Population biology of house mice (*Mus musculus* L.) on sub-Antarctic Marion Island

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Based on mark-recapture models, house mouse densities on sub-Antarctic Marion Island changed seasonally (up to 10-fold) and differed between habitats. Peak densities occurred towards the end of summer (May). On both the hummocky beach and vegetated lava study grids, densities at the end of summer were significantly higher than those recorded during 1979/80. During the rest of the year densities were significantly lower on these study grids than those recorded during 1979/80. Length of the breeding season (6,5 months) and mean litter size (7,24 ± 1,7) were of the same order as those recorded during 1979/80, as were age and sex specific mortality patterns. The incidence of pregnancy (7,27 litters/season) was higher (not significant) than that recorded during 1979/80. Prenatal mortality was positively correlated with ovulation rate. Differences in annual trends may result from yearly changes in environmental conditions and do not support speculation that these may have resulted from medium-term changes in climatic conditions in the sub-Antarctic.

Deur die gebruik van merk-hervang modelle is dit duidelik dat die digtheid van huismuise op die sub-Antarktiese Marioneiland seisoenaal verander (tot 10-voudig) en verskil tussen habitatte. Digthede het teen die einde van die somer (Mei) gepiek. Digtheid teen die einde van die somer op bioties beïnvloed gebiede en op begroeide lava was ook betekenisvol hoër as gedurende 1979/80. Gedurende die res van die jaar was digthede in hierdie habitatte betekenisvol laer as gedurende 1979/80. Die lengte van die teelseisoen (6,5 maande), gemiddelde werpselgrootte en ouderdom, sowel as geslagspesifieke mortaliteit, was soortgelyk aan waardes bepaal gedurende 1979/80. Die voorkoms van dragtigheid (7,27 werpsels/seisoen) was hoër (nie betekenisvol nie) as gedurende 1979/80. Prenatale mortaliteit en ovulasietempo het direk met mekaar verband gehou. Waargenome neigings kan toegeskryf word aan jaarlikse veranderinge in omgewingstoestande en onderskraag dus nie die voorstel dat toename in getalle te wyte is aan medium-termyn veranderinge in klimaatstoestande in die sub-Antarktiese gebied nie.

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Studies on the feral house mouse *Mus musculus* in habitats ranging from deserts and swamps to Antarctic islands provide a basis for comparison between populations, which can be related to prevailing environmental conditions (see Berry 1981). House mice have colonized at least eight sub-Antarctic islands including Marion Island, which they may have inhabited for 170 years (Berry, Peters & Van Aarde 1978). In the late 1970s this population was endocyclic and existed close to its physiological limits (Berry *et al.* 1978). Nevertheless, by then mice had become firmly established in the island's ecosystem (Gleeson 1981) and, with the removal of cats, are now considered the most important terrestrial mammalian 'carnivore' on the island.

Previous studies on mice at Marion Island focused on their demography and impact on the island's fauna and flora (Berry *et al.* 1978; Gleeson 1981; Gleeson & Van Rensburg 1982; Crafford & Scholtz 1987; Rowe-Rowe, Green & Crafford 1989; Crafford 1990; Smith & Steenkamp 1990). This study was motivated by suggestions that mouse densities have increased since the 1970s (Smith & Steenkamp 1990), possibly owing to an increase in ambient temperature. The associated increased predation on invertebrates responsible for litter turnover could have important consequences for ecosystem function.

This paper aims at analysing seasonal changes in the habitat specific densities of mice and attempts to explain these in terms of reproductive and age-specific survival patterns recorded over an 11-month period from May 1991 to March 1992. Some of these data are compared with those recorded earlier on Marion Island and with those for some other mouse populations.

Study area

Marion Island (46°54'S, 37°45'E) is volcanic in origin and lies about 2300 km SSE of Cape Town, South Africa. It extends over an area of 290 km² and rises to a height of 1230 m a.s.l. This study was conducted on the eastern coastal zone (<100 m a.s.l.) of the island south-east of the base station. The oceanic climate of the island is characterized by low temperatures (annual mean air temperature ≈ 5°C), high precipitation (>2500 mm/annum) and strong winds (Smith 1987). Since 1968, and especially over the last 10 years, mean surface air temperature has increased and annual precipitation has decreased (Smith & Steenkamp 1990; Smith 1992). Since Gleeson's (1981) study on these mice, temperatures have increased by ≈ 0,7°C.

Trapping took place on a hummocky beach, a hummocky vegetated black lava area and a dry swamp area. Hummocky beach areas near or at penguin and seal colonies are strongly influenced by manuring and trampling, are rich in nutrients and have an invertebrate biomass higher than elsewhere on the island (19 dry kg/ha; Gleeson 1981). Hummocky vegetated black lava areas consist of a mosaic of undulating lava, small mires and slopes dominated by fern-brakes. These dominated the study area and had a low invertebrate biomass (2 dry kg/ha; Gleeson 1981). Swamps cover large areas of the coastal plains and have high water tables. These have soft peat substrates and relatively low growing vegetation. Few refuges are available to mice but invertebrate biomass was 14 dry kg/ha (Gleeson 1981).

Materials and Methods

Density

Population densities based on capture-mark-recapture models were estimated monthly between May 1991 and March 1992 for two habitats, and bimonthly for a third, using the same grids and methods used by Gleeson (1981) during 1979/80. Each grid consisted of 10 × 10 trap stations with an interstation distance of 10 m, except for the first trapping session (May 1991), when the hummocky beach grid consisted of 7 × 7 stations. In this case two traps were placed at each station, whereas on all other trapping sessions a single Sherman trap, baited with a mixture of peanuts or oats and peanut butter, was set at each station. Trapping on a grid continued for five nights and was followed by two nights of trapping on eight assessment lines to determine the area of effect of the grid (Smith, Blessing, Chelton, Gentry, Golley & McGinnis 1971; O'Farrell, Kaufman & Lundahl 1977). Each assessment line comprised 13 stations, with five within the grid and eight extending beyond the perimeter thereof. All mice caught were marked by toe-clipping and released after the station of capture, sex, reproductive status and weight were recorded.

To compare our results directly with those obtained during 1979/80, the Petersen estimate was used to calculate densities and standard errors. For this estimate, captures for the first three nights were combined as the marking occasion and the fourth night was used as the recapture occasion. Jolly-Seber estimates, having fewer assumptions than the Petersen estimate, were used to analyse seasonal trends and differences between grids. For the Jolly-Seber estimate, all five nights were used as capture-recapture occasions, thus providing three estimates of density for each session. Mean densities and standard errors for each month are thus based on three estimates.

Comparisons between grids and seasons were based on densities not corrected for edge effects. Density on the hummocky beach grid during May (when a smaller grid was used) was corrected using assessment lines to make data comparable with other trap sessions. Monthly loss rates (mortality and emigration) were estimated from the proportion of marked mice which were not recaptured in subsequent trap sessions.

Reproduction

Each month about 120 mice were collected from the coastal zone. They were sexed, weighed and their reproductive status noted (i.e. males: testes weight; females: vaginal orifice perforate or imperforate, lactating or not lactating and pregnant or not pregnant). Age and weight at sexual maturity were estimated as the values when at least 50% of individuals in that age or weight class were reproductively active during the breeding season. Female mice which were pregnant or lactating, or had a perforated vaginal orifice were classed as reproductively active. Males were considered reproductively active when combined testes mass exceeded 60 mg (Rowe, Swinney & Quy 1983).

Ovulation rate was based on the number of corpora lutea in the ovaries after their routine preparation for histological examination, and litter size was based on embryo counts. Foetal mortality was calculated as the difference between the number of embryos and the number of corpora lutea. The incidence of pregnancy was calculated as described by Caughley (1977).

Age structure

The ages of mice were determined from molar tooth wear according to Gleeson (1981) and relevant data were treated following Caughley (1977).

Results

Density

Monthly densities in the three habitat types, estimated using the Petersen and Jolly-Seber models, are shown and compared with those recorded by Gleeson (1981) in Figures 1a–c. Densities on all three grids changed seasonally, with peak values at the end of summer (May) decreasing rapidly during autumn, and thereafter remaining relatively constant until the following summer when values again increased. Densities on the hummocky beach grid began to increase in early summer (December), whereas those on the vegetated lava and swamp grids only began to increase in mid-summer (February).

Densities on the hummocky beach grid derived from the Jolly-Seber model were significantly higher than those on the vegetated lava and swamp grids but there was no significant difference between the last-mentioned two grids ($F_{2,24}$ = 14; $p < 0,001$; Tukey multiple range test @$p = 0,05$). The peak density on the hummocky beach grid based on the Petersen estimate was significantly higher (t_1 = 49; $p < 0,05$) than the peak there during 1979/80. This peak on the vegetated lava grid was also significantly higher than that obtained during 1979/80 (t_1 = 18; $p < 0,05$). This was not the case on the swamp grid (t_1 = 3,28; $p > 0,1$).

Densities on the hummocky beach and vegetated lava grids, at the end of the breeding season (May), were significantly higher than those recorded during 1979/80 (Table 1). However, densities recorded at the end of the breeding season, and during the month prior to the beginning of recruitment (August), did not differ significantly. Values during 1979/80 were in all other cases significantly higher than those recorded during this study.

Table 1 A comparison between the number of mice per grid (± standard errors) during 1979/80 and 1991/92, recorded in three habitat types on Marion Island. All *t*-values have one degree of freedom

Habitat	Month	Density (1979)	Density (1991)	*t*-value	Significance level
Hummocky beach	May	126 ± 18	242 ± 33	42	<0,05
	Aug.	78 ± 5	56 ± 6	31	<0,05
	Nov.	68 ± 6	43 ± 3	40	<0,05
Vegetated lava	May	63 ± 7	89 ± 11	19	<0,05
	Aug.	51 ± 4	15 ± 2	53	<0,05
	Jan.	19 ± 2	7 ± 0	31	<0,05
Dry swamp	June	66 ± 15	51 ± 6	10	>0,05
	Aug.	29 ± 2	58 ± 15	16	<0,05
	Dec.	12 ± 2	9 ± 1	5	>0,05
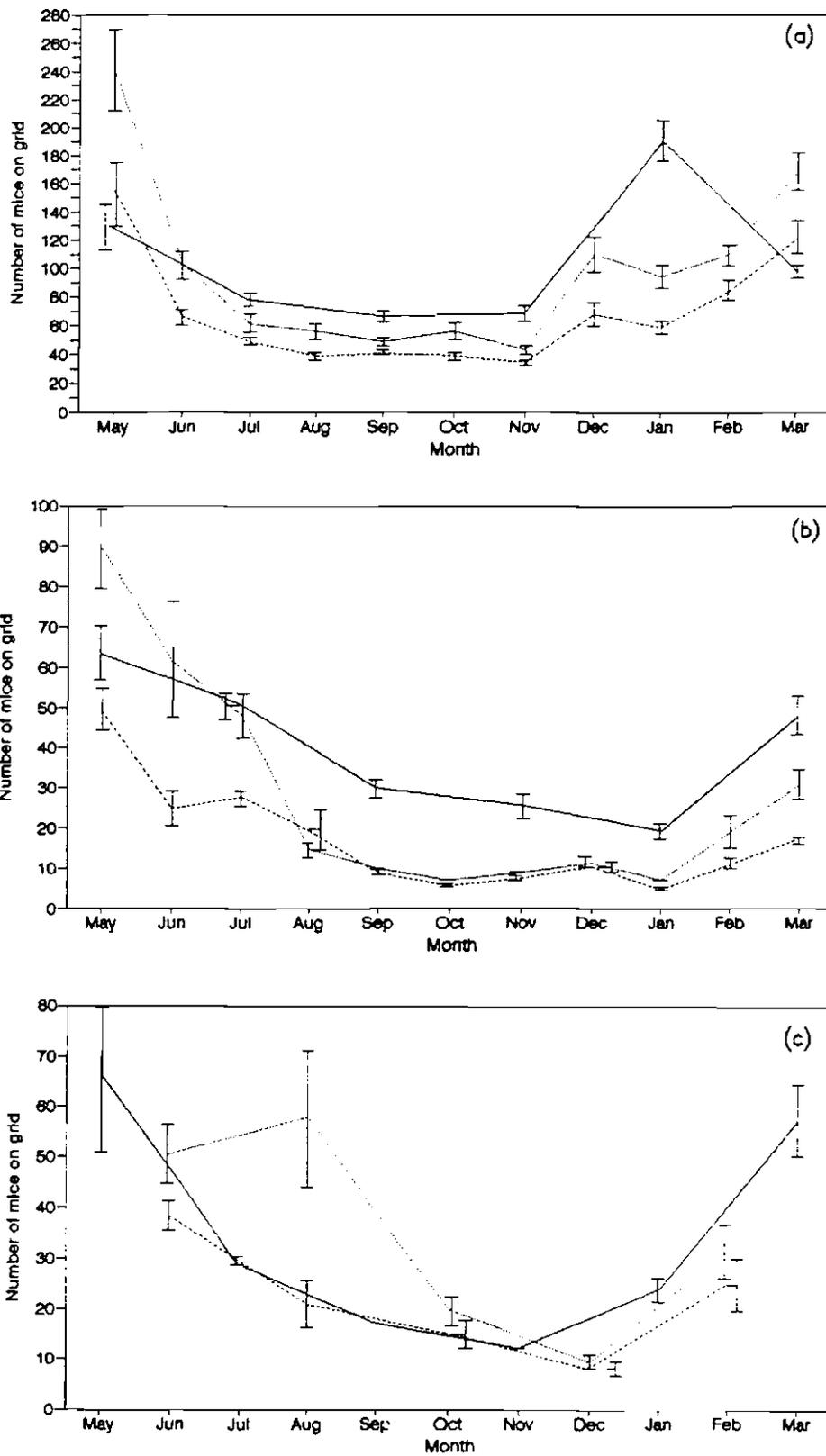
Figure 1   Petersen (....) and Jolly-Seber (---) estimates of the number of mice present monthly during 1991/92 on each of three 0,8-ha grids. Results obtained by Gleeson (1981) are also presented (—). Vertical bars denote one standard error of estimates. (a) = Hummocky beach, (b) = Vegetated black lava and (c) = Dry swamp.

Reproduction

Sexual maturity

Some females were pregnant or lactating from the age of two months but sexual maturity, based on the age when 50% were reproductively active, was reached at four months.

Based on 3-g weight classes, females reach sexual maturity at ≥20 g, with about 90% of females in all higher weight classes being reproductively active during the breeding season. Males attained sexual maturity at an age of two months and a weight of 11 g.
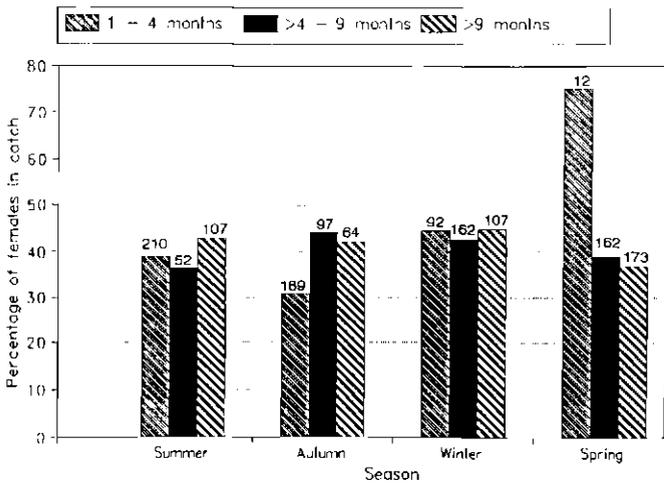
Figure 2 Season-specific sex ratios, represented as the percentage of females caught, for three age groups on Marion Island during 1991/92. Figures above bars denote sample sizes.

Sex ratios

Sex ratios of live-trapped mice were biased towards males in all age groups (1–4, >4–9, >9 months) and in all seasons, except in spring when females dominated the first age group (Figure 2). Differences in the sex ratios between the three age groups of killed mice existed only during autumn (Chi-square$_2$ = 6,21; p < 0,05). Season had no effect on the sex ratio of killed mice in any of the three age groups (1–4 months, Chi-square$_2$ = 5,8; p > 0,05; >4–9 months, Chi-square$_3$ = 1,34; p > 0,5 and >9 months, Chi-square$_3$ = 2,02; p > 0,5).

Seasonal breeding

Females in the killed sample were pregnant or lactating from September to May. Only two pregnant mice, however, were collected during September (n = 40) and one during May (n = 39). During October pregnant females were recorded only from the third week onwards (Figure 3).

On the live trap grid in the hummocky beach area, mice were reproductively active from October to March, when the trapping programme was terminated. Too few mice were present on the other two grids to allow a similar analysis. The first sign of reproductive activity occurred during December and January on the swamp and the vegetated lava grids, respectively, suggesting that reproduction began later in these areas than in the hummocky beach area.
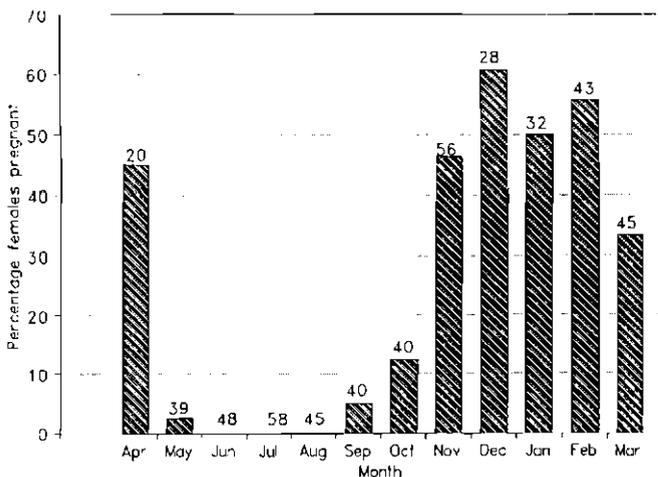
Female mice on Marion Island are therefore reproductively active for nine months of the year, but, based on periods when at least 50% were pregnant or lactating, the season of intense reproductive activity lasted about 6,5 months (mid-October – end April). The peak reproductive season for males extended from August to March. Mean testes weight remained low (<100 mg) from May to August for all age classes, increased rapidly during September and remained high (150 mg) until February/March. Significant monthly differences were recorded in all five adult weight classes (age class 3, $F_{8,200}$ = 70; p < 0,001; age class 4, $F_{10,252}$ = 238; p < 0,001; age class 5, $F_{10,124}$ = 48; p < 0,001; age class 6, $F_{10,59}$ = 29,3; p < 0,001 and age class 7, $F_{9,38}$ = 16,6; p < 0,001), with testes weight between May and August being significantly lower than during other months (Tukey multiple range test @0,05). Some males were reproductively active in all seasons but from September to February almost all male mice older than two months had testes weighing >60 mg.

Incidence of pregnancy

The ratio of pregnant to non-pregnant mature females did not differ significantly (Chi-square$_1$ = 0,479; p > 0,5) from that during 1979/80 (Gleeson 1981). The incidence of pregnancy during the breeding season of this study was 7,27 litters/female and also did not differ significantly (Chi-square$_1$ = 3,3; p > 0,05) from that recorded earlier (5,58; Gleeson 1981).

Ovulation rate, foetal mortality and litter size

Mean ovulation rate as suggested by the number of corpora lutea per female was 11,0 ± 3,6 and mean foetal loss 3,95

Figure 3 The percentage adult (>2 months) pregnant mice collected monthly on Marion Island during 1991/92. Values above bars denote sample sizes.
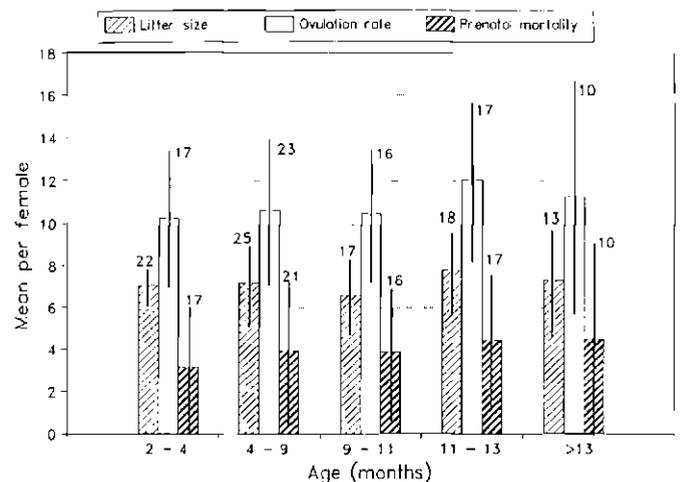
Figure 4 Age-specific mean ovulation rate, litter size and prenatal mortality for mice at Marion Island during 1991/92. Vertical bars denote one standard deviation of the means and numbers represent sample sizes.
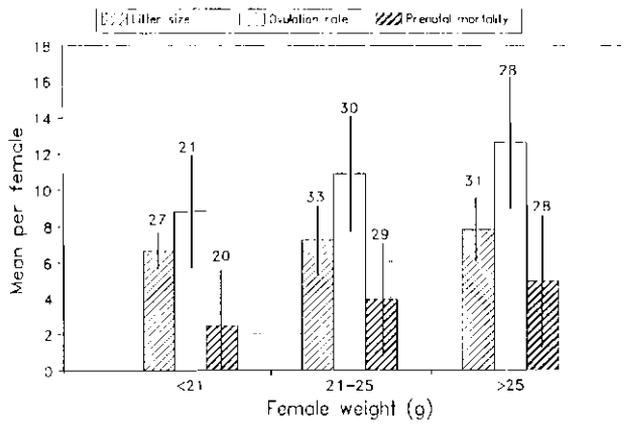
Figure 5 The influence of female body weight on mean ovulation rate, litter size and prenatal mortality. Vertical bars denote one standard deviation of the means and numbers represent sample sizes.

Table 2 Fecundity table constructed using data obtained from 320 female mice culled on Marion Island during the 1991/92 breeding season (October to April). f_x = number of females, B_x = number pregnant or lactating, m_x = fecundity/27 days and $m!$ = fecundity/year. The percentage of females in each age class which were pregnant or lactating is shown in the last column

Chronological age (months)	f_x	B_x	Females/ litter	B_x/f_x	m_x	$m!$	Per cent preg./lact.
>1 – ≤2	46	0	0,0	0,00	0,00	0,0	0
>2 – ≤4	78	21	3,5	0.27	0,95	2,1	27
>4 – ≤9	83	62	3,6	0,75	2,68	15,0	75
>9 – ≤11	45	38	3,3	0,84	2,80	6,3	84
>11 – ≤13	38	36	3,9	0,95	3,71	8,3	95
>13	30	25	3,7	0,83	3,04	21,9	83

± 3,5 foetuses/female. Mean litter size (7,24 ± 1,7 foetus/female; n = 88) did not differ significantly (t_{119} = 2; p > 0,1) from that during 1979/80 (6,91 ± 1,6 foetus/female; n = 33; Gleeson 1981). This suggests a prenatal loss of 36%. Neither ovulation rate ($F_{4,73}$ = 1,16; p > 0.1) nor litter size ($F_{4,84}$ = 1,63; p > 0,1) were affected by age (Figure 4). An analysis of three weight classes (<20 g, 20–25 g and >25 g) showed that larger females had significantly larger litters ($F_{2,87}$ = 4,21; p < 0,05) and higher ovulation rates ($F_{2,75}$ = 7,3; p < 0,005) than smaller females (Figure 5).

Significant seasonal changes occurred in both ovulation

rates ($F_{4,73}$ = 10,72; p < 0,001) and foetal mortality ($F_{4,71}$ = 7,44; p < 0,001), and ovulation rates were positively correlated with foetal mortality (Spearman's correlation; r_{76} = 0,90; p < 0,001). Prenatal mortality was not significantly affected by age ($F_{4,71}$ = 0,57; p > 0,5) or weight ($F_{2,73}$ = 2,61; p > 0,05). There was no discernible trend in the relationship between foetal age and foetal mortality. Litter size remained relatively constant throughout the season ($F_{4,84}$ = 1,76; p > 0,05).

A fecundity table constructed for 320 female mice killed during the breeding season is presented in Table 2. Reproductive output (number of females produced every 27,2
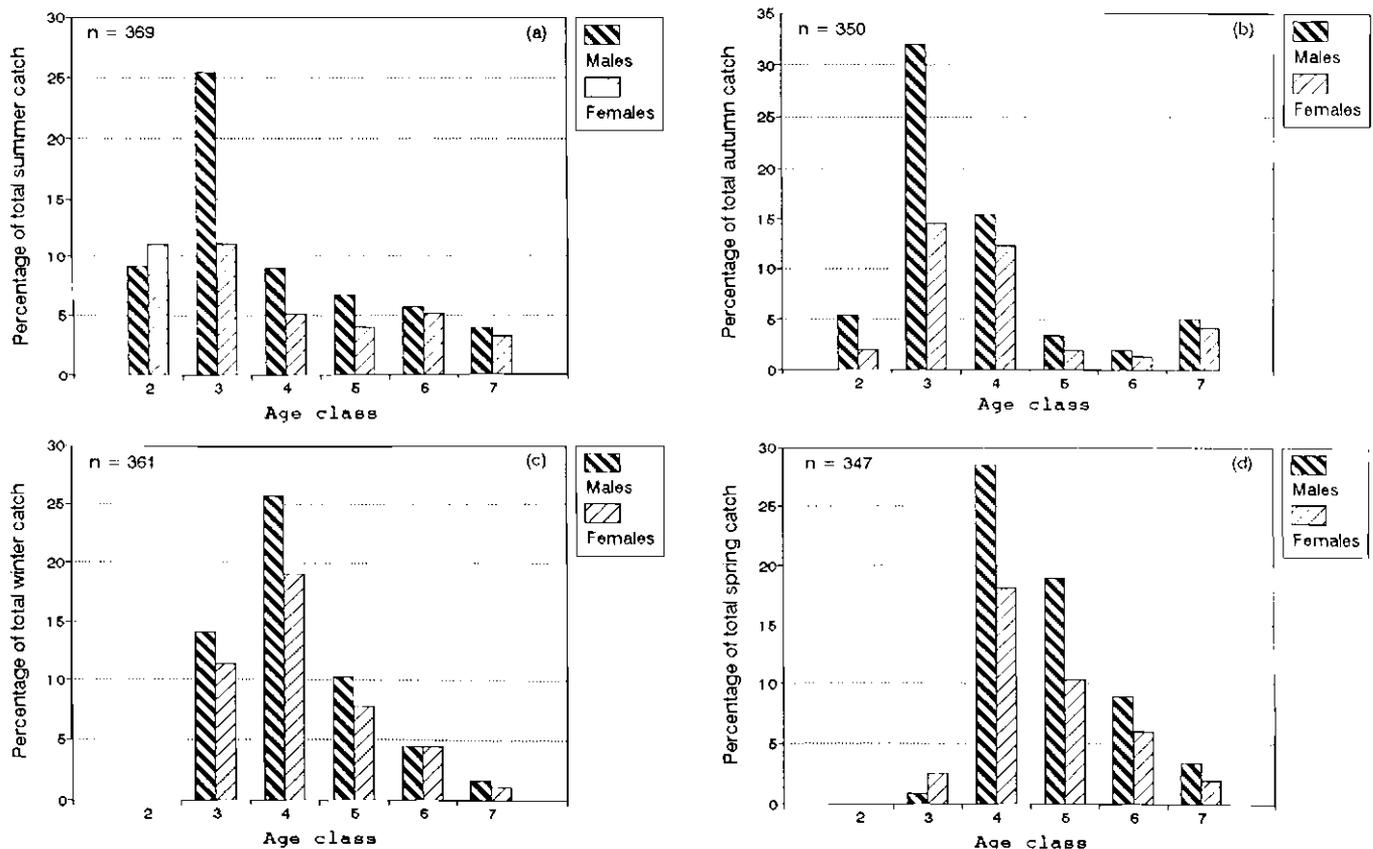
Figure 6 Age structure of mice killed during (a) summer, (b) autumn, (c) winter, and (d) spring of 1991/92 on Marion Island.

days) increased until mice reached 11 – 13 months of age (m_x = 3,71), and declined for mice in the oldest age class.

Age structure

The age structure of the population in relation to season is illustrated in Figures 6a–d. The age distribution changed significantly during the year (Chi-square$_6$ = 357; p < 0,001), being dominated by young mice ($\leq$4 months) during summer and older mice (>4 months) during spring. Juvenile mice (1 – $\leq$2 months), which first entered the trappable population during December, were born at the end of October. No juveniles (1 – $\leq$2 months) were caught between June and November.

The seasonal trend in the age structure was similar to that recorded during 1979/80 (see Gleeson 1981) with the exception of mice older than 13 months. Mice >13 months were recorded throughout the year opposed to only during summer in 1979/80 (see Gleeson 1981). These older mice, however, contributed <4% of the total winter population during this study. The present age structure was also similar to that recorded during 1975/76 (see Berry et al. 1978).

Increasing densities during summer were associated with an increase in the occurrence of juvenile mice. Declining densities during autumn were associated with a decrease in juvenile mice and an increase in the mean age of the population.

Loss rate

No trend was discernible in the highly fluctuating seasonal loss rates on the swamp and hummocky vegetated lava grids. On the hummocky beach area (where sample sizes were high), loss rate was high at the end of summer (May) and then declined to a low level, remaining relatively constant during the rest of the year (Table 3). The trends recorded for loss rate as well as the actual values were similar for males and females.

Table 3 Monthly survival and loss rates of male and female mice on the hummocky beach grid on Marion Island, recorded during 1991/92. n = number of marked mice, s = proportion of marked mice recaptured, l = proportion of marked mice not recaptured

Month	Females			Males		
	n	s	l	n	s	l
May	40	0,33	0,68	47	0,26	0,74
June	40	0,65	0,35	44	0,73	0,27
July	34	0,68	0,32	39	0,74	0,26
August	27	0,81	0,19	32	0,81	0,19
September	32	0,88	0,13	29	0,66	0,34
October	30	0,80	0,20	23	0,78	0,22
November	29	0,76	0,24	18	0,89	0,11
December	44	0,59	0,41	43	0,79	0,21
January	34	0,79	0,21	55	0,78	0,22
February	42	0,71	0,29	68	0,75	0,25

Discussion

Density

Differences in densities between the three grids representing different habitat types can be explained by food and refuge availability (Newsome 1969; Gleeson 1981; Rowe-Rowe & Crafford 1992). The hummocky beach and vegetated lava areas have numerous potential refuges, whereas in the dry swamp areas refuges are limited. On Marion Island, invertebrates form a major component of the diet of mice (Gleeson 1981; Gleeson & Van Rensburg 1982; Rowe-Rowe et al. 1989).

Changes in densities resulting from seasonal breeding, and possibly from seasonal changes in food availability (Gleeson & Van Rensburg 1982), have been reported for other feral house mouse populations (e.g. Newsome 1969; Berry 1981; Efford, Karl & Moller 1988). The higher and the lower densities recorded at the end of summer and winter, respectively (cf. those recorded some ten years ago), suggest that winter mortality has increased since then, but that more mice have survived or were produced during the present summer than then. Increased summer density may be ascribed to increased temperatures during the summer which affected reproductive output or summer survival. Moreover, actual peak densities may not have been recorded in 1979/80. Large inter-annual fluctuations due to differences in environmental conditions have been observed in many studies of house mice (see Newsome 1969; Berry 1981; Triggs 1991). Thus, higher summer densities recorded during the present study may not be sufficient to support speculations on a trend of increasing densities because of changed environmental conditions (Smith & Steenkamp 1990).

Sexual maturity

Female mice on Marion Island attain sexual maturity later than those living in other environments (see Pelikán 1981; Efford et al. 1988). Adverse conditions (low temperatures and food availability) may decrease the rate of development towards sexual maturity in house mice (Barnett 1973). In most studies, but not all (Efford et al. 1988), female mice mature before males (see Pelikán 1981; Rowe et al. 1983). On Marion Island, however, males attained sexual maturity at an earlier age than females, probably owing to maturation in males being less affected by unfavourable conditions than in females (Bronson 1984; Perrigo & Bronson 1985). No data are available on the age at which mice attained sexual maturity during 1979/80.

Seasonal breeding

Wild populations of mice usually breed seasonally (see Berry 1981; Pelikán 1981; Bomford 1987a) owing to a fluctuating food supply (Pryor & Bronson 1981), lack of specific nutrients (e.g. proteins; Bomford & Redhead 1987) or low temperatures (Barnett 1973; Bronson 1979; Pryor & Bronson 1981). Cold alone, however, does not prevent winter breeding, provided that the food supply is adequate (Bronson 1979; Berry 1981; Pelikán 1981; Bomford 1987b).

On Marion Island, mice bred during the warm period when invertebrate biomass was highest (see Gleeson 1981). Breeding in the swamp and vegetated lava areas may have

been delayed by lower food availability (see Gleeson 1981) while the cessation of breeding at the end of April may have been due to decreasing temperatures and the subsequent seasonal decline in food supplies (see Gleeson 1981).

The length of the breeding season was similar to that recorded earlier (see Gleeson 1981) and also resulted in seasonal changes in population densities and age structure. High densities at the end of summer may also have contributed to the cessation of breeding, as Bomford & Redhead (1987) suggested that high densities may suppress breeding intensity, owing to the effects of food abundance and spacing behaviour of the mice.

On Marion Island, male mice showed a distinct reproductive season. Bronson (1979) showed that food availability (whether nutritional or energetic) affects the reproductive condition of male mice, and cold conditions would compound these effects. Until now, this has only been illustrated for two other mice populations (see Lidicker 1966; Efford et al. 1988) and Pryor & Bronson (1981) concluded that male reproductive condition only declines seasonally under severe environmental conditions. Thus, despite elevated temperatures on Marion Island (Smith & Steenkamp 1990), reproduction in male mice continues to be inhibited during winter, supporting earlier notions (Berry et al. 1978) that mice here are experiencing the effects of severe environmental conditions.

Male mice on Marion Island became reproductively active earlier in the season than did females. This also occurred in the two other populations referred to above in which males showed seasonal reproductive activity, and probably resulted from males being less affected by harsh environmental conditions than females, presumably because their energetic costs of reproduction are lower than those of females (Perrigo & Bronson 1985; Efford et al. 1988).

Reproductive output

The incidence of pregnancy is affected by the length of the breeding season, temperature and food availability. Barnett (1973) showed that low temperatures increased age at first oestrus and length of the oestrous cycle, reduced the number of effective post-partum pregnancies and increased the length of gestation to 26 days in lactating female mice. Pryor & Bronson (1981) also showed that a wet and variable cold environment reduced the incidence of pregnancy in mice. The higher incidence of pregnancy recorded during this study (not significant), cf. 1979/80, may be the result of a subsequent increase in temperature (Smith & Steenkamp 1990; Smith 1992). The incidence of pregnancy determined during 1979/80, however, was based on only 121 females, most of which were collected towards the end of the breeding season (March/April), when the incidence of pregnancy was already declining (Gleeson 1981). Therefore, differences in the incidence of pregnancy may be an effect of insufficient sampling.

The percentage of excess corpora lutea recorded during this study (36%) was similar to that recorded in other island populations of mice (Batten & Berry 1967). Ovulation rates were correlated with prenatal mortality; thus, despite monthly variations in ovulation rates, litter size remained relatively constant throughout the breeding season. This

suggests a physiological limit to the number of embryos that can be supported by a female, probably determined by energetic constraints affecting foetal mortality (Pelikán 1981).

The number of litters produced per annum by mice varied from 5,5 on Skokholm Island to 10,9 in a feral population in California (Berry 1981), and the present value falls within this range of values; litter size was also similar to that recorded earlier on Marion Island (Berry et al. 1978; Gleeson 1981), despite maximum fecundity being associated with older and thus heavier females than during 1979/80. Batten & Berry (1967) ascribed the lack of influence of body weight on litter size in three island populations to harsh living conditions. In this study ovulation rate, as in some other studies on rodents (e.g. Batten & Berry 1967; Rowe et al. 1983), was affected by body weight.

Age structure and mortality

Seasonal changes in the age structure of mice probably result from seasonal breeding and mortality. For Marion mice this is supported by juveniles first entering the trappable population at the beginning of the breeding season. No young mice, however, were caught between June and November, suggesting that although litters were still delivered during April, relatively few juveniles survived.

Gleeson (1981) recorded no change in sex ratios and in this study changes were small and not consistent. The change resulted from a single month's capture, probably due to transitory sex-specific differences in trappability.

Patterns of loss due to mortality and emigration in the hummocky beach area were similar and were closely reflected by changes in monthly densities. The high loss rate during May on the hummocky beach grid and the much lower and more constant loss rates during the rest of the year, despite a continual decline in temperature and food supply (see Gleeson & Van Rensburg 1982), indicate a density associated loss, also recorded in other house mouse populations (e.g. Triggs 1991).

High mortality was associated with declining food supply during winter (Gleeson & Van Rensburg 1982). During the colder months of the year, the surface can be covered by a glassy film of ice which prevents the mice from finding food. High summer densities, reduction in food availability or accessibility, declining temperatures and increased metabolic requirements may account for the high mortality rate during May.

Conclusion

Our study was motivated by suggestions that mouse numbers have increased since the 1970s (Smith & Steenkamp 1990) owing to changes in climatic conditions. The implied increased predation on invertebrates responsible for litter turn-over could have important consequences for ecosystem function. Increased temperatures may, however, affect invertebrate productivity and may offset the influences of depredation by mice.

Length of the breeding season (6,5 months) and mean litter size (7,24 young/litter) were similar to those recorded earlier (Gleeson 1981), but the incidence of pregnancy was slightly higher (7,28 litters/year) than during 1979/80. Mouse densities on Marion Island appear to be affected by

food and refuge availability. The highest densities were recorded in biotically influenced areas (156 mice/ha) and habitat specific densities showed large seasonal fluctuations related to changes in temperature, food availability and seasonal breeding. Peak densities recorded during this study were higher than those recorded during 1979/80 but this could be the result of inter-annual fluctuations in environmental conditions. Higher summer densities recorded during the present study may only be incidental and do not provide sufficient evidence to support speculation that mice now occur at higher densities than before because of changed environmental conditions (Smith & Steenkamp 1990).

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