

Sub-antarctic House mice: colonization, survival and selection

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(With 1 plate and 2 figures in the text)

House mice have colonized and survived successfully on a number of Sub-Antarctic islands, where the mean annual temperature is only about 5°C, but where there is little seasonal fluctuation in climate. Surprisingly this allows almost continuous breeding. On at least two islands (Macquarie and Marion), there are significant changes in gene frequency in electrophoretically detected enzymes between young (less than three months of age) and old animals from the same population. This indicates natural selection acting in opposite directions at different stages of the life cycle. However the genetical compositions of the Macquarie and Marion populations are more distinct from each other than either is from most British samples. This means that detailed studies of the Sub-Antarctic mouse populations are likely to reveal much about local adaptation, while comparison between the responses of different populations may lead to important generalisations about the possible reaction to evolutionary challenges of a species living close to its physiological limit.

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Introduction

The seas around the Antarctic Continent contain a number of islands lying near to and north of the Antarctic convergence, where the cold surface water of the polar region sinks below the warmer water moving from the north. Botanically these islands are said to lie in a Sub-Antarctic zone, defined by the presence of closed phanerogamic communities but completely lacking trees or woody shrubs (Wace, 1960; Greene, 1964). In the early years of the nineteenth century most of the islands were raided for Fur and Elephant seals; subsequently attempts were made to establish sheep farms on the more temperate ones. During these periods of human contact, a variety of animals and plants were introduced (Holdgate & Wace, 1961; Holdgate, 1967). Among the inadvertently introduced species was the House mouse (*Mus musculus*), which now has thriving populations on at least seven of the colder islands: Amsterdam, St. Paul, Crozet, Kerguelen, Macquarie, Marion and South Georgia (Holdgate & Wace, 1961; Prévost & Mougín, 1970; Anderson & Condry, 1974; W. N. Bonner, *pers comm.*) (Fig. 1). This is surprising, since the temperature on these islands rarely (if ever) rises above the point at which reproduction stops in House

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mice living in less extreme climates (Smith, 1954; DeLong, 1967; Berry, 1968). Mice in cold stores may continue to breed down to at least -3°C , but only if undisturbed and supplied with ample food and bedding material (Barnett & Little, 1965, Barnett, 1973). Furthermore cold is the limiting factor controlling survival and hence population size in mice from temperate areas (Pearson, 1963; Berry, Jakobson & Triggs, 1973), and even in Britain there are genotypic differences in the ability to survive winter temperatures (Berry & Murphy, 1970; Berry & Jakobson, 1975a). Consequently the Sub-Antarctic mice must be living close to their physiological limits and hence likely to respond detectably to environmental stresses in ways unnecessary for animals in more temperate environments.

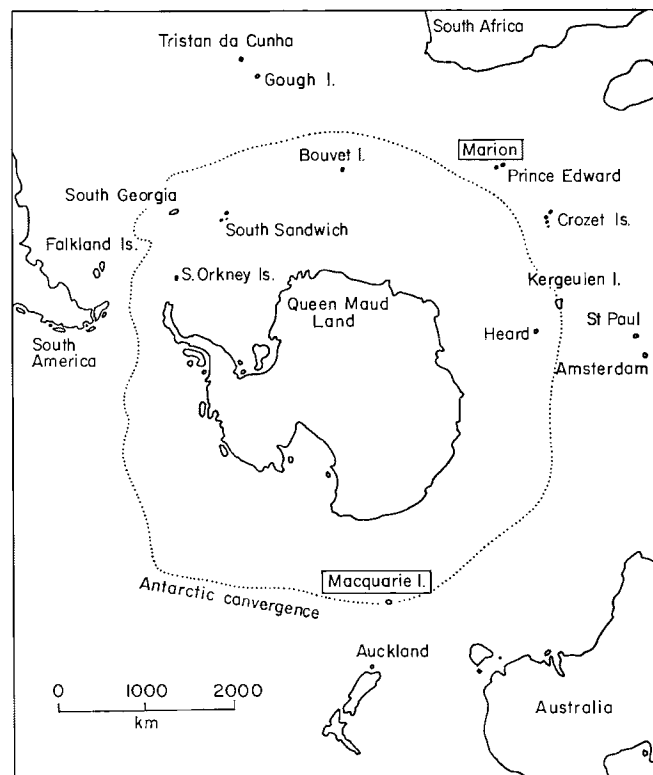


FIG. 1. Map of the Antarctic, showing the convergence and the islands mentioned in the text.

The correctness of this reasoning, allowing an approach to adaptation by using Sub-Antarctic mice as a natural experiment, has been proved in the one study so far carried out—on the mouse population of Macquarie Island ($54^{\circ} 37'S$; $158^{\circ} 54'E$) (Berry & Peters, 1975). This paper is a report on the mice from another island in the Sub-Antarctic and an attempt to generalize from these two studies to the critical pressures for small mammals exposed to climates which are harsh to them. It is based on 92 mice (49♂♂, 43♀♀) killed on Marion Island ($46^{\circ} 54'S$; $37^{\circ} 45'E$) by one of us (R. J. Van A) between December 1975 and March 1976, and subsequently examined in London.

Marion Island and its mice

Marion Island (and its neighbour, Prince Edward Island) is the summit of a basaltic volcano rising from the Atlantic-Indian Ocean median ridge, 2300 km south-east of Cape Town. The nearest land is Crozet Island, 925 km to the east. Marion is roughly circular (Fig. 2), with an area of 290 km² and rising to a height of 1230 m above sea-level (Swart Peak). High laval ridges run radially from the central mountain, dividing the lower ground near the coast into several relatively discrete areas (Plate I). The vegetation of the wet regions behind the coast is largely *Agrostis magellanica* mire, grading into feldmark communities where exposure to strong winds inhibits the development of complete vegetational cover; along the better drained cliffs, Tussock grass (*Poa cookii*) is dominant; and around the rocky beaches, where moulting Elephant seals (*Mirounga leonina*) and breeding Gentoo penguins (*Pygoscelis papua*) have an influence on the substrate, *Cotula plumosa* is the most common plant (Huntley, 1967, 1971).

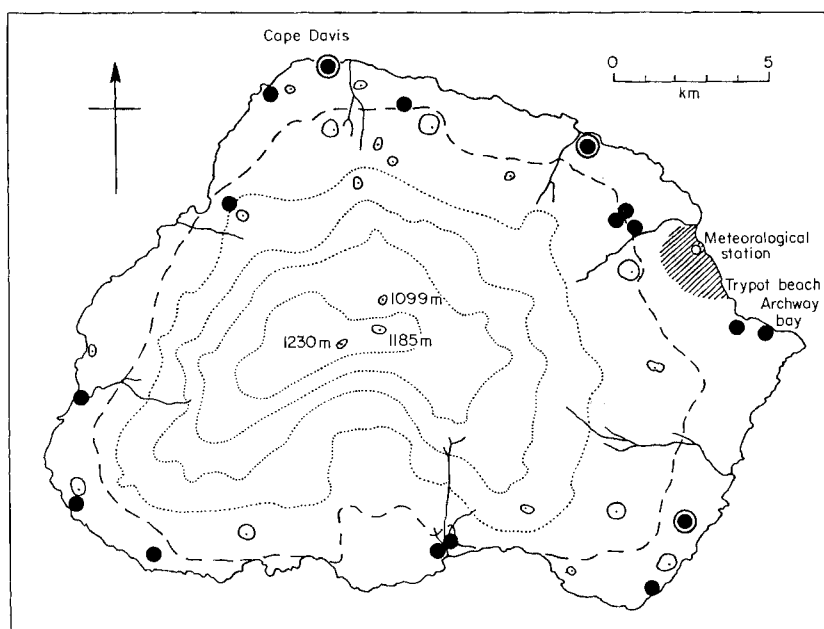


FIG. 2. Marion Island. Most of the mice were trapped in the shaded area round the Meteorological Station. Sitings of mice in other parts of the island (Anderson & Condy, 1974) are shown with ●; mice used in the present study by ○. The limits of the coastal plateau (approx. 150 m above sea level) are marked by a broken line.

Wind and rain dominate the climate of Marion to the extent that the island has been described as a "wind desert" (Schulze, 1971): on average 150 days every year have wind speeds of moderate to full gale force, whilst 25 days a month have some precipitation—snow has been recorded in every month. The mean annual rainfall is 260 cm. The effect of this is that not more than half of the possible solar radiation reaches the ground. Pollen studies have shown that practically all the flowering plants and ferns in the present day flora of Marion were present 16,000 years ago, suggesting that the island was not fully glaciated during the Pleistocene (Schalke & Van Zinderen Bakker, Sr., 1971).

23
1
250



PLATE I (a) Marion Island: typical coastal habitat type. Trypot Beach is to the right of the cove in the centre of the photograph. (b) Marion Island: beach habitat (Archway Bay).

Extreme temperatures are rare: the warmest month is February (mean 7.8° C) and the coldest is August (mean 3.6° C); the annual average is 5.5° C. Marion is slightly warmer than Macquarie Island: the annual mean there is 4.7° C, ranging from an average 6.7° C in January to 3.1° C in July. Of the southern islands with mice, only Kerguelen (mean annual temperature 4.3° C) and South Georgia (annual mean 1.6° C) are colder than Macquarie. Huntley (1971) has calculated an "index of oceanicity" for Marion of 1900. This compares with *c.* 400 for west Norway, 300–400 for the wetter parts of the Scottish Highlands, and 590 for Gough Island (40° S) which lies in the temperate waters of the South Atlantic. He has described life on Marion in uncomfortably graphic terms as "almost ceaseless rain and wind, and endless quaking bogs and rough lava flows (which) certainly detract from the joys of field work". In these respects Marion is typical of the Sub-Antarctic islands with a wet, windy and cloudy climate, and little seasonality.

The origins of the Marion mice are unknown. The island was discovered in 1772 by a French expedition led by Marion-Dufresne, and named in his honour by Cook who rediscovered the island in 1776. By 1802 sealers were living on both Marion and Prince Edward Islands, and a number of wrecks on the islands were already present (Marsh, 1948). Presumably the mice managed to colonize Marion during this phase of the island's history. Most of the seals on the islands were slaughtered during the nineteenth century, and the activities of the sealers must have come to an end early in the present century (Van Zinderen Bakker, Sr., 1971). German marines lived on Marion for short periods during both World Wars. The island was annexed by South Africa in 1948; since then that country has maintained a meteorological station there. Knowledge of the island's natural history largely stems from an expedition led by E. M. Van Zinderen Bakker, Sr., in 1965–6 (Van Zinderen Bakker, Sr., Winterbottom & Dyer, 1971). In 1973 more intensive investigations of mammal, bird and plant ecology began (Condy, 1975). This study of the mice is part of the mammal research programme.

In 1949 there were five cats at the meteorological station, taken there to control mice which reasserted their commensal habit when a human population returned to the island. Two of the cats were male; the sex of the others was unknown, but at least one must have been female, because a population of feral cats now occurs over much of the island, up to an altitude of at least 400 m (Anderson & Condy, 1974). However, mice have been found in the stomachs of only 16% of the cats, making up 4.4% by volume of all food items. There are no other regular predators on the mice, although skuas (*Stercorarius skua*) and gulls (*Larus dominicanus*) have been seen trying to catch them. Sheathbills (*Chionis minor*) may eat dead or injured mice, but they are principally scavengers.

Prior to the mammal studies of which this report is part, the only notes on the mice were by Van Zinderen Bakker, Jr. (1967) that they "do not cause much damage to plant and animal life" and by Van Zinderen Bakker, Sr. (1971) that they were "a nuisance to expedition members by doing much damage to clothing and food, and they even nibble the hair of the oblivious man sleeping in his tent". There are no rats on Marion.

Methods and material

One of us (R. J. Van A) lived on Marion Island from December 1974 to April 1976 studying the cat population. However during the summer of 1975–76, research was carried out also on mice which were trapped at various sites within 4 km of the meteorological station. In some places,

traps were set for three successive nights, at others for only one or two nights. Trouble was experienced with Sheathbills interfering with the mouse traps; the traps had to be well hidden to prevent this. Enough animals were collected during this and previous trappings to demonstrate that the species is well distributed over the island (Fig. 2). Mice occur up to at least 300 m on the central high ground, and probably up to the limit of vegetational cover at about 500 m (Anderson & Condy, 1974).

The habitat in which mice were caught was noted in every case, and all mice caught were killed. The following data were recorded: sex and body weight (and weight of uterus if gravid); head and body, tail and hind foot lengths; haemoglobin concentration and packed red cell volume (haematocrit value) (determined by standard methods); weights of the two kidneys (separately), adrenals and inter-scapular brown fat. The red cells and sera were separated, and frozen (together with the kidneys, liver and heart) for electrophoretic separation and staining of protein and enzyme isozymes on starch gels. This was carried out in London by J. P. using accepted techniques. Twenty-four loci were examined in this way: haemoglobin β -chain (*Hbb*), dipeptidase-1 and 3 (*Dip-1*, *Dip-3*), tripeptidase-1 (*Trip-1*), four esterases (*Es-1*, *Es-2*, *Es-3*, *Es-5*), red cell acid phosphatase (*Acp*), glucose phosphate isomerase (*Gpi-1*), mannose phosphate isomerase (*Mpi*), transferrin (*Trf*), mitochondrial isocitrate dehydrogenase (*Id-2*), supernatant and mitochondrial malic enzymes (*Mod-1*, *Mod-2*), mitochondrial and supernatant malate dehydrogenase (*Mor-1*, *Mor-2*), glutamate oxalate transaminases (*Got-1*, *Got-2*), indophenol oxidase-1 (*Ipo-1*), adenosine deaminase (*Ada*), phosphoglucomutase-1 and -2 (*Pgm-1*, *Pgm-2*), and albumen (*Alb-1*) (Henderson, 1965; DeLorenzo & Ruddle, 1969, 1970; Petras & Martin, 1969; Ruddle, Shows & Roderick, 1969; Selander & Yang, 1969; Berry & Murphy, 1970; Shows, Chapman & Ruddle, 1970; Harris & Hopkinson, 1976).

The animals were aged from the amount of molar tooth wear, using criteria described by Lidicker (1966). This is the most accurate way currently available of assigning age to a wild-caught mouse (Varshavskii, 1949; Berry, 1970). The distinctions between age-classes shown by the rate of wear is similar in mice from the Welsh island of Skokholm and in those originally used by Lidicker from Brooks Island, San Francisco Bay (Bellamy, Berry, Jakobson, Lidicker, Morgan & Murphy, 1973). The method produced plausible results when applied to mice caught on Macquarie Island, and it seems reasonable to apply the same criteria to the Marion sample.

In the comparison of the results from Marion, we have included data from Macquarie Island (52♂♂, 26♀♀) (Berry & Peters, 1975) and a number of apparently comparable populations. These are:

- Sandøy (62°N; mean annual temperature 7.1°C, average range 4.3°C)—one of the six Faroe islands which support mice, lying at the approximate northern limit of wild-living House mice. The sample (16♂♂, 36♀♀) was trapped on and around the small island farms by K. Meitil in October 1972.
- Shetland (60°N; mean annual temperature 7.6°C, average range 4.9°C)—mice from Berry, near Scalloway on the Mainland (main island) of the Shetland group. The sample (18♂♂, 35♀♀) was caught by hand when an oat rick was threshed in March 1973; it can be regarded as a random sample of the local mouse population (Berry, 1963, 1977).
- Orkney (59°N; mean annual temperature 8.0°C, average range 4.6°C)—mice from the island of Sanday. As in the case of Shetland, the sample (41♂♂, 36♀♀) was caught by hand at a threshing in March 1973 (Berry & Jakobson, 1975b).
- Skokholm (52°N; mean annual temperature 10.4°C, average range 5.1°C)—mice (58♂♂, 59♀♀) live-trapped on an effectively uninhabited island 3 km off the Welsh coast, where they were subject to a variety of environmental stresses (Berry, 1968; Berry & Peters, 1976).

Taunton (51°N; mean annual temperature 10.4°C, average range 7.7°C)—mice (41♂♂, 63♀♀) caught by hand at a threshing on a farm 10 km east of Taunton, Somerset, southern England in March 1974 (Berry & Jakobson, 1975b).

The "genetic distances" between the Marion sample and the above samples were calculated on the basis of the frequencies of electrophoretic variants, using Rogers' (1972) Statistic.

Results

All but five of the 92 mice trapped on Marion island came from an area of about 4 km² around the Meteorological Station and Laboratory (Fig. 2). In the intensively trapped area, animals were caught in a range of habitats:

- on cliff-tops intermittently inhabited by Rockhopper penguins (*Eudyptes crestatus*) during the summer breeding season;
- behind beaches, where Elephant seals moult during the late summer, and where Gentoo penguins breed in the late winter and moult in summer. These areas are dominated by either *Poa cookii* tussocks or trampled *Cotula plumosa*;
- in wet grassy mire areas (*Agrostis magellanica*) inland from the immediate coastal area.

Seven sites were trapped around the human-inhabited area, but the numbers from each were too small to distinguish differences between mice from each. Consequently the mice have been pooled and treated as a single population in all analyses. The average trap success was 29.6%.

TABLE I
Age-structure and estimated dates of birth of the Marion mice

	Age-class 1-3	4	5	6	7	8	Average
Modal age (months)	1.5	* 2.0	3.5	5.3	7.7	12+	temp. (C°)
Estimated month of birth of mice caught	Numbers caught						
January	6	17				4	7.2
February	3					1	7.8
March						1	7.5
April							6.2
May					3		4.9
June					1		4.3
July				4	6		3.8
August				1			3.6
September			4	2			3.6
October		4		4			4.8
November	2	8	8				5.7
December	1	4	8				6.4
Total	12	33	20	11	10	6	
% of each age-class	13.0	35.9	21.7	12.0	10.9	6.5	
% of each age-class on Macquarie I. (during December-March)	33.3	20.0	26.7	6.7	6.7	6.7	

The available records are inadequate to determine unequivocally whether or not breeding is continuous on Marion (Table I). Obviously extrapolating backwards from the apparent age of mice when caught to their estimated time of birth is imprecise. Nevertheless there seems good evidence that mice were being born in September and October, which means they were conceived in the coldest months of August and September. Together with the estimate that 10 mice were born in the winter month of July and the high proportion of older animals in the sample trapped from December to March (when compared with Macquarie), it seems that breeding is probably continuous on Marion, as on Macquarie where the evidence is much better.

TABLE II
Average sizes and weights in Marion Island and other mouse population samples

	Marion I.		Macquarie I.	Sandøy, Faroe	Berry, Shetland	Skokholm	Taunton
	♂♂	♀♀					
Lengths of (mm)							
Head & body	78.1±13.0	78.7±10.3	89.7± 8.3	95.5± 9.2	83.2±10.3	90.5± 9.5	86.6± 9.3
Tail	79.1± 6.3	78.4± 7.4	73.5± 6.3	83.2± 7.5	72.8± 9.2	80.1 ± 7.0	74.3± 8.7
Hind-foot	17.7± 0.7	17.8± 0.7	17.0± 0.8	19.3± 0.7	18.1± 0.6	17.0± 0.7	16.8± 0.8
Weights of							
Body (g)	21.4± 4.7	20.6± 5.9	15.8± 3.6	21.1± 6.2	15.5± 6.8	18.7± 5.2	13.4± 4.4
Left kidney (mg)	200.5±78.3		142.0±40.5	143.8±46.6	98.3±42.5	133.1±52.0	85.7±29.6
Adrenals (mg)	9.6± 3.8		8.7± 3.2	8.1± 2.9	5.6± 2.2	6.1± 1.7	5.2± 2.0
Brown fat	74.4±25.3		97.0±33.0	80.6±24.3	80.2±34.3	48.9±12.5	66.1±22.9
Haemoglobin (g/100 ml)	18.1± 2.7		13.7± 2.3	15.8± 1.1	14.9± 1.3	17.1± 1.6	17.3± 1.4
Haematocrit (%)	49.5± 7.0		50.1± 7.0	46.6± 2.8	48.7± 3.5	47.3± 4.9	50.6± 3.2
N	49	43	78	52	53	177	104

TABLE III
Relative organ weights (mg/g total body weight)

	Marion I.		Macquarie I.	Sandøy, Faroe	Berry, Shetland	Skokholm	Taunton
	♂♂	♀♀					
Heart	9.25	9.20	—	6.53	7.02	7.49	7.20
Spleen	3.01	3.12	—	1.99	4.01	4.77	1.89
Adrenals	0.40	0.52	0.55	0.38	0.36	0.32	0.39
Kidneys: left	9.49	9.07	8.99	6.82	6.34	7.12	6.35
right	9.96	9.15	—	7.28	6.57	7.26	6.53
Brown fat	3.49	3.81	6.14	3.82	5.17	2.61	4.90

Eight pregnant mice were caught (19% of females), carrying an average of 7.5 embryos each. The body weights of females (Table II) excludes the weight of gravid uteri. Since organ weights are obviously dependent on body size, we have calculated the mean organ weight (mg) per g of body weight in order to detect any allometric differences between populations (Table III).

The stomachs of all mice killed were fixed, and their contents examined. It proved impossible to carry out a complete analysis of ingested food, but there is no doubt that plant material (particularly small seeds) constitute the major part of the diet.

Sixteen of the 24 loci scored electrophoretically were invariable (*Trip-1*, *Dip-2*, *Dip-3*, *Mor-2*, *Got-1*, *Ada*, *Acp*, *Ipo-1*, *Id-2*, *Pgm-1*, *Pgm-2*, *Trf*, *Alb-1*, *Es-1*, *Es-5*, and *Mpi*). Apparently all possessed the "normal" wild-type allele. The remaining eight loci had two alleles segregating at each. The numbers of each genotype and the frequency of the rarer allele are set out in Table IV for younger (less than three months) and older mice. There were no sex differences in gene frequencies. With the small sample sizes involved, the change in gene frequency between age-groups is statistically insignificant for all loci except *Mod-1*,

TABLE IV
Numbers and % frequencies of alleles at segregating loci in Marion mice

		Up to 3 months (Age-classes 1-4)		Older than 3 months (Age-classes 5-8)	
		N	% of rarer allele	N	% of rarer allele
<i>Hbb</i>	dd	4	} 23.3 ± 5.5	0	} 18.2 ± 4.7
	ds	6		12	
	ss	20		21	
<i>Gpi</i>	aa	2	} 27.3 ± 4.7	3	} 21.7 ± 4.3
	ab	20		14	
	bb	22		29	
<i>Mor-1</i>	aa	29	} 10.3 ± 3.7	14	} 6.5 ± 2.6
	ab	3		4	
	bb	2		1	
<i>Mod-1</i>	aa	18	} 37.5 ± 5.2	29	} 22.8 ± 4.4
	ab	19		13	
	bb	7		4	
<i>Mod-2</i>	aa	33	} 1.5 ± 2.1	34	} 1.4 ± 1.4
	ab	1		1	
<i>Es-2</i>	bb	31	} 15.0 ± 4.0	28	} 22.1 ± 4.5
	bc	6		11	
	cc	3		4	
<i>Es-3</i>	bb	22	} 6.0 ± 3.4	26	} 11.3 ± 4.0
	bc	3		3	
	cc	0		2	
<i>Got-2</i>	aa	3	} 26.7 ± 5.7	2	} 20.0 ± 5.2
	ab	10		8	
	bb	17		20	

The figures for the frequencies are for the rarer allele at each locus

where the observed difference has a probability of occurring by chance of less than 3%. *Mpi* is linked to *Mod-1* on linkage group II (although 20 map units distant), but is unfortunately monomorphic on Marion. No locus showed any deviation from the expected binomial proportions of genotypes. There is a very slightly higher proportion of heterozygotes in the eight segregating loci in mice under four months of age (23.4%) than in those from four months to a year (19.8%).

The allele frequencies and overall heterozygosity of some of the commonly polymorphic allozymic loci are listed in Table V; genetic distances calculated by the method devised by Rogers (1972) and based on 12 electrophoretically detected loci are set out in Table VI.

TABLE V
Percentage frequencies of allozymic alleles

	Marion I.	Macquarie I.	Sandøy, Faroe	Berry, Shetland	Sanday, Orkney	Skokholm	Taunton
<i>Hbb</i> ^a	20.6	61.9	0	21.2	14.0	46.1	0
<i>Gpi-1</i> ^d	24.4	100	—	100	100	100	40.2
<i>Mor-1</i> ^a	7.2	0	0	0	0	0	0
<i>Mod-1</i> ^b	30.0	83.3	35.7	19.8	30.4	48.6	0
<i>Es-2</i> ^a	0	40.8	0	37.8	11.8	79.0	13.8
<i>Es-2</i> ^c	18.7	4.4	0	0	0	0	1.0
<i>Es-3</i> ^a	0	0	97.0	35.0	0	0	0
<i>Es-3</i> ^c	8.9	33.0	0	1.0	0	95.0	91.0
<i>Got-2</i> ^b	23.3	15.8	90.0	1.0	0	0	97.1
<i>Got-2</i> ^c	0	0	0	0	0	0	2.9
% of loci polymorphic*	36.4	31.6	37.5	36.8	21.1	28.6	36.1
% of heterozygotes per locus	7.7	6.5	7.8	5.6	5.1	7.9	5.4

*Defined as loci with the commonest allele having a frequency of less than 99%

TABLE VI
Distance statistics between population samples

Sample size*		Macquarie Island	Faroe: Sandøy	Shetland: Berry	Orkney: Sanday	Skokholm	Taunton
89	Marion Island	0.180	0.066	0.114	0.115	0.200	0.138
70	Macquarie Island		0.104	0.104	0.118	0.100	0.227
48	Faroe: Sandøy			0.148	0.094	0.251	0.119
52	Shetland: Berry				0.050	0.147	0.171
75	Orkney: Sanday					0.176	0.164
109	Skokholm						0.171
100	Taunton						

*Number of animals typed for most loci

Discussion

Colonization is an unpredictable event with a high chance of failure. The evidence for this is largely indirect since an unsuccessful introduction leaves no traces. Circumstantial support for the difficulty of successful colonization comes from the many failures experienced by the multitudinous Naturalization Societies taking birds and mammals from Britain to North America and Australasia, and also the absence of commensal forms such as rats and mice on many small islands susceptible to human influences (Bumpus, 1896; Baker & Stebbins, 1965). Nevertheless, as far as oceanic islands are concerned, those with a more benign climate often support highly successful populations of House mice. For example, R. H. Taylor (*pers. comm.*) has described on Antipodes Island (49°S) "a tussock and sedge community . . . where there were literally thousands of mice, and numbers were seen feeding on *Carex* seed heads", but even under these conditions some islands have only recently acquired mice—House mice did not successfully colonize the Galapagos Islands

until the 1939–45 war (Eibl-Eibesfeldt, 1955). Since the mouse populations on (at least) the different islands of the North Atlantic Shetland and Faroe groups are genetically highly heterogeneous between islands (Berry & Peters, 1977; also Berry, 1969; Berry & Rose, 1975), this implies that the inherited constitution is less important than the ecological problems of establishment. However, three studies of House mice living under different conditions have shown genetical differences between young and old individuals in the same population, indicating the existence of opposing selection pressures at different stages of the life cycle (on Skokholm: Bellamy, *et al.*, 1973; Berry & Jakobson, 1975a; on fields in northern California: Myers, 1974; and on Macquarie Island: Berry & Peters, 1975). The Marion Island mice show exactly the same: although the only formally significant shift in gene frequency is a loss of *Mod-1^b* alleles in older mice when compared with younger, there is a change of 5% or more at five of the other seven segregating loci (Table IV). Most importantly, the *Hbb^a* allele shows a decline with age as on Macquarie—where the change was greater in mice living completely separate from man. The change on Macquarie was from 71% to 54%, on Marion from 23 to 18%.

A serious practical problem of investigating adaptation in British mice is the extent of physiological acclimation they undergo at the beginning of winter: the oxygen consumption falls about 10%, while haemoglobin concentration increases about 10% (Jakobson & Moore, 1971; Maclean & Lee, 1973; Berry & Jakobson, 1975b). Since the Macquarie and apparently the Marion mice breed throughout the year, it seems reasonable to assume that they do not undergo seasonal physiological adjustment. In populations which seasonally acclimatize, the phenotypic change must act to reduce climatic stress and hence reduce the need for genetical adaptation. It is therefore of interest to compare physiological indicators of response to low temperatures (haemoglobin concentration and haematocrit value; brown fat and heart weights), and general responses to stress (adrenal and spleen weights) in the Marion and Macquarie mice, and both of them with other populations (Tables II, III).

Surprisingly, both the Marion and Macquarie mice are rather small when compared with north temperate mice, being approximately the size of animals from Tristan da Cunha (37°S) and Gough Island (40°S) (Hill, 1959). These islands have a mean annual temperature of 12.2°C and 11.7°C respectively (Holdgate, 1960). Relative body area is generally considered to be critical in adaptation to cold (*e.g.* Sealander, 1962) and mice on islands almost invariably increase in size—possibly as a response to a reduced need to escape from ground predators (Corbet, 1961; Foster, 1964). Even odder, the Marion and Macquarie animals are entirely different shapes: the Marion mice are 20% heavier than the Macquarie ones but are 10% shorter; the head & body to tail ratio is 1.00 for Marion but 1.22 for Macquarie—the latter similar to British island mice. The Marion mice have relatively large hearts compared to northern mice. Both Marion and Macquarie animals have large kidneys, which could be significant since kidney weight is a factor affecting survival in two British island populations—Skokholm and the Isle of May (Bellamy *et al.*, 1973; Berry, Jakobson & Triggs, 1973). Brown fat amount is a direct indicator of metabolic capability but varies greatly between animals. Marion mice have on average a similar amount of brown fat to northern mice, while Macquarie mice have more.

There is slight evidence that the Marion population may have originated from Denmark, since they possess the *Es-2^e* allele, described by Hunt & Selander (1973) in Danish mice and hitherto only recorded elsewhere from the Faroe Islands (which have had strong links

with Denmark for many years) (Berry & Peters, 1977). However there is little point in speculating about the relationships of the mice on the Sub-Antarctic islands. Their origins are almost certainly highly diverse, but even closely related populations in a species like the House mice may be very distinct because of their variability and ability of small numbers to found new populations (Berry, 1975; Berry & Peters, 1977) (Table VI).

The genetic distances in Table VI can be calibrated by the "distances" between samples trapped on Skokholm in successive years. No immigration is likely into this island population, so change between years must be due to genetical forces acting on the island mice (Berry & Jakobson, 1974, 1975*a*). The mean distance from year to year is 0.025 (Berry & Peters, 1977). This has to be compared with distances between rick samples collected from three farms near Taunton about 3 km from each other where the mean distance is 0.088—presumably due to chance founder sampling in an otherwise continuous species range. The Marion population is closest to that of Sandøy, perhaps reflecting a joint Danish origin of the two populations; it is also more like the southern English rick sample from Taunton than either Macquarie or the wild-living populations from Skokholm. This illustrates the importance of ancestry rather than contemporary selective pressures in determining the genetical compositions of local populations (Berry & Warwick, 1974; Berry, 1975).

Is it possible to generalize at all about the mice on Sub-Antarctic islands from present knowledge? Even from the limited comparisons possible between the Marion and Macquarie populations, it is clear that the two islands support genetically distinct populations. Indeed there is no obvious pattern at all in gene frequencies in the two southern populations or the four northern populations compared in Table VI, although it is of interest that the mean level of heterozygosity is similar in all the samples listed, despite the fact that only one (Taunton) does not come from a relatively small island (Table V). In a much larger and more detailed series of comparisons between 26 populations (from the Faroe, Shetland, and Orkney island groups, and from sites on Great Britain itself), Berry & Peters (1977) found the same prolixity of variation, but drew the conclusion that the apparent inter-population genetical randomness could not be regarded as evidence for the irrelevance of genetical constitution, since natural selection was acting strongly to influence the frequency of at least some alleles or genotypes under certain conditions.

This applies even more strongly to Sub-Antarctic populations where endocyclic selection seems to be a regular feature of mouse existence (selection, that is, which operates in different directions at different times in a mouse's life). Allozymic variants may be linked markers or pleiotropic effects of physiologically important characters; or they may be expressions of important characters themselves. Nevertheless the genetical adjustments undergone by mice living under conditions like those on Marion and Macquarie Islands provide an excellent opportunity to discover those traits which limit survival at different times of life, and thence the possibility of evaluating the relative importance of each by comparing the responses of mice on different islands. Waddington (1965) has argued that "what is needed, at the present state of our understanding of evolution, is not so much a greater elaboration of formal theories of quantitative and population genetics, or even more analyses of wild populations in terms of genetics divorced from their ecology. What we need is more knowledge about the ways in which populations, in fact, meet evolutionary challenges". Further study of the Sub-Antarctic mouse populations seems likely to give highly pertinent information about such "evolutionary challenges".

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REFERENCES

- Anderson, G. D. & Condry, P. R. (1974). A note on the feral cat and house mouse on Marion Island. *S. Afr. J. antarct. Res.* **4**: 58–61.
- Baker, H. G. & Stebbins, G. L. (eds) (1965). *Genetics of colonizing species*. New York & London: Academic Press.
- Barnett, S. A. (1973). Maternal processes in the cold-adaptation of mice. *Biol. Rev.* **48**: 477–508.
- Barnett, S. A. & Little, M. J. (1965). Maternal performance in mice at -3°C : food consumption and fertility. *Proc. R. Soc. (B)* **162**: 492–501.
- Bellamy, D., Berry, R. J., Jakobson, M. E., Lidicker, W. Z., Morgan, J. & Murphy, H. M. (1973). Ageing in an island population of the house mouse. *Age & Ageing* **2**: 235–250.
- Berry, R. J. (1963). Epigenetic polymorphism in wild populations of *Mus musculus*. *Genet. Res., Camb.* **4**: 193–220.
- Berry, R. J. (1968). The ecology of an island population of the house mouse. *J. anim. Ecol.* **37**: 445–470.
- Berry, R. J. (1969). History in the evolution of *Apodemus sylvaticus* (Mammalia) at one edge of its range. *J. Zool., Lond.* **159**: 311–328.
- Berry, R. J. (1970). The natural history of the house mouse. *Fld Stud.* **3**: 219–262.
- Berry, R. J. (1975). On the nature of genetical distance and island races of *Apodemus sylvaticus*. *J. Zool., Lond.* **176**: 293–296.
- Berry, R. J. (1977). The population genetics of the house mouse. *Sci. Progr., Oxford.* **64**: 341–370.
- Berry, R. J. & Jakobson, M. E. (1974). Vagility in an island population of the House mouse. *J. Zool., Lond.* **173**: 341–354.
- Berry, R. J. & Jakobson, M. E. (1975a). Ecological genetics of an island population of the House mouse. *J. Zool., Lond.* **175**: 523–540.
- Berry, R. J. & Jakobson, M. E. (1975b). Adaptation and adaptability in wild-living House mice. *J. Zool., Lond.* **176**: 391–402.
- Berry, R. J., Jakobson, M. E. & Triggs, G. S. (1973). Survival in wild-living mice. *Mamm. Rev.* **3**: 46–57.
- Berry, R. J. & Murphy, H. M. (1970). Biochemical genetics of an island population of the house mouse. *Proc. R. Soc. (B)* **176**: 87–103.
- Berry, R. J. & Peters, J. (1975). Macquarie Island house mice: a genetical isolate on a Sub-Antarctic island. *J. Zool., Lond.* **176**: 375–389.
- Berry, R. J. & Peters, J. (1976). Genes, survival and adjustment in an island population of the house mouse. In *Population genetics and ecology*: 23–48. Karlin, S. & Nevo, E. (Eds). New York: Academic Press.
- Berry, R. J. & Peters, J. (1977). Heterogeneous heterozygosities in *Mus musculus* populations. *Proc. R. Soc. (B)* **197**: 485–503.
- Berry, R. J. & Rose, F. E. N. (1975). Islands and the evolution of *Microtus arvalis* (Microtinae). *J. Zool., Lond.* **177**: 395–409.
- Berry, R. J. & Warwick, T. (1974). Field mice (*Apodemus sylvaticus*) on the Castle Rock, Edinburgh: an isolated population. *J. Zool., Lond.* **174**: 325–331.
- Bumpus, H. C. (1896). The variations and mutations of the introduced sparrow, *Passer domesticus*. *Biol. Lect., Woods Hole* **1896**: 1–15.
- Condry, P. R. (1975). Mammal research on the Prince Edward Islands. *Publ. Univ. Pretoria*, (n.s.) No. 97: 56–59.
- Corbet, G. B. (1961). Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. *Nature, Lond.* **191**: 1037–1040.
- DeLong, K. T. (1967). Population ecology of feral house mice. *Ecology* **48**: 611–634.
- DeLorenzo, R. J. & Ruddle, F. H. (1969). Genetic control of two electrophoretic variants of glucosephosphate isomerase in the mouse (*Mus musculus*). *Biochem. Genet.* **3**: 151–162.
- De Lorenzo, R. J. & Ruddle, F. H. (1970). Glutamate oxalate transaminase (GOT) genetics in *Mus musculus*: linkage, polymorphism and phenotypes of the *Got-2* and *Got-1* loci. *Biochem. Genet.* **4**: 259–273.

- Eibl-Eibesfeldt, I. (1955). Über der Massenausbreiten der Hausmaus auf Süd-Seymour, Galapagos. *Saugetierk. Mitt.* **3**: 175–176.
- Foster, J. B. (1964). Evolution of mammals on islands. *Nature, Lond.* **202**: 234–235.
- Greene, S. W. (1964). Plants of the land. In *Antarctic research*: 240–253. Priestley, R. E., Adie, R. J. & Robin, G. de Q. (Eds). London: Butterworth.
- Harris, H. & Hopkinson, D. A. (1976). *Handbook of enzyme electrophoresis*. Amsterdam: North-Holland.
- Henderson, N. S. (1965). Isozymes of isocitrate dehydrogenase: subunit structure and intracellular location. *J. exp. Zool.* **158**: 263–273.
- Hill, J. E. (1959). Rats and mice from the islands of Tristan de Cunha and Gough, South Atlantic Ocean. *Results Norw. scient. Exped. Tristan da Cunha* No. 46: 1–5.
- Holdgate, M. W. (1960). The fauna of the mid-Atlantic islands. *Proc. R. Soc. (B)* **152**: 350–567.
- Holdgate, M. W. (1967). The influence of introduced species on the ecosystems of temperate oceanic islands. *Publ. Int. Union Conserv. Nat.* **9**: 151–176.
- Holdgate, M. W. & Wace, N. M. (1961). The influence of man on the floras and faunas of southern islands. *Polar Rec.* **10**: 465–493.
- Hunt, W. G. & Selander, R. K. (1973). Biochemical genetics of hybridisation in European house mice. *Heredity* **31**: 11–33.
- Huntley, B. J. (1967). A preliminary account of the vegetation of Marion and Prince Edward Island. *S. Afr. J. Sci.* **63**: 235–241.
- Huntley, B. J. (1971). Vegetation. In *Marion and Prince Edward Islands*: 98–160. Van Zinderen Bakker, Sr., E. M., Winterbottom, J. M. & Dyer, R. A. (Eds). Cape Town: Balkema.
- Jakobson, M. E. & Moore, R. E. (1971). Season and metabolic rate in house mice on an island. *J. Physiol., Paris* **63**: 296–299.
- Lidicker, W. Z. (1966). Ecological observations on a feral house mouse population declining to extinction. *Ecol. Monogr.* **36**: 27–50.
- Maclean, G. S. & Lee, A. K. (1973). Effects of season, temperature and activity on some blood parameters of feral house mice (*Mus musculus*). *J. Mammal.* **54**: 660–667.
- Marsh, J. H. (1948). *No pathway here*. Cape Town: Timmins.
- Myers, J. H. (1974). Genetic and social structure of feral house mouse populations on Grizzly Island, California. *Ecology* **55**: 747–759.
- Pearson, O. P. (1963). History of two local outbreaks of feral house mice. *Ecology* **44**: 540–549.
- Petras, M. L. & Martin, J. E. (1969). Improved electrophoretic resolution of some Hb variants in *Mus musculus*. *Biochem. Genet.* **3**: 303–309.
- Prévost, J. & Mougou, J.-L. (1970). *Guide des Oiseaux et Mammifères de Terres Australes et Antarctiques Françaises*. Paris: Delachaux & Niestlé.
- Rogers, J. S. (1972). Measures of genetic similarity and genetic distance. *Univ. Texas Publ.* No. 7213, *Studies in Genetics* **7**: 145–153.
- Ruddle, F. H., Shows, T. B. & Roderick, T. (1969). Esterase genetics of *Mus musculus*: expression, linkage and polymorphism of locus *Es-2*. *Genetics* **62**: 393–399.
- Schalke, H. J. W. G. & Van Zinderen Bakker, Sr., E. M. (1971). History of the vegetation. In *Marion and Prince Edward Islands*: 89–97. Van Zinderen Bakker, Sr., E. M., Winterbottom, J. M. & Dyer, R. A. (Eds). Cape Town: Balkema.
- Schulze, B. R. (1971). The climate of Marion Island. In *Marion and Prince Edward Islands*: 16–31. Van Zinderen Bakker, Sr., E. M., Winterbottom, J. M. & Dyer, R. A. (Eds). Cape Town: Balkema.
- Sealander, J. A. (1961). Seasonal changes in blood values of deer mice and other small mammals. *Ecology* **43**: 107–119.
- Selander, R. K. & Yang, S. Y. (1969). Protein polymorphism and genic heterozygosity in a wild population of the House mouse (*Mus musculus*). *Genetics* **63**: 653–667.
- Shows, T. B., Chapman, V. M. & Ruddle, F. H. (1970). Mitochondrial malate dehydrogenase and malic enzyme: Mendelian inherited electrophoretic variants in the mouse. *Biochem. Genet.* **4**: 707–718.
- Smith, W. W. (1954). Reproduction in the house mouse *Mus musculus* L. in Mississippi. *J. Mammal.* **35**: 509–515.
- Van Zinderen Bakker, Sr., E. M. (1971). Introduction. In *Marion and Prince Edward Islands*: 1–15. Van Zinderen Bakker, Sr., E. M., Winterbottom, J. M. & Dyer, R. A. (Eds). Cape Town: Balkema.
- Van Zinderen Bakker, Sr., E. M., Winterbottom, J. M. & Dyer, R. A. (1971). *Marion and Prince Edward Islands. Report on the South African Biological & Geological Expedition, 1965–1966*. Cape Town: Balkema.

- Van Zinderen Bakker, Jr., E. M. (1967). Observations on animal life on Marion and Prince Edward Islands. *S. Afr. J. Sci.* **63**: 242-246.
- Varshavskii, S. N. (1949). [The age composition of the house mouse population (*Mus musculus* L.).] *Zool. Zh.* **28**: 361-371 (in Russian).
- Wace, N. (1960). The botany of the southern oceanic islands. *Proc. R. Soc. (B)* **152**: 575-590.
- Waddington, C. H. (1965). Introduction. In *Genetics of colonizing species*: 1-6. Baker, G. H. & Stebbins, G. L. (Ed). New York & London: Academic Press.