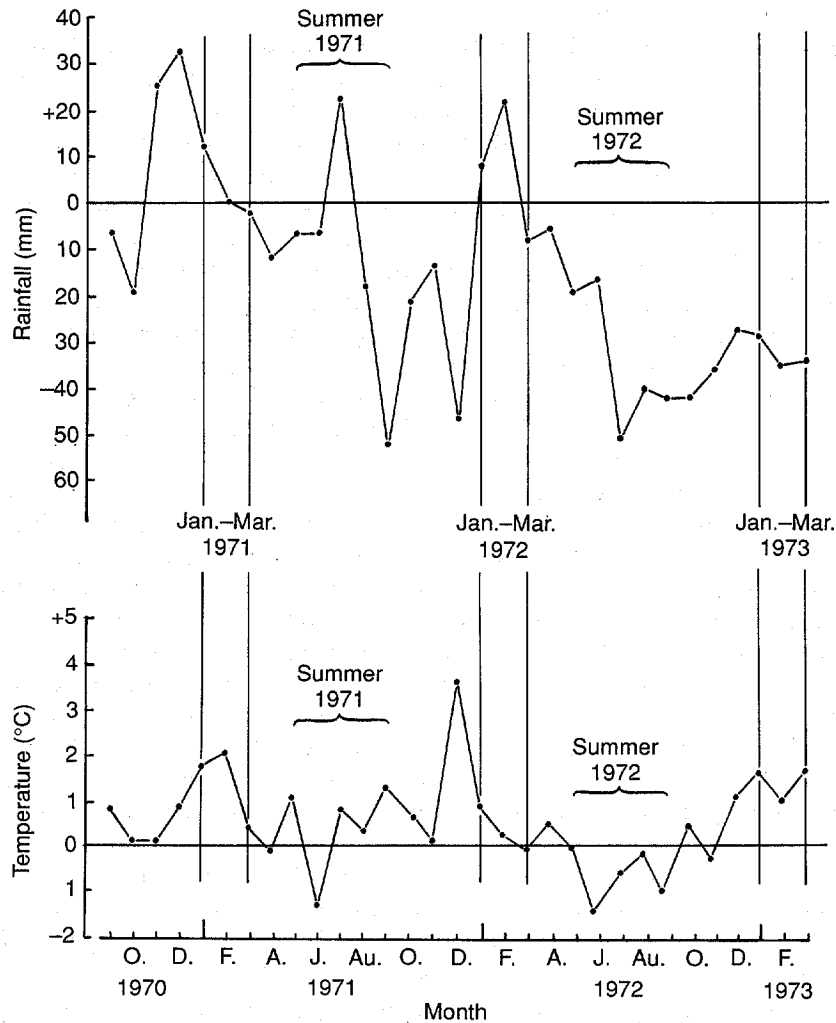


FIG. 10. Rainfall (mm; Isle of May) and mean air temperature (°C; St Andrews, Fife) for 1970-73 expressed as the difference from the 1941-70 average (Leuchars meteorological station, Fife).

greatest during February/April, the period with the lowest mean minimum temperatures. Mortality on the 'South End' study area was greater during the colder and wetter winter of 1971-72 than during that of 1972-73. January and February 1972 were not only colder in absolute terms but the effect of the cold may have been more acute because it occurred abruptly, following a mild December. Food shortage perhaps accompanied this inclement weather, for it was notable that the mice sampled for physiological tests during February 1972 were the only group to gain large amounts of weight during their first night in captivity when given food ad lib (Triggs, 1977). In general, mice gained weight during winter, which suggests that there was no overall food shortage. However, growth of autumn-weaned females was slow (Fig. 6) and accompanied by delayed

sexual maturation. Breakey (1963) observed such a breeding delay in wild house mice on the salt-marshes of San Francisco Bay, California. A female reaching the age of two months in June on the Isle of May would have bred at that age, while one reaching the same age during October would not have bred until the following spring, some seven or eight months later.

The reduction in population size in winter resulted from the combined effects of increased mortality and low recruitment. Breeding declined in the autumn concurrently with the sharp autumnal drop in ambient temperature, at which time major metabolic acclimatization also took place (Triggs, 1977).

In the mild winter of 1970-71, small numbers of mice were pregnant in every month except January. During February, 10-15% were pregnant, a percentage which rose steeply to 35-45% in March-April 1971. This resulted in rapid population growth during summer 1971; the population size at the end of the year was the largest recorded during the study.

Other workers have noted that a relatively large spring population can be a prelude to subsequent population explosion. Pearson (1963) correlated the outbreaks of *M. domesticus* in the San Francisco Bay region with unusually warm winter temperatures during the preceding two years. Berry (1968) used historical records to show that mild winter temperatures regularly resulted in mouse 'highs' on Skokholm. However, in the present study the spring 1972 population size (2100) was approximately double that of spring 1971 (1100), yet the subsequent autumn population sizes were 2500 and 1800, respectively: the large spring 1972 population failed to expand in the summer. Notably, temperatures were below average during 1972 (Fig. 10) and breeding activity was reduced. No pregnant mice were observed in January-February 1972, and from late March to early May 1972 a maximum of only 15% of adult females were pregnant. Likewise, the proportion of females which were pregnant in mid-summer 1972 was lower than in the preceding year, and breeding ended earlier in autumn 1972 than in autumn 1971 (Fig. 4). Taken together, these observations suggest that climate has considerable influence on population dynamics, the spring and summer conditions being potentially as influential as the severity of the winter.

Lowered ambient temperatures produced considerable thermoregulatory adaptation in individual mice. Physiological measurements on animals sampled between autumn and spring showed metabolic and other energy-saving adjustments (Triggs, 1977; Jakobson, 1978). Relative to summer, winter acclimatization was characterized by:

1. Lowered heat production at 5 °C for the maintenance of a particular colonic temperature.
2. Reduced weight loss during exposure to cold.
3. Increased amounts of brown fat, haematocrit and haemoglobin levels.

Similar adjustments have been found in other feral populations, e.g. on Skokholm (Jakobson, 1971) and in Australia (Maclean & Lee, 1973). Summary statements of acclimatization trends obscure the fact that the physiological measurements on wild mice showed wide variation in response, both within and between samples. Jakobson (1981) presents a synthesis of data from Skokholm and May Island (from Triggs, 1977) which shows that changes between summer and winter in metabolism and body temperature of mice maintained in a cold test (225 min at 5 °C) largely reflect a reduction in variability of response in winter: high and low metabolizers are present at all times of the year but the proportion of low metabolizers is much higher during winter, as is the proportion of mice which can resist body temperature decline in the cold. In essence, the winter-acclimatized mouse has a 'more stable' response to imposed tests (Jakobson, 1981). Multivariate differences in thermoregulatory performance were identified between groups

of May mice which related to their subsequent chance of survival during winter (Berry, Jakobson & Triggs, 1973). However, there was no consistent pattern through time, either within or between sexes, as to the particular set of characteristics which favoured survival in either Skokholm or May mice (Triggs, 1977; Jakobson, 1978).

The probability of survival depends not only on physiological performance but on interaction with age, genotype, social relationships, behaviour, etc. (Berry, Jakobson & Triggs, 1973; Berry, Jakobson & Peters, 1987). Death may result from a short-term or fortuitous stress such as lack of food, loss of nest (through flooding), or coincidence of wind, rain and cold imposed on acclimatization patterns not very different from those of survivors. Significant differences in cold adaptation may still be present, for example in thermoregulatory behaviour (Sealand, 1952; Barnett & Scott, 1964; Lynch & Hegmann, 1972), but these will not necessarily be detected in a study of thermoregulatory physiology. Thus, day-time huddling of mice is probably commonplace during winter on the Isle of May. Two nests were uncovered which contained four and five mice, respectively; five artificial nests which were installed to monitor activity patterns regularly contained up to 18 mice (Triggs, 1977). Huddling has well-documented energy-saving effects (Prychodko, 1958; Hart, 1971; Bryant & Hails, 1975). Alternatively, huddling in the nest might conceivably sustain individual mice which otherwise have relatively poor cold tolerance. More importantly, huddling is implicated as being a prerequisite for the energy-saving adaptation of torpor (Webb, Jagot & Jakobson, 1982). Early accounts of torpidity in house mice were circumstantial (e.g. Degerbøl, 1942, see Berry, 1970). More recently, unequivocal evidence of torpidity has been recorded in feral house mice (Morton, 1978) and described in laboratory studies (Fertig & Edmonds, 1969; Hudson & Scott, 1979). Triggs (1977) measured colonic temperatures of May mice huddled in natural and artificial nests on several occasions. Ten of 22 mice had temperatures in the range 32–36 °C (compared with a typical range of 36–38 °C). One mouse from a natural nest had a body temperature of 26.8 °C 20 min after disturbance; it attained 37.6 °C after a further 30 min (air temperature, 6 °C). Such observations suggest that May mice can utilize huddling and torpidity as an adaptability mechanism. The opportunity to huddle could therefore have a significant impact on survival, that chance depending on the density of mice, the availability of nest sites and social interactions. Unfortunately, these factors are difficult to quantify in the field; consequently, the extent to which thermoregulatory behaviour affects mortality remains largely unknown.

The global distribution of house mice is indicative of their adaptability, the major components of which are individual (physiological) and population (genetical) adjustment. The brevity of life would suggest that mice live close to their physiological limits and are exposed periodically to substantial selection pressure. Post-weaning life expectancy for May mice is about 150 days, half as long again as Skokholm mice (Berry & Jakobson, 1971). Females survive longer than males, a finding of most house mouse population studies (Petrusewicz & Andrzejewski, 1962; DeLong, 1967; Newsome, 1969; Berry & Jakobson, 1971; Stickel, 1979). Maximum life-span is about 18 months. This is markedly shorter than the average 3–4 year life-span of wild house mice kept under animal-house conditions. Evidence for response to selection pressure comes from observations of seasonal endocyclic change in genotype frequency at the haemoglobin β -chain locus in Skokholm mice. Spring-caught samples have fewer Hbb^s/Hbb^d heterozygotes than autumn ones (Berry & Murphy, 1970). Heterozygotes are also under-represented in older mice, compared to younger ones, of autumn-caught samples (Berry, 1978) indicative of an apparent advantage of heterozygosity at this locus to young mice in autumn which declines through winter. Unfortunately, there is still no satisfactory correlation between such genetic differences and survivorship (Jakobson, 1981; Newton & Peters, 1983).

In complete contrast, electrophoretic analysis of tissue and blood proteins coded by 22 loci in 93 May Island mice showed the population to be completely monomorphic* (Berry & Peters, 1977) compared with 18% of loci polymorphic in Skokholm mice, 30% in northern Scotland and 50% on Hawaii Island (Berry, 1981). Surprisingly, the long-term studies of Skokholm and May Island mice have revealed gross similarity in the biological characteristics of the two populations (i.e. in terms of breeding, mortality, social structure, thermoregulatory performance, etc.), yet the underlying genotypic variation between individuals is so fundamentally different. The monomorphic condition seems, albeit from a limited set of observations, not seriously to have compromised individual adaptability, nor the population's capacity for continued successful existence. It would be interesting to know whether the monomorphic condition was of recent origin or long-standing. Had it been perpetuated after colonization by a few genetically invariant 'founder' mice, or did it arise as a result of a severe genetic 'bottleneck'? Was it a selected genome which conferred on individuals a sufficiently wide spectrum of physiological flexibility for them to cope with the typical range of environmental challenge imposed by existence on the Isle of May? Or was it a non-adaptive condition, potentially leading along an evolutionary 'blind alley' whereby the population would face extinction if conditions were to change substantially? Unfortunately the genetical history of the May mice is unknown and answers to such questions remain conjecture. Notwithstanding, the fact remains that the genetically invariant May mouse population showed biological characteristics comparable to those of the genetically variable Skokholm population. As is true for much scientific pursuit, these findings beg further questions of animal-environment interactions and adaptability rather than revealing answers. What is clear is that house mice have achieved success in colonizing island and mainland landmasses by a plethora of biological mechanisms and that it may potentially be misleading to make generalizations from any particular study. Berry (1981) states that 'All our knowledge of mouse populations leads to two general conclusions:

1. Every population is genetically unique and highly adaptable.
2. The adaptability involves genes affecting and potentially adjusting all the constituents of mortality, natality, and movement which control population numbers.'

The Isle of May mouse population study upholds the former tenet; as regards the latter, the individuals certainly show adaptability but the contribution of the genome remains unresolved.

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*The population is no longer monomorphic following hybridization with Eday Island (Orkney Group) house mice introduced on to May Island during 1982 (see Berry *et al.*, 1991).

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