Manaaki Whenua
Landcare Research

Systematic review of the population and spatial ecology of invasive rats and house mice (*Rattus* spp. and *Mus musculus*) in New Zealand

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Systematic review of the population and spatial ecology of invasive rats and mice (*Rattus* spp. and *Mus musculus*) in New Zealand

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Summary

Project and client

Predator Free 2050 Ltd Auckland (PF2050 Ltd) is conducting a wide-ranging exploration of potential tools to eradicate invasive mammals from New Zealand. As part of its Science Strategy, PF2050 Ltd is interested in developing and exploring realistic population models of genetic approaches to rodent control.

Constructing realistic population models requires adequate knowledge of the system being modelled and input parameters to populate such models. PF2050 Ltd proposed the research reported here to collect data and information on the population and spatial ecology of rodents in New Zealand that can be used to support realistic models.

Objectives

- To produce databases of the spatial and population ecology parameters of three species of rodents (ship rat, Norway rat, and house mouse) that are representative of the wild populations of New Zealand. These databases will inform the development of realistic models of rodent population dynamics.
- To produce recommendations for constructing realistic models of rodent population dynamics in New Zealand aimed at informing models of genetic approaches to rodent control.

Methods

I conducted a systematic literature review following standardised procedures to collect a representative sample of studies of the population and spatial ecology of the three species of rodents in New Zealand, including mainland and offshore islands.

Results and discussion

- A total of 99 studies were included in the qualitative synthesis.
- Only 52 of those 99 (52.5%) sourced relevant quantitative data for any of the three rodent species. Some studies provided more than one value of relevance for this project, resulting in a final sample of 94 data points for the three species.
- The quantitative data were used to build databases on the spatial and population ecology of the three rodent species. These databases are available from the Manaaki Whenua – Landcare Research Data Store: https://datastore.landcareresearch.co.nz/dataset/rodent-review-datasets.
- Ship rats were the most studied species, followed by Norway rats and house mice. Populations of Norway rat and house mice were studied more frequently on islands than on the mainland. In the case of the ship rat, mainland populations had been marginally more studied than island populations.
- Detailed studies of the spatial and population ecology of any of the three species are relatively scarce. Further research could help alleviate this scarcity.

- More research is needed to understand the role of density-dependence in influencing the population dynamics of the three rodent species.

Conclusions and recommendations

Quantitative models of rodent population dynamics and management using genetic control could benefit from considering the following recommendations.

1. Develop models and scenarios specific to islands and the mainland separately.
2. For mainland rodent populations, consider developing models and scenarios specific to forest (native and non-native), rural and urban habitats. In the case of native forests, the capacity of the models to replicate each of the six population dynamics classes identified by Walker et al. (2019) should be evaluated.
3. Compare the population dynamics in heterogeneous and homogeneous landscapes. Heterogeneous landscapes include patchy (fragmented) landscapes and landscapes where the rodent densities vary locally.
4. Ensure the models explore the role of incumbent advantage (i.e. individuals already present in an area excluding outsiders) in preventing or hampering self-dissemination of genetic control throughout rodent populations.
5. Explore the role of strong resource fluctuations (e.g. masting events) in driving rodent eruptive dynamics.
6. Investigate the role of density-dependence in shaping rodent population dynamics.
7. Incorporate interactions between the three rodent species. The three species seem to compete, and this competition affects their population dynamics.

1 Introduction and background

Rats (*Rattus* spp.) and house mice (*Mus musculus*) are some of the most widespread invasive species in the world, and are a major threat to biodiversity and the social and economic bottom-line in the recipient regions (Long, 2003; Jones et al., 2016, 2008; Shiels et al., 2014). New Zealand is not an exception to this global pattern (Innes in press; Russell & Innes in press; Ruscoe & Pech, 2010; Russell & Clout, 2004).

Four rodent species have been introduced, become established (self-sustaining populations), and spread in New Zealand:

- the ship or black rat (*Rattus rattus*)
- the Norway rat (*Rattus norvegicus*)
- the kiore or Pacific rat (*Rattus exulans*)
- the house mouse.

These four species produce severe negative impacts on the native biodiversity of New Zealand and are intensively managed to mitigate their impacts through a mix of eradication on islands and population control in mainland scenarios, where eradication is not feasible (Atkinson, 1973; Blackwell, 2000; Campbell & Atkinson, 2002; Ruscoe et al., 2004; Russell & Clout, 2005; Russell et al., 2005, 2009; Bellingham et al., 2010; Ruscoe & Pech, 2010; MacKay et al., 2011; King et al., 2011; Jones et al., 2016; Parkes et al., 2017; Murphy & Nathan in press; Walker et al., 2019). Invasive rats are a core target species for eradication under New Zealand's Predator Free 2050 mission (https://www.doc.govt.nz/nature/pests-and-threats/predator-free-2050/).

The likelihood of eradicating rodents from New Zealand depends on a good understanding of their spatial and population ecology, and the capacity to plan and implement effective, complex eradication programmes under varied ecological and social circumstances (Russell et al., 2005, 2008; Holmes et al., 2015; Groves & Game, 2016; Jones et al., 2016; Parkes et al., 2017; Walker et al., 2019). This is a typical 'wicked' problem in conservation and invasive species management (Game et al., 2014; Woodford et al., 2016).

Quantitative ecological models of rodent population dynamics can be a powerful tool to explore the ecology of rodent species under different ecological situations and to investigate the likely effectiveness of proposed management strategies – including eradication (Blackwell et al., 2001; Russell & Clout, 2004; Coutts, 2005; Russell et al., 2016; Parrott, 2017; García-Díaz et al., 2019b). However, the reliability of these models – and, by extension, the adequacy of their predictions and recommendations – hinges on both the quality of the input data used to parameterise them and the accuracy of the model in representing real-life dynamics (Prowse et al., 2016, 2017; Dietze, 2017; Wilkins et al., 2018; García-Díaz et al., 2019b).

The objective of this research project was to collect a representative sample of the spatial and population ecology of three of the four invasive rodents in New Zealand to inform and populate realistic models of population dynamics. (Kiore were excluded from this project.) I conducted a systematic review to produce a database for each of the three species. These three databases are representative of the current knowledge of the spatial and population ecology in New Zealand of ship rats, Norway rats and house mice (Figure 1).

A systematic review of the existing literature is a well-established procedure to summarise data and evidence in ecology and environmental conservation and management (Pullin & Stewart, 2006; Moher et al., 2009; Collaboration for Environmental Evidence, 2013; Schwartz et al., 2018). In the context of developing and using quantitative models to understand and manage invasive rodents in New Zealand, a systematic review will ensure the parameters used in the models are adequate and accurately reflect the ecology of these species in this country. The data were aggregated into island and mainland populations. Note that the databases are not necessarily comprehensive because the objective was to collect a representative sample.

2 Objectives

- To produce databases of spatial and population ecology parameters of three species of rodents that are representative of the wild populations of New Zealand. These databases will inform the development of realistic models of rodent population dynamics.
- To recommend parameter values to be used in models of rodent population dynamics in New Zealand.

3 Methods

I conducted a systematic literature review following standardised procedures and quantified the population and spatial ecology of the three species of rodents in mainland and island habitats (Pullin & Stewart, 2006; Moher et al., 2009; Collaboration for Environmental Evidence, 2013). The first stage of the literature review (Figure 1) involved searching online databases for potentially relevant publications using the keywords 'rat population New Zealand' and 'Mouse population New Zealand' (Web of Science and Google Scholar databases searched on 09/05/2018). These databases were complemented with additional references sourced from the chapters on the target species in the upcoming revision of the *Handbook of New Zealand Mammals* (draft chapters provided by the authors) and five additional publications suggested by collaborators when approached by email. References (see Figure 1) were compiled in a digital library stored in the Zotero Reference Manager system.

The title, keywords, and abstract of 405 references were screened to assess their relevance to this project. References that met any of these three criteria were excluded:

- not about New Zealand (61 references excluded)
- not about rodents (58 excluded)
- not about the spatial or population ecology of invasive rodents (102 excluded).

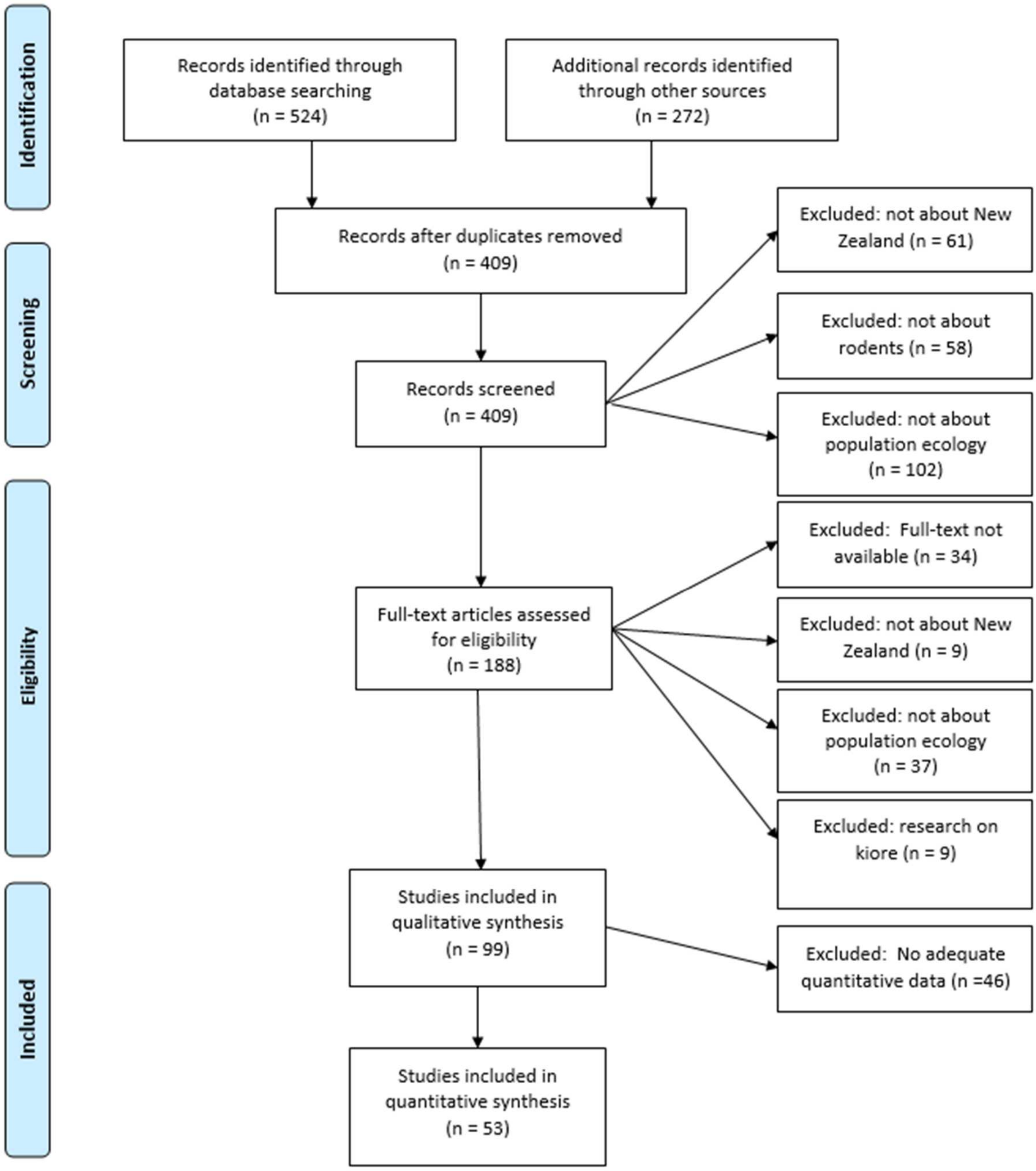

Figure 1. Process for the literature review to identify and screen studies on the population and spatial ecology of invasive rodents, excluding kiore, in New Zealand.

Subsequently, in the next stage, I evaluated the full texts of 188 references (Figure 1) and excluded references that met any of the following criteria:

- full text not readily available (34 references excluded)
- not about New Zealand (nine excluded)
- not about the spatial or population ecology of invasive rodents (37 excluded)
- about kiore (nine excluded).

In total, 99 studies were kept for the spatial and population ecology synthesis (Figure 1). Quantitative estimates of population and spatial ecology parameters were extracted from these studies, including, whenever possible, the mean or median value, a measure of uncertainty in the parameters reported (e.g. standard error), and a range of values. The parameters collected are available from the Manaaki Whenua – Landcare Research Data Store: https://datastore.landcareresearch.co.nz/dataset/rodent-review-datasets.

Also, information on the location, type of habitat (island or mainland), and period of study was compiled from the studies. After consultation with Dan Tompkins (PF2050 Ltd) and collaborators based at Cornell University (Assistant Professor Philipp Messer Research Group), the quantitative data available from the systematic review were summarised by season. The entire databases, in comma-separated values format, are stored and available from the Manaaki Whenua – Landcare Research Data Store: https://datastore.landcareresearch.co.nz/dataset/rodent-review-datasets.

4 Results and discussion

The systematic review found 99 relevant published studies, of which only 52 (52.5%) provided quantitative data that could be used to summarise the population and spatial ecology of ship rats, Norway rats, and house mice in New Zealand. The studies not included in the quantitative synthesis mostly provided indexes of abundance (e.g. number of captures per 100 trap-nights), which are not straightforward to translate into densities (individuals per hectare). Nevertheless, those studies report important information on the relative spatial and temporal dynamics of rodent populations in New Zealand. A digital library listing the 99 studies considered is available from the Manaaki Whenua – Landcare Research Data Store (https://datastore.landcareresearch.co.nz/dataset/rodent-review-datasets) and in Appendix 1 of this report.

The 52 studies with quantitative data produced a total of 94 data points of a variety of parameters describing the population and spatial ecology of rodents in New Zealand. Some studies provided more than one value, which explains the discrepancy between the number of studies and the number of values obtained. Ship rats were the subject of most studies (34 of 52; 65.4%), followed by Norway rats (10 of 52; 19.2%) and house mice (8 of 52; 15.4%). Not surprisingly, the number of data points collected was higher for the ship rat (54 of 94; 57.4%) but identical for the Norway rat (20 of 94; 21.3%) and house mouse (20 of 94; 21.3%). Most of the data points for the Norway rat and house mouse came from islands (18 of 20; 90%, and 11 of 20; 55%, respectively). Data points were more evenly distributed between islands and the mainland for the ship rat (22 of 54; 40.7%, and 32; 59.3%, respectively).

The systematic review highlighted potential knowledge gaps and discrepancies across species. Overall, it found detailed studies only of populations in a few selected locations across New Zealand. Examples include ship rats in fragmented landscapes around Hamilton (Innes et al., 2010; King et al., 2011), ship rat populations in the Orongorongo Valley (Efford et al., 2006), house mice on Mana Island (Efford et al., 1988), and Norway rats in the Pureora Forest (Innes et al., 2001). Long-term data from other locations across the country would be useful to better understand the spatial ecology and demography of these three species in different habitats.

Both Norway rats and house mice seem to be relatively understudied considering their wide distribution in New Zealand. Additional studies would be beneficial to improve understanding of the variability in the demography and ecology of these two species across different New Zealand habitats. Recent studies published after the date the database search was carried out provide additional information on the ecology of house mice (Wilson et al., 2018).

Density dependence has been included in models of rodent population dynamics in New Zealand (Coutts, 2005; Tompkins et al., 2013; Holland et al., 2018), and it is important when considering the likely efficacy of genetic control approaches for rodent eradication (Wilkins et al., 2018). However, further research is needed to clarify the role of density dependence in New Zealand rodent populations. Empirical data on density dependence in the three species were relatively scarce, with some studies suggesting that density-dependent effects might not always affect the home range sizes and juvenile dispersal of ship rats (Miller & Miller, 1995; Harper, 2006).

5 Conclusions and recommendations

This systematic review of the population parameters of three species of invasive rodents in New Zealand establishes the basis for making progress towards three main goals of Predator Free New Zealand:

1. to establish the basis for a synthesis of the knowledge on the population and spatial ecology of three rodent species in the country
2. related to the previous point, to highlight potential knowledge gaps that can be the target of future research
3. to provide representative data to build realistic models of rodent population dynamics under different scenarios in New Zealand.

All the data collated during the systematic review of the literature are available from the Manaaki Whenua – Landcare Research Data Store (https://datastore.landcareresearch.co.nz/dataset/rodent-review-datasets), which facilitates the use of these databases. These databases can be updated when new information is collected or appears in the literature.

Based on the systematic review presented here, quantitative models of rodent population dynamics and management using genetic control could benefit from considering the following recommendations.

1. Develop models and scenarios specific to islands and the mainland separately.
2. In the case of models for mainland rodent populations, consider developing models and scenarios specific to forest (native and non-native), rural, and urban habitats. In the case of native forests, the capacity of the models to replicate each of the six population dynamics classes identified by Walker et al. (2019) should be evaluated.
3. Compare the population dynamics in heterogeneous and homogeneous landscapes. Heterogeneous landscapes include patchy (fragmented) landscapes and landscapes

where rodent densities vary locally. In these types of landscapes, the population dynamics of rodents is different from that in homogeneous landscapes (Innes et al., 2010; King et al., 2011). Landscape-level processes (including rescue effects, whereby one population subject to control is rescued by immigrants; (Frankham, 2015; Banks et al., 2018) can affect the efficacy of novel management strategies such as gene drives. For example, a gene-drive may not spread quickly and efficiently in a metapopulation inhabiting a fragmented landscape compared with a well-mixed population (i.e. with panmictic mating) (Frankham et al., 2017; Prowse et al., 2017; Noble et al., 2018).

4 Ensure models explore the role of incumbent advantage in preventing or hampering self-dissemination of genetic control throughout rodent populations. In the case of rats, extant populations tend to exclude newly arrived individuals (Russell et al., 2014, 2019), something that may affect the efficacy of control.

5 Explore the role of strong resource fluctuations (e.g. masting events) in driving rodent eruptive dynamics and how they potentially affect the efficacy of novel management strategies (Coutts, 2005; Kelly et al., 2013; Tompkins et al., 2013; Holland et al., 2018; Walker et al., 2019).

6 Investigate the role of density dependence in shaping rodent population dynamics, and how it could affect novel management strategies and the recovery of rodent populations after control (Wilkins et al., 2018; García-Díaz et al., 2019a).

7 Incorporate interactions between the three rodent species. The three species seem to compete with each other, and this (direct or indirect) competition affects their population dynamics (Russell & Clout, 2005; Innes in press; Murphy & Nathan in press; Russell & Innes in press).

6 Acknowledgements

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7 References

Atkinson UAE 1973. Spread of the ship rat (Rattus r. rattus L.) III New Zealand. Journal of the Royal Society of New Zealand 3: 457–472.

Banks PB, Byrom AE, Pech RP, Dickman CR 2018. Reinvasion is not invasion again. BioScience: biy076–biy076.

Bellingham PJ, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmshurst JM, Mulder CP 2010. New Zealand island restoration: seabirds, predators, and the importance of history. New Zealand Journal of Ecology 34: 115–136.

Blackwell G, Potter M, & Minot E 2001. Rodent and predator population dynamics in an eruptive system. Ecological Modelling 142: 227–245.

Blackwell GL 2000. An investigation of the factors regulating house mouse (Mus musculus) and ship rat (Rattus rattus) population dynamics in forest ecosystems at Lake Waikaremoana, New Zealand. Unpublished PhD thesis, Massey University, Palmerston North.

Campbell DJ, Atkinson IAE 2002. Depression of tree recruitment by the Pacific rat (Rattus exulans Peale) on New Zealand's northern offshore islands. Biological Conservation 107: 19–35.

Collaboration for Environmental Evidence 2013. Guidelines for systematic review and evidence synthesis in environmental management, Version 4.2. Bangor University, UK, Centre for Evidence-Based Conservation.

Coutts SR 2005. A stochastic computer simulation of island group colonisation by Rattus norvegicus in small near shore island systems: specifically Tia Island and the Boat group. Unpublished MSc Thesis, University of Otago, Dunedin.

Dietze MC 2017. Ecological forecasting. Princeton, NJ, Princeton University Press.

Efford MG, Fitzgerald BM, Karl BJ, Berben PH 2006. Population dynamics of the ship rat Rattus rattus L. in the Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 33: 273–297.

Efford MG, Karl BJ, Moller H 1988. Population ecology of Mus musculus on Mana Island, New Zealand. Journal of Zoology 216: 539–563.

Frankham R 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Molecular Ecology 24: 2610–2618.

Frankham R, Ballou JD, Ralls K, Eldridge M, Dudash MR, Fenster CB, Lacy RC, Sunnucks P 2017. Genetic management of fragmented animal and plant populations. Oxford University Press, Oxford, UK.

Game ET, Meijaard E, Sheil D, McDonald-Madden E 2014. Conservation in a wicked complex world: challenges and solutions. Conservation Letters 7: 271–277.

García-Díaz P, Anderson DR, Lurgi M 2019a. Evaluating the effects of landscape structure on the recovery of an invasive vertebrate after population control. Landscape Ecology, https://doi.org/10.1007/s10980-019-00796-w.

García-Díaz P, Prowse TAA, Anderson DP, Lurgi M, Binny RN, Cassey P 2019b. A concise guide to developing and using quantitative models in conservation management. Conservation Science and Practice 1: e11.

Groves CR, Game ET 2016. Conservation planning: informed decisions for a healthier planet. Greenwood Village, Colorado, Roberts and Company Publishers.

Harper GA 2006. Habitat use by three rat species (Rattus spp.) on an island without other mammalian predators. New Zealand Journal of Ecology: 321–333.

Holland EP, Binny RN, James A 2018. Optimal control of irrupting pest populations in a climate-driven ecosystem. PeerJ 6: e6146.

Holmes ND, Griffiths R, Pott M, Alifano A, Will D, Wegmann AS, Russell JC 2015. Factors associated with rodent eradication failure. Biological Conservation 185: 8–16.

Innes J in press. Norway rat, Rattus norvegicus (Berkenhout, 1769). In: Handbook of the mammals of New Zealand.

Innes JG, King CM, Flux M, Kimberley MO 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983–87. New Zealand Journal of Zoology 28: 57–78.

Innes J, King CM, Bridgman L, Fitzgerald N, Arnold G, Cox N 2010. Effect of grazing on ship rat density in forest fragments of lowland Waikato, New Zealand. New Zealand Journal of Ecology 34: 227–232.

Jones HP, Holmes ND, Butchart SH, Tershy BR, Kappes PJ, Corkery I, Aguirre-Muñoz A, Armstrong DP, Bonnaud E, Burbidge AA 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113: 4033–4038.

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22: 16–26.

Kelly D, Geldenhuis A, James A, Penelope Holland E, Plank MJ, Brockie RE, Cowan PE, Harper GA, Lee WG, Maitland MJ, Mark AF, Mills JA, Wilson PR, Byrom AE 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. Ecology Letters 16: 90–98.

King CM, Innes JG, Gleeson D, Fitzgerald N, Winstanley T, O'Brien B, Bridgman L, Cox N 2011. Reinvasion by ship rats (Rattus rattus) of forest fragments after eradication. Biological Invasions 13: 2391–2408.

Long J 2003. Introduced mammals of the world: their history, distribution and influence. Melbourne, Australia, CSIRO Publishing.

MacKay JWB, Murphy EC, Anderson SH, Russell JC, Hauber ME, Wilson DJ, Clout MN 2011. A successful mouse eradication explained by site-specific population data. Island invasives: eradication and management. Gland, Switzerland, IUCN. Pp. 198–203.

Miller CJ, Miller TK 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. New Zealand Journal of Ecology 19: 19–27.

Moher D, Liberati A, Tetzlaff J, Altman DG, Prisma Group 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. PLOS medicine 6: e1000097.

Murphy E, Nathan HW in press. House mouse, Mus musculus. In: Handbook of the mammals of New Zealand.

Noble C, Adlam B, Church GM, Esvelt KM, Nowak MA 2018. Current CRISPR gene drive systems are likely to be highly invasive in wild populations. Elife 7: e33423.

Parkes JP, Byrom AE, Edge K-A 2017. Eradicating mammals on New Zealand island reserves: what is left to do? New Zealand Journal of Ecology 41: 263–270.

Parrott L 2017. The modelling spiral for solving ‘wicked’ environmental problems: guidance for stakeholder involvement and collaborative model development. Methods in Ecology and Evolution 8: 1005–1011.

Prowse TA, Cassey P, Ross JV, Pfitzner C, Wittmann TA, Thomas P 2017. Dodging silver bullets: good CRISPR gene-drive design is critical for eradicating exotic vertebrates. Proceedings of the Royal Society B 284: 20170799.

Prowse TAA, Bradshaw CJA, Delean S, Cassey P, Lacy RC, Wells K, Aiello-Lammens ME, Akçakaya HR, Brook BW 2016. An efficient protocol for the global sensitivity analysis of stochastic ecological models. Ecosphere 7: e01238.

Pullin AS, Stewart GB 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology 20: 1647–1656.

Ruscoe WA, Wilson D, McElrea L, McElrea G, Richardson SJ 2004. A house mouse (Mus musculus) population eruption in response to rimu (Dacrydium cupressinum) seedfall in southern New Zealand. New Zealand Journal of Ecology: 259–265.

Ruscoe WR, Pech RP 2010. Rodent outbreaks in New Zealand. In: Singleton GR, Belmain SR, Brown PR, Hardy B eds. Rodent outbreaks: ecology and impacts. Philippines, Los Banos. Pp. 239–251.

Russell JC, Abdelkrim J, Fewster RM 2009. Early colonisation population structure of a Norway rat island invasion. Biological Invasions 11: 1557–1567.

Russell JC, Beaven BM, MacKay JW, Towns DR, Clout MN 2008. Testing island biosecurity systems for invasive rats. Wildlife Research 35: 215–221.

Russell JC, Binnie HR, Oh J, Anderson DP, Samaniego-Herrera A 2016. Optimizing confirmation of invasive species eradication with rapid eradication assessment. Journal of Applied Ecology 54: 160–169.

Russell JC, Clout MN 2004. Modelling the distribution and interaction of introduced rodents on New Zealand offshore islands. Global Ecology and Biogeography 13: 497–507.

Russell JC, Clout MN 2005. Rodent incursions on New Zealand islands. In: Parkes J, Statham M, Edwards G comps. Proceedings of the 13th Australasian vertebrate pest conference. Lincoln, New Zealand, Landcare Research. Pp. 324–330.

Russell JC, Innes J in press. Ship rat, Rattus rattus (Linnaeus, 1758). In: Handbook of the mammals of New Zealand.

Russell JC, Robins JH, Fewster RM 2019. Phylogeography of invasive rats in New Zealand. Frontiers in Ecology and Evolution 7: 48.

Russell JC, Sataruddin NS, Heard AD 2014. Over-invasion by functionally equivalent invasive species. Ecology 95: 2268–2276.

Russell JC, Towns DR, Anderson SH, Clout MN 2005. Intercepting the first rat ashore. Nature 437: 1107.

Schwartz MW, Cook CN, Pressey RL, Pullin AS, Runge MC, Salafsky N, Sutherland WJ, Williamson MA 2018. Decision support frameworks and tools for conservation. Conservation Letters 11: e12385.

Shiels AB, Pitt WC, Sugihara RT, Witmer GW 2014. Biology and impacts of Pacific Island invasive species. 11. Rattus rattus, the Black Rat (Rodentia: Muridae). Pacific Science 68: 145–184.

Tompkins DM, Byrom AE, Pech RP 2013. Predicted responses of invasive mammal communities to climate-related changes in mast frequency in forest ecosystems. Ecological Applications 23: 1075–1085.

Walker S, Kemp JR, Elliott GP, Mosen CC, Innes JG 2019. Spatial patterns and drivers of invasive rodent dynamics in New Zealand forests. Biological Invasions: 1–16.

Wilkins KE, Prowse TAA, Cassey P, Thomas PQ, Ross JV 2018. Pest demography critically determines the viability of synthetic gene drives for population control. Mathematical Biosciences 305: 160–169.

Wilson DJ, Innes JG, Fitzgerald NB, Bartlam S, Watts C, Smale MC 2018. Population dynamics of house mice without mammalian predators and competitors. New Zealand Journal of Ecology 42: 192–203.

Woodford DJ, Richardson DM, MacIsaac HJ, Mandrak NE, van Wilgen BW, Wilson JR, Weyl OL 2016. Confronting the wicked problem of managing biological invasions. NeoBiota 31: 63.

Appendix 1 – List of documents used in the rodent population and spatial ecology synthesis

Abdelkrim J, Byrom AE, Gemmell NJ 2010. Fine-scale genetic structure of mainland invasive *Rattus rattus* populations: implications for restoration of forested conservation areas in New Zealand. Conservation Genetics 11:1 953–1964.

Alterio N, Moller H, Brown K 1999. Trappability and densities of stoats (*Mustela erminea*) and ship rats (*Rattus rattus*) in a South Island Nothofagus forest, New Zealand. New Zealand Journal of Ecology 23: 95–100.

Atkinson UAE 1973. Spread of the ship rat (*Rattus r. rattus* L.) III New Zealand. Journal of the Royal Society of New Zealand 3: 457–472.

Bagasra A, Nathan HW, Mitchell MS, et al. 2016. Tracking invasive rat movements with a systemic biomarker. New Zealand Journal of Ecology 40: 267–272.

Bellingham PJ, Towns DR, Cameron EK, et al. 2010. New Zealand island restoration: seabirds, predators, and the importance of history. New Zealand Journal of Ecology 34: 115-136.

Bettesworth DJ, Anderson GRV 1972. Diet of *Rattus norvegicus* on Whale Island, Bay of Plenty, New Zealand. Tane 18: 189–195.

Blackwell G, Potter M, Minot E 2001. Rodent and predator population dynamics in an eruptive system. Ecological Modelling 142: 227–245.

Blackwell GL 2000. An investigation of the factors regulating house mouse (*Mus musculus*) and ship rat (*Rattus rattus*) population dynamics in forest ecosystems at Lake Waikaremoana, New Zealand. Unpublished PhD thesis, Massey University, Palmerston North.

Blackwell GL, Potter MA, McLennan JA 2002. Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? New Zealand Journal of Ecology 26: 43–51.

Bowie MH, Kavermann M, Ross JG 2010. The Quail Island story-thirteen years of multi-species pest control: successes, failures and lessons learnt. In: Veitch CR, Clout MN, Towns DR eds. Island invasives: Eradication and management. IUCN/SSC and CBB, Auckland, New Zealand. Pp. 157–161

Bridgman LJ 2012. Interactions between ship rats and house mice. Unpublished PhD thesis, University of Waikato.

Brockie RE, Moeed A 1986. Animal biomass in a New Zealand forest compared with other parts of the world. Oecologia 70: 24–34.

Brown KP, Moller H, Innes J, et al. 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. New Zealand Journal of Ecology 30: 271–275.

Carter A, Barr S, Bond C, et al. 2016. Controlling sympatric pest mammal populations in New Zealand with self-resetting, toxicant-free traps: a promising tool for invasive species management. Biological Invasions 18: 1723–1736.

Caughley J, Bomford M, Parker B, et al. 1998. Managing vertebrate pests: rodents. Canberra, Australia, Bureau of Resource Sciences and Grains Research and Development Corporation.

Choquenot D 2006. Bioeconomic modeling in conservation pest management: effect of stoat control on extinction risk of an indigenous New Zealand passerine, *Mohua ochrocephala*. Conservation Biology 20: 480–489.

Christie JE, MacKenzie DI, Greene TC, et al. 2015. Using passive detection devices to monitor occupancy of ship rats (*Rattus rattus*) in New Zealand temperate rainforest. New Zealand Journal of Ecology 39: 79–86.

Christie JE, Wilson PR, Taylor RH, et al. 2017. How elevation affects ship rat (*Rattus rattus*) capture patterns, Mt Misery, New Zealand. New Zealand Journal of Ecology 41: 113–119.

Clapperton BK 2006. A review of the current knowledge of rodent behaviour in relation to control devices. Science & Technical Pub. Wellington, New Zealand, Department of Conservation.

Clout MN 1980. Ship rats (*Rattus rattus* L.) in a *Pinus radiata* plantation. New Zealand Journal of Ecology 3: 141–145.

Clout MN, Denyer K, James RE, et al. 1995. Breeding success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in relation to control of introduced mammals. New Zealand Journal of Ecology 19: 209–212.

Connolly TA, Day TD, King CM 2009. Estimating the potential for reinvasion by mammalian pests through pest-exclusion fencing. Wildlife Research 36: 410–421.

Coutts SR 2005. A stochastic computer simulation of island group colonisation by *Rattus norvegicus* in small near shore island systems: specifically Tia Island and the Boat group. Unpublished PhD thesis, University of Otago.

Daniel MJ 1978. Population ecology of ship and Norway rats in New Zealand. In: Dingwall PR, Atkinson IAE, Hay C eds. The ecology and control of rodents in New Zealand nature reserves. Wellington, Department of Lands and Survey. Pp. 145–152.

Dingwall PR, Atkinson IAE, Hay C 1978. The ecology and control of rodents in New Zealand nature reserves. Wellington, Department of Lands and Survey.

Dowding JE, Murphy EC 1994. Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland, New Zealand. New Zealand Journal of Ecology 18: 19–27.

Efford M 2004. Density estimation in live-trapping studies. Oikos 106: 598–610.

Efford MG, Fitzgerald BM, Karl BJ, et al. 2006. Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 33: 273–297.

Efford MG, Karl BJ, Moller H 1988. Population ecology of *Mus musculus* on Mana Island, New Zealand. Journal of Zoology 216: 539–563.

Empson RA, Miskelly CM 1999. The risks, costs and benefits of using brodifacoum to eradicate rats from Kapiti Island, New Zealand. New Zealand Journal of Ecology 23: 241–254.

Fitzgerald BM, Gibb JA 2001. Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. Biological Conservation 99: 97–108.

Gillies C, Leach M, Coad N, et al. 2003. Six years of intensive pest mammal control at Trounson Kauri Park, a Department of Conservation 'mainland island', June 1996-July 2002. New Zealand Journal of Ecology 30: 399–420.

Gillies CA, Pierce RJ 1999. Secondary poisoning of mammalian predators during possum and rodent control operations at Trounson Kauri Park, Northland, New Zealand. New Zealand Journal of Ecology 23: 183–192.

Girardet SAB, Veitch CR, Craig JL 2001. Bird and rat numbers on Little Barrier Island, New Zealand, over the period of cat eradication 1976–80. New Zealand Journal of Zoology 28: 13–29.

Harper G, Veitch D 2006. Population ecology of Norway rats (*Rattus norvegicus*) and interference competition with Pacific rats (*R. exulans*) on Raoul Island, New Zealand. Wildlife Research 33: 539–548.

Harper GA 2005. Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura. New Zealand Journal of Zoology 32: 155–162.

Harper GA 2006. Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators. New Zealand Journal of Ecology 30: 321–333.

Harper GA, Dickinson KJ, Seddon PJ 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. New Zealand Journal of Ecology 29: 251–260.

Harper GA, Rutherford M 2016. Home range and population density of black rats (*Rattus rattus*) on a seabird island: a case for a marine subsidised effect? New Zealand Journal of Ecology 40: 219–228.

Hickson RE, Moller H, Garrick AS 1986. Poisoning rats on Stewart Island. New Zealand Journal of Ecology 9: 111–121.

Hone J, Duncan RP, Forsyth DM 2010. Estimates of maximum annual population growth rates (rm) of mammals and their application in wildlife management. Journal of Applied Ecology 47: 507–514.

Hooker S, Innes J 1995. Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum. New Zealand Journal of Ecology 22: 291–304.

Innes J in press. Norway rat, *Rattus norvegicus* (Berkenhout, 1769). In: Handbook of the mammals of New Zealand.

Innes J, King CM, Bridgman L, et al. 2010. Effect of grazing on ship rat density in forest fragments of lowland Waikato, New Zealand. New Zealand Journal of Ecology 34: 227–232.

Innes J, Warburton B, Williams D, et al. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. New Zealand Journal of Ecology 19: 5–17.

Innes J, Watts C, Fitzgerald NL, et al. 2011. Behaviour of invader ship rats experimentally released behind a pest-proof fence, Maungatautari, New Zealand. In: Island invasives: eradication and management. Proceedings of the International Conference on Island

Invasives. Gland, Switzerland and Auckland, New Zealand, IUCN (International Union for Conservation of Nature). Pp. 437–440.

Innes JG, King CM, Flux M, et al. 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983–87. New Zealand Journal of Zoology 28: 57–78.

Innes JG, Skipworth JP 1983. Home ranges of ship rats in a small New Zealand forest as revealed by trapping and tracking. New Zealand Journal of Zoology 10: 99–110.

James RE, Clout MN 1996. Nesting success of New Zealand pigeons (*Hemiphaga novaeseelandiae*) in response to a rat (*Rattus rattus*) poisoning programme at Wenderholm Regional Park. New Zealand Journal of Ecology 20: 45–51.

Jones C, Pech R, Forrester G, et al. 2011. Functional responses of an invasive top predator Mustela erminea to invasive meso-predators *Rattus rattus* and *Mus musculus*, in New Zealand forests. Wildlife Research 38: 131–140.

Keedwell RJ, Brown KP 2001. Relative abundance of mammalian predators in the upper Waitaki Basin, South Island, New Zealand. New Zealand Journal of Zoology 28: 31–38.

King C, Innes J, Flux M, et al. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. New Zealand Journal of Ecology 20: 215–240.

King C, Winstanley T, Innes J, et al. 2014. Multiple paternity and differential male breeding success in wild ship rats (*Rattus rattus*). New Zealand Journal of Ecology 38: 76–85.

King CM, Innes JG, Gleeson D, et al. 2011. Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. Biological Invasions 13: 2391–2408. doi: 10.1007/s10530-011-0051-6

Latham JE 2006. The ecology of ship rats (*Rattus rattus*) on Ponui Island: implications for North Island brown kiwi (*Apteryx mantelli*). Unpublished MSc thesis, University of Auckland.

Masuda BM, Jamieson IG 2013. Response of a reintroduced bird population to a rat reinvasion and eradication. New Zealand Journal of Ecology 37: 224–231.

Miller CJ, Miller TK 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. New Zealand Journal of Ecology 19: 19–27.

Miller SD, Russell JC, MacInnes HE, et al. 2010. Multiple paternity in wild populations of invasive *Rattus* species. New Zealand Journal of Ecology 34: 360–363.

Moller H, Tilley JAV 1986. Rodents and their predators in the eastern Bay of Islands. New Zealand Journal of Zoology 13: 563–572.

Moors PJ 1985. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao Islands, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 8: 37–54.

Murphy E, Nathan HW in press. House mouse, *Mus musculu*s. In: Handbook of the mammals of New Zealand.

Murphy EC, Bradfield P 1992. Change in diet of stoats following poisoning of rats in a New Zealand forest. New Zealand Journal of Ecology 16: 137–140.

Murphy EC, Clapperton BK, Bradfield PM, et al. 1998. Effects of rat-poisoning operations on abundance and diet of mustelids in New Zealand podocarp forests. New Zealand Journal of Zoology 25: 315–328.

Norbury G, Byrom A, Pech R, et al. 2013. Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. Ecological Applications 23: 1707–1721.

Nugent G, Warburton B, Thomson C, et al. 2011. Effect of prefeeding, sowing rate and sowing pattern on efficacy of aerial 1080 poisoning of small-mammal pests in New Zealand. Wildlife Research 38: 249–259.

Pryde M, Dilks P, Fraser I 2005. The home range of ship rats *(Rattus rattus*) in beech forest in the Eglinton Valley, Fiordland, New Zealand: a pilot study. New Zealand Journal of Zoology 32: 139–142.

Reardon JT, Whitmore N, Holmes KM, et al. 2012. Predator control allows critically endangered lizards to recover on mainland New Zealand. New Zealand Journal of Ecology 36: 141–150.

Robins JH, Miller SD, Russell JC, et al. 2016. Where did the rats of Big South Cape Island come from? New Zealand Journal of Ecology 40: 229–234.

Ruffell J, Didham RK, Barrett P, et al. 2014. Discriminating the drivers of edge effects on nest predation: forest edges reduce capture rates of ship rats (*Rattus rattus*), a globally invasive nest predator, by altering vegetation structure. PLOS One 9: e113098.

Ruscoe WA, Ramsey DS, Pech RP, et al. 2011. Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. Ecology Letters 14: 1035–1042.

Ruscoe WA, Sweetapple PJ, Perry M, et al. 2013. Effects of spatially extensive control of invasive rats on abundance of native invertebrates in mainland New Zealand forests. Conservation Biology 27: 74–82.

Ruscoe WA, Wilson D, McElrea L, et al. 2004. A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. New Zealand Journal of Ecology 28: 259–265.

Ruscoe WR, Pech RP 2010. Rodent outbreaks in New Zealand. In: Singleton GR, Belmain SR, Brown PR, Hardy B eds. Rodent Outbreaks: Ecology and Impacts. Los Banos, Philippines, International Rice Research Institute. Pp. 239-251.

Russell J 2007. Invasion ecology and genetics of Norway rats on New Zealand islands. Unpublished PhD thesis, University of Auckland.

Russell JC, Abdelkrim J, Fewster RM 2009. Early colonisation population structure of a Norway rat island invasion. Biological Invasions 11: 1557–1567.

Russell JC, Beaven BM, MacKay JW, et al. 2008. Testing island biosecurity systems for invasive rats. Wildlife Research 35: 215–221.

Russell JC, Clout MN 2005. Rodent incursions on New Zealand islands. In: Parkes J, Statham M, Edwards G comps. Proceedings of the 13th Australasian vertebrate pest conference. Lincoln, New Zealand, Landcare Research. Pp. 324–330.

Russell JC, Innes J in press. Ship rat, *Rattus rattus* (Linnaeus, 1758). In: Handbook of the mammals of New Zealand

Russell JC, Mackay JW, Abdelkrim J 2009. Insular pest control within a metapopulation context. Biological Conservation 142: 1404–1410.

Russell JC, McMorland AJ, MacKay JW 2010. Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79: 159–164.

Russell JC, Miller SD, Harper GA, et al. 2010. Survivors or reinvaders? Using genetic assignment to identify invasive pests following eradication. Biological Invasions 12:1 747–1757.

Russell JC, Sataruddin NS, Heard AD 2014. Over-invasion by functionally equivalent invasive species. Ecology 95: 2268–2276. doi: 10.1890/13-1672.1

Russell JC, Towns DR, Anderson SH, et al. 2005. Intercepting the first rat ashore. Nature 437: 1107.

Russell JC, Towns DR, Clout MN 2008. Review of rat invasion biology: implications for island biosecurity. Wellington, Department of Conservation.

Rutherford M, Harper GA, Moller H 2009. Denning behaviour of ship rats (*Rattus rattus*) on Taukihepa, a seabird breeding island. New Zealand Journal of Ecology 36: 343–353.

Shiels AB, Pitt WC, Sugihara RT, et al. 2014. Biology and impacts of Pacific Island invasive species. 11. *Rattus rattus*, the Black Rat (Rodentia: Muridae). Pacific Science 68: 145–184.

Smith DH, Murphy EC, Christie JC, et al. 2009. The effectiveness of poison bait stations at reducing ship rat abundance during an irruption in a *Nothofagus* forest. New Zealand Journal of Zoology 36: 13–21.

Sweetapple PJ, Nugent G 2007. Ship rat demography and diet following possum control in a mixed podocarp—hardwood forest. New Zealand Journal of Ecology 31: 186–201.

Taylor DP 1984. Identification and detection of the rats in New Zealand and the eradication of ship rats on Tawhitinui Island. Unpublished PhD thesis, Lincoln College, University of Canterbury.

Taylor RH 1978. Distribution and interactions of rodent species in New Zealand. Dingwall PR, Atkinson IA, Hay C comps: The ecology and control of rodents in New Zealand nature reserves. Wellington, New Zealand, Department of Lands and Survey Information Series. Pp. 135–143.

Thomas MD, Brown JA, Henderson RJ, et al. 1999. Feasibility of using wax-blocks to measure rat and possum abundance in native forest. In: Proceedings of the New Zealand Plant Protection Conference. New Zealand Plant Protection Society;. Pp. 125–129.

Tompkins DM, Byrom AE, Pech RP 2013. Predicted responses of invasive mammal communities to climate-related changes in mast frequency in forest ecosystems. Ecological Applications 23: 1075–1085.

Tompkins DM, Veltman CJ 2006. Unexpected consequences of vertebrate pest control: predictions from a four-species community model. Ecological Applications 16: 1050–1061.

Watkins AF, McWhirter JL, King CM 2010. Patchiness in distribution of rodents and mustelids in New Zealand forests. Wildlife Research 37: 13–18.

Watkins AF, McWhirter JL, King CM 2010. Variable detectability in long-term population surveys of small mammals. European Journal of Wildlife Research 56: 261–274.

Weihong JI, Veitch CR, Craig JL 1999. An evaluation of the efficiency of rodent trapping methods: the effect of trap arrangement, cover type, and bait. New Zealand Journal of Ecology 23: 45–51.

Wilson DJ, Efford MG, Brown SJ, et al. 2007. Estimating density of ship rats in New Zealand forests by capture-mark-recapture trapping. New Zealand Journal of Ecology 31: 47–59.

Wilson DJ, Wright EF, Canham CD, et al. 2007. Neighbourhood analyses of tree seed predation by introduced rodents in a New Zealand temperate rainforest. Ecography 30: 105–119.

Wilson PR, Karl BJ, Toft RJ, et al. 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. Biological Conservation 83: 175–185.