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Density-impact functions for invasive house mouse (*Mus musculus*) effects on indigenous lizards and invertebrates

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Abstract House mice are among the most widely distributed mammals in the world, and adversely affect a wide range of indigenous biota. Suppressing mouse populations, however, is difficult and expensive. Cost-effective suppression requires knowing how low to reduce mouse numbers to achieve biodiversity outcomes, but these targets are usually unknown or not based on evidence. We derived density-impact functions (DIFs) for mice and small indigenous fauna in a tussock grass/shrubland ecosystem. We related two indices of mouse abundance to five indices of indigenous lizard and invertebrate abundance measured inside and outside mammal-resistant fences. Eight of 22 DIFs were significantly non-linear, with positive responses of skinks

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D. Clarke e-mail: dclarke@doc.govt.nz (*Oligosoma maccanni*, *O. polychroma*) and ground wētā (*Hemiandrus* spp.) only where mice were not detected or scarce (<5% footprint tunnel tracking rate or printing rate based on footprint density). Kōrero geckos (*Woodworthia* spp.) were rarely detected where mice were present. A further 9 DIFs were not differentiated from null models, but patterns were consistent with impacts at 5% mouse abundance. This study suggests that unless mouse control programmes commit to very low abundances, they risk little return for effort. Impact studies of invasive house mice are largely restricted to island ecosystems. Studies need to be extended to other ecosystems and species to confirm the universality or otherwise of these highly non-linear DIFs.

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Introduction

Invasive house mice (Mus musculus) are among the most widely distributed mammals in the world, and are increasingly recognised for their negative impacts on a range of indigenous invertebrate, lizard, seabird and plant species (Angel et al. 2009; Jones et al. 2003; Nelson et al. 2016; Newman 1994; Norbury et al. 2014; Russell et al. 2020; Smith et al. 2002; St Clair 2011; Wanless et al. 2007; Wanless et al. 2012; Wilson et al. 2007). These impacts are further increased following control and eradication of toporder predators and rats, which sometimes suppress mouse numbers (Angel et al. 2009; Goldwater et al. 2012; Wilson et al. 2018). Whilst tools are available for eradicating mice on offshore islands, they are not scalable or transferable to mainland systems due to economic, logistical, and social limitations. Existing control tools are constrained by their brief suppression effect or limitation to modestly proportioned areas enclosed by mammal-proof fencing (Nelson et al. 2016; Reardon et al. 2012; Wilson et al. 2018). For control to be cost-effective, and to avoid underor over-expenditure, it is necessary to know how low mouse numbers need to be reduced to achieve desirable biodiversity outcomes. Most species that are vulnerable to mice in New Zealand, for example, require mouse suppression to low levels (Nelson et al. 2016), but these levels have not been quantified. Several studies have inferred mice as harmful predators of small indigenous lizards (Hoare et al. 2007a; Knox et al. 2012; Lettink and Cree 2006; Newman 1994; Towns and Elliott 1996) and invertebrates (St Clair 2011), but impacts are often unquantified, based on uncontrolled and un-replicated designs, or sometimes confounded with impacts of other rodent species (St Clair 2011).

One of the fundamental tenets of cost-effective management of pests, including mice, is knowing the minimum control effort, or maximum allowable pest density, that achieves a required outcome, yet this knowledge is lacking for many invaded systems (Caughley and Gunn 1996; Grice 2009), although see Cooke et al. (2010). Consequently, managers risk

not applying enough effort, or conversely, overcommitting scarce resources. A useful way of quantifying pest targets is by deriving the relationship between pest density and their impact (i.e., a 'pest densityimpact function' or DIF, sensu Norbury et al. 2015). The shapes of these relationships can take various linear or non-linear forms. Non-linear forms are especially interesting as they suggest threshold pest densities at which impacts change rapidly, suggesting a tangible management target (Edge et al. 2011).

Norbury et al.'s (2015) review of DIFs showed that 'highly vulnerable' functions (i.e., positive resource responses only at very low pest densities) are common for many prey taxa in relation to mammalian predators, reported solely from New Zealand: mostly forest birds in relation to stoats (Mustela erminea), ship rats (Rattus rattus), or brushtail possums (Trichosurus vulpecula) (Basse et al. 1999; Binny et al. 2020; Innes et al. 1999; Whitehead et al. 2008), tree wētā (Hemideina thoracica) in relation to ship rats in forests (Ruscoe et al. 2013), and ground weta (Hemiandrus spp.) and juvenile McCann's skinks (Oligosoma maccanni) in relation to European hedgehogs (Erinaceus europaeus occidentalis) in dryland habitat (Jones et al. 2013). The only DIFs previously published in relation to mice are for Mahoenui giant wētā (Deinacrida mahoenui) (Watts et al. 2017) and other ground-dwelling invertebrates (Watts et al. 2022) in New Zealand forest, which were also typical of 'highly vulnerable' functions. Otherwise, relationships between mouse abundance and biodiversity outcomes are largely unknown.

Here, we derive DIFs for mice and small indigenous lizards and invertebrates in a tussock grass/ shrubland ecosystem. We relate three indices of mouse abundance to five indices of indigenous lizard and invertebrate abundance, measured inside and outside two mammal-resistant fences. We evaluate intercept-only, linear, and exponential functions for observed DIFs and compare them with alternative types described in Norbury et al. (2015) to reveal the kind of mouse management that might be required to protect these taxa.

Materials and methods

Study area

Our study was located in the Macraes Conservation Area in eastern Otago, New Zealand, near the township of Macraes Flat (45°25'S, 170°28'E). The area contains extensive rock outcrops of Haast schist at an altitude of 400–600 m. The vegetation is a mosaic of close-cropped introduced grasses (e.g., *Agrostis capillaris*), indigenous tussock grasses (*Chionochloa rigida*, *C. rubra*), and mixed shrublands with mānuka (*Leptospermum scoparium*) and matagouri (*Discaria toumatou*) as the dominant woody species. No tussock masts (i.e., years with heavy flowering and seeding) occurred during the study.

Study design

We derived DIFs by calculating abundance indices of mice, small lizards, and invertebrates (see methods below) simultaneously and at the same locations, and plotting lizard and invertebrate indices against mouse indices. We conducted two studies.

- In the 'landscape' study in December 2010, we a. sampled across a 4000-ha area containing uncontrolled mouse populations and suppressed populations of larger predators: feral cats (Felis catus), weasels (Mustela nivalis vulgaris), stoats, feral ferrets (M. putorius furo), and European hedgehogs. Ship rats and Norway rats, R. norvegicus, were present in small, localised numbers and were only occasionally captured. The area had been subjected to more than 10 years of extensive predator trapping, beginning at least in 1999 over a smaller area of 2700 ha (Tocher 2006), designed to recover populations of Nationally Endangered grand skinks (Oligosoma grande) and Otago skinks (O. otagense) (see Reardon et al. 2012 for details). These larger predators were at low densities-mean numbers caught per 100 kill-trap-nights from 2005 to 2014 were 0.12 for cats, 0.12 for ferrets, and 0.38 for hedgehogs (New Zealand Department of Conservation, unpublished data).
- b. In the 'fence' study in November 2012 and April 2013, we sampled inside and outside two mammal-resistant fences located within the predator

suppression zone. The 18-ha 'Wildlife' fenced area contained tussock grassland and shrubland dominated by *Coprosma* spp. and was cleared of the mammals listed above in 2005. The 9-ha 'Redbank' fenced area contained primarily tussock and was cleared of mammals in 2007. The fences consisted of panels of stainless-steel 6×24 mm mesh, 1.8 m-high with a subterranean skirt at the base and a metal rolled hood barrier at the top (Reardon et al. 2012). Mouse incursions occurred 3 or 4 times before our study began, but mice were immediately eradicated or suppressed to undetectable levels after they were first detected.

Landscape study sampling

We indexed mouse, lizard and invertebrate abundances at 50 independent grids (each 45×45 m) distributed across the predator suppression zone (Fig. 1), and equally apportioned to three habitat types: sparse $(<1 \text{ per m}^2)$ tussock grasses of short (<40 cm high)to tall (>40 cm high) stature; dense tall tussock (>1 per m^2); and mixed shrubland (matagouri or mānuka) with sparse tall tussocks. Sixteen grids were distributed randomly within each habitat type, plus an extra grid inside each of the two mammal-free fences. Each grid consisted of 16 'Black Trakka' inked footprint tracking tunnels (500×100×100 mm; Gotcha Traps 2 Young Street, RD2, Warkworth, New Zealand) laid in a 4×4 arrangement at 15-m spacing, baited with peanut butter, and set for 3 nights. Mice, small skinks (mainly McCann's skinks and southern grass skinks O. aff. polychroma Clade 5), and ground weta (large flightless orthopterans) were detected in tracking tunnels. Skink prints could not be differentiated by species (Jarvie and Monks 2014), although we know both species do use tunnels. Korero gecko (Woodworthia spp. "Otago/Southland large") prints could be differentiated but they rarely tracked the tunnels, so these data are not presented. Weta were identified by tarsal pad prints. Abundance indices were expressed in two ways: percentage of tunnels tracked (tracking rates), and percentage of 300 1-cm² squares tracked per tunnel (printing rates), measured by overlaying gridded transparency film onto the tracking cards (see Watts et al. 2011). The former index is the convention used in most studies, but unlike the latter index,





Fig. 1 Map of study area showing the boundary of the 4000ha predator trapping area (red line), 50 landscape study sampling grids (red circles), and 16 fence study sampling grids (black and yellow closed squares). The two predator-free fences (northern red open square = 'Redbank' fence, southern red open square = 'Wildlife' fence) each contained four fence sampling grids, which were paired with four fence grids containing similar habitat outside the fences. The layout of a land-

is insensitive to the number of prints on a given card (e.g., a single print on a card is scored the same tracking rate as 100 prints).

Grids also contained nine artificial refuges (3×3) arrangement, 15-m spacing) nested within the tunnel layout. Each refuge consisted of three brown Onduline® corrugated plates $(20 \times 30 \text{ cm})$ placed on top of one another and separated by 1-cm spacers to allow lizards and invertebrates to occupy the gaps (Lettink and Cree 2007). These refuges provide reasonably robust indices of skink abundance, given optimal weather conditions (Lettink et al. 2011; Wilson et al. 2017). We did not account for weather conditions in our analyses, but we sampled whenever we could during optimum conditions

scape study grid $(45 \times 45 \text{ m})$ is shown as a 4×4 arrangement of tracking tunnels (T) and a 3×3 arrangement of artificial refuges (R). The layout of a fence study grid $(105 \times 105 \text{ m})$ is shown as an 8×8 arrangement of Elliott traps (E), a 4×4 arrangement of tracking tunnels (T, plus one tunnel at each grid corner), a 10×10 arrangement of artificial refuges (x), and a 10×10 arrangement of pitfall traps (o)

(see Hoare et al. 2009), although occasionally this was not possible. Onduline is a lightweight corrugated roofing product made of organic fibres saturated with bitumen. Refuges were deployed 6 weeks before each sampling to allow colonisation. Then, at the start and end of 5 days (spanning the deployment of tracking tunnels), the numbers of skinks (separated by species), geckos, and invertebrates were counted in early morning before it was too warm for animals to remain within the refuges (see Wilson et al. 2017). To make counting easier, invertebrates of an arbitrary body length of $\geq 2 \text{ mm}$ were counted. Invertebrates mainly comprised cockroaches (Blattodea; 53% of all invertebrates counted), earthworms (Oligochaeta; 14%), and beetles (Coleoptera; 12%) (other taxa listed in Table 1, online resource 1). Invertebrate taxa were pooled. Animals were not marked, so abundance indices were based on total numbers counted per grid per day and calculated per 100 refuge-nights.

Fence study sampling—inside and outside mammal-resistant fences

We sampled more intensively at 16 larger grids $(105 \times 105 \text{ m})$ in total inside and outside the two mammal-resistant fences (Fig. 1). Mammals were generally absent inside the fences, and uncontrolled mice and suppressed populations of large predators were present outside. In April 2013, mice were detected inside the Redbank fence, and had probably been there for 5–6 weeks before we began sampling. Eight grids were located inside the fences (four in each fence), and another eight grids were placed outside in locations chosen to match the predominant habitat types within each fence (tussock and woody). As for the landscape study, the fence study provided indices of indigenous fauna abundance in the presence of mice on some of the grids outside the fences, and in the absence of mice inside the fences, so were integrated into the analysis of the DIFs.

Sixteen Black Trakka tunnels baited with peanut butter were nested inside each grid in a 4×4 arrangement at 30 m spacing, and four large tracking tunnels (one at the corner of each grid) were set for 5 nights. Large tunnels consisted of corrugated plastic $(1000 \times 200 \times 200 \text{ mm})$ stapled to a heavy wooden base (Pickerell et al. 2014), baited with peanut butter (replaced every 2 days) and rabbit meat (replaced daily) to detect predatory mammals larger than mice (large mammal data were sparse and excluded from the analysis). Tracking rates of mice, skinks, geckos, and ground wētā were derived from all tunnels. Printing rates were derived from Black Trakka tunnels only.

Artificial refuges (n=100) were arranged in a 10×10 grid at 2-m spacing within each larger grid. Skinks, geckos, and invertebrates were counted at the start and end of 5 days and expressed as the number counted per 100 refuge nights. Invertebrates (≥ 2 mm body length, taxa pooled) mainly comprised hoppers (Amphipoda; 25%), cockroaches (23%), and spiders (Araneae;16%) (other taxa listed in Table 1, online resource 1).

A similar grid of 100 pitfall traps (10×10 , at 2-m spacing) was arranged within each larger grid, located 60 m away from the refuge grid (Fig. 1). A pitfall trap consisted of a plastic cup (20 cm high, 15 cm diameter) dug at ground level, baited with a 1 cm^3 piece of tinned pear, and covered with a small wooden board supported above the ground to allow access by lizards and invertebrates. Traps were checked daily for only 3 days in 2012 (due to disruption by high rainfall) and for 5 days in 2013. Total counts of wētā and 'other invertebrates' ($\geq 2 \text{ mm}$ body length, taxa pooled) were expressed per 100 pitfall nights. Because skinks may eat invertebrates caught in the same pitfall trap, we counted invertebrates only if the trap did not contain a skink. Invertebrates mainly comprised beetles (48%) and spiders (25%) (other taxa are listed in Table 1, online resource 1). Skinks were marked with unique codes by applying dots and dashes to their backs with a xylene-free paint pen. These codes remained legible for the 3-5-day mark-recapture sessions. The number of unique skinks captured was expressed per 100 pitfall nights.

Given that activity, and therefore capture probability, of ectotherms is highly influenced by environmental conditions such as ambient temperature (Spence-Bailey et al. 2010), we conducted all animal sampling inside and outside the fences simultaneously to ensure identical weather conditions. Data from the November 2012 and April 2013 samplings were pooled for analysis.

Mouse abundance was also measured by setting grids of 64 aluminium Elliott live-capture traps (Tasker and Dickman 2002) in an 8×8 arrangement at 15-m spacing, and baited with peanut butter mixed with rolled oats. Polyester fibre was placed inside each trap to provide thermal insulation. Traps were checked daily during the morning for 4 days. Mice were marked with numbered metal ear tags and released. The number of unique individuals captured was recorded, but there were too few mice captured for density estimation (and few new mice were captured after 4 days), so only 'minimum number alive' was derived. No Elliott traps were placed inside the fences, which were expected to be free of mice.

Relationships between the above animal abundance indices and population density are not entirely clear. For mice, Ruscoe et al. (2001) and Wilson et al. (2018) found poor relationships between density and tunnel tracking rates, but Ruscoe et al. (2001) found a reasonably good relationship with minimum number alive. Unfortunately, we captured too few mice for robust estimates of minimum number alive in our study. For lizards, relationships between density and numbers counted in artificial refuges are significant, but highly dependent on weather and time of day (Lettink et al. 2011; Wilson et al. 2017).

Analytical methods

Animal count data were converted to continuous predictor and response variables (abundance indices) by pooling total animal counts from monitoring devices in a grid and dividing by the total capture effort (number of devices or device nights). We determined the most representative shapes of density-impact functions by comparing several linear and non-linear models fitted to the same predictor and response data. Fitted models were intercept-only (no relationship), linear (y=a+bx), exponential growth $(y=ax^b)$ and exponential decay models ($y = ae^{bx}$). The interceptonly model relates to the theoretical 'insensitive' relationship in Norbury et al. (2015), the linear and exponential growth models relate to the 'indirectly advantaged' relationship, and the exponential decay model relates broadly to the 'proportionate,' 'highly vulnerable,' and 'resistant' relationships. Model selection was based on the small-sample-corrected Akaike Information Criterion (AICc, Sugiura 1978). Given the abundance of zeros in the predictor variable (mouse abundance), we decided to narrow our inference rather than pursue analyses using mixed error terms, such as zero-inflated models (see Campbell 2021). We compared the strength of evidence for each relationship shape, relative to the other relationship shapes, using non-linear regression because it is flexible for the wide range of predictor and response combinations measured. Therefore, AICc was used only to summarise the evidence for the shape of each relationship (see Burnham and Anderson 2002). No other inferences relying on error term distributions (standard errors, confidence intervals or hypothesis tests) were taken from the models. The model with the lowest AICc value and >2 from the next closest model was chosen as the model best representing the shape of the density-impact function. However, if there was evidence to select a set of models within 2 AICc units of each other but > 2 AICc units from other models, that set of models was chosen to represent the relationship. Finally, if the intercept-only model had the lowest AICc, only that model was selected.

Where datasets were available from both the landscape and fence studies (12 of the 31 DIFs derived; see Table 2, online resource 1), data were combined for the analyses. Because counts are integers and abundance indices are real numbers, conventional statistical analyses of these different data types, for example using generalized linear models, assume different error term distributions. We used non-linear models to maintain a similar analytical approach to past studies (sensu Norbury et al. 2015), but this made specifying models with the correct error term distribution difficult. This is addressed in online resource 3.

We tested whether habitat (tussock and woody) was a confounding factor in the DIFs for skink printing rates, counts of McCann's skinks in refuges, and wētā printing rate in relation to the most sensitive mouse index (printing rate). We tested these response variables because they consisted of sufficient nonzero data (measured in both the landscape and fence study samplings) and had clear support for either the linear or exponential-decay models. In each case, we fitted a model for the combined tussock and woody habitats, and a separate model with a habitat interaction term so that the regressions could vary between these habitats. The models were compared with AICc.

Results

There were positive responses of skinks and ground wētā only where mice were not detected or scarce (<5% footprint tunnel tracking rate or printing rate based on footprint density). Where mouse printing or tracking rates were high, lizards and invertebrates were consistently scarce. Geckos were an extreme example: they were rarely detected where mice were present. All eleven DIFs based on mouse printing rates appeared to be strongly inflected 'highly vulnerable' functions, according to their shape (sensu Norbury et al. 2015) (Figs. 2, 3). Of these, exponential decay functions were selected based on AICc (i.e., delta AICc>2, Table 2, online resource 1) for skink printing rates and counts of McCann's skinks



Fig. 2 Density-impact functions for mice and lizards at the Macraes Conservation Area, eastern Otago. Mouse abundance indices derived from printing rates, i.e., percentage of the area of tracking cards printed by mice in inked tunnels. Lizard abundance indices derived from: printing rates by skinks (**a**, n=82) and geckos (**b**, n=32) (same cards as mice); number

of McCann's skinks (**c**, n=32) and southern grass skinks (**d**, n=32) per 100 pitfall trap nights; and number of McCann's skinks (**e**, n=82), southern grass skinks (**f**, n=82) and Körero geckos (**g**, n=82) per 100 artificial refuge nights. Relationship shapes with considerable support are indicated (and bolded in Table 2, online resource 1). Some data points are overlapping

in refuges (Fig. 2a, e). They showed mouse printing rate thresholds of 5% or less, below which printing rates and counts suddenly increased. Both linear and exponential decay functions were supported for numbers of grass skinks in pitfall traps and wētā printing rates (2d, 3a). However, for McCann's skink in pitfall traps, grass skinks in refuges, geckos in refuges, and invertebrates in pitfall traps, the intercept-only, linear, and exponential functions all received similar support (Figs. 2c, f, g, 3c). These ambiguities were due to highly variable lizard and invertebrate abundances where mice were not detected i.e., when the corresponding mouse index was zero. Most of the ambiguous DIFs, however, were consistent with the 5% mouse abundance threshold, with higher thresholds apparent for skinks and invertebrates in pitfall traps. For the remaining three DIFs based on mouse printing rates, the intercept-only model had the lowest AICc, and hence relationships with gecko printing rate, wētā in pitfall traps, and invertebrates in Fig. 3 Density-impact functions for mice and invertebrates at the Macraes Conservation Area, eastern Otago. Mouse abundance indices derived from printing rates, i.e., percentage of the area of tracking cards printed by mice in inked tunnels. Wētā abundance indices derived from printing rates $(\mathbf{a}, n = 82)$ (same cards as mice) and number of wētā per 100 pitfall trap nights (**b**, n = 32). Abundance indices of other invertebrates are derived from number per 100 pitfall trap nights (c, n = 32) (same pitfall traps as weta), and number per 100 artificial refuge nights (\mathbf{d} , n = 82). Relationship shapes with considerable support are indicated (and bolded in Table 2, online resource 1). Some data points are overlapping



refuges were not supported statistically (Figs. 2b, 3b, d). Habitat differences in fauna abundance indices did not confound the results for skink printing rates, McCann's skinks in refuges, or wētā printing rates, because inclusion of habitat interaction terms in the three DIFs tested did not improve the models (see Fig. 1, online resource 2, for graphs separated by habitat; and Table 3, online resource 1 for statistics).

Density-impact functions based on the conventional, but less sensitive, tracking rate index of mouse activity were generally less inflected than those based on printing rates. Of these eleven DIFs, both linear and exponential decay functions were supported for skink tracking rates, grass skinks in pitfall traps, McCann's skinks in refuges, and wētā tracking rates (Table 2, online resource 1, and Figs. 4a, d, e, 5a). For gecko tracking rates, McCann's skinks in pitfall traps, grass skinks in refuges, invertebrates in pitfall traps, and invertebrates in refuges, the intercept-only, linear and exponential functions all received similar support (Figs. 4b, c, f, 5c, d). For geckos in refuges and wētā in pitfall traps, the intercept-only model had the lowest AICc (Figs. 4g, 5b).

Density-impact functions based on the minimum number of mice alive were less clear (Figs. 2, 3, online resource 2), but too few mice were captured to interpret these functions, and spatial replication was limited to eight grids. Of the nine DIFs, both linear and exponential decay functions were supported for only grass skinks in pitfall traps (Table 2, online resource 1; and Fig. 2c, online resource 2). For grass skinks in refuges, invertebrates in pitfall traps, and invertebrates in refuges, the intercept-only, linear, and exponential functions all received similar support (Figs. 2e, 3c, d, online resource 2). For skink printing rate, McCann's skinks in pitfall traps, McCann's skink in refuges, wētā printing rates, and wētā in pitfall traps, the intercept-only model had the lowest AICc (Figs. 2a, b, d, 3a, b, online resource 2).

Discussion

Of the three house mouse abundance indices measured, printing rate was the most sensitive to mouse activity because it accounted for variable footprint density. All the DIFs based on this index, and about



Fig. 4 Density-impact functions for mice and lizards at the Macraes Conservation Area, eastern Otago. Mouse abundance indices derived from tracking rates, i.e., percentage of inked tracking tunnels marked by mice. Lizard abundance indices derived from: tracking rates by skinks (**a**, n = 82) and geckos (**b**, n = 32) (same cards as mice); number of McCann's skinks

(c, n=32) and southern grass skinks (d, n=32) per 100 pitfall trap nights; and number of McCann's skinks (e, n=82), southern grass skinks (f, n=82) and Körero geckos (g, n=82) per 100 artificial refuge nights. Relationship shapes with considerable support are indicated (and bolded in Table 2, online resource 1). Some data points are overlapping

half of those derived from less sensitive indices, took the visual shape of 'highly vulnerable' functions (sensu Norbury et al. 2015), with statistical support for exponential decay/linear relationships in 4 of 11 cases for each of the mouse printing rate and mouse tunnel tracking rate indices. In a further 9 cases, support for these inverse relationships did not differ significantly from support for null (intercept-only) models. The highly variable lizard and invertebrate abundance indices recorded where mice were not detected imply that other unmeasured variables, such as food abundance or refuge from predators, may be important in determining the abundance of small native animals. Despite these ambiguities, the relationships suggest that small lizards, wētā, and other invertebrates, in New Zealand at least, are highly palatable to mice or behaviourally naïve to mice, and/or that their fecundity rates may be insufficient to recover from predation. In addition, mice may be highly efficient consumers of these fauna or have few constraints on their foraging behaviour so that even a few individuals may have severe negative impacts. Fig. 5 Density-impact functions for mice and invertebrates at the Macraes Conservation Area, eastern Otago. Mouse abundance indices derived tracking rates, i.e., percentage of inked tracking tunnels marked by mice. Wētā abundance indices derived from tracking rates (a, n = 82) (same cards as mice) and number of weta per 100 pitfall trap nights (b. n=32). Abundance indices of other invertebrates are derived from number per 100 pitfall trap nights (c, n=32) (same pitfall traps as wētā), and number per 100 artificial refuge nights (d, n = 82). Relationship shapes with considerable support are indicated (and bolded in Table 2, online resource 1). Some data points are overlapping



Mice may have even greater negative impacts on larger lizard species given the slow life histories of these lizards (Cree 1994), and their fewer suitable habitat refuges that are small enough to exclude mice. Therefore, mouse control is warranted, combined with research to assess how factors, such as microhabitat characteristics, may affect mouse density and hence abundance of small indigenous taxa (see Lennon et al. 2021).

Mice can affect abundance of indigenous fauna in several ways. Direct predation is commonly reported (Hoare et al. 2007a; Jones et al. 2003; Knox et al. 2012; Lettink and Cree 2006; Newman 1994; Norbury et al. 2014; O'Donnell et al. 2017; Russell et al. 2020; Smith et al. 2002; St Clair 2011; Towns and Elliott 1996; Wanless et al. 2012; Wilson and Lee 2010). A less obvious effect is alteration of thermoregulatory behaviour of ectotherms. When exposed to predator cues in captivity, McCann's skinks taken from a high predation site basked less often than those from a low predation site (Cliff et al. 2022). Basking returned to normal levels immediately after predator cues were removed, suggesting high fitness costs of reduced thermo-regulation for this species. Mice may also compete with indigenous fauna for food. Skinks, geckos and mice are omnivorous and have some overlap in diet (Miller and Webb 2001; Patterson 1992; Watts 2001; Whitaker 1980). Invertebrates are the primary food of all three taxa, notably for mice during non-mast years when seed is less abundant (Wilson and Lee 2010). Differences in gape size and diet quality between mice and indigenous fauna (Baumans 2010; Wotton 2002) might weaken competition, but competition between these groups is largely unstudied and requires further investigation. Given that mice also consume seeds and other plant material (Angel et al. 2009), DIFs might be a useful approach for understanding mouse impacts on vegetation.

Density-impact functions are correlations only they do not necessarily imply causation. An alternative to the mouse impact hypothesis is habitat effects. It could be argued, for example, that high mouse numbers occur in habitat types that are less suited to small indigenous fauna. However, previous studies in the same modified grassland system studied here show the opposite—mice are usually more abundant in mature grasslands where many invertebrates and small lizards, particularly southern grass skinks, also enjoy the extra food and shelter mature grasslands provide (Norbury et al. 2009), provided mice are not overly abundant (Norbury et al. 2013). Clearly, indigenous fauna are affected by many factors besides mouse predation, including habitat type and top-order predators (Lettink et al. 2010; Moseby et al. 2009; Norbury et al. 2009; Reardon et al. 2012). The wide range of lizard and invertebrate abundances measured in this study where mice were not detected clearly demonstrates other factors at work. However, our analysis showed that tussock or woody habitat had little effect on the shape of the DIFs, and top-order predators were either absent inside the mammalresistant fences or present in low numbers outside (mean total trap rates for cats, ferrets and hedgehogs = 0.62 per 100 trap nights, New Zealand Department of Conservation, unpublished data). In any case, negative effects of top-order predators on small prey are often equivocal (e.g., Norbury et al. 2013; Risbey et al. 2000). Given that low numbers of cats, ferrets and hedgehogs were moving over considerably larger areas than mice, we considered that local abundances of small lizards and invertebrates were influenced more by locally abundant, uncontrolled populations of mice than by sparse scattered populations of toporder predators.

A potentially confounding factor in this study is behavioural interference by mice affecting detectability of indigenous fauna, rather than an effect on their density. For example, lizards and invertebrates might reduce their activity in the presence of mice (Duvaucel's geckos, *Hoplodactylus duvaucelii*, are known to avoid avoid rats, *Rattus exulans*; Hoare et al. 2007b), they might detect mouse odour in tracking tunnels and avoid them, or they may be less likely to enter tunnels after mice remove the bait. Chemosensory-mediated antipredator behaviours, however, are not well developed in New Zealand lizards, presumably because they evolved with predators (birds, tuatara and larger lizards) that hunt primarily by sight (Monks et al. 2019).

Given we did not measure mouse density, the term 'density-impact function' in not strictly correct, unless our abundance indices are linearly related to mouse density, which may not be the case (Ruscoe et al. 2001; Wilson et al. 2018). Similarly, more research is needed to understand the relationships between abundance indices and densities of lizards and invertebrates, such as those measured in this study (Hoare et al. 2009; Lettink et al. 2011, 2022; Wilson et al. 2017). In this case, 'density index-impact function' is a more appropriate term.

If mice affect small indigenous fauna as severely as some of these DIFs suggest, it raises the question of how these taxa manage to persist in the study area. They would need to experience regular periods of very few or no mice during non-mast years to survive the occasional mouse irruption caused by tussock mast (see O'Donnell and Hoare 2012). Indeed, occasional mouse irruptions are the normal pattern in this and other tall tussock systems (Norbury et al. 2013; Wilson and Lee 2010). In modified grass/shrubland systems, however, exotic pasture species produce masses of seed every year, resulting in high mouse numbers every autumn (Norbury et al. 2013). Mice are usually patchily distributed in these systems, with high affinity to woody components of grassland habitats (Norbury et al. 2013). Temporal and spatial refuges may allow a dynamic coexistence between mice and suppressed levels of small indigenous fauna.

Implications for management

Despite the global distribution of invasive house mice, impact studies of mice are largely restricted to island ecosystems. The highly non-linear DIFs in New Zealand imply that mouse numbers must be reduced to zero or very low levels to achieve positive outcomes for small lizards, ground weta, and other invertebrates, but these studies need to be extended to other ecosystem types and species. Our results imply that conservation managers should commit to reach and maintain these mouse levels, otherwise they risk gaining little return for effort and wasting resources. The mouse suppression target proposed to achieve conservation outcomes for lizards in New Zealand is a 5% tunnel tracking rate (James Reardon, pers. comm.). Our data support this target for McCann's skinks in artificial refuges (Fig. 4e) based on statistical analyses, and for Korero geckos in tracking tunnels and refuges (Fig. 4b, g), and for grass skinks and invertebrates in refuges (Figs. 4f, 5d) based on the visual shapes of these relationships. It is important to note, however, that we deployed tunnels for 3-5 nights in grids at 15-30 m spacings, whereas the New Zealand standard for rodents is 1 night at 50-m spacing along lines. We sampled in this way to obtain sufficient detections of lizards and invertebrates in the absence of standard tracking protocols for monitoring these groups. The threshold in our study might therefore have been lower had we deployed tunnels for 1 night along lines, but this requires further testing. Clearer support for a 5% target (or lower in some cases) was evident in our DIFs based on the more sensitive printing rate index, which was developed for wētā by Watts et al. (2011). Although tracking rate indices are commonly used to monitor rodent populations, they are at best a crude tool, aimed at detecting large fluctuations in mouse abundance. In this case, the more sensitive printing rate index for mice may be the best possible compromise. We recommend that printing rates should be derived from tracking tunnel cards in the future but recognise that this method requires extra processing time.

Reducing mouse numbers directly by lethal means is the conventional management approach, but methods to do this sustainably on inhabited mainland systems are currently limited. Defending against reinvasion in open landscapes, especially for small management areas, is a further challenge. An alternative approach is to manage the drivers of mouse abundance. Bottom-up processes are usually more important regulators of mouse dynamics than top-down predation (Norbury et al. 2013; Ruscoe et al. 2011). Cessation of livestock grazing in modified ecosystems increases growth of exotic pastures, followed by proliferation of rodents and subsequent declines in lizards (Hoare et al. 2007a; Knox et al. 2012; Newman 1994). These studies imply that judicious grazing (e.g., constant light stocking rates or pulsed grazing to reduce pasture density prior to seeding) may reduce mouse abundance in some circumstances. Whether this technique can help recover lizard populations will depend on whether mice can be reduced to sufficiently low levels indicated by the DIFs, and whether lizards can tolerate the reduction in vegetation cover. This is a topic for research.

New Zealand is embarking on an ambitious program to eradicate introduced brushtail possums, mustelids and rats by 2050 (Russell et al. 2015). Mesopredator release of rodents following removal of apex predators, coupled with sufficient food supply, have been shown in a range of ecosystems globally (Báez et al. 2006; Crooks and Soulé 1999; Ritchie and Johnson 2009; Schmidt and Ostfeld 2003), including New Zealand (Choquenot and Ruscoe 2000; Norbury et al. 2013). Therefore, there is a risk of increasing house mouse numbers in some areas following eradication of apex predators. The net outcomes for indigenous fauna are unclear, but small indigenous lizards and invertebrates, such as those studied here, may be at increased risk.

In conclusion, this study suggests that for some indigenous fauna, unless mouse control programmes commit to very low mouse abundance, they risk little return for effort and wasted expenditure.

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Data availability Data will be made available upon reasonable request.

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