

# Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island

S. M. Ferreira · R. J. van Aarde · T. D. Wassenaar

Received: 30 January 2006 / Revised: 3 May 2006 / Accepted: 15 May 2006 / Published online: 7 July 2006  
© Springer-Verlag 2006

**Abstract** Recent changes in the climate of the sub-Antarctic may influence the number of house mouse (*Mus musculus sensu lato*) living on islands in the region. An increase in mouse numbers, as conditions became milder, could amplify the effects of climate change on native prey species. However, we have no direct evidence of the influence of climate on mouse numbers in the sub-Antarctic. We, therefore, assessed demographic trends in the mouse population on Marion Island between 1991 and 2001. Both the climate and mouse numbers were relatively stable during our study. Mice, however, increased their reproductive output in years when ambient temperatures were relatively high. Moreover, reduced reproductive output followed high densities at the onset of a breeding season, implying density-dependent limitation. We conclude that both temperature and density limited the increase in numbers during the summer breeding season. Major die-offs during winter probably limit population size and explain the relative stability in numbers across the 10 years of our study.

## Introduction

For the past 50 years, ambient and sea temperatures increased across several parts of the Antarctic and sub-Antarctic (Smith 2002; Mélice et al. 2003; Turner et al. 2005). Such changes may influence the biota of the sub-Antarctic, especially their response to variation in ambient temperature (e.g. Klok and Chown 2001; Sinclair and Chown 2005). This may hold for house mice (*Mus musculus sensu lato*) introduced to several sub-Antarctic islands (see Berry et al. 1978).

At the sub-Antarctic Marion Island, mice may both reduce invertebrate numbers through predation and alter ecosystem function (van Aarde et al. 2004). The assumed increase in mouse numbers in response to warmer conditions may amplify their impact (Smith and Steenkamp 1990; Chown and Smith 1993; Bergstrom and Chown 1999; Smith et al. 2002). The perceived link between climate change and mouse numbers implies that low temperatures limit the reproductive output and survival of mice. Climate models have some capability to predict mouse outbreaks (Krebs et al. 2004). However, we do not know of data that support long-term increases in mice densities when temperatures rise in the sub-Antarctic. In addition, the link between changes in numbers and changes in climate is complex, as factors other than climate may limit populations. For instance, high densities may limit population size by reducing both reproductive output and survival (Krebs 2003) most likely through lower food availability to individuals at higher densities (Batzli 1992; Ylönen et al. 2003) or social stresses (Sutherland and Singleton 2006). Mice at Marion only breed during the relatively warm summer months from November to March (Matthewson et al.

---

S. M. Ferreira · R. J. van Aarde (✉) · T. D. Wassenaar  
Conservation Ecology Research Unit,  
Department of Zoology and Entomology,  
University of Pretoria, Pretoria, South Africa  
e-mail: rjvaarde@zoology.up.ac.za

*Present Address:*

S. M. Ferreira  
Department of Statistics, University of Auckland,  
Auckland, New Zealand

*Present Address:*

T. D. Wassenaar  
African Wilderness Restoration, PO Box 11997,  
Klein Windhoek, Windhoek, Namibia

1994). Consequently, their numbers peak at the end of the breeding season. More than 90% of mice die during winter and before the onset of breeding (van Aarde et al. 1996).

Any increase in mouse numbers due to temperature changes on Marion Island is important, as they prey on invertebrates and plants (Gleeson and van Rensburg 1982; van Aarde et al. 1996, 2004; Smith et al. 2002). More mice, therefore, may amplify the effects of climate change on the Island's native species. Moreover, Marion Island is a Special Nature Reserve that is of importance for conservation (Anonymous 1996). It is thus imperative to protect its native biota against the impacts of introduced species. Marion Island is not alone in these constraints—other sub-Antarctic islands also have protected area status and several support house mice (Berry et al. 1978; Frenot et al. 2005). A resolution on the response of mice to climate change may be of wide-ranging value.

Mice have been part of Marion Island's ecosystem for over 200 years (Berry et al. 1978). Here they function as predators (Burger 1978; Gleeson and van Rensburg 1982; Rowe-Rowe et al. 1989; van Aarde et al. 1996; Smith et al. 2002), once served as prey to introduced domestic cats, *Felis catus* (van Aarde 1980), and may compete for food with a native bird (Huyser et al. 2000). However, their negative effect on some of the Island's invertebrates may be much smaller than that of other limiting factors (see van Aarde et al. 2004). Even so, the removal of mice from the Island could benefit the integrity of the ecosystem and the conservation of native species (Chown and Cooper 1995).

To remove mice from an island is technically challenging, costly, and may have unpredictable outcomes (Jackson and van Aarde 2003). Such a campaign would benefit from understanding how climate and mouse numbers interact. In this paper, we address the influence of temperature and density on reproductive output and survival rates in mice over a period of 10 years. Reproduction and survival in free-living house mice are limited by intrinsic (e.g. Singleton et al. 2005; Sutherland et al. 2005) and extrinsic factors (e.g. Meikle and Westberg 2001; Ruscoe et al. 2005). On the basis of these suggestions and on the work of others, we hypothesize for Marion Island's mice that, across years, (1) survival will be high during relatively warm winters (e.g. Berry and Jakobson 1971; Berry et al. 1973); (2) reproductive output will be high during relatively warm summers (e.g. Berry and Jakobson 1971; Stickel 1979); (3) survival during winter will decrease with increasing densities (e.g. Berry et al. 1973; Sutherland and Singleton 2006); and (4) reproductive

output will decrease with increasing summer densities (e.g. Batzli 1992).

## Methods

### Study site

Marion (270 km<sup>2</sup>; 46°54'S, 37°45'E) is situated in the sub-Antarctic Prince Edward Island group. The climate is oceanic, yearly rainfall exceeds 2,000 mm (Smith 2002), and the biota is typical of the sub-Antarctic (Gremmen 1981). August is the coolest month (minimum 1.6°C to maximum 6.7°C), whereas warmest temperatures are in February (6.1–12.1°C) (data from the South African Weather Bureau). Diversity is relatively low, with several endemic species and no indigenous terrestrial mammals (Smith 1987). Domestic cats, introduced in 1948 to control mice, preyed mostly on petrels (van Aarde 1980, 1983). Cats were exterminated in 1991 (Bester et al. 2000) when the present study commenced. Mice have lived on Marion for at least 200 years, but never on the neighbouring Prince Edward Island (Berry et al. 1978). Mice occur on Marion up to 800 m a.s.l. (Matthewson et al. 1994), whereas Avenant and Smith (2003) noted mice up to 1,200 m a.s.l.

Our study focused on the eastern coastal zone. Most trapping grids were located within a 3-km radius from the meteorological research station. During the season of 1996 and 1997, we also located trapping grids within 3-km radii from huts located on the coastal regions around the Island. These huts included Kildalkey, Watertunnel, Rook's Bay, Swartkop, Mixed Pickle, Cape Davis, and Reppetto's.

Trapping grids focused on sampling three habitat types. Swamps typically cover large areas, have high water tables, and peat substrates covered by low vegetation (Gremmen 1981). Even though mice refuges are scarce (Avenant and Smith 2003), mice densities in summer range from 65 to 115 individuals per hectare (Matthewson et al. 1994; van Aarde et al. 1996). Invertebrate biomass is relatively high (Burger 1978; Gleeson and van Rensburg 1982; Crafford 1990).

The second habitat type comprises hummocky vegetated black lava in a mosaic of lava, small mires, and fern-brake slopes (Gremmen 1981). Here invertebrate biomass (Burger 1978; Gleeson and van Rensburg 1982; Crafford 1990) and mice densities are the lowest of the three habitats we studied (Matthewson et al. 1994; van Aarde et al. 1996).

The third habitat is made up of biotically influenced areas near or at penguin or seal colonies that experience trampling, are enriched through manuring (Gremmen 1981), and have the highest invertebrate biomass on the Island (Burger 1978; Gleeson and van Rensburg 1982; Crafford 1990). Mouse densities here are usually higher than on the other two habitat types (Matthewson et al. 1994; van Aarde et al. 1996).

#### Data collection

We used capture–mark–recapture techniques to estimate the minimum numbers alive (Krebs 1998) per unit area ( $n \text{ ha}^{-1}$ ) during 5 study years between 1991 and 2001. We also collated the data collected by Gleeson (1981) during 1979 and 1980. For our study, trapping stations were spaced 10 m apart on replicate grids ( $10 \times 10$  from 1991 to 1995 and  $7 \times 7$  from 1996 to 2001) placed in the three habitat types (biotically influenced areas, vegetated black lava, and swamps). None of the trapping grids included in this analysis was experimentally manipulated during our study (Table 1). Each trapping station included in our analyses comprised a Sherman live trap set for 6 h from sunset onwards on 5 successive nights. We used raisins, peanuts, or oats rolled in peanut butter as bait, marked trapped mice (toe-clipping) and recorded their sex and weight before releasing them at the point of capture. The University of Pretoria's ethics committee sanctioned all handling procedures. The South African Weather Bureau recorded monthly minimum daily temperatures for the Island. Trapping grids, with the exception of regional ones (Table 1), were within 3 km from the weather station where temperatures were recorded as described by Smith (2002). This enabled us to calculate mean minimum temperature for each month between 1975 and 2002.

#### Data analysis

We first tested whether densities changed during our study by finding the slope (an index of intrinsic growth) of a linear regression of the natural logarithm of densities against time (Caughley 1977) and testing whether these differed from zero. We also tested whether temperature changes during our study was the same as that recorded over the long-term (Smith 2002) using least-square linear regression analysis.

We calculated reproductive output as the number of mice  $< 16 \text{ g}$  ( $n_j$ ) in body weight per adult ( $> 19 \text{ g}$ ,  $n_f$ ) female for each trapping grid during the breeding season (November to May; see Matthewson et al. 1994). Reproductive output therefore included a

survival component. We also calculated monthly juvenile ( $< 16 \text{ g}$  at the onset of winter) and adult ( $> 19 \text{ g}$  at the onset of winter) survival rates separately for each of the winters. These were the inverse of mortality rate. Mortality rate is the rate of decrease per month in the natural log of the number of individuals that we marked on the first month (June) of trapping at each grid (see Caughley 1977).

We limited our analyses of survival to the winter (June to October) for three reasons. First, mice on Marion do not breed during these months. Second, we expected climate influences on survival to be strongest then. Third, we followed the fate of a large number of individuals marked at the beginning of the winter. Due to large winter die-offs (van Aarde et al. 1996), too few individuals were available at the beginning of summer to calculate realistic survival rates for summer.

We focused on minimum daily temperatures as we expected the strongest influence from the lowest temperatures. For each month, we calculated the mean values for daily minimum temperatures and used standardized residuals (SRs) to determine the deviation of these values from long-term (1991–2001) mean values. We defined an SR value as  $(x_j - \bar{x}_j)/\bar{x}_j$ , where  $x_j$  is the minimum temperature in month  $j$  and  $\bar{x}_j$  the mean for each month  $j$  in all years of the study period. Negative values suggested that a month was cooler than the mean and vice versa. We then calculated the mean monthly SR values for a season that reflects on the minimum ambient temperatures that mice experienced during that season. For each of the habitats, we plotted reproductive output against the mean summer SR values, but used only winter SR values for survival. We used  $r^2$  values as a model selection criterion (Johnson and Omland 2004) to fit either exponential or linear models for which we used least-square regression analyses to find which of the slopes described by these models differed significantly from zero.

To study the influence of density on reproductive output, we calculated an SR value for density at the onset of the breeding season, i.e. density in November. Here the SR value was the difference between the recorded density on a specific trapping grid in November of a particular year and the mean monthly density for the relevant habitat type in November over the study period.

To study the influence of density on survival, we calculated SR values for density in a specific month as we did for minimum temperatures. Here we defined monthly SR values for density as  $(d_{ij} - \bar{d}_{ij})/\bar{d}_{ij}$ , where  $d_{ij}$  is the density in month  $j$  on habitat  $i$  and  $\bar{d}_{ij}$  the mean for each month  $j$  in habitat  $i$  of all years of the study period. Mean monthly SR values for density in a

**Table 1** A summary of monthly mice captures recorded on trapping grids during 5 years of data collection at Marion Island

Month	1991–1992				1993–1994				2000–2001							
	VBL 1	Swamp 1	Biotic 1	VBL 1	Swamp 1	Biotic 1	VBL 2	VBL 3	VBL 4	Swamp 2	Swamp 3	Swamp 4	Swamp 5	Biotic 2	Biotic 3	Biotic 4
April	–	–	–	–	–	–	85 (47)	116 (56)	115 (62)	108 (77)	91 (60)	110 (71)	–	112 (65)	137 (81)	117 (73)
May	215 (82)	–	294 (155)	167 (87)	171 (106)	182 (124)	–	–	–	–	–	–	127 (68)	–	–	–
June	93 (33)	151 (51)	203 (86)	186 (86)	123 (66)	119 (75)	–	–	–	–	–	–	109 (42)	–	–	–
July	150 (46)	–	190 (60)	134 (72)	139 (80)	177 (108)	–	–	–	–	–	–	–	–	–	–
August	38 (15)	109 (43)	165 (53)	111 (58)	108 (67)	137 (77)	–	–	–	–	–	–	70 (35)	–	–	–
September	47 (12)	–	151 (52)	48 (38)	109 (67)	128 (82)	–	–	–	–	–	–	–	–	–	–
October	24 (8)	57 (19)	127 (51)	68 (36)	127 (64)	174 (94)	–	–	–	–	–	–	31 (17)	–	–	–
November	45 (9)	–	135 (41)	64 (29)	100 (50)	123 (72)	–	–	–	–	–	–	18 (11)	–	–	–
December	53 (11)	42 (18)	168 (88)	74 (33)	59 (28)	111 (76)	–	–	–	–	–	–	–	–	–	–
January	43 (9)	–	194 (83)	54 (19)	46 (18)	159 (101)	–	–	–	–	–	–	10 (5)	–	–	–
February	79 (19)	86 (29)	216 (105)	111 (55)	47 (34)	187 (141)	–	–	–	–	–	–	37 (26)	–	–	–
March	135 (35)	–	282 (148)	105 (57)	93 (53)	206 (154)	–	–	–	–	–	–	–	–	–	–
April	–	–	–	152 (89)	91 (61)	193 (147)	66 (43)	70 (41)	88 (54)	106 (79)	87 (62)	–	64 (40)	–	–	–
April	–	–	–	–	–	–	–	–	–	–	–	–	–	157 (89)	115 (79)	158 (97)
Month	1996–1997															
May	99 (52)	–	–	164 (55)	–	–	–	–	177 (87)	230 (98)	282 (126)	273 (134)	–	–	–	–
June	–	84 (39) <sup>C</sup>	146 (44) <sup>C</sup>	–	122 (57)	131 (54)	152 (58) <sup>R</sup>	151 (57) <sup>R</sup>	–	–	–	–	–	–	–	–
July	–	–	–	–	140 (40)	115 (40)	–	–	–	160 (66)	116 (49)	154 (66)	–	–	–	–
August	–	27 (11) <sup>W</sup>	29 (16) <sup>W</sup>	–	–	–	36 (11) <sup>S</sup>	62 (19) <sup>S</sup>	–	–	–	–	81 (43) <sup>K</sup>	55 (27) <sup>K</sup>	–	–
September	–	–	–	–	39 (22)	41 (19)	–	–	–	75 (33)	59 (28)	72 (33)	–	–	–	–
October	–	7 (3) <sup>B</sup>	3 (1) <sup>B</sup>	–	–	–	33 (18) <sup>C</sup>	26 (12) <sup>C</sup>	–	–	–	–	90 (47) <sup>R</sup>	97 (43) <sup>R</sup>	–	–
November	–	–	–	–	17 (7)	42 (22)	–	7 (5) <sup>K</sup>	–	31 (21)	52 (27)	57 (30)	–	–	–	–
December	–	10 (5) <sup>Ro</sup>	11 (8) <sup>Ro</sup>	–	–	–	0 (0) <sup>K</sup>	–	–	66 (43)	63 (47)	63 (46)	–	–	–	–
January	–	–	–	–	57 (30)	58 (38)	–	–	–	–	–	–	84 (54) <sup>S</sup>	75 (44) <sup>S</sup>	–	–
February	–	49 (28) <sup>R</sup>	38 (23) <sup>R</sup>	–	–	–	–	–	–	92 (61)	78 (52)	63 (44)	–	–	–	–
March	–	–	–	–	42 (30)	46 (34)	–	–	–	162 (89)	212 (111)	201 (112)	–	–	–	–
April	–	44 (24) <sup>K</sup>	35 (20) <sup>K</sup>	–	–	–	104 (59) <sup>M</sup>	90 (54) <sup>M</sup>	–	–	–	–	–	–	–	–
May	63 (40)	–	–	98 (63)	–	–	–	–	–	–	–	–	–	–	–	–
Month	1998–1999															
April	71 (43)	88 (46)	81 (52)	–	110 (79)	103 (69)	60 (43)	96 (57)	96 (57)	76 (60)	132 (78)	146 (92)	–	–	–	–
May	99 (42)	106 (39)	115 (46)	85 (69)	117 (67)	102 (66)	–	90 (52)	90 (52)	–	89 (47)	124 (57)	121 (73)	85 (43)	–	–
June	36 (19)	47 (24)	83 (23)	–	130 (51)	94 (38)	–	133 (48)	133 (48)	–	117 (49)	76 (39)	104 (40)	104 (40)	–	–
July	30 (19)	31 (20)	–	–	61 (21)	63 (25)	–	54 (28)	54 (28)	–	97 (38)	70 (27)	80 (30)	80 (30)	–	–
August	43 (13)	58 (16)	71 (18)	–	65 (20)	80 (28)	–	52 (17)	52 (17)	–	53 (18)	38 (12)	78 (24)	78 (24)	–	–
September	33 (11)	24 (11)	38 (16)	–	42 (12)	72 (22)	–	32 (14)	32 (14)	–	42 (14)	33 (13)	57 (16)	57 (16)	–	–
October	35 (9)	11 (7)	25 (7)	–	36 (12)	60 (21)	–	27 (10)	27 (10)	–	45 (16)	34 (12)	51 (20)	51 (20)	–	–

**Table 1** continued

Month	1998–1999															
	VBL 2	VBL 3	VBL 4	Swamp 1	Swamp 2	Swamp 3	Swamp 4	Swamp 8	Swamp 9	Biotic 2	Biotic 3	Biotic 4				
November	27 (8)	11 (5)	40 (11)	-	36 (18)	55 (23)	-	-	-	43 (21)	-	30 (16)	39 (19)	30 (15)		
December	28 (13)	21 (10)	26 (9)	-	67 (28)	75 (36)	-	-	-	52 (15)	-	110 (40)	81 (37)	116 (66)		
January	29 (11)	19 (8)	35 (16)	-	57 (34)	101 (45)	-	-	-	75 (38)	-	-	-	-		
February	60 (25)	53 (19)	78 (30)	-	-	-	-	-	-	-	-	144 (62)	122 (61)	133 (66)		
March	49 (25)	49 (24)	90 (32)	-	83 (57)	91 (62)	-	-	-	105 (59)	-	150 (66)	147 (76)	139 (76)		
April	68 (42)	84 (42)	87 (46)	-	145 (93)	105 (60)	-	-	-	131 (78)	-	180 (74)	133 (69)	136 (68)		

Trapping occurred on three habitat types: vegetated black lava (VBL), swamp (Swamp), and biotically influenced areas (Biotic) (see text for a description of habitat types). Values represent the total number of captures (first value) followed by the number of individuals (second value in parentheses) recorded for those months when a specific trapping grid was sampled. A hyphen means that no trapping occurred in that specific grid and year. Trapping grids have unique numbers. For instance, "Swamp 1" always refers to the same grid, sampled in different years. Grids trapped during 1991–1992 and 1993–1994 were in a 10x10 arrangement, while the rest were all 7x7. C Cape Davis Region, W Watertunnel Region, B Base Region, Ro Rook's Bay Region, R Reppetto's Region, K Kildalkey Region, S Swartkop Region, M Mixed Pickle Region. <sup>a</sup>Habitats that were outside our focal study area

season thus reflected on whether mice then experienced low, average, or high densities during that season. We used these SR values in least-square regressions to assess the influence of density in the different habitat types on reproductive output and survival.

We also calculated winter (May–October) and summer (November–April) intrinsic growth rates for the populations on each trapping grid following Caughley (1977). We used least-squares regression analyses to evaluate growth rates as functions of density at the onset of each season. This approach has inherent statistical flaws—growth is estimated from densities and thus dependent on population estimates which may also have errors. Our use of minimum numbers alive minimizes the influences of errors in population estimates. Dependence of growth on density still provides small flaws, but we reasoned that these will not obscure the general result (see van Aarde et al. 1999).

**Results**

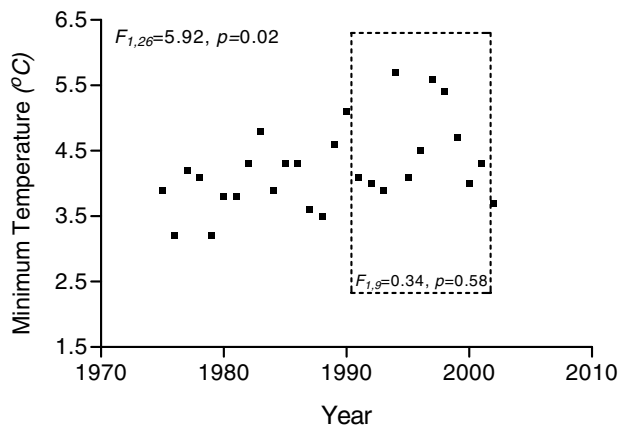
Climate changes

The mean minimum temperature at Marion Island increased between 1975 and 2002 (Fig. 1, but see also Table 2). However, over our shorter study period (1991–2001), mean minimum temperature did not increase significantly for 9 months of the year (Table 2). Temperature changes that we detected over our study were thus inconsistent with the long-term trend (see Table 2). The lack of short-term trends did not allow us to study the response of mice to an increase in temperature. We therefore relied on the analyses of year-to-year differences in temperature and demographic variables.

Density changes

The monthly mouse densities ( $n\ ha^{-1}$ ) were similar during each study year. Numbers peaked during April or May, and very few mice were present at the end of winter (Fig. 2). Values for the studies during 1979–1980 and 1990s were similar for two of the three habitats. Values on the swamps seemed lower during 1979–1980 than during 1990s (Fig. 2).

Mouse densities remained constant over our study period (Fig. 3) and the intrinsic growth rate ( $r$ ) for the Island as a whole was  $0.029 \pm 0.018$  ( $\bar{x} \pm SE; t_{69} = 1.62, P = 0.11$ ). Growth rate in biotically influenced areas was  $0.0009 \pm 0.0236$  ( $t_{23} = 0.038, P = 0.98$ ), that on vegetated black lava was  $0.036 \pm 0.020$  ( $t_{20} = 1.77,$



**Fig. 1** An example of climate change at Marion Island as represented by the mean daily minimum temperatures recorded during December at Marion Island between 1975 and 2002. We based our analyses on data collected by the South African Weather Bureau. The *broken block* indicates our study period (1991–2001). The *F* statistics are for the linear regressions calculated for the two periods. Values during our trapping period did not follow a specific trend. This was typical for most of the months (Table 2)

$P = 0.09$ ), and that on swamps was  $0.088 \pm 0.021$  ( $t_{22} = 4.22$ ,  $P < 0.01$ ; Fig. 3).

#### Influence of temperature and density on reproductive output and survival

Reproductive output was higher during summers with above average minimum temperatures than ones with below average minimum temperatures (Fig. 4). However, these differences were much greater on the swamps ( $y = 0.79 e^{6.15x}$ ,  $r^2 = 0.71$ ) than on biotically

influenced areas ( $y = 0.48 e^{14.08x}$ ,  $r^2 = 0.89$ ) or vegetated black lava ( $y = 0.81 e^{9.58x}$ ,  $r^2 = 0.57$ ). Reproductive output was also lower in the biotically influenced areas when densities here were above average compared with when they were below average (Fig. 5,  $y = 1.67 e^{-3.22x}$ ,  $r^2 = 0.45$ ), but did not follow a specific trend on the other two habitats. A generalized linear model ( $F_{3,9} = 5.45$ ,  $P < 0.01$ ,  $r^2 = 0.71$ ) showed that minimum temperature influenced reproductive output irrespective of density or habitat type (Table 3).

The SRs of minimum temperature and density on their own explained little of the SRs in survival rates. In a single case, adults survived better on the vegetated black lava when temperatures were relatively warm (Fig. 4,  $y = 2.47x + 0.80$ ,  $r^2 = 0.90$ ,  $F_{1,3} = 25.91$ ,  $P = 0.01$ ). No generalized linear model that included the SRs of temperature, density, and habitat type explained variation in the survival of juveniles ( $F_{3,3} = 2.07$ ,  $P = 0.29$ , Table 3). However, for adults the model suggested that minimum temperature had some influence on their survival ( $F_{3,9} = 5.86$ ,  $P < 0.01$ ,  $r^2 = 0.73$ , Table 3).

Intrinsic growth rate during summer decreased with an increase in density at the onset of summer. This did not hold for the relationship between winter growth rates and the density of mice at the onset of winter (Fig. 6).

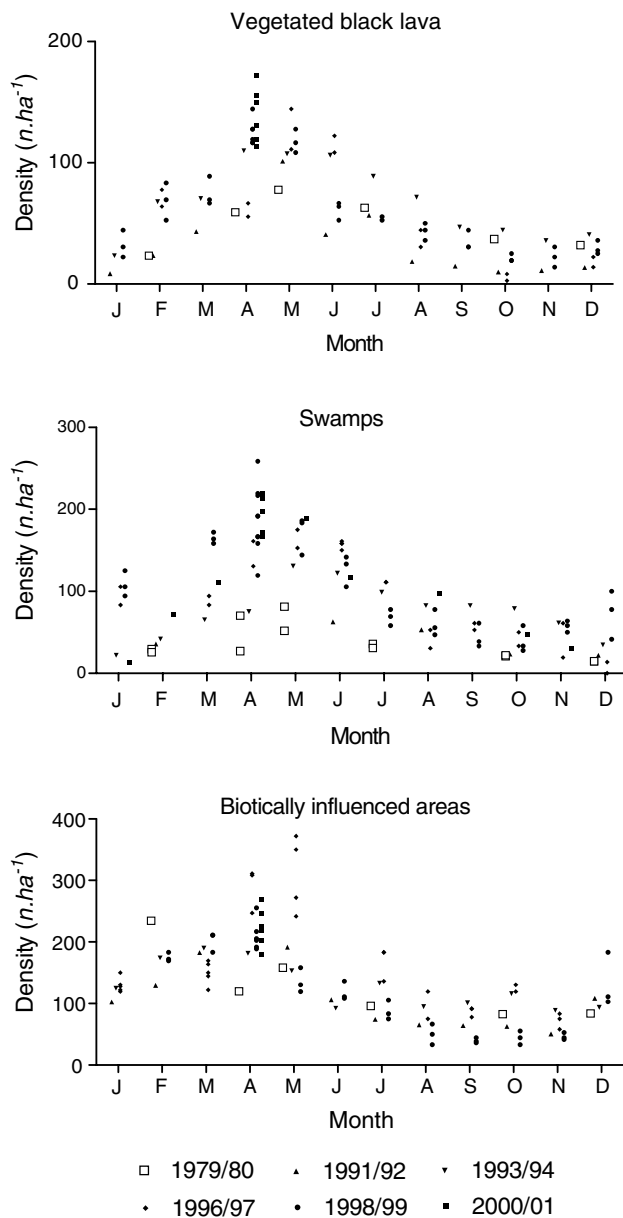
## Discussion

Our study focused on how measures of reproductive output and survival in feral mice may respond to

**Table 2** Summary of linear regression results reflecting on changes in mean monthly minimum temperatures (calculated from daily minimums) at Marion Island during 1975–2002 and for our study period from 1991 to 2001

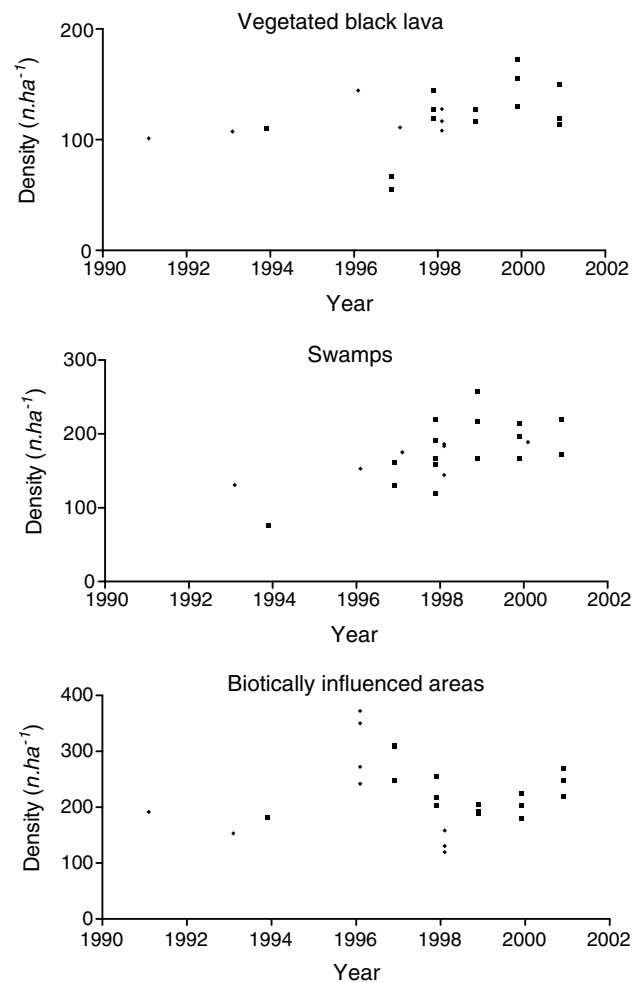
	1975–2002			1991–2001		
	Range	Slope	<i>F</i> value	Range	Slope	<i>F</i> value
January	3.7–6.7	$0.04 \pm 0.02$	$F_{1,26} = 8.27^*$	4.1–6.7	$0.16 \pm 0.05$	$F_{1,9} = 8.85^*$
February	4.5–6.7	$0.04 \pm 0.01$	$F_{1,26} = 9.82^*$	5.3–6.7	$0.01 \pm 0.05$	$F_{1,9} = 0.03$
March	4.1–6.5	$0.03 \pm 0.01$	$F_{1,25} = 6.61^*$	4.4–6.5	$0.04 \pm 0.06$	$F_{1,9} = 0.58$
April	2.8–5.5	$0.03 \pm 0.01$	$F_{1,26} = 5.57^*$	2.8–5.5	$-0.04 \pm 0.07$	$F_{1,9} = 0.37$
May	1.6–4.8	$0.03 \pm 0.02$	$F_{1,26} = 3.66$	2.1–4.8	$0.06 \pm 0.07$	$F_{1,9} = 0.67$
June	1.2–3.7	$0.01 \pm 0.01$	$F_{1,26} = 0.15$	1.3–3.1	$0.13 \pm 0.05$	$F_{1,9} = 7.71^*$
July	0.6–3.7	$0.05 \pm 0.02$	$F_{1,26} = 7.39^*$	0.9–3.2	$0.12 \pm 0.07$	$F_{1,9} = 3.55$
August	-0.3–2.8	$0.04 \pm 0.02$	$F_{1,24} = 4.74^*$	1.1–2.3	$0.05 \pm 0.04$	$F_{1,8} = 1.17$
September	0.6–2.6	$0.01 \pm 0.01$	$F_{1,26} = 0.80$	0.8–2.6	$0.04 \pm 0.05$	$F_{1,9} = 0.49$
October	1.2–3.9	$0.04 \pm 0.01$	$F_{1,26} = 8.56^*$	1.8–3.9	$0.05 \pm 0.06$	$F_{1,9} = 0.63$
November	2.0–5.3	$0.05 \pm 0.01$	$F_{1,26} = 11.0^*$	2.6–5.3	$0.16 \pm 0.06$	$F_{1,9} = 6.09^*$
December	3.2–5.7	$0.03 \pm 0.01$	$F_{1,26} = 5.92^*$	3.9–5.7	$0.04 \pm 0.07$	$F_{1,9} = 0.34$

*F* value is the ANOVA result for the slope (change in temperature, °C per year). Asterisks indicates a *P* value of  $< 0.05$ . We present the range of mean minimum temperatures (°C) recorded for each month across the two study periods



**Fig. 2** Monthly variation in density of house mice on trapping grids in three habitat types at Marion Island recorded during 6 years of surveys between 1979 and 2001. We extracted the data for 1979/1980 from Gleeson (1981). Note that the number of trapping grids varied between months and years (see Table 1). We separate years using a column plot to minimize overlap of symbols for ease of presentation

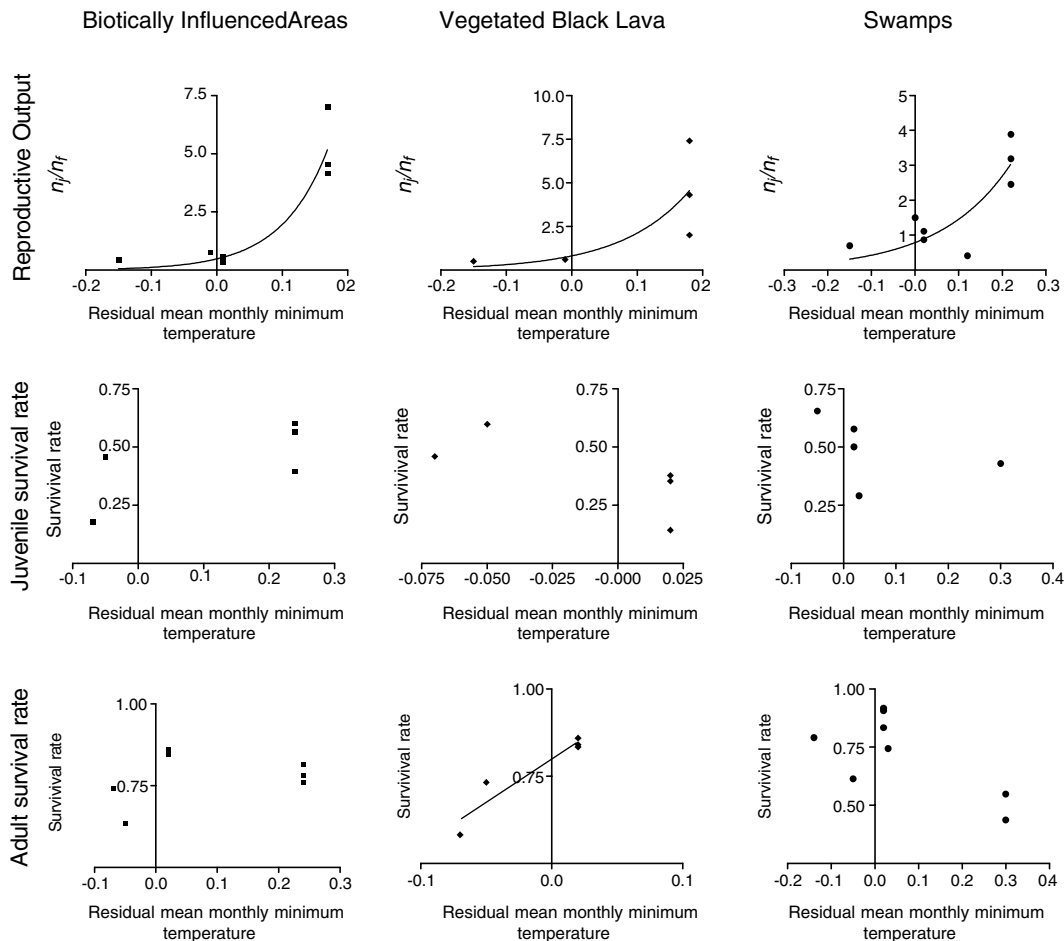
density and ambient minimum temperature at sub-Antarctic Marion Island. More specifically, we focussed our analyses on responses to residual differences thereby taking cognisance of strong seasonal variation in temperature and densities. In contrast to our first hypothesis, minimum ambient temperature did not have a strong effect on survival during winter. Mice always died in large numbers then, irrespective of



**Fig. 3** Mouse densities recorded for three habitat types at Marion Island during April (filled square) and May (filled diamond) from 1991 to 2001. Densities during our study increased only on swamps. Note that the number of trapping grids varied between months and years (see Table 1)

the severity of winters. However, as we expected, reproductive output in summer increased when ambient temperature did. Unexpectedly, survival in winter did not decrease with increased densities, probably due to the masking effect of temperatures. Reproductive output decreased with increased summer densities on at least one of the habitat types.

We appreciate that factors such as predation (e.g. Arthur et al. 2004) and interspecific competition (e.g. Fox and Pople 1984; Scott and Dueser 1992) may be important in limiting mouse numbers. However, mice on the Island are mainly active at night when potential predators (e.g. kelp gulls, *Larus dominicanus dominicanus*, and sub-Antarctic skuas, *Catharacta antarctica*) are inactive. These species took some mice that on



**Fig. 4** Reproductive output, juvenile, and adult winter survival as functions of residual minimum temperature ( $SR$  value) recorded for biotically influenced areas, vegetated black lava, and swamps. On all habitats, reproductive output increased as  $SR$  values of minimum temperature increased. However, only

adult survival rates on vegetated black lava increased significantly with  $SR$  values of minimum temperature. We only show curves that met statistical significance. Note that we excluded trapping grids for which we did not have complete temperature data sets across the relevant period for which a value was derived

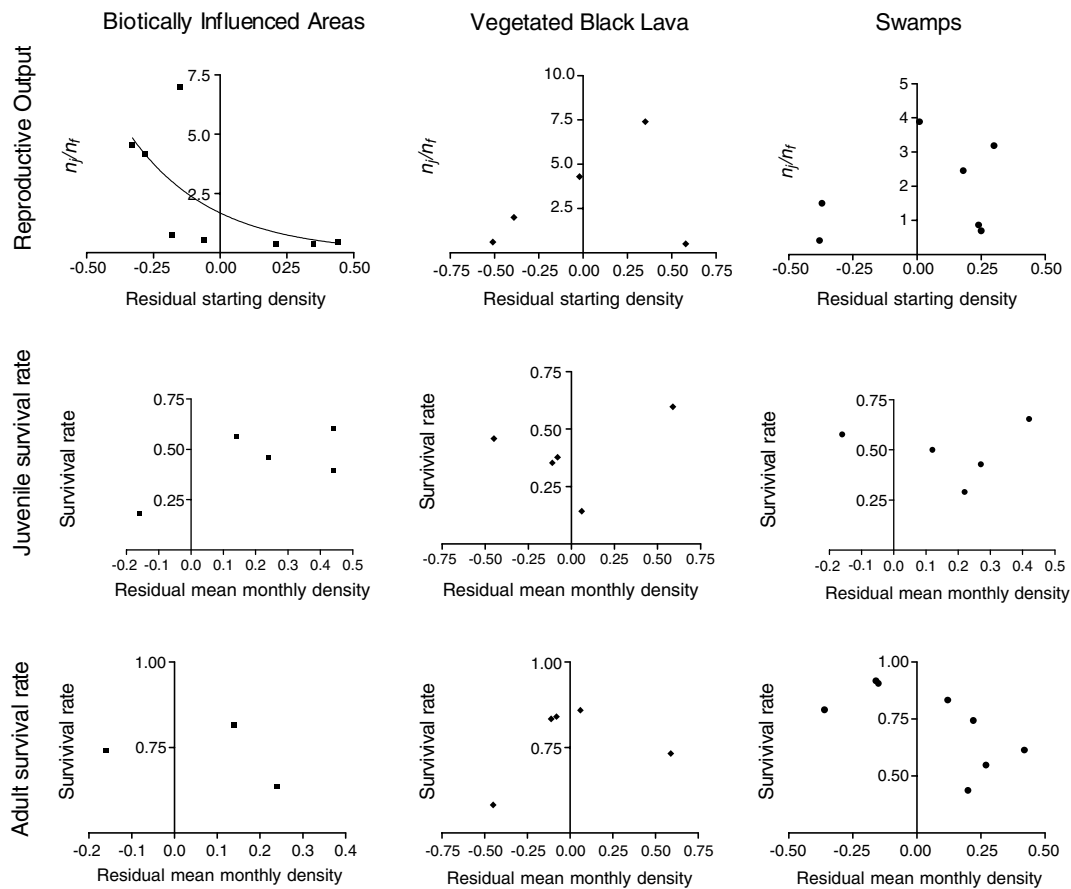
occasion ventured from burrows during the day (personal observations). Apparent overlap in niches and a decrease in lesser sheathbill, *Chionis minor*, numbers suggest that mice may compete with sheathbills (Huyser et al. 2000). Although the effect of predation and interspecific competition may be small, we concede that these may have induced some variation in survival.

On the basis of an earlier assessment of trends in temperatures and rainfall, the climate of the Island is changing (Smith 2002). Therefore, mice presently experience a climate different to that which prevailed earlier. Consequently, earlier comments (see Smith and Steenkamp 1990; Chown and Smith 1993; Bergstrom and Chown 1999; Smith et al. 2002) that change in climate on Marion Island induced mouse numbers to increase through increased reproductive

output may have been right, but lacked supporting data.

Like ours, several earlier studies conducted elsewhere noted high numbers of mice at the end of summer and autumn (e.g. Berry and Jakobson 1971; Stickel 1979). By focussing our analysis of long-term trends on data collected during April and May over a period of 10 years, we showed that mouse numbers increased significantly on only one of the three habitat types that we studied. Reproductive output was higher during warmer than average summers, but lower during years when densities were above average. However, survival rates varied independent of minimum temperature and density. This suggests that the increase in mouse numbers on swamps may have resulted from increased reproductive output. Reproductive output as we defined it included both a fecundity and





**Fig. 5** Reproductive output, juvenile, and adult survival as functions of residual density ( $SR$  values) recorded for biotically influenced areas, vegetated black lava, and swamps. Reproductive output declined as residual density increased on the

biotically influenced areas. We show only curves that met statistical significance. Note that we excluded trapping grids for which we did not have complete density data sets at the start or across the relevant period for which a value was derived

survival component so that the increase in numbers could be due to increases in either or both of them. However, we cannot ignore the role of inter-habitat dispersal, even though we did not record such movements during our study.

The increase in mouse numbers on swamps may also be due to rising temperatures that boosted invertebrate biomass. However, should this have been the case, then mouse numbers should also have increased elsewhere on the Island. Perhaps more importantly, lowered rainfall (Smith 2002) could have induced the drying of swamps, making a once marginal habitat type more accessible to both mice and invertebrates. Other studies outside the sub-Antarctic noted that rain influenced food supply and access to burrows for mice (see Newsome 1969; Brown and Singleton 1999; Ylönen et al. 2003). However, such drying clearly had no influence on mouse numbers elsewhere on the coastal plains of the Island.

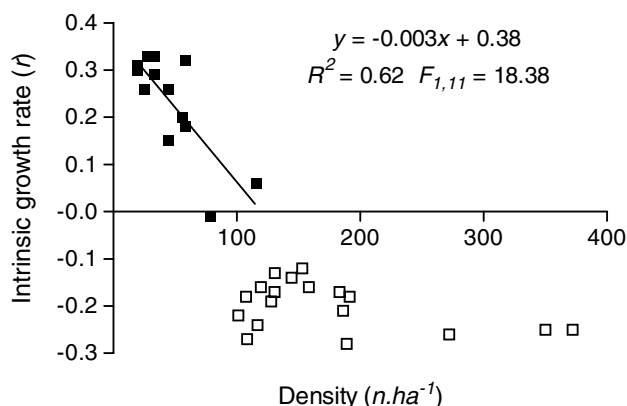
Different to some studies that ignored the influence of season on rodent demography (e.g. Hansen et al. 1999; Turchin and Ostfeld 1997), our results illustrate strong seasonal differences in mechanisms that may explain population fluctuations such as those that also have been noted by Åström et al. (1996) and Batzli (1999). On Marion Island, more than 90% of mice die every year during winter (van Aarde et al. 1996). The extreme winter weather conditions thus have a limiting role that acts independent of density and yearly changes in minimum temperatures. The relationship between density and population growth during summer adjusts this limitation. Such adjustment appears to come from lowered reproductive output that reduces growth rates in sub-populations on habitats where densities are high at the onset of summer. Some earlier studies on rodents also reported seasonal density dependence (e.g. Hansen et al. 1999; Yoccoz et al. 2001), and in one

**Table 3** Results of general linear models that summarize the effect of habitat (categorical variable), density, and temperature (continuous variables) on reproductive output, juvenile, and adult survival

Effect	Sum of squares	df	Mean sum of squares	F value	p value
<b>Reproductive output</b>					
Constant	21.671	1	21.671	15.49	<0.01
Habitat (H)	4.344	2	2.172	1.55	0.26
Density (D)	2.799	1	2.799	2.00	0.19
Temperature (T)	23.170	1	23.170	16.55	<0.01
H × D	3.344	2	1.672	1.17	0.35
H × T	5.069	2	2.535	1.81	0.22
D × T	0.009	1	0.009	0.001	0.93
H × D × T	10.011	2	5.005	3.58	0.07
Error	12.599	9	1.401	–	–
<b>Juvenile survival rate</b>					
Constant	0.326	1	0.326	25.63	<0.01
Habitat (H)	0.006	2	0.003	0.25	0.79
Density (D)	0.001	1	0.001	0.11	0.76
Temperature (T)	0.021	1	0.021	1.69	0.28
H × D	0.050	2	0.025	1.96	0.29
H × T	0.169	2	0.084	6.63	0.08
D × T	0.092	1	0.092	7.20	0.07
H × D × T	0.071	2	0.036	2.79	0.21
Error	0.038	3	0.013	–	–
<b>Adult survival rate</b>					
Constant	8.531	1	8.531	1994.36	<0.01
Habitat (H)	0.014	2	0.007	1.62	0.25
Density (D)	0.011	1	0.011	2.48	0.15
Temperature (T)	0.035	1	0.035	7.90	0.02
H × D	0.012	2	0.006	1.35	0.31
H × T	0.025	2	0.013	2.85	0.11
D × T	0.001	1	0.001	0.098	0.76
H × D × T	0.024	2	0.012	2.73	0.12
Error	0.039	9	0.004	–	–

case, high densities delayed maturation of females during summer (Yoccoz et al. 2001).

Predation by feral cats before their removal in 1992 (Bester et al. 2000) could have suppressed mouse



**Fig. 6** Winter (open symbols) and summer (closed symbols) intrinsic growth rates presented as functions of the density of mice at the onset of winter and summer, respectively. Summer growth rates declined with increased densities at the onset of summer

numbers. We showed, however, that mouse numbers at the time were similar to those during the 1990s on all but one habitat. Mice were never an important prey item for cats (van Aarde 1980) and it is likely that cat predation did not limit the mouse population (van Aarde et al. 1996). We cannot dispute that cats may have had some influence on mouse demography.

Mouse numbers during our study may have reached a new equilibrium (Fig. 3) and reproductive output certainly was higher when the minimum temperatures were above average. Minimum temperatures rose between 1975 and 2002, a period that spans the time between the first (1979/1980) and the last mouse surveys (2000/2001). Litter sizes and the fraction of females that breed in a season were also higher in 1992/1993 than in 1979/1980 (Matthewson et al. 1994). These results suggest that reproductive output increased since 1979/1980. We, therefore, expect mouse numbers to have been higher during our study than during 1979/1980 when minimum temperatures were lower. The only support that we have for this notion comes from the swamps where there were more mice during the 1990s than before.

Perhaps the most important reason for relatively stable numbers during the 1990s is that minimum ambient temperature then did not follow a specific trend. Variability in minimum ambient temperature did indeed explain year-to-year differences in reproductive output in our study. We know that cold spells or food-shortage can halt breeding in mice (Bronson 1979). Furthermore, in our study, lower than normal winter temperatures did not reduce survival beyond background values, even though a number of studies reported a positive association between survival of rodents and temperature in cool climates (Berry 1968; Berry and Jakobson 1971, 1975). Mice on Marion live close to their physiological limit (Berry et al. 1978), but construct burrow systems and runways that allow them to escape extreme weather (Avenant and Smith 2003). This and other physiological adaptations to cold (Webb et al. 1997) may reduce energy needs and explain why temperature did not affect survival rates strongly.

Our measure of reproductive output is not a true reflection of reproductive rate and represents a cumulative measure of reproductive rate and juvenile survival. We have no means through which to separate variability in reproductive rates from juvenile survival. In spite of this, we have illustrated that the reproductive output of mice was greater at higher temperatures. We also showed that high densities lowered reproductive output in biotically influenced areas. This is in line with Singleton et al. (2005) who recorded

decreases in litter size when mice densities were high at the beginning of the breeding season in Australia. Several earlier studies recorded physiological changes in the individuals of a population when densities increase—foetal resorptions rise, sexual maturation is later, oestrous cycles are irregular, and surviving weaned pups per female are fewer (see references in Stueck and Barrett 1978). We noted fewer juveniles per female at higher densities, but cannot dispute that other density-dependent effects on reproductive output may operate at Marion Island.

In addition, temperature and density interact at Marion in such a way that mouse numbers are probably higher now than in the 1970s, but kept stable by density dependence. The responses of mice to temperature and densities may hold for other sub-Antarctic islands where increase in numbers could amplify their impact on native biota. Our study suggests that mouse numbers may increase as the climate warms. However, density-dependent reproductive output will modulate such an increase. Managers of sub-Antarctic islands thus have reason to be concerned about how climate may influence the impact of mice on native biota. They also need to consider the influence of density on numbers when designing management plans. This is especially important when density-dependent responses may compensate for the reduction of mouse numbers.

**Acknowledgments** The South African Department of Environmental Affairs and Tourism and the University of Pretoria supported this project logistically and financially. We are grateful for field assistance provided by Jaco Delpont, DG Erasmus, Jo Fourie, Rob Guldemond, Tim Jackson, Anina Koekemoer, Paddy Kuun, Charles Louw, Donald Matthewson, Lukas Niemandt, and Jaco van Wyk at various stages of the project. The comments of three anonymous referees added to the quality of the typescript.

## References

- Anonymous (1996) Prince Edwards Islands Management Plan. Department of Environmental Affairs and Tourism, Pretoria
- Arthur AD, Pech RP, Dickman CR (2004) Habitat structure mediates the non-lethal effects of predation on enclosed populations of house mice. *J Anim Ecol* 73:867–877
- Åström M, Lundberg P, Lundberg S (1996) Population dynamics with sequential density-dependence. *Oikos* 75:174–181
- Avenant NL, Smith VR (2003) The microenvironment of house mice on Marion Island (sub-Antarctic). *Polar Biol* 26:129–141
- Batzli GO (1992) Dynamics of small mammal populations: a review. In: McCullough DR, Barrett RH (eds) *Wildlife 2001 populations*. Elsevier, London, pp 831–850
- Batzli GO (1999) Can seasonal changes in density dependence drive population cycles? *TREE* 14:129–131
- Bergstrom DM, Chown SL (1999) Life at the front: history, ecology and change in southern ocean islands. *Trends Ecol Evol* 14:472–477
- Berry RJ (1968) The ecology of an island population of house mouse. *J Anim Ecol* 37:445–470
- Berry RJ, Jakobson ME (1971) Life and death in an island population of the house mouse. *Exp Gerontol* 6:187–197
- Berry RJ, Jakobson ME (1975) Adaptation and adaptability in wild-living house mice. *J Zool Lond* 176:391–402
- Berry RJ, Jakobson ME, Triggs GS (1973) Survival in wild-living mice. *Mammal Rev* 3:46–57
- Berry RJ, Peters J, van Aarde RJ (1978) Sub-Antarctic house mice: colonization, survival and selection. *J Zool Lond* 184:127–141
- Bester MN, Bloomer JP, Bartlett PA, Muller DD, van Rooyen M, Buchner H (2000) Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *S Afr J Wildl Res* 30:53–57
- Bronson FH (1979) The reproductive ecology of the house mouse. *Q Rev Biol* 54:265–299
- Brown PR, Singleton GR (1999) Rate of increase as a function of rainfall for house mouse *Mus domesticus* populations in a cereal-growing region in southern Australia. *J Aple Ecol* 36:484–493
- Burger AE (1978) Terrestrial invertebrates: a food resource for birds at Marion Island. *S Afr J Antarct Res* 8:87–99
- Caughley G (1977) *Analysis of vertebrate populations*. Wiley, New York
- Chown SL, Cooper J (1995) The impact of feral house mice at Marion Island and the desirability of eradication, In: Report on a workshop held at the University of Pretoria, 16–17 February 1995. Department of Environmental Affairs and Tourism Directorate, Antarctica & Islands
- Chown SL, Smith VR (1993) Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* 96:508–516
- Crafford JE (1990) The role of feral mice in ecosystem functioning on Marion Island. In: Kerry KR, Hempel G (eds) *Antarctic ecosystems: ecological change and conservation. Proceedings of the 5th SCAR biology symposium, 29 August–3 September 1988*, Hobart, Tasmania. Springer, Heidelberg, pp 359–364
- Fox BJ, Pople AR (1984) Experimental confirmation of interspecific competition between native and introduced mice. *Aust J Ecol* 9:323–334
- Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicky M, Bergstrom DM (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biol Rev* 80:45–72
- Gleeson JP (1981) Ecology of the house mouse *Mus musculus* Linnaeus, on Marion Island. M.Sc. Thesis, University of Pretoria, Pretoria
- Gleeson JP, van Rensburg PJJ (1982) Feeding ecology of the house mouse *Mus musculus* on Marion Island. *S Afr J Antarct Res* 12:34–39
- Gremmen NJM (1981) The vegetation of the sub-Antarctic islands Marion and Prince Edward. D.R.W. Junk Publishers, The Hague
- Hansen TF, Stenseth NC, Henttonen H (1999) Multi-annual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *Am Nat* 154:129–139
- Huysen O, Ryan PG, Cooper J (2000) Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biol Conserv* 92:299–310

- Jackson TP, van Aarde RJ (2003) Advances in vertebrate pest control: implications for the control of feral house mice on Marion Island. *S Afr J Sci* 99:130–136
- Johnson JB, Omland KO (2004) Model selection in ecology and evolution. *TREE* 19:100–108
- Klok CJ, Chown SL (2001) Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic kelp fly, *Paractora dreuxi* (Diptera: Helcomyzidae). *J Insect Physiol* 47:95–109
- Krebs CJ (1998) Ecological methodology. Benjamin Cummings, Menlo Park
- Krebs CJ (2003) Two complementary paradigms for analysing population dynamics. In: Sibly RM, Hone J, Clutton-Brock TH (eds) *Wildlife population growth rates*. The Royal Society, Cambridge University Press, Cambridge, pp 110–126
- Krebs CJ, Kenney AJ, Singleton GR, Mutze G, Pech RP, Brown PR, Davis SA (2004) Can outbreaks of house mice in southeastern Australia be predicted by weather models? *Wildl Res* 31:465–474
- Matthewson DC, van Aarde RJ, Skinner JD (1994) Population biology of house mouse (*Mus musculus* L.) on sub-Antarctic Marion Island. *S Afr J Zool* 29:99–106
- Meikle D, Westberg M (2001) Maternal nutrition and reproduction of daughters in wild house mice (*Mus musculus*). *Reproduction* 122:437–442
- Mélice J-L, Lutjeharms JRE, Roualt M, Ansoorge IJ (2003) Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *S Afr J Sci* 99:363–366
- Newsome AE (1969) A population study of house-mice temporarily inhabiting a South Australian wheatfield. *J Anim Ecol* 38:341–359
- Rowe-Rowe DT, Green B, Crafford JE (1989) Estimated impact of feral house mice on sub-Antarctic invertebrates at Marion Island. *Polar Biol* 9:457–460
- Ruscoe WA, Elkinton JS, Choquenot D, Allen RB (2005) Predation of beech seed by mice: effects of numerical and functional responses. *J Anim Ecol* 74:1005–1019
- Scott DE, Dueser RD (1992) Habitat use by indular populations of *Mus* and *Peromyscus*: what is the role of competition? *J Anim Ecol* 61:329–338
- Sinclair BJ, Chown SL (2005) Deleterious effects of repeated cold exposure in a freeze-tolerant sun-Antarctic caterpillar. *J Exp Biol* 208:869–879
- Singleton GR, Brown PR, Pech RP, Jacob J, Mutze G, Krebs CJ (2005) The genus *Mus* as a model for evolutionary studies. *Biol J Linn Soc* 84:617–627
- Smith VR (1987) The environment and biota of Marion Island. *S Afr J Sci* 83:211–220
- Smith VR (2002) Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* 52:345–357
- Smith VR, Steenkamp M (1990) Climatic change and its ecological implications at a sub-Antarctic island. *Oecologia* 85:14–24
- Smith VR, Avenant NL, Chown SL (2002) The diet and impact of house mice on a sub-Antarctic island. *Polar Biol* 25:703–715
- Stickle LF (1979) Population ecology of house mice in unstable habitats. *J Anim Ecol* 48:871–887
- Stueck KL, Barrett GW (1978) Effects of resource partitioning on the population dynamics and energy utilization strategies of feral house mice (*Mus musculus*) populations under experimental field conditions. *Ecology* 59:539–551
- Sutherland DR, Singleton GR (2006) Self-regulation within outbreak populations of feral house mice: a test of alternative models. *J Anim Ecol* 75:584–594
- Sutherland DR, Spencer PBS, Singleton GR, Taylor AC (2005) Kin interactions and changing social structure during a population outbreak of feral house mice. *Mol Ecol* 14:2803–2814
- Turchin P, Ostfeld RS (1997) Effects of density and season on the population rate of change in the meadow vole. *Oikos* 78:355–361
- Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. *Int J Climatol* 25:279–294
- van Aarde RJ (1980) The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. *S Afr J Wildl Res* 10:123–128
- van Aarde RJ (1983) Demographic parameters of the feral cat *Felis catus* population at Marion Island. *S Afr J Wildl Res* 13:2–16
- van Aarde RJ, Ferreira SM, Wassenaar TD, Erasmus DG (1996) With the cats away the mice may play. *S Afr J Sci* 92:357–358
- van Aarde RJ, Whyte I, Pimm SL (1999) The consequences of culling for the dynamics of the African elephant population of Kruger National Park. *Anim Conserv* 2:287–294
- van Aarde RJ, Ferreira SM, Wassenaar TD (2004) Do feral house mice have an impact on invertebrate communities on sub-Antarctic Marion Island? *Aust Ecol* 29:215–224
- Webb P, Ellison G, Skinner JD, van Aarde RJ (1997) Are feral house mice from the sub-Antarctic adapted to cold? *Z Säugetierkd* 62:58–62
- Ylönen H, Jacob J, Runcie NJ, Singleton GR (2003) Is reproduction of the Australian house mouse (*Mus domesticus*) constrained by food? A large-scale field experiment. *Oecologia* 135:372–377
- Yoccoz NG, Stenseth NC, Henttonen H, Prévot-Julliard A-C (2001) Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. *J Anim Ecol* 70:713–720