Responses to pest control in Nelson beech forests

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Abstract

Being responsible for some of the greatest losses to native biodiversity in New Zealand, brushtail possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*) and ship rats (*Rattus rattus*) are the main targets of predator control. The common methods used to control these species include trapping, poison bait stations, and aerially applied sodium fluoroacetate (1080). In New Zealand beech (*Nothofagus* spp.) forests, the outcome of predator control operations can be difficult to predict due to species interactions, variation in beech seedfall, and altitude. The objective of my study was to determine the effect of different pest control methods (trapping, and poisoning with diphacinone, pindone or 1080, both ground based and aerial) on ship rat and common forest bird populations, particularly how these effects are influenced by altitudinal gradients and beech masting events.

This study used long-term tracking tunnel and five-minute bird count (5MBC) data from areas of beech forest at six treatment and one non-treatment sites in Kahurangi and Nelson Lakes National Parks, South Island, New Zealand. The monitoring data were collected at a range of altitudes and time spans over the course of 14 years (2002-2015), spanning a range in beech seedfall levels including several high-seed years, and an altitudinal range of 600-1450 m a.s.l.

The only pest control method analysed here that effectively reduced ship rat abundance was 1080 application. The efficacy of 1080 was not affected by beech seedfall levels but was reduced with altitude since ship rat abundance is greatly reduced above 1000 m a.s.l. The 12 most common bird species detected across all sites included four introduced and eight native species. Most native bird species showed significant declines in response to increased ship rat abundance, and the effect of this was reduced with altitude, indicating that high altitude is a refuge for native birds to escape predation. This study also found evidence for mesopredator release of ship rats following stoat control, and for competition between native and introduced bird species; however both of these findings require further study.

Analysis of the long-term data sets confirmed some findings from previous studies but found contrary results to others, which indicated important avenues for future research. This study also highlights the importance of long-term data sets and applying pest control treatments in a standardized way that allows us to optimize methods to manage introduced species for native species conservation.

Chapter 1. Introduction

Pest control operations are a key component of native ecosystem conservation and restoration in New Zealand forests (Clout 2001, Saunders & Norton 2001, Kelly et al. 2005, Innes et al. 2010, Pech & Maitland 2016). Introduced mammalian pests are responsible for altering the foliar composition of native forests as well as competing with and/or preying upon the vulnerable indigenous fauna (Innes et al. 1999, Craig et al. 2000, Moorhouse et al. 2003, Baber et al. 2009, Elliott et al. 2010, Innes et al. 2010). Although there are many examples of successful pest management efforts in New Zealand (e.g. Dilks 1999, Gillies et al. 2003, Whitehead et al. 2008, Starling-Windhof, Massaro & Briskie 2011, O'Donnell & Hoare 2012, Byrom, Innes & Binny 2016), bird and mammal population responses to pest control are still difficult to predict. Food availability, species interactions, and environmental gradients such as altitude can alter faunal responses to different pest control methods, but little is known about how these factors interact to produce differing results within New Zealand forest ecosystems (Beggs 1991, Rayner et al. 2007, Langham & Kelly 2011, Christie et al. 2017, O’Donnell, Weston & Monks 2017).

1.1 Mammalian predators in New Zealand

The colonization of New Zealand, first by Polynesians and then by Europeans, led to the introduction of a variety of invasive pest species including mammalian predators, the likes of which were not previously found in the New Zealand archipelago (Holdaway 1989, Craig et al. 2000, King 2005). Of the 32 introduced mammalian species that established wild populations in New Zealand (King 2005), some of the greatest losses to native biodiversity have been from brushtail possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*) and ship rats (*Rattus rattus*), all of which prey on native animals while the first two also damage native vegetation (Craig et al. 2000, Saunders & Norton 2001, Innes et al. 2010). In addition to this, introduced possums have been responsible for the spread of bovine tuberculosis (*Mycobacterium bovis*) through farmed cattle and red deer in New Zealand (Livingstone et al. 2015, Warburton & Livingstone 2015). Stoats, ship rats, and brushtail possums were either introduced to New Zealand intentionally for economic and biological benefits (possums for fur, stoats to control rabbits) or unintentionally as stowaways (ship rats), and since their introductions, have established populations throughout nearly all of New Zealand’s mainland (the North, South and Stewart Islands) and on many smaller offshore islands (Cowan 2005, Innes 2005, King & Murphy 2005).

Stoat - *Mustela erminea*

Stoats were intentionally imported into New Zealand in the 1880s to control rabbit populations that were damaging sheep pastures to the detriment of the colonial economy (King & Murphy 2005). Within six years of their liberation, sightings of stoats were recorded in forests and other areas far from release sites or any rabbit populations, and it is likely that stoats spread throughout both main islands before the end of the nineteenth century (King & Murphy 2005), although they have never reached Stewart Island/Rakiura. Since their establishment, stoats have played a major role in the extinction and decline of a number of native bird populations and have been termed "one of the worst ecological mistakes made by European colonists in New Zealand" (King & Murphy 2005).

Stoats are very active and thorough searchers of prey, and will kill animals much larger than themselves (Moors 1983, King & Murphy 2005). Stoats are opportunistic consumers and in New Zealand their diet consists of a variety of birds, insects, rodents (rats and mice), lagomorphs (rabbits and hares indistinguishable in gut contents), possums and lizards (King & Moody 1982, Murphy, E. C. & Dowding 1994, Smith, D. H. V. et al. 2008). Stoat populations are able to significantly increase as a direct response to increased availability of food. For example, during high-seed years in native New Zealand beech (*Nothofagus* spp.) forests, the populations of rodents increase dramatically and this is followed by an increase in stoat populations (King & Murphy 2005). The increased numbers of stoats subsequently reduce native forest bird populations (see section 1.6 for further detail on beech mast events).

Ship Rat – *Rattus rattus*

Ship rats made their way to New Zealand with the European settlers aboard their ships as stowaways and subsequently spread throughout the North and South islands in the late 1800s also reaching Stewart Island/Rakiura, and approximately 60 smaller offshore islands (Atkinson 1973, Innes 2005). The reasons that they did not arrive with earlier European sailors between 1769 and the late 1880s are unclear (Atkinson 1973). Although there are three *Rattus* species present in New Zealand: the kiore or Pacific rat (*R. exulans*), the Norwegian rat (*R. norvegicus*), and the ship rat or black rat (R. rattus), the ship rat is by far the most arboreal of the three, is likely to have had the most significant negative impact on native New Zealand wildlife, and is the most widely distributed *Rattus* species in New Zealand (Innes 2005).

Ship rats are omnivorous generalists, eating both plant and animal foods, but are also known to be selective (Innes 2005, McQueen & Lawrence 2008). In New Zealand, ship rats feed on seeds, fruits, other plant matter and invertebrates (Miller & Miller 1995, Sweetapple & Nugent 2007, McQueen & Lawrence 2008), as well as forest birds' eggs, chicks, and incubating adults (Brown 1997, Brown et al. 1998b, Innes et al. 1999, McQueen & Lawrence 2008). Although bird matter does not always make up a large proportion of the ship rat diet (McQueen & Lawrence 2008), the wide distribution of ship rats and the high numbers that their populations are able to reach (particularly during a beech mast), means the number of birds consumed is enough to threaten the viability of some native forest bird populations.

Brushtail possum - *Trichosurus vulpecula*

The first successful introduction of brushtail possums from Australia to New Zealand took place in the late 1850s with the intention of establishing a fur trade (Cowan 2005). Possums subsequently spread through the North and South Islands and to Stewart Island/Rakiura and a national fur industry was established, however the negative effects of brushtail possums in New Zealand soon became apparent to both farmers and conservationists (Cowan 2005, Clout 2006). In New Zealand brushtail possums have adapted new diets and habitats, and have fewer natural parasites and predators compared to Australian populations and these differences have led to greatly increased population densities, increasing the amount of damage they cause to the native flora and fauna (Cowan 2005).

Possum selective browsing in New Zealand forests leads to changes in forest composition and structure and the disappearance or severe reduction of preferred species, e.g. fuchsia (*Fuchsia exortica*), titoki (*Alectryon excelsus*), kāmahi (*Weinmannia racemosa*), southern rātā (*Metrosideros umbellata*), and tawa (*Beilchmiedia tawa*), from areas with high possum densities (Fitzgerald, A. E. & Wardle 1979, Sweetapple, Fraser & Knightbridge 2004, Cowan 2005, Clout 2006). Although brushtail possums were initially thought to be primarily herbivorous, they are now known to also feed on native invertebrates, eggs, and nestlings (Fitzgerald, A. E. & Wardle 1979, Cowan & Moeed 1987, Sweetapple et al. 2004, Clout 2006). As herbivores, competitors, predators, and disease vectors, brushtail possums pose a major threat to native wildlife in New Zealand as well as to the agricultural industry (Cowan 2005, Clout 2006, Elliott et al. 2010, Warburton & Livingstone 2015).

1.2 Mammal impacts on the New Zealand avifauna

A total of 41.4 % of endemic bird species and 31 % of all bird species breeding in New Zealand in pre-human times have become locally or globally extinct since the arrival of humans (Holdaway, Worthy & Tennyson 2001). Although habitat loss and fragmentation had some influence, invasive alien species, in particular predation by introduced mammals, have been identified as the leading cause of decline for native New Zealand birds (Clout 2001, Saunders & Norton 2001, Innes et al. 2010, Elliott & Kemp 2016). A lack of evolutionary history with mammalian predators means that native New

Zealand birds, as with many other island bird species, are particularly vulnerable to predation because they do not have anti predator behaviours appropriate for mammals (Holdaway 1989, Maloney & McLean 1995, Sanders & Maloney 2002, Stanbury & Briskie 2015). As a result many native birds have suffered range contractions, population declines, or extinctions as a consequence of predation and competition with introduced pests (Craig et al. 2000, Saunders & Norton 2001, Innes et al. 2010).

Evidence of mammalian predation on New Zealand forest birds is common in the literature. Stoats, ship rats, and/or brushtail possums are associated with the decline of kiwi (*Apteryx spp.*) (McLennan et al. 1996, Basse, McLennan & Wake 1999), North Island kōkako (*Callaes cineria wilsoni*) (Innes et al. 1999), yellow crowned parakeets (kākāriki, *Cyanoramphus auriceps*) (Elliott, Dilks & O'Donnell 1996, O’Donnell 1996), New Zealand pigeons, (kererū, *Hemiphaga novaeseelandiae*) (Powlesland, R. G. et al. 2003), yellowheads (mohua, *Mohua ochrocephala*) (Elliott 1996, Dilks 1999, Dilks et al. 2003), kākā (*Nestor meridionalis*) (Beggs & Wilson 1991, Dilks et al. 2003, Moorhouse et al. 2003), and robins and tomtits (*Petroica spp.*) (Brown 1997 Remeš, Matysioková & Cockburn 2012). Predation by introduced mammals is also associated with the extinctions of endemic species including the South Island kōkako (*Callaes c. cinerea*) and piopio (*Turnagra capensis*) (King & Murphy 2005). Although more than 30 % of New Zealand’s total land area is formally reserved for conservation (Craig et al. 2000, Saunders & Norton 2001) native species are still declining in these areas when their predators are not effectively managed (Clout 2001, Saunders & Norton 2001).

1.3 Mammalian predator control methods

Given the evidence of the negative effects of introduced mammalian predators on native bird populations, it is not surprising that a number of efforts have been made on their control or eradication. Predator control methods vary in intensity from intermittent or seasonally targeted control, to sustained control, or complete eradication of the target species (Saunders & Norton 2001, Courchamp, Chapuis & Pascal 2003, Parkes & Murphy 2003, Parkes et al. 2017). Although eradication of pests is favoured, it is rarely a feasible option on the mainland, so sustained control and seasonal control are the most common methods used (Parkes & Murphy 2003, Parkes et al. 2017). Stoats, brushtail possums, and ship rats are the main targets of predator control on the New Zealand mainland and the regular methods used include targeted trapping, poison bait stations, and aerially applied sodium fluoroacetate (1080) (Craig et al. 2000, Parkes & Murphy 2003, Baber et al. 2009, Green & Rohan 2012, O'Donnell & Hoare 2012, Russell et al. 2015).

Trapping

Targeted trapping is used to control stoats, brushtail possums, and sometimes ship rats with the key advantage of being able to exclude or reduce the unintentional capture of native birds, thereby reducing non-target mortality (Courchamp et al. 2003). Managing stoat populations with targeted trapping has been successful in reducing predation on native bird populations such as North Island brown kiwi (*A.mantelli*), bellbirds (korimako, *Anthornis melanura*), blue ducks (whio, *Hymenolaimus malacorhynchos*), and kākā (Gillies et al. 2003, Moorhouse et al. 2003, Kelly et al. 2005, Whitehead et al. 2008). However, individual stoats can learn to become wary and avoid traps thus maintaining stoat trapping networks can be labour intensive and costly (King & Murphy 2005).

Rats are a by-catch in stoat traps (Christie et al. 2006) and targeted snap-trapping of rats is often done in conjunction with stoat trapping with the purpose of keeping stoat traps clear of rats, and sometimes with the aim of controlling the rats themselves. Possum trapping is often carried out in conjunction with other control methods e.g. poisoning with 1080, cyanide, or various anticoagulants (Cowan 1992, Innes et al. 1999, Courchamp et al. 2003, Cowan 2005).

Ground-based toxins

A variety of toxins are used to directly target ship rats and brushtail possums, and sometimes stoats through secondary poisoning (Brown, Alterio & Molleir 1998a, Murphy, E. C. et al. 1998, Moorhouse et al. 2003, Long et al. 2016). Ground based poison operations typically employ the use of bait station networks for seasonally targeted or sustained control and a variety of toxins have been used in these bait stations including brodifacoum, diphacinone, pindone, cyanide, and 1080 (Innes & Barker 1999, Warburton & Thomson 2002, Courchamp et al. 2003, Parkes & Murphy 2003, Parkes et al. 2017).

Some toxins have been proven more successful than others, for example Eason et al. (1993) found that poisoning with brodifacoum was more effective at reducing possum densities than pindone. Furthermore, brodifacoum is also successful at reducing ship rat populations (Eason et al. 1993, Innes et al. 1995, Parkes et al. 2017) but it is now used less regularly for pest control because it is not as readily degradable, which means it builds up in food chains and has higher associated dangers of non-target mortality than other toxins such as 1080 (Dowding, Murphy & Veitch 1999, Innes & Barker 1999).

Other anticoagulants, such as diphacinone, have also been applied with varied success due to bait shyness and lowered bait uptake when natural food sources are abundant (Harper, G. et al. 2013). In ground based poison operations, 1080 has been used (e.g. Alterio 2000, Gillies et al. 2003), but since it is readily biodegradable and does not persist in the environment to the degree that anticoagulants can, 1080 is also used in aerial control operations (Murphy, E. C. et al. 1999, Warburton & Livingstone 2015). Ground based pest control can be costly and difficult to maintain over large areas and cannot cover areas inaccessible by foot, therefore aerial toxin application is often the preferred method of control (Parkes & Murphy 2003, Warburton & Livingstone 2015, Parkes et al. 2017).

Aerially applied 1080

In the past, aerial application of 1080 has primarily been used for large-scale possum control (Coleman, Fraser & Nugent 2007, Green & Rohan 2012, Van Klink, Kemp & O'Donnell 2013) and has been shown to result in more than 90% mortality rates in possum populations (Coleman et al. 2007). Controlling invasive possum populations by the Animal Health Board (later renamed Tb Free New Zealand and subsequently OSPRI) has helped New Zealand's agricultural industry by reducing infection rates of bovine tuberculosis (Tb, *Mycobacterium bovis*) while also helping native flora and fauna through associated reductions in predation on nesting birds and herbivory on palatable native plants (Warburton & Livingstone 2015). Other mammals, e.g. rats, stoats and deer, are also susceptible to 1080 poisoning, providing even further benefits to native birds and plants through reduced predation (Nugent & Morriss 2013, Warburton & Livingstone 2015).

Studies investigating the direct impact of 1080 poisoning on non-target native species have found evidence of 1080 residue in dead birds including South Island fernbirds (mātātā, *Bowdleria punctata*), kea (*Nestor notabilis*), and North Island tomtits (miromiro, *Petroica macrocephala toitoi*) (Powlesland, R. G., Knegtmans & Styche 2000, Veltman & Westbrooke 2011, Van Klink et al. 2013) but field studies have concluded that the negative effect of direct mortality resulting from poisoning is outweighed by the benefits to the survivors from reduced predation that lead to subsequent overall increases in survival and nesting success in these bird populations (Eason et al. 2011, Schadewinkel et al. 2014). More recently it is also becoming apparent that direct impacts of 1080 poisoning on non-target natives have been greatly reduced due to the advances in bait delivery technologies (Orr-Walker et al. 2012, Greene, T. C. et al. 2013, Clapperton et al. 2014, Morriss, Nugent & Whitford 2016).

1.4 Species interactions

Due to interactions between predators, effective targeted control of one pest species can have inadvertent, and sometimes negative, consequences for other important species within the system (Murphy, E. C. & Bradfield 1992, Zavaleta, Hobbs & Mooney 2001, Tompkins & Veltman 2006, Rayner et al. 2007, Ruscoe et al. 2011). Although pest control has regularly resulted in lower predation rates for many bird species, control programs may target only one or two pest species, which can produce an unfavourable response elsewhere in the system (Tompkins & Veltman 2006, Rayner et al. 2007, Ruscoe et al. 2011, Tompkins, Byrom & Pech 2013). The duration of benefits from a successful control operation are also variable since some target species are able to recover within 1-2 years for stoats and as little as 3-6 months for ship rats, compared to around 6 years for brushtail possums (Innes et al. 1995, Nugent et al. 2010, Griffiths & Barron 2016). Therefore care must be taken to consider the population dynamics of other species and the wider ecosystem as well as the target species when applying predator control.

Mesopredator/competitive release

In the absence of a dominant or apex predator, smaller omnivores and predators can undergo significant population increases due to release from predation, known as mesopredator release (Soulé et al. 1988, Crooks & Soulé 1999, Ritchie & Johnson 2009). Similarly, control of a target species can result in competitive release of a non-target species through reduced competition for resources (Caut et al. 2007, Trewby et al. 2008, Ruscoe et al. 2011).

Both mesopredator and competitive release can have detrimental effects on prey species that are more susceptible to the released predator than to the controlled one (Prugh et al. 2009). For example, disappearance of a top predator, the coyote (*Canis latrans*), from urbanised areas of California allowed several mesopredator populations to increase, resulting in local extinctions of native scrub-breeding birds (Crooks & Soulé 1999). Mesopredator release has also been demonstrated in New Zealand with the endemic Cook's petrel (tītī, *Pterodroma cookii*) suffering reduced nesting success following the eradication of cats (*Felis catus*) and subsequent increases in kiore on Little Barrier Island/Hauturu (Rayner et al. 2007). Mesopredator release is also demonstrated in ship rat populations following the control of stoats (Tompkins & Veltman 2006, Masuda, McLean & Gaze 2014). However, Ruscoe et al. (2011) found that at some North Island sites rat abundance was unaffected by stoat control and was instead only sensitive to changes in brushtail possum abundance, apparently due to competitive release. This suggests that rat populations are regulated by food resources and not by predation. The possibility of competitive release and/or mesopredator release of ship rats following the control of possums and/or stoats must therefore be included as a key risk when designing a predator control operation and measuring its success.

Competition with introduced birds

Recent reviews have indicated that introduced birds can have a strong negative impact on native bird populations through predation and competition (Baker, Harvey & French 2014, Martin-

Albarracin et al. 2015) but little is known about negative interactions between introduced and native bird populations in New Zealand (Massaro, Stanbury & Briskie 2013, Lawrence et al. 2016). The introduced European starling (*Sturnus vulgaris*) is a nest predator of the endangered native New Zealand black robin (toutouwai, *Petroica traversi*) and has been recorded taking over nesting sites from both black robins and orange fronted parakeets (kākāriki, *Cyanoramphus malherbi*) and (Kearvell 2013, Massaro et al. 2013, Lawrence et al. 2016) and the introduced common myna (*Acridotheres tristis*) has also been implicated in reducing populations of native birds on Moturoa island through predation and competition (Tindall, Ralph & Clout 2007). However, there are no confirmed cases of interspecific competition with introduced birds being the primary cause of decline in a native species, and the role of introduced birds as predators and competitors of native birds in New Zealand has gained relatively little attention (Innes et al. 2010, Lawrence et al. 2016).

1.5 Environmental interactions

Beech masting

It is widely recognised internationally that mast seeding events (the intermittent mass production of seed by a plant population, Kelly 1994) are followed by a number of population eruptions by other species in the community (Wolff 1996, Ostfeld & Keesing 2000, Alley et al. 2001, Kelly, Koenig & Liebhold 2008a, Bergeron et al. 2011). Southern beech (*Nothofagus* spp.) forests in New Zealand experience mast seeding events that occur at irregular intervals in response to particular temperature cues (Schauber et al. 2002, Kelly et al. 2013). The added source of food provided by a high-seed year allows rodent (rat and mouse) populations in these forests to irrupt, followed by an increase in stoat populations that prey upon the rodents (King 1983, Choquenot & Ruscoe 2000, Kelly et al. 2008a). Several native seed-eating birds also directly benefit from the increased food supply that masting provides, for example in beech forests kākā only nest during mast years and yellow-crowned parakeets re-nest more often and over a longer season with increased seedfall (Elliott et al. 1996, Wilson et al. 1998, Dilks et al. 2003). Unfortunately for these birds, losses due to increased predation from concurrent population increases in stoats and ship rats outweigh the benefits provided by increased food supplies if predator populations are not effectively managed (McQueen & Lawrence 2008, Tompkins et al. 2013).

Altitude

Environmental gradients such as altitude also affect the distribution of both birds and mammals. In New Zealand, ship rat abundance appears to decline strongly with altitude. Ship rats have an effective upper limit of around 1000 m a.s.l. (Christie et al. 2017) and bird population distributions also vary with elevation; some species are more common at mid to high altitudes, e.g. rifleman (tītīpounamu, *Acanthisitta chloris*) and brown creeper (pīpipi, *Mohoua novaeseelandiae*), while others are more common at lower altitudes e.g. bellbird and tū (*Prosthemadera novaeseelandiae*) (Elliott et al. 2010, Langham & Kelly 2011). Competition, predation, and food resources also vary across these gradients (Wardle 1984, Moeed & Meads 1985, Beggs 1991, Christie et al. 2006, Elliott et al. 2010) therefore the relationship between altitude and local species composition and abundance is not surprising. Due to these altitudinal differences in species composition, some predator control operations may result in unexpected altitudinal shifts by different species when the pressures of competition and/or predation are altered (Rayner et al. 2007, Elliott et al. 2010, Langham & Kelly 2011).

1.6 Measuring success

Effectively measuring the results of a pest control operation is almost as important as the pest control itself. It is essential to measure the outcomes of pest management in order to evaluate success or potential failure, and to guide future management strategies (Sweetapple & Nugent 2011, MacLeod et al. 2012, Greene, T. C. et al. 2013, Christie et al. 2015). Wildlife monitoring is common practice in New Zealand where bird and mammal abundances are frequently monitored to quantify the effects of pest control and to detect changes in native biodiversity (e.g. Whitehead et al. 2008, Greene, T. C. et al. 2013, Masuda et al. 2014). It is important that these monitoring techniques are standardised to enable comparisons to be made across time and space (Hartley 2012). Various techniques are used to monitor bird and mammal abundance and the chosen method will depend on the particulars of the study and any existing resource constraints (Courchamp et al. 2003, Sweetapple & Nugent 2011).

The five-minute bird count (5MBC) as first described by Dawson & Bull (1975) has been the standard method used to measure bird abundance in New Zealand since the 1970s and has been used in over 260 studies across New Zealand (Hartley 2012, Masuda et al. 2014). Studies use 5MBC data to analyse long-term, pre- versus post-treatment, or treatment versus non-treatment changes in bird abundance (e.g. Elliott et al. 2010, Greene, T. C. et al. 2013, Hoare, Monks & O'Donnell 2013, Iles & Kelly 2014). Five minute bird counts are advantageous because multiple species can be counted simultaneously and large numbers of counts can be undertaken using relatively little time, money and equipment (Dawson & Bull 1975, Hartley & Greene 2012). Additionally, because 5MBCs have been the standard method applied in New Zealand for such an extended period, analysis of long-term trends requires the continued use of this method so that mismatching collection techniques do not confound data comparisons.

Changes in bird abundance can be used to determine the effectiveness of a given predator control regime. For example, an increase in kākā (*Nestor meridionalis*) abundance in an area of targeted stoat control could indicate that predator management has been successful. However, it is important to measure mammal abundance (biodiversity outputs) directly, and not just control effort (management inputs), in order to more accurately test for interactions between predators and explain any disparity found in bird responses to control techniques (Langham & Kelly 2011). Mammal populations within forest habitats may be monitored using tracking tunnels, wax tags, chew cards, hair tubes, trail cameras, mark-recapture trapping or kill traps depending on the focal species, objectives, and funding (Sweetapple & Nugent 2011). Some studies use only one method such as tracking tunnels (e.g. Dilks et al. 2003, Kelly et al. 2005, Whitehead et al. 2008) but a combination of methods is often required to monitor a variety of mammals and detect them efficiently. For example, Ruscoe et al. 2011 used hair tubes and tracking tunnels for monitoring stoat abundance, and mark-recapture techniques to monitor mouse, rat and possum populations, all within the same study. Possums are often monitored using leg-hold kill traps, wax tags or chew cards, while stoats and rodents are most often monitored with tracking tunnels or chew cards (Sweetapple & Nugent 2011, Pickerell et al. 2014).

Monitoring mammals can be time consuming, costly, and difficult after pest control operations due to low densities resulting in low detectability (Sweetapple & Nugent 2011, Christie et al. 2015). When a combination of methods is feasible, tracking tunnels and chew cards can be used together to effectively detect stoats, ship rats, and brushtail possums at relatively low costs in time and money, and are regularly used for mammal monitoring in New Zealand by DOC, the AHB, and various volunteer organisations.

1.7 Thesis outline and objectives

In New Zealand beech forests, the outcome of a given predator control operation can be difficult to predict due to species interactions, variation in beech seedfall, and altitude. The benefits of predator control may also be short-lived if predator populations are able to recover quickly following operations (Ruscoe et al. 2011, Parkes et al. 2017). Although ship rats are only one of three main targets of predator control (along with stoats and brushtail possums), within this study I focus on ship rats because they are important predators of native birds, show strong altitudinal variations in their distribution, have been variously controlled either effectively or ineffectively with a variety of methods, are able to recover quickly from pest control operations, and respond strongly to high-seed years. As well as analysing ship rat responses to pest control I will also focus on responses of common forest bird species within beech forest communities. Common species are important for ecosystem structure and function and since they are the most abundant species, changes in their population densities and distributions will be easier to detect than for rare species, which would often require a species-specific monitoring programme.

This study takes advantage of the use of consistent wildlife monitoring techniques that have provided long-term data sets for pest mammal and common forest bird abundance over the course of various pest control operations in areas of native mixed beech forest in the upper South Island, New Zealand. Using tracking tunnels and five-minute bird counts, both birds and mammals have been consistently monitored through beech masting events from approximately 400-1450 m a.s.l. in Nelson Lakes and Kahurangi National Parks. Therefore, the overall objective of my study was to determine the effect of different pest control methods (targeted trapping, and poisoning with diphacinone, pindone or 1080, both ground based and aerial) on ship rat and forest bird populations, with a specific focus on how these effects are influenced by altitudinal gradients and beech masting events. Specifically, I address the following questions:

Ship rats (Chapter 3)

1. How does ship rat abundance vary with altitude?
2. How does ship rat abundance respond to beech seedfall events?
3. Which pest control regime is most effective at reducing ship rat abundance?
4. Do ship rat responses to pest control vary with altitude?
5. Is the efficacy of ship rat control altered by beech masting events?

Birds (Chapter 4)

1. How does forest bird abundance vary with altitude?
2. How does forest bird abundance respond to beech seedfall events?
3. How does forest bird abundance respond to ship rat abundance?
4. How does forest bird abundance respond to different pest control methods?
5. Do bird responses to ship rat populations vary with altitude and/or beech seedfall?

Chapter 2. Study sites and methods

2.1 Site selection

Two sites from Kahurangi National Park and five sites (including one non-treatment site) from Nelson Lakes National Park were chosen for this study because of their similarities in habitat type, the long-standing data sets that are available, and because together they reflect a range of pest control methods that are most commonly used in New Zealand forests. Stoats, ship rats, and possums tend to be the main targets of mammal control in New Zealand and the common methods used to control these include trapping, poison bait stations, and aerially applied 1080, all of which are represented within my study sites.

All study sites are located within National Parks (protected areas administered by DOC) in the upper South Island of New Zealand. Each site contains habitat characteristic of the mixed beech (*Nothofagus* spp.) forest type commonly found in the northern South Island, representing approximately 22 % of New Zealand’s total native forest cover (Wardle 1984). These mixed beech forests are dominated by red beech (*Nothofagus fusca*), silver beech (*N. menziesii*), and mountain beech (*N. solandri* var. *cliffortioides*). Because all sites are within areas of beech forest they have all experienced variable mast seed crops with the associated animal population changes, the effects of which have been monitored for both birds and mammals. A recent revision (Heenan & Smissen 2013) suggested splitting *Nothofagus* into separate genera (in New Zealand, *Fuscospora* and *Lophozonia*) but in this thesis I follow the older taxonomic treatment.

Birds and mammals have been monitored within these sites for between three and 20 years by the Department of Conservation (DOC), University of Canterbury (UC), Friends of Cobb (FOC), Friends of Flora (FOF), with the help of the Animal Health Board (AHB) (more detail in site descriptions; sections 2.2 and 2.3). Wildlife monitoring over the years has therefore provided an extensive data log for these sites which covers the responses of birds and mammals to a variety of pest control techniques and beech masting events at different altitudes with an appropriately comparative non-treatment site.

Table 2.1 Names and locations of the seven sites that were used within this study.

Area	Site	Latitude	Longitude
Kahurangi	Cobb	41°13'S	172°61'E
Kahurangi	Flora	41°18'S	172°73'E
Nelson Lakes	Big Bush	41°79'S	172°84'E
Nelson Lakes	Lakehead	41°83'S	172°83'E
Nelson Lakes	Rotoiti core	41°82'S	172°86'E
Nelson Lakes	Rotoiti new	41°80'S	172°88'E
Nelson Lakes	Rotoroa	41.92'S	172.67'E

2.2 Nelson Lakes National Park

Nelson Lakes National Park includes an area of 101,733 ha situated in the northern South Island of New Zealand within the northern most ranges of the Southern Alps. The Rotoiti Nature Recovery Project (RNRP) is a mainland island project within the National Park that currently includes approximately 5000 ha managed by DOC and an additional 5000 ha managed by the volunteer group Friends of Rotoiti (FOR) (Long et al. 2016). It is one of six mainland island projects funded within a national programme that focuses on the ecological restoration and conservation of various native habitats in New Zealand (Butler 2000, Saunders & Norton 2001).

The RNRP and adjacent non-treatment site, Rotoroa, lie within an expanse of cool-temperate, original mixed beech forest with an average annual rainfall between 2000 and 3000 mm. Vegetation here has been classified into five altitudinal zones; silver/red beech with mataī (*Prumnopitys taxifolia*) and kahikatea (*Dacrycarpus dacrydioides*) (455–475m a.s.l); red/silver beech (485-540 m a.s.l); red/silver beech with kamahi (*Weinmannia racemosa*) or mountain beech (550-1020 m a.s.l); mountain/silver beech (1050-1425 m a.s.l); and tussock grassland (*Chionochloa* spp.) (1455-1590 m a.s.l) (Beggs 1991). There are high densities of endemic scale insects (*Ultracoelostoma* spp.) up to around 800 m a.s.l that provide an important food resource to the system in the form of honeydew (Beggs 1991, Elliott et al. 2010). The avifauna includes several common introduced species, a range of relatively common widespread native species (for a full list see Chapter 3), and some less common native species including great spotted kiwi (roroa, *Apteryx haastii*), yellow crowned parakeets, kākā, and kea (*Nestor notabilis*) which have been the focus of a lot of conservation efforts within the RNRP (Elliott et al. 2010, Long et al. 2016).

The RNRP was established in the spring of 1996 with the first year of monitoring carried out in 1996/1997 and subsequent pest control initially undertaken in 1997/1998 (Butler 2000). The main targets of pest control are cats (*Felis catus*), stoats, ship rats, possums, and wasps (*Vespula* spp.). There are four treatment sites within the RNRP; Rotoiti core, Lakehead, Big Bush, and Rotoiti “new” (Table 2.1). The adjacent non-treatment site, Rotoroa, is also monitored by the RNRP. Although the

RNRP was established in 1997, here I will concentrate on data from 2002 onwards because of gaps in bird monitoring at the non-treatment site (i.e. no counts between February 1996 and February 2002) and lack of mammal monitoring at the non-treatment site pre-2002.

Rotoiti core

When the RNRP was established, the total area managed included 825 ha and since the expansion of the project, this area has been named the Rotoiti core site. Rotoiti core is situated on the slopes of the St Arnaud range; bordering Lake Rotoiti and the St Arnaud Village (Figure 2.1). Stoats, ship rats, and possums have all been targeted for control here with some control programs more sustained than others. Possums and stoats have been controlled consistently within the Rotoiti core site since the project commenced, by way of targeted poisoning and/or trapping (Table 2.2). Rodents have not been controlled constantly within the core site and the methods that have been used include bait stations with brodifacoum (pre-2002), targeted trapping, aerial 1080 poisoning, and bait stations with 1080, diphacinone, or pindone (post-2002) (Table 2.2). Bird and mammal populations have been monitored here by DOC every year since the establishment of the project (Tables 2.10 and 2.11).

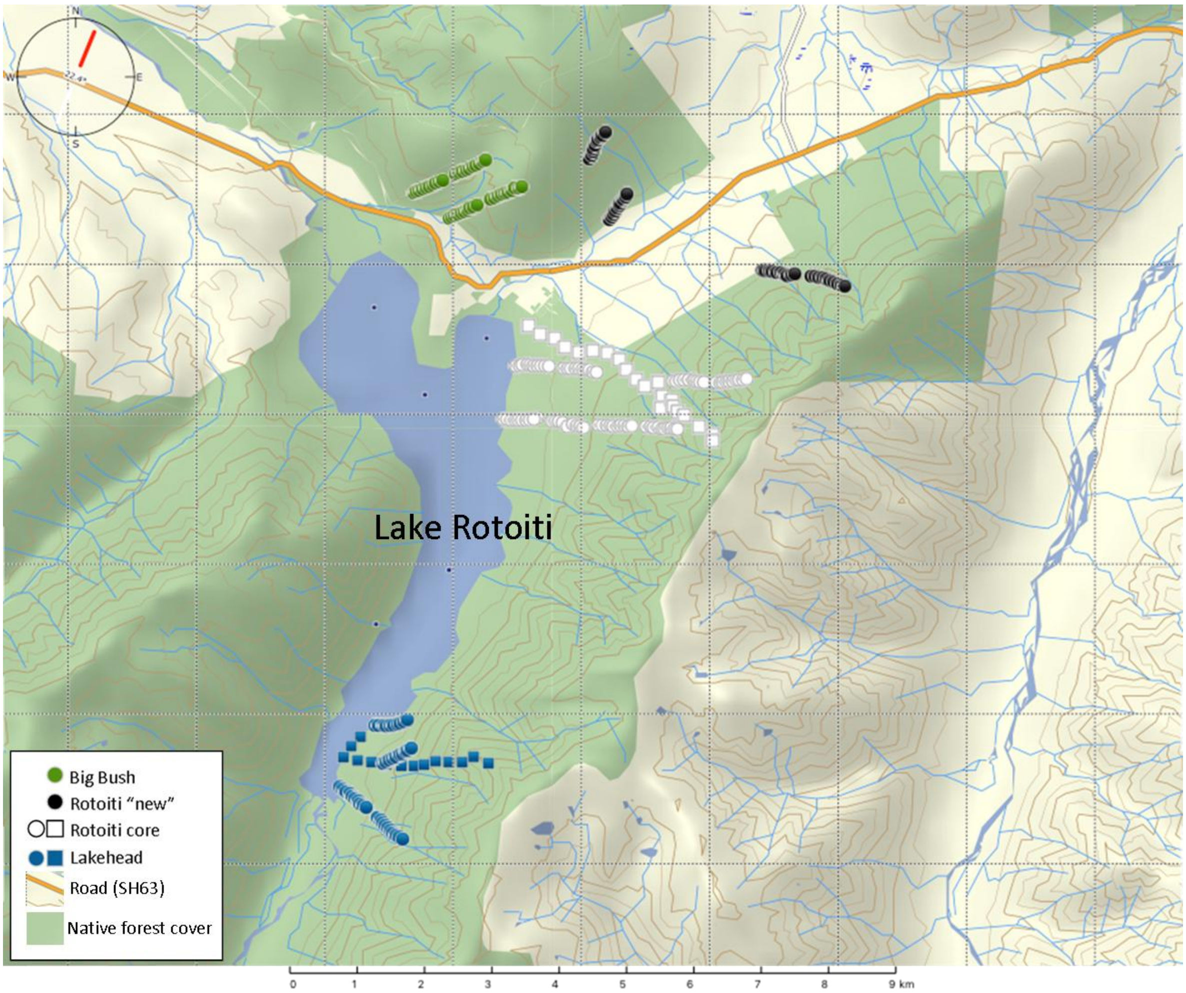


Figure 2.1 Five-minute bird count stations and tracking tunnel locations for RNRP sites; Lakehead, Rotoiti core, Rotoiti "new" and Big Bush as they stand in 2016. Map shows eight tracking tunnel lines in Rotoiti core and four each in Lakehead, Big Bush and Rotoiti "new" with individual tracking tunnels marked by circles and one bird count line each in Lakehead and Rotoiti core with individual bird count stations marked by squares. Map created using Garmin Basecamp.

Table 2.2 Method of pest control used for stoat, ship rat, and possum control from 2002 - 2015 within the Rotoiti core site of the RNRP in Nelson Lakes National Park (information collated from Department of Conservation Rotoiti Nature Recovery Project annual reports; 2001-02, 2002-03, 2003-04, 2004-05, 2005-06, 2006-07, 2007-08, 2008-09, 2009-10, 2010-11, 2011-12, 2012-13, 2013-14, 2014-15, available from www.doc.govt.nz/our-work/mainland-islands/rotoiti/docs-work/rotoiti-nature-recovery-project-annual-reports/).

Year	Stoat control	Possum control	Ship rat control
2002	trapping	feratox/cyanide/ trapping	trapping
2003	trapping	feratox/trapping	trapping
2004	trapping	trapping	trapping
2005	trapping	trapping	trapping
2006	trapping	trapping	1080
2007	trapping	trapping	absent
2008	trapping	trapping	absent
2009	trapping	trapping	absent
2010	trapping	trapping	diphacinone
2011	trapping	trapping	diphacinone
2012	trapping	trapping	diphacinone
2013	trapping	trapping	pindone
2014	trapping	trapping	aerial 1080
2015	trapping	trapping	absent

Lakehead

The Lakehead site is also situated on the slopes of the St Arnaud range and lies south of the Rotoiti core site at the head of Lake Rotoiti on the eastern side (Figure 2.1). Stoats, ship rats, and possums have also been targeted for control at Lakehead. When the RNRP was established, the Lakehead site was originally a full non-treatment area, and then pre-2002 became a stoat-treatment-only area that would be used as a non rat treatment comparison to the Rotoiti core site. Since 2012 however, the bait station networks for ship rat control have been extended at the RNRP to include the Lakehead area and Lakehead was also included in the 2014 Battle for our Birds (BFOB) 1080 drop (Table 2.3.). Bird and mammal populations have been monitored here by DOC every year since the establishment of the project (Tables 2.10 and 2.11).

Table 2.3 Method of pest control used for stoat, ship rat, and possum control from 2002 - 2015 within the Lakehead site of the RNRP in Nelson Lakes National Park (see Table 2.2 for sources).

Year	Stoat control	Possum control	Ship rat control
2002	trapping	absent	absent
2003	trapping	feratox	absent
2004	trapping	absent	absent
2005	trapping	absent	absent
2006	trapping	absent	absent
2007	trapping	absent	absent
2008	trapping	absent	absent
2009	trapping	trapping	absent
2010	trapping	trapping	absent
2011	trapping	trapping	absent
2012	trapping	trapping	diphacinone
2013	trapping	trapping	pindone
2014	trapping	trapping	aerial 1080
2015	trapping	trapping	absent

Big Bush

The Big Bush site is situated at the northern end of Lake Rotoiti, to the north west of the Rotoiti core site and St Arnaud village (Figure 2.1). The stoat and rat trapping networks were expanded to include the Big Bush area in 2002 but rat trapping ceased in 2005 and the area has not received any targeted rat control since 2005. Targeted trapping of possums in the RNRP also now includes the Big Bush area (Table 2.4). Bird populations are not monitored at this site but mammal populations have been monitored by DOC every year since the establishment of the project (Tables 2.10 and 2.11).

Table 2.4 Method of pest control used for stoat, ship rat, and possum control from 2002 - 2015 within the Big Bush site of the RNRP in Nelson Lakes National Park (see Table 2.2 for sources).

Year	Stoat control	Possum control	Ship rat control
2002	trapping	absent	trapping
2003	trapping	absent	trapping
2004	trapping	absent	trapping
2005	trapping	absent	trapping
2006	trapping	absent	absent
2007	trapping	absent	absent
2008	trapping	absent	absent
2009	trapping	absent	absent
2010	trapping	absent	absent
2011	trapping	absent	absent
2012	trapping	absent	absent
2013	trapping	trapping	absent
2014	trapping	trapping	absent
2015	trapping	trapping	absent

Rotoiti “new”

Rotoiti “new” includes areas either side of SH63, north of Rotoiti core and east of Big Bush (Figure 2.1). The Rotoiti “new” site is included in the stoat and possum trapping network at the RNRP but to date has not received any targeted rat control. Stoats have been controlled here by trapping since 2002 and possums controlled by trapping since 2013. Bird populations are not monitored at this site and mammal populations were monitored here by DOC in 2002-2004, 2006, and 2012-2015 (Tables 2.10 and 2.11).

Table 2.5 Method of pest control used for stoat, ship rat, and possum control from 2002 - 2015 within the Rotoiti “new” site of the RNRP in Nelson Lakes National Park (see Table 2.2 for sources).

Year	Stoat control	Possum control	Ship rat control
2002	trapping	absent	trapping
2003	trapping	absent	trapping
2004	trapping	absent	trapping
2005	trapping	absent	trapping
2006	trapping	absent	absent
2007	trapping	absent	absent
2008	trapping	absent	absent
2009	trapping	absent	absent
2010	trapping	absent	absent
2011	trapping	absent	absent
2012	trapping	absent	absent
2013	trapping	trapping	absent
2014	trapping	trapping	absent
2015	trapping	trapping	absent

Rotoroa

The non-treatment site, Rotoroa, is located on Mt Misery at the southern end of Lake Rotoroa in Nelson Lakes National Park (Figure 2.2). To date there has been no pest control within the Rotoroa site (Table 2.6) as this was set aside during the establishment of the RNRP to remain a non-treatment site to always be used to compare the effects of the various pest control treatments applied within the treatment sites of the RNRP. Bird and mammal populations have been monitored here by DOC every year since the establishment of the project (Tables 2.10 and 2.11).

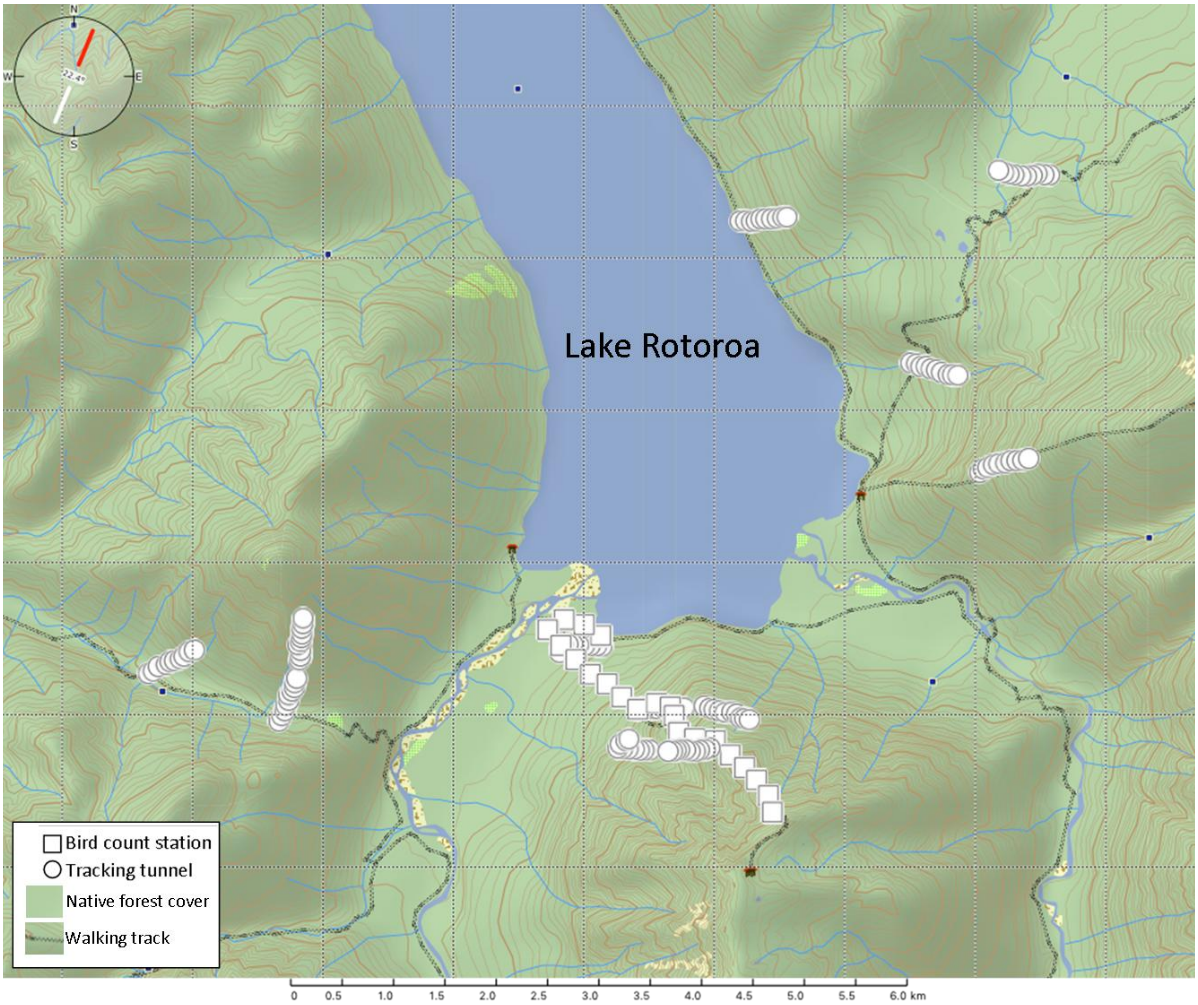


Figure 2.2 Five-minute bird count stations and tracking tunnel locations in Rotoroa as they stand in 2016. Map shows 10 tracking tunnel lines with 10 individual tracking tunnels each marked by white circles and one bird count line with individual bird count stations marked by white squares. Map created using Garmin Basecamp.

Table 2.6 Method of pest control used for stoat, ship rat, and possum control from 2002 - 2015 within the Rotoroa (non-treatment) site in Nelson Lakes National Park. No pests have been managed at this site by DOC (see Table 2.2 for sources).

Year	Stoat control	Possum control	Ship rat control
2002	absent	absent	absent
2003	absent	absent	absent
2004	absent	absent	absent
2005	absent	absent	absent
2006	absent	absent	absent
2007	absent	absent	absent
2008	absent	absent	absent
2009	absent	absent	absent
2010	absent	absent	absent
2011	absent	absent	absent
2012	absent	absent	absent
2013	absent	absent	absent
2014	absent	absent	absent
2015	absent	absent	absent

2.3 Kahurangi National Park

Kahurangi National Park encompasses most of the north western corner of New Zealand's South Island. With a total area of 452,002 ha it is New Zealand's second largest natural protected area. Kahurangi is largely managed by DOC but there are also volunteer organisations that have run predator control operations in the area including FOC and FOF. The Cobb Valley and Flora Stream areas are located near the eastern edge of Kahurangi near the Arthur/Wharepapa Range and Tablelands. In the low and mid slopes of this area, the forest canopy is dominated by silver beech with small scattered areas of red beech and a typical understory of *Griselinia littoralis*, *Pseudopanax* spp., and *Coprosma* spp. (Wardle 1984, Masuda et al. 2014). The treeline is between 1300 m and 1400 m a.s.l with the upper 200 m of the forest dominated by silver beech with little mountain beech in Flora and a mixture of silver beech and mountain beech in Cobb. There are also small patches of southern rātā (Masuda et al. 2014, personal obs.). Low densities of scale insects are found in small patches but do not dominate the lowlands as in Nelson Lakes (personal obs.). The avifauna is similar to that of Nelson Lakes with several common introduced species and a range of both common and vulnerable native bird species; great spotted kiwi, yellow crowned parakeets, kākā, kea, and blue ducks are present here (personal obs.).

Over the years both Cobb and Flora have received targeted control of stoats, possums, and/or ship rats coupled with bird and mammal monitoring. Although FOC and FOF have monitored bird and mammal populations since 2006 (Cobb) and 2001 (Flora), the methods used to monitor birds have differed from those used in Nelson Lakes and these bird counts were only performed along the valley floor at approximately 800 m a.s.l. Therefore only the bird and mammal monitoring data collected by UC (post-2013 at approximately 650 – 1350 m a.s.l, including standard 5 minute bird counts) are used here.

Cobb

FOC was established in 2006 with the aim of restoring and maintaining native biodiversity in the Cobb Valley area of Kahurangi National Park. In affiliation with DOC, Forest and Bird, and the NZ Deerstalkers Association, the FOC project area now covers approximately 5000 ha including 449 stoat traps and around 30 possum traps. During the DOC BFOB response to the 2014 beech mast, the Cobb Valley area was initially proposed as a non-treatment site to be compared to other areas receiving aerial 1080 poisoning (i.e. Flora) but ultimately Cobb also received aerial 1080 poisoning in November 2014 (Table 2.7). However, this 1080 application occurred after the mammal monitoring took place that year so data collected in 2014 were considered non-rat-treatment observations. Bird and mammal populations have been monitored in the area by UC since November 2013 (Tables 2.10 and 2.11).

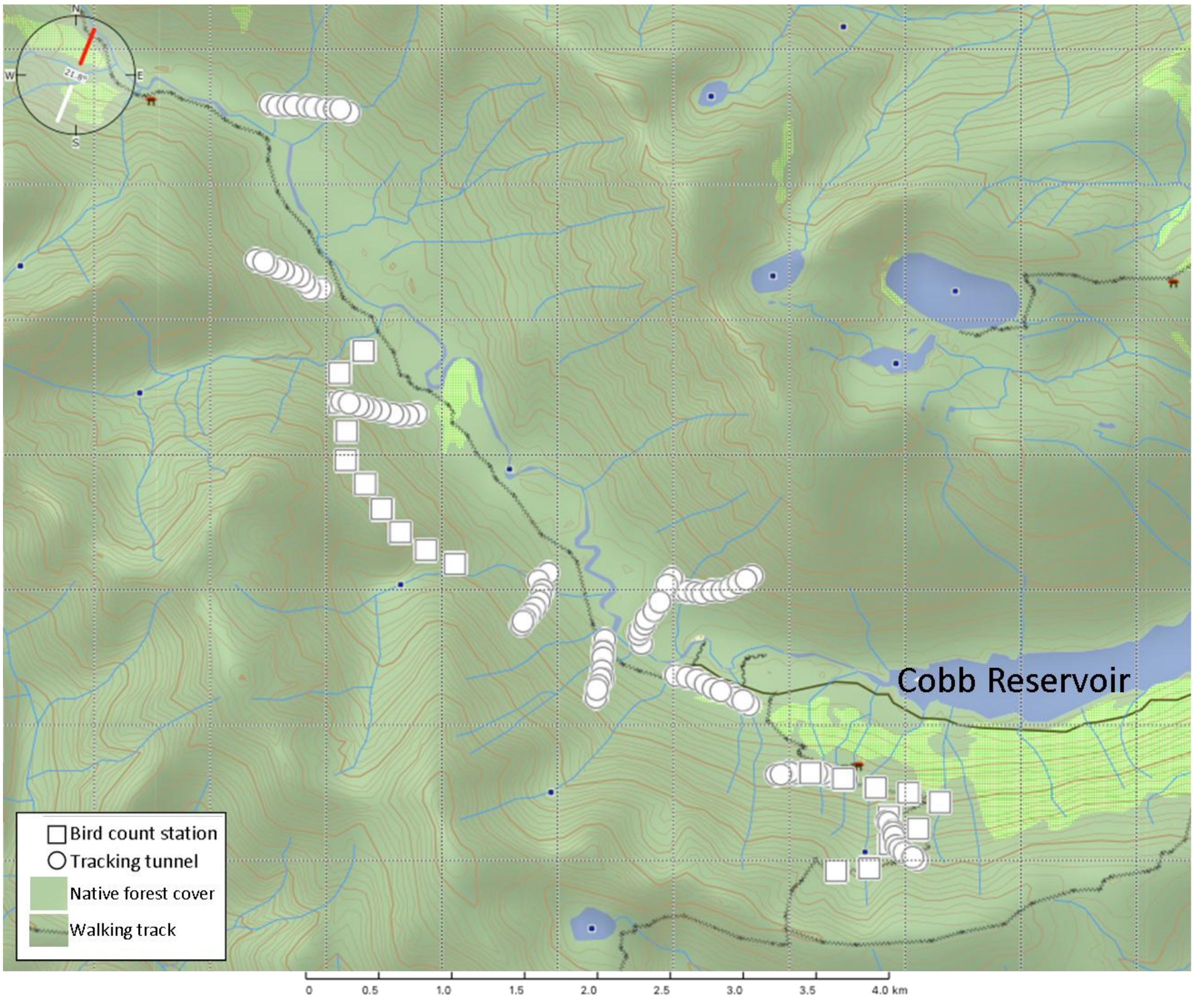


Figure 2.3 Five-minute bird count stations and tracking tunnel locations in Cobb. Map shows 10 tracking tunnel lines with 10 individual tracking tunnels each marked by white circles and two bird count lines with 10 individual bird count stations each marked by white squares. Map created using Garmin Basecamp.

Table 2.7 Method of pest control used for stoat, ship rat, and possum control from 2013 - 2015 within the Cobb site in Kahurangi National Park.

Year	Stoat control	Possum control	Ship rat control
2013	trapping	trapping	absent
2014	trapping	trapping	aerial 1080
2015	trapping	trapping	absent

Flora

FOF was established in 2001 with the goal of protecting and returning endangered and threatened native species to the Flora Stream catchment area in Kahurangi National Park. In partnership with DOC, FOF now manages trap lines covering 8,000 ha with 1125 stoat traps, some of which also have possum traps nearby. During DOC's BFOB operation, the Flora area received aerial 1080 treatment. Bird and mammal populations have been monitored in the area by UC since November 2013 (Tables 2.10 and 2.11).

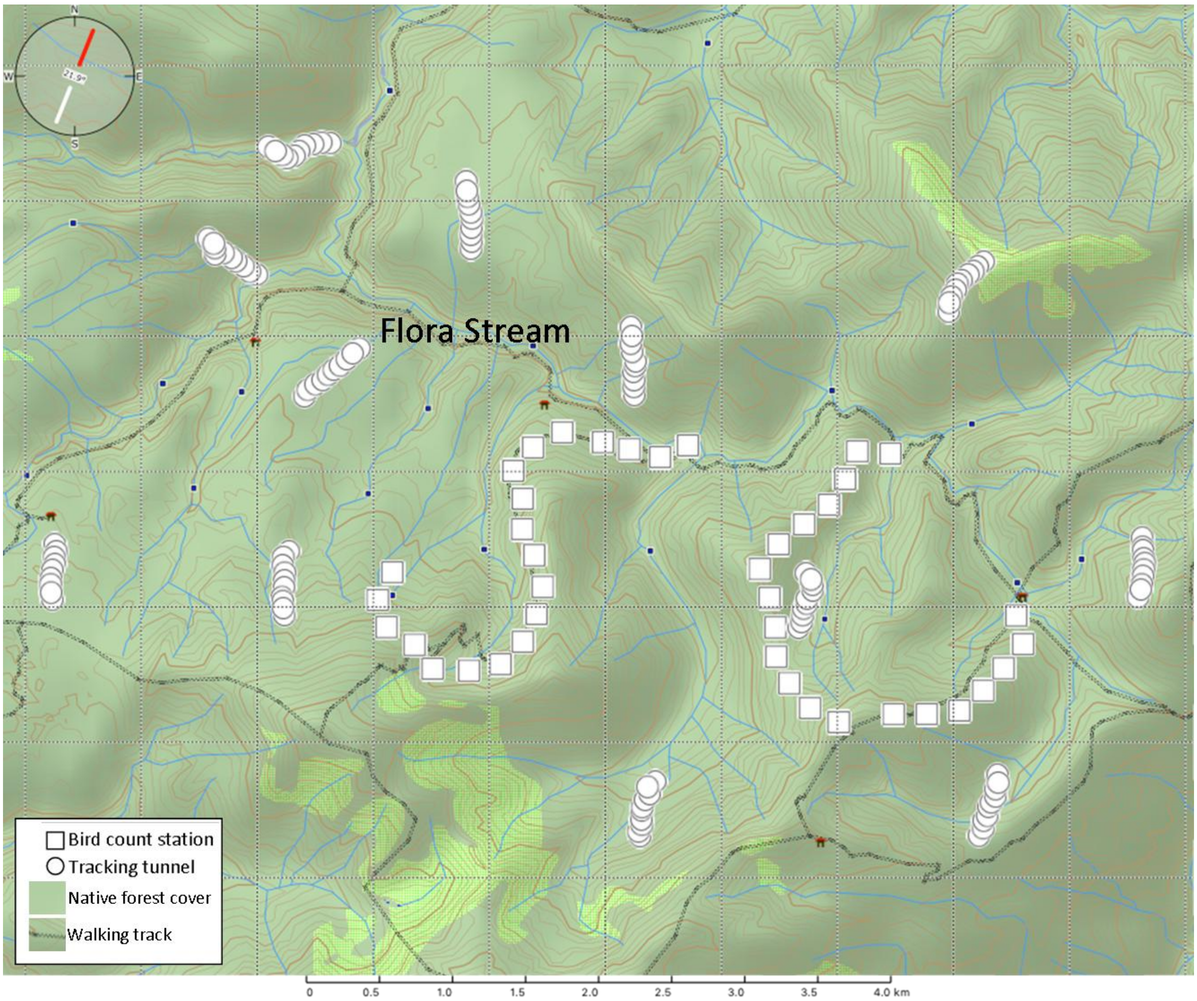


Figure 2.4: Five-minute bird count stations and tracking tunnel locations in Flora. Map shows 12 tracking tunnel lines with 10 individual tracking tunnels each marked by white circles and two bird count lines with 20 individual bird count stations each marked by white squares. Map created using Garmin Basecamp.

Table 2.8 Method of pest control used for stoat, ship rat, and possum control from 2013 - 2015 within the Flora site in Kahurangi National Park.

Year	Stoat control	Possum control	Ship rat control
2013	trapping	trapping	absent
2014	trapping	trapping	aerial 1080
2015	trapping	trapping	absent

2.4 Monitoring methods

To monitor mammal populations, a combination of tracking tunnels and chew cards were used by UC within Cobb and Flora to detect rodents and possums, and tracking tunnels used by DOC within the remaining sites to detect rodents and stoats. Due to reasons listed in Chapter one and because stoats and possums are rarely detected within these sites (owing to successful control of possums and low detectability of stoats) I chose to analyse only ship rat populations with tracking tunnel rates for the mammal monitoring component of this study. For birds, 5MBCs were used at both Kahurangi and Nelson Lakes sites to detect any bird species present, providing the data to analyse trends in populations of the 12 most common bird species detected across all sites. Birds were monitored between 455 m and 1481 m a.s.l and mammals between 463 m and 1391 m a.s.l (Table 2.9).

Table 2.9 Altitudinal distribution of monitoring lines for birds and mammals across all study sites. NA means no bird counts performed at that site.

Area	Site	Tracking tunnels (m a.s.l.)	Bird counts (m a.s.l.)
Kahurangi	Cobb	830 - 1196	828 - 1258
Kahurangi	Flora	636 -1342	877 - 1214
Nelson Lakes	Big Bush	569 - 906	NA
Nelson Lakes	Lakehead	612 - 1023	622 - 1445
Nelson Lakes	Rotoiti core	616 - 1389	656 - 1481
Nelson Lakes	Rotoiti new	617 - 1115	NA
Nelson Lakes	Rotoroa	463 - 1391	455 - 1425

Mammal monitoring

Permanent tracking tunnel lines were established to detect the presence of rodents at all study sites (Figures 2.1-2.4). Each tracking tunnel line includes 10 individual tracking tunnels that are spaced 50 m apart, giving each tracking tunnel transect a total length of 500 m. The Kahurangi tracking tunnel lines were established by DOC, FOC, and FOF, and the Nelson Lakes tracking tunnels established by DOC. Most tracking tunnel lines have been used consistently every sampling season but in some sites at Nelson Lakes, not all tracking tunnel lines have been monitored every year (Table 2.10). The 10 tracking tunnel lines at Cobb and 12 lines at Flora were monitored by fieldworkers from UC (Tim Galloway, Archie MacFarlane, Josh Van Vianen, and myself) from 2013 to 2015 while all tracking tunnel lines in the Nelson Lakes sites were monitored by DOC Nelson Lakes staff and volunteers from 2002 to 2015. Tracking tunnels were monitored for one night during November (or as close to November as possible; Table 2.10) on a clear night when rodents were likely to be active. Tracking tunnel cards were inserted in to the tunnels with a peanut butter lure and collected the following day to be scored for presence/absence of rats and mice. Ship rats are the most abundant *Rattus* species across all sites however, it must be noted that no distinctions are made between *Rattus* species when scoring tracking tunnel cards.

Table 2.10 Number of tracking tunnels (TTs) and dates monitored for all tracking tunnel lines at all sites. Total is the number of tunnels and the total times monitored across all years for each site.

	Rotoiti core		**Lakehead**		**Big Bush**		**Rotoiti "new"**		**Rotoroa**		**Cobb**		**Flora**	
Year	**Date**	**TTs**	**Date**	**TTs**	**Date**	**TTs**	**Date**	**TTs**	**Date**	**TTs**	**Date**	**TTs**	**Date**	**TTs**
2002	9 Dec	100	9 Dec	40	9 Dec	40	9 Dec	60	2 Dec	160	-	-	-	-
2003	17 Nov	100	17 Nov	40	17 Nov	40	17 Nov	60	10 Nov	160	-	-	-	-
2004	22 Nov	100	22 Nov	40	22 Nov	40	22 Nov	60	29 Nov	160	-	-	-	-
2005	21 Nov	100	21 Nov	40	21 Nov	40	-	-	28 Nov	150	-	-	-	-
2006	27 Nov	100	27 Nov	40	27 Nov	40	27 Nov	60	20 Nov	160	-	-	-	-
2007	5 Nov	100	5/11/2007	40	5/11/2007	40	-	-	15 Nov	160	-	-	-	-
2008	10 Nov	100	10 Nov	40	10 Nov	40	-	-	20 Nov	110	-	-	-	-
2009	16 Nov	100	16 Nov	40	16 Nov	40	-	-	31 Dec	120	-	-	-	-
2010	22 Nov	100	22 Nov	40	22 Nov	40	-	-	4 Nov	100	-	-	-	-
2011	31 Oct	100	31 Oct	40	31 Oct	40	-	-	7 Nov	120	-	-	-	-
2012	date unknown	80	date unknown	40	date unknown	40	date unknown	20	22 Nov	120	-	-	-	-
2013	31 Oct	80	31 Oct	40	31 Oct	40	31 Oct	20	14 Nov	120	2 Nov	100	18 Nov and 23 Nov	120
2014	11 Dec	80	11 Dec	40	11 Dec	40	11 Dec	60	15 Dec	120	1 Nov	100	13 Nov and 19 Nov	120
2015	5 Nov	80	5 Nov	40	5 Nov	40	5 Nov	20	16 Nov	100	5 Nov	100	13 Nov and 20 Nov	120
Total		**1320**		**890**		**560**		**360**		**1860**		**300**		**360**

Bird monitoring

Bird count transects were established to measure the abundance of common bird species present at Rotoiti core, Lakehead, Rotoroa, Cobb, and Flora using 5MBCs (Figure 2.1-2.4). Bird count transects at Cobb and Flora were established by UC with the help of the AHB, FOC, and FOF, and the bird count transects at Lakehead, Rotoiti core, and Rotoroa were established by DOC. Each transect has between 10 and 21 5MBC stations and each of these was counted several times per season resulting in 600 to 2600 counts per site across 2002-2016 in total (Table 2.11). 5MBCs were completed in November 2013-2015 and February 2014 at Cobb and Flora, and were usually completed tri annually (in February, May, and November) at Lakehead, Rotoiti core, and Rotoroa. Bird counts at Cobb and Flora were conducted by UC fieldworkers (Tim Galloway, Archie MacFarlane, Josh Van Vianen, and myself) and at Lakehead, Rotoiti core, and Rotoroa by DOC staff and volunteers (including myself in February 2016).

Table 2.11 Total five-minute bird counts per site per year from February 2002 – May 2016. Totals include the number of stations counted per year for February, May, and November for all years combined.

Year	Rotoiti counts	Lakehead counts	Rotoroa counts	Cobb counts	Flora counts
2002	168	112	126	0	0
2003	189	126	189	0	0
2004	168	112	126	0	0
2005	168	112	126	0	0
2006	188	126	105	0	0
2007	168	112	147	0	0
2008	188	126	104	0	0
2009	187	126	126	0	0
2010	189	126	189	0	0
2011	189	126	188	0	0
2012	189	112	168	0	0
2013	190	127	188	150	160
2014	126	84	105	307	295
2015	168	112	118	160	160
2016	123	70	104	0	0
Total	**2598**	**1709**	**2109**	**617**	**615**

Beech seedfall data

Twenty seedfall traps (metal funnels of DSIR design) each are located at Rotoroa and Rotoiti core and ten at Flora at varying altitudes where they were monitored by DOC. Collection bags were fitted to the seed traps in early March and collected in mid April when a new set of bags were fitted and then collected in mid-June giving two seed counts per trap per year (total 20-40 seed counts per site per year). Seeds were sorted into species i.e. red beech, silver beech, and mountain beech and total number of viable and non-viable seeds recorded in the national seed data base where they were available for use in this study. In this analysis I used total seedfall (not viable) and summed both collection samples within a season to get a yearly total per trap. I averaged across all three beech species so my predictor used in analysis is mean seedfall per m^2 per year.

Chapter 3. Factors affecting ship rat abundance

3.1 Objectives

Effective management of mammalian predators through sustained control (e.g. trapping) or seasonal control (e.g. aerial 1080 poisoning) requires a complex understanding of the target populations in regard to population dynamics, responses to the environment, and responses to resources (Parkes & Murphy 2003, Rouco, Norbury & Anderson 2016, Parkes et al. 2017). The purpose of monitoring introduced predator populations, such as ship rats, in New Zealand forests has been to determine how they respond to pest control and to detect any changes in their populations that may require a change in the method and scale of pest control being applied.

The ship rat control methods investigated in this study include targeted trapping and targeted poisoning with diphacinone, pindone, and 1080. Additionally, most treatment sites also have extensive trapping networks for sustained targeted control of stoats (Chapter 2; Tables 2.2 - 2.8). The rat tracking data has been collected at a range of altitudes and time spans over the course of 14 years which saw a range in annual beech seedfall levels including several high-seed years. Here I use the index of rat abundance (probability of detection in tracking tunnels) under each pest control regime, at a range of altitudes, with a range of seedfall levels, to answer the following key questions:

1. How does ship rat abundance vary with altitude?
2. How does ship rat abundance respond to beech seedfall events?
3. Which pest control regime is most effective at reducing ship rat abundance?
4. Do ship rat responses to pest control vary with altitude?
5. Is the efficacy of ship rat control altered by beech masting events?

The overall aim is to determine the most effective way to control ship rats for native bird conservation and to determine the conditions under which the effects of different pest control techniques on ship rat populations may change.

3.2 Methods

A total of 4910 tracking tunnel observations were used in the ship rat analyses for this study. These observations included tracking tunnel data from seven sites; Big Bush, Cobb, Flora, Lakehead, Rotoiti core, Rotoiti new, and Rotoroa. A further 440 observations from tracking tunnels that were placed at altitudes equal to or less than 610 m a.s.l. (426 and 14 observations from Rotoroa and Big Bush respectively) were excluded because these were outside of the altitudinal range of the remaining five sites. Furthermore, the majority of the low-altitude tracking tunnel data was from the Rotoroa site which was unusual in the context of this study, being the only site of the seven which never had any pest control (Table 2.6). Tracking tunnels therefore covered a range from 612 m to 1391 m a.s.l.

Tracking tunnel data were analysed using binomial GLMMs (generalised linear mixed models) in R with the *lme4* package (Bates et al. 2015). Tunnels were analysed as independent points so that the full altitudinal range of a tracking tunnel line could be considered, however random terms for individual tunnels, tunnel lines, and sites were included in the models to control for the nested nature of the data. Fixed terms included in the final model were rat treatment, stoat treatment, altitude, seedfall, rat treatment x altitude, and rat treatment x seedfall (Table 3.1).

Altitude (m a.s.l) and seedfall (mean annual beech seeds per m^2) were included as continuous variables. Seed counts covered three species combined (*Nothofagus fusca*, *N. solandri* and *N. menziesii*). The abundance of each beech species varied with altitude, but the three tend to be correlated in their high-seed years (Schauber et al. 2002), so the combined average is a reliable indication of which years were high-seed years. Seed counts were log-transformed (log10) to allow for the right-skewed nature of the seed data. Because very low mean annual seed counts from the Flora site were rounded to 0.00 seeds per m^2, I converted any zeros in the data set to 0.01 seeds per m^2 (less than the next lowest mean annual seed count of 0.07 seeds per m^2) to allow log-transformation. Seed count data from the Rotoiti core site was used as a predictor for the nearby Big Bush, Lakehead, and Rotoiti new sites, and Flora used for the nearby Cobb site, because seedfall data were only available from three locations (Rotoiti core, Rotoroa and Flora). Since masting events in *Nothofagus* spp. occur over large geographical areas in New Zealand (Schauber et al. 2002), applying seedfall data from nearby sites is reliable. Unfortunately an altitude x seedfall interaction would not run in this model due to a convergence error so had to be excluded from the analysis.

Stoat treatment included two levels, either trapping or absent (non-treatment), and rat treatment initially included six levels but this was reduced to four levels after some data exploration. The six levels originally included for rat treatment were; aerially-applied 1080, ground-based 1080, diphacinone, pindone, trapping, and absent (non-treatment). Diphacinone was applied at Rotoiti core from 2010 to 2012 and at Lakehead in 2012, and pindone applied at Rotoiti core and Lakehead in 2013 by DOC (Tables 2.2 and 2.3). Because pindone was only applied once, in 2013, the rat treatment x seedfall interaction could not be run using these levels. Therefore, I merged the diphacinone and pindone treatments to create one level and renamed this “other toxins”. A further combination of aerially-applied 1080 treatment and ground-based 1080 treatment was also made because the ground-based 1080 treatment only occurred once during this study, in response to a high-seed year in 2006 at Rotoiti core. Therefore, the final four levels for rat treatment were 1080, other toxins, trapping, and absent. The R code used for the final GLMM was as follows:

```
ratglmm.4<-glmer(rat~stoat.tmnt
                 + rat.tmnt4
                 + rat.tmnt4 * altitude
                 + rat.tmnt4 * mean.seed.log10
                 +(1|tunnel.ID) + (1|line.code) + (1|site),
                 family=binomial, data=allTT)
```

For a full listing of sites with years of treatment and data collection methods see chapter 2.

3.3 Results

The proportion of tracking tunnels marked by rats was highest in 2006 and 2014 (and in 2012 in Lakehead) (Figure 3.1) which coincided with peaks in the mean annual beech seedfall per m^2 (Figure 3.2). Rat tracking rates have generally been highest at the Lakehead site which was included in the RNRP stoat trapping network from 2002 onwards but has only received rat control since 2012. Beech seedfall levels in 2014 were the highest recorded within this study (Figure 3.2). The proportion of tunnels tracked by rats in 2014 in areas that were treated with 1080 (Flora, Lakehead, and Rotoiti core) were very low relative to the sites that were not treated with 1080 that year (Big Bush, Rotoiti new, and Rotoroa), or were treated with 1080 but not until after the rat tracking data were collected (Cobb).

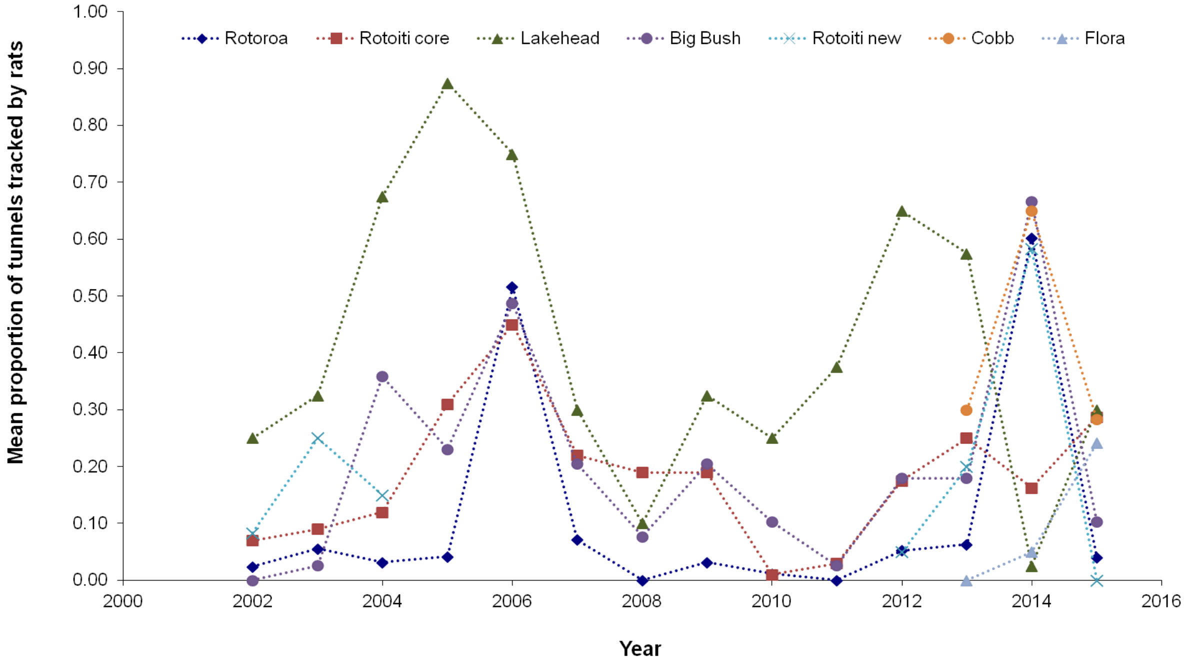


Figure 3.1 Mean proportion of tracking tunnels tracked by rats at all study sites from 2002 to 2015. Note that tracking tunnel data were not collected at Rotoiti new between 2005 and 2011.

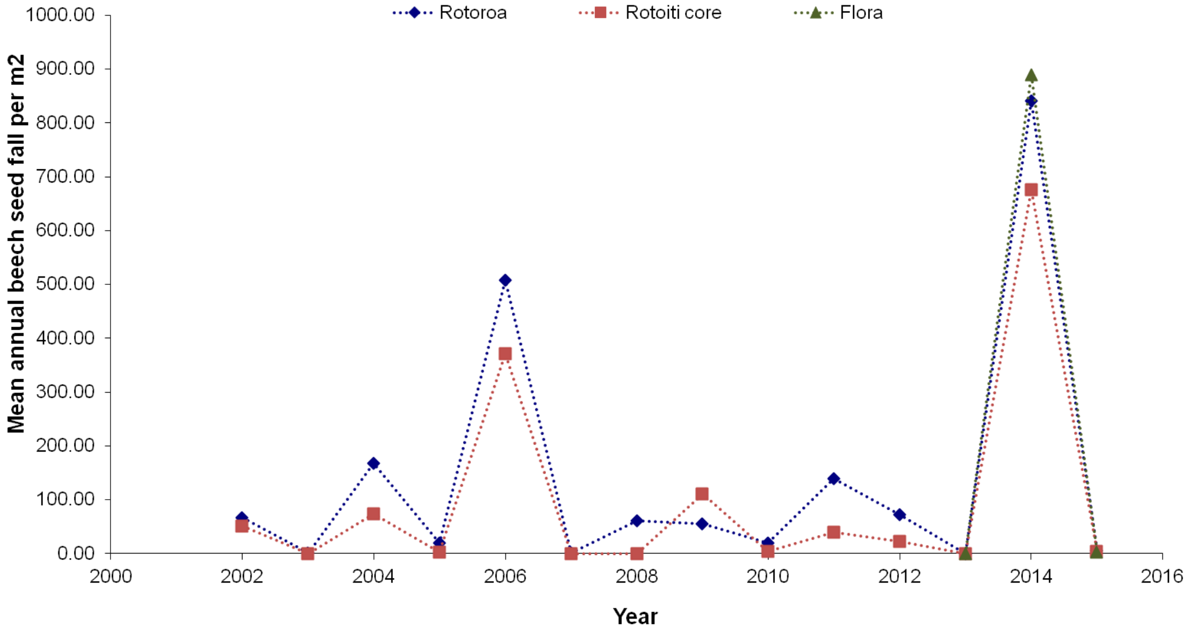


Figure 3.2 Mean annual beech seedfall per m^2 (total seed, for *Nothofagus fusca*, *N. solandri* and *N. menziesii* combined) at Rotoroa and Rotoiti core from 2002 to 2015 and at Flora from 2012 to 2015.

Rat tracking rates decreased significantly with altitude and increased significantly with seedfall, showing that rats were more common at low elevations and in high-seed years (Table 3.1). Unexpectedly, stoat trapping had a significant positive effect on rat tracking rates relative to rat tracking in the absence of stoat control (Table 3.1). The only effective pest control method at reducing ship rat tracking rates investigated here was 1080 poisoning (estimate = -2.722) (Table 3.1). Results for targeted rat trapping treatment found no significant effect on rat tracking rates (Table 3.1). The GLMM analysis suggested that “other toxins” (the few years with pindone or diphacinone) had a significant *positive* effect on rat tracking, but it is more likely that this is an artifact - these treatments were probably only applied in years when rats were anticipated to increase, and the treatments were then ineffective at halting the increase in rat tracking, as opposed to having a direct positive effect on tracking rates.

Table 3.1 GLMM analysis output using rat tracking data from all sites combined (Big Bush, Cobb, Flora, Lakehead, Rotoiti core, Rotoiti new, and Rotoroa) at altitudes between 612 m and 1391 m a.s.l. with significant p values indicated in bold.

Random effects	**Variance**	**Std. Dev.**
tracking tunnel	0.088	0.296
tracking tunnel line	0.559	0.748
site	0.190	0.436

Fixed effects	**Estimate**	**Std. Error**	***z* value**	***P* value**
(intercept)	-1.194	0.734	-1.627	0.104
stoat trapping	1.428	0.538	2.653	**0.008**
1080	-2.722	0.952	-2.859	**0.004**
other toxin	5.255	1.232	4.265	**< 0.001**
rat trapping	1.444	0.939	1.537	0.124
altitude	-0.002	0.001	-3.262	**0.001**
seedfall	0.486	0.038	12.737	**< 0.001**
1080 x altitude	0.002	0.001	2.073	**0.038**
other toxin x altitude	-0.007	0.002	-4.195	**< 0.001**
rat trapping x altitude	-0.002	0.001	-1.791	0.073
1080 x seedfall	-0.107	0.177	-0.603	0.546
other toxin x seedfall	-0.886	0.123	-7.218	**< 0.001**
rat trapping x seedfall	-0.532	0.130	-4.096	**< 0.001**

In general, the proportion of tracking tunnels tracked by rats decreased with altitude (Table 3.1) and was highest between 600 m and 800 m a.s.l (Figures 3.3 and 3.4). Rat tracking rates decreased with altitude for all treatment levels (Figures 3.3 and 3.4). The significant 1080 x altitude interaction and other toxins x altitude interaction show that the effect of 1080 and other toxin treatments on rat detection were not independent of altitude. The 1080 treatment significantly reduced rat densities but as altitude increased, the treatment effect was reduced. In contrast, rat densities decreased with altitude under the other toxin treatments, compared to increased rat densities at lower altitudes with this treatment. Rat trapping not only had no significant effect on rat tracking rates (see above), it also had no significant interaction with altitude (Table 3.1). When stoats were trapped, rat tracking rates were greater at lower altitudes relative to rat tracking rates when stoats were not trapped (Figure 3.4). This difference was reduced as altitude increased and rat tracking rates became similar between stoat treatment and non-stoat treatments at approximately 1300 m a.s.l (Figure 3.4).

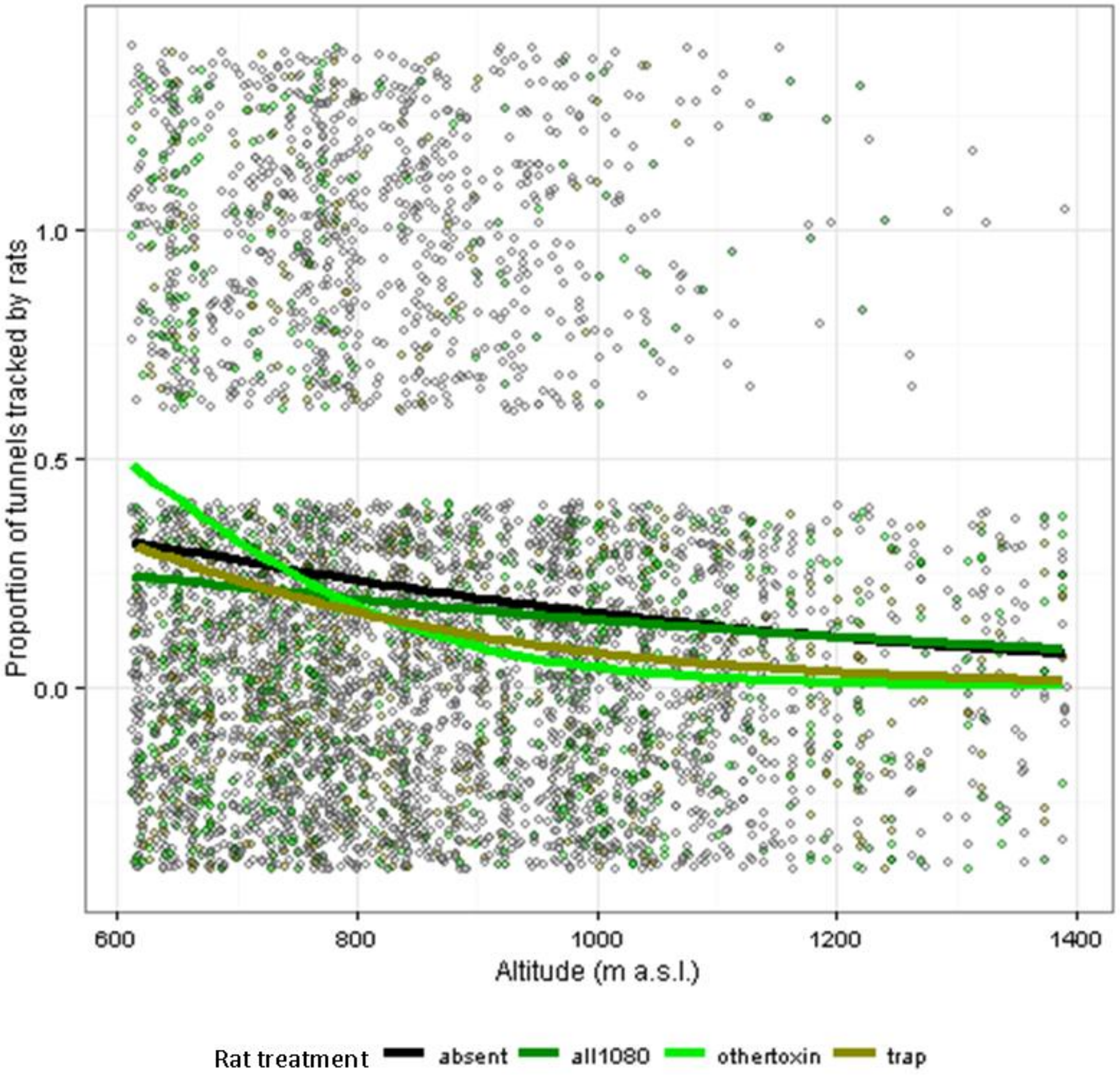


Figure 3.3 Proportion of tracking tunnels tracked by rats against altitude (m a.s.l). Graph shows the differences in rat tracking rates between rat treatments; non-treatment (absent), targeted rat trapping, 1080 poisoning, and poisoning by other toxins (diphacinone and pindone). The jitter function was applied to show repeat counts of the binomial data. The fitted lines come from local smoothing functions (geom_smooth... formula = y ~ x, method = "glm", family = "binomial"), for statistical testing see Table 3.1.

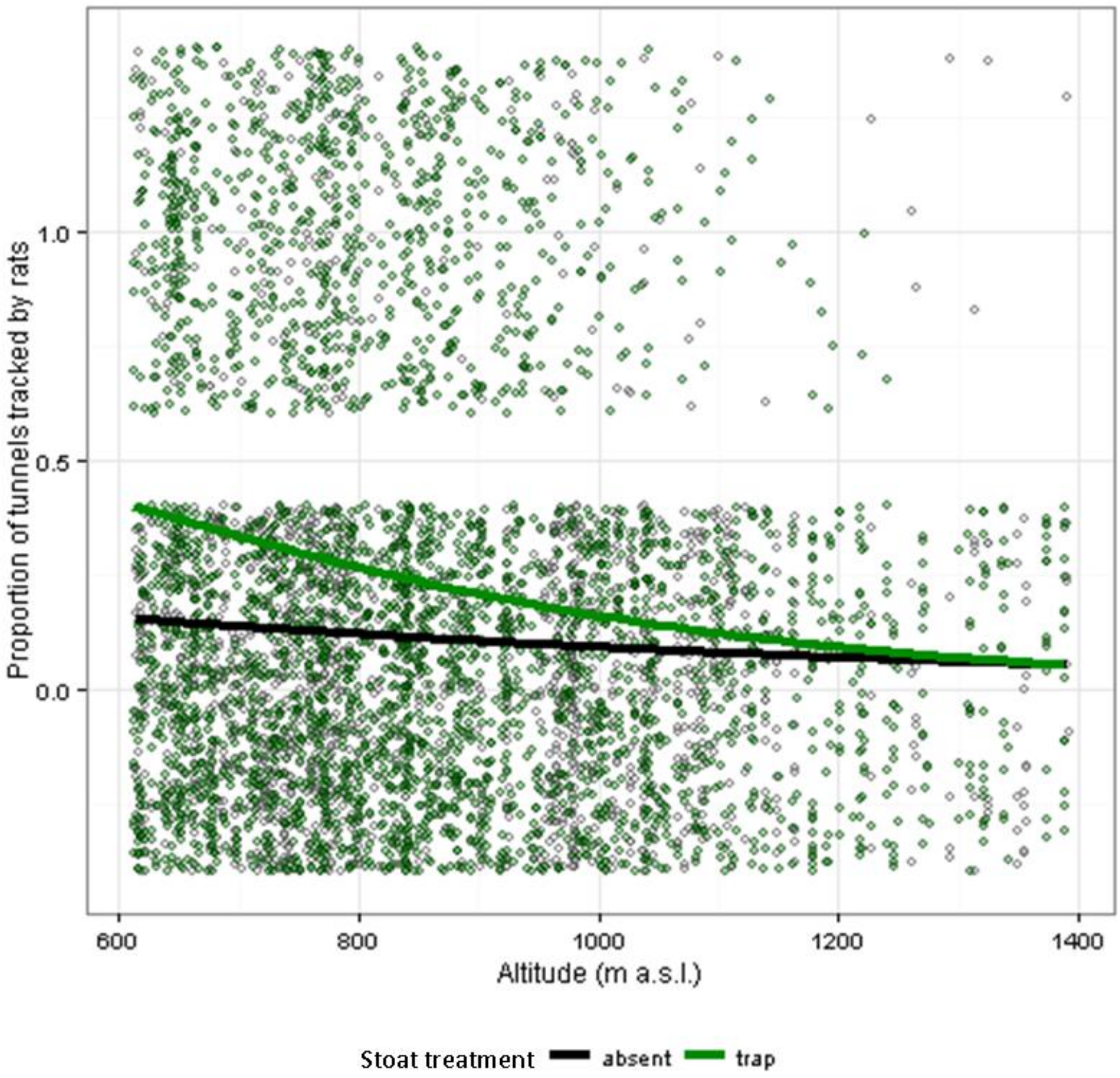


Figure 3.4 Proportion of tracking tunnels tracked by rats against altitude (m a.s.l). Graph shows the differences in rat tracking rates between stoat treatments; absent (non-treatment) and targeted stoat trapping. The jitter function was applied to show repeat counts of the binomial data. The fitted lines come from local smoothing functions (geom_smooth... formula = y ~ x, method = "glm", family = "binomial"), for statistical testing see Table 3.1.

The efficacy of some ship rat control methods was altered by beech mast events. Rat tracking rates in general showed a significant increase with increased seedfall, but the effect of 1080 poisoning was not affected by seedfall (non-significant 1080 treatment x seedfall interaction; Table 3.1). For rat trapping and other-toxin treatments, rat tracking rates decreased with increased seedfall (Figure 3.5). These results suggested that the effects of rat trapping and other toxin application increased (i.e. rat density increased further) when seedfall increased and the effect of the 1080 treatment was unaffected by seedfall levels. However, observations were lacking for rat trapping and other toxin treatments during high-seed years (Figure 3.5). The increased densities in rat abundance following stoat trapping were apparently reduced during high-seed years (Figure 3.6) but this conclusion is tentative as I did not include a stoat trapping x seedfall interaction in the models because I only had one site without stoat trapping (Chapter 2).

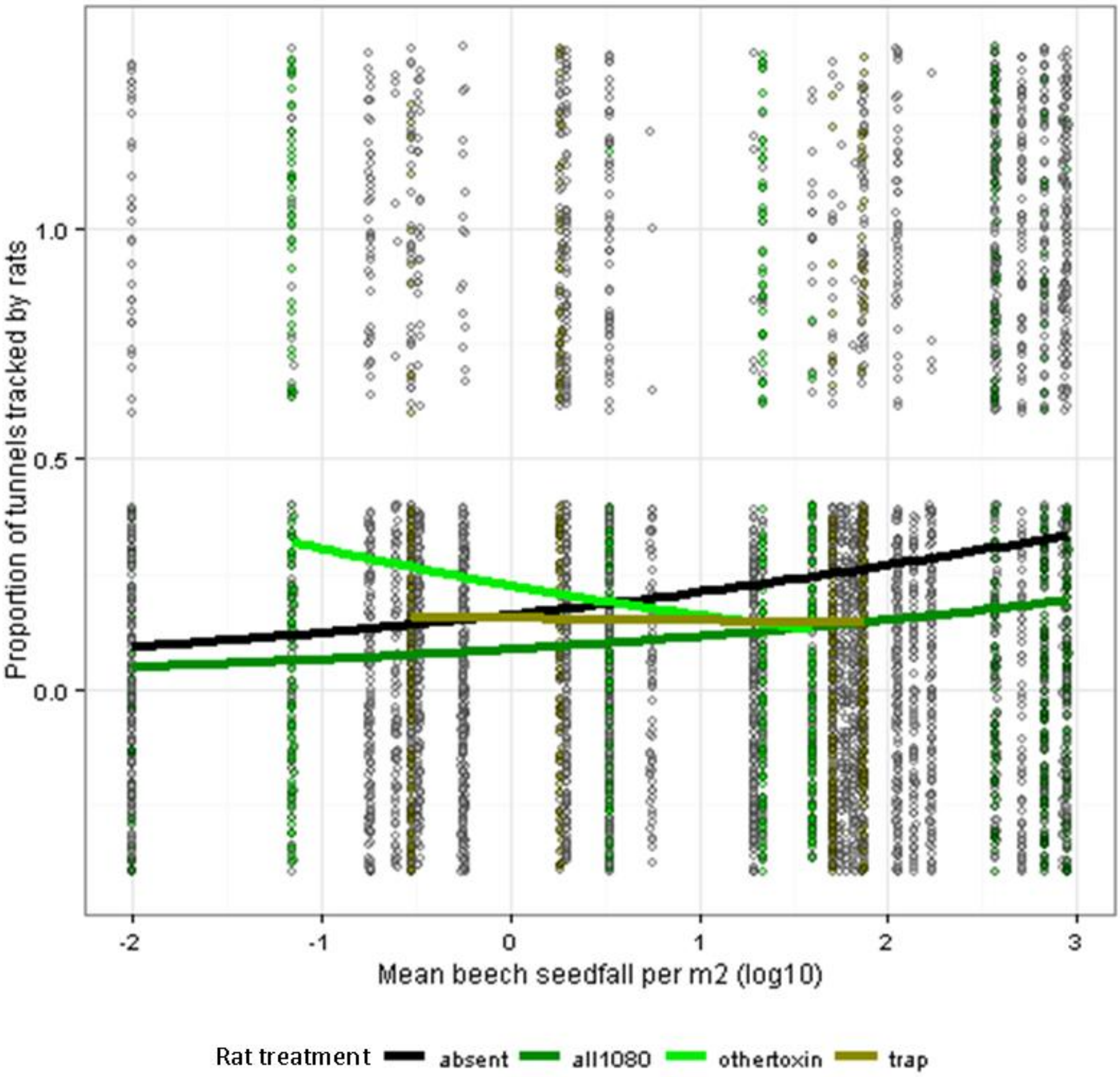


Figure 3.5 Proportion of tracking tunnels tracked by rats against mean annual beech seedfall per m^2 (log10). Graph shows differences in rate tracking rates between rat treatments; non-treatment (absent), targeted rat trapping, 1080 poisoning, and poisoning by other toxins (diphacinone and pindone). The jitter function was applied to show repeat counts of the binomial data. The fitted lines come from local smoothing functions (geom_smooth... formula = y ~ x, method = "glm", family = "binomial"), for statistical testing see Table 3.1.

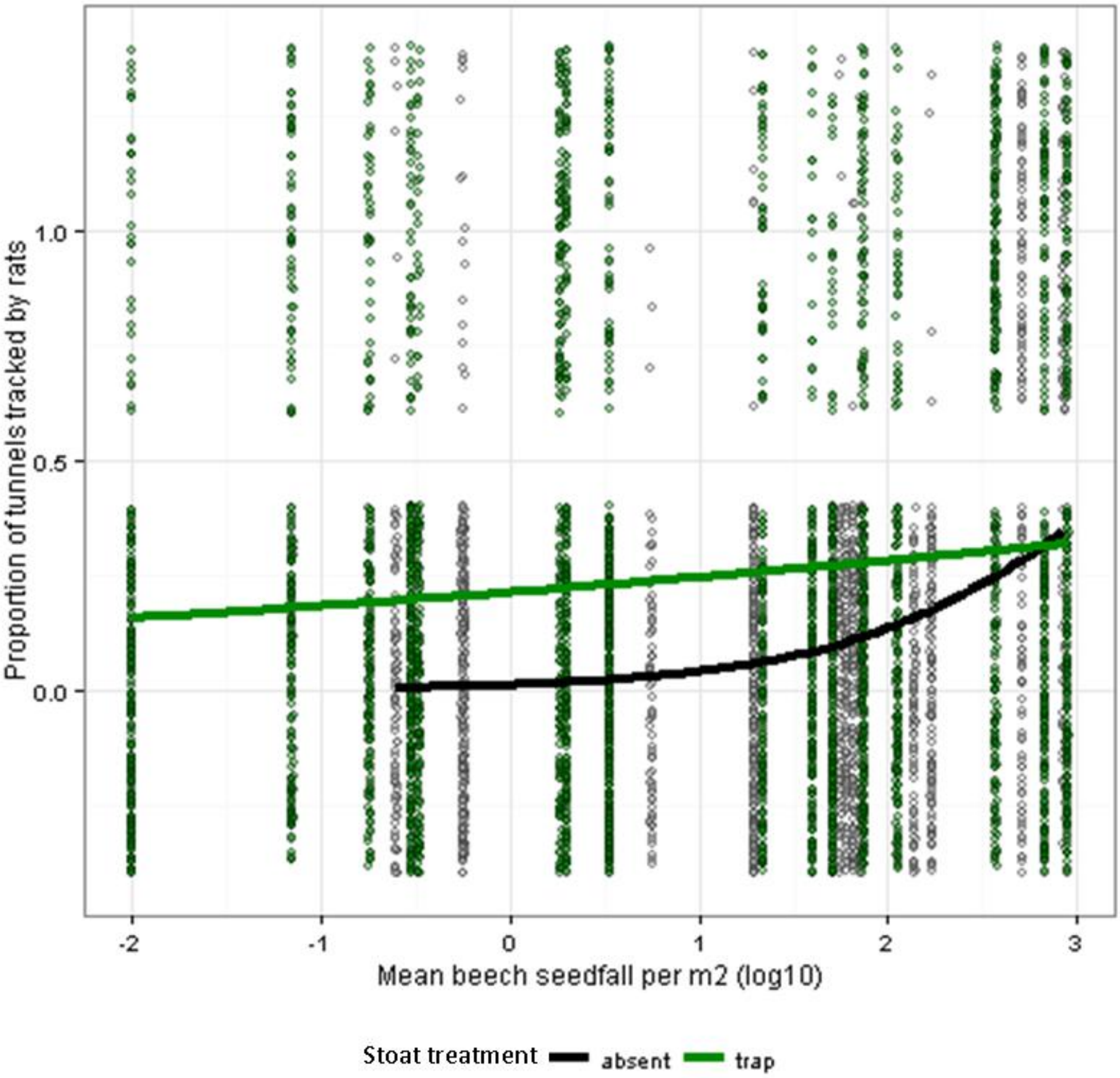


Figure 3.6 Proportion of tracking tunnels tracked by rats against mean annual beech seedfall per m^2 (log10). Graph shows the differences in rat tracking rates between stoat treatments; absent (non-treatment) and targeted stoat trapping. The jitter function was applied to show repeat counts of the binomial data. The fitted lines come from local smoothing functions (geom_smooth... formula = y ~ x, method = "glm", family = "binomial"), for statistical testing see Table 3.1.

3.4 Discussion

The information collected here has been successful in providing information to answer the key questions in this chapter and helps to confirm the more effective ways to control ship rat populations. Rat detection decreased with altitude: rat tracking levels were highest at altitudes between 600 m and 800 m a.s.l. Rat detection also increased when stoats were controlled relative to the non-stoat treatment rat tracking rates, which is consistent with the occurrence of mesopredator release. Rat detection exhibited a significant increase when beech seedfall levels increased and underwent obvious spikes at these times unless there was local effective rat control. The tracking tunnel monitoring results indicated that the application of 1080 poisoning was the only method that reduced ship rat abundance. The application of diphacinone, pindone, or targeted rat trapping did not result in reduced rat abundance. The proportion of tracking tunnels tracked by rats was significantly lower when 1080 was applied relative to the non-treatment rat tracking rates.

Ship rat responses to altitude and seedfall

In New Zealand, ship rats are largely absent from higher elevation habitats including upland beech forest and above the treeline (Studholme 2000, Harper, G. A., Dickinson & Seddon 2005, Christie et al. 2006, Christie et al. 2017). In accordance with this, findings from my study indicate that ship rats residing in beech forest habitats are most abundant between 600 and 800 m a.s.l and their presence decreases rapidly at altitudes greater than 1000 m a.s.l. Studholme (2000) suggested that ship rats prefer lower altitudes because they are confined to areas with mean monthly temperatures of no less than 2°C. However, several studies have detected increased rat capture success in winter (e.g. Alterio, Moller & Brown 1999, Efford et al. 2006, Christie et al. 2017). Christie et al. (2017) suggest that increased rat capture in colder months is indicative of increased capture probability rather than increased rat abundance. Rats have a fast metabolism and may undergo increased food requirements in the winter, consequently, increased time spent foraging may increase the likelihood that they will enter a baited trap (Innes 2005, Christie et al. 2017). Therefore elevation may be less of a limiting factor to rat abundance or detectability when food supplies are high i.e. during a high-seed year.

This study provides further evidence that ship rat abundance increases with increased beech seedfall in New Zealand forests, which supports findings from other studies investigating the relationships between rodents and mast seed events (e.g. King 1983, Wolff 1996, Choquenot & Ruscoe 2000, Ostfeld & Keesing 2000, Fitzgerald, B. M., Efford & Karl 2004, Harper, G. A. 2005, Kelly et al. 2008b, Long et al. 2016, Christie et al. 2017). The proportion of ship rats detected in tracking tunnel observations in this study showed marked increases during 2006 and 2014, both of which were high-seed years. Whether or not ship rat abundance increases at higher altitudes during high-seed years cannot be concluded from this study, however, Christie et al. (2017) found that more rats were captured at higher altitudes when beech seed fall increased but rats were still not captured at altitudes greater than 1100 m a.s.l.

Ship rat responses to pest (rat and stoat) control

1080 poisoning was the only effective technique at reducing ship rat detection in tracking tunnels across all study sites. This is not surprising because previous studies have found that poisoning with 1080, specifically via aerial application, will substantially reduce stoat, possum, and/or ship rat populations immediately following 1080 operations (Miller & Miller 1995, Murphy, E. C. et al. 1999, Veltman & Pinder 2001, Gillies et al. 2003, Nugent & Morriss 2013, Elliott & Kemp 2016, Griffiths & Barron 2016). Aerial application is also beneficial in terms of geographical area coverage; areas inaccessible on foot can still be reached for predator control using the aerial application of toxins (Elliott & Kemp 2016, Griffiths & Barron 2016).

Other toxins (i.e. diphacinone and pindone), which were applied using a network of poison bait stations at the Rotoiti core and Lakehead sites, were found to be associated with increases in rat detection in this study. It is unlikely that poisoning with toxins other than 1080 would cause an increase in rat abundance and more likely that these techniques have been ineffective at controlling ship rat populations, particularly those that are undergoing a natural increase for other reasons.

Rat trapping apparently did not work at RNRP: it did not have a significant effect on the proportion of tracking tunnels tracked by rats relative to tracking tunnel rates under non-treatment conditions. Studies investigating the effect of different ship rat control methods have found that targeted rat trapping or ground based poisoning with toxins other than 1080 can in fact reduce ship rat populations (Innes et al. 1995, Murphy, E. C. et al. 1998, Hill, Vel & Shah 2003, Ruscoe et al. 2011) but the degree to which these populations are reduced varies greatly and in some cases it is likely that the population reductions observed may not meet the requirements for an operation to be deemed successful and provide real conservation benefits (i.e. the DOC recommended target rat tracking rates of ≤ 5 %; Elliott & Suggate 2007).

It has been advised that ground-based control of ship rats (either trapping or poisoning) should be applied following aerial 1080 operations to kill the remaining survivors of a large-scale operation and to maintain the benefits provided by aerial control (Parkes et al. 2017). Ship rat populations are known to recover within as little as 6 months following aerial 1080 operations and it is suggested that their populations are able to surpass pre-operation densities (Innes et al. 1995, Miller & Miller 1995) which could be due to reduced predation from stoats and/or reduced competition with possums (Tompkins & Veltman 2006, Rayner et al. 2007, Ruscoe et al. 2011, Masuda et al. 2014).

In this study I found evidence for mesopredator release of rats following the control of stoats. Rat detection levels were higher when targeted stoat trapping was applied compared to when there was no targeted stoat control. These results support evidence for mesopredator release found in a number of other studies (Caut et al. 2007, Rayner et al. 2007, Prugh et al. 2009, Ritchie & Johnson 2009), and in particular, a simulation model constructed by Tompkins and Veltman (2006) that predicted an increase in rat abundance in the presence of stoat control in mixed beech forest. However, this is contrary to findings from Ruscoe et al. (2011) who tested for mesopredator release empirically and found evidence for competitive release of rats when possums were controlled but not for mesopredator release when stoats were controlled. A possible reason for this may be that my study and Tompkins and Veltman's (2006) model involve mixed beech forest in the South Island, whereas the study by Ruscoe et al. (2011) occurred within a mixed podocarp forest in the North Island. Since beech forests have more food for ship rats when beech trees are masting (McQueen & Lawrence 2008), this may reduce food competition between rats and possums in beech forests. Evidence for mesopredator release in my study is discussed further in Chapter 5.

Interactions between pest control and altitude

Since the proportion of tunnels tracked by rats was lower with increasing altitude, it is expected that rats should display a reduced response to pest control at higher elevations, as is shown here with the application of 1080. Although the results here suggest that the use of toxins other than 1080 result in higher rat tracking rates at lower altitudes and lower rat tracking rates than all other treatments at higher altitudes, these findings are confounded by the artefact of increased rat tracking during diphacinone and pindone applications between 2011 and 2013. Other toxin treatment applications were applied following a period of prolonged stoat trapping with no targeted rat control. This suggests that rats were able to reach higher densities under the influence of mesopredator release. My study found that the effect of mesopredator release on rats is greatest between 600 m and 800 m a.s.l. Therefore, the relatively high rat tracking rates under the other toxins treatment regime at lower elevations may also be an artefact of mesopredator release.

Interactions between pest control and masting events

The peak in rat tracking rates at the non-rat-treatment sites (Big Bush, Cobb, Rotoiti new, and Rotoroa), compared to the steep decline in rat tracking rates at the rat-treatment sites (Flora, Lakehead, and Rotoiti core), outlines the benefit of 1080 poisoning to control ship rat populations during high-seed years. The efficiency of 1080 as a rat control tool is not significantly affected by the level of mean annual seedfall per m^2; however rat tracking rates were only reduced down to the DOC recommended target (≤ 5 %) in Flora and Lakehead and not in Rotoiti core following aerial 1080 application in 2014. Elliot and Kemp (2016) found that aerial 1080 application substantially reduced rat abundance at 25/25 South Island sites; however the target of ≤ 5 % rat tracking was only reached in 72 % of the sites they analysed.

The lack of application of other toxins and rat trapping during high-seed years through the course of this study means that we cannot conclude what heavy seed crops would mean for the efficacy of these treatments. However, because previous studies show that ground-based treatments are not enough to control increased rat populations during high-seed years (Elliott & Suggate 2007) and the ground based treatments did not reduce ship rat populations in this study, my analyses suggest that during high-seed years, ground-based treatments would be ineffective at controlling ship rat populations within my study sites.

Conclusions

Rat control is not usually applied at higher altitudes (> 1000 m a.s.l) due to lower rat tracking rates at these elevations. Findings here suggest that this strategy is justified because the benefit of effective rat control is reduced as altitude increases and it is unlikely that rat populations will expand over this threshold during high-seed years. Based on new information provided by this study, I suggest that rat control at lower altitudes is most important when stoat populations are also being controlled, but using stoat control as a proxy for stoat abundance must be interpreted with caution. Targeted rat trapping and poisoning with diphacinone were ineffective at reducing ship rat densities but these options may be useful when rat densities are not particularly high (i.e. following an aerial 1080 operation).

Future study and analysis of this data could include mustelid tracking tunnel observations to make direct comparisons between stoat and ship rat abundance to confirm that ship rat populations increase when stoat populations are reduced. Including possum treatments as an additional level in the analysis would provide evidence for the presence/absence of competitive release of rats which is also an important factor to consider, however less important than mesopredator release at these sites since possum abundance is relatively low.

Chapter 4. Factors affecting bird abundance

4.1 Objectives

Understanding the mechanisms that alter faunal responses to pest control operations is important in order to optimise the outcomes of pest control operations (Parkes & Murphy 2003, Ruffell & Didham 2017). The purpose of monitoring bird populations at these sites has been to determine how they are responding to predator control, to inform native species conservation, within these areas. Here I investigated the responses of individual bird species to a variety of variables that potentially affected their populations, including rat tracking rates, predator (stoat and ship rat) control methods, total native bird abundance, total introduced bird abundance, altitude, and level of beech seedfall.

Similar to the rat tracking data (Chapter 3), the bird count data has been collected at a range of altitudes and time spans over the course of 15 years (February 2002 – May 2016; Chapter 2; Tables 2.10 and 2.11). This is a period in which there was a wide range in annual beech seedfall levels, including several high-seed years. A full list of the bird species detected within these sites is given in Table 4.1. Here I use the index of bird abundance (as measured using 5MBCs) of the 12 most commonly detected species under each pest control regime, at a range of altitudes, with a range of seedfall levels, to answer the following key questions:

1. How does forest bird abundance vary with altitude?
2. How does forest bird abundance respond to beech seedfall events?
3. How does forest bird abundance respond to ship rat abundance?
4. How does forest bird abundance respond to different pest control methods?
5. Do bird responses to ship rat populations vary with altitude and/or beech seedfall?

As with the ship rat monitoring (Chapter 3), the overall aim was to determine the most effective way to control ship rats for native bird conservation and to determine the conditions under which the effects of different pest control techniques on common forest bird populations may change.

Table 4.1 Mean number of birds detected per bird count for all species detected using 5MBCs across all sites. Species are listed in order of most frequently detected (The first 12 being the species that were included in the analysis). The 40 species include 15 introduced species and 25 native species, 17 of which are endemic to New Zealand. Native species are indicated by the inclusion of their Māori name and endemic species indicated with an *. The list does not include birds that were detected but not identified. A mean of + indicates species whose mean abundance was < 0.001. Common redpolls, Eurasian blackbirds and New Zealand fantails are hereafter referred to simply as redpolls, blackbirds and fantails.

Common name	**Scientific name**	**Māori name**	**Mean**
bellbird	*Anthornis melanura*	korimako*	2.55
silvereye	*Zosterops lateralis*	tauhou	2.03
chaffinch	*Fringilla coelebs*	-	0.74
tomtit	*Petroica macrocephala*	miromiro*	0.72
song thrush	*Turdus philomelos*	-	0.69
grey warbler	*Gerygone igata*	riroriro*	0.60
rifleman	*Acanthisitta chloris*	tītīpounamu*	0.55
common redpoll	*Carduelis flammea*	-	0.52
brown creeper	*Mohoua novaeseelandiae*	pīpipi*	0.29
Eurasian blackbird	*Turdus merula*	-	0.28
tui	*Prosthemadera novaeseelandiae*	tūī*	0.23
New Zealand fantail	*Rhipidura fuliginosa*	pīwakawaka*	0.19
kaka	*Nestor meridionalis*	kākā*	0.15
South Island robin	*Petroica australis*	toutouwai*	0.15
European goldfinch	*Carduelis carduelis*	-	0.10
yellow crowned parakeet	*Cyanoramphus auriceps*	kākāriki*	0.09
European greenfinch	*Carduelis chloris*	-	0.03
weka	*Gallirallus australis*	weka*	0.01
kea	*Nestor notabilis*	kea*	0.01
paradise shelduck	*Tadorna variegata*	pūtakitaki*	0.01
dunnock	*Prunella modularis*	-	0.01
shining cuckoo	*Chrysococcyx lucidus*	pīpīwharauroa	0.01
New Zealand falcon	*Falco novaeseelandiae*	kārearea*	0.01
common starling	*Sturnus vulgaris*	-	0.01
New Zealand pipit	*Anthus novaeseelandiae*	pīhoihoi*	0.004
Eurasian skylark	*Alauda arvensis*	-	0.004
Australasian harrier	*Circus approximans*	kāhu	0.004
long tailed cuckoo	*Eudynamys taitensis*	koekoeā*	0.003
New Zealand pigeon	*Hemiphaga novaeseelandiae*	kererū*	0.003
welcome swallow	*Hirundo neoxena*	warou	0.002
house sparrow	*Passer domesticus*	-	0.001
spur winged plover	*Vanellus miles*	-	0.001
black backed gull	*Larus dominicanus*	karoro	0.001
sacred kingfisher	*Todiramphus sanctus*	kōtare	0.001
mallard	*Anas platyrhynchos*	-	+
Canada goose	*Branta canadensis*	-	+
black swan	*Cygnus atratus*	kakīānau	+
yellowhammer	*Emberiza citrinella*	-	+
California quail	*Callipepla californica*	-	+
morepork	*Ninox novaeseelandiae*	ruru	+

4.2 Methods

A total of 6856 5MBC observations from February 2002 – May 2016 were used in the analysis for this study. These observations included bird count data from Cobb, Flora, Lakehead, Rotoiti core, and Rotoroa. My data set excluded 802 observations from bird count stations at altitudes below 600 m a.s.l. at Rotoroa because these were outside of the altitudinal range of the remaining four sites. Bird count stations therefore covered an altitudinal range of 615 m to 1481 m a.s.l.

Bird count data for each bird species were analysed using GLMs (generalised linear models) with a poisson error distribution using the *lme4* package in R (Appendix A) (Bates et al. 2015). Bird count stations were analysed as independent points so that the full altitudinal ranges of each bird count transect could be considered as well as the pest control method applied in relation to a given count. Three models were tested to explore the relationships between forest bird abundance and altitude, seedfall, ship rat abundance, pest control, and other bird populations (Table 4.2). Ideally I would have used GLMMs as with the rat analysis (Chapter 3) but due to the data structure, only GLMs would run. Had the GLMMs run for the bird analyses, I would have included random terms for bird count station, transect and site, to allow for the nested nature of the data. Since this was not an option, measuring bird count stations independently was acceptable because the birds counted change rapidly over time and the differences in birds counted between one station and the next are important in this study. Furthermore, no statistical controls were added to control for observer bias because all the observers that contributed to the data for this study were either volunteers, employees, or students from UC and DOC that had received proper training.

ANOVA (analysis of variance) chi square tests were run for each model for each species to compare residual degrees of freedom and residual deviance of each level within the models to check for over-dispersion. All three models for redpolls and silvereyes were subsequently corrected for over-dispersion by using a quasi-poisson error distribution. Over-dispersion was not detected in any of the models for the remaining species (see ANOVA summary outputs in Appendix A).

The effect of ship rats on birds was tested two different ways: directly using rat tracking rates, and indirectly using management treatment regimes. To test for the effect of rat tracking on bird abundance, the annual mean rat tracking proportions per site, calculated from the rat tracking data used in Chapter 3, were included as a fixed term within Model 1 (Table 4.2). Rat tracking rates from November tracking tunnel observations were applied to bird counts made in the same November and for the two counts that followed (February and May the following year). The same technique was also used to match pest control treatments to the bird count data (Model 2). To allow for potential indirect effects of pest control via competition among bird species, counts of total introduced birds and total native birds were used as a measure of total abundance of potential avian competitors to use as fixed effects predicting individual species abundance (Model 3). For native species this was calculated by subtracting the focal species abundance from the total native species detected at each count, and similarly for focal introduced species subtracted from the introduced species totals. Within the GLMs, stoat treatment included two levels, either trapping or absent (non-treatment), and rat treatment included four levels; 1080, other toxins, trapping, and absent (non-treatment), as in Chapter 3. As well as the fixed terms, I included a few specific interaction terms (Table 4.2) where those were directly relevant to my questions. The R code used for the final GLMs was as follows (example here for bellbirds):

MODEL 1

```
> belglm.1<-glm(bellbird ~  rat.tracking * altitude
+               + rat.tracking * mean.seed.log10,
+               family = poisson, data = allBC)
> summary(belglm.1)
```

MODEL 2

```
> belglm.2<-glm(bellbird ~ stoat.tmnt
+               + rat.tmnt4 * altitude
+               + rat.tmnt4 * mean.seed.log10,
+               family = poisson, data = allBC)
> summary(belglm.2)
```

MODEL 3

```
> allBC$tn.bel <- (as.numeric(allBC$total.native) -
as.numeric(allBC$bellbird))
> belglm.3<-glm(bellbird ~  total.exotic
+               + as.numeric(allBC$tn.bel)
+               + altitude
+               + mean.seed.log10,
+               family = poisson, data = allBC)
> summary(belglm.3)
```

As with the rat tracking analysis, altitude (m a.s.l.) and seed fall (mean annual beech seeds per m^2) were included as continuous variables and seed count observations were log-transformed (log10) (Chapter 3). Seed count data from the Rotoiti core site was used as a predictor for the nearby Lakehead site, and Flora used for the nearby Cobb site, because seedfall data were only available from three locations (Rotoiti core, Rotoroa and Flora). For a full list of sites with years of treatment and data collection methods see Chapter 2.

Table 4.2 Fixed terms and interactions used in three GLMs for bird count data analysis. Rat tracking, total native birds and total introduced birds are described in detail in this Chapter. See Chapter 3 for detailed descriptions of the remaining fixed terms (altitude, seed fall, stoat treatment, and rat treatment).

Model 1 (rat abundance)	Model 2 (treatments)	Model 3 (competition)
rat tracking	stoat treatment	total native birds
altitude	rat treatment	total introduced birds
seed fall	altitude	altitude
rat tracking x altitude	seed fall	seed fall
rat tracking x seed fall	rat treatment x altitude	
	rat treatment x seed fall	

4.3 Results

The 12 most commonly detected bird species during 5MBCs across all sites included four introduced species and eight native species (seven endemic) (Table 4.1). Of these, the most common was bellbirds (mean = 2.55 birds per 5MBC). There was variation between species in their responses to beech seedfall, altitude, and pest control, while responses to rat tracking rates were more consistent. Comparing models by their AIC (Akaike Information Criterion) value indicates that Model 1 (i.e. rat abundance) was the best predictor of bird species abundance for most species. The exceptions were fantails, which were best described by Model 3 (i.e. total bird abundance), and song thrushes, best described by Model 2 (i.e. pest control method) (Table 4.3). The best models for silvereyes and redpolls could not be specified because there was no AIC data for these species. For a list of GLM summary outputs from R and associated ANOVA chi square tests refer to Appendix A.

Table 4.3 AIC values for the three models used to predict changes in bird population abundance using bird count data for the 12 most common species from all sites combined (Cobb, Flora, Lakehead, Rotoiti new, and Rotoroa). Species are listed in order of most common. The lowest AIC values for each species are the models with the best fit and are indicated in bold. AIC values were not given in R output for redpolls and silvereyes because of the quasi-poisson error distribution.

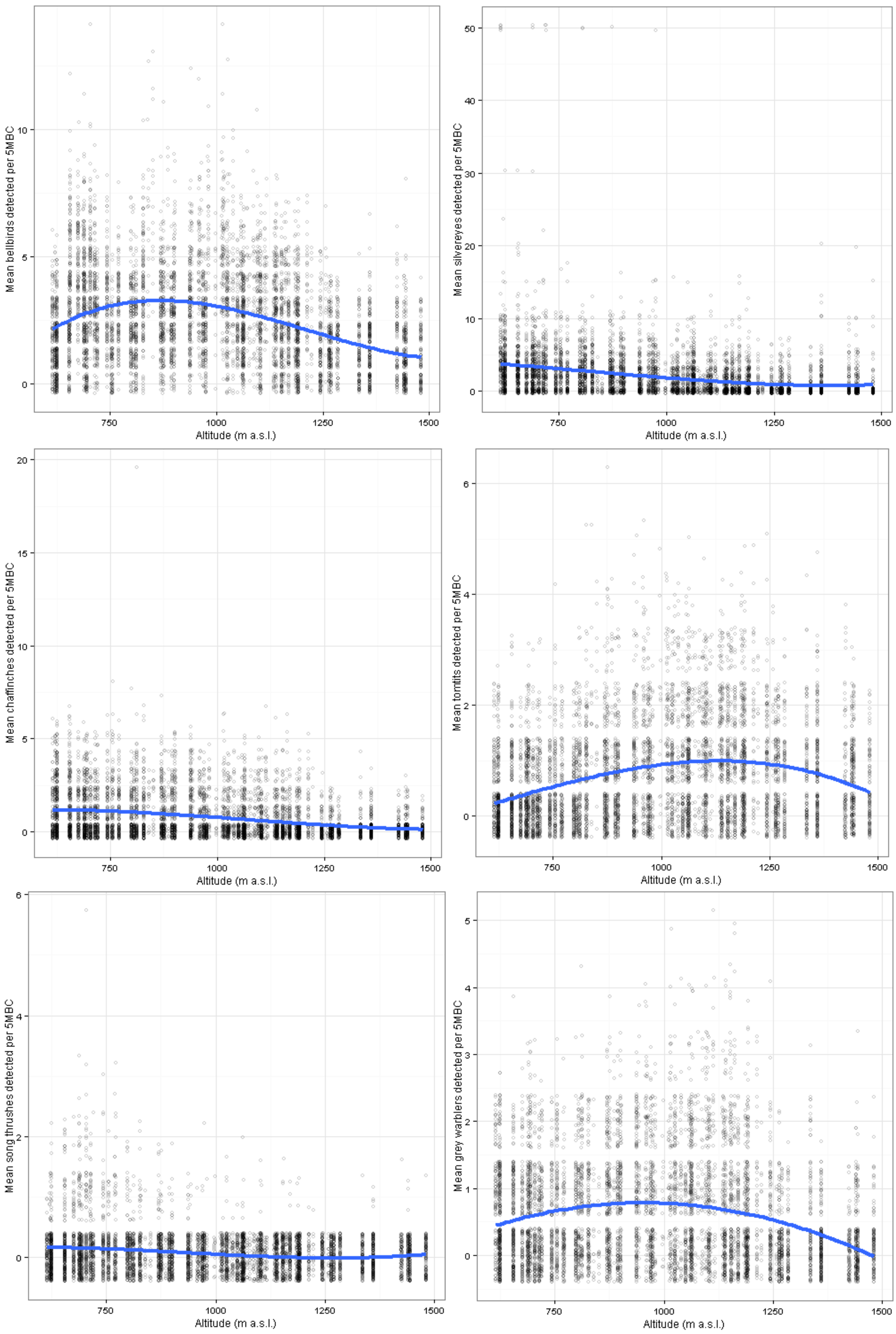
Species	**Model 1**	**Model 2**	**Model 3**
bellbird	**25976**	26439	27004
silvereye	NA	NA	NA
chaffinch	**15981**	16257	16481
tomtit	**15037**	15298	15371
song thrush	3075	**3015**	3121
grey warbler	**13622**	13959	13950
rifleman	**14158**	14529	14834
redpoll	NA	NA	NA
brown creeper	**9802**	9841	10044
blackbird	**8606**	8650	8671
tūī	**7653**	7801	7888
fantail	6960	6947	**6935**

Bird abundance varied significantly with altitude for all species except redpolls (Table 4.4). Brown creeper, tomtit, and rifleman abundance increased with altitude, while the remaining nine species (four introduced and five native) showed declines in abundance with increased elevation (Table 4.4). Bellbirds, grey warblers, riflemen, and tomtits all showed similarly curved responses to altitude (according to the shape of the smoothed lines in Fig 4.1) relative to the other bird species (Figure 4.1). Each of these four species were most common at mid to high altitudes and demonstrated obvious peaks in abundance at around 900 m, 1000 m, 1150 m, and 1200 m a.s.l., respectively (Figure 4.1).

Bird responses to beech seed fall were more varied than that of altitude (Table 4.4, Figure 4.2). Redpoll and tūī abundance did not change significantly in response to seedfall (Table 4.4). Brown creeper, fantail, and rifleman abundance increased with increased seedfall and the remaining species responded negatively to increased seed fall (Table 4.4). Brown creepers and rifleman therefore were the only species to respond positively to both increased seedfall and elevation, and redpolls were the only species lacking a response to either factor (Table 4.4).

Bird populations showed consistent responses to ship rat abundance (i.e. rat tracking rates). Brown creepers, chaffinches, fantails, and redpolls (two introduced species and two native species) did not respond to ship rat abundance, while all remaining species decreased in response to ship rat abundance (Table 4.4, Figure 4.3). Riflemen and tūī showed the greatest population reductions as a result of rat tracking, -5.394 and - 3.948, respectively (see Appendix A for GLM summary outputs).

None of the bird populations analysed here increased in response to increased rat tracking (Table 4.4). The positive rat tracking by altitude interactions shown by bellbirds, grey warblers, riflemen, silvereyes, and tūī (Table 4.4) mean that the declines in abundance observed in these species in response to rat tracking are reduced at higher elevations.


Mean bellbirds detected per 5MBC
10
5
0
750
1000
1250
1500
Altitude (m a.s.l.)
Mean silvereyes detected per 5MBC
50
40
30
20
10
0
750
1000
1250
1500
Altitude (m a.s.l.)
Mean chaffinches detected per 5MBC
20
15
10
5
0
750
1000
1250
1500
Altitude (m a.s.l.)
Mean tomtits detected per 5MBC
6
4
2
0
750
1000
1250
1500
Altitude (m a.s.l.)
Mean song thrushes detected per 5MBC
6
4
2
0
750
1000
1250
1500
Altitude (m a.s.l.)
Mean grey warblers detected per 5MBC
5
4
3
2
1
0
750
1000
1250
1500
Altitude (m a.s.l.)

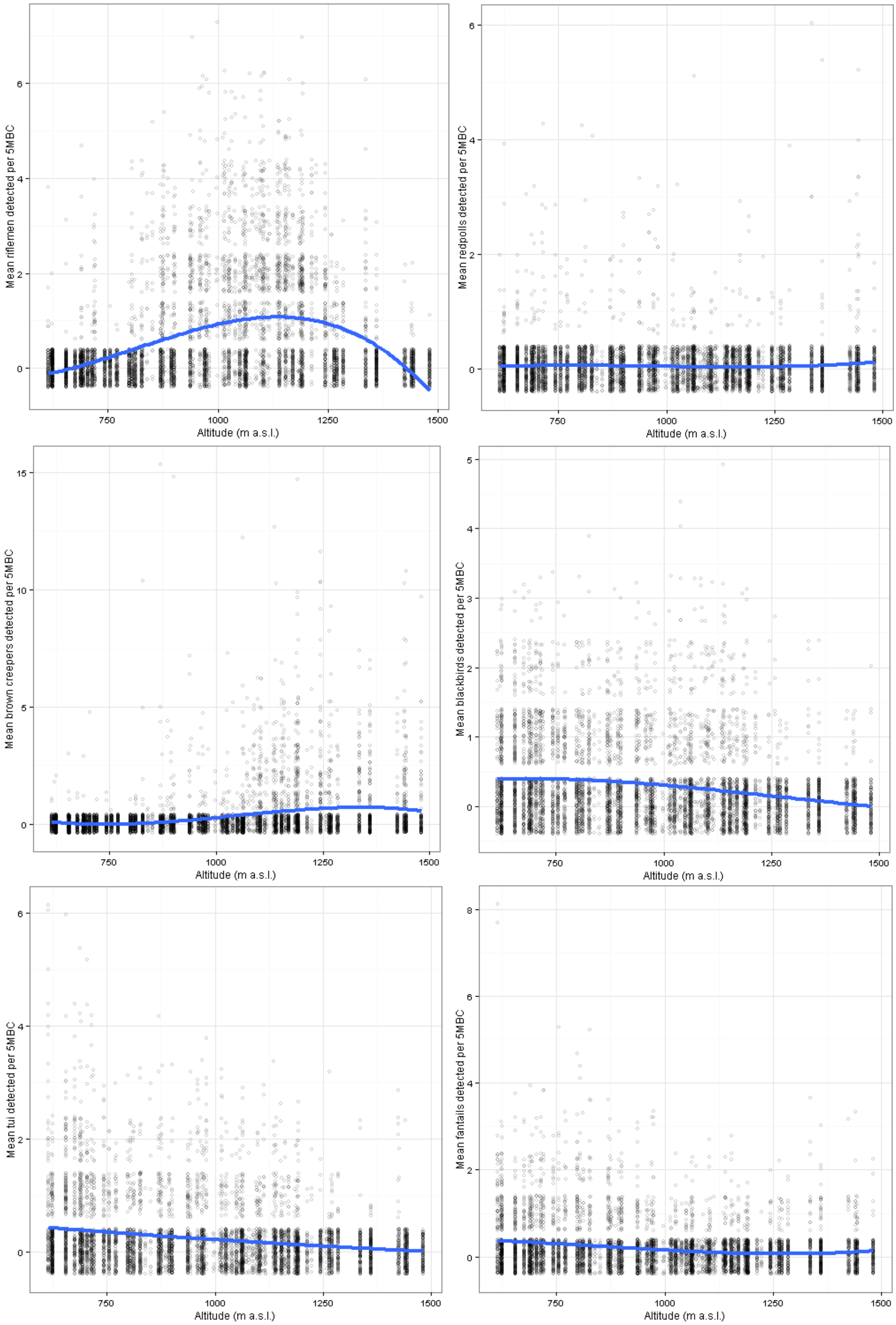
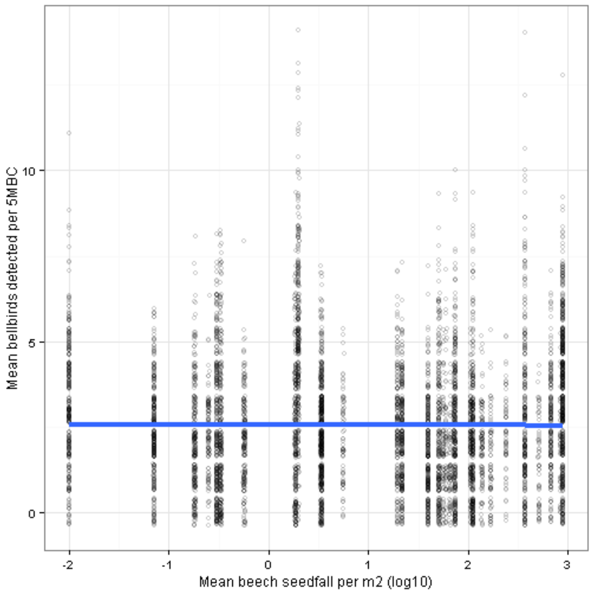
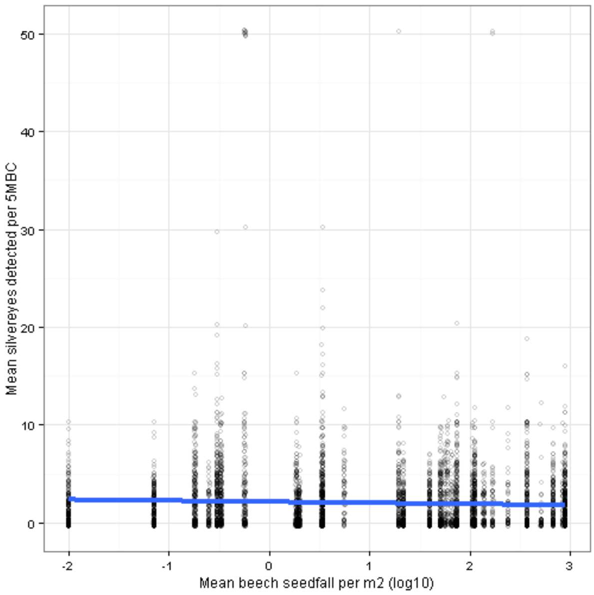
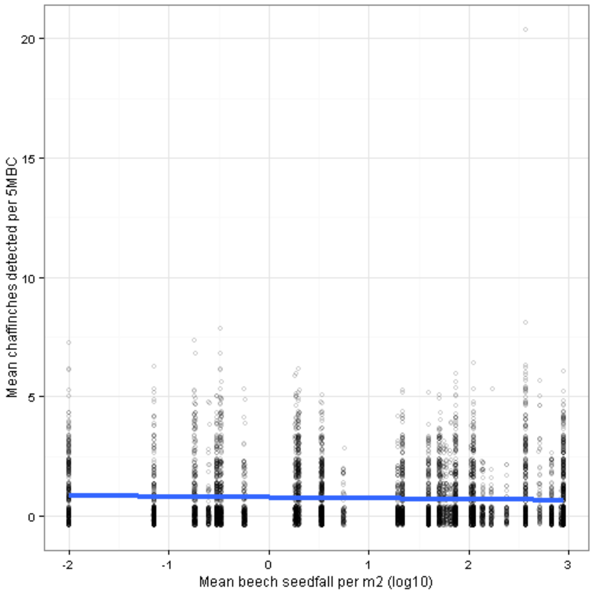
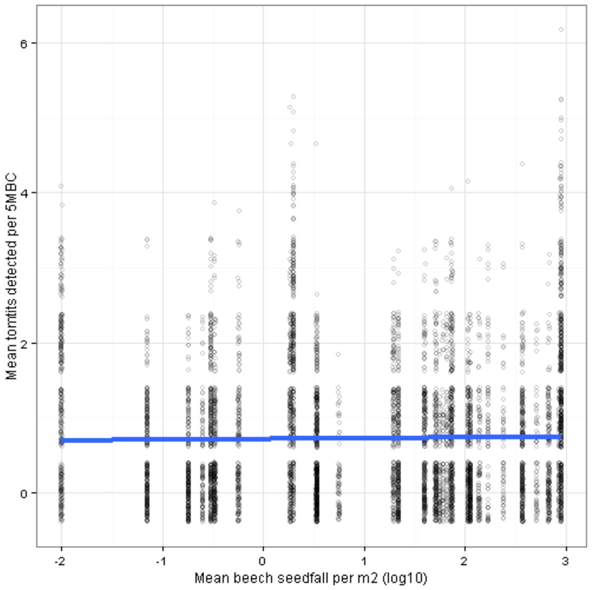


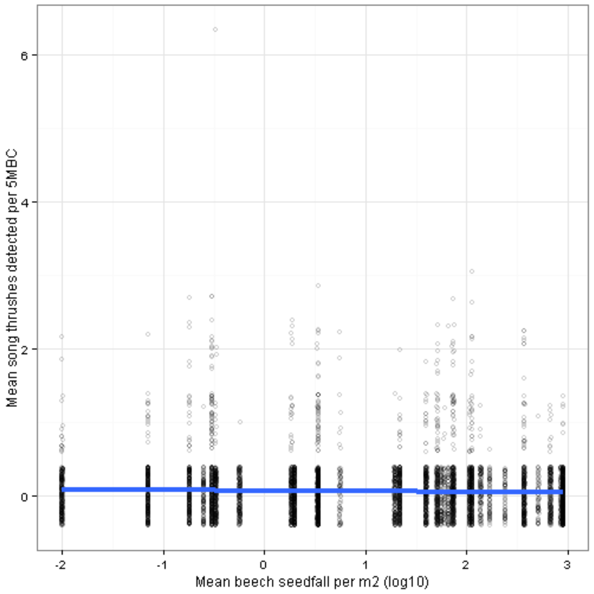
Figure 4.1 Mean number of birds detected per 5MBC against altitude (m a.s.l.) for the 12 most commonly detected bird species across all sites. The jitter function was applied to show the number of repeat counts in the data. The lines are smoothed fits to show the general trends. Silvereye counts of 50 birds per 5MBC are from observations of large silvereye flocks. For statistical testing see Appendix A.

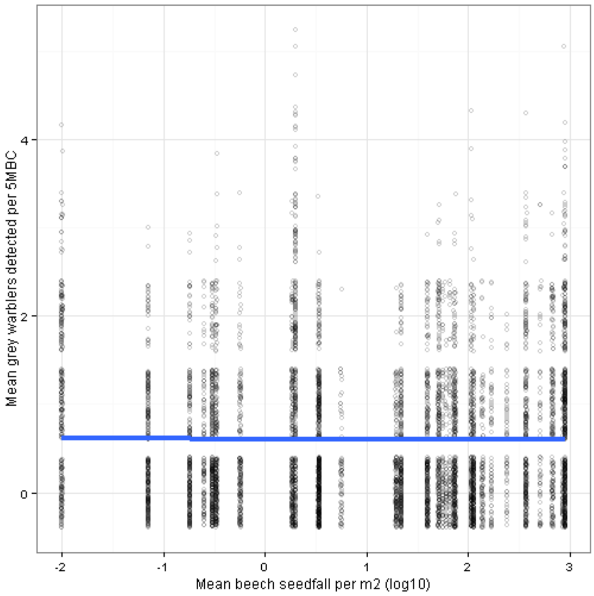

Mean bellbirds detected per 5MBC
0
5
10
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)


Mean silvereyes detected per 5MBC
0
10
20
30
40
50
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)


Mean chaffinches detected per 5MBC
0
5
10
15
20
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)


Mean tomtits detected per 5MBC
0
2
4
6
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)


Mean song thrushes detected per 5MBC
0
2
4
6
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)


Mean grey warblers detected per 5MBC
0
2
4
-2
-1
0
1
2
3
Mean beech seedfall per m2 (log10)

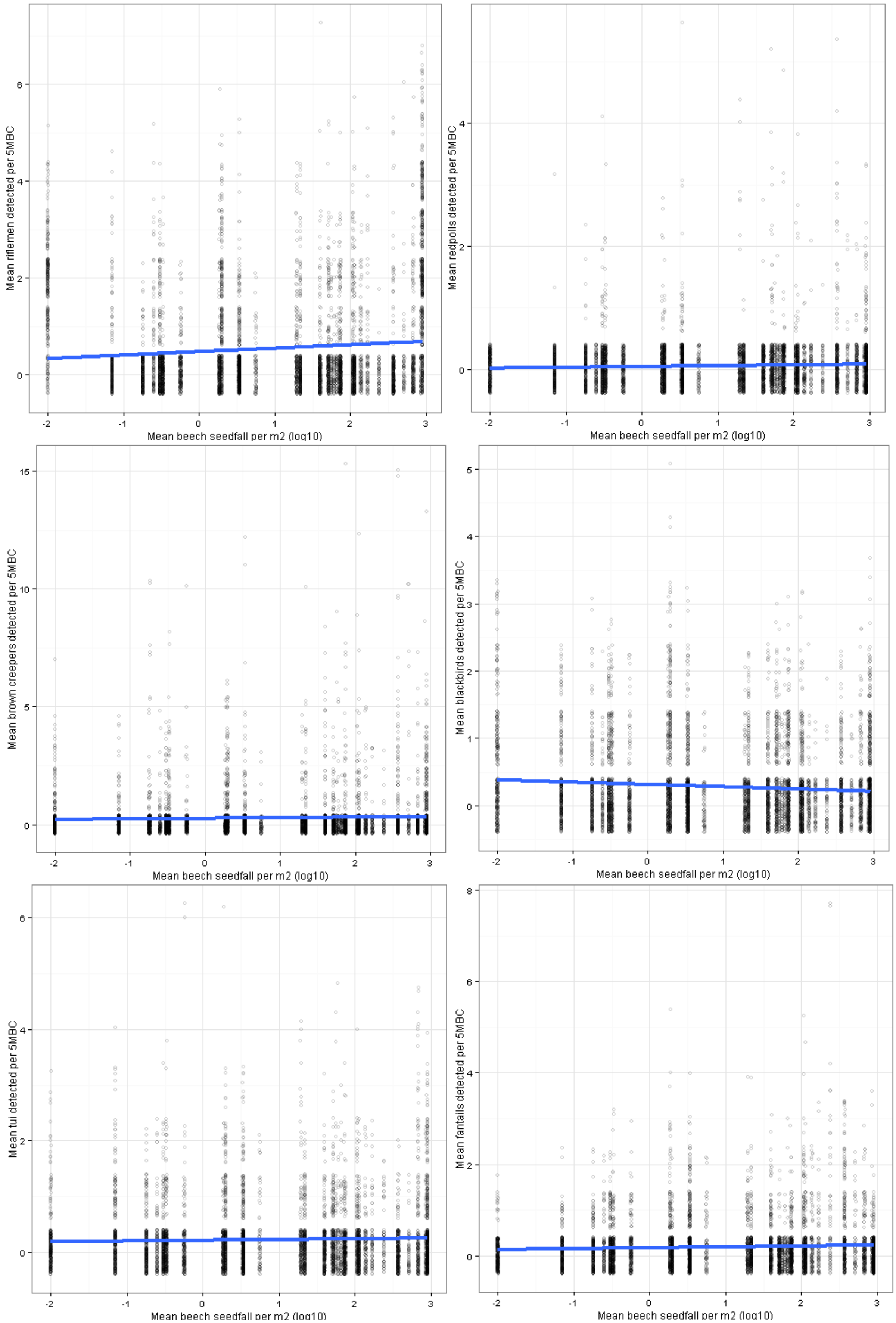
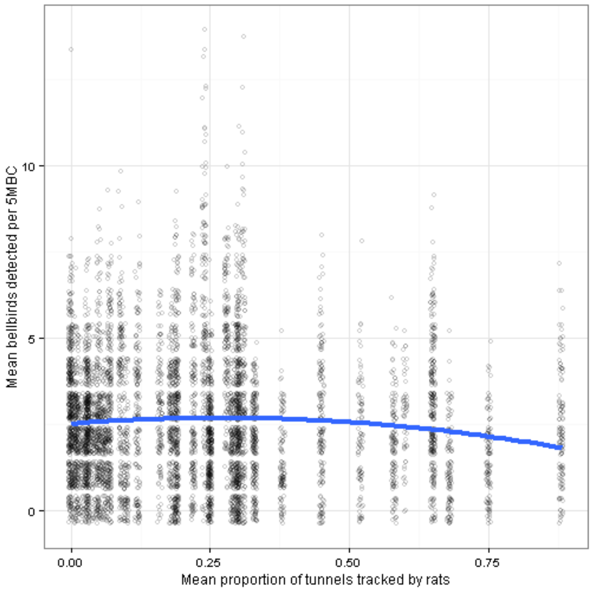
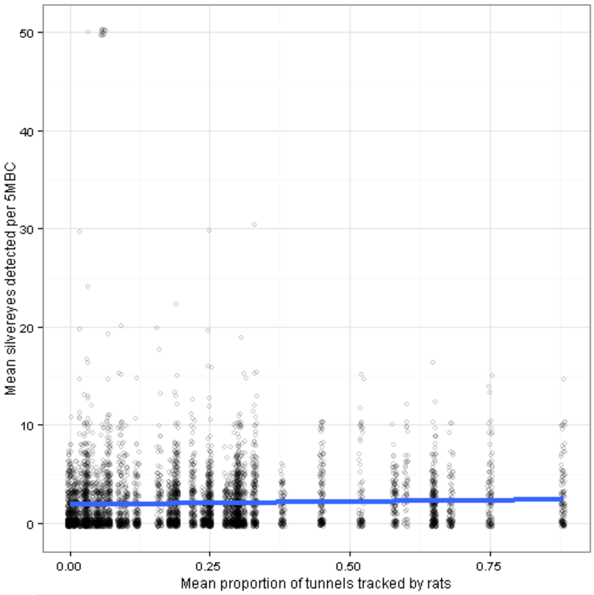
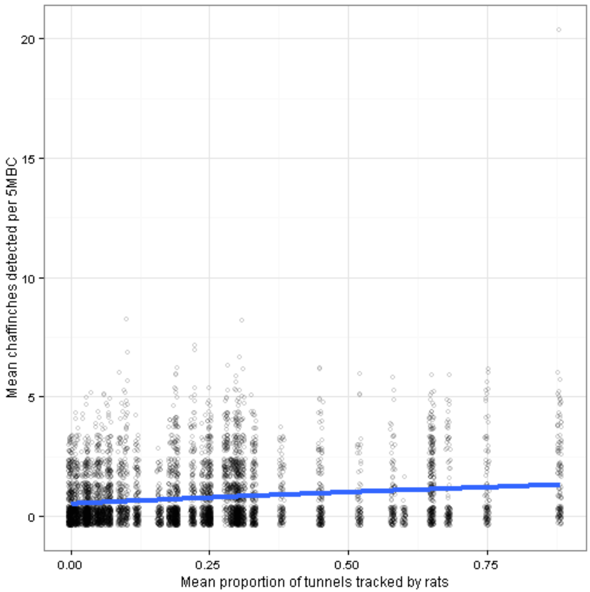
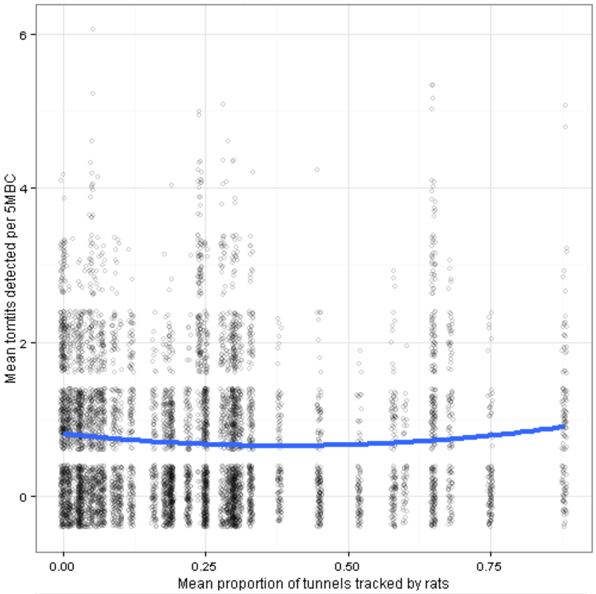


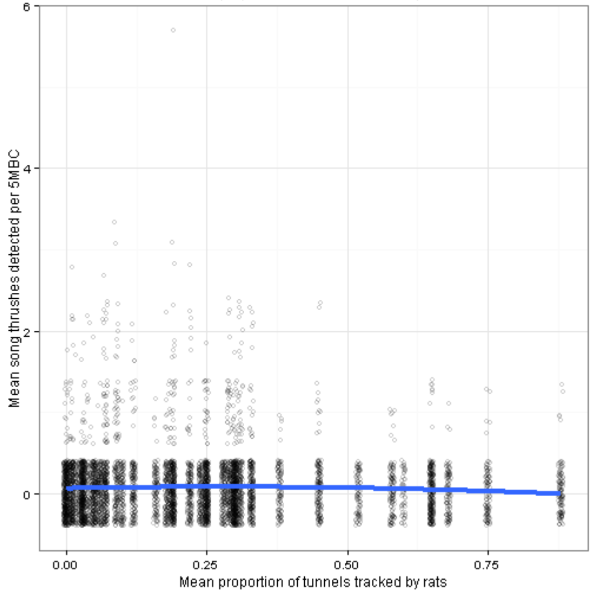
Figure 4.2 Mean number of birds detected per 5MBC against mean annual beech seedfall per m^2 for the 12 most commonly detected bird species across all sites. The jitter function was applied to show the number of repeat counts in the data. The lines are smoothed fits to show the general trends. Silvereye counts of 50 birds per 5MBC are from observations of large silvereye flocks. For statistical testing see Appendix A.

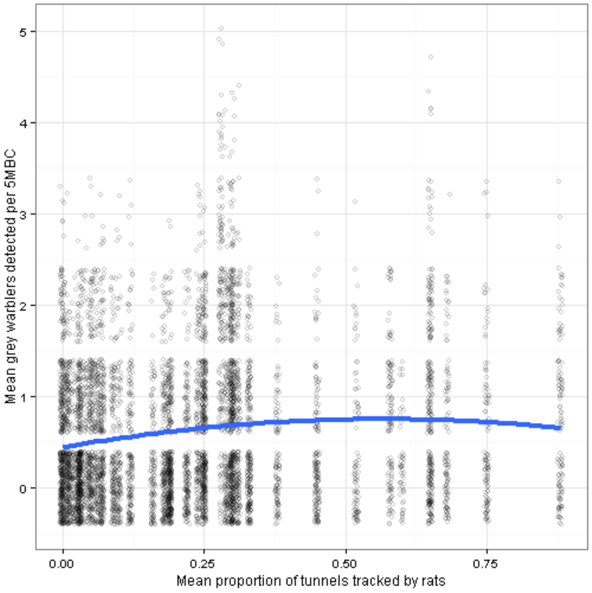

Mean bellbirds detected per 5MBC
0
5
10
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats


Mean silvereyes detected per 5MBC
0
10
20
30
40
50
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats


Mean chaffinches detected per 5MBC
0
5
10
15
20
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats


Mean tomtits detected per 5MBC
0
2
4
6
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats


Mean song thrushes detected per 5MBC
0
2
4
6
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats


Mean grey warblers detected per 5MBC
0
1
2
3
4
5
0.00
0.25
0.50
0.75
Mean proportion of tunnels tracked by rats

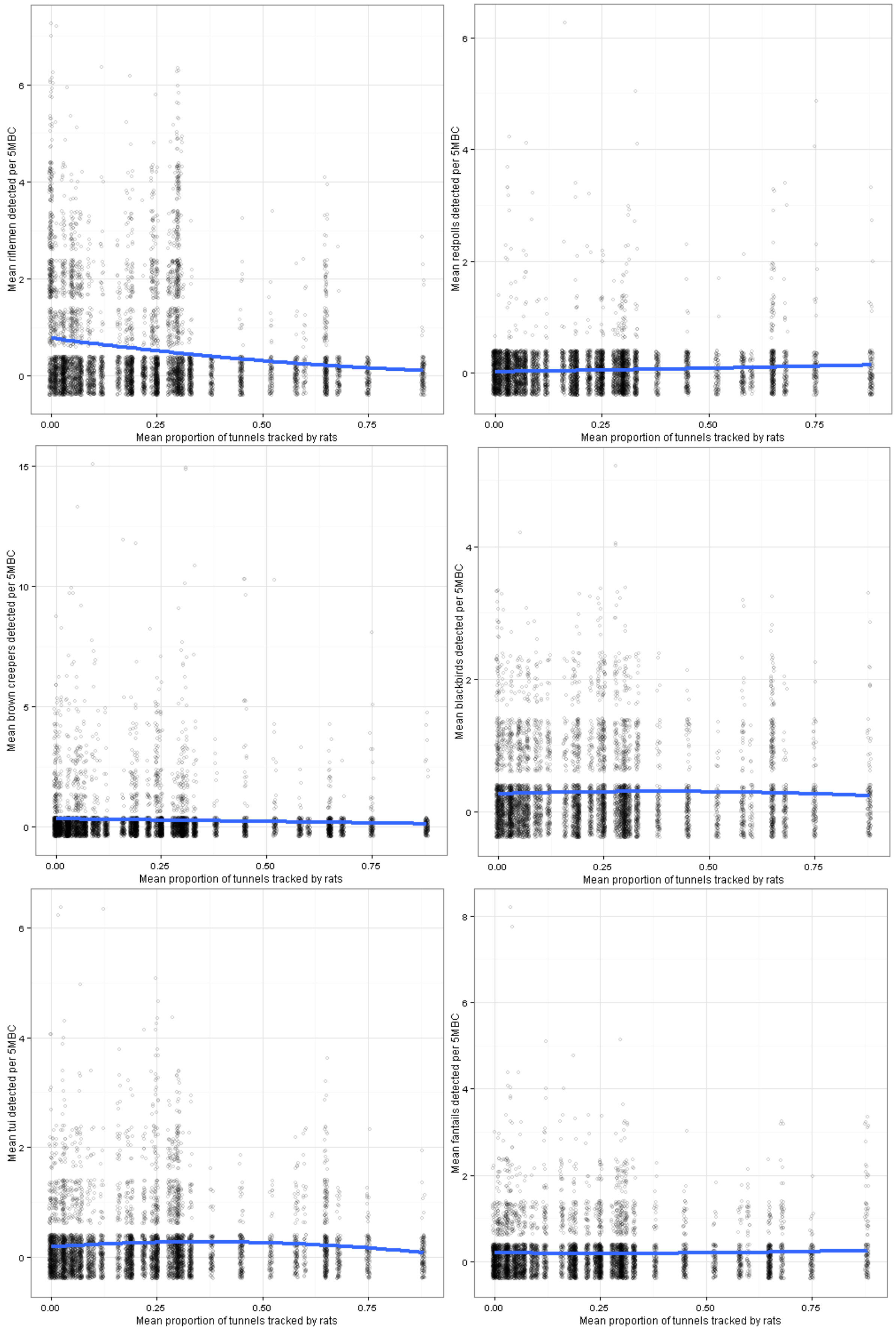


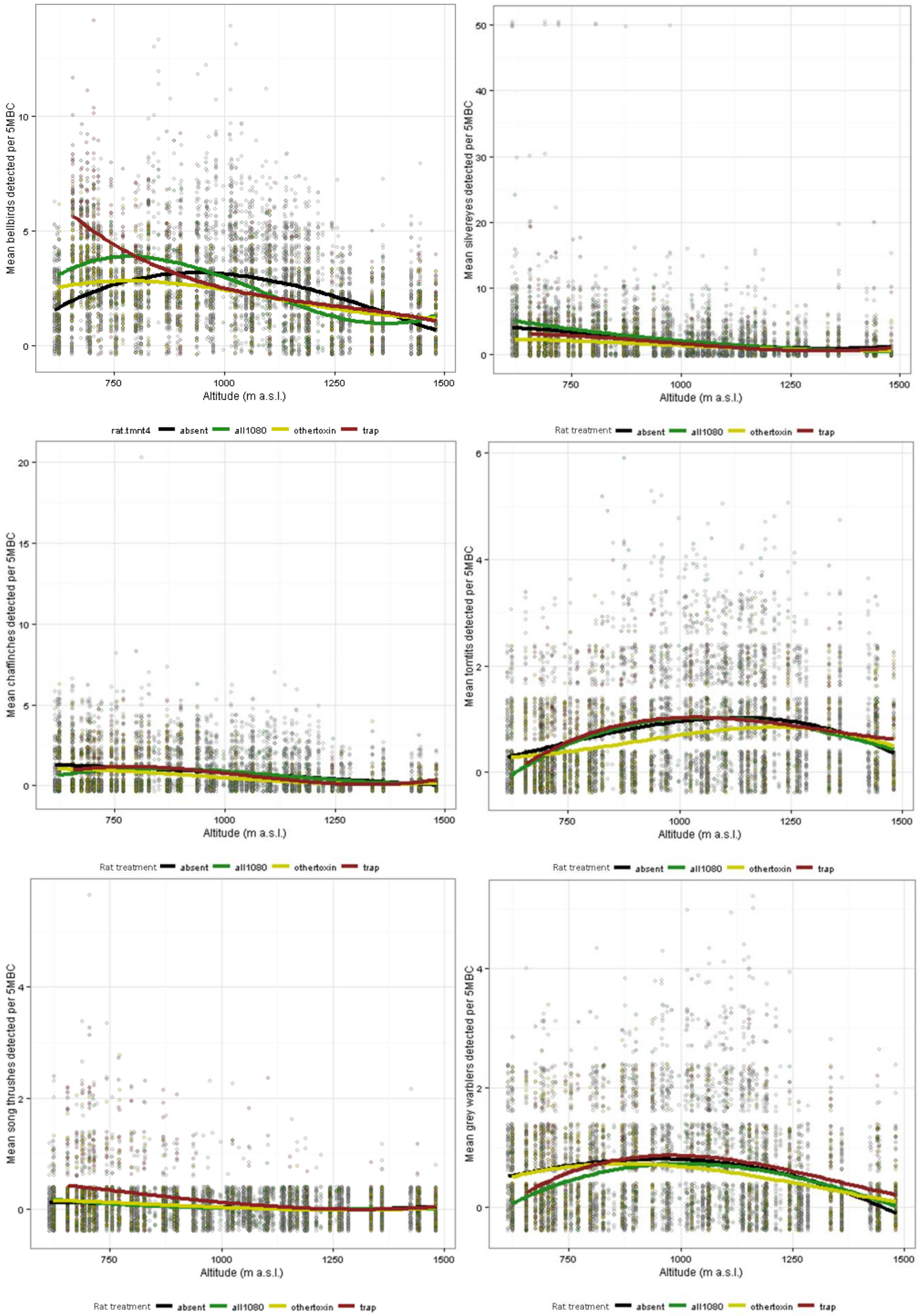
Figure 4.3 Mean number of birds detected per 5MBC against mean proportion of tunnels tracked by rats for the 12 most commonly detected bird species across all sites. The jitter function was applied to show the number of repeat counts in the data. The lines are smoothed fits to show the general trends. Silvereye counts of 50 birds per 5MBC are from observations of large silvereye flocks. For statistical testing see Appendix A.

Table 4.4 Summary of results from bird count GLMs for model 1 (rat abundance) using bird count data for the 12 most common species from all sites combined (Cobb, Flora, Lakehead, Rotoiti new, and Rotoroa) at altitudes between 615 m and 1481 m a.s.l. Species are listed in order of most common. Significant effects are expressed by either - (negative) or + (positive), and non-significant effects are listed as 0. Full details of each GLM are given in Appendix A.

Species	Rat tracking	Altitude	Seedfall	Rat tracking x altitude	Rat tracking x seedfall
bellbird	-	-	-	+	+
silvereye	-	-	-	+	+
chaffinch	0	-	-	0	+
tomtit	-	+	-	0	+
song thrush	-	-	-	0	+
grey warbler	-	-	-	+	+
rifleman	-	+	+	+	+
redpoll	0	0	0	0	+
brown creeper	0	+	+	0	0
blackbird	-	-	-	0	+
tūī	-	-	0	+	+
fantail	0	-	+	0	0

The population responses of birds to ship rat and stoat control (i.e. stoat trapping, rat trapping, 1080 and other toxins) showed high levels of variation between species (Table 4.5). Most species responded positively to stoat trapping; only fantails and silvereyes decreased in abundance and tūī showed no response. Bellbirds were the only species that increased in abundance in response to all ship rat and stoat control treatments. In contrast, tūī populations increased in response to all rat control treatments but did not respond to stoat treatment. Rat trapping resulted in the second highest number of positive responses. Bellbirds, tūī, brown creepers, blackbirds and song thrushes all increased with rat trapping. Bellbirds, brown creepers, and tūī were therefore the only native species that showed a significant increase as a direct result of a rat control treatment; all other native species populations either declined or did not change significantly in response to rat control.

Grey warblers, riflemen and tomtits were similar in their altitudinal responses to pest control (Figure 4.4 and 4.5). Their altitudinal distributions were similar under all rat control treatments (including no rat control) and stoat treatments; however in the absence of stoat control all three species show changes in altitudinal distribution (Figure 4.5) compared to when stoat control was applied. In the absence of stoat control, grey warbler abundance was greatest at ~600 m, riflemen at ~900 m, and tomtits at ~1450 m a.s.l. (Figure 4.5), compared to their treatment altitudinal peaks of approximately 1000 m, 1150 m, and 1200 m a.s.l., respectively (Figure 4.5). Without stoat control, there was a shift to lower altitudes for grey warblers and riflemen and a shift to higher altitudes for tomtits. Bellbirds also show different altitudinal responses to different pest control treatments (Figure 4.4 and 4.5). Bellbird abundance increased at low to mid altitudes (600 – 900 m a.s.l.) in response to all pest control treatments, relative to non-treatment abundances (Figure 4.4 and 4.5).


Mean bellbirds detected per 5MBC
0
5
10
750
1000
1250
1500
Altitude (m a.s.l.)
rat.tmnt4
absent
all1080
othertoxin
trap
Mean silvereyes detected per 5MBC
0
10
20
30
40
50
Altitude (m a.s.l.)
Rat treatment
absent
all1080
othertoxin
trap
Mean chaffinches detected per 5MBC
0
5
10
15
20
Altitude (m a.s.l.)
Rat treatment
Mean tomtits detected per 5MBC
0
2
4
6
Altitude (m a.s.l.)
Rat treatment
Mean song thrushes detected per 5MBC
0
2
4
Altitude (m a.s.l.)
Rat treatment
Mean grey warblers detected per 5MBC
0
2
4
Altitude (m a.s.l.)
Rat treatment

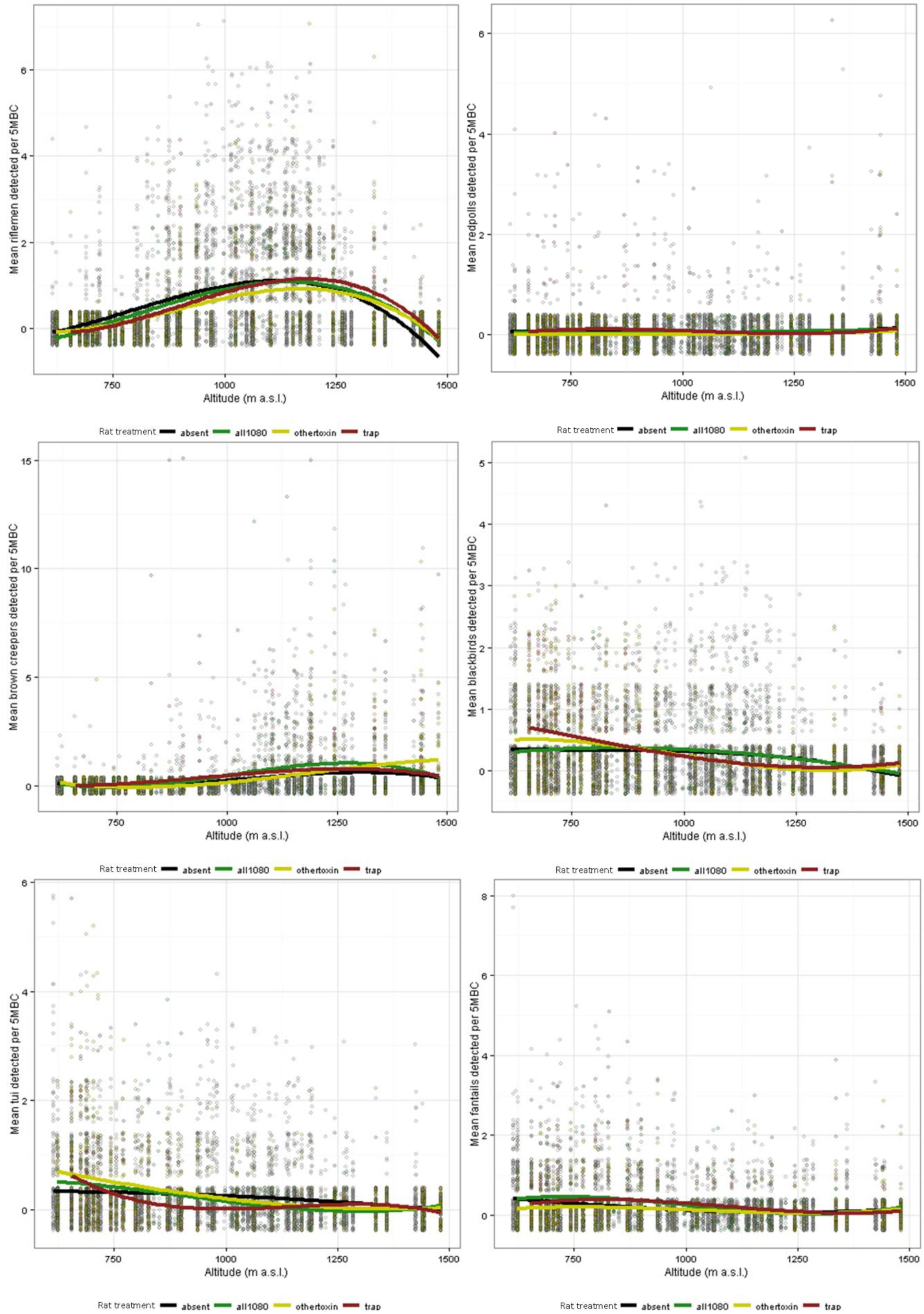
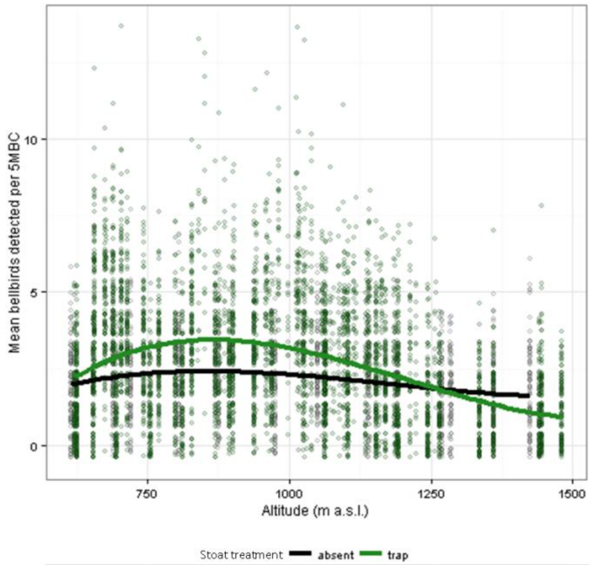
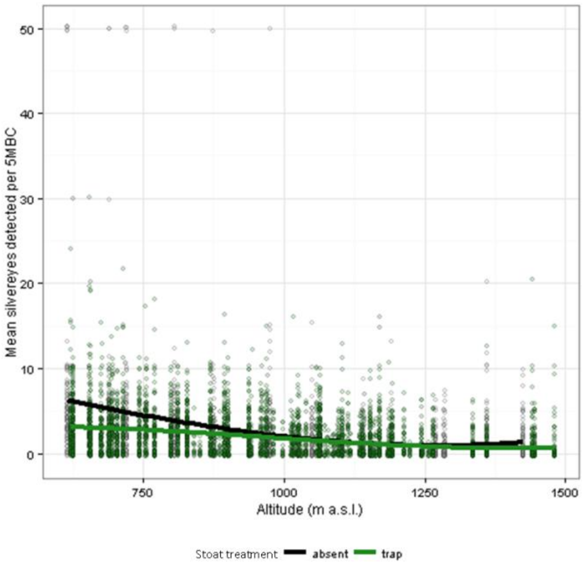
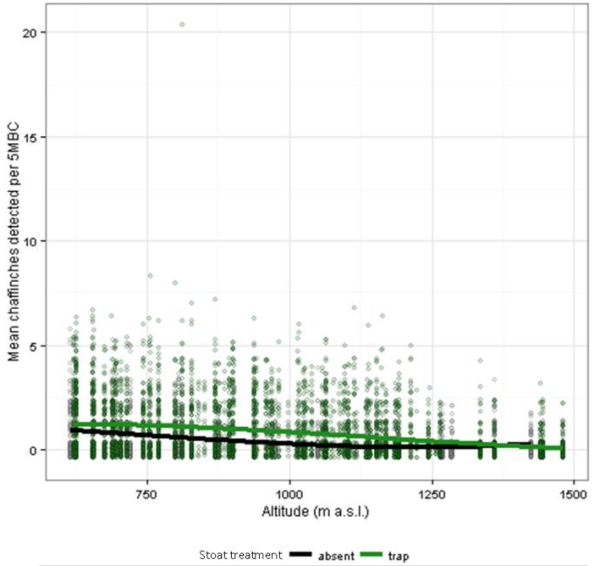
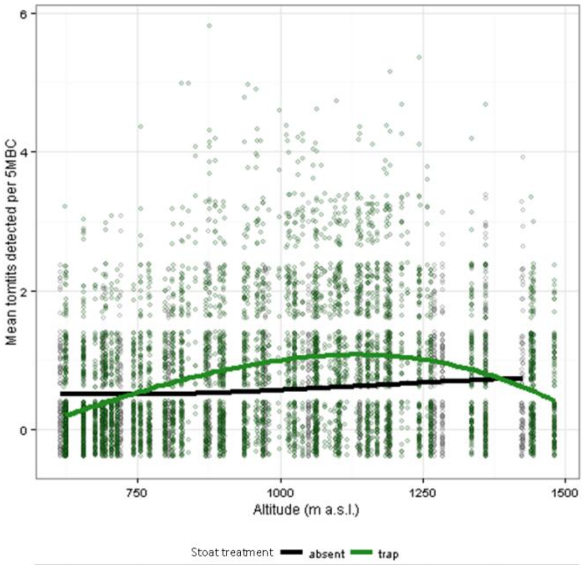


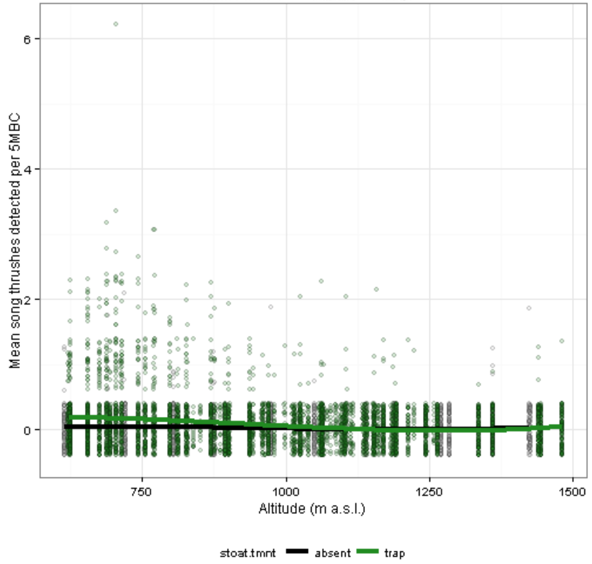
Figure 4.4 Mean number of birds detected per 5MBC against altitude (m a.s.l.) for the 12 most commonly detected bird species across all sites. Graphs show differences between the four rat treatments; absent (non-treatment), 1080, other toxins, and targeted rat trapping. The jitter function was applied to show the number of repeat counts in the data. The lines are smoothed fits to show the general trends. Silvereye counts of 50 birds per 5MBC are from observations of large silvereye flocks. For statistical testing see Appendix A.

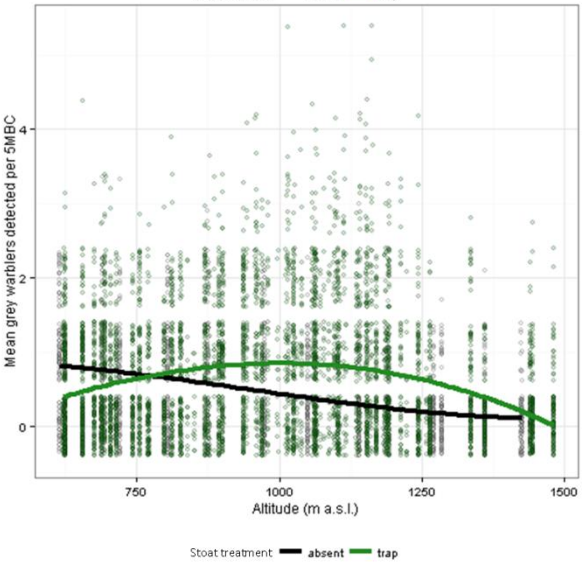

Mean bellbirds detected per 5MBC
0
5
10
750
1000
1250
1500
Altitude (m a.s.l.)
Stoat treatment
absent
trap


Mean silvereyes detected per 5MBC
0
10
20
30
40
50
750
1000
1250
1500
Altitude (m a.s.l.)
Stoat treatment
absent
trap


Mean chaffinches detected per 5MBC
0
5
10
15
20
750
1000
1250
1500
Altitude (m a.s.l.)
Stoat treatment
absent
trap


Mean tomtits detected per 5MBC
0
2
4
6
750
1000
1250
1500
Altitude (m a.s.l.)
Stoat treatment
absent
trap


Mean song thrushes detected per 5MBC
0
2
4
6
750
1000
1250
1500
Altitude (m a.s.l.)
stoat.tmnt
absent
trap


Mean grey warblers detected per 5MBC
0
2
4
750
1000
1250
1500
Altitude (m a.s.l.)
Stoat treatment
absent
trap

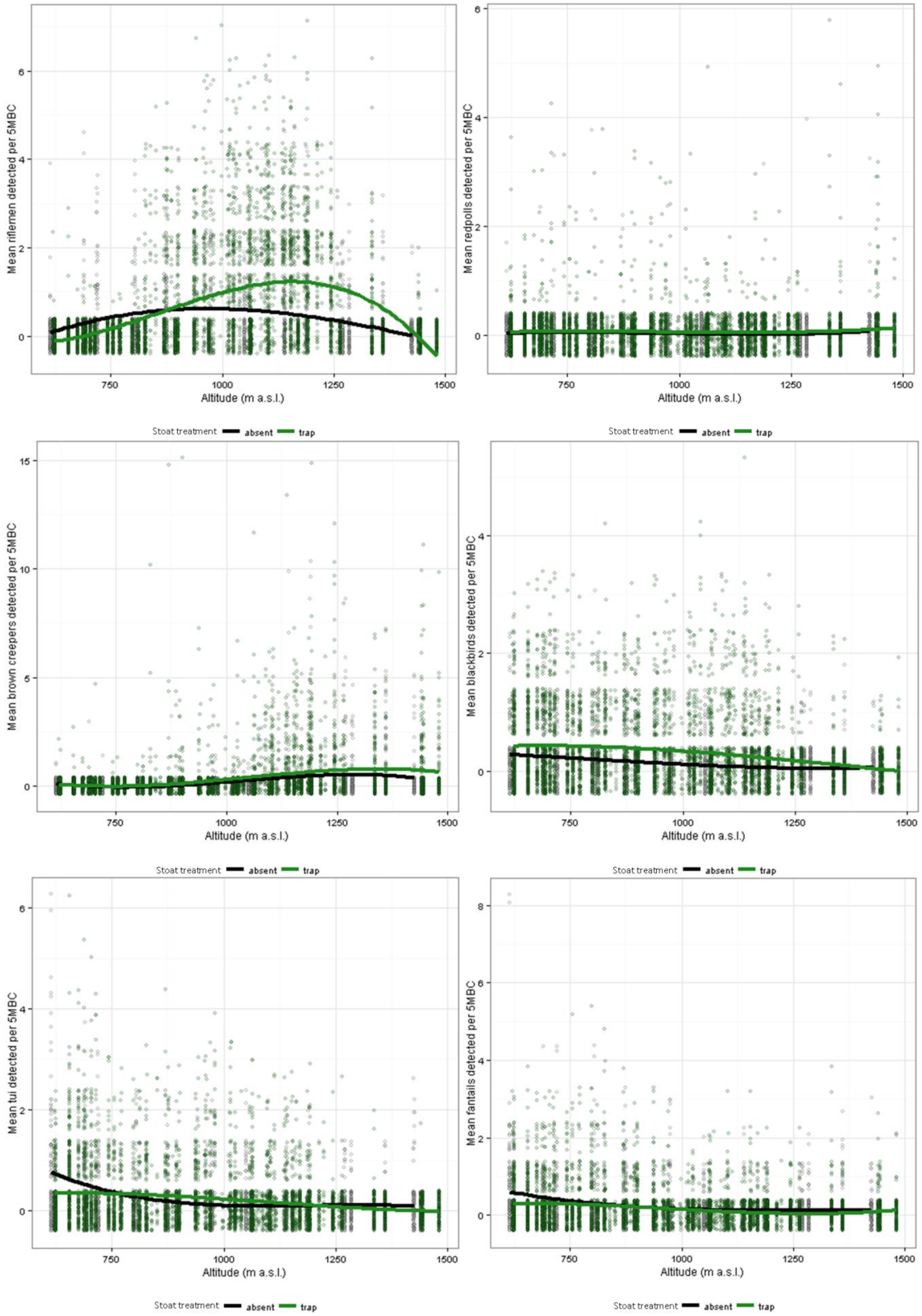


Figure 4.5 Mean birds detected per 5MBC against altitude (m a.s.l.) for the 12 most commonly detected bird species across all sites. Graphs show differences between the two stoat treatments; absent (non-treatment) and targeted stoat trapping. The jitter function was applied to show the number of repeat counts in the data. The lines are smoothed fits to show the general trends. Silvereye counts of 50 birds per 5MBC are from observations of large silvereye flocks. For statistical testing see Appendix A.

Table 4.5 Summary of results from bird count GLMs for model 2 (treatments) using bird count data for the 12 most common species from all sites combined (Cobb, Flora, Lakehead, Rotoiti new, and Rotoroa) at altitudes between 615 m and 1481 m a.s.l. Species are listed in order of most common. Significant effects are expressed by either - (negative) or + (positive), and non-significant effects are listed as 0. Full details of each GLM are given in Appendix A.

Species	Stoat trapping	1080	Other toxins	Rat trapping
bellbird	+	+	+	+
silvereye	-	0	-	0
chaffinch	+	-	0	0
tomtit	+	-	-	0
song thrush	+	0	0	+
grey warbler	+	-	0	-
rifleman	+	-	-	-
redpoll	+	0	-	0
brown creeper	+	0	-	+
blackbird	+	0	+	+
tūī	0	+	+	+
fantail	-	0	-	0

Three native species (brown creepers, fantails, and riflemen) declined when the total number of introduced bird species increased (Table 4.6). Silvereyes were unaffected by increased abundance of introduced species, while the remaining eight species (four native and four introduced) increased with total introduced species abundance. Therefore, only native species were negatively affected by increasing populations of introduced species. Fantails, silvereyes, and song thrushes showed no response to increased total native bird abundance and the remaining eight species (six native and two introduced) responded positively to increased native bird abundance (Table 4.6). Redpolls were the only species that responded negatively to an increase in overall native bird species abundance (Table 4.6).

Table 4.6 Summary of results from bird count GLMs for model 3 (competition) using bird count data for the 12 most common species from all sites combined (Cobb, Flora, Lakehead, Rotoiti new, and Rotoroa) at altitudes between 615 m and 1481 m a.s.l. Species are listed in order of most common. Significant effects are expressed by either - (negative) or + (positive), and non-significant effects are listed as 0. Full details of each GLM are given in Appendix A.

Species	Total introduced	Total native
bellbird	+	+
silvereye	0	0
chaffinch	+	+
tomtit	+	+
song thrush	+	0
grey warbler	+	+
rifleman	-	+
redpoll	+	-
brown creeper	-	+
blackbird	+	+
tūī	+	+
fantail	-	0

4.4 Discussion

The information collected here confirms findings from previous studies as well as presenting new information. The bird populations investigated here showed varying responses to altitude, beech seedfall, and pest control. Most bird populations responded negatively to increased rat tracking (i.e. ship rat abundance), consistent with other evidence showing rats are important bird predators. However, while 1080 application was the most effective method at reducing ship rat populations, this was often not reflected in bird abundance increases after 1080 application. This study has also confirmed that high altitude may provide a refuge for some native bird species to escape predation. Several native species also declined in response to increased introduced bird populations.

Forest bird responses to altitude and seedfall

Positive responses to seedfall were exhibited here by brown creepers, fantails and riflemen. Since these three species are largely insectivorous (Heather & Robertson 1996), and increased beech seedfall tends only to directly benefit seed eaters i.e. kākā and yellow crowned parakeets (Elliott et al. 1996, Wilson et al. 1998, Dilks et al. 2003), it is unlikely that increased beech seed fall was directly beneficial to these species. However, since they are insectivores, they could be benefiting from the increased abundance of invertebrates that are associated with high-seed years (Alley et al. 2001, Kelly et al. 2008a). The most common response to increased seed fall was decreased bird abundance, a pattern I found in 7 of the 12 species. Since predator (i.e. ship rat and stoat) populations are known to increase during high-seed years (King 1983, Murphy, E. C. & Dowding 1995, Fitzgerald, B. M. et al. 2004, Kelly et al. 2008a, Chapter 3) it is expected that increased seed fall will have an indirect negative impact on bird abundance as was reflected here in negative bird responses to rat tracking rates, and in a number of previous studies (Elliott 1996, Dilks et al. 2003, White & King 2006, O'Donnell et al. 2017).

Several studies have also investigated variation in bird population densities with altitude in New Zealand beech forests. For example, Elliot et al. (2010) and Langham & Kelly (2011) both found that some bird species (e.g. brown creepers and riflemen) occur more commonly at mid to high altitudes (> 1000 m a.s.l.) while others (e.g. bellbirds and tūī) prefer lower altitudes (< 1000 m a.s.l.). My study supports these findings and shows that all species underwent significant changes in abundance in response to altitudinal gradients, with the exception of the introduced redpoll. Because the vegetative composition and availability of resources (i.e. insects, seeds, and honeydew) in these areas change with altitude (Wardle 1984, Moeed & Meads 1985, Beggs 1991) it is not surprising that the abundance of bird populations relying on these resources should vary across an altitudinal range as well (Elliott et al. 2010, Langham & Kelly 2011). However, there is limited evidence for how much these altitudinal shifts in bird densities are governed by pressures from introduced species, and how much are due to natural population gradients responding to resource composition and/or competition with their naturally occurring counterparts (Rayner et al. 2007, Elliott et al. 2010).

Forest bird responses to ship rat abundance

Introduced mammalian predators are largely responsible for declines in native New Zealand forest bird populations, and of these, ship rats are implicated in a large proportion of losses (Brown 1997, Innes 2005, Innes et al. 2010). The role of ship rats in the decline of native bird species was confirmed here because all but two native species (brown creepers and fantails), demonstrated population declines in response to increased ship rat abundance. I found that the greatest losses to native bird populations in response to ship rats were suffered by bellbirds, riflemen and tūī. However, within the study sites examined here bellbird and tūī populations are probably lower in areas with increased rat tracking compared to those with fewer rats for additional reasons.

Tūī and bellbirds feed on invertebrates, fruits, nectar and honeydew depending on what is available (Heather & Robertson 1996, Williams & Karl 1996, Murphy, D. J. & Kelly 2001, 2003). Large densities of introduced wasps are associated with honeydew crops in New Zealand beech forests for around 4 months of the year (Thomas et al. 1990, Beggs 1991, 2001). When invasive wasp populations are not controlled, they are capable of reducing a standing crop of honeydew by more than 90 % of its natural size (Beggs 2001, Beggs & Wardle 2006). Within this study, areas that have received effective rat control and therefore lower rat abundance include areas that have also undergone wasp control e.g. Rotoiti core and Lakehead (Long et al. 2016). Effective wasp control using Fiprinol in poison bait stations has resulted in increased honeydew droplet abundance within the RNRP (Long et al. 2016) increasing the amount of honeydew available for bellbirds and tūī. Additionally, these areas have also received long-term targeted stoat trapping therefore the effect of rat abundance on bellbird and tūī populations may be exaggerated by these supplementary factors.

Altitudinal shifts in bird populations observed in this study, and other studies, could be due to altitudinal shifts in the abundance and influence of introduced pests (Beggs 1991, Elliott et al. 2010, Langham & Kelly 2011). Elliot et al. (2010) found that bird abundance has been mostly affected at lower altitudes. In beech forests, ship rat abundance is highest at low to mid altitudes (600 – 800 m a.s.l.) (Christie et al. 2017, Chapter 3) and in honeydew beech forests wasp populations are also most abundant at low to mid altitudes (Beggs 1991). Therefore, it is likely that bird populations are largely affected by ship rat and wasp densities at low to mid altitudes. This study also found evidence that the negative impact of ship rats on native birds is smaller as altitude increases for bellbird, grey warbler, rifleman, silvereye, and tūī populations, which suggests that high altitude provides a refuge for native birds through lower predation by ship rats.

It is unclear why brown creepers and fantails did not respond significantly to changes in ship rat abundance. For brown creepers, it may be the case that because they are most abundant at elevations where ship rats are rare (>1000 m a.s.l.) (Elliott et al. 2010, Langham & Kelly 2011, Christie et al. 2017) they do not suffer great losses from ship rat predation. Fantails have a relatively high rate of nest productivity compared to some other native species, with an average of 3 broods of 3-5 eggs per year, and records of up to 5 broods per year, compared to riflemen for example, with an average of 2 broods of 2-5 eggs per year (Heather & Robertson 1996, Powlesland, R.G. 2013). Therefore, fantails may be able to cope with increased predation rates better than other native species. Instead, fantails appear more limited by harsh winters since fantail survival is sensitive to adverse weather conditions (Powlesland, M. H. 1982, Powlesland, R.G. 2013).

Forest bird responses to pest control

Although 1080 application was the only effective tool found to reduce ship rat populations (Chapter 3) and most forest bird populations studied here showed significant declines when ship rat populations increased, 1080 application only elicited a positive population response in bellbirds and tūī. Additionally, brown creepers, which in my analysis showed no response to rat abundance, responded positively to targeted rat trapping. All remaining native species either lacked a response or responded negatively to 1080, other toxins, and targeted rat trapping. This suggests that pest control is not a reliable proxy for rat abundance when predicting bird population responses.

Three native species, tomtits, grey warblers, and riflemen, declined in response to the 1080 treatment. Since the use of 1080 has been associated with non-target mortality of native birds in the past (Powlesland, R. G., Knegtmans & Marshall 1999, Powlesland, R. G. et al. 2000), it is possible that these birds suffered from 1080 poisoning. However recent studies indicate that mortality of native birds following 1080 applications are now minimal to absent (Schadewinkel et al. 2014, Morriss et al. 2016), therefore it is more likely that tomtit, grey warbler, and rifleman populations reduced in response to increased rat abundance associated with years when 1080 is applied. Within these sites (as with most of New Zealand), 1080 is only applied for rat control when high rat densities are expected, so although 1080 may be successful in reducing rat abundance, in some cases reductions in rat abundance may only be from high to medium rat density, instead of to low density (i.e. < 5% rat tunnel tracking) (Elliott & Kemp 2016). Therefore, the 1080 treatment may be effective at reducing rat densities but not always to low enough levels for tomtits, grey warblers, and riflemen to evade predation.

Most bird species showed similar altitudinal ranges under each rat control treatment compared to their non-treatment ranges. Stoat trapping however, produced altitudinal differences in the abundance of several species compared to non-treatment abundances, particularly for bellbirds, grey warblers, riflemen and tomtits. Bellbirds increased at lower altitudes when stoats were controlled while tomtits, grey warblers, and riflemen decreased at lower altitudes and increased at mid to high altitudes when stoats were controlled. These results are contrary to findings from Langham & Kelly (2011) who found stronger altitudinal responses to rat control than to stoat control for bellbirds, tomtits, grey warblers and riflemen. Responses of tomtits, grey warblers, and riflemen also do however reflect findings from Chapter 3 that suggest ship rat density increases, particularly at lower altitudes, when stoats are controlled. Since tomtits, grey warblers, and riflemen decrease at lower altitudes when stoats are controlled, this could be the result of them suffering increased predation via the mesopredator release of ship rats at lower altitudes, which may be especially true for grey warblers and riflemen which have demonstrated the use of altitude as a refuge.

The disparity I found between bird population responses to ship rat abundance and rat control methods may indicate the need to measure the delayed responses to rat control, rather than the immediate responses. It should also be noted that the Rotoroa site is the main source of non-stoat trapping data, as all other stoat trapping data has come from areas that have had some degree of rat control so these may also be additive effects of control. Measuring a change in bird abundance in response to rat control would also provide more information on the actual effects of pest control. Nevertheless, when information on predator population abundance is not available, the only option is to use control regimes as a substitute for measuring predator abundance, but clearly this should be done with caution.

Effects of other bird populations

This study indicates that brown creeper, fantail, and rifleman populations all experienced declines in response to the abundance of introduced bird populations. Because chaffinches were the most commonly detected introduced bird and the third most commonly detected species overall (mean = 0.74 birds detected per 5MBC), it is possible that population declines in native species are in response to increased chaffinch abundance. Brown creepers, fantails, and riflemen, all feed mainly on beetles, caterpillars, moths, and spiders (Heather & Robertson 1996, McKinlay 2013, Powlesland, R.G. 2013, Withers 2013). Chaffinches are predominantly seed eaters in the winter however, during the breeding season invertebrates including beetles, caterpillars, moths, and spiders, make up a large portion of the diet of both adults and chicks (Heather & Robertson 1996, Angus 2013). The altitudinal distribution of chaffinches also overlaps with that of brown creepers, fantails, and riflemen; therefore it is possible that these native species are suffering from competition with introduced chaffinches, although this needs to be confirmed with more detailed studies of diet and estimates of the level of interspecific competition.

The role of introduced birds in the decline of native birds has been largely ignored to date, probably as a result of the clear and well-documented effects of introduced mammalian predators on native birds (Innes et al. 2010). Nevertheless, there is some evidence of introduced birds having negative impacts on native bird populations in New Zealand (Tindall et al. 2007, Massaro et al. 2013, Lawrence et al. 2016). Massaro et al. (2013) found that predation by the European starling was the leading cause of nest failure for the endangered black robin (toutouwai, *Petroica traversi*) on the Chatham Islands. Tindall et al. (2007) found that tūī populations increased significantly on Moturoa Island when introduced common myna (*Acridotheres tristis*) populations were controlled which may have been the result of interference competition. To my knowledge, however, my study provides the first empirical evidence that under certain conditions, native bird populations may be suppressed by competition with introduced bird populations in New Zealand.

Conclusion

Each bird species varies in their individual responses to the factors considered here. Brown creepers, fantails, and riflemen are interesting because they benefit from increased seedfall and respond negatively to introduced bird abundance additionally, brown creepers and fantails appear unaffected by ship rat abundance. Riflemen are sensitive to rat tracking rates so therefore may be suffering from a combination of predation from ship rats and competition with introduced chaffinches which appear to be unlimited by ship rat populations. By contrast, bellbirds and tūī may be benefiting from the increased availability of honeydew and reduced predation as a result of rat control, stoat control, and wasp control.

Future analysis of these data should include measuring changes in bird abundance instead of direct measures of abundance for example, change in birds detected from 2014 to 2015 in response to rat tracking and pest control in 2014, instead of direct measures of abundance in 2015. Fitting terms to measure stoat treatment by rat treatment interactions may also be a useful addition to minimise disparity between the non-treatment and treatment sites when measuring the effect of ship rat control. However, the latter would be more robust if there were a better range of sites with all combinations of stoat control (trapping/non-treatment) and rat control (trapping/toxins/non-treatment). In the current dataset, only one site had consistent absence of stoat control (Rotoroa), and that site has also never had control of any other pest i.e. ship rats. Therefore, the current data set is somewhat limited because it doesn’t allow for analysis of ship rat control in the absence of stoat control.

Hopefully the findings here provide further confirmation of the most effective ways to control ship rat populations to increase native bird species abundance or at least determine the sources of disparity sometimes found when measuring bird population responses to pest control.

Chapter 5. Discussion

5.1 Importance of long-term data sets: 5MBCs

Distribution and abundance data are vital sources of information when determining the population responses of a species to a given factor (Sullivan 2012). Long-term monitoring is often required to measure the full extent of species' responses, particularly when there is a lag response that short-term studies cannot capture (Byrom et al. 2016). Following pest control operations in New Zealand that are designed to benefit native bird populations, it is important to monitor the outcomes to determine whether the operation was a success and using long-term data sets is beneficial because these will take into account natural population fluctuations and possible lag responses to pest control (Byrom et al. 2016).

There are several methods used by ecologists and ornithologists to measure the abundance of birds e.g. fixed-width strip transect counts, distance-sampling, audio-visual surveys, presence-absence surveys, and 5MBCs, and each of these vary in accuracy and suitability to particular circumstances (Westbrooke & Powlesland 2005, Greene, T. et al. 2010, Masuda et al. 2014, Basile et al. 2016). As outlined in Chapter 1, 5MBCs are an advantageous method that has been used widely by multiple studies to measure pre- versus post- treatment, treatment versus non-treatment, or historic versus contemporary changes in bird abundance (e.g. Harper, G. A. 2009, Elliott et al. 2010, Barnett 2011, O'Donnell & Hoare 2012, Iles & Kelly 2014). This technique requires the observer to record all birds seen or heard from a designated point within a five minute time frame allowing multiple species to be counted simultaneously (Dawson & Bull 1975, Hartley & Greene 2012), but the 5MBC has also been under much scrutiny (Hartley 2012, Sullivan 2012).

Use of 5MBCs has been the subject of unpublished debate over its accuracy (Hartley 2012), especially when bird surveys are undertaken by volunteers and community groups and the time and resources are not available to provide adequate training for them (Masuda et al. 2014). Assumptions of the 5MBC are that the number of detections of a bird species is a relative measure of its population abundance and that observers do not differ significantly in their ability to detect (see and hear) the birds present (Hartley & Greene 2012). This latter assumption is violated if observers are not adequately trained and their detection abilities vary (Dawson & Bull 1975, Hartley & Greene 2012). Observer skill is particularly important in 5MBCs because many birds are heard rather than seen, often from rather short and/or distant calls, so a high level of familiarity with bird calls is required to accurately identify all bird species. To some extent observer bias can be controlled for during statistical analysis; however this can only compensate for modest levels of differential detection among observers, whereas very inexperienced observers may miss many birds and misidentify others. Hence, it is best practice to restrict 5MBC observers to those with adequate skills and training.

An unavoidable disadvantage of this method of bird surveying is its limited ability to detect rare bird species (Hartley & Greene 2012). Therefore 5MBCs should be used in conjunction with other methods when the species of interest is uncommon, but can be used on their own to measure population abundances of more common widespread species. Measuring changes in the populations of common and widespread native birds is important because common and widespread species are the main contributors to ecosystem structure, functioning, and biomass (Gaston & Fuller 2007, Elliott et al. 2010). Detecting important changes in common native species in New Zealand has been made possible with the use of the 5MBC over long time spans which allow us to compare current and historic changes in abundance, further enabling us to predict species changes in the future.

5.2 Interactions between mammals

Both mesopredator release and competitive release can have detrimental effects on prey species that, as a result, suffer from increased predation (Courchamp et al. 2003, Prugh et al. 2009). Understanding why these differences occur is important to help direct appropriate responses to inadvertent species responses to pest control (Elmhagen & Rushton 2007, Rayner et al. 2007). Furthermore, prey species may be at elevated risk when released species are fast breeders (like ship rats) that can undergo rapid population increases under the right conditions (Ruscoe et al. 2011).

Mesopredator release occurs when an apex predator is reduced or becomes extinct within a community (Soulé et al. 1988). These apex predators may be native species that are lost through habitat destruction and/or exploitation (Soulé et al. 1988, Crooks & Soulé 1999, Myers et al. 2007, Prugh et al. 2009), or they may be introduced species that are removed intentionally for predator control (Caut et al. 2007, Norbury et al. 2013, Masuda et al. 2014). Once the apex predator is removed from the system, predators from the next trophic level may undergo significant population increases to the detriment of their prey species (Ritchie & Johnson 2009). Competitive release may occur through the same pathways (Trewby et al. 2008, Ruscoe et al. 2011) however there is substantially less evidence for competitive release in the literature than for mesopredator release, indicating that it is either less studied, or less common.

In a controlled and replicated experiment, Trewby et al. (2008) found that increases in red fox (*Vulpes vulpes*) populations in the United Kingdom were the result of reduced densities of their sympatric competitors, the Eurasian badger (*Meles meles*), that were being culled in the area for disease control. This study provided strong evidence for competitive release; however, understanding the pathways that lead to competitive release will be much more complicated in a system that undergoes control of multiple predatory invaders, at different trophic levels (Ruscoe et al. 2011), which is generally the case in New Zealand.

Stoats, ship rats, and brushtail possums are all predators of native birds and/or their eggs and chicks, therefore it is important that the predator populations are controlled (Saunders & Norton 2001, Innes et al. 2010). Nevertheless, some control operations may only target one or two of these species potentially allowing uncontrolled species to increase through mesopredator or competitive release, thereby increasing predation pressure on the prey, which has potential to outweigh the benefits of the pest control operation (Zavaleta et al. 2001, Spurr & Anderson 2004). For example, in an area where stoats are controlled but rats are not, bird species such as kiwi and blue ducks are likely to benefit because they are sensitive to predation by stoats but relatively insensitive to ship rats (McLennan et al. 1996, Whitehead et al. 2008). In contrast, birds sensitive to ship rat predation e.g. North Island kōkako (Innes et al. 1999), would likely suffer increased predation if the rats experience mesopredator release (Spurr & Anderson 2004, Rayner et al. 2007). Similarly, when possums are controlled and rats are not, birds sensitive to rat predation could suffer increased predation rates if the rats experience competitive release (Spurr & Anderson 2004, Ruscoe et al. 2011). Ruscoe et al. (2011) tested for both mesopredator and competitive release in a four-species assemblage containing stoats, ship rats, brushtail possums, and house mice (*Mus musculus*), and found evidence for competitive release of ship rats following possum control, but no evidence for mesopredator release of rats following stoat control.

Ruscoe et al.'s finding is contrary to my results, where I found evidence for mesopredator release of ship rats within the same four-species assemblage. There are several reasons that could explain these differences. Firstly, Ruscoe et al. (2011) suggest that their stoat removal treatment may have failed to successfully reduce stoat numbers enough for ship rats to benefit. But based on some calculations of animal densities and feeding rates, they conclude that the rates of stoat predation on ship rats have been overestimated and that stoat predation should usually be insufficient to regulate rodent populations within New Zealand forests (Blackwell, Potter & Minot 2001, Blackwell et al. 2003). This appeared to be the case in their North Island study where stoat control caused no increase in rats, but doesn't appear true within my South Island study since ship rat populations increased when stoats were controlled compared to when they were not. However their study was a replicated balanced design run specifically to test these interactions, whereas mine was a long-term study using existing unbalanced combinations of various types of pest control. Moreover, without the inclusion of mustelid tracking data within my analysis, I cannot be sure that the apparent responses of rats to mustelid control were driven by changes in stoat density.

Secondly, possum densities within the majority of my study sites were thought to be very low, because of repeated possum control at all sites except Rotoroa coupled with the normally slow rate of recovery of possums post-treatment. Possum abundance is not monitored at the Nelson Lakes sites (Big Bush, Lakehead, Rotoiti and Rotoroa), but all sites within the RNRP have ongoing possum trapping and signs of possum presence are very rare (Long et al. 2016). Chew card analysis from a separate study in Cobb and Flora found possum densities were extremely low (< 5 % average chew cards marked by possums, Dave Kelly, Univ. Canty., pers. comm.). Lack of possum abundance data (particularly at the Rotoroa non-treatment site) means that testing for competitive release is difficult, however future analysis could include possum control as a proxy for possum abundance, and may give an indication whether competitive release is occurring in my study areas.

Thirdly, the areas within my study that are managed by extensive stoat trapping have also received targeted possum and/or rat control at some stage (see Chapter 2; Tables 2.2 to 2.8) with switching on/off of possum and rat control but never switching off stoat control. This means the effect of possum control alone on ship rat populations cannot be measured and any effect seen is instead the combined effect of possum control and stoat control.

Although my study, for historical reasons, lacked representation of all treatment combinations (was unbalanced), and was therefore less robust than Ruscoe et al. (2011), my results indicate that ship rat populations were higher in areas that received stoat control compared to areas that did not. Whether this difference from Ruscoe et al. is due to the different experimental approaches, or correctly reflects different rat responses in the North versus South Islands, is unknown. Regardless of the true mechanism behind this population difference, it outlines the importance of managing and monitoring all species within an invasive mammal assemblage to detect inadvertent consequences of pest control operations.

5.3 Interactions between birds

Recent reviews have indicated the importance of considering introduced birds when determining the reasons for native bird population declines (Baker et al. 2014, Martin-Albarracin et al. 2015). For example, introduced populations of rose-ringed parakeets (*Psittacula krameri*) in Belgium outcompete native Eurasian nunthatches (*Sitta europaea*) for cavity nesting sites (Strubbe & Matthysen 2007, 2009), and the introduced Japanese white-eye (*Zosterops japonica*) outcompetes native populations of Hawaiian akepa (*Loxops coccineus*) for food resources resulting in reduced akepa juvenile body mass and bill length (Freed & Cann 2009). Yet the effects of introduced birds on native bird populations have received little attention in New Zealand, particularly during conservation management planning (Lawrence et al. 2016). This is probably because, in the past, introduced birds were considered poor invaders of native forest that could only establish populations in these habitats after enough habitat destruction and reduction in native bird abundance has occurred (Diamond & Veitch 1981, Morgan, Waas & Innes 2006). Also, when compared to the impact of invasive mammals, the relative impact of invasive birds was viewed as small (Innes et al. 2010).

In New Zealand, examples of negative impacts from introduced birds on native birds include the European starling stealing and preying on the nests of native black robins and orange fronted parakeets, and the common myna potentially competing with tūī and preying on other native birds (Tindall et al. 2007, Kearvell 2013, Massaro et al. 2013). In this study, I found evidence that competition from introduced birds may be suppressing native rifleman populations. Although this needs to be confirmed with more detailed studies of diet and estimates of the level of interspecific competition, it points to a potentially important pathway that requires further investigation.

Measuring the impact of competition from introduced birds may be especially important for species that are suffering population declines regardless of pest control, such as the rifleman (Smith, A. N. H. & Westbrooke 2004). Rifleman populations are declining throughout New Zealand but the cause of this is unknown (Innes et al. 2010). Since these declines are occurring in areas even where pest management regimes are in place (Smith, A. N. H. & Westbrooke 2004), other contributions to decline, in addition to invasive mammals, need to be considered. I found that introduced bird abundance had a negative effect on riflemen populations. Since chaffinches were the most abundant introduced bird within my study sites and their diet overlaps with the rifleman during the breeding season (Heather & Robertson 1996), competition with chaffinches for food is a possible source of this negative impact. In the last 30 years, riflemen abundance has declined at low altitudes but has remained steady at mid to high altitudes in beech forest (Elliott et al. 2010, Langham & Kelly 2011). Riflemen populations are negatively affected by introduced mammals and it appears that altitude is a refuge from predation (Harper, G. A. 2009, Elliott et al. 2010, Withers 2013, Chapter 4). However, riflemen may also use altitude as a refuge to escape competition. Although not found in this study, there is also evidence in the literature of native birds attacking riflemen such as tomtits, brown creepers, and bellbirds and this could also contribute to their high-altitude distribution (Withers 2009). If riflemen are in fact suffering a combination of predation from introduced mammals and competition with introduced birds (as well as attacks from native birds), it is not surprising that their populations are declining. If predator control is not enough to alleviate the pressures on their populations, my findings suggest that the effect of introduced birds should be given more attention.

5.4 Disparity between bird responses

Until the 1980s, aerial 1080 operations resulted in high levels of mortality in some native bird species (Morriss et al. 2016). Since then, extensive research and subsequent changes in baiting practices appear to have largely minimized these risks (Crowell et al. 2016, Morriss et al. 2016, Parkes et al. 2017). In this study, I found negative responses associated with 1080 application in tomtit, rifleman, and grey warbler abundance. To my knowledge, no studies have found evidence for the direct by-kill of either grey warblers or riflemen following 1080 operations. Ground-foraging insectivores (e.g. robins and tomtits), are more susceptible to 1080 poisoning (Lloyd & McQueen 2000) rather than birds with feeding behaviours like grey warblers and riflemen that spend their time foraging in the canopy and on tree trunks, and gleaning insects from leaves and branches (Heather & Robertson 1996, Withers 2013). Therefore, it is unlikely that grey warbler and rifleman populations declined in response to direct 1080 poisoning, but it is possible that tomtit populations were negatively affected by non-target poisoning.

My study also found that grey warblers, riflemen and tomtits responded negatively to rat abundance, and rat abundance is reduced by 1080 control operations. Therefore, either some bird populations suffered as a direct response to 1080 application, or pest control is not a reliable predictor of bird abundance/bird responses to control operations. Furthermore, immediate responses to pest control are not reliable because they do not take into account the lag effect of control operations (Byrom et al. 2016) and may give contradictory results if a control operation has been unsuccessful at regulating a predator population eruption.

The disparity found in my study between bird population responses to pest control immediately following control operations (assumed to be a proxy for predator abundance) and bird population responses to rat abundance (a direct measure of predator abundance), indicate not only that pest control is an unreliable proxy for ship rat abundance but also that determining the lag or long-term responses of native bird populations is more important than determining their immediate responses. Therefore, when mammal abundance data, e.g. tracking tunnel indices, are not available, a change in bird abundance from one breeding season to the next could be a more reliable indicator of bird population patterns.

5.5 Future research

In this study I identified a range of factors that can contribute to variations in faunal responses to pest control within mixed beech forest communities. In doing so, I have also identified several possible avenues for future research, with particular regard to taking advantage of long-term data sets, similar to the one used here. Some of the key areas for future include:

- Measuring changes in bird population abundance (from one year to the next) instead of static abundance (density in a particular year).
- Determining levels of competition between native and introduced bird species and the relative importance of these in native species declines.
- Finding confirmation for mesopredator or competitive release of ship rats so that controls for these can be put in place when needed.
- Measuring the interactions between stoat control and rat control treatments instead of the combined effect of both treatments on both bird and mammal populations.

This study has also identified shortcomings in the experimental datasets for answering some of my initial questions, because of historical factors at the various study sites. Answering some of these questions accurately may not be possible with the information that is currently available. My study sites do not currently provide an opportunity to measure the effect of rat control alone (in the absence of stoat and/or possum control) on both bird and ship rat populations. All areas within this study that currently or historically have been treated with rat control have simultaneously been treated with stoat control. There are no areas which have had rat control without stoat control (or rat control without possum control). There are also no areas within my study sites which have had stoat control turned on since 1997 which have ever had it turned off again. This lack of representation for all treatment and non-treatment combinations means that only the combined effects of stoat treatment and rat treatment could be measured and not the effect of rat treatment alone. Additionally, having a full representation of all treatment combinations would provide the data needed to determine whether ship rat populations here undergo mesopredator release, competitive release, or a combination of the two.

Another aspect that I was interested in measuring within this community was the interaction between altitude, seedfall and pest control on rat tracking rates, but due to the nature of the data when I included this interaction in my models they would not run. I specifically wanted to measure this interaction to determine whether it is necessary to control ship rat populations at higher altitudes during high-seed years in beech forests and whether the presence of stoat trapping would influence the outcomes of this.

The best way to correct these issues would be to try more variable combinations of pest management treatments over the next few years; specifically, to switch off stoat trapping within an area of the RNRP (perhaps intermittently over a number of years with low and high beech seed crops) and control only ship rats so that all important treatment combinations are represented and studies such as these can provide more robust information. There is no denying the hard work that has gone into the management and implementation of the RNRP and the numerous positive results it has produced. Although the idea of stopping stoat trapping for a period may be unnerving, especially when stoat trapping is thought to be having an important positive impact on native species conservation, switching off a predator control programme may be worth doing considering the information that could be gained by such an approach.

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Appendix A: GLM coefficient output tables and ANOVA chi square test tables from R for each bird species.

Bellbird

Model 1

```
Coefficients:
                              Estimate Std. Error z value Pr(>|z|)    
(Intercept)                  2.141e+00  4.702e-02  45.523  < 2e-16 ***
rat.tracking                -2.258e+00  1.465e-01 -15.408  < 2e-16 ***
altitude                    -1.128e-03  4.723e-05 -23.892  < 2e-16 ***
mean.seed.log10             -5.406e-02  8.110e-03  -6.666 2.63e-11 ***
rat.tracking:altitude        1.858e-03  1.447e-04  12.839  < 2e-16 ***
rat.tracking:mean.seed.log10  2.225e-01  2.492e-02   8.926  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 10449.9  on 6641  degrees of freedom
Residual deviance:  9714.4  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 25976

Number of Fisher Scoring iterations: 5


Analysis of Deviance Table
Model: poisson, link: log
Response: bellbird
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641    10449.9              
rat.tracking                  1    17.96      6640    10431.9  2.26e-05 ***
altitude                      1   462.17      6639     9969.7 < 2.2e-16 ***
mean.seed.log10               1     0.10      6638     9969.6     0.757    
rat.tracking:altitude         1   175.53      6637     9794.1 < 2.2e-16 ***
rat.tracking:mean.seed.log10  1    79.69      6636     9714.4 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                     Estimate Std. Error z value Pr(>|z|)    
(Intercept)                         9.752e-01  4.515e-02  21.598  < 2e-16 ***
stoat.tmnttrap                      2.204e-01  2.240e-02   9.840  < 2e-16 ***
rat.tmnt4all1080                    1.248e+00  1.231e-01  10.135  < 2e-16 ***
rat.tmnt4othertoxin                 4.846e-01  9.035e-02   5.363 8.16e-08 ***
rat.tmnt4trap                       1.741e+00  9.434e-02  18.455  < 2e-16 ***
altitude                           -2.357e-04  3.923e-05  -6.009 1.87e-09 ***
mean.seed.log10                    -5.359e-03  6.714e-03  -0.798  0.42475    
rat.tmnt4all1080:altitude          -1.327e-03  1.339e-04  -9.913  < 2e-16 ***
rat.tmnt4othertoxin:altitude       -6.697e-04  9.480e-05  -7.064 1.62e-12 ***
rat.tmnt4trap:altitude             -1.768e-03  1.019e-04 -17.352  < 2e-16 ***
rat.tmnt4all1080:mean.seed.log10    4.442e-02  2.015e-02   2.204  0.02752 *  
rat.tmnt4othertoxin:mean.seed.log10  7.683e-03  1.555e-02   0.494  0.62128    
rat.tmnt4trap:mean.seed.log10       5.786e-02  1.862e-02   3.107  0.00189 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 10855  on 6855  degrees of freedom
Residual deviance:  9704  on 6843  degrees of freedom
AIC: 26439
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: bellbird
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                      6855    10855.0              
stoat.tmnt                1   154.49      6854    10700.5 < 2.2e-16 ***
rat.tmnt4                 3   138.89      6851    10561.6 < 2.2e-16 ***
altitude                  1   442.31      6850    10119.3 < 2.2e-16 ***
mean.seed.log10           1     0.12      6849    10119.2  0.730828    
rat.tmnt4:altitude        3   402.03      6846     9717.2 < 2.2e-16 ***
rat.tmnt4:mean.seed.log10  3    13.15      6843     9704.0  0.004321 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)    
(Intercept)               1.397e+00  3.758e-02  37.182  < 2e-16 ***
total.exotic              2.177e-02  4.564e-03   4.771 1.84e-06 ***
as.numeric(allBC$tn.bel)  1.392e-02  1.579e-03   8.817  < 2e-16 ***
altitude                 -5.843e-04  3.343e-05 -17.480  < 2e-16 ***
mean.seed.log10           8.639e-04  5.416e-03   0.160    0.873    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 10855  on 6855  degrees of freedom
Residual deviance: 10285  on 6851  degrees of freedom
AIC: 27004
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: bellbird
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev Pr(>Chi)    
NULL                                      6855      10855             
total.exotic              1  130.111      6854      10725   <2e-16 ***
as.numeric(allBC$tn.bel)  1  131.708      6853      10593   <2e-16 ***
altitude                  1  308.236      6852      10285   <2e-16 ***
mean.seed.log10           1    0.025      6851      10285   0.8732    
```

Blackbird

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)    
(Intercept)                   0.9310771  0.1439863   6.466    1e-10 ***
rat.tracking                 -1.6157084  0.4283489  -3.772 0.000162 ***
altitude                     -0.0020093  0.0001534 -13.099  < 2e-16 ***
mean.seed.log10              -0.3182648  0.0233468 -13.632  < 2e-16 ***
rat.tracking:altitude         0.0006249  0.0004597   1.359 0.174067    
rat.tracking:mean.seed.log10  0.8229976  0.0713230  11.539  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5918.4  on 6641  degrees of freedom
Residual deviance: 5409.5  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 8605.8
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: blackbird
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641     5918.4              
rat.tracking                  1     0.12      6640     5918.3    0.7247    
altitude                      1   324.98      6639     5593.3 < 2.2e-16 ***
mean.seed.log10               1    49.40      6638     5543.9 2.085e-12 ***
rat.tracking:altitude         1     2.57      6637     5541.3    0.1089    
rat.tracking:mean.seed.log10  1   131.83      6636     5409.5 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)    
(Intercept)                         -0.5516346  0.1450383  -3.803 0.000143 ***
stoat.tmnttrap                       0.7566047  0.0845248   8.951  < 2e-16 ***
rat.tmnt4all1080                    -0.1901645  0.4205838  -0.452 0.651165    
rat.tmnt4othertoxin                  1.4076939  0.2924977   4.813 1.49e-06 ***
rat.tmnt4trap                        1.7112092  0.3154868   5.424 5.83e-08 ***
altitude                            -0.0012957  0.0001263 -10.259  < 2e-16 ***
mean.seed.log10                     -0.1914466  0.0200902  -9.529  < 2e-16 ***
rat.tmnt4all1080:altitude           -0.0010892  0.0004694  -2.321 0.020306 *  
rat.tmnt4othertoxin:altitude        -0.0019269  0.0003498  -5.509 3.61e-08 ***
rat.tmnt4trap:altitude              -0.0020823  0.0003677  -5.662 1.49e-08 ***
rat.tmnt4all1080:mean.seed.log10     0.7447509  0.0777963   9.573  < 2e-16 ***
rat.tmnt4othertoxin:mean.seed.log10  0.1333223  0.0435984   3.058 0.002228 ** 
rat.tmnt4trap:mean.seed.log10        0.1890785  0.0561380   3.368 0.000757 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 6071.8  on 6855  degrees of freedom
Residual deviance: 5367.2  on 6843  degrees of freedom
AIC: 8649.7
Number of Fisher Scoring iterations: 6
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: blackbird
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855     6071.8
stoat.tmnt                 1  159.456      6854     5912.4 < 2.2e-16 ***
rat.tmnt4                  3    5.949      6851     5906.4    0.1141
altitude                   1  310.441      6850     5596.0 < 2.2e-16 ***
mean.seed.log10            1   38.335      6849     5557.6 5.958e-10 ***
rat.tmnt4:altitude         3   67.047      6846     5490.6 1.830e-14 ***
rat.tmnt4:mean.seed.log10  3  123.413      6843     5367.2 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)              -0.397070   0.111429  -3.563 0.000366 ***
total.native              0.027892   0.003388   8.232  < 2e-16 ***
as.numeric(allBC$te.bla)  0.181640   0.010197  17.813  < 2e-16 ***
altitude                 -0.001324   0.000107 -12.371  < 2e-16 ***
mean.seed.log10          -0.115752   0.016098  -7.191 6.45e-13 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 6071.8  on 6855  degrees of freedom
Residual deviance: 5404.5  on 6851  degrees of freedom
AIC: 8671.1
Number of Fisher Scoring iterations: 6
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: blackbird
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855     6071.8
total.native              1   120.06      6854     5951.8 < 2.2e-16 ***
as.numeric(allBC$te.bla)  1   336.08      6853     5615.7 < 2.2e-16 ***
altitude                  1   159.99      6852     5455.7 < 2.2e-16 ***
mean.seed.log10           1    51.17      6851     5404.5 8.481e-13 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Brown creeper

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                  -5.2047842  0.1890693 -27.528  < 2e-16 ***
rat.tracking                 -0.9526515  0.6642944  -1.434 0.151549
altitude                      0.0036731  0.0001519  24.176  < 2e-16 ***
mean.seed.log10               0.0809592  0.0242097   3.344 0.000826 ***
rat.tracking:altitude         0.0002385  0.0005303   0.450 0.652908
rat.tracking:mean.seed.log10  0.0167420  0.0803082   0.208 0.834861
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 9305.7  on 6641  degrees of freedom
Residual deviance: 7738.4  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 9801.7
Number of Fisher Scoring iterations: 6
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: brown.creeper
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                          6641     9305.7
rat.tracking                  1    57.76      6640     9248.0 2.964e-14 ***
altitude                      1  1483.02      6639     7764.9 < 2.2e-16 ***
mean.seed.log10               1    26.33      6638     7738.6 2.877e-07 ***
rat.tracking:altitude         1     0.19      6637     7738.4    0.6605
rat.tracking:mean.seed.log10  1     0.04      6636     7738.4    0.8348
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)
(Intercept)                         -5.716e+00  1.827e-01 -31.290  < 2e-16 ***
stoat.tmnttrap                       3.616e-01  6.711e-02   5.388 7.12e-08 ***
rat.tmnt4all1080                    -1.855e-01  4.671e-01  -0.397 0.691268
rat.tmnt4othertoxin                 -2.278e+00  4.358e-01  -5.227 1.72e-07 ***
rat.tmnt4trap                        1.078e+00  3.280e-01   3.286 0.001017 **
altitude                             3.770e-03  1.391e-04  27.100  < 2e-16 ***
mean.seed.log10                     -2.291e-02  2.042e-02  -1.122 0.261968
rat.tmnt4all1080:altitude           -2.621e-05  3.662e-04  -0.072 0.942955
rat.tmnt4othertoxin:altitude         1.650e-03  3.327e-04   4.959 7.10e-07 ***
rat.tmnt4trap:altitude              -1.193e-03  2.659e-04  -4.488 7.19e-06 ***
rat.tmnt4all1080:mean.seed.log10     3.887e-01  5.683e-02   6.839 7.99e-12 ***
rat.tmnt4othertoxin:mean.seed.log10  1.638e-01  4.719e-02   3.471 0.000519 ***
rat.tmnt4trap:mean.seed.log10        3.929e-01  6.251e-02   6.286 3.26e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 9488.6  on 6855  degrees of freedom
Residual deviance: 7721.6  on 6843  degrees of freedom
AIC: 9841.3
Number of Fisher Scoring iterations: 7

Analysis of Deviance Table
Model: poisson, link: log
Response: brown.creeper
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855     9488.6
stoat.tmnt                 1    15.34      6854     9473.2 8.991e-05 ***
rat.tmnt4                  3    41.43      6851     9431.8 5.302e-09 ***
altitude                   1  1536.95      6850     7894.8 < 2.2e-16 ***
mean.seed.log10            1    25.40      6849     7869.4 4.655e-07 ***
rat.tmnt4:altitude         3    62.27      6846     7807.2 1.922e-13 ***
rat.tmnt4:mean.seed.log10  3    85.62      6843     7721.6 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)              -5.3674338  0.1697146 -31.626  < 2e-16 ***
total.exotic             -0.0818333  0.0201939  -4.052 5.07e-05 ***
as.numeric(allBC$tn.brc)  0.0139187  0.0058321   2.387    0.017 *
altitude                  0.0036674  0.0001211  30.290  < 2e-16 ***
mean.seed.log10           0.0729428  0.0165633   4.404 1.06e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 9488.6  on 6855  degrees of freedom
Residual deviance: 7940.6  on 6851  degrees of freedom
AIC: 10044
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: brown.creeper
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855     9488.6
total.exotic              1   290.74      6854     9197.8 < 2.2e-16 ***
as.numeric(allBC$tn.brc)  1   171.75      6853     9026.1 < 2.2e-16 ***
altitude                  1  1065.77      6852     7960.3 < 2.2e-16 ***
mean.seed.log10           1    19.69      6851     7940.6 9.128e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Chaffinch

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                   1.699e+00  9.225e-02  18.416   <2e-16 ***
rat.tracking                 -2.617e-01  2.326e-01  -1.125    0.260
altitude                     -2.125e-03  9.954e-05 -21.352   <2e-16 ***
mean.seed.log10              -2.446e-01  1.556e-02 -15.717   <2e-16 ***
rat.tracking:altitude         4.156e-04  2.543e-04   1.634    0.102
rat.tracking:mean.seed.log10  6.660e-01  4.053e-02  16.432   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 11368.5  on 6641  degrees of freedom
Residual deviance:  9737.2  on 6636  degrees of freedom
```

```
AIC: 15981
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: chaffinch
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                          6641    11368.5
rat.tracking                  1   318.81      6640    11049.7 < 2.2e-16 ***
altitude                      1  1022.26      6639    10027.4 < 2.2e-16 ***
mean.seed.log10               1    16.02      6638    10011.4 6.281e-05 ***
rat.tracking:altitude         1     4.79      6637    10006.6   0.02863 *
rat.tracking:mean.seed.log10  1   269.39      6636     9737.2 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)
(Intercept)                          1.033e+00  8.321e-02  12.415  < 2e-16 ***
stoat.tmnttrap                       7.510e-01  4.818e-02  15.586  < 2e-16 ***
rat.tmnt4all1080                    -7.041e-01  2.614e-01  -2.693  0.00707 **
rat.tmnt4othertoxin                  2.320e-01  1.940e-01   1.196  0.23183
rat.tmnt4trap                       -1.246e-01  1.927e-01  -0.647  0.51783
altitude                            -1.922e-03  7.563e-05 -25.415  < 2e-16 ***
mean.seed.log10                     -8.844e-02  1.198e-02  -7.383 1.54e-13 ***
rat.tmnt4all1080:altitude           -6.360e-04  2.949e-04  -2.157  0.03101 *
rat.tmnt4othertoxin:altitude        -9.168e-04  2.304e-04  -3.980 6.89e-05 ***
rat.tmnt4trap:altitude              -3.160e-04  2.137e-04  -1.478  0.13930
rat.tmnt4all1080:mean.seed.log10     6.585e-01  4.891e-02  13.464  < 2e-16 ***
rat.tmnt4othertoxin:mean.seed.log10  1.416e-02  2.980e-02   0.475  0.63457
rat.tmnt4trap:mean.seed.log10        1.673e-01  3.794e-02   4.409 1.04e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 11663.4  on 6855  degrees of freedom
Residual deviance:  9888.7  on 6843  degrees of freedom
AIC: 16257
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: chaffinch
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855    11663.4
stoat.tmnt                 1   310.98      6854    11352.4 < 2.2e-16 ***
rat.tmnt4                  3   125.24      6851    11227.2 < 2.2e-16 ***
altitude                   1  1063.20      6850    10164.0 < 2.2e-16 ***
mean.seed.log10            1     8.25      6849    10155.8  0.004084 **
rat.tmnt4:altitude         3    26.43      6846    10129.3  7.76e-06 ***
rat.tmnt4:mean.seed.log10  3   240.62      6843     9888.7 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)               1.081e+00  6.914e-02  15.641  < 2e-16 ***
total.native              9.703e-03  2.619e-03   3.705 0.000212 ***
as.numeric(allBC$te.cha)  2.656e-01  1.224e-02  21.692  < 2e-16 ***
altitude                 -1.711e-03  6.569e-05 -26.045  < 2e-16 ***
mean.seed.log10          -3.688e-02  1.012e-02  -3.644 0.000268 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 11663  on 6855  degrees of freedom
Residual deviance: 10129  on 6851  degrees of freedom
AIC: 16481
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: chaffinch
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855      11663
total.native              1   109.86      6854      11554 < 2.2e-16 ***
as.numeric(allBC$te.cha)  1   687.72      6853      10866 < 2.2e-16 ***
altitude                  1   723.87      6852      10142 < 2.2e-16 ***
mean.seed.log10           1    13.22      6851      10129 0.0002773 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fantail

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)    
(Intercept)                   0.4450810  0.1740820   2.557   0.0106 *  
rat.tracking                 -0.3368320  0.5062678  -0.665   0.5058    
altitude                     -0.0024334  0.0001909 -12.744  < 2e-16 ***
mean.seed.log10               0.1488567  0.0328954   4.525 6.04e-06 ***
rat.tracking:altitude         0.0004558  0.0005728   0.796   0.4262    
rat.tracking:mean.seed.log10 -0.0737228  0.0926471  -0.796   0.4262    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5201.3  on 6641  degrees of freedom
Residual deviance: 4805.1  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 6960.2
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: fantail
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641     5201.3              
rat.tracking                  1     1.56      6640     5199.7    0.2117    
altitude                      1   354.49      6639     4845.2 < 2.2e-16 ***
mean.seed.log10               1    38.97      6638     4806.2  4.31e-10 ***
rat.tracking:altitude         1     0.51      6637     4805.7    0.4741    
rat.tracking:mean.seed.log10  1     0.63      6636     4805.1    0.4265    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)    
(Intercept)                          0.9015280  0.1547901   5.824 5.74e-09 ***
stoat.tmnttrap                      -0.4810796  0.0727815  -6.610 3.85e-11 ***
rat.tmnt4all1080                     0.4384388  0.3932370   1.115 0.264873    
rat.tmnt4othertoxin                 -1.5265009  0.3683821  -4.144 3.42e-05 ***
rat.tmnt4trap                       -0.4612147  0.3343614  -1.379 0.167775    
altitude                            -0.0026261  0.0001610 -16.312  < 2e-16 ***
mean.seed.log10                      0.1083115  0.0280440   3.862 0.000112 ***
rat.tmnt4all1080:altitude            0.0005698  0.0004448   1.281 0.200173    
rat.tmnt4othertoxin:altitude         0.0014094  0.0003936   3.581 0.000343 ***
rat.tmnt4trap:altitude               0.0008303  0.0003584   2.317 0.020527 *  
rat.tmnt4all1080:mean.seed.log10    -0.3971269  0.0710727  -5.588 2.30e-08 ***
rat.tmnt4othertoxin:mean.seed.log10  0.1490015  0.0678205   2.197 0.028021 *  
rat.tmnt4trap:mean.seed.log10        0.1756175  0.0707037   2.484 0.012997 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5310.2  on 6855  degrees of freedom
Residual deviance: 4761.3  on 6843  degrees of freedom
AIC: 6946.6
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: fantail
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                       6855     5310.2              
stoat.tmnt                 1    19.63      6854     5290.5 9.387e-06 ***
rat.tmnt4                  3    65.15      6851     5225.4 4.668e-14 ***
altitude                   1   373.88      6850     4851.5 < 2.2e-16 ***
mean.seed.log10            1    21.56      6849     4829.9 3.421e-06 ***
rat.tmnt4:altitude         3    15.97      6846     4814.0  0.001149 ** 
rat.tmnt4:mean.seed.log10  3    52.71      6843     4761.3 2.114e-11 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)    
(Intercept)               0.8688276  0.1374032   6.323 2.56e-10 ***
total.exotic             -0.2374787  0.0210132 -11.301  < 2e-16 ***
as.numeric(allBC$tn.fan)  0.0094384  0.0053719   1.757   0.0789 .  
altitude                 -0.0026832  0.0001333 -20.132  < 2e-16 ***
mean.seed.log10           0.1120200  0.0212104   5.281 1.28e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5310.2  on 6855  degrees of freedom
Residual deviance: 4765.6  on 6851  degrees of freedom
AIC: 6934.9
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: fantail
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                      6855     5310.2              
total.exotic              1    42.07      6854     5268.1 8.810e-11 ***
as.numeric(allBC$tn.fan)  1    33.74      6853     5234.3 6.287e-09 ***
altitude                  1   440.19      6852     4794.2 < 2.2e-16 ***
mean.seed.log10           1    28.56      6851     4765.6 9.107e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Grey warbler

Model 1

```
Coefficients:
                              Estimate Std. Error z value Pr(>|z|)    
(Intercept)                  2.247e-01  1.001e-01   2.245 0.024744 *  
rat.tracking                -7.499e-01  2.729e-01  -2.748 0.005998 ** 
altitude                    -8.087e-04  9.965e-05  -8.115 4.86e-16 ***
mean.seed.log10             -8.040e-02  1.718e-02  -4.680 2.87e-06 ***
rat.tracking:altitude        1.051e-03  2.707e-04   3.882 0.000104 ***
rat.tracking:mean.seed.log10  2.667e-01  4.718e-02   5.652 1.59e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 7370.7  on 6641  degrees of freedom
Residual deviance: 7180.1  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 13622
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: grey.warbler
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641     7370.7              
rat.tracking                  1   79.924      6640     7290.8 < 2.2e-16 ***
altitude                      1   61.494      6639     7229.3 4.440e-15 ***
mean.seed.log10               1    0.133      6638     7229.1    0.7155    
rat.tracking:altitude         1   17.128      6637     7212.0 3.495e-05 ***
rat.tracking:mean.seed.log10  1   31.921      6636     7180.1 1.606e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                     Estimate Std. Error z value Pr(>|z|)    
(Intercept)                        -2.204e-01  9.076e-02  -2.429 0.015159 *  
stoat.tmnttrap                      4.647e-01  4.795e-02   9.692  < 2e-16 ***
rat.tmnt4all1080                   -1.250e+00  3.045e-01  -4.104 4.05e-05 ***
rat.tmnt4othertoxin                -9.551e-04  1.845e-01  -0.005 0.995869    
rat.tmnt4trap                      -8.353e-01  2.006e-01  -4.164 3.13e-05 ***
altitude                           -5.747e-04  7.876e-05  -7.297 2.93e-13 ***
mean.seed.log10                    -4.460e-02  1.313e-02  -3.396 0.000683 ***
rat.tmnt4all1080:altitude           4.323e-04  3.010e-04   1.436 0.150936    
rat.tmnt4othertoxin:altitude       -4.169e-04  1.943e-04  -2.146 0.031876 *  
rat.tmnt4trap:altitude              5.198e-04  1.950e-04   2.666 0.007673 ** 
rat.tmnt4all1080:mean.seed.log10    3.442e-01  4.851e-02   7.095 1.29e-12 ***
rat.tmnt4othertoxin:mean.seed.log10  1.432e-01  3.210e-02   4.460 8.18e-06 ***
rat.tmnt4trap:mean.seed.log10       1.575e-01  4.294e-02   3.669 0.000244 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 7595.6  on 6855  degrees of freedom
Residual deviance: 7291.0  on 6843  degrees of freedom
AIC: 13959
Number of Fisher Scoring iterations: 5
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: grey.warbler
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                       6855     7595.6              
stoat.tmnt                 1   95.168      6854     7500.4 < 2.2e-16 ***
rat.tmnt4                  3   47.155      6851     7453.3 3.222e-10 ***
altitude                   1   65.161      6850     7388.1 6.904e-16 ***
mean.seed.log10            1    1.187      6849     7386.9 0.2759980    
rat.tmnt4:altitude         3   20.758      6846     7366.2 0.0001182 ***
rat.tmnt4:mean.seed.log10  3   75.209      6843     7291.0 3.268e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)    
(Intercept)              -6.018e-01  8.075e-02  -7.453 9.13e-14 ***
total.exotic              1.207e-01  7.927e-03  15.230  < 2e-16 ***
as.numeric(allBC$tn.grw)  1.500e-02  2.984e-03   5.026 5.00e-07 ***
altitude                 -1.934e-04  6.918e-05  -2.795  0.00519 ** 
mean.seed.log10           4.824e-03  1.101e-02   0.438  0.66118    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 7595.6  on 6855  degrees of freedom
Residual deviance: 7297.3  on 6851  degrees of freedom
AIC: 13950
Number of Fisher Scoring iterations: 5
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: grey.warbler
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                      6855     7595.6              
total.exotic              1  260.485      6854     7335.1 < 2.2e-16 ***
as.numeric(allBC$tn.grw)  1   29.836      6853     7305.3 4.701e-08 ***
altitude                  1    7.836      6852     7297.4  0.005121 ** 
mean.seed.log10           1    0.192      6851     7297.3  0.661066    
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Redpoll

Model 1

```
Coefficients:
                               Estimate Std. Error t value Pr(>|t|)    
(Intercept)                  -3.2960347  0.5387007  -6.118 9.98e-10 ***
rat.tracking                  0.1654408  1.2083107   0.137   0.8911    
altitude                     -0.0002938  0.0005161  -0.569   0.5692    
mean.seed.log10               0.0689566  0.0978846   0.704   0.4812    
rat.tracking:altitude         0.0009865  0.0011219   0.879   0.3793    
rat.tracking:mean.seed.log10  0.4718630  0.2350803   2.007   0.0448 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 1.967496)
    Null deviance: 2361.9  on 6641  degrees of freedom
Residual deviance: 2228.9  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: NA
Number of Fisher Scoring iterations: 6
```

```
Analysis of Deviance Table
Model: quasipoisson, link: log
Response: redpoll
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641     2361.9              
rat.tracking                  1   87.526      6640     2274.3 2.562e-11 ***
altitude                      1    0.365      6639     2274.0   0.66689    
mean.seed.log10               1   35.189      6638     2238.8 2.347e-05 ***
rat.tracking:altitude         1    1.820      6637     2237.0   0.33620    
rat.tracking:mean.seed.log10  1    8.077      6636     2228.9   0.04275 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error t value Pr(>|t|)    
(Intercept)                         -3.910e+00  4.398e-01  -8.890  < 2e-16 ***
stoat.tmnttrap                       9.306e-01  2.408e-01   3.864 0.000112 ***
rat.tmnt4all1080                    -2.565e+00  1.656e+00  -1.549 0.121322    
rat.tmnt4othertoxin                 -8.105e+00  2.813e+00  -2.881 0.003973 ** 
rat.tmnt4trap                        4.100e-01  8.210e-01   0.499 0.617547    
altitude                            -2.884e-05  3.590e-04  -0.080 0.935978    
mean.seed.log10                      2.904e-01  6.557e-02   4.428 9.66e-06 ***
rat.tmnt4all1080:altitude            1.813e-03  1.441e-03   1.258 0.208317    
rat.tmnt4othertoxin:altitude         5.762e-03  2.116e-03   2.723 0.006495 ** 
rat.tmnt4trap:altitude              -4.054e-04  7.940e-04  -0.511 0.609712    
rat.tmnt4all1080:mean.seed.log10     1.705e-02  2.354e-01   0.072 0.942249    
rat.tmnt4othertoxin:mean.seed.log10 -2.365e-01  2.814e-01  -0.840 0.400675    
rat.tmnt4trap:mean.seed.log10        4.033e-02  1.816e-01   0.222 0.824204    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 1.911587)
    Null deviance: 2532.2  on 6855  degrees of freedom
Residual deviance: 2367.8  on 6843  degrees of freedom
AIC: NA
Number of Fisher Scoring iterations: 7

Analysis of Deviance Table
Model: quasipoisson, link: log
Response: redpoll
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                       6855     2532.2              
stoat.tmnt                 1   17.898      6854     2514.3  0.002214 ** 
rat.tmnt4                  3   66.835      6851     2447.5 1.240e-07 ***
altitude                   1    1.005      6850     2446.5  0.468309    
mean.seed.log10            1   51.727      6849     2394.7 1.973e-07 ***
rat.tmnt4:altitude         3   25.460      6846     2369.3  0.003996 ** 
rat.tmnt4:mean.seed.log10  3    1.465      6843     2367.8  0.857535    
---
```

Model 3

```
Coefficients:
                           Estimate Std. Error t value Pr(>|t|)    
(Intercept)               0.2994648  0.2272906   1.318  0.18770    
total.native             -0.0267947  0.0103526  -2.588  0.00967 ** 
as.numeric(allBC$te.red)  0.3056193  0.0104873  29.142  < 2e-16 ***
altitude                 -0.0037986  0.0002669 -14.231  < 2e-16 ***
mean.seed.log10          -0.1291125  0.0322358  -4.005 6.26e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 0.8851959)
    Null deviance: 2772.7  on 6855  degrees of freedom
Residual deviance: 1988.8  on 6851  degrees of freedom
AIC: NA
Number of Fisher Scoring iterations: 8

Analysis of Deviance Table
Model: quasipoisson, link: log
Response: song.thrush
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev Pr(>Chi)    
NULL                                      6855     2772.7             
total.native              1     0.66      6854     2772.1   0.3864    
as.numeric(allBC$te.red)  1   530.92      6853     2241.2  < 2e-16 ***
altitude                  1   238.31      6852     2002.9  < 2e-16 ***
mean.seed.log10           1    14.04      6851     1988.8  6.8e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Rifleman

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)    
(Intercept)                  -1.053e+00  1.051e-01 -10.019  < 2e-16 ***
rat.tracking                 -5.394e+00  4.554e-01 -11.845  < 2e-16 ***
altitude                      7.771e-04  9.364e-05   8.300  < 2e-16 ***
mean.seed.log10               5.714e-02  1.657e-02   3.449 0.000564 ***
rat.tracking:altitude         2.778e-03  3.905e-04   7.114 1.13e-12 ***
rat.tracking:mean.seed.log10  4.183e-01  6.737e-02   6.208 5.35e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 10591  on 6641  degrees of freedom
Residual deviance:  9583  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
```

```
AIC: 14158
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: rifleman
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                          6641    10591.2
rat.tracking                  1   445.56      6640    10145.6 < 2.2e-16 ***
altitude                      1   354.20      6639     9791.4 < 2.2e-16 ***
mean.seed.log10               1   117.60      6638     9673.8 < 2.2e-16 ***
rat.tracking:altitude         1    51.73      6637     9622.1 6.370e-13 ***
rat.tracking:mean.seed.log10  1    39.13      6636     9583.0 3.959e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)
(Intercept)                         -2.501e+00  1.019e-01 -24.547  < 2e-16 ***
stoat.tmnttrap                       7.598e-01  5.042e-02  15.071  < 2e-16 ***
rat.tmnt4all1080                    -1.717e+00  3.698e-01  -4.642 3.45e-06 ***
rat.tmnt4othertoxin                 -1.206e+00  2.383e-01  -5.062 4.16e-07 ***
rat.tmnt4trap                       -8.876e-01  2.414e-01  -3.676 0.000237 ***
altitude                             1.259e-03  8.008e-05  15.716  < 2e-16 ***
mean.seed.log10                      1.176e-01  1.347e-02   8.734  < 2e-16 ***
rat.tmnt4all1080:altitude            2.042e-04  3.118e-04   0.655 0.512625
rat.tmnt4othertoxin:altitude         5.192e-04  2.103e-04   2.469 0.013560 *
rat.tmnt4trap:altitude               5.502e-04  2.108e-04   2.610 0.009065 **
rat.tmnt4all1080:mean.seed.log10     5.875e-01  6.256e-02   9.392  < 2e-16 ***
rat.tmnt4othertoxin:mean.seed.log10 -1.491e-02  3.946e-02  -0.378 0.705443
rat.tmnt4trap:mean.seed.log10       -1.681e-01  4.820e-02  -3.487 0.000488 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 10894.8  on 6855  degrees of freedom
Residual deviance:  9825.8  on 6843  degrees of freedom
AIC: 14529
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: rifleman
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855    10894.8
stoat.tmnt                 1   104.64      6854    10790.1 < 2.2e-16 ***
rat.tmnt4                  3   211.38      6851    10578.8 < 2.2e-16 ***
altitude                   1   446.94      6850    10131.8 < 2.2e-16 ***
mean.seed.log10            1   150.71      6849     9981.1 < 2.2e-16 ***
rat.tmnt4:altitude         3    11.59      6846     9969.5  0.008917 **
rat.tmnt4:mean.seed.log10  3   143.68      6843     9825.8 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)              -2.542e+00  9.404e-02 -27.031  < 2e-16 ***
total.exotic             -7.069e-02  1.223e-02  -5.782 7.37e-09 ***
as.numeric(allBC$tn.rif)  4.407e-02  2.772e-03  15.897  < 2e-16 ***
altitude                  1.513e-03  7.371e-05  20.529  < 2e-16 ***
mean.seed.log10           1.265e-01  1.196e-02  10.579  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 10895  on 6855  degrees of freedom
Residual deviance: 10146  on 6851  degrees of freedom
AIC: 14834
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: rifleman
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855      10895
total.exotic              1   146.27      6854      10748 < 2.2e-16 ***
as.numeric(allBC$tn.rif)  1    59.32      6853      10689 1.338e-14 ***
altitude                  1   427.91      6852      10261 < 2.2e-16 ***
mean.seed.log10           1   115.08      6851      10146 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Silvereye

Model 1

```
Coefficients:
                               Estimate Std. Error t value Pr(>|t|)
(Intercept)                   3.3212178  0.1162992  28.558  < 2e-16 ***
rat.tracking                 -2.1519320  0.3271606  -6.578 5.15e-11 ***
altitude                     -0.0027825  0.0001280 -21.732  < 2e-16 ***
mean.seed.log10              -0.0976543  0.0202921  -4.812 1.52e-06 ***
rat.tracking:altitude         0.0024016  0.0003566   6.735 1.77e-11 ***
rat.tracking:mean.seed.log10  0.1546317  0.0573072   2.698  0.00699 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 4.49022)
    Null deviance: 23407  on 6641  degrees of freedom
Residual deviance: 19752  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: NA
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: quasipoisson, link: log
Response: silvereye
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                          6641      23407
rat.tracking                  1     53.7      6640      23354 0.0005437 ***
altitude                      1   3290.4      6639      20063 < 2.2e-16 ***
mean.seed.log10               1     70.5      6638      19993 7.397e-05 ***
rat.tracking:altitude         1    208.3      6637      19784 9.681e-12 ***
rat.tracking:mean.seed.log10  1     32.6      6636      19752 0.0070389 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error t value Pr(>|t|)
(Intercept)                          3.176e+00  8.949e-02  35.487  < 2e-16 ***
stoat.tmnttrap                      -3.837e-01  4.316e-02  -8.889  < 2e-16 ***
rat.tmnt4all1080                     5.161e-01  2.652e-01   1.946  0.05165 .
rat.tmnt4othertoxin                 -7.183e-01  2.326e-01  -3.089  0.00202 **
rat.tmnt4trap                       -1.875e-02  2.421e-01  -0.077  0.93826
altitude                            -2.222e-03  9.019e-05 -24.639  < 2e-16 ***
mean.seed.log10                     -7.908e-02  1.515e-02  -5.220 1.84e-07 ***
rat.tmnt4all1080:altitude           -2.478e-04  3.060e-04  -0.810  0.41799
rat.tmnt4othertoxin:altitude         2.904e-04  2.629e-04   1.105  0.26939
rat.tmnt4trap:altitude              -7.162e-05  2.717e-04  -0.264  0.79212
rat.tmnt4all1080:mean.seed.log10    -8.810e-02  4.539e-02  -1.941  0.05228 .
rat.tmnt4othertoxin:mean.seed.log10  1.044e-01  3.870e-02   2.698  0.00699 **
rat.tmnt4trap:mean.seed.log10        5.689e-04  4.738e-02   0.012  0.99042
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 3.981376)
    Null deviance: 24044  on 6855  degrees of freedom
Residual deviance: 19741  on 6843  degrees of freedom
AIC: NA
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: quasipoisson, link: log
Response: silvereye
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855      24044
stoat.tmnt                 1    235.6      6854      23808 1.435e-14 ***
rat.tmnt4                  3    179.6      6851      23629 8.783e-10 ***
altitude                   1   3682.2      6850      19946 < 2.2e-16 ***
mean.seed.log10            1    139.5      6849      19807 3.215e-09 ***
rat.tmnt4:altitude         3     14.8      6846      19792  0.294222
rat.tmnt4:mean.seed.log10  3     50.9      6843      19741  0.005143 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error t value Pr(>|t|)    
(Intercept)               2.841e+00  8.584e-02  33.093  < 2e-16 ***
total.exotic             -1.829e-02  1.078e-02  -1.697   0.0898 .  
as.numeric(allBC$tn.sil) -6.976e-03  5.710e-03  -1.222   0.2219    
altitude                 -2.185e-03  8.548e-05 -25.562  < 2e-16 ***
mean.seed.log10          -5.364e-02  1.317e-02  -4.072 4.72e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for quasipoisson family taken to be 4.520746)
    Null deviance: 24044  on 6855  degrees of freedom
Residual deviance: 20507  on 6851  degrees of freedom
AIC: NA
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: quasipoisson, link: log
Response: silvereye
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                      6855      24044              
total.exotic              1    203.4      6854      23840 1.975e-11 ***
as.numeric(allBC$tn.sil)  1     18.0      6853      23822   0.04596 *  
altitude                  1   3240.5      6852      20582 < 2.2e-16 ***
mean.seed.log10           1     74.4      6851      20507 4.977e-05 ***
```

Song Thrush

Model 1

```
Coefficients:
                              Estimate Std. Error z value Pr(>|z|)    
(Intercept)                   2.253401   0.335197   6.723 1.78e-11 ***
rat.tracking                 -2.858555   1.093418  -2.614  0.00894 ** 
altitude                     -0.005148   0.000411 -12.525  < 2e-16 ***
mean.seed.log10              -0.285072   0.051361  -5.550 2.85e-08 ***
rat.tracking:altitude         0.001412   0.001369   1.031  0.30234    
rat.tracking:mean.seed.log10  0.688104   0.165278   4.163 3.14e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 2704.2  on 6641  degrees of freedom
Residual deviance: 2262.9  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 3075.4
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: song.thrush
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                          6641     2704.2              
rat.tracking                  1     6.11      6640     2698.1 0.0134222 *  
altitude                      1   404.55      6639     2293.6 < 2.2e-16 ***
mean.seed.log10               1    12.30      6638     2281.2 0.0004525 ***
rat.tracking:altitude         1     1.18      6637     2280.1 0.2773793    
rat.tracking:mean.seed.log10  1    17.18      6636     2262.9   3.4e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                     Estimate Std. Error z value Pr(>|z|)    
(Intercept)                         2.574e-01  3.637e-01   0.708 0.479164    
stoat.tmnttrap                      8.562e-01  2.075e-01   4.126 3.68e-05 ***
rat.tmnt4all1080                    1.683e+00  1.227e+00   1.371 0.170290    
rat.tmnt4othertoxin                 1.255e+00  8.312e-01   1.510 0.130946    
rat.tmnt4trap                       1.180e+00  5.278e-01   2.236 0.025345 *  
altitude                           -4.360e-03  3.786e-04 -11.516  < 2e-16 ***
mean.seed.log10                    -1.987e-01  5.163e-02  -3.848 0.000119 ***
rat.tmnt4all1080:altitude          -3.233e-03  1.672e-03  -1.933 0.053229 .  
rat.tmnt4othertoxin:altitude       -1.833e-03  1.109e-03  -1.653 0.098233 .  
rat.tmnt4trap:altitude             -4.491e-05  6.506e-04  -0.069 0.944962    
rat.tmnt4all1080:mean.seed.log10    6.238e-01  1.774e-01   3.516 0.000437 ***
rat.tmnt4othertoxin:mean.seed.log10 1.534e-01  9.555e-02   1.606 0.108277    
rat.tmnt4trap:mean.seed.log10       7.670e-02  8.597e-02   0.892 0.372327    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 2772.7  on 6855  degrees of freedom
Residual deviance: 2171.1  on 6843  degrees of freedom
AIC: 3014.8
Number of Fisher Scoring iterations: 7
```

```
Analysis of Deviance Table
Model: poisson, link: log
Response: song.thrush
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855     2772.7
stoat.tmnt                 1    70.20      6854     2702.5 < 2.2e-16 ***
rat.tmnt4                  3   132.86      6851     2569.7 < 2.2e-16 ***
altitude                   1   368.78      6850     2200.9 < 2.2e-16 ***
mean.seed.log10            1    11.63      6849     2189.3 0.0006486 ***
rat.tmnt4:altitude         3     4.11      6846     2185.2 0.2502369
rat.tmnt4:mean.seed.log10  3    14.06      6843     2171.1 0.0028196 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)              0.9060545  0.2481563   3.651 0.000261 ***
total.native            -0.0212779  0.0104460  -2.037 0.057152 .
as.numeric(allBC$te.sth)  0.1880075  0.0197720   9.509  < 2e-16 ***
altitude                -0.0041802  0.0002776 -15.056  < 2e-16 ***
mean.seed.log10         -0.1168812  0.0344440  -3.393 0.000690 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 2772.7  on 6855  degrees of freedom
Residual deviance: 2293.7  on 6851  degrees of freedom
AIC: 3121.4
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: song.thrush
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855     2772.7
total.native              1    0.664      6854     2772.1 0.4151412
as.numeric(allBC$te.sth)  1  164.813      6853     2607.3 < 2.2e-16 ***
altitude                  1  302.199      6852     2305.1 < 2.2e-16 ***
mean.seed.log10           1   11.414      6851     2293.7 0.0007288 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Tomtit

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)
(Intercept)                  -1.014e+00  9.338e-02 -10.864  < 2e-16 ***
rat.tracking                 -7.650e-01  2.880e-01  -2.657  0.00789 **
altitude                      8.025e-04  8.552e-05   9.384  < 2e-16 ***
mean.seed.log10              -7.965e-02  1.469e-02  -5.420 5.95e-08 ***
rat.tracking:altitude         1.827e-04  2.633e-04   0.694  0.48762
rat.tracking:mean.seed.log10  3.937e-01  4.587e-02   8.583  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 7950.5  on 6641  degrees of freedom
Residual deviance: 7653.8  on 6636  degrees of freedom
  (214 observations deleted due to missingness)
AIC: 15037
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: tomtit
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev Pr(>Chi)
NULL                                          6641     7950.5
rat.tracking                  1    2.287      6640     7948.2   0.1304
altitude                      1  217.423      6639     7730.8   <2e-16 ***
mean.seed.log10               1    2.241      6638     7728.5   0.1344
rat.tracking:altitude         1    0.755      6637     7727.8   0.3848
rat.tracking:mean.seed.log10  1   73.922      6636     7653.8   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)    
(Intercept)                         -1.448e+00  8.667e-02 -16.703  < 2e-16 ***
stoat.tmnttrap                       3.752e-01  4.137e-02   9.069  < 2e-16 ***
rat.tmnt4all1080                    -6.022e-01  2.772e-01  -2.172  0.02982 *  
rat.tmnt4othertoxin                 -5.427e-01  1.854e-01  -2.928  0.00342 ** 
rat.tmnt4trap                        1.102e-01  1.842e-01   0.598  0.54952    
altitude                             8.794e-04  7.093e-05  12.398  < 2e-16 ***
mean.seed.log10                     -3.029e-03  1.186e-02  -0.255  0.79839    
rat.tmnt4all1080:altitude           -2.027e-04  2.564e-04  -0.791  0.42906    
rat.tmnt4othertoxin:altitude         1.207e-04  1.723e-04   0.701  0.48353    
rat.tmnt4trap:altitude              -1.318e-04  1.715e-04  -0.769  0.44201    
rat.tmnt4all1080:mean.seed.log10     3.958e-01  4.306e-02   9.193  < 2e-16 ***
rat.tmnt4othertoxin:mean.seed.log10  2.657e-02  3.150e-02   0.844  0.39891    
rat.tmnt4trap:mean.seed.log10       -1.186e-01  3.823e-02  -3.103  0.00192 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 8206.8  on 6855  degrees of freedom
Residual deviance: 7730.9  on 6843  degrees of freedom
AIC: 15298
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: tomtit
Terms added sequentially (first to last)


                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)    
NULL                                       6855     8206.8              
stoat.tmnt                 1   38.009      6854     8168.8 7.043e-10 ***
rat.tmnt4                  3   85.716      6851     8083.1 < 2.2e-16 ***
altitude                   1  233.121      6850     7850.0 < 2.2e-16 ***
mean.seed.log10            1    4.118      6849     7845.8   0.04243 *  
rat.tmnt4:altitude         3    1.314      6846     7844.5   0.72575    
rat.tmnt4:mean.seed.log10  3  113.597      6843     7730.9 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)    
(Intercept)              -1.822e+00  8.011e-02 -22.744  < 2e-16 ***
total.exotic              4.571e-02  8.958e-03   5.103 3.35e-07 ***
as.numeric(allBC$tn.tom)  3.280e-02  2.547e-03  12.878  < 2e-16 ***
altitude                  1.175e-03  6.401e-05  18.355  < 2e-16 ***
mean.seed.log10           1.500e-02  1.000e-02   1.500    0.134    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 8206.8  on 6855  degrees of freedom
Residual deviance: 7820.2  on 6851  degrees of freedom
AIC: 15371
Number of Fisher Scoring iterations: 5

Analysis of Deviance Table
Model: poisson, link: log
Response: tomtit
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev Pr(>Chi)    
NULL                                      6855     8206.8             
total.exotic              1     0.03      6854     8206.8   0.8530    
as.numeric(allBC$tn.tom)  1    43.93      6853     8162.8  3.4e-11 ***
altitude                  1   340.37      6852     7822.5  < 2e-16 ***
mean.seed.log10           1     2.25      6851     7820.2   0.1332    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Tūī

Model 1

```
Coefficients:
                               Estimate Std. Error z value Pr(>|z|)    
(Intercept)                   1.7245694  0.1640227  10.514  < 2e-16 ***
rat.tracking                 -3.9477468  0.4747309  -8.316  < 2e-16 ***
altitude                     -0.0034843  0.0001843 -18.902  < 2e-16 ***
mean.seed.log10              -0.0021950  0.0296035  -0.074   0.9409    
rat.tracking:altitude         0.0039424  0.0005100   7.730 1.07e-14 ***
rat.tracking:mean.seed.log10  0.2564368  0.0872743   2.938   0.0033 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
```

```
    Null deviance: 5770.6  on 6641  degrees of freedom
Residual deviance: 5219.8  on 6636  degrees of freedom
AIC: 7652.9
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: tui
Terms added sequentially (first to last)
                             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                          6641     5770.6
rat.tracking                  1     0.05      6640     5770.6 0.8278741
altitude                      1   467.56      6639     5303.0 < 2.2e-16 ***
mean.seed.log10               1    13.65      6638     5289.4 0.0002197 ***
rat.tracking:altitude         1    60.91      6637     5228.4 5.968e-15 ***
rat.tracking:mean.seed.log10  1     8.69      6636     5219.8 0.0032014 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 2

```
Coefficients:
                                      Estimate Std. Error z value Pr(>|z|)
(Intercept)                          0.0153268  0.1412006   0.109 0.913562
stoat.tmnttrap                      -0.0892940  0.0689799  -1.294 0.195496
rat.tmnt4all1080                     2.8931310  0.5303853   5.455 4.90e-08 ***
rat.tmnt4othertoxin                  2.4565873  0.3167137   7.756 8.73e-15 ***
rat.tmnt4trap                        4.0173225  0.5994917   6.701 2.07e-11 ***
altitude                            -0.0016616  0.0001358 -12.232  < 2e-16 ***
mean.seed.log10                      0.1118240  0.0240744   4.645 3.40e-06 ***
rat.tmnt4all1080:altitude           -0.0034563  0.0006793  -5.088 3.62e-07 ***
rat.tmnt4othertoxin:altitude        -0.0026118  0.0003918  -6.666 2.63e-11 ***
rat.tmnt4trap:altitude              -0.0050268  0.0007827  -6.423 1.34e-10 ***
rat.tmnt4all1080:mean.seed.log10    -0.0835943  0.0814584  -1.026 0.304787
rat.tmnt4othertoxin:mean.seed.log10 -0.0311579  0.0451178  -0.691 0.489823
rat.tmnt4trap:mean.seed.log10       -0.2752118  0.0772783  -3.561 0.000369 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5943.1  on 6855  degrees of freedom
Residual deviance: 5256.9  on 6843  degrees of freedom
AIC: 7800.7
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: tui
Terms added sequentially (first to last)
                          Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                       6855     5943.1
stoat.tmnt                 1     0.27      6854     5942.8 0.6045354
rat.tmnt4                  3    44.73      6851     5898.1 1.058e-09 ***
altitude                   1   481.27      6850     5416.8 < 2.2e-16 ***
mean.seed.log10            1    14.43      6849     5402.4 0.0001451 ***
rat.tmnt4:altitude         3   132.37      6846     5270.0 < 2.2e-16 ***
rat.tmnt4:mean.seed.log10  3    13.14      6843     5256.9 0.0043520 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3

```
Coefficients:
                           Estimate Std. Error z value Pr(>|z|)
(Intercept)               0.2077362  0.1263400   1.644 0.100122
total.exotic              0.0308991  0.0140424   2.200 0.027777 *
as.numeric(allBC$tn.tui)  0.0351607  0.0034668  10.142  < 2e-16 ***
altitude                 -0.0022873  0.0001254 -18.239  < 2e-16 ***
mean.seed.log10           0.0726940  0.0188342   3.860 0.000114 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for poisson family taken to be 1)
    Null deviance: 5943.1  on 6855  degrees of freedom
Residual deviance: 5360.3  on 6851  degrees of freedom
AIC: 7888.1
Number of Fisher Scoring iterations: 6

Analysis of Deviance Table
Model: poisson, link: log
Response: tui
Terms added sequentially (first to last)
                         Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                      6855     5943.1
total.exotic              1    71.46      6854     5871.6 < 2.2e-16 ***
as.numeric(allBC$tn.tui)  1   133.29      6853     5738.3 < 2.2e-16 ***
altitude                  1   362.96      6852     5375.4 < 2.2e-16 ***
mean.seed.log10           1    15.09      6851     5360.3 0.0001025 ***
```