



## RESEARCH

## Population trends of house mice during tussock mast seeding on Auckland Island

Rachael L. Sagar<sup>1\*</sup> , Finlay S. Cox<sup>1</sup>, Stephen R. Horn<sup>1</sup> and James C. Russell<sup>2</sup> <sup>1</sup>Department of Conservation, PO Box 743, Invercargill 9840, New Zealand<sup>2</sup>University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

\*Author for correspondence (Email: rsagar@doc.govt.nz)

Published online: 28 November 2022

**Abstract:** House mice (*Mus musculus*) are an invasive species on Auckland Island in the New Zealand subantarctic and planning for their eradication is underway. Mast seeding events cause rodent populations to irrupt, though little is known about this phenomenon in snow tussock grass (*Chionochloa* spp.) systems on Southern Ocean islands. The aim of this study was to understand population fluctuations of mouse abundance on Auckland Island for the 2 years following a mast event, and with which tools to monitor abundance, to inform planning of bait application for eradication. Mouse populations were studied using kill and live trapping at two sites on Auckland Island, and mouse density was estimated using spatially explicit capture-recapture models. Mouse population density was highest during summer mast seeding of *Chionochloa antarctica* and then declined the following winter and subsequently remained low for the following year. Breeding remained seasonal, with a pulse in early summer and a very low level continuing through winter in both years, regardless of mast conditions. These results are similar to those from other cool temperate Southern Ocean islands where seasonal resource availability appears to drive breeding. Throughout the study the capture probability of mice was generally higher when population density was lower, which highlights that conclusions about population trends could be misleading if abundance indices are not calibrated to measures of population density. Mouse eradication should preferentially take place outside of a mast event but would likely still succeed during and following a mast event. Our work fills a key knowledge gap about rodent population trends during mast events for Southern Ocean islands, which is particularly important where eradications are planned.

**Keywords:** *Chionochloa antarctica*, density, spatially explicit capture-recapture, eradication, *Mus musculus*, rodent, Southern Ocean

## Introduction

The phenomenon of irruptive rodent population responses to periods of high seed production (mast seeding or masting) by grasses or forest trees is well documented (Bogdziewicz et al. 2016). In New Zealand, these dynamics are best known in southern beech (*Nothofagus* spp.) forest, where rodent populations, including house mice (*Mus musculus*), irrupt in response to periodic beech masting (King 1983). Beech forest is not the only mast seeding system that drives mouse population dynamics in New Zealand. Alpine grasses including snow tussocks (*Chionochloa* spp.) have periodic mast seeding, which has a similar impact on mouse population dynamics on the main islands of New Zealand to beech mast events, though evidence is limited to a single study (Wilson & Lee 2010). Mouse populations rise in the autumn following a mast summer, and may remain high through the following winter, spring and summer, then decline prior to the next winter, likely owing to resource limitations and predation (King 1983; Wilson & Lee 2010). Studies of mouse population trends in response to cereal crop availability in Australia show that the length of breeding seasons, population density and rate of

population increase varies from year to year, influenced by multiple factors including the population density at the start of breeding, disease prevalence and the level of the preceding winter's rainfall (Singleton et al. 2005). Such a variable context-specific population response is likely to be found in other systems.

House mice are a highly successful invasive species, present on all continents except Antarctica (Boursot et al. 1996). Their introduction has been almost entirely accidental, assisted by human movement, or their range expanded through human-mediated changes to landscapes (Auffray et al. 1990). Mice are present on many Southern Ocean islands where they have negative impacts on native biodiversity (Courchamp et al. 2003; Angel et al. 2009). There is widespread documentation of the consumption of plant matter and macroinvertebrates by mice on Southern Ocean islands (e.g. Angel et al. 2009; Houghton et al. 2019; Russell et al. 2020). Over the last decade evidence of significant negative impacts of mice on avian species, including predation on large live seabirds, has emerged from Southern Ocean islands (Wanless et al. 2012; Dilley et al. 2015). Unsurprisingly, eradicating mice and other mammalian pests from such islands is becoming an increasingly common

and effective conservation strategy (Russell & Broome 2016; Holmes et al. 2019; Spatz et al. 2022).

Mice have been documented since 1840 on Auckland Island, the main island in the Auckland Island group in the New Zealand Subantarctic Islands Area (NZSIA; Fig. 1), and a World Heritage area recognised for its significant natural and cultural values (World Heritage Convention 1998). The nuclear DNA of Auckland Island mice reveals they are the subspecies *M. musculus domesticus*, are distinct from other mouse populations in New Zealand, and likely arrived with sealers from North America (Veale et al. 2018). Mice are found at all altitudes and across all habitats on Auckland Island (Harper 2010b; Russell et al. 2019). Population fluctuations on Auckland Island are suspected to be driven by the pulsed availability of seed from tussock mast seeding events, with other plants and invertebrates sustaining smaller populations between masting events (Harper 2010b; Russell et al. 2018, 2019).

The eradication of feral pigs (*Sus scrofa*), mice and feral cats (*Felis catus*) from Auckland Island is considered feasible (Horn et al. 2022) and planning for its implementation is underway. There is a history of pioneering eradications on Southern Ocean islands, and in particular within the NZSIA (Russell et al. 2022 and references therein). To date the largest successful mouse eradication in the world was on subantarctic Macquarie Island (12 785 ha), which was cleared of rabbits (*Oryctolagus cuniculus*), ship rats (*Rattus rattus*) and mice in 2014 (Springer 2016). Subantarctic Antipodes Island (2012 ha) in the NZSIA was cleared of mice in 2016 (Horn et al. 2019). If successful, the eradication of mice from Auckland Island (45 891 ha) would be a 350% increase in the global land area cleared of mice, a huge jump in the scale of operations.

The logistical challenges of completing bait spread at the scale of Auckland Island requires a deviation from current best practice (Horn et al. 2022; Livingstone et al. 2022; Oyston et al. 2022). A lower bait sowing rate (two applications, each of 4 kg ha<sup>-1</sup> brodifacoum) and timing operations during summer have been proposed, c.f. two applications, each of 8 kg ha<sup>-1</sup> of brodifacoum during winter (best practice: Broome et al. 2017). A bait uptake trial simulating these adjusted methods was successfully carried out on Auckland Island during summer (early February) 2019 (Russell et al. 2019), leading to confidence this method would expose every individual if the bait application strategy encompassed two baiting applications a few weeks apart. However, during summer 2018/2019 a mast-seeding of tussock occurred on Auckland Island. Tussock mast events occur every few years and are suspected to cause significant fluctuations in mouse populations on Auckland Island (Harper 2010b; Russell et al. 2018). Uncertainty over the population dynamics of mice (e.g. density, home range size and breeding activity) following a mast event on Auckland Island translates to uncertainty in eradication success under such circumstances. Potentially, mice will not consume toxic bait when other food sources are plentiful, and/or they might have fewer opportunities to encounter bait if population densities are higher and home ranges smaller. Understanding the legacy of mast events on mouse populations across Auckland Island is important to inform the risk to success should an eradication follow a mast event. The objective of this study was to understand population fluctuations of mice on Auckland Island in relation to seeding cycles of the dominant tussock grass *Chionochloa antarctica*. In addition, we compared two methods of measuring mouse abundance.

## Methods

### Site description

This study was undertaken at two sites across three habitat types on Auckland Island (45 891 ha), the main island in the Auckland Island Motu Maha group (56 816 ha; 50.69°S, 166.08°E) in the New Zealand subantarctic area, 465 km south of mainland New Zealand (Fig. 1). The climate is characterized by strong, prevailing westerly winds and frequent rain and cloud cover and cool temperatures (2–12°C) all year round (Fraser 2020). Three major distinct vegetation types cover the island. A thin band of coastal forest (approx. 5000 ha) extends up to 50 m inland along the more sheltered eastern and southern side of the island. Coastal forest is dominated by rātā (*Metrosideros umbellata*). A thick scrub band (approx. 20 000 ha) extends from the coast in places, to approx. 250 m a.s.l.. Scrub is dominated by dracophyllum (*Dracophyllum longifolium*), myrsine (*Myrsine divaricata*) and stunted rātā. Above 250 m a.s.l. and in exposed coastal areas, tussock grasses dominate (approx. 20 000 ha). The predominant species is snow tussock (*Chionochloa antarctica*). *Chionochloa antarctica* tussock flowered heavily during summer 2018/19, leading to a mast seeding event.

Live and kill trapping were undertaken around the Smith Harbour area (Fig. 1), and only kill trapping was undertaken in the Deas Head area (Fig. 1). Trap grids and transects were established in the three main habitat types: coastal forest, scrub and tussock. Trapping grids and transects were established in coastal forest close to sea level (<20 m a.s.l.), in scrub at 100–200 m a.s.l., and in tussock at 200–350 m a.s.l. (Fig. 1). Feral pigs and New Zealand sealion rāpoka (*Phocarctos hookeri*) were present in the study area and very occasionally interfered with traps. Field work at each site was done when it could take place alongside other work programs on feral pigs (Cox et al. 2022) and feral cats (Glen et al. 2022; Rodriguez-Recio et al. 2022), meaning sampling periods across sites were not always aligned.

### Mouse population density

#### Deas Head

Sampling was undertaken in early March 2019, late August 2019, late November 2019 and mid-March 2020. During each sampling event, nine kill trap transects were established in the Deas Head area, three in each of the three habitat types following Harper (2010b) (Fig. 2; Table 1). The exception was in March 2020 when logistical constraints meant only two transects were set in each habitat type (Table 1).

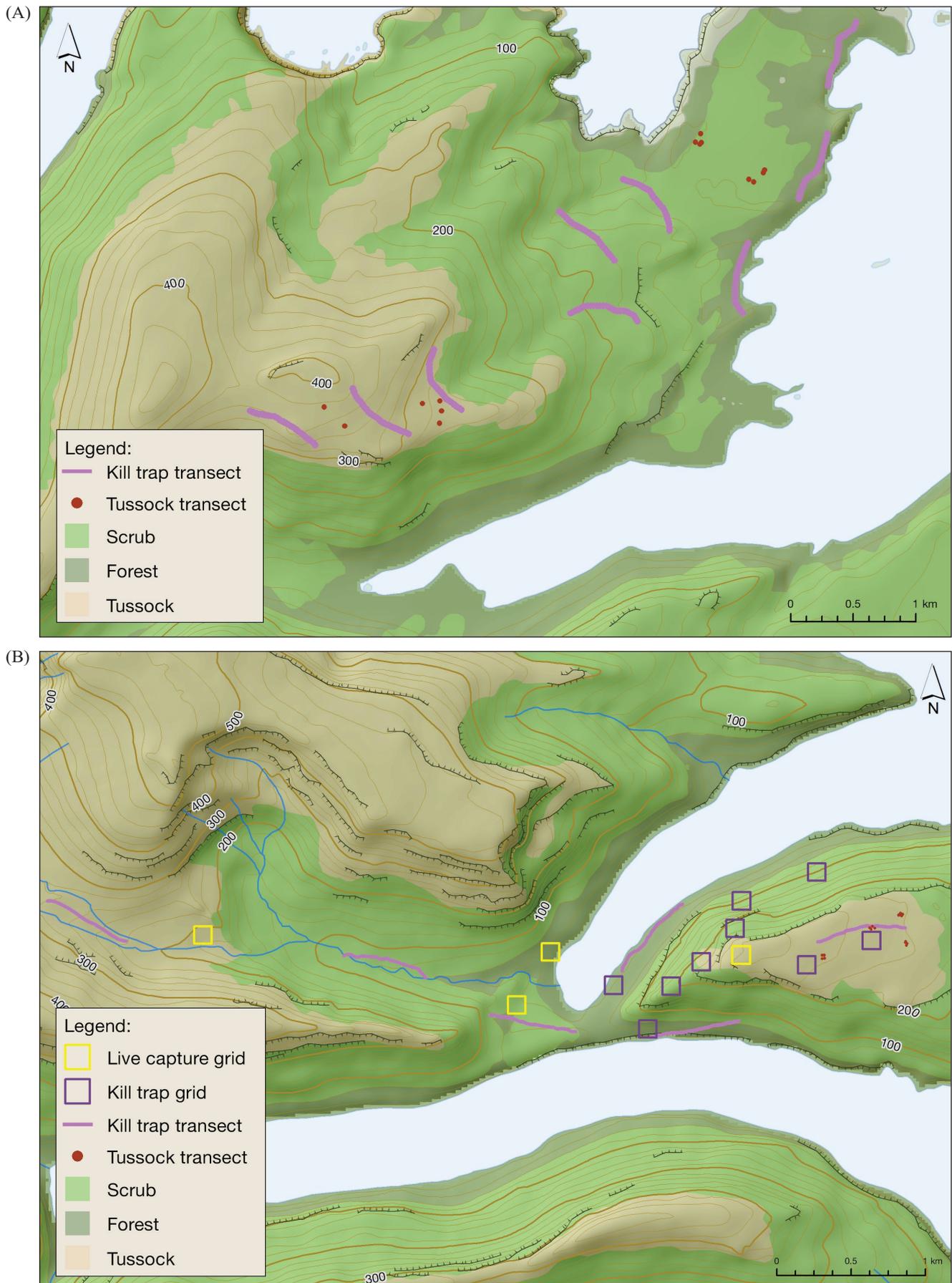
Transects were 625 m long and 500 m apart, each with 25 Victor® snap kill traps (Woodstream Corporation Inc., Lancaster, USA) spaced 25 m apart. Traps were baited with peanut butter and secured under small tunnels to reduce risks to non-target species and to prevent precipitation setting traps off. Traps were opened when deployed and were checked and cleared daily for 3 days. All killed mice were necropsied and their sex, reproductive status and weight (nearest 1 g) were recorded. Females with perforate vaginas and males with scrotal testes were considered to be reproductively active. Typically, mice weighing ≥17 g were in reproductive condition and considered adult; lighter mice were considered juvenile. To investigate patterns of cohort recruitment, the distribution of weights within trips was examined for patterns of bimodality.



**Figure 1.** Subantarctic Auckland Island relative to mainland New Zealand showing study sites at Deas Head and Falla Peninsula during house mouse population studies in 2019–2020.

**Table 1.** Number of live or kill trapping grids (G) or transects (T) in each habitat by site during each sampling event in 2019–2020 at Auckland Island. Shading indicates when traps were not operated.

Site	Habitat	Feb 2019		Aug 2019		Nov 2019		Jan 2020		Mar 2020		Aug 2020	
		Live	Kill										
Deas Head	Forest		3T		3T		3T				2T		
	Scrub		3T		3T		3T				2T		
	Tussock		3T		3T		3T				2T		
Smith Harbour	Forest	1G	5G	1G				1G				1G	2T
	Scrub	1G	2G	1G				1G				1G	2T
	Tussock	2G	2G	1G				1G				2G	2T



**Figure 2.** Study sites at Auckland Island: (A) Deas Head and (B) Smith Harbour, including Falla Peninsula, showing positions of live and kill trapping grids and transects set for house mice.  $n = 25$  traps per transect;  $n = 49$  traps per grid ( $7 \times 7$ ; only perimeters shown).

### Smith Harbour

In February 2019, 13 grids of 49 traps, 10 m apart in seven rows and seven columns (following Russell 2012), were established around the Smith Harbour area, including Falla Peninsula, spread across the three habitat types (Fig. 2; Table 1). Four of these grids had Longworth traps (Penlon Ltd, Oxfordshire, UK), baited with carrot and peanut butter and provided with dry polyester wool bedding (Table 1). The four grids included two tussock grids because the first tussock grid (west of Falla Peninsula) caught no mice. These traps were operated for 7 nights, checked daily, with mice euthanised by cervical dislocation on the final 2 nights. At the same time, nine grids of Victor® snap kill traps were baited with peanut butter and secured under small tunnels as above. These traps were checked and cleared daily for 7 days. In August 2019 and January 2020 three live capture grids were repeated (all on Falla Peninsula; Table 1).

In August 2020 all four live capture grids were repeated. Additionally, in August 2020 six kill trap transects were operated, two in each of the three habitat types (Fig. 1; Table 1). Transects were set 500 m away from other transects or grids. Each transect was 625 m long, with 25 Victor® snap kill traps spaced 25 m apart. Traps were baited with peanut butter and secured under small tunnels as above. Traps were opened when deployed and checked and cleared daily for 3 days.

All killed mice were necropsied and measurements recorded for sex, reproductive status and weight (nearest 1 g).

### Tussock monitoring

Flowering intensity (inflorescences per tussock) is a predictor of seed production (Kelly et al. 2008). Sixteen permanent transects (20–25 m) were established in tussock habitat at each of Falla Peninsula and Deas Head in February 2019 (Fig. 2). Transect locations and bearings were randomized within areas dominated by *C. antarctica*. The first 20 individual tussocks where the centre of the tussock canopy was located within 1 m either side of the transect line were sampled and tagged for repeat measures. Following Kelly et al. (2008), the number of flowering culms on each plant was counted, along with the basal diameter and a visual estimation of the percent of the basal area carrying live tillers. Tussocks were re-sampled following the same protocol at Falla Peninsula in January 2020 ( $n = 16$  transects) and Deas Head in March 2020 ( $n = 6$  transects).

### Density estimation

The density of mice was estimated using spatially explicit capture–recapture models with half-normal detection curves, fitted with the package secr in R (Borchers & Efford 2008). Known deaths (in kill traps, at the end of live trap sessions, and accidental deaths in live traps) were incorporated into these models. Previous modelling of mouse density at Smith Harbour using only the January 2019 live and kill-trap grid data showed that habitat, trap type (Longworth or Victor®), sex and body weight did not affect density estimates (Russell et al. 2019). Therefore, full likelihood models were used to determine how capture probability ( $g_0$ ) and the scale of movement ( $\sigma$ ) varied with temporal covariates only, while density was always allowed to fully vary by grid and transect set in each habitat to give unique estimates (Efford 2004).

Because no recaptures could occur in kill traps, only data from the live trapping grids at Smith Harbour could be used to estimate  $\sigma$  and its covariates. Therefore, the first model set

estimated  $\sigma$ , and how it varied with year (2019 or 2020) and season (warm or cold) either individually or additively, or with month (3 levels: Jan, Feb, Aug), trip (4 levels: Feb 2019, Aug 2019, Jan 2020, Aug 2020) or session (12 levels: the individual grids), all while  $g_0$  was held constant (7 models). This process determined the most important temporal covariate for  $\sigma$ .

The second model set investigated how  $g_0$  varied with the same temporal covariates in the live trapping grids at Smith Harbour, while  $\sigma$  was held constant (7 models). This process determined the most important temporal covariates for  $g_0$ , on the same dataset used to do so for  $\sigma$ .

Because capture probability can be estimated from both live and kill traps, data from both Smith Harbour and Deas Head could be used to estimate  $g_0$  and its covariates. Therefore, the third model set investigated how  $g_0$  varied with the temporal covariates for the combined live trapping grids and kill trapping grids and transects at both Smith Harbour and Deas Head, while  $\sigma$  was held constant (7 models). This process determined the most important temporal covariates for  $g_0$ , on the entire trapping dataset, to contrast with the most important temporal covariates identified solely from live trapping data.

A model combining the most supported covariates of capture probability and scale of movement from the first three model set comparisons was then constructed. An additional fourth model set based on this most supported temporal model was then used to investigate if there were additional consistent effects of site (Smith Harbour or Deas Head) on capture probability and/or density (4 models), with density still fully varying with grid or transect. All models in each model set (see Appendix S1) were compared using Akaike's information criterion (AIC) and model weights (Burnham & Anderson 2002).

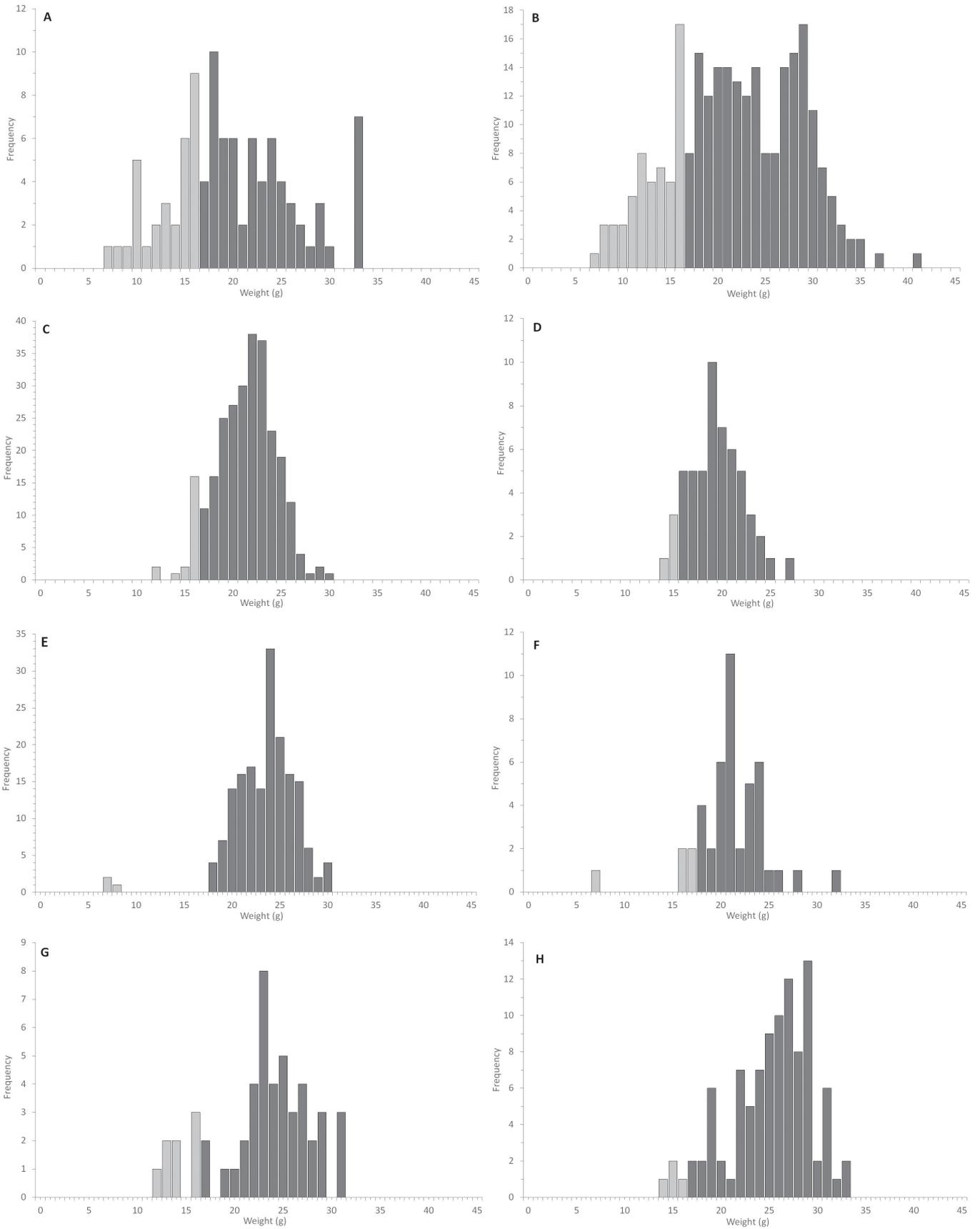
This final most supported model that emerged was then used to provide estimates of mouse density at all trapping grids and transects on Auckland Island. However, due to the inferential limitations from extrapolating live to kill trap data across sites, the density estimates should be interpreted only as indicating patterns in space and time rather than as absolute estimates at each grid.

The trapping rate (mice per 100 corrected trap nights (CTN)) was used as an index of mouse abundance. CTN was calculated by removing half a trap night for every night a trap was unavailable due to a mouse capture or to non-target interference (Nelson & Clark 1973). CTN was calculated for each grid and transect set in each habitat and averaged for each habitat at each sampling event.

## Results

In total, 1116 mice were caught over 2 years. At Smith Harbour, 201 mice were caught in the live-trap grids (Feb 2019, Aug 2019, Jan 2020, Aug 2020), 232 in the kill-trap grids (Feb 2019) and 98 in the kill-trap transects (Aug 2020). At Deas Head 585 mice were caught in the kill-trap transects (Feb 2019, Aug 2019, Nov 2019, Mar 2020). The bimodal distribution of body weights in November 2019 indicated mice were beginning to breed with the recruitment of a new cohort (Fig. 3E), followed by a second cohort in Jan 2020 (Fig. 3F), which by March 2020 (and also by Feb 2019 the previous year) was mostly fully incorporated into the adult population (Figs. 3G, A, B). In August, breeding was largely absent with only a few large juveniles in the population (Figs. 3C, D, H).

For the 201 mice caught in the Smiths Harbour live-trap



**Figure 3.** Frequency distribution of body weights (g) of adult (dark grey) and juvenile (light grey) house mice captured on Auckland Island during Feb 2019–Aug 2020. (A) Deas Head Feb 2019; (B) Smith Harbour Feb 2019; (C) Deas Head Aug 2019; (D) Smith Harbour Aug 2019; (E) Deas Head Nov 2019; (F) Smith Harbour Jan 2020; (G) Deas Head Mar 2020; (H) Smith Harbour Aug 2020.

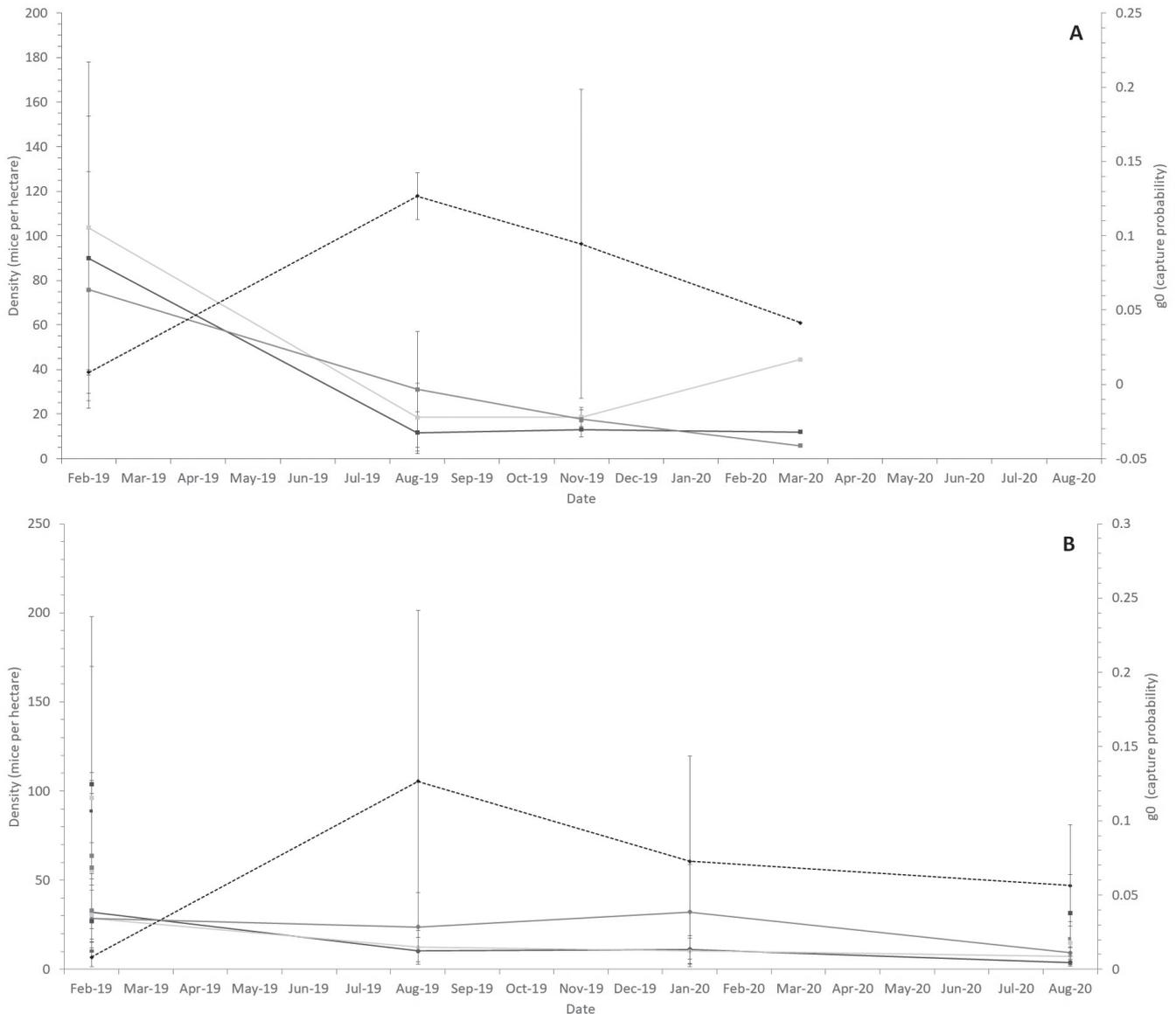
grids, there were an additional 264 recaptures that allowed estimation of mouse scale of movement ( $\sigma$ ) (first model set). Mouse scale of movement was best estimated by a model where it varied with session i.e. unique to every grid (model weight = 1). However, because session-specific  $\sigma$  models cannot be extrapolated to kill-traps where no recaptures occurred, we removed this model from further consideration. The next best fitting model was the null model with constant  $\sigma$  (model weight = 0.52), although there was some evidence that  $\sigma$  varied with trip (model weight = 0.24) or season (model weight = 0.21).

The same data from live-trap grids were used to determine covariates of mouse capture probability (second model set). Mouse capture probability was best estimated by a model where it varied with session i.e. unique to every grid (model weight = 0.56) or trip (model weight = 0.44). Repeating this analysis on the entire dataset of live trapping grids and kill trapping grids and transects at both Smith Harbour and Deas Head (third model set), mouse capture probability was best

estimated by a model where it varied with trip (model weight = 0.96).

Together these results suggested the best model to fit to the entire mouse trapping data set was one where capture probability varied with trip and scale of movement was constant. This model remained the best fitting model (model weight = 0.38) although there was also evidence of site effects on capture probability (model weight = 0.33) and density (model weight = 0.19).

Mouse density was highest during the first summer (Feb 2019 Smith Harbour: 28–104 mice  $\text{ha}^{-1}$  and Deas Head: 76–104 mice  $\text{ha}^{-1}$ ) and declined thereafter at both sites (Fig. 4; Aug 2019 Deas Head: 12–31 mice  $\text{ha}^{-1}$  and Smith Harbour: 12–24 mice  $\text{ha}^{-1}$ ). Density remained low the following summer (Nov 2019 Deas Head: 13–19 mice  $\text{ha}^{-1}$ ; Mar 2020 Deas Head: 6–45 mice  $\text{ha}^{-1}$ ; Jan 2020 Smith Harbour: 10–32 mice  $\text{ha}^{-1}$ ) and remained at a similar level through the subsequent winter (Fig. 4; Aug 2020 Smith Harbour 4–31 mice  $\text{ha}^{-1}$ ). Capture



**Figure 4.** Density ( $\pm$ SE) of house mice estimated at each trapping grid and by broad habitat classification: coastal forest (dark grey), scrub (light grey) and tussock (mid-grey) and capture probability ( $g_0$ ; dashed line) over time at two sites, Deas Head (A) and Smith Harbour (B), sampled under different trapping regimes: kill traps (squares) and live traps (circles).

probability ( $g_0$ ) was highest when density was first observed to decline, i.e. in the first winter (Fig. 4). The mouse abundance index (mice 100 per CTN) followed a similar pattern to capture probability (Fig. 5). Overall, mouse density, capture probability and abundance indices trends were consistent between sites, though all measures were generally higher at Deas Head than Smith Harbour (Figs. 4 & 5). Trends were also largely consistent between habitat types, except for the first trip at Smith Harbour, where mouse density in kill-trap grids varied across habitats as much as 28–104 mice  $ha^{-1}$  (Fig. 4).

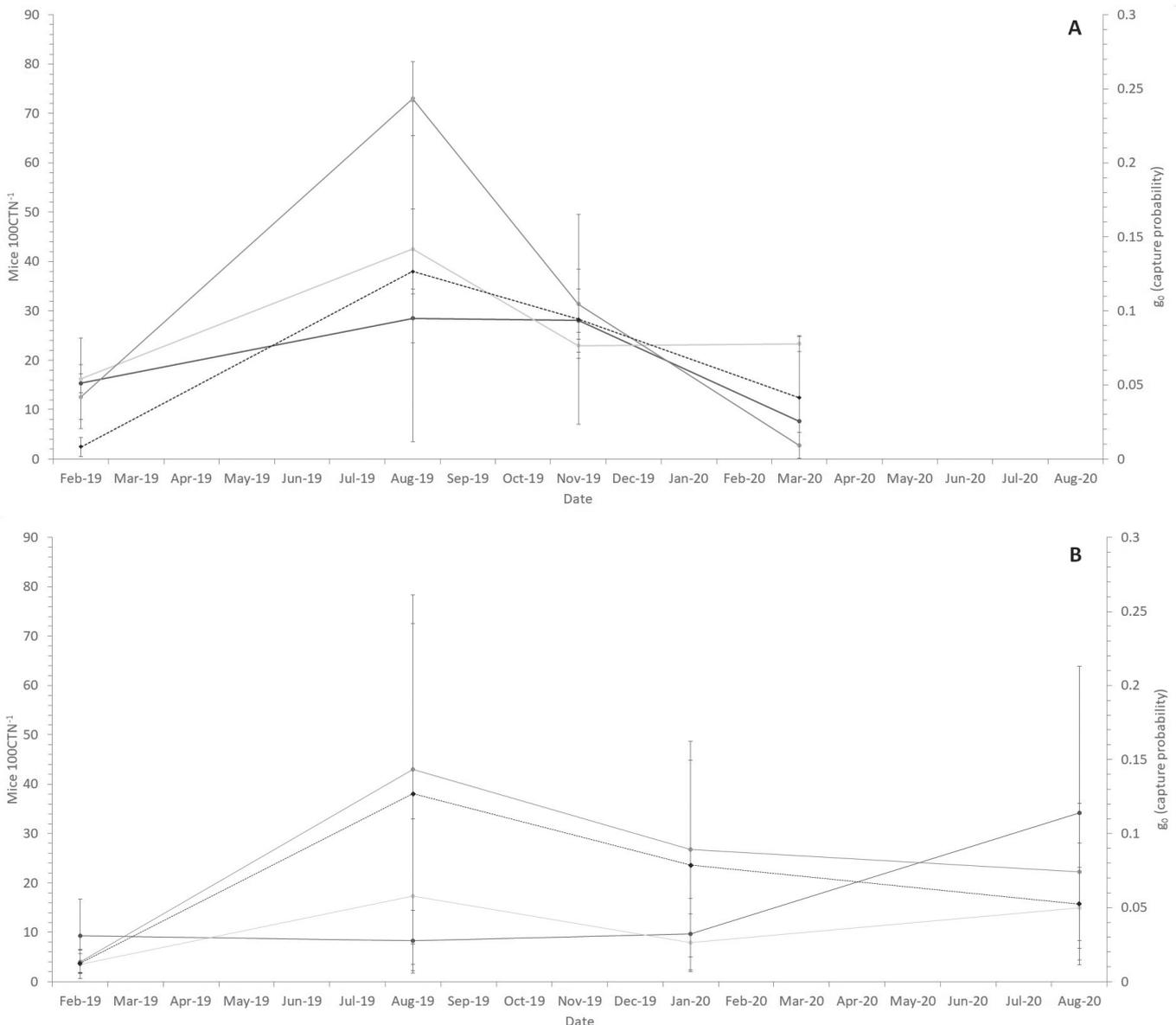
Very little bycatch or trap interference occurred at either site. At Deas Head, three tomtits (*Petroica macrocephala marrineri*) were caught in traps, while pigs interfered with traps on 27 occasions and sealions did so on three occasions. At Smith Harbour, pigs interfered with traps on only three occasions (pigs were being locally eradicated at the start of our study and allowed to repopulate thereafter; Cox et al.

2022) and three bellbirds (*Anthornis melanura*) were caught in snap traps.

Snow tussock *C. antarctica* was flowering heavily in summer 2019 with >92% of plants having at least one flowering culm (mean  $\pm$  SEM = 22.7  $\pm$  1.7 culms per flowering plant). This result contrasted with summer 2020, when <1% of plants were flowering, with an average of 4.5  $\pm$  0.9 culms per flowering plant.

## Discussion

The population trends of mice on Auckland Island broadly follow the irruptive patterns of house mice in relation to masting in other temperate New Zealand systems (Ruscoe et al. 2001; Wilson & Lee 2010). However, both population densities and the timing of the increase on cool-temperate



**Figure 5.** An index of abundance (mean captures per 100 corrected trap nights  $\pm$  SE) of house mice at each site by broad habitat classification: coastal forest (dark grey), scrub (light grey) and tussock (mid grey) and capture probability ( $g_0 \pm$  SE; dashed line) over time at two sites, Deas Head (A) and Smith Harbour (B).

Auckland Island differed from warm-temperate New Zealand systems. Following an autumn seed fall in warm-temperate New Zealand systems, mouse population peaks are generally seen during the following winter-spring and sometimes as late as summer (Wilson & Lee 2010). On Auckland Island the highest mouse population densities were observed immediately during the first sampling period (Feb), following several months of high food availability. The seeding of tussock on cool-temperate subantarctic Auckland Island (Nov–Feb) is earlier and briefer than New Zealand South Island tussock (Edgar & Connor 2000) and beech (*Fuscospora* spp.) forests (Jan–Apr; Wilson & Lee 2010). This timing likely accounts for the earlier population increase on Auckland Island than in warm temperate systems. The mouse population density on Auckland Island had declined by the winter following the mast event and remained at a similar level during the subsequent summer and winter. This result is further supported by evidence from Russell et al. (2018), where very low mouse population density was measured at the same Deas Head site outside of a mast year. Although the highest density recorded was in the first summer of monitoring, given the separated sampling periods it is possible the true population peak was not sampled. Furthermore, we only studied two sites, and found variation in density even among sites of seemingly identical habitat, and starkly different from densities at the same Deas Head sites outside of mast seeding (Russell et al. 2018). Accordingly, we only have a coarse view of mouse population dynamics on a very large island.

Estimated mouse densities on Auckland Island around the population peak were lower than reported from summer studies on subantarctic Gough Island (R. Cuthbert unpubl. data in Rexer-Huber et al. 2013) and Marion Island (Matthewson et al. 1994), though comparable to Antipodes Island (Russell 2012). Winter density on Auckland Island was comparable to winter densities on other Southern Ocean islands, including Steeple Jason Island (Rexer-Huber et al. 2013) and Marion Island (Matthewson et al. 1994; Ferreira et al. 2006), which are all at much higher latitudes than Gough Island (R. Cuthbert unpubl. data in Rexer-Huber et al. 2013). However, comparison of densities among studies, and even of densities within our study, must be undertaken with caution, due to use of different capture devices, and assumptions made when estimating density. Mice were or are the sole extant introduced mammal on Steeple Jason, Antipodes, Gough and Marion Islands, in contrast to Auckland Island where they co-exist with pigs and cats. Evidence from Marion Island before and after the eradication of cats shows that abiotic factors, not predation pressure, drive mouse density there (Aarde & Jackson 2007). While cats undoubtedly prey on mice on Auckland Island (Harper 2010a), the apparent large demographic responses of mice to masting mean it is unlikely cat predation has any significant effect on mouse populations on Auckland Island and the bottom-up role of resource availability drives population responses.

As in warm-temperate New Zealand beech (King 1983; Fitzgerald et al. 2004) and tussock (Wilson & Lee 2010) systems, the mouse population increase on Auckland Island is likely the result of high juvenile survival and subsequent recruitment as a result of increased food supply. However, our study appears not to have captured the initial breeding pulse in response to the mast event. The first sampling event occurred toward the end of seeding and the wide distribution of weights shows juveniles were recruiting to the population and adults were still breeding at this time. The similar distribution

of weights from both winters studied suggests that breeding largely ceases through this season, regardless of if a mast event occurred the previous summer. The bi-modal distribution of weights from summers shows that multiple seasonal breeding pulses occurs during this time, and outside of a mast event breeding slows again by late summer. Very few mice breed over winter on Southern Ocean islands, including Auckland Island (Matthewson et al. 1994; Avenant & Smith 2004; Harper 2010b; Rexer-Huber et al. 2013; Elliott et al. 2015). Studies on other Southern Ocean islands have occurred in the absence of mast seeding events and this is the first study to report that winter breeding is not elevated in a mouse population on a Southern Ocean island following a mast event the previous summer. In contrast elevated winter breeding following tussock or tree masting the previous summer is typical in warm temperate New Zealand island systems (King 1983; Wilson & Lee 2010).

Social factors when mouse density is high may influence how likely individuals are to interact with traps. Throughout the study the capture probability of mice ( $g_0$ ) was generally higher when density was lower. This finding likely reflects that the resource limitation that has constrained density at these times probably also motivates mice to interact with traps more. Furthermore, when population density is high mouse home ranges are smaller, meaning they will have fewer opportunities to interact with traps (Efford et al. 2016).

Abundance indices such as corrected captures are often used as a proxy for population trends (Fitzgerald et al. 2004 and references therein). In this study, capture probability and an abundance index (captures per 100 CTN) followed similar trends and likely reflected patterns in resource availability. Abundance index values for the winter following masting are considerably higher than Harper (2010b) reported for the same trapping regime on Auckland Island, also assumed to be following a mast event. Harper's (2010b) study was undertaken earlier in winter (June–July c.f. late August here) and it is possible tussock seeds and invertebrates remained more plentiful during this period, leading to lower catch rates. Data from Antipodes Island show that although density was similar between trapping periods in summer 2011 (60–147 mice  $ha^{-1}$ ) and winter 2013 (74–104 mice  $ha^{-1}$ ), abundance indices were lower in winter 2013 (21.7–22.9 mice  $100CTN^{-1}$ ) than summer 2011 (28.7–33.1 mice  $100CTN^{-1}$ ) (Russell 2012; Elliott et al. 2015). Likewise, mice abundance indices declined during winter (Jun–Aug 2005) on Macquarie Island, though mouse densities for this period are lacking (K. Springer unpubl. data). Reduced captures in winter is surprising, because resource availability presumably declines in winter on Southern Ocean islands (fewer seabirds present, invertebrate activity and vegetation growth reduced) compared to summer, and as a result capture probability should be higher. Together these results highlight that index of abundance measures, such as CTN, do not reliably indicate actual population density, and at least on Auckland Island more strongly reflect capture probability. Site and species-specific links between target species abundance and index measures need to be established and studies that assume a linear relationship between indices and population density may be misleading (Ruscoe et al. 2001).

This study shows the bait uptake trial undertaken on Auckland Island in summer 2019 (Russell et al. 2019) coincided with the highest estimates of mouse density and lowest capture probability during a mast seeding event. Thus the successful bait uptake by 99% of mice in that trial remains particularly encouraging for the feasibility of eradicating mice from Auckland Island at any stage of a tussock mast

seeding cycle (Russell et al. 2019). This outcome is critical because the timing of mouse baiting on Auckland Island will be influenced by logistical and practical considerations that require determinations months if not years in advance of any eradication.

Our work on mouse population trends fills an important gap in knowledge for Southern Ocean islands, particularly where tussock mast seeding occurs and is a consideration in eradication planning. Increasingly, larger or more complex eradications are being proposed that will require adaptation of best practice (e.g. Horn et al. 2022; Livingstone et al. 2022; Oyston et al. 2022). We recognize the interaction of pests, food resources and the environment mean there is likely no ‘one size fits all’ solution for these complex projects. Accordingly, site or species-specific investigations can be built into operational planning to reduce uncertainty and risk where departure from best practice is required.

## Author contributions

RLS, FSC, SRH and JCR designed the study and undertook fieldwork; RLS and JCR analysed the data; and RLS and JCR wrote the manuscript with input from FSC and SRH.

## Acknowledgements

Thanks to Paul Jacques, Rose Hanley-Nickolls, Lindsay Chan, Kirsten Rogers, Veronika Frank, Mark Le Lievre, Micaela Kirby-Crowe, Richard Griffiths, Will Bannister, Sasha Roselli, Graham Parker, Kalinka Rexer-Huber, Brent Barret, Jenny Rickett, Penny Pascoe, Iain Graham, Caitlyn Thomas, Rose Collen, Rowan Hindmarsh-Walls and James Ware for assistance with field work. Many thanks to Steve Kafka and the crew of MY Evohe, MV Awesome, MV Searanger and HMNZS Canterbury for safe transport to and from the island. Thanks to the Murihiku district team and Kaitiaki Roopu for their support of the work. Performed under University of Auckland animal ethics R2095. Thanks to a reviewer for feedback on the manuscript.

## References

- Aarde R, Jackson T 2007. Food, reproduction and survival of mice on sub-Antarctic Marion Island. *Polar Biology* 30: 503–511.
- Angel A, Wanless RM, Cooper J 2009. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions* 11: 1743–1754.
- Auffray J-C, Vanlerberghe F, Britton-Davidian J 1990. The house mouse progression in Eurasia: a palaeontological and archaeozoological approach. *Biological Journal of the Linnean Society* 41: 13–25.
- Avenant NL, Smith VR 2004. Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). *Polar Biology* 27: 99–111.
- Bogdziewicz M, Zwolak R, Crone EE 2016. How do vertebrates respond to mast seeding? *Oikos* 125: 300–307.
- Borchers D, Efford M 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64: 377–385.
- Boursot P, Din W, Anand R, Darviche D, Dod B, Von Deimling F, Talwar GP, Bonhomme F 1996. Origin and radiation of the house mouse: mitochondrial DNA phylogeny. *Journal of Evolutionary Biology* 9: 391–415.
- Broome KG, Golding C, Brown K, Horn SR, Corson P, Bell P 2017. Mouse eradication using aerial baiting: current agreed best practice used in New Zealand (Version 1.0). New Zealand Department of Conservation internal document DOC-3034281. Wellington, New Zealand, Department of Conservation Te Papa Atawhai. 23 p.
- Burnham KP, Anderson DR 2002. Model selection and inference a practical information-theoretic approach. 2nd edn. Springer-Verlag. 488 p.
- Courchamp F, Chauis J-L, Pascal M 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78: 347–383.
- Cox FS, Horn SR, Bannister WM, Macdonald NL 2022. A local eradication pilot study of methods for feral pig eradication on Auckland Island. *New Zealand Journal of Ecology* 46: 3490.
- Dilley BJ, Schoombie S, Schoombie J, Ryan PG 2015. “Scalping” of albatross fledglings by introduced mice spreads rapidly at Marion Island. *Antarctic Science* 28: 73–80.
- Edgar E, Connor HE 2000. *Flora of New Zealand Volume V: Gramineae (Grasses): Vol. V.* Manaaki Whenua Press.
- Efford M 2004. Density estimation in live-trapping studies. *Oikos* 106: 598–610.
- Efford MG, Dawson DK, Jhala YV, Qureshi Q 2016. Density-dependent home-range size revealed by spatially explicit capture-recapture. *Ecography* 39: 676–688.
- Elliott GP, Greene TC, Nathan HW, Russell JC 2015. Winter bait uptake trials and related field work on Antipodes Island in preparation for mouse (*Mus musculus*) eradication. DOC Research and Development Series 345. Wellington, New Zealand, Department of Conservation. 34 p.
- Ferreira SM, VanAarde RJ, Wassenaar TD 2006. Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island. *Polar Biology* 30: 83–94.
- Fitzgerald B, Efford M, Karl B 2004. Breeding of house mice and mast seeding of southern beeches in the Orongorongo Valley, New Zealand. *New Zealand Journal of Ecology* 31: 167–184.
- Fraser A 2020. The climate and weather of the Auckland Islands. Unpublished Report - prepared for the Department of Conservation Te Papa Atawhai. Invercargill, New Zealand, 45°S Weather Service Ltd. 40 p.
- Glen AS, Sagar RL, Brav-Cubitt T, Jacques PM 2022. Monitoring and detection of feral cats on Auckland Island. *New Zealand Journal of Ecology* 46: 3494.
- Harper GA 2010a. Diet of feral cats on subantarctic Auckland Island. *New Zealand Journal of Ecology* 34: 259–261.
- Harper GA 2010b. Habitat use by mice during winter on subantarctic Auckland Island. *New Zealand Journal of Ecology* 34: 262–264.
- Holmes ND, Spatz DR, Oppel S, Tershy B, Croll DA, Keitt B, Genovesi P, Burfield IJ, Will DJ, Bond AL, Wegmann A, Aguirre-Muñoz A, Raine AF, Knapp CR, Hung CH, Wingate D, Hagen E, Méndez-Sánchez F, Rocamora G, Yuan HW, Fric J, Millett J, Russell JC, Liske-Clark J, Vidal E, Jourdan H, Campbell K, Springer K, Swinnerton K, Gibbons-Decherong L, Langrand O, de Brooke ML, McMinn M, Bunbury N, Oliveira N, Sposimo P, Gerald

- P, McClelland P, Hodum P, Ryan PG, Borroto-Páez R, Pierce R, Griffiths R, Fisher RN, Wanless R, Pasachnik SA, Cranwell S, Micol T, Butchart SHM 2019. Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLoS One* 14: e0212128.
- Horn SR, Greene T, Elliott GP 2019. Eradication of mice from Antipodes Island, New Zealand. In: Veitch CR, Clout MN, Martin AR, Russell JC, West CJ eds. *Island invasives: scaling up to meet the challenge*. Proceedings of the International Conference on Island Invasives 2017. Occasional Paper of the IUCN Species Survival Commission 62. Gland, Switzerland, IUCN. Pp. 131–137.
- Horn SR, Sagar RL, Frank VK, Cox FS, Jacques PM, Ware J, Hanley-Nickolls R, Leask EP, MacDonald NL, Kirby-Crowe MS, Le Lievre ME, Broome KG 2022. The next frontier: assessing the feasibility of eradicating mammalian pests from Auckland Island. *New Zealand Journal of Ecology* 46: 3500.
- Houghton M, Terauds A, Merritt D, Driessen M, Shaw J 2019. The impacts of non-native species on the invertebrates of Southern Ocean Islands. *Journal of Insect Conservation* 23: 435–452.
- Kelly D, Turnbull MH, Pharis RP, Sarfati MS 2008. Mast seeding, predator satiation, and temperature cues in *Chionochloa* (Poaceae). *Population Ecology* 50: 343–355.
- King CM 1983. The relationships between beech (*Nothofagus* Sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *The Journal of Animal Ecology* 52: 141.
- Livingstone J, Horn SR, Broome KG, Sagar RL 2022. How low can you sow? House mouse eradication on Motuareronui/Adele Island. *New Zealand Journal of Ecology* 46: 3498.
- Matthewson DC, Van Aarde RJ, Skinner JD 1994. Population biology of house mice (*Mus musculus*) on sub-Antarctic Marion Island. *South African Journal of Zoology* 29: 99–106.
- Nelson L, Clark FW 1973. Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy* 54: 295–298.
- Oyston ED, Horn SR, Murphy EC 2022. A trial on Te Pākeka/Maud Island for reducing aerial baiting sow-rates for the eradication of house mice. *New Zealand Journal of Ecology* 46: 3499.
- Rodriguez-Recio M, Sagar RL, Chan L, Cox FS, Jacques PM 2022. Spatial ecology meets eradication of feral cats on Auckland Island. *New Zealand Journal of Ecology* 46: 3493.
- Rexer-Huber K, Parker GC, Reeves M, Stanworth AJ, Cuthbert RJ 2013. Winter ecology of house mice and the prospects for their eradication from Steeple Jason (Falkland Islands). *Polar Biology* 36: 1791–1797.
- Ruscoe WA, Goldsmith R, Choquenot D 2001. A comparison of population estimates and abundance indices for house mice inhabiting beech forests in New Zealand. *Wildlife Research* 28: 173–178.
- Russell JC 2012. Spatio-temporal patterns of introduced mice and invertebrates on Antipodes Island. *Polar Biology* 35: 1187–1195.
- Russell JC, Broome KG 2016. Fifty years of rodent eradications in New Zealand: another decade of advances. *New Zealand Journal of Ecology* 40: 197–204.
- Russell JC, Horn SR, Harper GA, McClelland P 2018. Survey of introduced mammals and invertebrates on Auckland Island, March–April 2015. DOC Research and Development Series 352. Wellington, New Zealand, Department of Conservation. 17 p.
- Russell JC, Griffiths R, Bannister WM, Le Lievre ME, Cox FS, Horn SR 2019. Mouse bait uptake and availability trials on Falla Peninsula, Auckland Island. DOC Research and Development Series 363. Wellington, New Zealand, Department of Conservation. 11 p.
- Russell JC, Peace JE, Houghton MJ, Bury SJ, Bodey TW 2020. Systematic prey preference by introduced mice exhausts the ecosystem on Antipodes Island. *Biological Invasions* 22: 1265–1278.
- Russell JC, Horn SR, Broome KG 2022. Restoration of New Zealand subantarctic islands. *New Zealand Journal of Ecology* 46: 3482.
- Singleton GR, Brown PR, Pech RP, Jacob J, Mutze GJ, Krebs CJ 2005. One hundred years of eruptions of house mice in Australia - a natural biological curio. *Biological Journal of the Linnean Society* 84: 617–627.
- Spatz DR, Holmes ND, Will DJ, Hein S, Carter ZT, Fewster RM, Keitt B, Genovesi P, Samaniego A, Croll DA, Tershy BR, Russell JC 2022. The global contribution of invasive vertebrate eradication as a key island restoration tool. *Scientific Reports* 12: 13391.
- Springer K 2016. Methodology and challenges of a complex multi-species eradication in the sub-Antarctic and immediate effects of invasive species removal. *New Zealand Journal of Ecology* 40: 273–278.
- Veale AJ, Russell JC, King CM 2018. The genomic ancestry, landscape genetics and invasion history of introduced mice in New Zealand. *Royal Society Open Science* 5: 170879.
- Wanless RM, Ratcliffe N, Angel A, Bowie BC, Cita K, Hilton GM, Kritzing P, Ryan PG, Slabber M 2012. Predation of Atlantic Petrel chicks by house mice on Gough Island. *Animal Conservation* 15: 472–479.
- Wilson DJ, Lee WG 2010. Primary and secondary resource pulses in an alpine ecosystem: snow tussock grass (*Chionochloa* spp.) flowering and house mouse (*Mus musculus*) populations in New Zealand. *Wildlife Research* 37: 89–103.
- World Heritage Convention 1998. New Zealand sub-antarctic islands. United Nations Educational, Scientific and Cultural Organization. <http://whc.unesco.org/en/list/877/>

Editorial board member: George Perry

Received 21 April 2021; accepted 10 August 2022

## Supplementary Material

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Model sets for estimating density, capture probability ( $g_0$ ) and scale of movement ( $\sigma$ ) using spatially explicit capture-recapture.

The New Zealand Journal of Ecology provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.