ORIGINAL PAPER

Food, reproduction and survival in mice on sub-Antarctic Marion Island

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Abstract The house mouse *Mus musculus* is the most widespread introduced mammal on sub-Antarctic islands, where it may alter ecosystem function. Ambient temperature and food availability affect reproduction and survival for mice. It is unclear how these factors influence mouse demography in the sub-Antarctic, and we tested the influence of food experimentally on Marion Island. Using food supplementation trials, we did not alter reproduction or overwinter survival. Alternatively, we argue ongoing climatic change on Marion could increase mouse densities through summer, while increased winter survival may reduce population growth rates the following summer through density dependence. The overall influence of these apposing forces depends on their relative strengths but may limit changes in mouse numbers with ongoing changes in climate in the sub-Antarctic.

Introduction

Climatic change is a reality for the southern ocean islands (Bergstrom and Chown 1999) and has been recorded for a number of sub-Antarctic islands, including Macquarie (Adamson et al. 1988), Kerguelen (Frenot et al. 1997), Marion (Rouault et al. 2005), Heard (Budd 2000; Pockley 2001) and South Georgia (Gordon and Timmis 1992). This change is characterised by an increase in annual mean surface temperature at nearly

double the global average rate (Tett et al. 1999), a decrease in annual total precipitation and an increase in annual total hours of sunshine (Smith 2002). The biota of sub-Antarctic islands are impoverished and climate change may have serious implications, especially for indigenous terrestrial species (Barendse and Chown 2000).

Currently though, by far the greatest threat to sub-Antarctic island biotas stems from the invasion of alien species (Bergstrom and Chown 1999). Prominent amongst these are mammals—presently nine mammal species, whether introduced accidentally or deliberately, persist on sub-Antarctic islands (Chapuis et al. 1994). One well-known alien of southern oceans islands is the house mouse *Mus musculus* (*sensu lato*), which has successfully colonised at least eight sub-Antarctic islands (Berry et al. 1978). Mice have been held responsible for impacting directly on species through predation (Gleeson and van Rensburg 1982; Crafford and Scholtz 1987; Chown and Smith 1993; van Aarde et al. 2004), or indirectly through competition for food (Huyser et al. 2000), nutrient cycling (Crafford 1990) or habitat modification (Chown and Smith 1993). While their eradication from these islands seems desirable, the logistics of such an operation are considerable and have limited chances of success (Jackson and van Aarde 2003).

On Marion mice prey principally on invertebrates (Crafford 1990; van Aarde et al. 1996; van Aarde et al. 2004), the numbers of which have either been declining (Chown and Smith 1993) or are much lower than on the neighbouring mouse-free Prince Edward Island (Crafford and Scholtz 1987). Marion's mice may therefore be experiencing food limitation, which could explain why numbers there have not increased over the

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last decade, though major die-offs during winter probably limit population size and explain the relative stability in numbers (see Ferreira et al. 2006).

Sub-Antarctic mouse populations may be living close to their physiological limits (Berry et al. 1978). Furthermore, it has been speculated that high mortality and declining food availability in winter prevent expansion of mouse populations on sub-Antarctic islands (Gleeson and van Rensburg 1982; Matthewson et al. 1994; Ferreira et al. 2006). On Marion Island mouse numbers change seasonally in response to seasonal breeding, where mice only breed during summer (Matthewson et al. 1994). These peak at the end of summer at densities as high as 300 mice per hectare, most (93–97%) of which die during the winter (van Aarde et al. 1996). In the present study we test a food limitation hypothesis, by supplementing food supply to mice on a year round basis. We predict that, should food limit reproduction or survival, reproductive parameters will be higher and mortality rates lower when food supply is increased artificially.

Study site and methods

Study site

Fieldwork was conducted on sub-Antarctic Marion Island (46°54′S, 37°45′E), 2,300 km SSE of Cape Town, South Africa. Thermally, Marion is exceptionally stable, the difference in mean temperature of the coldest and warmest months being only 3.6°C, while mean diurnal temperature fluctuation is 1.9°C (Smith 2002; Rouault et al. 2005). Presently, mean annual air temperature is ∼6.6°C, total annual precipitation 2,000 mm/year and annual total sunshine 1,430 h (Smith 2002). However, annual mean surface air temperature has increased by 1.2°C between 1969 and 1999. Annual precipitation has decreased since records

began in the 1960s, with the 1990s being the driest decade on record. At the same time annual total hours sunshine have increased by 3.3 h per year from 1951 to 1999 (Smith 2002).

Methods

Live trapping was conducted using sets of 49 Sherman live traps, laid out in a 7 × 7 grid configuration, with 10 m intervals between each trapping station. A total of five control and five treatment grids were established, all in similar habitat along the coastal plains of the island, and with a minimum inter-grid distance >200 m to ensure individuals were not trapped on both treatment and control grids. We trapped at each grid for five consecutive nights, through a series of seven capture events, in a 5–6 week cycle. During every trapping session, both a control and a treatment grid were trapped. The dates on which we started each trapping session are detailed in Table 1. In our results we refer to each of these as "capture events". Traps were baited with a mixture of raisins and peanut butter, were opened just before sunset and checked 3–4 h after complete darkness fell. Traps could not be left open for longer periods due to the danger of hypothermia to occupants. Seven trapping cycles were completed for each of the grids over a period of 11 months from May 2000 to March 2001 (Table 1).

Captured mice were marked using toe-clipping techniques, weighed and sexed. Breeding males were definon-breeding males were non-descended. Breeding females were defined by having a perforate vaginal orifice, or as lactating (following Matthewson et al. 1994). Determining pregnancy is subjective in all but the most gravid females and was therefore not used as a reliable field characteristic to define a female's reproductive status.

Custom-made feeding stations were manufactured from upturned 25 cm plastic plant pots, with two 3 cm

Table 1 Dates on which each five-night live trapping session commenced, through a series of seven trapping cycles at each grid

| Capture event | Period | Trapping grid number | | | | |
		Grid 1	Grid 2	Grid 3	Grid 4	Grid 5
1	May–June	1 May 2000	8 May 2000	15 May 2000	22 May 2000	29 May 2000
2	June–July	12 June 2000	26 June 2000	3 July 2000	11 July 2000	17 July 2000
3	August–September	7 August 2000	21 August 2000	29 August 2000	06 September 2000	06 September 2000
4	October–November	3 October 2000	11 October 2000	18 October 2000	29 October 2000	29 October 2000
5	November–December	20 November 2000	4 December 2000	15 December 2000	25 December 2000	25 December 2000
6	January–February	8 January 2001	16 January 2001	29 January 2001	05 February 2001	12 February 2001
7	February–March	26 February 2001	5 March 2001	12 March 2001	19 March 2001	25 March 2001

During every trapping session, both a treatment and control grid were trapped. Each grid was trapped every 5–6 weeks, from May 2000 to March 2001. The capture events referred to in our figures correspond to these capture periods

holes drilled near their rims to allow entry. These pots were positioned evenly in a 6×6 configuration within each of the trapping grids between the rows of trapping stations. Drainage holes on the top end of the upturned pots were blocked to improve waterproofing and pots were secured to the ground with pegs to protect them from being disturbed by wind or scavenging birds. During the first trapping cycle supplementary food was not provided at treatment or control grids in order to estimate initial mouse numbers. Thereafter, supplementary feeding started on the treatment grids, but not the control grids. Supplementary feeding consisted of the weekly supply, through the course of the experiment, of 5,000 g of proprietary mouse pellets (18% protein content; Epol Animal Feed Manufacturers, P.O. Box 19096, Pretoria West, South Africa), distributed evenly amongst the feeding stations on treatment grids. Pellets were either consumed or stored in underground nests (see Avenant and Smith 2003). On average mice removed 637 ± 30 g/day (mean $\pm$ SD) of pellets from each of the treatment grids, while all the pellets were taken from a treatment grid on only two occasions. As 89.2% of the supplemented food was removed, we argue that sufficient food was available to mice without becoming depleted between weekly replenishment.

Population estimates, survival probabilities, numbers joining and reproductive outputs were calculated to determine the effects of supplementary feeding on demography. We estimated population sizes using the Peterson (PT) and Jolly-Seber (JS) methods and the software of Krebs (1998). As the first and last population estimates cannot be computed using JS methods (Krebs 1998), PT estimates were used to extend the estimates to April and May when mouse densities are expected to peak on the island (Matthewson et. al. 1994; Ferreira et al. 2006). Thus, the PT method was only used to demonstrate the overall pattern of mouse numbers, while all analyses were performed using the JS estimates, which are regarded as more conservative (Krebs 1998).

The rate of change in population numbers per grid from August to February were estimated by regressing the $\log_e$ values of the JS estimates against the month for each capture event (see Caughley 1977). The slopes of the least square linear regressions were compared statistically to determine differences in trends (Zar 1996).

We calculated reproductive output as:
(number of mice <16 g)/(number of females >19 g), thus estimating the number of offspring weaned per adult female, given that more than 90% of females on Marion Island are reproductively mature during the breeding season when there mass is ≥ 20 g (Matthewson et al. 1994).

Immigration and survival rates were also calculated using JS methods and software provided by Krebs (1998). Survival rates reflect numbers surviving from the previous capture event. We estimated immigration from the estimates of numbers joining, though the JS method cannot calculate numbers joining for the first and the last two capture events. Therefore, our analysis was performed using only the estimates for August, October, November and December. Similarly, the JS method cannot calculate survival rates for the last two capture events. Thus, the statistical analysis of survival rates only relied on values for June–December.

Residential times were calculated by determining the number of days between the first and last capture of each individual throughout the study period. Mice were placed into three body weight classes (<16, 16–19 and >19 g) depending on weight at first capture. Using these data, the mean number of days spent on treatment and control grids were calculated for each weight class.

Data analysis

Unless otherwise stated statistical analyses were performed using the mean values from each of the five replicate control and treatment grids for each of the seven capture events. Data were only compared for periods following food supplementation. To compare data, which were not independent, we used a repeated measures analysis of variance (rm ANOVA) design. Data calculated as percentages were arcsine transformed before performing parametric statistical procedures (Zar 1996, pp282–283). We considered capture sessions on the individual trap sites as the repeated measures and treatment (control or food supplementation) as the grouping variables (see Zar 1996). When interaction terms were significant, differences were examined using the Tukey HSD test for equal sample sizes (Zar 1996). Analyses were conducted using the ANOVA/MANOVA module of STATISTICA 6.0 (StatSoft Inc. 1995). Residential times were initially compared using a nested three-way ANOVA design, taking treatment (control or food supplementation), sex (male or female) and body mass classes (<16, 16–19 and >19 g) as the grouping variables (Zar 1996). Individual trapping grids were nested within the control and food supplementation treatments.

Results

Population demography

In total, we captured 1,274 individual mice (608 females, 666 males) on treatment and 629 individuals (320 females, 309 males) on control grids. Population

estimates, based on the JS method, showed significant effects of both time (rm ANOVA, $F_{4, 32} = 4.20$, $P < 0.01$) and treatment ($F_{1,8} = 73.62$, $P < 0.0001$), with a near-significant interaction between the two variables (rm ANOVA, $F_{4,32} = 2.30$, $P = 0.08$, Fig. 1). The JS estimates on the control grids decreased through the study period until January–February, in the austral summer, before increasing again. In comparison, with the addition of supplementary food, populations on the treatment grids increased until June–September, before declining until January–February. The JS estimates on the treatments remained consistently more than four times greater than on the controls (Fig. 1). A similar pattern was found for the PT estimates, with a significant effect of time (rm ANOVA, $F_{5,25} = 3.84$, $P < 0.02$) and treatment (rm ANOVA, $F_{1,5} = 33.51$, $P < 0.005$), while the interaction between the variables was near-significant (rm ANOVA, $F_{5,25} = 2.54$, $P = 0.054$). Thus, supplementary food increased mouse numbers substantially, both during summer and winter periods, though food supplementation did not avert population decline during winter. Indeed, the overall rate of population decline did not differ significantly between food treatments and controls ($F_{1,46} = 0.57$, $P = 0.46$, Fig. 2).

Reproduction

The reproductive output of females on control and food addition grids indicate a near-significant effect of food supplementation (rm ANOVA, $F_{1,8} = 4.63$, $P = 0.064$, Fig. 3) and a significant time effect (rm ANOVA, $F_{5,40} = 25.44$, $P < 0.0001$), with an interaction between time and treatment (rm ANOVA, $F_{5,40} = 4.70$, $P < 0.002$). Reproductive output only differed significantly with treatment during the final capture event in February–March, when the reproductive output of females was unexpectedly higher on control grids.

There was also a significant effect of time on the percentage of perforate females (rm ANOVA, $F_{6, 48} = 5.33$, $P < 0.0005$, Fig. 4) and the percentage females lactating (rm ANOVA, $F_{6,48} = 21.92$, $P < 0.0001$, Fig. 4), but no significant effect of treatment, or interaction between treatment and time.

Immigration

Reproductive output on all grids were very low from June–July to October–November (Fig. 3) and the JS estimates for these months represent immigration onto the treatment grids and not births. More mice immigrated onto treatment grids (rm ANOVA, $F_{1,8} = 40.44$, $P < 0.0002$, Fig. 5), while the lower
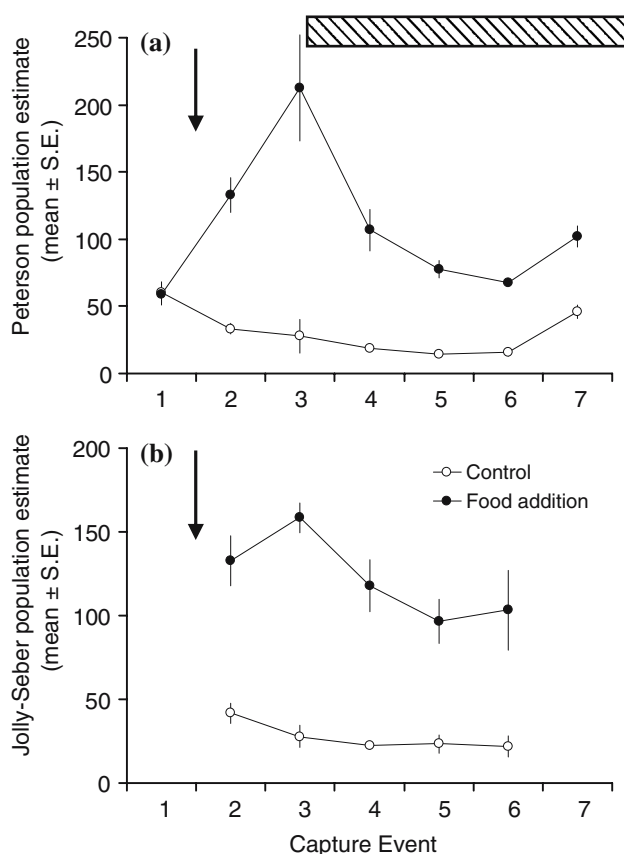

Fig. 1 Temporal differences in population numbers (mean ± SE) of *Mus musculus* using **a** Peterson and **b** JS estimates, for food addition ($n = 5$) and control ($n = 5$) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period. For a description of the times periods represented by capture events please refer to Table 1

numbers of immigrants recorded in August–September resulted in a significant time effect (rm ANOVA, $F_{3,24} = 3.37$, $P < 0.05$), as well as an interaction between time and numbers of individuals immigrating on to grids (rm ANOVA, $F_{3,24} = 3.20$, $P < 0.05$). The treatment effect was due to the large number of individuals joining the food supplement grids in June–July.

Survival rates

Food addition (rm ANOVA, $F_{1,8} = 11.62$, $P < 0.01$, Fig. 6) but not time significantly increased survival from the previous capture event, while there was a near-significant interaction between treatment and time on individual survival ($F_{4,32} = 2.46$, $P = 0.065$, Fig. 6). This difference, however, could only be attributed to the higher survival of individuals on the treatment sites during the first winter capture event after treatment started (Tukey HSD test, $P = 0.03$), while supplementary feeding had no effect on survival during subsequent winter months.
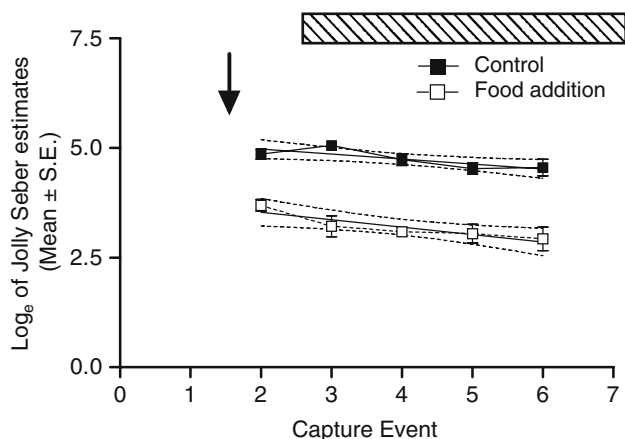
Fig. 2 Population decline rates of *Mus musculus* based on the JS population estimates for food addition ($n = 5$) and control ($n = 5$) grids, showing no significant difference in the rate of population decline during winter ($F_{1,46} = 0.57$, $P = 0.46$). For food addition slope $= -0.11 \pm 0.04$, for control grids slope $= -0.17 \pm 0.06$. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period

Male body mass

Males were significantly heavier in January–February during the breeding period, than in June–September through non-breeding periods (rm ANOVA, $F_{5,40} = 5.32$, $P < 0.001$, Fig. 7). In addition, males on the food supplementation grids were significantly heavier than those on control grids ($F_{1,8} = 65.56$, $P < 0.0001$, Fig. 7), while there was no interaction between time and treatment on male body mass.

Residential times

Individual residential times were significantly higher on food supplementation than control grids (hierarchical nested random effects ANOVA; $F_{2,1,677} = 13.26$, $P < 0.0001$, Fig. 8), though no gender-specific differences occurred ($F_{1,1,677} = 2.50$, $P = 0.11$, Fig. 8). Furthermore, residency times were lower for individuals weighing <16 g than for intermediately sized or large individuals ($F_{2,1,677} = 13.26$, $P < 0.0001$, Fig. 8) whose residency times did not differ significantly from each other. No interactions were recorded between sex, body mass or treatment. The increase in residential times on treatment grids probably contributed to the higher number of mice encountered under conditions of food supplementation.

Discussion

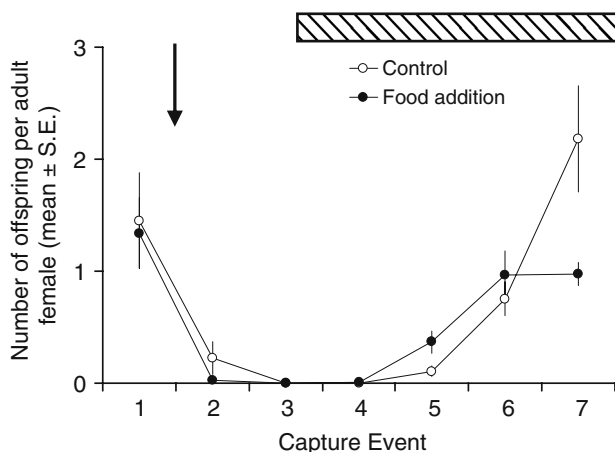In our study, like those of others (reviewed by Boutin 1990) food supplementation affected a number of

Fig. 3 Temporal trends in number off *Mus musculus* offspring recruits (<16 g) per adult female (>19 g) for treatment ($n = 5$) and control ($n = 5$) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period
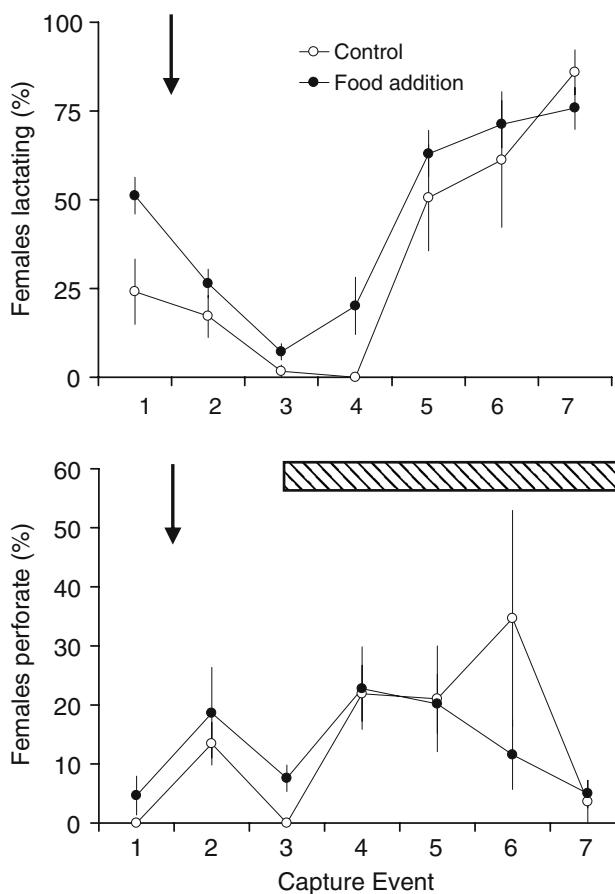

Fig. 4 Temporal trends in the percentage *Mus musculus* females lactating and perforate for treatment ($n = 5$) and control ($n = 5$) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period

population variables. Food supplementation did not increase reproductive output or extend the breeding season. In addition, survival rates were only higher on
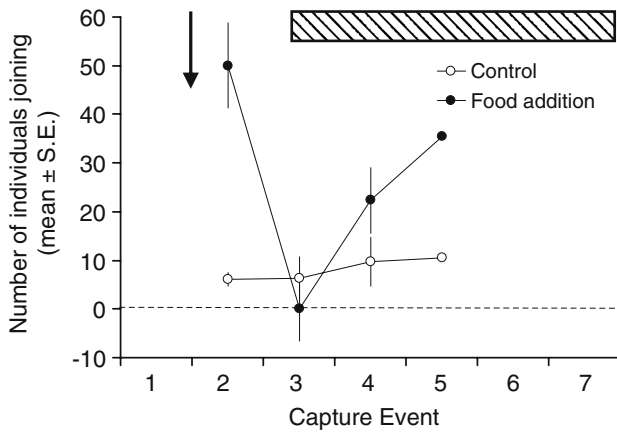
Fig. 5 Temporal trends in immigration of *Mus musculus* onto treatment (*n* = 5) and control (*n* = 5) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period
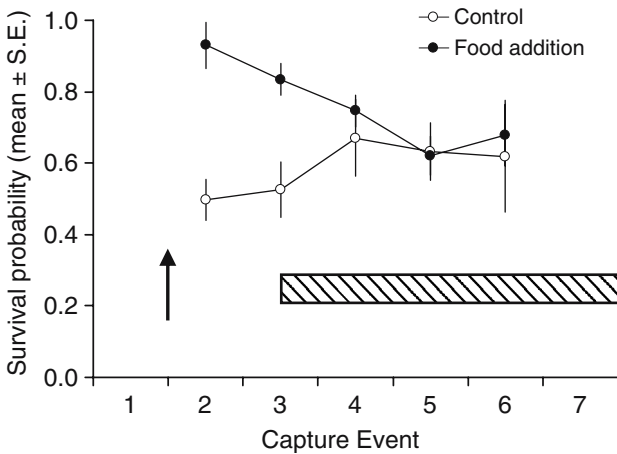

Fig. 6 Temporal trends in JS survival estimates of *Mus musculus* from the previous trapping event, for treatment (*n* = 5) and control (*n* = 5) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period

Fig. 7 Temporal trends in mean body mass of male *Mus musculus* for treatment (*n* = 5) and control (*n* = 5) grids. *Arrow* shows commencement of food addition, *hatched bar* indicates summer breeding period

Fig. 8 Mean residential times for **a** female and **b** male *Mus musculus* for three weight classes on treatment and control grids

treatment grids during the summer. Thus, patterns of population decline could not be averted during winter through food supplementation, despite the effective increase in over-winter mass (at least of males) receiving supplementary food. The initial increase in mouse numbers in response to food supplementation is a common artefact of such an experimental design (reviewed by Boutin 1990). It normally results from immigration onto treatment grids and from longer residential times on these grids.

We conclude that food availability has only marginal effects on survivorship and reproductive parameters for mice on sub-Antarctic Marion Island. Similarly, under the temperate conditions that prevail in Australia, reproduction does not appear to be limited by food constraints (see Ylönen et al. 2003 and references
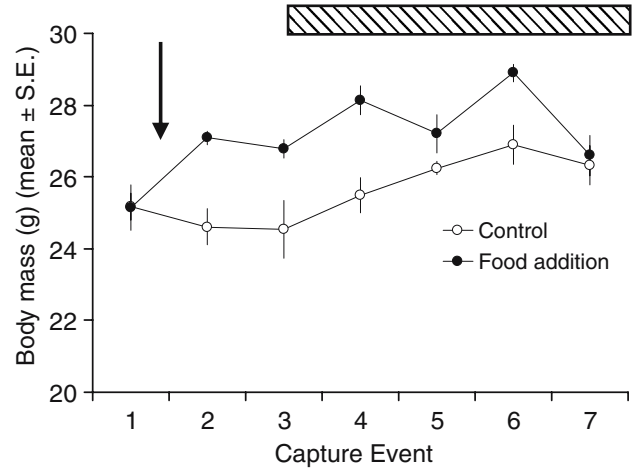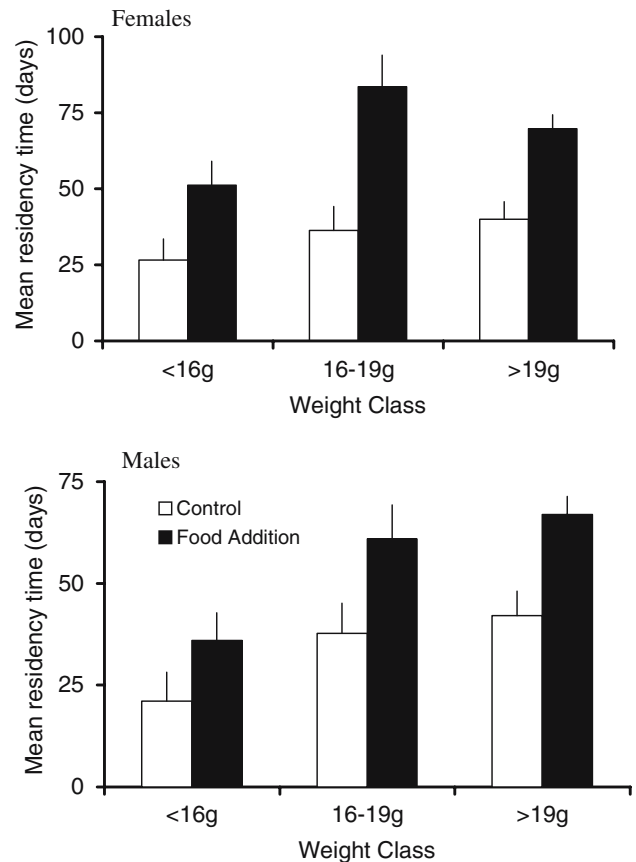
therein). This suggests that seasonal changes in numbers are not dictated by food availability. Our contention that seasonal food availability may not be limiting is supported by the observation that mice on Marion eat more during winter (Gleeson and van Rensburg

1982; Smith et al. 2002). Similarly, le Roux et al. (2002) recorded a predominance of protein-rich invertebrate food items in the diet of mice during winter months at the Kerguelen Archipelago. This seasonal variation in food quality or quantity may, however, be mediated by a decrease in ambient temperature over winter, for which an increase in food consumption would be predicted in order to offset increased metabolic costs (Konarzewski and Diamond 1994).

Our findings are of obvious concern to the conservation of sub-Antarctic island biotas, such as those of Marion, as they suggest that factors other than food availability limit reproductive output and survival. The reproductive ability of house mice has been studied extensively in both the field and laboratory, indicating several constraining factors. Unlike many rodents, day length is unlikely to affect reproductive seasonality (Bronson 1979; Pryor and Bronson 1981). Rather the breeding biology of female house mice appears to be directly related to their energetic balance (Bronson and Perrigo 1987). Even when provided with unlimited food, low-ambient temperatures (Pryor and Bronson 1981), increased foraging effort and reduced feeding efficiency (Perrigo and Bronson 1983) reduce reproductive output and sexual development. Exposure to cold during lactation increases maternal food intake (Johnson and Speakman 2001), reflecting the greater energy constraint on homeothermy, while also reducing the number or mass of pups reared (Johnson and Speakman 2001). Similarly, food shortages during pregnancy lead to reduced litter sizes through selective foetal resorption and infanticide (Perrigo 1987). It also reduces pup mass, offspring growth rates and survival (Perrigo 1987).

The resting metabolic rate (RMR) of house mice does not show adaptation to cold conditions (Webb et al. 1997; Johnson and Speakman 2001). Given that annual mean surface temperatures are increasing on Marion, this warmer environment may allow females to expend less energy in thermoregulation and more energy could be allocated to reproduction. Thus, we predict that pup survival, mass and litter sizes may increase, whereas foetal resorption rates should decline. In addition, higher ambient temperatures should allow for a longer breeding season. Furthermore, reduced rainfall and the disappearance of the snowline (Sumner et al. 2004) may allow mice to forage more efficiently and enhance their rate of food gain. Our predictions are in keeping with the higher incidences of pregnancy and higher fecundity rates recorded on Marion Island during the 1990s than the 1970s (van Aarde et al. 1996), while Ferreira et al. (2006) demonstrated that Marion's mice increased

their reproductive output in years when minimum ambient temperatures were relatively high. Climate change could therefore increase the size of mouse populations on sub-Antarctic islands during the summer breeding months when mice breed through mechanisms linked directly to metabolic requirements and their influence on female reproductive rates.

As no natural rodent predators occur on most sub-Antarctic islands, predation should not limit mouse population numbers at the onset of the breeding period, when mouse densities are low (see Sinclair et al. 1990). Consequently, island populations should inherently increase more rapidly during spring than mainland populations. Subsequently islands populations may reach relatively high densities, a factor we argue is likely to be aggravated by climate warming. Mouse populations are regulated in part by density dependent factors (Krebs et al. 1995; Choquenot and Ruscoe 2000). Therefore, if mice can be expected to reach higher summer-autumn densities due to climatic change, this should intensify density-dependence. Thus, Ferreira et al. (2006) suggest that the mouse densities on Marion Island are controlled by density-dependent factors, with lower growth rates in years following higher overwinter densities. Similarly Triggs (1991) demonstrated a negative correlation between spring population size and changes in mouse numbers from spring to autumn, showing a density-dependent effect that may be attributed to social depression or food availability/quality. We therefore predict that climatic warming will alter mouse population dynamics on these islands through an increase in peak densities, followed by reduced overwinter survival. Thus, the amplitude of population fluctuations should increase.

Presently mouse populations are largely restricted to the coastal regions of islands such as Marion, South Georgia (Berry et al. 1979) and Gough (Rowe-Rowe and Crafford 1992) where they occur mainly in lower altitude areas. Reduced rainfall, snow cover and climate warming are likely to lead to extensive changes in plant community structure and succession (Smith and Steenkamp 1990; Chapin et al. 1995; Smith et al. 2001; Sumner et al. 2004). This should favour range expansion for mice on sub-Antarctic islands. For instance, indications are that desiccation is rapidly drying out mire habitats through a reduction in peat moisture content (Chown and Smith 1993), making them more suitable for exploitation by mice (Ferreira et al. 2006). Range expansion is also likely to be facilitated by the further expansion of alien vegetation types that would provide suitable habitat for mice.

In conclusion, increasing food through supplementation had little influence on reproductive biology. Food,

however, did increase early but not late winter survival. Cold climate rather than food therefore is important in determining the number of mice that will survive to breed during the following summer. On Marion continuing climatic warming during winter may increase the size of the subsequent summer breeding cohort, as mortality could be reduced. It also may increase female fecundity through the lengthening of the breeding season or increased litter sizes. We argue that these changes could increase mouse densities through the summer. However, increased winter survival could reduce population growth rates the following summer through density-dependence (Ferreira et al. 2006). The sum total of these apposing forces depends on their relative strengths but may give rise to no or to limited changes in mouse numbers with changes in climate. This does not hold for the impact of mice as this arises from the cumulative pressures they exert on their prey and the impact that climate change may have for invertebrates and their environment.

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