Drivers of predatory behavior and extreme size in house mice *Mus musculus* on Gough Island

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In comparison to the mainland, populations of rodents on islands are often characterized by a suite of life history characteristics termed the "island syndrome." Populations of rodents introduced to islands are also well known for their impacts on native species that have evolved in the absence of mammalian predators. We studied the ecology and behavior of introduced house mice *Mus musculus* on Gough Island where they are the only terrestrial mammal and where their predatory behavior is having a devastating impact on the island's burrowing petrel (order *Procellariiformes*) population and the Critically Endangered Tristan albatross *Diomedea dabbenena*. Mice on Gough exhibit extreme features of the island syndrome, including: a body mass 50–60% greater than any other island mouse population, peak densities among the highest recorded for island populations, and low seasonal variation in numbers compared to other studied islands. Seasonal patterns of breeding and survival were linked to body condition and mass, and mice in areas with high chick predation rates were able to maintain higher mass and condition during the winter when mouse mortality rates peak. Within-site patterns of chick predation indicate that proximity to neighboring predated nests and nesting densities are important factors in determining the likelihood of predation. We conclude that selection for extreme body mass and predatory behavior of mice result from enhanced overwinter survival. Small mammal populations at temperate and high latitudes are normally limited by high mortality during the winter, but on Gough Island mice avoid that by exploiting the island's abundant seabird chicks.

Key words: invasive species, island syndrome, *Mus musculus*, predatory behavior

INTRODUCTION

Intraspecific comparisons of island and mainland populations have provided many important insights into ecology and evolution. Island populations are often characterized by larger body mass, lower reproductive output, greater survival rates, higher and more stable population densities, reduced intraspecific aggression, and greater spatial overlap in home ranges (Gliwicz 1980; Stamps and Buechner 1985; Adler and Levins 1994; Gray and Hurst 1998). This suite of characteristics is termed the "island syndrome" (Adler and Levins 1994) and occurs among numerous taxonomic groups from invertebrates to mammals (Goltsman et al. 2005; Niebering et al. 2006; Raia et al. 2010; Lomolino et al. 2012). Many studies of the island syndrome have focused on rodents (Muridae), which are often generalists and exhibit

high levels of demographic and behavioral plasticity (Silver 1995; Adler 1996). Their widespread distribution and often relatively recent introduction to many islands has allowed patterns of microevolution to be investigated (Pergrams and Ashley 2001). Island populations of rodents often undergo rapid morphological changes (Lomolino 2005; Meiri et al. 2008) and their population densities can change rapidly when normal ecological constraints, such as those imposed by predators and competitors, are absent (Gray and Hurst 1998; Goldwater et al. 2012).

The island biology of the house mouse *Mus musculus* has been particularly well studied in this context, including investigations in temperate and subantarctic regions (e.g., Berry 1964, 1968; Berry et al. 1978; Pye 1993; Avenant and Smith 2004). This includes studies from Gough Island in the South Atlantic Ocean, where it is assumed that house mice arrived with sealing

boats in the early nineteenth century and where the mouse population is unusual in having extremely large body size, high population densities, and a large proportion of avian tissue in their diet (Rowe-Rowe and Crafford 1992; Jones et al. 2003). The other key factor that distinguishes mice on Gough Island is that they regularly prey upon seabird chicks, including those of the Tristan albatross *Diomedea dabbenena* that are over 300 times their body mass (Cuthbert and Hilton 2004). Groups of mice gnaw at the rump, flanks, and abdominal cavity (Wanless et al. 2007; Cuthbert et al. 2013a) and chicks die from their wounds 2–5 days after an attack begins (Davies et al. 2015). The impact of this unusual predatory behavior is most severe on small-bodied, winter-breeding species (Cuthbert et al. 2013b; Dilley et al. 2015), with most of the island's 13 burrowing petrel species (order *Procellariiformes*) predicted to be in decline (Cuthbert et al. 2013b). For the Tristan albatross, the predatory behavior of mice in combination with fisheries mortality (Wanless et al. 2009; Cuthbert et al. 2014) has resulted in the species being classified as Critically Endangered (IUCN 2012).

We describe the biology and behavior of mice on Gough Island in relation to the species' predatory behavior and predictions from the island syndrome. We report mouse population density, spatial overlap, breeding, and survival, and the effect of mass and body condition on mouse demography at sites with varying levels of albatross predation. Lastly, we evaluate whether the density and distribution of nesting Tristan albatrosses influence mouse behavior and assess the implications of seabird nesting density on the prevalence of predatory behavior on Gough Island.

MATERIALS AND METHODS

Study site and fieldwork methods.—Gough Island (40°S, 10°W) is a 65 km² mountainous island, with a cold-temperate climate (mean monthly minimum and maximum temperatures in lowland areas of 6.5°C and 11.6°C in August/September, and 11.7°C and 17.7°C in February) and high annual precipitation (2,600–3,750 mm). A total of 4 principal vegetation communities occur on the island, of which the 3 most widespread are fernbush in lowland areas (< 400 m), wet heath in the uplands (400–700 m), and high elevation feldmark vegetation (> 700 m; Fig. 1—Ryan 2007). Millions of burrowing petrels nest within lowland areas throughout the year at densities of up to 3,700–4,600 burrows/ha (Cuthbert 2004), along with thousands of Atlantic yellow-nosed albatrosses, *Thalassarche chlororhynchos*, and sooty albatrosses, *Phoebetria fusca*. Upland areas hold smaller populations (tens of thousands) of burrowing petrels as well as 1,500 to 2,400 pairs of Tristan albatrosses (Wanless et al. 2009).

Fieldwork was undertaken from 2003 to 2012, with intensive year-long field seasons of mouse research in 2003/2004, 2005/2006, and 2008/2009, along with annual monitoring of Tristan albatross chicks in all years. Mouse research was undertaken in lowland areas near the weather station in the southeast of the island (Fig. 1), where mouse densities are highest, and 2 adjacent upland areas. The upland areas are characterized by similar elevation, climate, habitat, and albatross nesting density (1.16–1.17 nests/ha) but experience contrasting rates of albatross chick predation: mortality rates over the chick-rearing period at the high predation site "Green Hill" averaged 77% (95% confidence interval [*CI*] 66–99%) from 2001 to 2009, two-thirds higher than mortality rates at the low predation site "Gonydale" over the same period (45% *CI* 31–58%). Year-round data were obtained on mice in lowland areas, whereas studies in upland areas were restricted to March–September, coinciding with chick-rearing and depredation of Tristan albatross chicks, as well as mid-summer (December). Monitoring
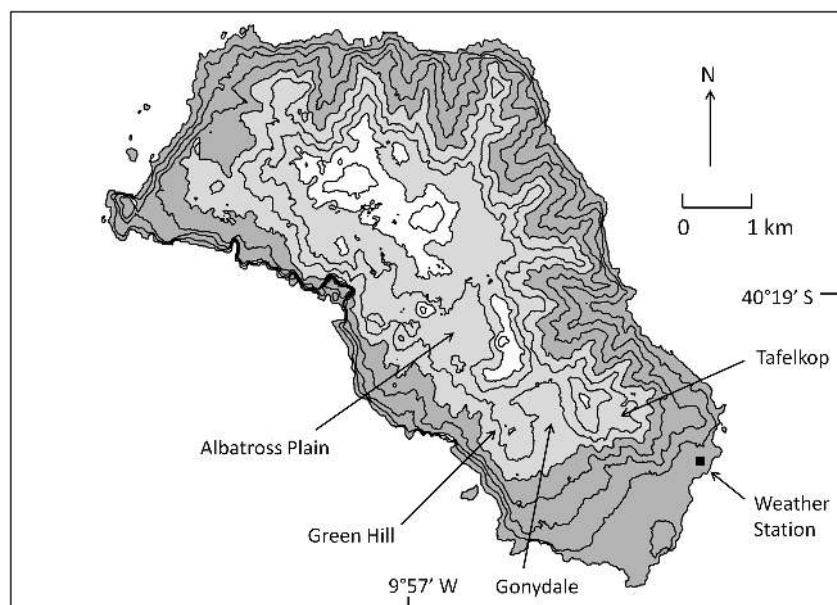

Fig. 1.—Map of Gough Island (40°S, 10°W) indicating the main distribution of fernbush (medium gray shading, < 400 m in elevation), upland wet heath (light gray shading, 400–700 m), and high-altitude feldmark vegetation (white shading, >700 m) and the location of sites named in the text. Contour lines are at 100 m intervals.

of Tristan albatrosses in the uplands was undertaken across 9 count areas of the island (Cuthbert et al. 2004), with more intensive research undertaken in the Gonydale, Green Hill, and Albatross Plain areas (Fig. 1). The numbers of incubating Tristan albatrosses (January/February) and large surviving chicks (September) were counted to estimate nesting density and breeding failure. Further information on albatross chick survival and GPS locations of each nest was obtained from Gonydale, Green Hill, Albatross Plain, and the Tafelkop count areas during the 2010 breeding season.

Mice were studied through a combination of snap-trapping (all years of study) and live-trapping (in 2005/2006), with trapping taking place on 72 × 72 m grids of 100 traps rotated among 3–4 representative sites within lowland and the 2 upland areas. Snap-trapping grids were run for 1–4 nights and live-trapping sessions (using Scientific Supa-Kill traps, Kempton Park, South Africa) were undertaken over 3–6 consecutive nights (Table 1). All snap-trapped mice were sexed, weighed, and body and tail length measured. Live-trapped mice were individually marked by toe clipping (Berry 1970), sexed and measured on the 1st trapping occasion, and thereafter weighed on recapture. Pregnancies (as revealed by dissection) were only observed in mice > 21 g in mass so following Matthewson et al. (1994) we used a cutoff mass of 20 g to differentiate juvenile and adult mice. On Gough Island, male mice can exhibit scrotal testes in all months (Jones et al. 2003) so the breeding season was defined by the occurrence of pregnant or lactating females.

Data analysis.—Data from mouse live capture sessions were analyzed in DENSITY 5.0 (Efford 2012), where spatially explicit capture–recapture models (SECRs) were used to calculate density, recapture probability (g_0), and the spatial scale of the detection function (σ). For each live capture session, we specified a buffer of 80 m (> 3 times the calculated mean maximum distance moved for the majority of sessions) and incorporated information on mortalities and individual trap history (i.e., if a trap was lost or unset). Estimated densities (mice/ha) were selected through maximum likelihood procedures (ML-SECR). Values of the detection function (σ) were used to estimate home range area, which is approximated by the 95% circular probability density area of capture, where home range = $\pi \times (2.45 \times \sigma)^2$ (Borchers and Efford 2008). For each capture session, we used the home range area and density estimate to calculate the average home range overlap between neighboring home ranges.

Monthly survival rates were obtained using live recapture models in MARK (White and Burnham 1999). To account for the uneven intervals between trapping sessions, models were fitted with varying trapping intervals (44–107 days) and the resulting daily survival rates were standardized to a 30-day period for comparison with other studies. A total of 15 of 674 mice died during capture and these individuals were coded as not released. As we were interested in seasonal variation in survival, we only fitted models with variable survival [$\phi(t)$], and variable and constant recapture probability [models $\phi(t)p(.)$ and $\phi(t)p(t)$]. Goodness-of-fit tests were run for each capture site ($n = 4$) to evaluate if the global model for each site was overdispersed. Where overdispersion occurred, data and estimated *CI*s were corrected for ĉ with model selection based on the lowest DAIC$_c$ or QAIC$_c$ values (Cooch and White 2014).

To explore factors that influenced mouse survival, we constructed generalized linear models (GLMs) with recapture or no capture at the $t + 1$ capture session as a binary dependent variable (with recapture or no capture coded as a binomial distribution) and with body mass, month, elevation, and sex as factors. We assessed the best-fitting model from the set of candidate models in an information-theoretic model-testing framework (Burnham and Anderson 2002) in program R (v3.1.2—R Core Team 2013), with the best model determined by the lowest Akaike's Information Criteria (AIC$_c$). When there was no clear top model (AIC$_c$ < 0.7), we explored the top models, depending on the degree of support from the weighted AIC$_c$ values. Candidate models were Mass, Elevation, Month, Mass + Month, Mass + Month + Elevation, Mass + Month + Elevation + Sex, and one null model with no explanatory variables to represent

Table 1.—Results of spatially explicit capture–recapture (SECR) models for house mice, *Mus musculus*, on Gough Island in 2 lowland areas and upland areas with high (HP) and low (LP) albatross chick, *Diomedea dabbenena*, predation rates, indicating month of each capture session, number of nights of trapping, total number of mice (total captures), estimated density (95% confidence limits), probability of detection g_0, spatial scale of detection function σ, 95% home range (HR) probability density, and percent overlap in ranges.

Site	Month	Nights	Mice (*n* captures)	Density (mice/ha)	g_0	σ (m)	HR (ha)	Overlap
Lowland 1	Oct	5	64 (114)	72 (54–97)	0.04	12.5	0.29	95%
Lowland 1	Nov	5	112 (239)	91 (71–115)	0.05	15.6	0.46	98%
Lowland 1	Jan	6	134 (311)	115 (95–140)	0.06	13.7	0.35	98%
Lowland 1	May	5	199 (300)	266 (218–325)	0.02	14.6	0.40	99%
Lowland 2	Feb	6	138 (306)	138 (115–167)	0.05	12.4	0.29	98%
Lowland 2	Mar	5	79 (153)	131 (98–175)	0.06	12.0	0.27	97%
Lowland 2	Jun	5	90 (201)	124 (94–164)	0.11	12.0	0.27	97%
Lowland 2	Sep	4	82 (140)	81 (62–107)	0.06	14.2	0.38	97%
Upland HP	Dec	6	29 (58)	22 (13–35)	0.03	18.9	0.68	93%
Upland HP	May	5	96 (226)	98 (79–121)	0.09	10.4	0.21	95%
Upland HP	Aug	3	66 (96)	107 (78–147)	0.06	9.5	0.17	95%
Upland LP	Dec	5	30 (54)	27 (16–46)	0.03	17.2	0.56	93%
Upland LP	Mar	5	97 (180)	122 (97–153)	0.04	11.0	0.23	96%
Upland LP	Jun	5	85 (250)	74 (58–93)	0.10	12.1	0.28	95%
Upland LP	Sep	4	44 (89)	34 (23–52)	0.07	15.8	0.47	94%

a baseline candidate model. The analysis included data from lowland areas (*n* = 526 mice, from October to August) and upland areas (*n* = 341, from December to August), with 340 mice recaptured at *t* + 1 and 527 not recaptured. Due to variable intervals between captures in upland and lowland areas, we also undertook a separate analysis for mice from upland areas. In these models, elevation was replaced with site in order to evaluate if albatross chick predation was an important factor in explaining patterns of mouse survival.

Mouse body condition was estimated as body mass divided by the mass predicted from a linear regression of ln(mass) against ln(tail length—Hayes and Shonkwiler 2001). Separate regressions were calculated for each of the 3 study years, and for each year the condition index was standardized to a mean of 1.0 to account for interobserver differences in measurements. The regressions were calculated from kill-trapping data, which in 2005/2006 was supplemented by data from 1st recorded capture of live-trapped animals. There was substantial monthly and altitudinal variation in mass and condition and seasonal differences in trapping effort; therefore, in order to standardize the data for different years, the regression equations used data only for lowland mice from November to August each year, because these were the time/place in which mice were trapped every year. Patterns of variation in body condition (coded as a Gaussian distribution in the analysis) were investigated with GLMs and a set of candidate models based on a priori consideration of the factors that may be most significant for explaining patterns of variation in body condition. For lowland areas these models were Year, Month, Sex, Year + Month, Year + Sex, Month + Sex, Year + Month + Sex, and one null model. For upland areas, we introduced site as an additional factor. Analyses were undertaken in Program R as described above. To verify that patterns of body condition were related to individual changes in condition, and not driven by differential mortality of lighter or heavier individuals, or recruitment of juveniles, we also examined within-individual patterns of mass change from retrapped live mice. Due to different time periods between trapping sessions, changes in individual body mass were calculated as the daily rate of mass change (g/day), with seasonal differences in rates of daily mass gain tested through a GLM with trapping period as a factor.

We used GLMs to investigate factors that influenced survival of Tristan albatross chicks following hatching, including site, nearest neighbor distance, and nearest neighbor chick fate (survive/fail to fledge) with chick survival coded as a binomial distribution. Competing models were assessed in program R as described above. To examine the effect of nest density on annual breeding success at the site scale, we constructed a generalized linear mixed model using the LME4 package (Ver. 1.1-7) in R v3.1.2. For each site–year combination, the model used the number of fledglings divided by number of nests in an "events/trials" formula as the response variable, with a binomial error distribution and logit link function. The fixed explanatory variable was scaled and centered on nest density (nests/ha). We used AIC to compare random intercept, random intercept and slope, and fixed effects only models. The best-fit model (lowest AIC) was the random intercept and slope model.

Unless stated otherwise, statistical tests were 2-tailed with $P < 0.05$ as the cutoff for significance, and means are presented ± 1 *SD*. Proportions were arcsine transformed prior to analysis. Live-trapping and kill-trapping in this study followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Permission and approval to undertake this fieldwork was granted by the Administrator and the Conservation Department of Tristan da Cunha.

RESULTS

Population density and spatial overlap.—Mouse densities in lowland areas ranged from 72/ha in October to 266/ha in early May, a 3.7-fold increase. Following this peak, mouse numbers decreased from May to September (Fig. 2; Table 1). The population peak occurred at the end of the mouse breeding season (see below) and prior to high winter mortality in August and September (Fig. 3; Table 2). Mouse densities in upland areas were less than one half of those in the lowlands (Table 1) and underwent a 4–5-fold seasonal variation. Home range size averaged 0.35 ± 0.14 ha (range among sites 0.17–0.68), with an average home range overlap of $95 \pm 2\%$ (range 93–99%; Table 1).
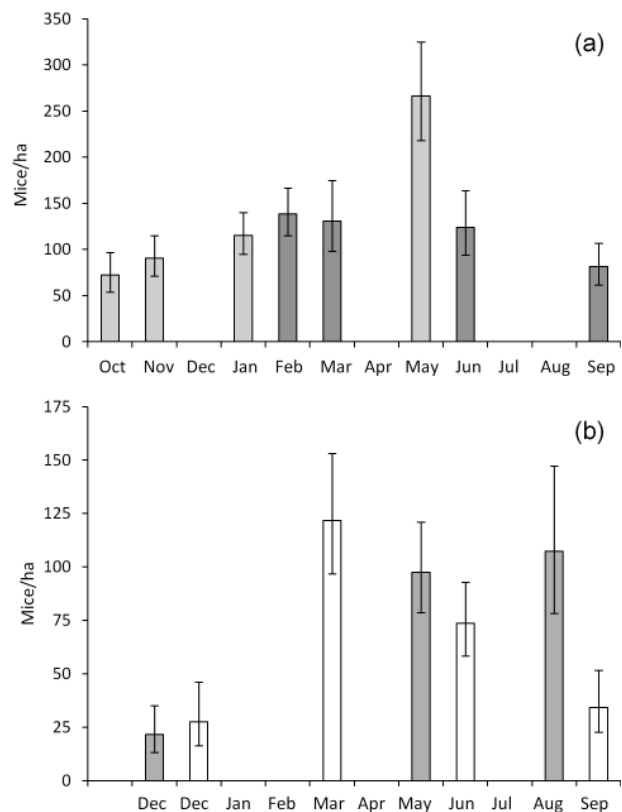

Fig. 2.—Seasonal variation in population density of house mice on Gough Island in (a) lowland areas and (b) upland areas. The 2 trapping sites in the lowland areas are indicated by different shades of gray: upland areas with low albatross predation by open bars and high predation by shaded bars (upland trapping began in December for both sites). Error bars are 95% confidence intervals around the mean.
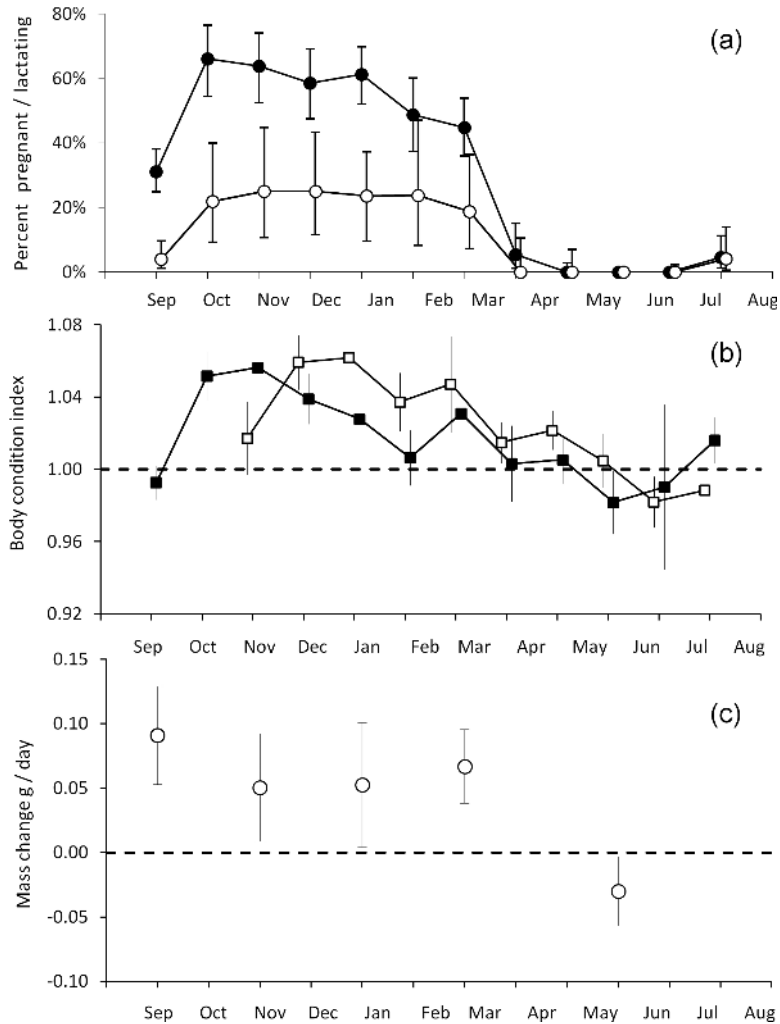
Fig. 3.—Seasonal variation in (a) the percentage of pregnant (filled circle symbols) and lactating (unfilled circles) female house mice, (b) body condition (both sexes combined) in 2003/2004 (unfilled squares) and 2008/2009 (filled squares), and (c) rates of daily mass gain (both sexes) for lowland areas. Error bars are 95% confidence intervals around the mean.

Table 2.—Results from mark-recapture models with variable survival and constant recapture probability [$\phi(t)p(.)$] indicating lowland and upland areas, the mid-date and duration of each trapping period, number of house mice, *Mus musculus*, released at *t*, and estimated 30-day survival and 95% confidence limits.

Altitude	Mid trap date	Trap days	Mice	30-day S	L95%	U95%
Lowland	02 Nov 2005	51	71	0.78	0.66	0.86
Lowland	20 Dec 2005	45	112	0.71	0.58	0.81
Lowland[a]	27 Feb 2006	53	138	0.81	0.57	0.92
Lowland[a]	30 Apr 2006	71	108	0.87	0.62	0.96
Lowland[a]	11 Jul 2006	72	86	0.72	0.51	0.85
Lowland[a]	07 Sep 2006	45	40	0.24	0.09	0.41
Upland	25 Jan 2006	100	30	0.63	0.45	0.77
Upland	23 Feb 2006	134	29	0.52	0.28	0.71
Upland	08 May 2006	107	75	0.91	0.55	0.98
Upland	11 Aug 2006	83	83	0.22	0.09	0.38
Upland	31 Aug 2006	45	52	0.41	0.26	0.55

[a] Confidence limits adjusted for overdispersion.

Breeding seasonality, body condition, and within-individual patterns of mass change.—Pregnant and lactating females were recorded from August to March (2003/2004) and August to April (2008/2009), with a peak of breeding during October–March (Fig. 3) when $23.0\pm2.3\%$ ($n = 6$ months) of females were pregnant. There was no significant monthly variation in litter size (1-way analysis of variance [ANOVA] $F_{7,78} = 1.86$, $P = 0.09$) with an average 8.3 ± 2.3 embryos per

litter (range 2–16, $n = 86$). Variation in lowland mouse body condition was best explained by Year + Month ($w_i = 0.73$), with weak or no support for the remaining candidate GLMs (Supporting Information S1). Adult body condition in lowland areas in 2003/2004 and 2008/2009 showed similar seasonal patterns, although condition increased earlier in 2008/2009 (Fig. 3). Condition increased markedly from winter to spring and thereafter declined through the year, reaching a low point in June/July (Fig. 3). The monthly percentages of pregnant females and lactating females were both strongly correlated with mean monthly body condition in 2003/2004 (pregnant, Pearson's $r = 0.725$, $n = 10$, $P < 0.01$; lactating, $r = 0.771$, $n = 10$, $P < 0.005$) and 2008/2009 (pregnant, $r = 0.802$, $n = 12$, $P < 0.001$; lactating, $r = 0.791$, $n = 12$, $P < 0.001$). Analysis of within-individual patterns of body mass change indicated a significant effect of month on daily mass change (1-way ANOVA $F_{4,180} = 3.22$, $P = 0.014$), with Fisher post hoc tests indicating that mass change during June was different to all other periods (Fig. 3). Individual mice increased in mass during summer (September–March) but lost body mass during winter (April–August). This winter mass loss corresponded with the period when the population exhibited its lowest body condition and the cessation of breeding (Fig. 3).

Survival and body mass.—Variable survival and constant recapture probability [$\phi(t)p(.)$] models provided the best-fit to the retrap data at 3 trapping sites, but data at the 4th site were overdispersed and a model with variable recapture and survival [$\phi(t)p(t)$] had the best-fit. This latter model was adjusted for overdispersion ($\hat{c} = 2.91$), but the *CI*s were implausible for 2 periods (range 0.00–1.00). As the difference in QAIC$_c$ between the models for constant versus variable recapture was small (3.20) and the former provided biologically realistic estimates of survival and *CI*s (comparable to the other 3 sites), the results from the [$\phi(t)p(.)$] model were utilized. Monthly survival estimates for mice in lowland areas were high from November to mid-July (Table 2), whereas survival was around one-third of this value in August–September (Table 2). Survival estimates in upland areas exhibited the same pattern of high survival during January–May and low survival during August–September (Table 2).

Generalized linear models examining survival of live-trapped mice to the $t + 1$ retrapping indicated a best model with Mass + Month + Elevation as factors ($w_i = 0.70$; Supporting Information S2). In lowland areas, there was no difference in the body mass of mice that survived versus those that were not recaptured during October to February, however from March to August heavier mice were more likely to be recaptured (Fig. 4). The pattern was less clear cut in upland areas where mice were generally lighter and where heavier mice were more likely to be recaptured during the winter months of July and August (Fig. 4). A separate set of candidate GLMs for mice in upland areas indicated that Mass ($w_i = 0.50$) and Mass + Month ($w_i = 0.19$) influenced survival (Supporting Information S3). Site was not an important factor, suggesting that seasonal variation in mouse survival followed similar patterns in the high and low albatross predation sites.

Comparison between upland areas with varying albatross predation rates.—There were similar mouse densities at the 2 upland sites during December (Table 1) and similar peak values from March to June (Fig. 2). However, mouse density decreased in the low predation site from March to September, whereas densities at the high predation site remained constant from May to August (Fig. 2). There was no evidence for a marked difference between the sites in spatial overlap of home ranges or σ (Table 1). Variation in body condition of mice in upland areas was influenced by Year + Month + Site ($w_i = 0.67$), with lower support for a model with Year + Month + Site + Sex as factors ($w_i = 0.33$), and no support for the remaining candidate models (Table 3). Body condition in both years and sites was very similar in December. However, mouse condition increased from May to September (when Tristan albatross chicks have hatched and are vulnerable to predation) in the high predation site, whereas body condition in the low predation site remained constant from May to September in 2005/2006 and decreased during the same period in the 2003/2004 season (Fig. 5a). Within-individual patterns of mass gain during 2005/2006 indicated a significant site effect and site × period interaction (periods May/June and August; 2-way ANOVA; site × period $F_{1,115} = 12.36$, $P = 0.001$; site $F_{1,115} = 9.54$, $P = 0.003$; period $F_{1,115} = 6.48$, $P = 0.012$; overall model fit $R^2 = 0.193$), with rates
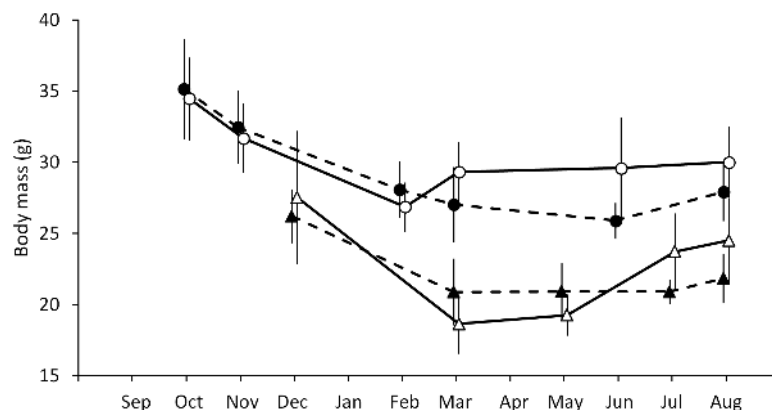

Fig. 4.—Relationship between body mass and month for house mice surviving to the $t + 1$ recapture session (unfilled symbols and solid lines) versus those not recaptured (filled symbols and dashed lines) for mice in lowland (circles) and upland (triangle) areas. Error bars are 95% confidence intervals around the mean.

Table 3.—Model results for body condition in upland areas in the 2003/2004 and 2005/2006 study seasons indicating the model, the number of parameters (K), Akaike's Information Criterion with a small sample correction (AIC_c, difference between current and top model (ΔAIC_c), the relative likelihood of the model (w_i), cumulative model weight (cum weight), and maximized value of the log-likelihood function (LL).

| Model	K	AIC_c	ΔAIC_c	w_i	Cum weight	LL
Year + month + site	5	−1,557.75	0.00	0.67	0.67	783.92
Year + month + site + sex	6	−1,556.33	1.42	0.33	1.00	784.23
Year + month	4	−1,544.69	13.05	0.00	1.00	776.38
Month + site	4	−1,536.77	20.98	0.00	1.00	772.42
Year	3	−1,535.74	22.01	0.00	1.00	770.89
Month + site + sex	5	−1,534.83	22.92	0.00	1.00	772.46
Site	3	−1,529.24	28.51	0.00	1.00	767.64
Month	3	−1,528.40	29.35	0.00	1.00	767.22
Null model	2	−1,518.52	39.22	0.00	1.00	761.27
Sex	3	−1,517.25	40.50	0.00	1.00	761.64
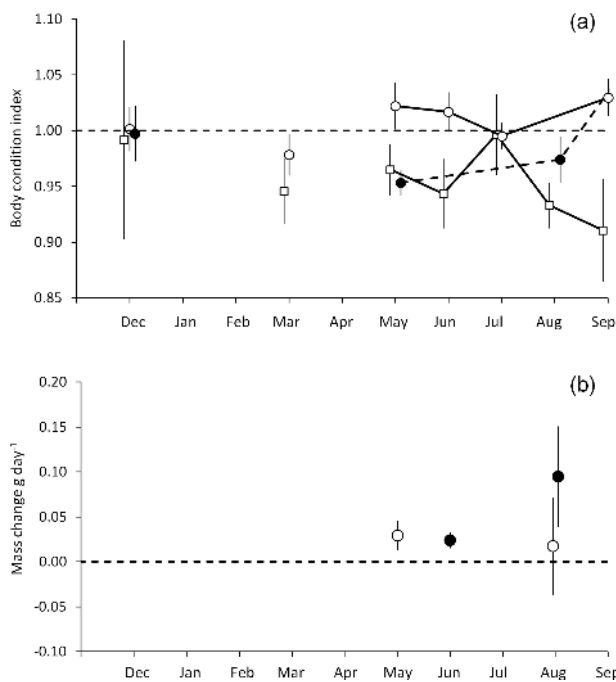
Fig. 5.—Seasonal variation in upland areas for (a) body condition and (b) rates of daily mass gain in house mice at sites with high rates of Tristan albatross predation in 2005/2006 (black filled circles and thick dashed line) and low albatross predation rates in 2005/2006 (open circles and solid line) and 2003/2004 (open squares and solid line). Error bars are 95% confidence intervals around the mean.

of mass gain remaining the same at the low albatross predation site but increasing in August for the high predation site (Fig. 5b).

Within-site and between-year patterns of albatross predation.— The likelihood of Tristan albatross chick survival was most influenced by the fate of the nearest neighboring nest ($w_i = 0.68$). For nests that were within 20 m of each other this relationship was very strong; the probability of survival was only 3.6% (95% *CI* 0.1–18.4%) if the neighboring nest failed, compared to 90% (*CI* 55.5–99.8%) if the neighboring chick survived (Fig. 6). There also was support for a model that included the distance to the nearest neighbor as well as its fate ($w_i = 0.25$), suggesting that the strength of the neighboring nest effect decreased with increasing nearest neighbor distance (Fig. 6; Table 4). There

was little support for models that included site as a factor, indicating that the relationship between chick survival and the fate and distance from its nearest neighbor was consistent across the island. Across years and sites, breeding success of Tristan albatrosses was negatively associated with nesting density (parameter estimate for scaled and centered nest density = −0.76 ± *SE* 0.31, *P* = 0.015), with higher mouse predation rates in areas with higher albatross nesting density.

DISCUSSION

Studies of rodents on islands have provided much evidence in support of the "island syndrome" (Adler and Levins 1994), and despite reviews that have questioned the generality of such "rules" (e.g., Meiri et al. 2008) the syndrome appears to be consistent among rodents (Lomolino 2005; Meiri et al. 2008; Lomolino et al. 2012). House mice on Gough Island exhibit many features predicted by the island syndrome: large body size, high and comparatively stable population densities, high survival rates, and a large degree of spatial overlap. However, some of these characters have evolved to an extreme degree in comparison to other island populations: body mass is 50–60% greater (Table 5); peak densities are among the highest recorded (Table 5); and there is low seasonal variation in numbers (4–5-fold in comparison to 10–13-fold on other islands— Triggs 1991; Matthewson et al. 1994). The other key feature that distinguishes mice on Gough Island is their large-scale predatory behavior on albatross and petrel chicks (Cuthbert and Hilton 2004; Wanless et al. 2007). We consider that this predatory behavior and the abundance of albatross and petrel chicks in the winter period has provided a unique set of circumstances that has freed the mice on Gough from normal ecological constraints that limit body size, with devastating consequences for the island's seabird populations.

Selection for predatory behavior by mice is indicated by the seasonal patterns of body condition and mass across all sites and from the comparison between the 2 uplands areas with varying predation rates. As with other rodent populations (e.g., Dobson and Michener 1995; Wauters and Dhondt 1995; Mutze 2009), reproduction of mice on Gough Island is influenced
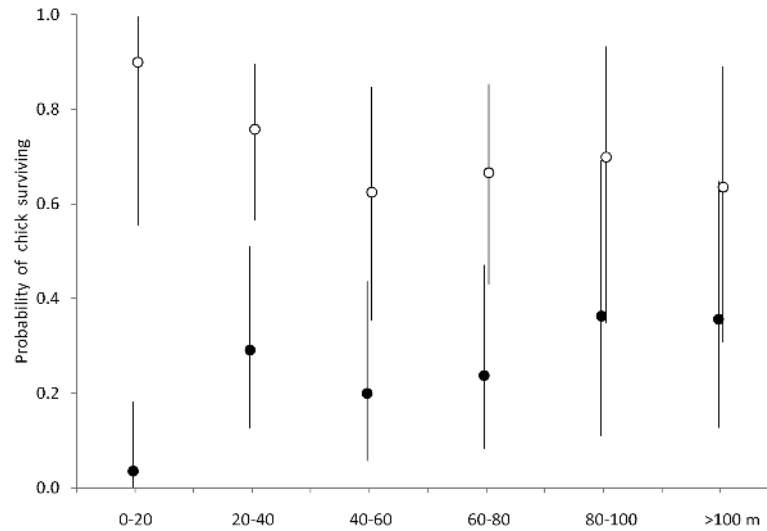
Fig. 6.—Relationship between nearest neighbour distance (m) and the probability that Tristan albatross chicks survive to fledge for chicks with failed nearest neighbours (black filled symbols) and surviving nearest neighbours (open symbols). Error bars are 95% dichotomous confidence intervals around the mean.

Table 4.—Model results for generalized linear models assessing the likelihood of survival of Tristan albatross chicks, *Diomedea dabbenena,* from hatching to fledging during the 2010 breeding season indicating the model, the number of parameters (K), Akaike's Information Criterion with a small sample correction (AIC_c, difference between current and top model (ΔAIC_c), the relative likelihood of the model (w_i), cumulative model weight (cum weight), and maximized value of the log-likelihood function (LL).

Model	K	AIC_c	ΔAIC_c	w_i	Cum weight	LL
Nearest fate	2	245.09	0.00	0.68	0.68	−120.52
Nearest fate + nearest distance	3	247.08	1.99	0.25	0.93	−120.48
Nearest fate + nearest distance + site	6	249.73	4.63	0.07	1.00	−118.66
Site	4	289.36	44.26	0.00	1.00	−140.58
Null model	1	297.16	52.07	0.00	1.00	−147.57
Nearest distance	2	299.07	53.98	0.00	1.00	−147.51

Table 5.—Demographic and population parameters for island populations of house mice, *Mus musculus*, in the Southern Hemisphere indicating island, latitude, mean adult body mass, breeding season and duration (months), average litter size, and maximum recorded density.

Island	Latitude	Mass (g)	Season (months)	Litter size	Maximum density	References
Gough	40°	35.7	Aug–Apr (9)	8.3	266	This study
Rangitoto	36°		Sep–Jun (10)	6.7		1
Tristan	37°	21.5[a]		6.8		2
Allports	40°	21.6		5.9		3
Mana	41°	21.1–22.2	Sep–Jun (10)	6.4–7.1		3,4
Marion	46°	20.6–21.4	Oct–May (8)	7.2–7.5	125–300	5,6,7,8
Antipodes	49°	19.7–22.7		5.8	147	3,9
Steeple Jason	51°	22.0		6.4	31[b]	10
Macquarie	54°	16–17[a]	Sep–Jun (10)	6.6		11
South Georgia	54°	21.4		7.1	2	2,12

[a] Mice on Macquarie Island and Tristan da Cunha occur with ship rats *Rattus rattus* and are consequently likely to be smaller sized in the presence of this competitor/predator (Goldwater et al. 2012), although this is only clearly seen for Maquarie Island.
[b] Density estimate for the winter period.
References: 1 Miller and Miller (1995); 2 R. J. Cuthbert, pers. obs.; 3 Murphy and Pickeral (1990); 4 Efford et al. (1988); 5 Berry et al. (1978), 6 Matthewson et al. (1994); 7 Avenant and Smith (2004); 8 Ferreira et al. (2006); 9 Russell (2012); 10 Rexer-Huber et al. (2013); 11 Pye (1993); 12 Cuthbert et al. (2012).

by body condition, with female reproductive rates correlated with condition. We also found evidence for the importance of body mass on winter survival of mice, as has been reported for a range of small mammals in temperate or Arctic regions (Murie and Boag 1984; Pucek et al. 1993; Karels et al. 2000; Korslund and Steen 2006; Schorr et al. 2009). Where Gough Island mice appear to differ from other mouse populations is in the pattern of mass gain and increasing body condition during the winter months in lowland areas (where winter predation rates on Atlantic petrel *Pterodroma incerta* chicks are very

high—Wanless et al. 2012; Dilley et al. 2015), and the similar pattern of stable or increasing mass and condition in the upland site with high albatross predation rates. In contrast, mass and condition showed no increase and in 1 year decreased in winter in the neighboring upland site with low predation rates. This pattern, of stable or increasing mass and condition, contrasts markedly with small mammal populations in Arctic and temperate regions where weight loss during winter is the norm (Iverson and Turner 1974; Hansson 1990, 1992; Aars and Ims 2002; Korslund and Steen 2006) and where high mortality in winter is a key factor in regulating many rodent populations (Berry 1968; Triggs 1991; Ferreira et al. 2006).

Given the positive effect of mass and body condition on survival and reproduction in mice and other small mammals, there is likely to be directional selection for large body size among other mouse populations; however, gigantism is only seen on Gough Island (Table 5). On the mainland, selection for increased size is likely to be limited by predation risk (Dickman 1992; Arthur et al. 2004; Powell and Banks 2004) and because larger animals require greater energetic resources particularly during winter (Peters 1993). Mice on islands that lack other introduced mammals or native avian predators are generally subject to little predation risk, but the need for larger individuals to maintain a higher energetic intake is still likely to be an important limiting factor (Triggs 1991; Ferreira et al. 2006). Gough Island, with its millions of winter-breeding seabirds, presents a rare case where an energetically rich prey source is abundant during the critical winter period (when avian material comprises a key dietary component—Jones et al. 2003). The abundance of seabird food, combined with predatory behavior, probably has favored the evolution of large body size in this population.

If seabird predation is advantageous, why do predation rates of albatross chicks differ between 2 uplands areas of Gough Island? We cannot exclude all extrinsic factors, but measurements of climatic and biotic variables indicated no large-scale differences between the sites. House mice exhibit a large degree of behavioral plasticity (Silver 1995) and differences in the prevalence of predatory behavior may evolve or be learned and vary between different subpopulations. Wild mouse populations typically have social organizations of individual territories or group/shared territories (Murphy and Pickeral 1990), with the latter more likely on Gough Island given the overlap in ranges and communal feeding on albatross chicks (Wanless et al. 2007). In this context, the prevalence of predatory behavior within different groups could be an important factor in determining chick predation rates on the island. Supporting this, the spatial scale of mouse movements (30–40 m) are broadly similar to the spatial scale of albatross predation where the likelihood of nest failure was strongly related to the fate of neighboring nests (0–40 m; Fig. 6). Given the apparent benefits of seabird predation on mouse mass and condition and winter survival, we would expect this behavior to spread: high rates of predation upon Tristan albatross in upland areas and on winter-breeding petrels in the lowlands are the norm (Wanless et al. 2012; Cuthbert et al. 2013b).

If predatory behavior of mice is favored on Gough Island, why is not seabird predation common at other islands where house mice occur? Mice are known to prey upon seabird and passerine chicks at several other islands (Fugler et al. 1987; Ainley et al. 1990; Campos and Granadeiro 1999; Jones and Ryan 2010; Bolton and Stanbury 2011), but it is only at Gough where the scale of predation is so severe that it is driving population declines across a wide range of birds (Wanless et al. 2007; Ryan and Cuthbert 2008; Cuthbert et al. 2013b). As well as the fitness benefits of predation in favoring the spread of this behavior, we suspect that the abundance of winter-breeding seabirds is also important. Nearest neighbor analysis of chick survival on Gough Island indicated that Tristan albatross chicks were far more likely to die if they were close to other chicks that died and there was a density-dependent relationship between albatross nesting density and predation rates: across years more chicks were killed in higher density areas. While some intersite differences in predation rates at Gough Island remain unexplained, the general pattern was of predation rates increasing with bird breeding densities. Comparison of winter nesting densities of albatross and petrel chicks at Gough Island and at 4 other islands where mice are the sole species of introduced rodent reveals substantial differences: densities range < 0.1 chicks/ha at Steeple Jason (Falklands Islands) and South Georgia, where winter-breeding *procellariiformes* are largely absent or in very low numbers, 0.2 chicks/ha on Marion Island, and 29 chicks/ha on the Antipodes Islands (densities estimated from the vegetated area of each island and population estimates for winter-breeding species). Mice at these 4 islands are of typical body size (Table 5) and, if it is recorded, only rarely prey upon chicks (Jones and Ryan 2010; Bolton and Stanbury 2011). In contrast, winter densities of burrowing petrel and albatross chicks across the whole of Gough Island are around 160 chicks/ha, with winter densities of Atlantic petrels in lowland areas reaching 430 chicks/ha (Cuthbert 2004). We consider this high density of chicks, one or more orders of magnitude greater than winter densities on other islands, has provided the conditions to allow directional selection for larger body size and high rates of predatory behavior in Gough Island's mouse population. These results suggest that the situation on Gough Island may well be unique and that the risk of such impacts occurring on other islands is low, unless such islands have mice as the sole species of introduced rodent as well as large populations of vulnerable prey in the winter when mouse populations are normally limited.

This study focused on understanding the ecology of mice and the factors that have driven their unusual predatory behavior and extreme biology on Gough Island, but in addition our findings reemphasize the conservation imperative to eradicate mice from the island (Dawson et al. 2014). Based on the large populations of burrowing petrels, albatrosses, and giant petrels on the island and their low values of breeding success (Cuthbert et al. 2013b, Cuthbert et al. 2014), more than 1 million seabird chicks are being predated by house mice each year (Wanless et al. 2012). In the context of a mouse eradication attempt, our study indicates that an operation should take

place during April to July, when mice are not breeding and their natural mortality rates are high, and prior to the hatching of Atlantic petrel chicks in August that would provide an alternative and abundant food supply to the bait pellets used in an eradication. Plans to eradicate mice from Gough Island are currently in preparation and if successful will result in the restoration of Gough Island as one of the world's most important seabird breeding islands.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Model results for Generalized Linear Model of mouse body condition in lowland areas in 2003/2004 and 2008/2009.

Supporting Information S2.—Model results for Generalized Linear Model of survival of live-trapped mice to the $t + 1$.

Supporting Information S3.—Model results for Generalized Linear Model of live-trapped mice to the $t + 1$ capture session in upland areas.

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