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Population dynamics of house mice without mammalian predators and competitors

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Abstract: Mesopredator and competitor release can lead to population increases of invasive house mice (*Mus musculus*) after larger introduced mammals are controlled or eradicated. In New Zealand, mammal-resistant fences have enabled multi-species mammal eradications in order to protect indigenous species. When house mice are the only mammals remaining in these biodiversity sanctuaries, they may reach a high population density, with potential consequences for their indigenous prey. We studied mouse populations in the absence of other mammals for 5 years at mammal-resistant fenced forest sites at Maungatautari, Waikato. We used spatially explicit capture–recapture (SECR) to estimate mouse population density quarterly in two independently fenced sites, with contrasting levels of mouse management that were switched half-way through the study. In the absence of mouse control, mouse population density reached 30–46 ha^{-1} at one site each year after summer breeding, and 23 ha^{-1} at the other site. Mouse tracking rates in inked footprint tunnels were positively related to numbers of mice captured in each session, but not significantly to mouse density. The highest mouse densities were similar to estimates in New Zealand forest and alpine ecosystems after mass seeding (masting) events, but lower than estimates in another sanctuary and on some islands lacking larger terrestrial mammals. We suggest that in the absence of competition and predation from other mammals, food limitation may have prevented mouse populations from attaining very high densities in this mainland forest location.

Keywords: biodiversity sanctuary; competitor release; food limitation; invasive species; island; mesopredator release; *Mus musculus*; New Zealand; population density; SECR

Introduction

Species introduced into an ecosystem are often managed by eradication or population reduction to protect indigenous flora and fauna (Myers et al. 2000; Courchamp et al. 2003; Smith et al. 2010). However, trophic or competitive interactions can cause non-target introduced species to respond numerically to these control programmes, inflicting additional or greater ecosystem damage (Zavaleta et al 2001; Courchamp et al. 2003). Removing a top predator can lead to increased abundance of smaller predators (mesopredator release; Soulé et al. 1988; Courchamp et al. 1999; Ritchie et al. 2012). Removing a competing species can lead to increased abundance of its inferior competitor, which benefits from reduced interference and/or greater access to shared resources (competitor release; Caut et al. 2007; Trewby et al. 2008; Ruscoe et al. 2011). Both of these ecological release mechanisms can result in increased predation on indigenous taxa in the managed ecosystem (e.g. Rayner et al. 2007; Ritchie & Johnson 2009; Norbury et al. 2013).

House mice (*Mus musculus*) are among the world's most prevalent invasive mammals, owing to their potentially rapid population growth, flexible omnivorous diet, and long association with humans (Bronson 1979; Auffray et al. 1990; Ruscoe & Murphy 2005). Wild, non-commensal house mice are usually uncommon and inconspicuous in ecosystems where larger mammals are present (Bronson 1979; Angel et al. 2009; Harper & Cabrera 2010). However, they become abundant on oceanic islands and the New Zealand mainland when their mammalian competitors and predators are absent or removed (e.g. Innes et al. 1995; Choquenot & Ruscoe 2000; Jones et al. 2003; Witmer et al. 2007). In turn, predation by abundant mice on oceanic islands lacking other terrestrial mammals can significantly affect indigenous biota (Angel et al. 2009; Simberloff 2009). Mice also become numerous when food is plentiful (King 1983; Wilson & Lee 2010). Extensive mouse plagues in the wheat-growing areas of south-eastern Australia follow rainfall and other possible prerequisites, such as reduced rates of predation and disease (Pech et al. 1999; Krebs et al. 2004; Singleton et al. 2007).

As these examples suggest, multiple factors may combine to limit mouse population size. Norbury et al. (2013) demonstrated mouse population growth after experimental predator removal, but only where grass seed provided ample food for mice. Other studies have attributed mouse population increases to relaxation of interference and/or exploitative competition after removal of ship rats (*Rattus rattus*) (e.g. Brown et al. 1996; Witmer et al. 2007; Harper & Cabrera 2010; Ruscoe et al. 2011) or Norway rats (*Rattus norvegicus*) (Ji et al. 1999; cf. Tennyson & Taylor 1999). However, as both ship rats (McQueen & Lawrence 2008; Bridgman et al. 2013) and Norway rats (O'Boyle 1974) may also prey on mice, competitor and mesopredator release combined may have caused these mouse population increases.

In New Zealand, house mice are the smallest of the mammalian species introduced since humans arrived in c. 1280 AD, when bats were the only terrestrial mammals (King 2005; Wilmshurst et al. 2008). Mice had reached New Zealand on European ships by the 1820s (King 2016) and they are now present in most habitats throughout the country (Ruscoe & Murphy 2005). They prey primarily on seeds and invertebrates (Ruscoe & Murphy 2005), and sometimes also on lizards

(Newman 1994; Norbury et al. 2014) and the eggs and chicks of birds (Cuthbert & Hilton 2004; O'Donnell et al. 2017). Biodiversity sanctuaries have been established to protect native species on the New Zealand mainland by removing invasive mammals and excluding them with mammal-resistant fences (Innes et al. 2012). In addition to ship rats and Norway rats (discussed above), other mammals that are removed and excluded are predators of mice – cat (*Felis catus*) and the mustelids stoat (*Mustela erminea*), ferret (*Mustela putorius*) and weasel (*Mustela nivalis*) – and a potential competitor (hedgehog, *Erinaceus europaeus*). Removal of most species is usually successful, but mice either survive eradication attempts or subsequently reinvade (Innes et al. 2012) through small openings in or under the fence. Hence, these mice occupy environments with reduced predation and interspecific competition.

We studied the population dynamics of house mice for 5 years in the absence of other introduced mammals within mammal-resistant fences at a forested biodiversity sanctuary. We compared mouse population densities between two independently fenced sites, with contrasting levels of mouse management that were switched half-way through the study. We also assessed mouse demographic parameters (body condition, body size and reproductive condition) that could be affected by differences between sites and management treatments, and could help to explain density variation.

Methods

Study site

Maungatautari is an extinct andesitic volcano in the Waikato region, North Island, New Zealand. Lowland forest on Maungatautari below 600 m a.s.l. is dominated by tawa (*Beilschmiedia tawa*) with frequent mangeao (*Litsea calicaris*) and kāmahi (*Weinmannia racemosa*), and above 600 m by tawa and kāmahi, with scattered rimu (*Dacrydium cupressinum*) and tāwari (*Ixerba brexioides*) (Nicholls 1967).

The Maungatautari Ecological Island Trust (MEIT) enclosed Maungatautari with a mammal-resistant fence (Day & MacGibbon 2007) in August 2006 (Table 1). Most pest mammals were eradicated inside the fence in a prolonged operation that started in November 2006 (Speedy et al. 2007). Mice became very scarce but were probably never eradicated entirely from the reserve. Since February 2012 no further mouse control was attempted, and mice became increasingly abundant.

An independent mammal-resistant fence was built in 2006 around a 17 ha private forest block, covenanted to the Queen Elizabeth II National Trust and separated from the main Maungatautari reserve by a vehicle track. Mammals were eradicated from this block during the next 2 years, but mice apparently reinvaded and had become abundant again by 2011 (Table 1).

Our study began in April 2011 at two independently fenced sites (Fig. 1) with contrasting levels of mouse management. Our Q block study site, the 17 ha independently fenced private forest block described above, had no mouse control and high mouse density at the beginning of the study. Our 24 ha M block (100 m north of Q block), received ongoing mouse control as part of the main fenced 3400 ha reserve; mice were undetectable there when this study began. Each site resembles a peninsula of forest partially surrounded by farmland (Fig. 1).

Midway through our study, in August 2013, we switched mouse management treatments between the two blocks, to assess experimentally how mouse abundance levels affect indigenous biota, in a related study (Watts et al. 2017). MEIT eradicated mice from Q block, and in M block the remaining mouse control was withdrawn (Table 1) and the mouse population was allowed to increase. Mouse population density in Q block was high from April 2011 to August 2013, and low from November 2013 to February 2016. We refer to these block–phase combinations as QH and QL, respectively. In contrast, mouse density in M block was low and then higher (ML and MH) in the same respective periods.

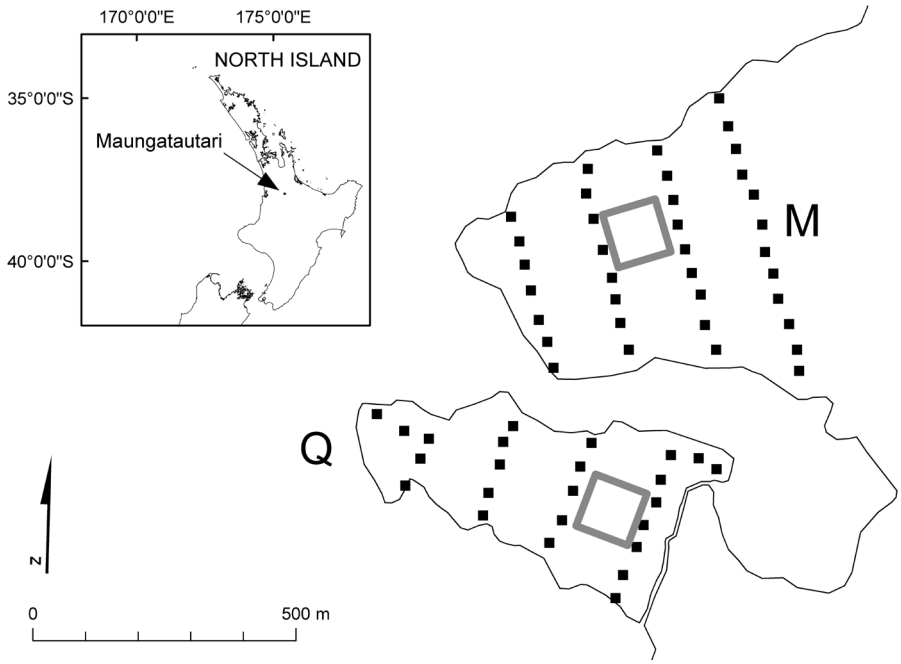

Figure 1. Locations of trapping grids (large grey squares) and tracking tunnels (small black squares) in our Q and M block study sites on the northwest edge of Maungatautari, central Waikato, North Island, New Zealand. Thin black lines indicate mammal-resistant fences surrounding 17 ha Q block and the 3400 ha area that includes M block.

Table 1. Mouse control and initial detections on two study blocks at Maungatautari, from 2006 to 2016. Q is a 17 ha privately owned forest block, enclosed by an independent mammal-resistant fence and adjacent to the Maungatautari biodiversity sanctuary. M is a 24 ha block within the main 3400 ha fenced reserve. MEIT refers to the Maungatautari Ecological Island Trust. The duration of the present study was April 2011 to February 2016.

Block	Date	Mouse control and detection
Q	2006	Independent mammal-proof fence completed
	2006–2008	Mammalian pests except mice eradicated and not detected since
	May 2008	Mice eradicated with hand-spread toxic brodifacoum baits
	August 2009	Mice detected with inked footprint tracking tunnels
	April and August 2011	Mice tracked > 90% of tunnels (our results)
	August 2013	Treatment switch: mice eradicated
	May 2014	Mice detected in tunnels placed by MEIT. Fence damage found and repaired, and additional toxin broadcast.
	February 2015	Mice detected in two tunnels (our results; 8% tracking rate), but none trapped and none detected in subsequent sessions
M	August 2006	Mammal-resistant fence completed around Maungatautari biodiversity sanctuary
	November 2006	Eradication of mammals within the fence began. Mice probably never entirely eradicated.
	April and August 2011	No mice captured in traps or detected with inked footprint tracking tunnels in M block (our results)
	November 2011	First mouse trapped and mice detected with tracking tunnels in M block (our results)
	February 2012	Mouse control ceased at Maungatautari
	August 2006 to August 2013	Some rat trapping and poisoning continued near M block in order to kill invading ship rats
	August 2013	Treatment switch: poison use ceased (only rat traps used when responding to fence breaches)
	November 2014	Toxin laid for 2 days at one fence-post south of M block, owing to an operational error
	January 2016	Toxin laid for 2 days along the fence north of M block, owing to an operational error

Estimating mouse population density with spatially explicit capture–recapture

We estimated the population density of mice (mice per hectare) with spatially explicit capture–recapture (SECR; Efford 2004; Borchers & Efford 2008). Mice were caught in live-capture Longworth traps (NHBS, Totnes, Devon, UK). A grid of 64 traps (8 rows × 8 columns, with 15 m spacing) was placed in each block (Fig. 1). Traps were baited with peanut butter and rolled oats and contained polyester fibre filling for warmth, and were checked daily in five-day capture sessions in April 2011, August 2011, and then quarterly until February 2016. Captured mice were marked with numbered metal ear-tags and released after weight, head and body length (HBL) and reproductive status were recorded. For reproductive status of females we recorded either perforate or imperforate vagina and obvious pregnancy (distended abdomen). For males we recorded testes position as scrotal or abdominal.

Mouse population density estimates were obtained by analysing the data from each quarterly capture session in each block, using the secr package (Efford 2016) in program R (R Core Team 2016). We analysed combined data from all capture sessions (20 per block) with > 1 captures (M block: 17 sessions, first three sessions had ≤ 1 capture; Q block: 10 sessions, last 10 sessions had 0 captures). Combining data from multiple sessions (White 2005) allowed us to estimate density for sessions with few (but > 1) captures (i.e. many of the M block sessions).

We assumed that populations were closed during each 5-day trapping session (i.e. that no reproduction, mortality, immigration or emigration occurred during these periods). Spatial detection models, representing daily capture probability as a half-normal function (g) of the distance between a trap and the centre of a mouse's home range (Efford 2004), were fitted to the capture data by maximising the conditional likelihood (Borchers & Efford 2008). Two spatial detection parameters were estimated: g_0, the probability of capture (per day) in a trap located at the centre of the home range (i.e. at 0 m), and spatial scale σ (m). Mouse home range centres were assumed to be distributed randomly and independently in space. Mouse density in each capture session was calculated as a derived parameter; i.e. the number of captures in that session n divided by the effective sampling area a, computed from the g_0 and σ estimates (Borchers & Efford 2008).

We selected a set of alternative spatial detection models of variation in the two spatial detection parameters, g_0 and σ, after comparing the performance of alternative models during the first 2 years of the study on the basis of AIC_c (Burnham & Anderson 2002). We then compared alternative models fitted to all the data from 2011 to 2016, also on the basis of AIC_c. In the alternative model set (Table 2), g_0 and σ were either both constant (i.e. the null model) or were both additive functions of the block–phase combination (QH, ML, MH; QL had no captures and was excluded) and/or season (spring, summer, autumn, winter). Models in which g_0 was also an additive function of mouse weight and/or a behavioural response to capture were also tested. Two alternative types of behavioural responses to capture (Efford 2016) were considered: b, a permanent response in which an animal's probability of capture increased (a trap-happy response) or decreased (trap-shy) after its first capture; and bk, a trap-specific permanent response in which an animal became trap-happy or trap-shy in relation to a particular trap (Royle et al. 2011; Wilson et al. 2017).

Table 2. Additive SECR models of variation in spatial detection parameters g_0 and σ, fitted to capture data of house mice at Maungatautari. At most one behavioural response to capture, *b* or *bk*, was included in a model. The variables block–phase and season were always applied to both g_0 and σ simultaneously, but *b*, *bk* and mouse weight (at first capture) were applied to g_0 only. For discrete variables, the number of levels is given in parentheses.

Parameter	Variable	Discrete (levels) or continuous	Values
g_0	—	—	— (i.e. g_0 constant)
	block–phase	discrete (3)	QH, ML, MH
	season	discrete (4)	spring, summer, autumn, winter
	b	discrete (2)	0 (first capture) or 1 (captured previously)
	bk	discrete (2)	0 (first capture) or 1 (captured previously)
	mouse weight	continuous	4–28.5 g
σ	—	—	— (i.e. σ constant)
	block–phase	discrete (3)	QH, ML, MH
	season	discrete (4)	spring, summer, autumn, winter

Comparing mouse demographics between block–phases QH and ML, and QH and MH

We used mixed-effects models to compare demographic parameters of the mouse population in block–phase QH (the reference block–phase) with populations in ML and MH. Explanatory variables were block–phase (QH, ML, MH), season, their interaction (where it could be fitted), and additional model-specific variables, as described below. Sampling date was fitted as a random effect (with 20 levels, up to 10 for each block–phase), to account for (1) annual variation and (2) sampling multiple mice from the same block on each date. Models were fitted in the lme4 package (Bates et al. 2015) in R version 3.3.0 (R Core Team 2016).

An explanatory variable was considered statistically significant ($P < 0.05$) if the 95% highest posterior density interval (HPDI) of its model coefficient excluded zero. We used HPDIs because the usual method of estimating 95% confidence intervals (CI) is not straightforward for mixed-effects models. Instead, we generated 1000 estimates of each fixed-effect coefficient, representing a sample of its posterior distribution (i.e. its distribution given our data), and calculated HPDIs from these samples. We used the sim function in the arm package for R (Gelman et al. 2016) and the mcmc and HPDinterval functions in the coda package (Plummer et al. 2006). We also calculated 99% and 90% HPDIs in order to quantify P-values relative to the respective probability levels of 0.01 and 0.1.

Relationship between body weight and head and body length

We fitted a linear mixed-effects model with the response variable $\log_e$(body mass) and the additional explanatory variables $\log_e$(HBL), sex, and their interactions with block–phase (QH, ML and MH, as above). The $\log_e$–$\log_e$ relationship between body mass and HBL is an indicator of small-mammal body condition (Krebs & Singleton 1993). The explanatory variable block–phase and its interaction with $\log_e$(HBL) represent differences between block–phases (QH vs ML and QH vs MH) in the intercept and slope, respectively, of the relationship between $\log_e$(body mass) and $\log_e$(HBL).

Size structure as a proxy for age structure

We assigned each mouse to one of three size classes, as a proxy for age classes, based on the 25% and 75% quantiles of body weight of all captures combined: small (≤ 13.5 g), medium (> 13.5 g and ≤ 19.5 g), and large (> 19.5 g). We used two generalised linear mixed-effects models for binomial data (with $\log_e$ link functions) to investigate these multinomial data (Dobson & Barnett 2008). We tested for block–phase differences in the probabilities that a captured small or medium mouse would be small (model 1), and a captured large or medium mouse would be large (model 2). The response variable in each case was the number of successes (captures of small mice for model 1 or large mice for model 2) given the number of independent trials (combined captures of medium mice and either small [model 1] or large [model 2] mice) on each capture date. An interaction between block–phase and season could not be fitted for model 1 because no small mice were captured in ML in winter.

Reproductive condition

We used two further generalised linear mixed-effects models for binomial data to test for block–phase differences in the probabilities that captured females (model 3) and males (model 4) would be in reproductive condition (perforate vagina or pregnant for females, scrotal testes for males). The response variable in each case was the number of successes (captures of reproductive mice) given the number of independent trials (all captures) on each capture date. Interactions between block–phase and season could not be fitted because no mice were in reproductive condition in ML in winter.

Indexing mouse abundance with inked footprint tracking tunnels

We calculated relative indices of mouse abundance in both blocks with footprint tracking based on Department of Conservation standard procedures (Gillies & Williams 2013). We placed inked tracking tunnels (24 in Q block and 36 in M block) in lines 150 m apart, each with 5–12 tunnels 50 m apart. Because of our small block sizes, this layout differed from the recommended lines ≥ 200 m apart, each with 10 tunnels. Tunnels were baited with peanut butter and checked the next morning, 1–7 days prior to each quarterly 5-day capture session (above). Tracking rate (percentage of tunnels tracked by mice) was calculated for each occasion on each block.

Relationship between mouse tracking, density, and number of mice captured

Although footprint-tracking tunnels are commonly used to index rodent abundance in New Zealand, the relationship between tracking rates and mouse population density has not often been assessed. We therefore tested whether the mouse-tracking rate (the percentage of inked tunnels tracked by mice) was related to mouse population density (n = 17 sessions on M block and 10 sessions on Q block). Because we lacked density estimates from 13 trapping sessions with ≤ 1 mouse capture (see above), we also tested whether tracking rate was related to the number of unique mice captured in each session (n = 20 sessions on each block). We used separate linear models (function gls in package nlme in R; Pinheiro et al. 2017) for these two predictor variables. Block (M or Q) and its interaction with density or number of mice captured were additional predictor variables.

The models included a correlation structure (an autoregressive process of order 1) to account for temporal autocorrelation; i.e. non-independence of sequential measures (Pinheiro & Bates 2000) within a block. The response variable was the percentage of tunnels tracked by mice in each block on each sampling date. Percentages of tunnels tracked were transformed before analysis to normalise the distribution of residuals, by expressing them as proportions and calculating the arcsine of their square-roots (Crawley 2002). Density estimates were $\log_e$-transformed and numbers of mice captured were square-root-transformed before analysis, to linearise relationships and limit the effects of very high values.

Comparing forest structure and composition between the two blocks

The presence of vascular plant species in each of six fixed-height tiers (< 30 cm, 0.3–2 m, 2–5 m, 5–12 m, 12–20 m, and > 20 m) was recorded at 36 circular 1 m^2 plots in each of the Q and M blocks in April 2015 (QL, MH). Each plot was placed 5 m from a tracking tunnel (Fig. 1), measured at right angles on alternating sides of each line of tunnels. In the Q block (with only 24 tracking tunnels), 12 additional plots were placed 10 m from other plots, on the opposite side of the line, to achieve equal numbers of plots per block.

Bray-Curtis distance was used to quantify the dissimilarity of each plot from the total species list. PERMANOVA analyses (Anderson 2001) of these Bray-Curtis dissimilarities were then used to test for differences in vegetation composition between the Q and M blocks. Separate comparisons were done for all height tiers combined and for each separate tier. In addition, to compare graphically the species composition of plots (all tiers combined) between the two blocks, a detrended correspondence analysis (DCA) ordination (Hill & Gauch 1980) was used. These analyses were done with the adonis and decorana functions in the R package vegan (Oksanen et al. 2017).

Results

Mouse population density

In the best-supported model of mouse population density (i.e. the model with the lowest AIC_c), both g_0 (probability of capture of an animal in a trap at the centre of its home range) and σ (home range width) varied as a function of mouse block–phase (QH, ML or MH) and season. In this model, g_0 also varied according to mouse weight and a behavioural response to capture *b*. Other models received much less support ($\Delta AIC_c \geq 11.1$; Table 3).

In QH, density was estimated at 9–46 mice per hectare in different capture sessions, until mice were eradicated there in August 2013. In ML, the first mouse was caught in our third capture session in November 2011, and density could not be estimated until February 2012. Thereafter, densities in MH increased up to 23 ha^{-1} but never attained the highest point density estimates in QH (30–46 ha^{-1}). Only the first QH density estimate differed significantly from the highest MH estimate, on the basis of non-overlapping 95% CIs (QH: 44 ha^{-1}, 95% CI 34–57 in April 2011; M: 23 ha^{-1}, 17–32 in February 2015). After February 2015, mouse density declined steadily in MH to 10 ha^{-1} at the end of the study, 1 year later.

Contrasting seasonal population trajectories between block–phases

Mouse population density fluctuated seasonally in both blocks. Most years were characterised by relatively high summer or autumn (February and May) densities, winter declines (May–August), and gradual increases during the next breeding season (August–February; Fig. 2). There were two notable deviations from this pattern. First, in winter–spring August to November 2012, density declined in QH, but increased in ML (Fig. 2). Second, in spring–summer November 2015 to February 2016, density decreased in MH, continuing a gradual population decline observed in MH throughout the final year of our study.

Spatial detection parameters

The estimated probability of capturing a mouse in a trap at the centre of its home range (parameter g_0) was similar in QH and MH but lower in ML (Fig. 3). Because we did not model the shapes or utilisation of individual mouse home ranges, our analysis does not yield realistic home-range size estimates. However, the average home range of mice (based on parameter σ) was smaller in QH and MH than in ML, indicated by a more

Table 3. Best-supported models of spatial detection parameters for house mice captured in Longworth traps in two forest blocks at Maungatautari. ΔAIC_c gives the increase in AIC_c relative to the best-supported model. Only the top three models are shown; all others had $\Delta AIC_c > 44$ and weight 0. Models are defined in Table 2.

Model		Parameters	Log(Likelihood)	ΔAIC_c	Model weight
g_0	σ				
block–phase + season + *b* + weight	block–phase + season	14	–6294.4	0	1.0
block–phase + *b* + weight	block–phase	8	–6306.1	11.1	0.0
season + *b* + weight	season	10	–6310.8	24.6	0.0

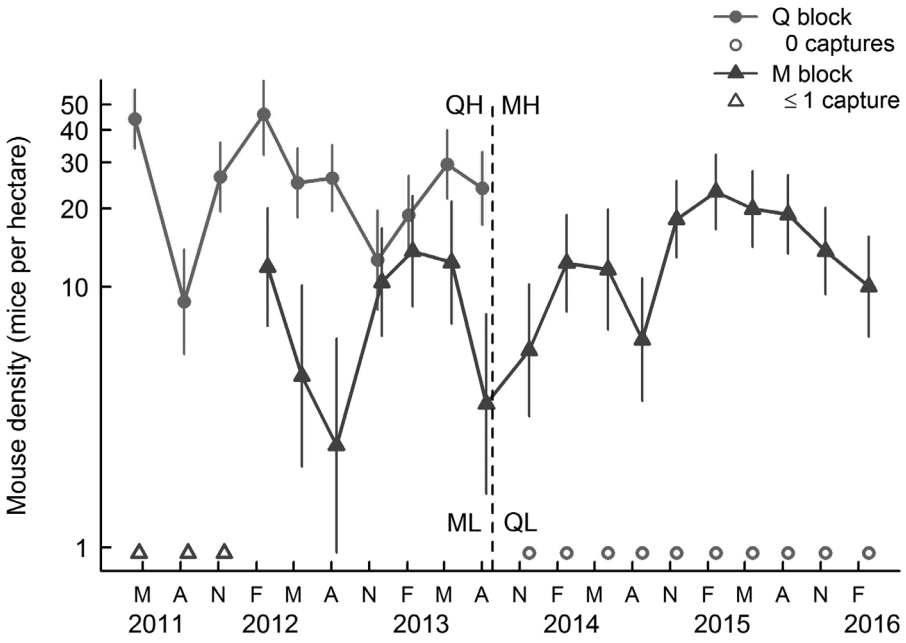

Figure 2. Estimated house mouse population density in Q and M blocks within Maungatautari Ecological Island. Vertical lines show 95% confidence intervals. Open symbols show trapping sessions when density could not be estimated; i.e. when ≤ 1 mice were captured in M block (triangles) early in the study, and when 0 mice were captured in Q block (circles) after eradication. Timing of the treatment switch in August 2013 is shown with a dashed vertical line. Density is plotted on a logarithmic scale. QH, QL, MH, and ML indicate block–phase combinations, i.e. mouse densities (High, Low) that switched between blocks (Q, M) at or around August 2013.

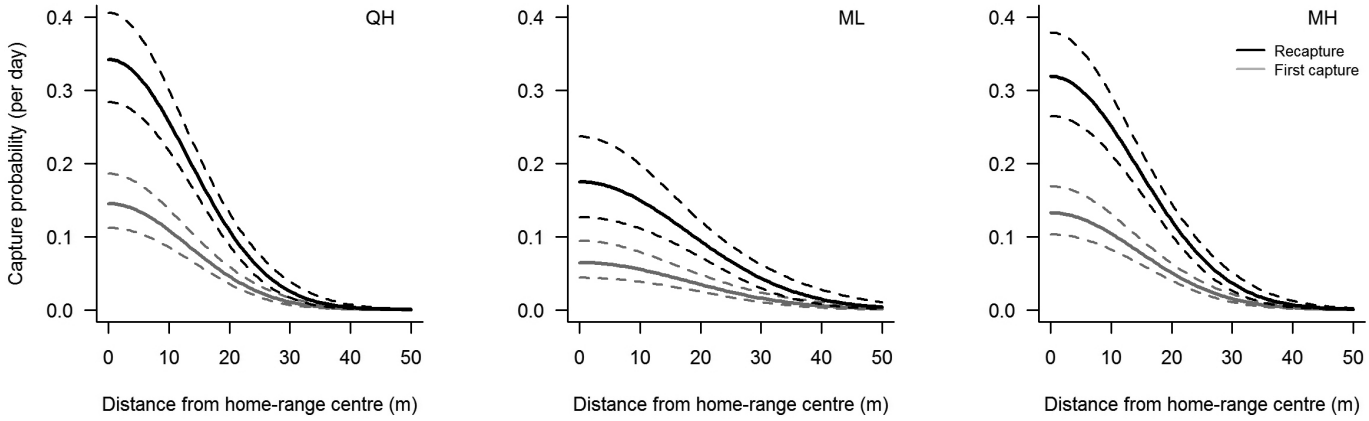

Figure 3. Modelled daily probability of capturing a mouse in a live-capture trap as a function of distance of the trap from the centre of the home range, in block–phases QH, ML and MH (i.e. block Q at high mouse population density and block M at low and high densities). Recapture probability refers to recapture during the same quarterly capture session. Capture probabilities for a 20 g mouse in spring are shown. Dashed lines indicate 95% confidence intervals.

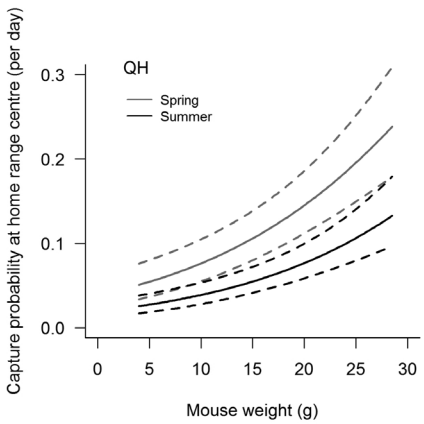

Figure 4. Modelled daily probability of capturing a mouse in a live-capture trap in the centre of its home range as a function of mouse weight. Capture probabilities for the first capture of a mouse in QH (block Q at high mouse population density) in spring and summer are shown. Dashed lines indicate 95% confidence intervals.

rapid decline in capture probability at increasing distance from the home range centre (Fig. 3). Capture probability increased for mice recaptured during the same capture session (a trap-happy response; Fig. 3), and was related positively to mouse weight (Fig. 4). Capture probability was highest in spring and lowest in summer (Fig. 4), and home range width was greater in summer than in other seasons.

Comparing mouse demographics between blocks QH and ML, and QH and MH

Relationship between body weight and HBL

There was no significant difference between QH and ML or QH and MH mouse block–phases in either the intercept or slope of the relationship between $\log_e$(body mass) and $\log_e$(HBL) ($P > 0.1$). Body mass was positively related to HBL (both variables on the $\log_e$ scale; $P < 0.01$). No other explanatory variables were statistically significant ($P > 0.05$).

Size structure as a proxy for age structure

On average, 34% of large and medium mice captured in QH were large (> 19.5 g), compared with 21% in MH (Table 4). The effect was more pronounced for males (39% vs 18%) than for females (30% vs 23%). The estimated probability that a captured large or medium mouse would be large was higher in QH than in MH ($P < 0.05$) but did not differ significantly between QH and ML. The probability of catching a large mouse was also higher in summer than in autumn (the reference level for testing seasonal differences; $P < 0.05$).

There were no significant block–phase differences in the probability that a small or medium mouse would be small (≤ 13.5 g; $P > 0.1$). The probability of catching a small mouse was higher in autumn than in spring ($P < 0.01$), summer ($P < 0.05$) and winter ($P < 0.01$).

Reproductive condition

The probability of a female mouse being reproductive was higher in spring ($P < 0.05$) and summer ($P < 0.01$; Table 4) than in autumn, but there were no significant seasonal effects for males ($P > 0.1$). There were no significant block–phase differences in the probability that captures of either sex would be in reproductive condition (QH vs ML $0.05 < P < 0.1$ for both sexes; QH vs MH ($P > 0.1$).

Relationship between mouse tracking, density, and number of mice captured

Mouse tracking rates (percentage of inked footprint-tracking tunnels tracked by mice) ranged from 0 to 100%, and 0 to 69 individual mice were captured in each session (Fig. 5). The percentage of tunnels with mouse tracks was positively related to the number of mice captured in each session (n = 20 sessions on each block; $t_{36} = 6.1$, $P < 0.0001$) (both variables transformed; see Methods), but was not significantly related to mouse density (n = 17 sessions on M block and 10 sessions on Q block, $t_{23} = 1.5$, $P = 0.16$). In both models, tracking rates did not differ significantly between the Q and M blocks, and interactions between block and mouse captures or density were not significant ($t_{36 \text{ or } 23} < 1.5$; $P > 0.16$). The estimated temporal autocorrelation parameters indicating the average correlation between consecutive tracking rate observations in each block were $\varphi = 0.12$ (95% CI −0.28, 0.48; numbers of captures model) and $\varphi = 0.53$ (0.004, 0.823; density model).

The correlation between the two predictor variables, density and number of captures, was $r = 0.95$ for the 27 sessions for which we had mouse population density estimates (i.e. sessions with > 1 capture). Mouse tracking rates were consistently low (0–11%) in the 13 sessions without density estimates (sessions with ≤ 1 capture).

Comparing forest structure and composition between the two blocks

There were no significant differences in vegetation composition between Q and M blocks, in all tiers combined ($F_{1,70} = 0.85$, $P = 0.63$) or in individual tiers (for 12–20 m, $F_{1,34} = 1.7$, $P = 0.08$; for other tiers, $F_{1,44–55} < 1.4$, $P > 0.19$). DCA plot ordination also did not identify any difference in vegetation composition between the two blocks.

Table 4. Numbers of mice in each of three size classes, and numbers of reproductive (Repr) and non-reproductive (NR) males and females captured in Q and M blocks before the experimental treatment switch (block–phases QH and ML) and in M block after the treatment switch (MH) at Maungatautari from 2011 to 2016. Animals with missing weight data are omitted from the size class columns, and juveniles with unidentified sex are omitted from the reproductive status columns. The table is sorted by block–phase and season in order to show seasonal variations.

Block–phase	Season	Date	Size class			Females		Males	
			Small	Medium	Large	Repr	NR	Repr	NR
QH	Autumn	12-Apr-2011	34	26	9	6	23	1	29
QH	Autumn	11-May-2012	9	19	13	2	13	12	5
QH	Autumn	9-May-2013	20	21	6	4	18	9	10
QH	Winter	9-Aug-2011	3	11	4	0	6	1	8
QH	Winter	3-Aug-2012	7	29	13	4	24	1	20
QH	Winter	2-Aug-2013	10	26	5	1	22	0	18
QH	Spring	5-Nov-2011	6	22	18	10	12	15	9
QH	Spring	21-Nov-2012	3	16	2	0	9	1	11
QH	Summer	18-Feb-2012	18	16	14	8	15	2	11
QH	Summer	4-Feb-2013	4	12	19	12	9	6	5
ML	Autumn	11-May-2012	5	1	0	0	3	0	0
ML	Autumn	9-May-2013	8	5	3	0	9	1	4
ML	Winter	3-Aug-2012	0	4	0	0	2	0	2
ML	Winter	2-Aug-2013	0	5	1	0	0	0	6
ML	Spring	21-Nov-2012	3	10	6	3	6	1	6
ML	Summer	18-Feb-2012	7	7	2	1	6	0	9
ML	Summer	4-Feb-2013	5	8	7	3	10	2	5
MH	Autumn	24-May-2014	11	4	0	1	6	1	7
MH	Autumn	10-May-2015	15	21	1	1	13	4	18
MH	Winter	15-Aug-2014	5	7	1	0	5	4	4
MH	Winter	4-Aug-2015	7	26	2	2	16	5	11
MH	Spring	14-Nov-2013	1	7	3	1	6	2	2
MH	Spring	6-Nov-2014	4	28	3	8	12	3	11
MH	Spring	3-Nov-2015	3	18	6	0	13	6	8
MH	Summer	13-Feb-2014	7	11	4	7	5	4	6
MH	Summer	10-Feb-2015	9	24	6	4	14	14	5
MH	Summer	16-Feb-2016	3	4	13	5	8	4	0

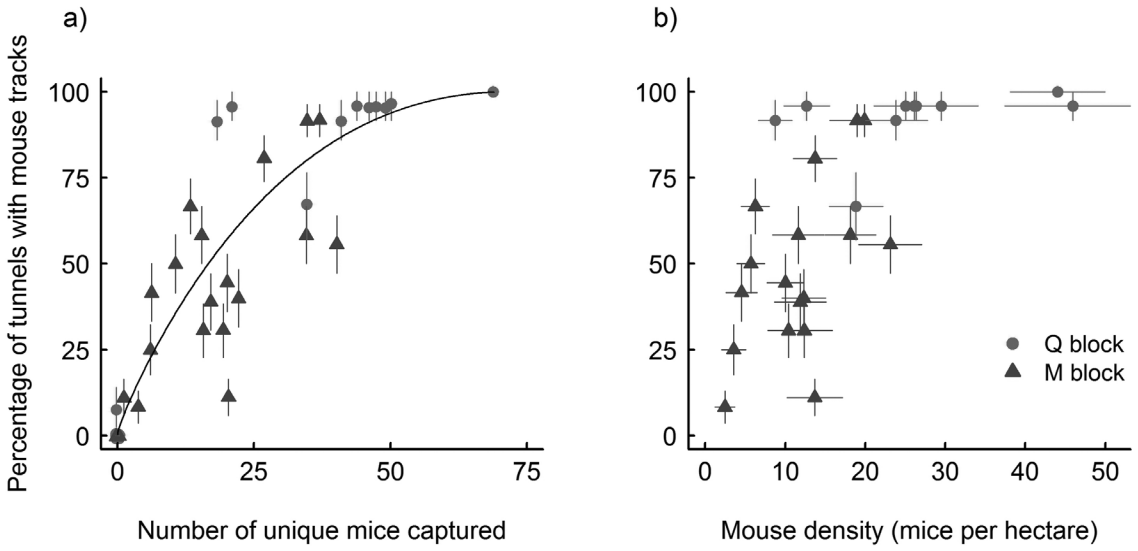

Figure 5. Mean mouse tracking rate (percentage of inked tracking tunnels tracked by mice) at the start of each trapping session, plotted as a function of (a) number of mice captured in each session and (b) estimated mouse population density in Q block and M block. The fitted curve in (a) corresponds to a model combining both blocks, as block effects were not significant. Points in (a) have been shifted by a small random amount (jittered) to reduce over-plotting. Error bars indicate standard errors.

Discussion

Mouse population density and potential limiting factors

In forests with other invasive mammals present on the New Zealand mainland, house mouse population density is usually < 6 mice ha^{-1} (Murphy 1989; Ruscoe et al. 2001, 2004; Wilson & Lee 2010), but can reach 50 ha^{-1} after periodic high seedfall (masting) in forests dominated by masting tree species (Ruscoe et al. 2001, 2004). The highest mouse population density estimate from the New Zealand mainland is 160 ha^{-1} in small forest patches surrounded by pasture and rank grass in the partially fenced biodiversity sanctuary on Tawharanui Peninsula, Auckland Region (Goldwater 2007; Goldwater et al. 2012). On New Zealand islands lacking other terrestrial mammals density estimates are intermediate: up to 20 ha^{-1} in forest (Murphy 1989; MacKay et al. 2011), 70 ha^{-1} in grassland–shrubland (Pickard 1984; Efford 2004), and 150 ha^{-1} in subantarctic grassland (Russell 2012). In other ecosystems worldwide, house mouse population densities have been estimated as high as 150–500 ha^{-1} on subantarctic islands lacking other terrestrial mammals (Parker et al. 2016; McClelland et al. 2018), in fluctuating populations in arid Peru (Arana et al. 2006), and during outbreaks on grassy California hillsides (Pearson 1963). Mouse plagues in Australian wheat-growing areas can exceed 2000 ha^{-1} (Singleton et al. 2007). Hence, the maximum mouse densities we recorded at Maungatautari (up to 46 ha^{-1} in Q block and 23 ha^{-1} in M block) were high when compared with most New Zealand forest ecosystems, but not with other ecosystems globally.

Although predation and interspecific competition by larger mammals may limit mouse population size (e.g. Innes et al. 1995; Witmer et al. 2007; Ruscoe et al. 2011), food supply or other factors (Pech et al. 1999; Singleton et al. 2007) may become limiting as mouse density increases following mesopredator and competitive release. This effect has been demonstrated in grassland/shrubland habitat, where lack of mouse population growth after experimental removal of higher-order mammalian predators was attributed to food limitation in locations with scarce grass seed (Norbury et al. 2013). At Maungatautari, depletion of the supply of invertebrates as food for mice when mice became abundant in our study blocks (Watts et al. 2017) may in turn have limited the mouse populations and prevented their continued increase to densities higher than those we observed.

Comparing study populations between blocks and phases: population change, spatial detection parameters and reproduction

In non-masting environments in New Zealand, mouse population density usually peaks in summer and autumn, and declines during winter (Ruscoe & Murphy 2005). Our density estimates generally followed this pattern, with two anomalies. First, apparent density-dependent rates of population change (mouse density declining in QH but increasing in ML) from August to November 2012 (winter–spring) were consistent with reduced food availability in QH relative to ML (discussed above). Second, declining density in MH throughout the final year of our study was also consistent with food limitation and contrasts with increasing spring–summer (November–February) densities in other years (QH 2011/12, 2012/13; MH 2012/13, 2013/14, 2014/15). However, because our study blocks were unreplicated, we are not able to demonstrate that differences between them caused these contrasting population dynamics.

Differences between the mouse populations at high density (QH and MH) and low density (ML) in the spatial detection parameters describing captures are also consistent with contrasting food availability at high and low mouse density (discussed above). Baited traps may have been more attractive to mice in higher-density populations that had depleted their invertebrate food supply (Watts et al. 2017). In addition, the apparently smaller home ranges of mice in QH and MH (based on spatial differences in capture probability) is consistent with the higher mouse densities in these block–phase combinations than in ML.

Intra-specific competition by mice for food could have limited population growth by lowering reproduction or survival, or by increasing emigration. This process could lead to a higher reproductive rate in ML than in QH, but we detected no differences in reproductive rate between these block–phase combinations. Survival and emigration were not measured directly.

Body size and restricted emigration may lead to a 'partial fence effect'

Because rodent population density often increases when dispersal is prevented by a fence enclosing the population, dispersal is thought to be necessary for normal rodent population regulation ('fence effect'; Krebs et al. 1969; Nelson et al. 2002; Krebs 2013). It is likely that at least some mice could emigrate over the mammal-resistant fences surrounding the 17 ha Q block and the 3400 ha main Maungatautari reserve (which contained M block), as these fences were not designed to contain mammals but to exclude them (Day & MacGibbon 2007; Connolly et al. 2009). Small, lightweight mice may have been more able than heavy mice to climb over the fence's curved metal hood.

Restriction by the fence of adult males seeking mates ('wandering'; Wolff 2008) may in part explain the higher proportion of large mice (especially males) in QH than in MH. Nelson et al. (2002) found that adult male house mice emigrated from experimental enclosures at a higher rate than adult females. Other habitat differences between our study blocks do not explain mouse body size differences between QH and MH, as mice in QH did not differ significantly in size from mice in ML, and forest composition in the two blocks is similar.

A 'partial fence effect' resulting from this restricted emigration from Q block may explain the generally higher mouse population density in QH than in MH throughout the study. In contrast, mice in M block could disperse throughout the larger fenced Maungatautari reserve. Immigrating mice from elsewhere in the reserve would not necessarily compensate for emigration from M block, owing to likely spatial variation in mouse population density (review in Krebs 2013) throughout the reserve.

Relationship between tracking index and density

Past tests of relationships between mouse tracking rates and population density had contrasting results, possibly owing to methodological differences (Nathan et al. 2013). The mouse tracking rate in inked tunnels was positively related to mouse density on Saddle Island, Hauraki Gulf, Auckland Region (Nathan et al. 2013), but not in a study in Fiordland, South Island (Ruscoe et al. 2001). Neither of these studies used standard (Gillies & Williams 2013) tunnel spacing or placement duration.

Our study supports the use of tracking tunnels placed using standard Department of Conservation guidelines (Gillies & Williams 2013) to roughly indicate mouse abundance, especially when populations are sparse. Tracking rates and numbers of unique mice captured were related despite the disparity in scale of the single live-trapping grid (1 ha) in each study block (a design driven by the high cost of live-trapping on multiple small grids per block), compared with the c. 20 times larger areas in which tracking tunnels were distributed. The method appeared to be most suitable for relatively sparse populations, because tracking rates approached 100% at intermediate mouse density (> 10–25 ha^{-1}, in sessions when > 20–40 mice were captured; Fig. 5). Although the relationship between tracking rates and mouse density was not statistically significant despite the high correlation between these variables, this test was relatively weak because of its smaller sample size (because density estimates were not available for sessions with ≤ 1 captures) and higher serial correlation between sequential tracking rates.

Conclusions

Population densities of house mice after larger mammals were removed from the Maungatautari forest were similar to those observed after masting events in New Zealand beech forest and alpine grassland (Ruscoe et al. 2001, 2004; Wilson & Lee 2010). If this mainland forest sanctuary is typical of non-masting forest locations in New Zealand, then eradication of larger mammals from these reserves may not generate the very high mouse population densities estimated on some offshore islands without other mammals (e.g. Efford 2004; Russell 2012; McClelland et al. 2018) or in forest patches surrounded by grassland on the predator-fenced Tawharanui Peninsula (Goldwater 2007).

House mouse populations are clearly often limited by predation and/or competition from other, larger pest mammals. However, the density of mice after removal of other mammals is likely to vary between locations, depending on food supply and whether any predatory mammals remain. For example, in managed urban areas it is possible that all wild and feral mammals may be removed but domestic cats remain. Therefore, given current support for Predator Free New Zealand (Russell et al. 2015), it is worth studying whether control of larger mammals in urban and rural settings leads to mouse population irruptions.

Even at moderately high density, house mice may have significant ecological impacts. In biodiversity sanctuaries they may have several additional negative consequences. First, mice may interfere with monitoring devices set to detect other species, in particular rats and mustelids, by stealing baits and obscuring footprints in tracking tunnels. Second, the extensive burrows created by house mice (Schmid-Holmes et al. 2001; Avenant & Smith 2003) may provide conduits out of the sanctuary into adjacent mouse-free exclosures, and into the sanctuary for weasels or other predators. Finally, visible mice and their sign detract from the enjoyment by visitors and volunteers of sanctuaries that are expected to be pest-free.

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