



Effect of one-hit control
on the density of possums
(*Trichosurus vulpecula*) and
their impacts on native forest

SCIENCE FOR CONSERVATION 304



Department of Conservation
Te Papa Atawhai

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G. Nugent, J. Whitford, P. Sweetapple, R. Duncan and P. Holland

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Cover: Kāmahī at Tahunamaere non-treatment site dying as a result of possum browse, 1996. Over the 8 years of the study, 39% of the kāmahī at Tahunamaere died, compared with an overall 8% (range 3–14%) in the seven Matemateonga sites where possums were aerially poisoned with 1080 in 1996.

Photo: Graham Nugent, Landcare Research.

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ABSTRACT

Introduced possums (*Trichosurus vulpecula*) have unwanted impacts on New Zealand's indigenous forest, but how forests respond to possum control is not well understood. Here, we document how possum populations, and the tree species they feed on, responded over 6–8 years following aerial 1080 poisoning. In each of three areas, possum density and tree condition were monitored at 2–7 poisoned sites and 1–3 unpoisoned sites (each 150–250 ha in area). Trap Catch Indices (TCIs) of possum density were much reduced after poisoning, but usually recovered quickly to near pre-control levels within 6 years. The overall mortality of possum-preferred tree species was about 25% lower at poisoned sites than at unpoisoned sites, but this varied between species. Browse levels initially fell sharply at most sites, but with greater declines at the poisoned sites. Browse pressure then increased again as possum numbers increased to previous levels. Canopy condition (as indexed by % Foliar Cover; FCI) increased at both poisoned and unpoisoned sites, but more so at the poisoned sites. Foliar cover of some the most common and widespread species such as kāmahi (*Weinmannia racemosa*), māhoe (*Melicytus ramiflorus*) and tawa (*Beilschmedia tawa*) continued to increase (i.e. recover from presumed previous defoliation) even when the possum numbers had substantially recovered. Although the interactions between possums and their food supply are complex, possum control does reduce possum browse, and therefore tree defoliation and, ultimately, tree mortality. Importantly, we infer that reducing possum density by 60% will usually be sufficient to protect most of the possum-preferred tree species we studied.

Keywords: possums, *Trichosurus vulpecula*, foliar cover, browse, rate of increase, tree mortality rates, New Zealand

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1. Introduction

The importance of introduced brushtail possums (*Trichosurus vulpecula*) in driving major changes in forest composition in New Zealand was questioned well into the latter half of the 20th century (e.g. Veblen & Stewart 1982). Uncertainty persisted because possum impacts are extremely variable, depending on a range of predisposing factors (Payton 2000). However, the weight of evidence from observational studies now leaves little doubt that possums do contribute to the sometimes catastrophic dieback of vulnerable forest types and can change forest composition through much increased mortality of vulnerable species such as northern rātā (*Metrosideros robusta*; Meads 1976) and Hall's tōtara (*Podocarpus hallii*; Bellingham et al. 1999a).

Since about 1960, the view that possums were affecting native forest structure and composition in unacceptable ways prompted large-scale control of possum populations in many areas to either prevent damage or allow the forest to 'recover' (Payton 2000). Initially, the perceived obviousness and urgency of the problem provided sufficient justification for the control. Doing something was seen as better than doing nothing, and it was presumed that reducing possum numbers would reduce browse pressure and at least prevent further damage. However, it is increasingly clear that simply removing or reducing a herbivore may not result in a rapid return to the previous ecosystem state, particularly where the herbivore has been long established (Schmitz & Sinclair 1997; Coomes et al. 2003). For example, species not eaten by the herbivore often increase in abundance (Bellingham et al. 1999b) and can prevent rapid re-establishment of eaten-out species, or any 'recovery' may take decades or centuries or occur only after some major ecological perturbation (Tanentzap et al. 2009).

Thus, although large-scale possum control has been implemented to try to limit or reverse the impacts of possums for four decades in New Zealand, the complexity in the outcomes of possum invasion has made it difficult to be certain that possum control will actually produce the desired mitigation and/or restoration responses. Much early possum control was implemented as a one-off or short-term attempt to avert anticipated catastrophic collapse of, for example, rātā (*Metrosideros* spp.)-kāmahi (*Weinmannia recemosa*) canopies. It is only in the last 10–15 years that most of the possum control aimed at protecting native vegetation has been conducted on an in-perpetuity basis. This is far too short a period to meaningfully measure medium- or long-term changes in forest canopy composition, and only one pair of related studies by Bellingham et al. (1999a, b) has attempted this using a large number of areas. In these studies, they did not detect consistent declines over time in any possum-preferred species other than a major decline in Hall's tōtara, which is an important food of possums (Nugent et al. 2000), and they detected no major differences in composition between areas that had or had not previously received some form of possum control. However, interpretation of these results is difficult, as neither the effectiveness of the control nor its extent were factored into the analysis, and the areas subject to possum control were not selected randomly (they were presumably targeted because the apparent impacts of possums were already severe).

To date, there are only six published studies that document short-term changes in plant biomass after possum control. Smale et al. (1995) did not detect any increase in canopy cover 5 years after possum control in a West Coast rātā-kāmahi forest. Likewise, Payton et al. (1997) did not detect any increase in foliar cover when possum control was implemented in kauri (*Agathis australis*) forest near Waipoua, Northland, not long after possums had colonised the area—although they did record a decrease in a nearby area where possums were not controlled, from which they inferred that the control had been effective in preventing a similar decline at Waipoua. In both these studies, however, the possum control was implemented to prevent canopy dieback and the trees were still in good health, so there was little scope for recovery.

The four remaining published investigations of short-term vegetation change after possum control all focussed mainly on just one or two highly impacted species and all showed substantial rapid increases in foliar biomass after possum control for those species. Nugent et al. (2002) demonstrated recovery of kohekohe (*Dysoxylum spectabile*) from near universal defoliation to almost full foliage cover within 2 years of possum control. Likewise, Sweetapple et al. (2002) showed the rapid accumulation of mistletoe stem-and-leaf biomass for 3–4 years following aerial poisoning of possums, whereas almost none had accumulated in the years before control (even though the size of the parasitic galls from which the stems emerged indicated that the plants were many years old). Rogers (1997) reported an increase over 2 years in the foliar biomass of Hall's tōtara in an area subject to possum control, but no change in a nearby area where possums were not controlled; for the other conifer monitored, pāhautea (*Libocedrus bidwillii*), there was a smaller increase for the banded trees and those in the area with possum control, but a decline in the area where possums were not controlled. Finally, Urlich & Brady (2005) recorded reduced mortality, increased basal area and higher foliar cover of tree fuchsia over 4–8 years after the initiation of possum control in five areas compared with one area with no possum control.

Pulsed intermittent or periodic control is frequently used to manage possum numbers and impacts in large, remote and rugged areas of native forest (Parkes et al. 2006). This strategy aims to minimise the adverse impacts of possums by reducing their numbers to well below some threshold density at which they are considered to cause unacceptable changes in forest structure and composition, and then repeating the control some years later once possum numbers have increased to close to or above that threshold. The gap of several years between successive control operations distinguishes this strategy from the so-called press or maintenance control strategies that are used in more accessible country where repeat control can be more readily undertaken each year (Parkes et al. 2006).

The period between successive controls has typically been of the order of 5–10 years (Parkes et al. 2006). However, that periodicity has not yet been related in any meaningful way to evidence-based threshold densities of possums at which their impacts are minimal or at least tolerable. As a consequence, there is little evidence to judge whether operations are being repeated too frequently or not frequently enough. This project therefore aimed to characterise those threshold densities and the optimal periodicity of control for the protection of a variety of tree species that are commonly affected by possums. The focus was on the response in canopy cover of existing forest trees, rather than on regeneration responses or native animal abundance.

In 1996, a medium-term study was commenced to determine the rates at which possum populations recovered after one-hit aerial poisoning and the threshold levels at which they again began to have an adverse impact on native forest canopies. The study was replicated in three areas, within each of which possums were controlled at 2-7 'treatment' sites and not controlled at 1-2 'non treatment' experimental control sites. An important design limitation was that the areas designated for treatment were selected by Department of Conservation (DOC) conservancies for conservation purposes, so the experimental treatment (possum control) was not randomly allocated to sites. To minimise the possibility of some selection bias, we endeavoured to select treatment and non-treatment areas that appeared to be similar with respect to the likely nature of the possum impact-density relationships for the indicator species monitored, and we have made extensive use of *in situ* controls in the form of unpalatable species and unbrowsed individuals within species. We report outcomes over the 6-8-year period following possum control.

2. Objective

The aim of this study was to gain a better understanding of how possum populations and forest canopy species responded to a single possum control operation, so that the level of control needed to maintain the desired level of protection of those tree species could be assessed.

3. Methods

3.1 STUDY DESIGN

In autumn 1996, we initiated a monitoring programme in the Matemateaonga Range, Wanganui Conservancy, and in the following year established similar programmes in the Richmond Range, Nelson/Marlborough Conservancy, and the Ikawhenua Range, in the former East Coast/Hawke's Bay Conservancy (Fig. 1). The full monitoring programme consisted of an initial survey of possum abundance and canopy condition prior to possum control, followed by three or four resurveys at biennial intervals, all in autumn. Within each of the three areas, we monitored 2–7 treatment sites and 1–2 non-treatment sites. The monitoring of multiple treatment sites within each area (rather than having each site as a fully independent replicate) reflected the desire to explore both between- and within-area variation.

At the treatment sites, possums were controlled by one-hit aerial 1080 poisoning soon after the first survey; there was no further control during the study, and none of the areas had previously been subject to official control. At non-treatment sites, possums were not intentionally controlled. Trends in indices of possum density and their impacts on vegetation in these blocks were assessed using modified variants of the Trap Catch Index (TCI; Warburton 1996) and Foliar Browse Index (FBI; Payton et al. 1999) methods, respectively.

Each study site consisted of a subcatchment of 150–250 ha. These subcatchments were sufficiently separate from each other for the resident possum populations within them to be independent of each other (i.e. the areas were too far apart for there to be any likelihood of overlap in the home ranges of resident possums, which are usually only a few hectares in size; Cowan & Clout 2000). Subcatchments were subjectively selected to represent the full range of variation in forest composition, susceptibility to possum damage, and the current extent of canopy dieback within the total area to be poisoned. The start points for five 400-m-long transects were established randomly along accessible ridgelines or creek beds (depending on area topography) and the transects were directed randomly within the physically accessible areas (i.e. avoiding bluffs). Possum abundance and tree condition were measured biennially along each transect. Forest composition was also assessed along these transects.

The overall study design therefore consisted of three true replicates (areas), within which were nested 2–7 poisoned and 1–3 unpoisoned sites, which also provided information on the variation in impact within areas. The three primary study areas are described below.

The scientific and common names of the most common plant species in each area are listed in Appendix 1, along with a measure of relative abundance (see section 3.4.1)

3.1.1 Matemateaonga Range

As part of a large, multi-stage programme, Wanganui Conservancy, DOC, aeri ally poisoned possums on the western end of the Matemateaonga Range (12 000 ha) in winter 1996 (Fig. 1A). Seven subcatchments were monitored in the poisoned

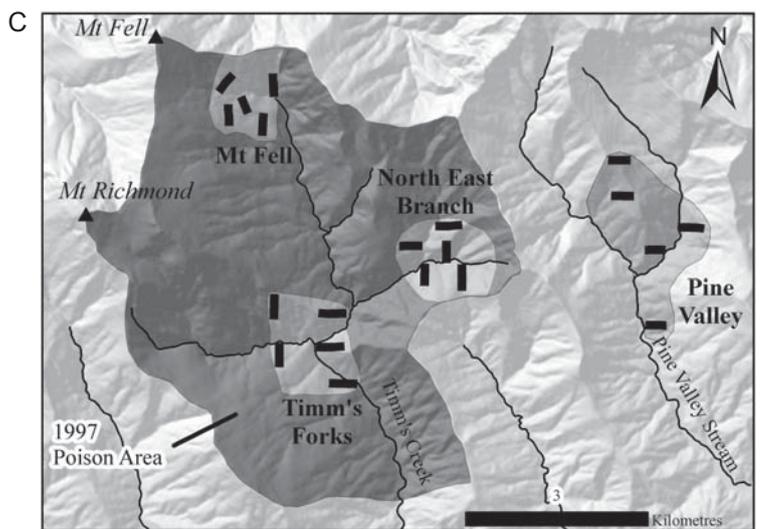
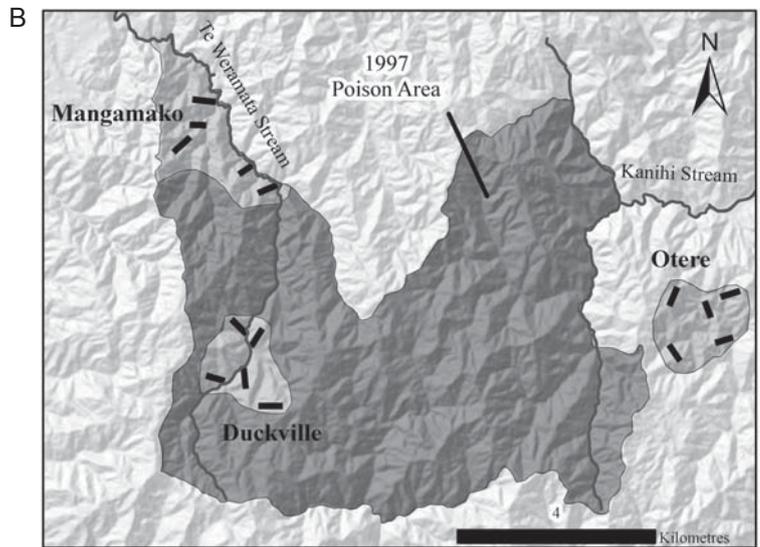
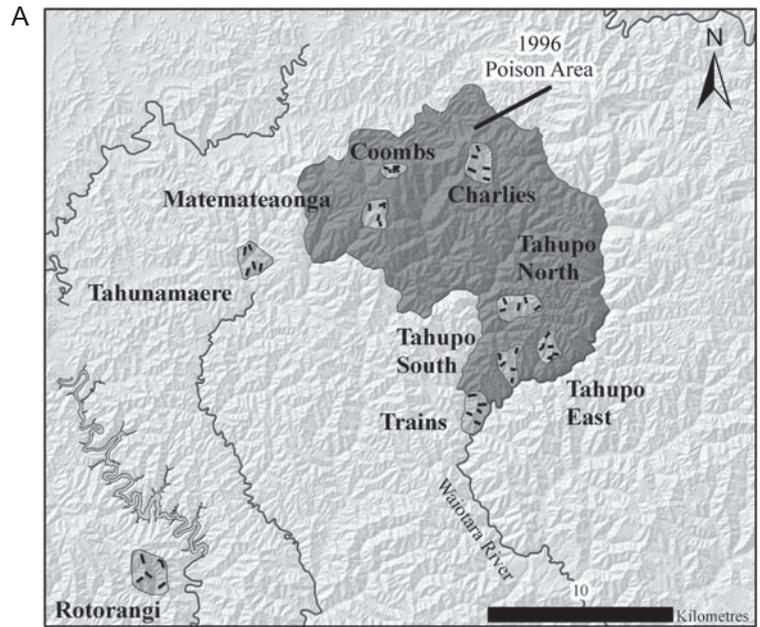
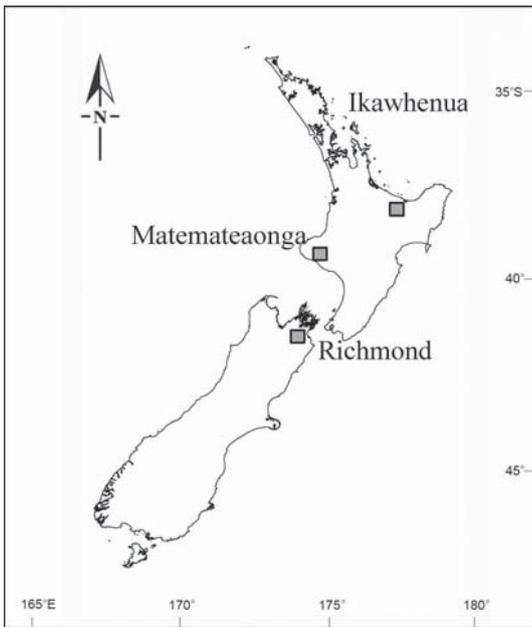


Figure 1. Location of study sites (medium grey) within study areas (light grey), showing locations of traplines and vegetation transects, and the boundaries of the various poisoning operations (dark grey) for A. Matemateaonga Range, B. Ikawhenua Range and C. Richmond Range.

areas, with sites (from north to south) assigned the following names: Charlies (CHA), Coombs (CMB), Matemateaonga Trig (MMO), Tahupo North (THN), Tahupo East (THE), Tahupo South (THS) and Trains (TRN). Two separate unpoisoned subcatchments to the south (Rotorangi; RTR) and southwest (Tahunamaere; THM) were monitored as experimental controls, and a limited amount of data were also gathered in the latter part of the study from a third unpoisoned area, Waitotara (WAI; not shown in Fig. 1A), immediately adjacent to the southern end of the poisoned area.

The Matemateaonga Range comprises soft mudstone (papa) hill country characterised by narrow gorges and ridges, with some flatter ridges to the north. The forest is predominantly mixed broadleaved-conifer forest with tawa (*Beilschmiedia tawa*) or kāmahi forming the main canopy. Kāmahi and northern rātā dominate the ridges, particularly towards the north. Black beech (*Nothofagus solandri* var. *solandri*) occurs on sandstone ridges to the south (Nicholls 1956; Wardle 1991). In the mid-1990s there was a north-south gradient in forest health, with major patches of canopy collapse (presumed by local managers to be possum-induced) in kāmahi-dominated stands in the northern part of the treatment area, but a largely intact canopy in the south. The possum control operation was intended to halt further canopy collapse. Possums were liberated at Wanganui as early as 1868 (Pracy 1974), but it is not known exactly when they first reached the Matemateaonga area. Goats (*Capra hircus*) and feral pigs (*Sus scrofa*) are common throughout the area, and the goats have severely depleted the understorey (Blaschke 1988). Red deer (*Cervus elaphus scoticus*) occur in small numbers at the northern end of the study area.

3.1.2 Ikawhenua Range

The former East Coast/Hawke's Bay Conservancy completed a 6000-ha poison operation in the middle of the Ikawhenua Range, Urewera National Park, in October 1997 (Fig. 1B). The two poisoned sites in this area were Mangamako (MKO) and Duckville (DVL), while the unpoisoned site, Otere (OTR), was located immediately east of the poisoned area.

The Ikawhenua Range is moderately steep hill country, with a largely intact mixed conifer-hardwood-beech forest. Tawa and kāmahi dominate much of the canopy, with rewarewa (*Knightia excelsa*) and hinau (*Elaeocarpus dentatus*) often also present. Northern rātā and rimu (*Dacrydium cupressinum*) are the most common emergents. Red beech (*Nothofagus fusca*) occurs as a canopy dominant on steeper spurs and at higher altitudes (Wardle 1984). Possums were first liberated at Lake Waikaremoana in 1898, and some subsequent liberations were made nearby (Pracy 1974). Red and rusa (*Cervus timorensis*) deer and pigs are present.

3.1.3 Richmond Range

The Nelson/Marlborough Conservancy completed a 2500-ha poison operation in the Timms Creek catchment in Richmond Forest Park in April 1997 (Fig. 1C). This area was selected for control as some possum-preferred species that were widespread as minor elements of this beech-dominated forest were showing evidence of possum impact and localised dieback. The three poisoned sites in this area were designated as Timms Forks (FRK), Mt Fell (MFL) and North East Branch (NEB). Pine Valley (PVA), the catchment immediately northeast of Timms Creek, was chosen as the unpoisoned site.

The Richmond Range has a complex geology, with the study area comprising Marlborough schist. Beech dominates the canopy, with hard (*Nothofagus truncata*) and red beech at lower altitudes intergrading into silver (*N. menziesii*) and finally mountain (*N. cliffortioides*) beech at the treeline (Wardle 1984). Possum-palatable species, including kāmahi, Hall’s tōtara, wineberry (*Aristotelia serrata*), haumakaroa (*Raukawa simplex*), māhoe (*Melicytus ramifloris*), lancewood (*Pseudopanax crassifolius*) and red flowering mistletoe (*Peraxilla tetrapetala*), occur occasionally in the canopy and/or commonly in the understorey. Southern rātā (*Metrosideros umbellata*) is present in small patches on steep rocky sites. Possums were not liberated in the Marlborough region until the late 1920s (Pracy 1974). Red deer occur throughout the Richmond Range, and pigs and goats are also present in low numbers.

3.2 TRAP CATCH INDEX OF POSSUM ABUNDANCE

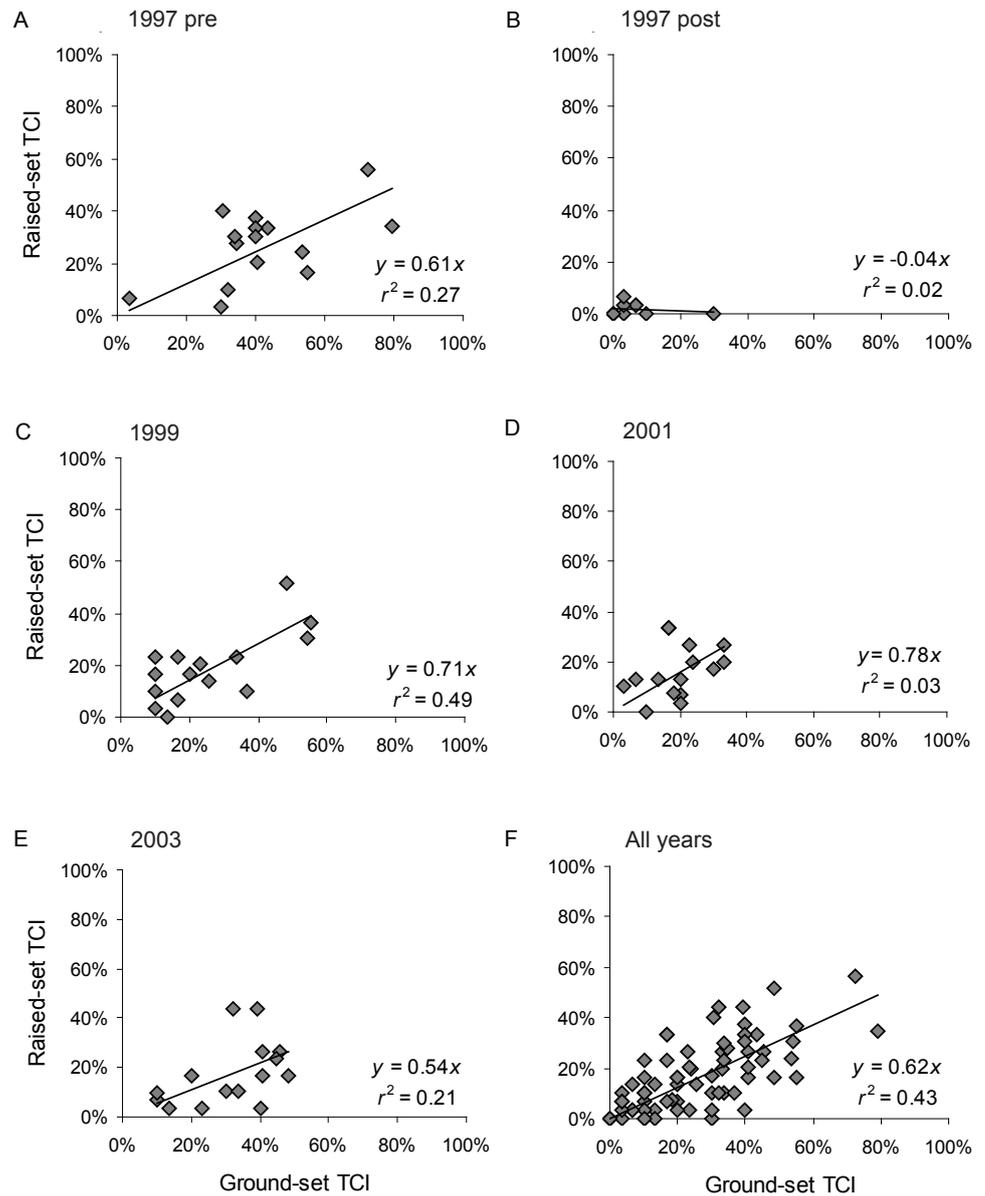
Along each of the five transects within each site, 20 Victor No. 1 traps were set 20 m apart for three fine nights where possible. Traps were set on raised platforms or boards 0.5–0.7 m above ground level to avoid catching ground birds. During all surveys except the first Matemateaonga survey (when heavy leaning-board raised sets were used), the raised sets used were ‘Scott Boards’, which comprised squares of plywood (15 × 18 cm) with routed holes designed to allow the trap to sit securely on top of the board when it was wedged between three nails hammered into a tree at the desired height. To minimise accidental capture of other small mammals or birds, traps were set so that reasonably heavy pressure was required to trip them.

For the Ikawhenua Range, conservancy staff required an estimate of trap-catch rates for ground-based traps so that the data from our study could be compared with TCI data from other nearby areas in which similar operations were being undertaken. To accommodate this management requirement, a comparison of catch rates using ground- and raised-set (Scott Board) traps was made by alternating five ground and five raised sets along each transect.

In each of the five assessments of trap catch in the Ikawhenua Range, fewer possums were caught overall on the raised sets than on ground sets (Fig. 2). There was considerable variability in the slope of the trend line, mainly reflecting very low catch rates for raised sets in late 1997, immediately after control (Fig. 2B): only five (21%) of the 24 possums captured in that survey were caught on raised sets. For the other four surveys, raised-set TCIs were 54–78% of ground-set TCIs, with an average of 62% for all five surveys combined (Fig. 2F). The slope of the regression forced through the origin was significantly different from 1, showing that catch rates were not equal ($t = 9.63$, $df = 69$, $P < 0.001$). Therefore, the equation $TCI_{\text{raised}} = 0.62 \times TCI_{\text{ground}}$ was subsequently used to adjust the trap-catch estimates for the ten ground sets on each line, so that these data could be combined with those from the raised sets. The adjusted Ikawhenua trap-catch data are treated as being directly comparable with the raised-set TCIs of the other two areas.

In the Matemateaonga Range area, surveys were initiated in 1996, with pre-control trapping in February–May, the poison operation in June, and the immediate post-control trapping in July. In the Richmond Range area, surveys were initiated

Figure 2. Correlations between trap catch indices (TCIs) recorded over 3 nights using alternating ground- and raised-set traps along 20-trap traplines in the Ikawhenua study area, for surveys carried out pre-control in 1997 (A), and post-control in 1997 (B), 1999 (C), 2001 (D) and 2003 (E), and for all five surveys combined (F). The trend lines have been forced through the origin.



in early 1997, with pre-control trapping in February, the poison operation in June, and post-control trapping in July. The Ikawhenua Range surveys were also initiated in 1997, with pre-control trapping in March–April 1997, the poison operation in October and post-control trapping in December. All subsequent resurveys were completed in March–May of 1998, 2000, 2002 and 2004 in the Matemateaonga Range, and 1999, 2001 and 2003 in the Richmond and Ikawhenua Range areas.

In the first Matemateaonga survey, separate pre- and post-poison trap lines were used to assess kill, and all possums captured before control were killed. The post-control trap lines were used as the vegetation transects. For the other two areas, we used only a single set of trap lines, but captured possums were marked with a temporary marker or ear tag and released unless they were seriously injured, in which case they were killed. The same mark-and-release approach was used in the subsequent reassessments in the Matemateaonga Range. The mark-and-release approach was adopted after it became apparent that there was wide variation in possum densities even within sites. By using this method, we

could use the same trap lines for all surveys, thereby reducing trapline location as a source of random error. In contrast, killing of captured possums would have affected subsequent assessment of possum abundance on the trapline and therefore would have required a new set of independent trap lines for each resurvey, adding another source of variability.

Very few marked possums were recaptured during the same trapping session, but those that were recaptured were treated as non-target captures for the purpose of analysis. Not many of the trapping sessions were completed in three successive fine nights, and in some instances extended poor weather meant only two nights' data were obtained. To overcome this inconsistency in the data, all TCI data in this report are based on the data from the first two fully fine nights. For the subset of 141 trap lines for which data from three successive fine nights were available, there was little difference between the 1-night, 2-night and 3-night indices ($17.9 \pm 1.2\%$ (SE), $18.7 \pm 1.3\%$, and $19.0 \pm 1.2\%$, respectively).

Evidence of seasonal variation in trap catch estimates (Nugent et al. 1997) prompted us to undertake further trapping in the Matemateaonga Range in August and December 1998, and in May 1999, in the two non-treatment blocks (Tahunamaere and Rotorangi) and two of the treatment blocks (Tahupo North and Tahupo East). This was to determine whether the apparent seasonal variation in trappability observed at high densities in this and other studies was real (and therefore provided some explanation for unexpected patterns in our data), and to assess whether there was also substantial seasonal variation in TCI at low possum densities. As a few possums injured during this additional trapping were killed, it will have had a small effect on our estimates of rates of increase for these sites over the first 2 years, but that bias will have been swamped by the large 'post-control' bias we identified in the first-2-year estimates for all sites (see results). The measurements of possum abundance and tree condition recorded during the first biennial resurvey of these sites will have reflected the actual number of possums that remained, so would be minimally biased in relation to the interaction between these variables.

3.3 POSSUM IMPACTS ON INDICATOR TREE SPECIES

Canopy condition and levels of possum browse were recorded for at least seven common tree species at each site during each biennial survey. The species chosen for monitoring at each site were mainly those designated as 'indicator species' known to be palatable to possums (see Appendix 1), but also included one largely unpalatable species at each site (pigeonwood (*Hedycarya arborea*) for North Island sites, and silver beech for South Island sites), as is standard for the FBI method (Payton et al. 1999). The unpalatable species were scored to allow some assessment of the variability in the FBI data that was independent of direct possum impacts or that resulted from differences between observers.

At every second trap site along the possum trap lines, 'scoreable' individuals of the chosen species (i.e. those whose canopies could be sufficiently distinguished from those of neighbouring or overhanging trees) were located and marked during the first survey. All subsequent reassessments then focused on this subset of marked trees. For the more common indicator species (e.g. tawa, kāmahi, pigeonwood, silver beech and māhoe), only the one or two scoreable trees

closest to the plot centre were scored at each plot, but for rarer indicators (e.g. northern and southern rātā, toro (*Myrsine salicina*), wineberry, Hall's tōtara and heketara (*Olearia rani*)), up to six trees within a 20-m radius of the plot centre were scored. For those rarer species, additional transects were also established to increase sample sizes to approximately 50 individuals of each species wherever possible. These additional transects were usually extensions of the main transects, but they were directed at readily re-locatable areas where the rare species could be found.

For each marked tree, we measured the percentage foliage cover index (FCI; in ten 10% classes from 5–95%), and the percentages (in five classes: 0%, 1–25%, 26–50%, 51–75%, >75%) of the whole canopy with dieback and with current season's possum browse (or hedging in the case of Hall's tōtara), as per Payton et al. (1999). Trees found dead in the resurveys were assigned a 0% canopy score in the field, and the numbers of such trees were used to assess rates of tree mortality during the study.

From 1998 onward, the 1–25% browse class was divided into two classes (1–5% and 6–25%), but this information was pooled when calculating mean browse scores to make those data fully comparable with the 1996–1997 data. Mean browse scores were calculated by taking the midpoint of the class range.

After the first two surveys (when only a single observer scored each tree), two observers were used to score all trees from the same position at the base of the tree, in an effort to reduce the effect of variation between observers. The score from each observer was recorded and averaged later, but inevitably there was occasional reassessment of scores when the pair of observers realised that their FCI scores differed by more than one 10% FCI class. Inspection of the frequency distributions of FCI scores indicated that this tended to reduce the FCI score for trees with very high cover but had little equivalent effect on below-average scores, because zero scores were possible, whereas scores >95% were not.

3.4 FOREST COMPOSITION AND FRUITFALL

3.4.1 Forest composition

Forest composition within each site was assessed by measuring species presence and canopy cover scores using a modification of the 'RECCE' method outlined by Allen (1993). Plots of approximately 10-m radius were located at every second trap site along the five pre-control trap lines, beginning at the second site of each line, so that there were ten assessments per trapline. The plant species present on these plots were assigned one of six cover scores (<1%, 1–5%, 5–25%, 25–50%, 50–75%, >75% of the plot area) in each of seven tiers (0–0.3, 0.3–2.0, 2.0–5.0, 5.0–12.0, 12.0–20.0 m above ground, emergent, and epiphyte). Approximately 20–30% of the RECCE plots were surveyed during each of the surveys, with the order and year in which plots were surveyed being dictated by the effect of weather on the amount of time and field effort required for the trapping and browse/FCI scoring that was being conducted at the same time. To save time, species that occurred mainly in the ground tier (<30 cm) and covered less than 1% of the plot were not recorded. Cover scores were summed by species and divided by the total all-species cover score to provide an index of relative abundance as a measure of availability to possums.

3.4.2 Fruitfall

To assess whether possum control had a major effect on fruit production, we monitored fruitfall under several species with moderate or large fruits that are known or believed to be eaten by possums. These included tawa, one or other of the *Elaeocarpus* spp. (hīnau or pōkākā *E. bookerianus*), pigeonwood, and māhoe. We placed litterfall traps made of a circular wire hoop supporting a shade-cloth funnel about 1 m off the ground and with a catching area of about 0.28 m² under six large specimens of each of the selected species along two or three of the accessible trap lines at eight of the sites. Half of the sites were poisoned (Tahupo East and Tahupo North in the Matemateaonga Range, Mangamako in the Ikawhenua Range, and Forks in the Richmond Range), while the remainder were the unpoisoned sites in each area. We endeavoured to collect material quarterly, with traps established at the time of the first survey. The collected material was sorted by species, dried to constant weight and weighed.

3.5 ANALYSIS AND MODEL FITTING

For each trapline, TCIs were calculated by deducting a half trap night for each sprung trap and for each non-target species caught. Sprung traps with possum fur (i.e. escapes) were treated as possum captures. To estimate rates of increase, TCIs were expressed as a proportion (f) of the trap nights with captures and, following Caughley (1977), the Poisson transformation $-\ln(1 - f)$ was then used to reduce the effect of trap saturation on the non-linearity of the relationship between trap catch data and actual possum density shown by Forsyth et al. (2005). The exponential rate of increase (r) was then calculated from $\ln(n_t/n_0)/t$, where n_0 and n_t values are the transformed TCIs recorded at the beginning and end, respectively, for the period t in years (Caughley 1977).

Browse pressure was expressed in several ways. Mean browse scores were calculated by taking the midpoint of class ranges. The resulting means are likely to be biased high, as within the lowest browse class (1–25% of leaves browsed), 57% of the 2321 observations in the post-control surveys indicated browse on less than 5% of leaves. Therefore, for some analyses browse pressure is represented simply as the percentage of trees browsed, while in other analyses browse is scored as present or absent, or as absent, light (< 25%) or heavy (> 25%).

Foliar cover was expressed in both absolute and relative terms. In absolute terms, the FCI score is used as a simple continuous variable. In relative terms, the mean FCI for browsed trees is expressed as a proportion of the mean FCI for an equivalent group of unbrowsed trees, to filter out some of the variability not related to possum browsing. This adjusted FCI was derived by calculating the mean FCI for each site for all of the unbrowsed main indicators, both across all surveys and separately for each survey (year), and then subtracting the difference between the overall mean and the mean for a particular year from all FCIs (browsed and unbrowsed) recorded that year. The browsed/unbrowsed classification is based on whether or not possum browse was recorded on a tree at any time during the study.

Tree mortality was expressed either in terms of the total number or percentage of trees that died during the study or, for biennial assessment periods, as simple finite annual rates.

The dry weight of fruit collected for each species was expressed as annual totals per trap, to overcome variability in the timing of seasonal collections.

The study was primarily designed as an observational study, rather than a hypothesis-testing one. We therefore rely mainly on simple summary statistics and standard tests of association, particularly linear correlation and/or regression for continuous data, and contingency tables for categorical data. However, to assess how possum control affected foliar cover and tree mortality, an Information-Theoretic model selection approach (Burnham & Anderson 2002) was used to compare the fit of a large number of competing models. This model-fitting approach uses the Akaike Information Criterion (AIC) to identify the most parsimonious models that are best supported by the data available.

To assess how possum abundance (as indexed by TCI) affected the scale and direction of change in foliar cover, the following logic was used to develop a model of the underlying process. The change in FCI (F) between time t and $t+\delta t$ was defined as:

$$\frac{dF}{dt} = \frac{\log(F_{t+\delta t}) - \log(F_t)}{\delta t} \quad \text{Equation 1}$$

The rate of change of FCI is assumed to depend on closeness to the ‘equilibrium’ FCI for that species (i.e. trees with FCI well below or well above the overall mean FCI will tend to increase or decrease, respectively, whereas those near the mean FCI will change little or not at all), as follows:

$$\frac{dF}{dt} = a + b \log(F) = r \log\left(\frac{F_K}{F}\right) \quad \text{Equation 2}$$

where a is a constant, $r = -b$, which is the intrinsic ability of the tree to recover foliage cover, and $F_K = \exp(-a/b)$, which is the equilibrium FCI.

The rate of change of FCI (for given values of F and F_K) was assumed to decrease as foliage consumption increased as a result of increasing possum abundance. However, there is heterogeneity in browse, and some trees are never browsed while others are browsed heavily. A linear model for rate of change of foliar cover index from time t to time $t+\delta t$ is therefore:

$$\frac{dF}{dt} = a_i + b \log(F) + c_i P + \varepsilon \quad \text{Equation 3}$$

where $i = 0,1$ representing whether the tree was never recorded as browsed during the study (0) or was browsed on at least one occasion (1); F is FCI at time t ; and P is the index used for possum abundance. Normal, random variation is represented by ε .

The most complex model fitted had a random effects structure that included trap line nested within site within area within year within species, affecting both the intercept of dF/dt and slope with respect to P . The random error structure accounted for species differences in foliage growth and rate of consumption by possums, which varied between years, and were subject to observer error and between- and within-site differences in each area and in different years.

Models were fitted using *lmer* from the *arm* package in R 2.9 (Gelman et al. 2009; R Development Core Team, 2009) for randomly varying intercept only, slope only and both. Because the relationship between possum density and TCI

is non-linear and potentially highly variable above TCI = 40% (Forsyth et al. 2005; Ramsey et al. 2005), TCI data were Poisson-transformed, and models used both absolute and relative measures of possum abundance. In total, five measures of possum abundance were used: actual TCI at time t (TCI), transformed TCI at time t (TCItrans), average TCI calculated from times t and $t+\delta t$ (AvTCI), closeness to maximum recorded TCI (%MaxTCI; used as an approximation indicating closeness to local carrying capacity) and average closeness to maximum recorded TCI (Av%MaxTCI; calculated from times t and $t+\delta t$).

The FCI model was also tested to see if the rate of change of FCI was sensitive to treatment (poisoned or unpoisoned). Biologically, poisoning should only affect possum abundance and not the intrinsic ability of the tree to recover foliage, so this was implemented via the parameter c_{ij} , where $j = 0,1$ indicating whether the site was poisoned (1) or not (0) and i is as before.

Finally, the FCI model was extended to include a fixed effect of species on foliage recovery rate, i.e. $b = b_s$ for each species s , was fitted to ascertain if explicitly different intrinsic recovery rates for different species was either important or supported by the data.

A similar model-selection approach and methodology was used to determine the relative importance of the major factors affecting tree mortality. Discrete-time failure-analysis models were fitted to a subset of the data. To reduce analytical complexity, trees added to the study after the first surveys were excluded. Likewise, species not recorded in both treatment and control blocks (mistletoe, fuchsia, haumakaroa and southern rātā) were excluded, as were those with a sample size of less than 100 (hīnau), those on which little or no browse was recorded (pōkākā, silver beech and pigeonwood), and any records for which not all the explanatory variables were recorded.

These models used the proportion of trees recorded as dead (FCI = 0) during each resurvey as a measure of the probability that a tree would fail (die) in any particular biennial period during the study. Initial models were developed to determine whether species, location (area, site and trapline) and initial FCI (the FCI recorded in the first survey, when all trees were alive) were important random effects on this probability. Models were fitted with a complementary log-log link function.

Using the best fitting of these initial models as a base, further models were constructed to determine the effect of treatment (i.e. possum control). Tree diameter was also included in these models to determine whether responses varied with tree size. The effect of treatment (i.e. possum control) was represented in these models in several different ways, along with species \times treatment interactions. Firstly, treatment was represented simply as a binary variable reflecting whether or not the site had been poisoned. In a set of alternative models, a cumulative measure of possum browse (the total browse score summed across surveys) was used to more directly and proximately represent the possum effect.

A final set of models was constructed using the TCI collected immediately after control (PostTCI) as the treatment effect. This analysis excluded the trees on supplementary lines because no trap catch data were collected on those lines.

4. Results

4.1 FACTORS AFFECTING POSSUM CATCH ESTIMATES

Results from this and other concurrent studies identified a series of methodological issues that potentially may have affected the accuracy of possum trap catch estimates. Therefore, those issues are dealt with before the main results (section 4.2 onward).

4.1.1 Seasonal variation and possum shyness

Four Matemateaonga blocks were monitored three times over an 8-month period (May, August and December) in 1998 to assess seasonal variation in trap-catch rate. The 2-night trap-catch rates for these blocks varied significantly between seasons ($F = 9.7$, $df = 2, 36$, $P < 0.001$), with a significant interaction between treatment and season ($F = 8.7$, $df = 2, 36$, $P < 0.001$). For the two unpoisoned blocks with high possum density (Tahunamaere and Rotorangi), the TCIs were about one-third lower in winter than in early summer or autumn. For the two low-density poisoned blocks, there was no evidence of seasonal variation that might have affected comparability of the first post-control estimates from trapping conducted at various times between July and December with subsequent estimates, which were all collected in autumn.

The 'mark-and-release' of possums appeared to result in short-term trap shyness in captured possums, as $< 1\%$ of the possums released on the first or second nights of a trapping session were recaptured later in that same session. There was weak evidence that some of this wariness may have persisted for at least several months, as in the two Tahupo blocks surveyed three times during 1998-1999, the TCI recorded in December 1998 on the set of trap lines used throughout this study was c. 20% lower than that recorded on a different set of trap lines surveyed in autumn 1999. However, we consider that any residual long-term effect will have been minor because only a small proportion of the population will have been trapped during any one survey.

During the biennial resurveys, an average of 16% of captured possums intended for release (287 of a sample of 1745 post-control captures for which the fate of trapped animals was recorded) were killed because they had injuries considered unlikely to heal. This is likely to have slightly reduced possum usage of the trap lines relative to areas away from the trapline in both poisoned and unpoisoned areas. However, the population effect will have been small, as only about a quarter of possums using a trapline are captured over three nights of trapping (GN, unpubl. data), suggesting only 4% would have been killed—small relative to many of the observed rates of increase (see below). Further, the immigration of possums would have diluted this even further.

4.1.2 Post-control bias in TCI

Over the first 18–22 months after control, the apparent exponential rate of increase for the 12 poisoned blocks averaged 0.917 ± 0.086 (range 0.29–1.44). This equates to a 2.5-fold increase in possum numbers annually, which is well beyond the reproductive capabilities of possums, even in the unlikely event that all females were able to produce two young each year.

Some of the high rate of increase can be explained by immigration, particularly at the Matemateaonga site where the two southernmost blocks, Trains and Tahupo South, were contiguous with unpoisoned areas during 1996–1997, and possums remained uncontrolled in the area west of the Trains site for the whole of the study. In other Matemateaonga areas, the sites were all at least 1 km inside the boundary of the poisoned area. When the TCIs for individual trap lines in the Matemateaonga surveys were plotted against distance to the nearest uncontrolled population, there was no correlation between TCI and distance to an uncontrolled source immediately after control ($r^2 = 0.006$, $df = 33$, $P = 0.65$) (Fig. 3A). However, by autumn 1998, the TCIs on all but one of the trap lines within 1 km of an uncontrolled possum population were above the average for the remainder. Further away from the boundary, however, there was again no relationship between distance and TCI ($r^2 < 0.001$) (Fig. 3B). Therefore, an immigration effect did not explain the impossibly high rates of reproductive increase recorded in blocks well away from an uncontrolled source. This indicated a bias in possum trappability, with the TCIs recorded in the first surveys conducted 1–2 months after poisoning underestimating the TCI that would be obtained from an undisturbed population at that density. The rates of subsequent increase using these data as the starting point will therefore be biased high.

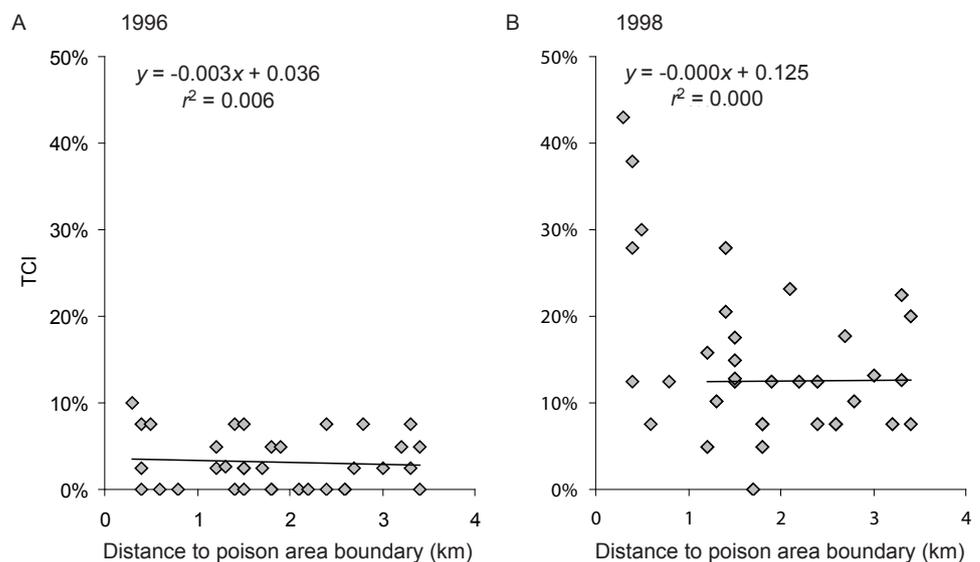


Figure 3. Relationship between trap catch index (TCI) for individual traplines in the Matemateaonga Ranges and the distance from the trapline to the nearest uncontrolled possum for A. the trapping conducted immediately following control (winter 1996), and B. 2 years later (autumn 1998). The trend line in B is fitted to only points more than 1 km from the boundary (i.e. traplines where it is considered reinvasion is unlikely to have greatly affected possum numbers).

4.2 PERCENT KILL AND POSSUM POPULATION RECOVERY

4.2.1 Percent kill

The 1996 and 1997 poison operations reduced the raised-set 2-night TCIs (hereafter simply referred to as TCI) in the poisoned sites by 75–100%, with the overall apparent average reduction for each of the three areas being between 89% and 96% (Appendix 2). By the standards at that time, these were deemed to be moderately successful operations. The highest post-control TCIs for individual trap lines were recorded at the two Ikawhenua sites. For that operation, the helicopter sowing bait was not permitted to sow bait within 150 m of major streams, so possums with range centres close to such streams are likely to have had poisoned baits in only parts of their ranges and therefore had a higher probability of survival.

4.2.2 Possum population recovery

At all sites, the TCIs increased rapidly following possum control, and returned to close to pre-control levels within 6 years (Appendix 2, Fig. 4). The bias in post-control TCIs identified above (section 4.1.2) precludes interpretation of the rate of change in TCI in the period immediately after control as a direct measure of the rate of increase of possums, but we assume that the TCIs for the surveys 2–8 years after control were unbiased.

Although the average TCIs for the poisoned sites within each area increased over each 2-year period after control for the first three remeasurements (Fig. 4), the exponential rate of possum increase generally declined over the 6- or 8-year periods, but with different patterns in each area (Fig. 5). In the Matemateaonga Range, there was a reasonably consistent pattern between sites, with the initial high increase in the first 2 years after control (1996–1998) followed by a smaller increase over the period 2–4 years after control (1999–2000; Fig. 5A). At two sites, TCI actually declined in the period 2–4 years after control (Appendix 2), with one of these declines caused by unscheduled

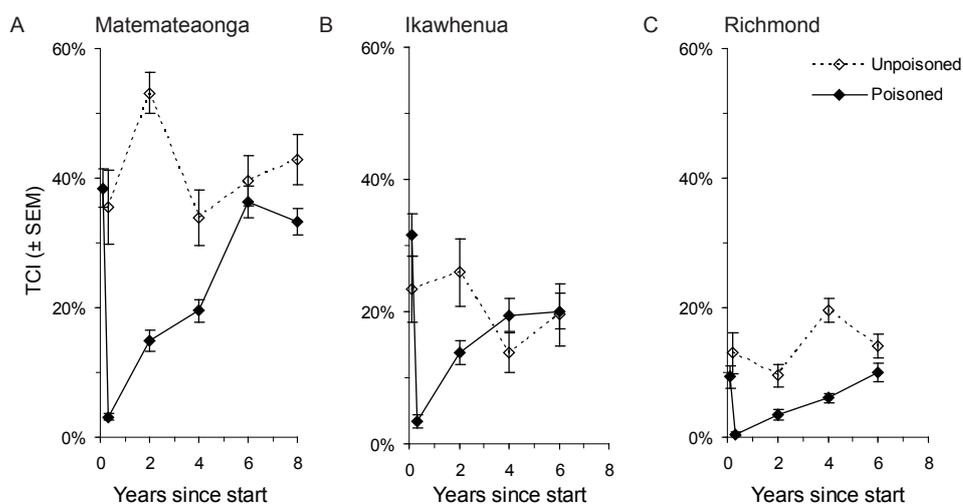


Figure 4. Changes in trap catch index (TCI) over 6 or 8 years following one-hit aerial poisoning for A. Matemateaonga Range, B. Ikawhenua Range and C. Richmond Range, for the poisoned and unpoisoned non-treatment sites within each area.

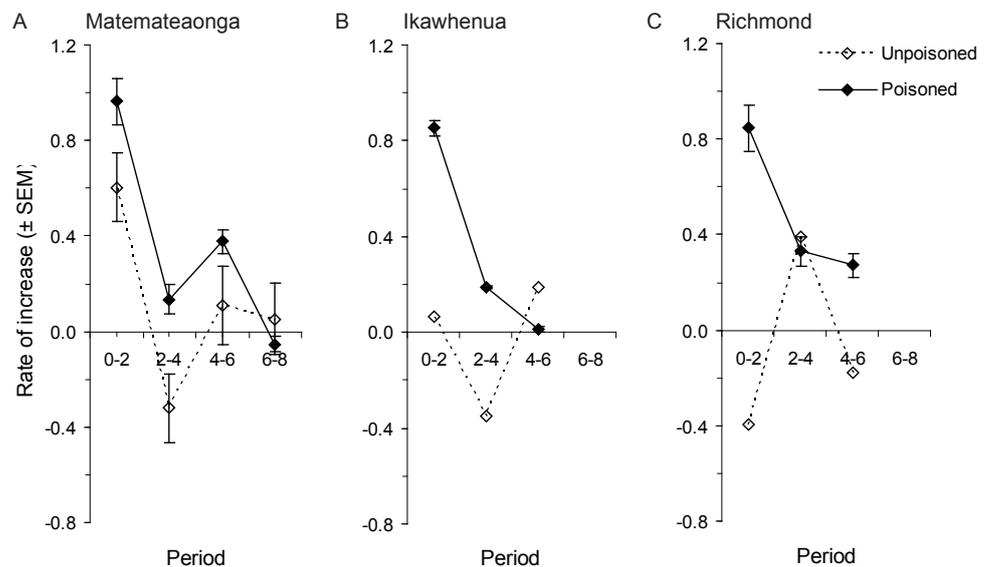


Figure 5. Mean exponential rate of annual increase in the transformed trap catch indices (TCIs) by area for each of the biennial periods after poisoning for A. Matemateaonga Range, B. Ikawhenua Range and C. Richmond Range. Data are the mean per site within each area, so no standard errors could be calculated for the unpoisoned areas in the Ikawhenua and Richmond Ranges where there was only a single site. The estimates for the period 0–2 years after the first survey reflect the increase between the immediate post-control TCIs and the values recorded 18–21 months later, but all other periods represent changes over two full years. The estimate for the unpoisoned Matemateaonga sites over the 0–2-year period is biased high because some traps in the first surveys were set too hard resulting in a low-biased TCI estimate.

trapping of possums on or near two of the trap lines at the Matemateaonga Trig (MMO) site. Excluding that site, the mean exponential rate of increase (r) for that period was 0.178 ± 0.055 . For the period 4–6 years after control (2000–2002), the mean r for the same six blocks was 0.386 ± 0.056 . Applying a one-tailed paired t -test (because we expected from theory a decline in the rate of increase as possum densities increased), there was weak evidence of an increase for the remaining six poisoned sites ($t = -1.69$, $df = 4$, $P = 0.07$). The TCIs for the two unpoisoned sites also increased substantially over this period after declining in the previous period. For the period 6–8 years after control (2002–2004), mean r for the seven poisoned sites was close to zero (-0.054 ± 0.030) as was also the case for both unpoisoned sites (Fig. 5A). This overall decline indicates that the population levels had reached or were above the short-term carrying capacity of those blocks in those years. The term ‘carrying capacity’ is used to refer loosely to the total amount of food and other resources needed by possums at their maximum sustainable level, and we assume that the highest TCI recorded during the study (usually the pre-control estimate) provides an approximate measure of possum abundance at carrying capacity.

In the Ikawhenua Range, the rate of increase in the two poisoned blocks also slowed during the period 2–4 years after control (1999–2001), and fell to zero 4–6 years after control (2001–2003) (Fig. 5B). There was no evidence of fur hunters using the blocks over the latter period, so the lack of increase again indicates that the populations were close to the current carrying capacity of these blocks for those years. In Otere (OTR), the non-treatment block, the presence of bait stations nailed to trees indicated that poisoning by fur hunters contributed to the reduced possum numbers during the 1999–2001 period, but by 2003 TCI was similar to initial levels once again.

In the Richmond Range, the rate of increase in TCI in the three poisoned blocks also slowed but remained positive during the period 2–4 years after control (1999–2001), and was also positive 4–6 years after control (2001–2003) (Fig. 5C). In contrast, the TCI in the unpoisoned block, Pine Valley, fell substantially during the first 2 years (1997–1999), then increased (1999–2001), and then declined again (2001–2003). The increase in the 1999–2001 period coincided with a beech masting event, which provided an abundance of beech seed, which possums eat when available (Sweetapple 2003).

Across all 12 poisoned sites, there was no correlation between the pre-control TCI and annual rate of increase for the first 4 years (Fig. 6A; General Linear Mixed Effects (GLME) model, slope = 0.05, $t = 0.90$, $df = 8$, $P = 0.39$), or the period 2–6 years after control (i.e. outside the period affected by post-control bias in TCI) (Fig. 6B; GLME model slope = -0.04, $t = 0.16$, $df = 8$, $P = 0.87$), or over any other period. This indicates that the rates of increase immediately after control were independent of the quality of the possum habitat at the site, at least as indexed by the pre-control TCI for the site.

The TCIs recorded 2, 4 and 6 years after control were all significantly related to those recorded before control (GLME models, $t = 6.03, 4.53, 5.44$, respectively, $df = 8$, $P < 0.006$ for all three regressions; Fig. 7), with regression slopes of 0.35, 0.43 and 0.76, respectively. These slopes represent the average recovery toward pre-control levels across the three areas; i.e. the populations had recovered to within 76% of pre-control levels with 6 years of control (for example).

Figure 6. Relationships between initial trap catch index (TCI) and the annual exponential rates of increase in TCI for the 12 poisoned blocks for the period
A. 0–4 years after control and
B. 2–6 years after control.

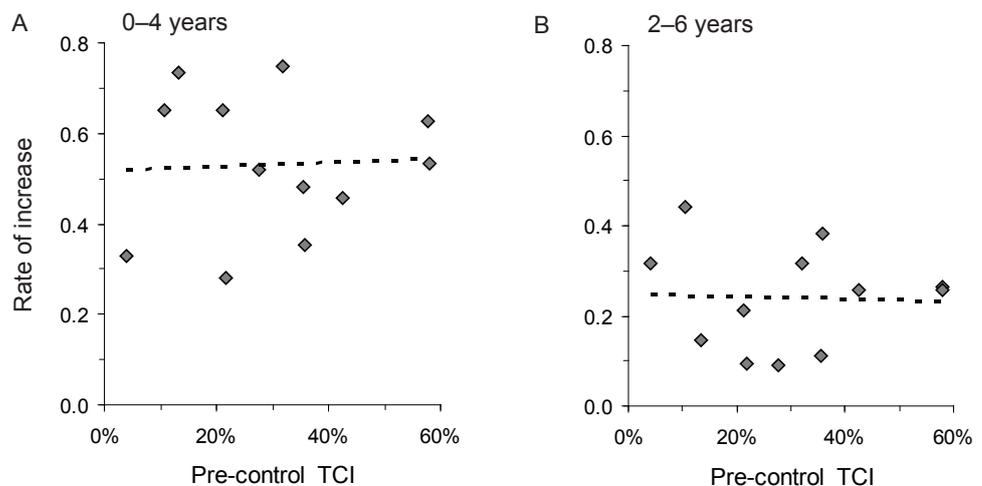
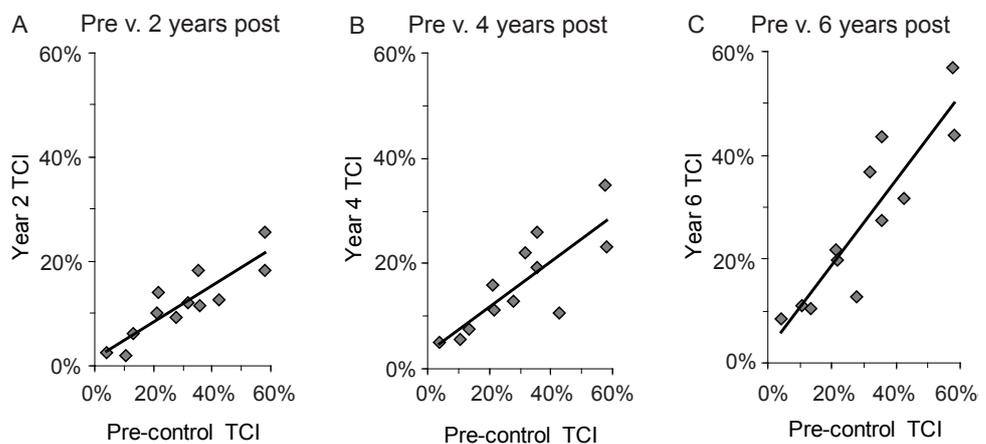


Figure 7. Relationships between initial trap catch index (TCI) and the TCI recorded A. 2 years after control, B. 4 years after control, and C. 6 years after control for all 12 poisoned blocks combined.



The TCIs in some non-treatment blocks differed between biennial surveys (repeated measures ANOVA: TAH $F = 3.97$, $df = 4, 16$, $P = 0.020$; ROT $F = 3.16$, $df = 3, 12$, $P = 0.007$; PVA $F = 3.16$, $df = 3, 12$, $P = 0.065$). Possum numbers seldom appeared to be stable, apparently either increasing relatively rapidly or declining equally rapidly.

4.3 CHANGES IN POSSUM BROWSE PRESSURE

In 1996–1997, possum browse was recorded on just under half of the indicator trees (i.e. all species excluding silver beech and pigeonwood; Appendix 3). There was no significant difference between poisoned and unpoisoned sites (Yates $\chi^2 = 2.14$, $df = 1$, $P = 0.14$; Table 1). In the poisoned areas, the percentage of trees browsed declined to 26% of pre-control levels over the first 2 years after control, then to 17% 4 years after control, before increasing again (Table 1). In the unpoisoned areas, much the same pattern occurred, but the size of the initial reduction was significantly smaller (log linear analysis, $G^2 = 27.8$, $P < 0.001$). Following control, the percentage of trees browsed in unpoisoned areas was always 1.5–2.0 times higher than in poisoned areas (log linear analysis, $G^2 = 163.3$, $P < 0.001$).

Browse pressure varied widely between species, both before and after control (Fig. 8; Appendix 3). The two species designated as unpalatable controls (silver beech and pigeonwood) were never or rarely browsed, and very little browse was ever recorded on hinau and pōkākā. There was also little evidence of browse on fuchsia (*Fuchsia excorticata*), suggesting it was not a highly favoured species at the single Richmond Range site where it was recorded, at least at the time of the survey. Hall’s tōtara was usually the most heavily browsed species, although browse on some minor species that occurred at only a few sites sometimes surpassed it. After control, the pre-eminence of Hall’s tōtara as the most heavily browsed species increased, with the area-specific mean for browse on Hall’s tōtara being almost always at least three times higher than on any other species that occurred in the same area. For the three most commonly abundant indicator trees—tawa, māhoe and kāmahī—browse levels were usually moderate before control and mostly very low afterward.

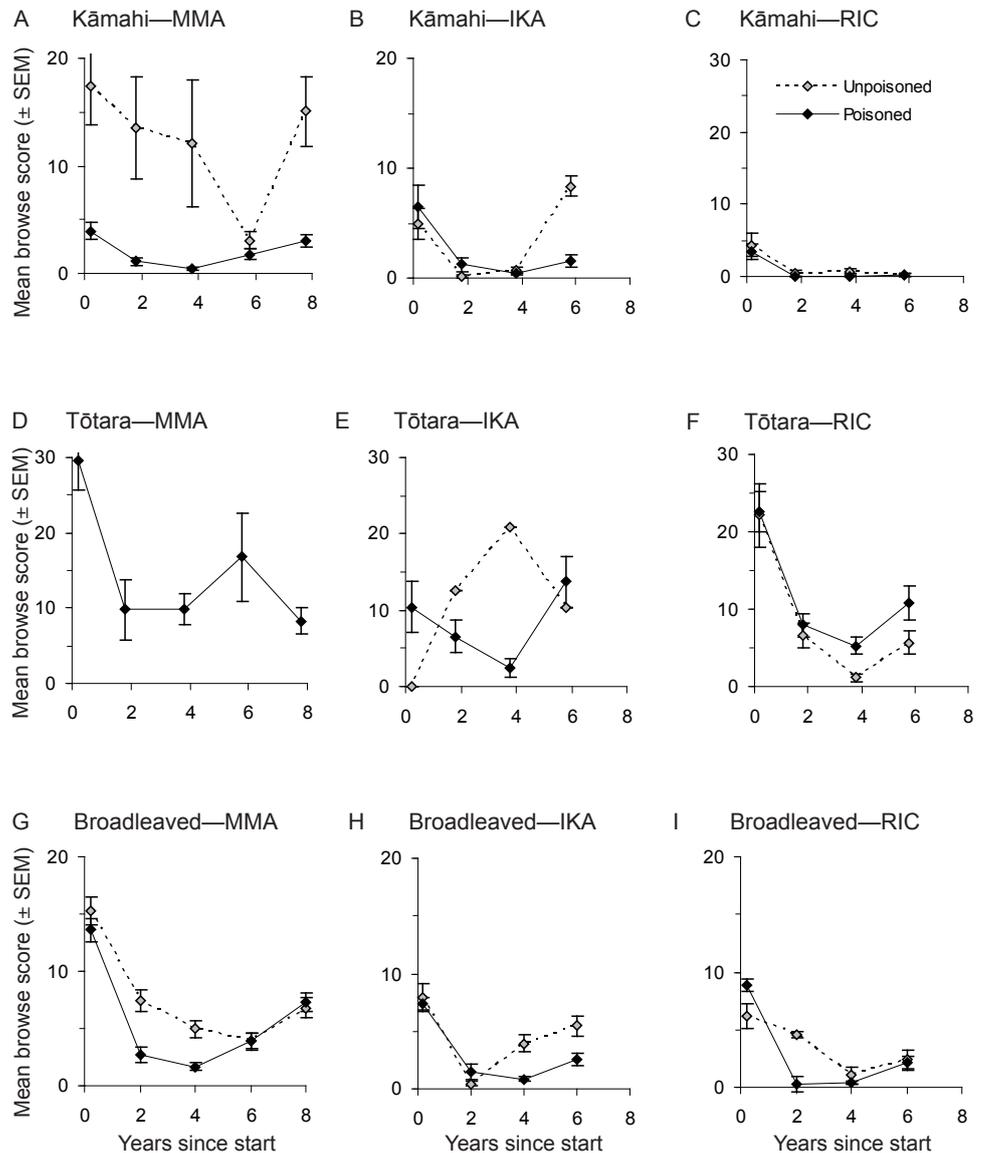
In general, the species most heavily browsed before control were also the most heavily browsed afterwards. However, there were some notable exceptions. Browse pressure on red mistletoe was higher after control than before. This species was monitored at only a single site, Mt Fell, and at that site the TCI

TABLE 1. CHANGES IN THE PERCENTAGE OF INDICATOR TREES (i.e. ALL SPECIES EXCLUDING SILVER BEECH *Notbofagus menziesii* AND PIGEONWOOD *Hedycarya arboreus*) BROWSED BY POSSUMS (*Trichosurus vulpecula*), BY TREATMENT.

Note: Data from Tahupo South in 1998 and from Waitotara are excluded because of observer error and incompleteness, respectively. Year 8 data (when only the Matemateaonga blocks were remeasured) are not included here. Sample size declined through time because some trees died.

YEARS SINCE CONTROL	UNPOISONED		POISONED	
	% BROWSED	<i>n</i>	% BROWSED	<i>n</i>
0	55.8	953	53.0	3619
2	24.7	827	13.6	3367
4	20.3	867	9.2	3355
6	31.4	844	19.2	3228

Figure 8. Mean % browse by area (MMA = Matemateaonga; IKA = Ikawhenua, RIC = Richmond) for kāmahi (*Weinmannia racemosa*) (A-C), Halls tōtara (*Podocarpus hallii*) (D-F) and all other possum-preferred broadleaved indicator species combined (G-I). Data are the repeated-measures averages per transect for all transects in which more than five trees of the species or species group was measured in each survey.



6 years after control was double the pre-control TCI. Therefore, the higher browse pressure may reflect higher possum numbers. In contrast, there was almost no browse recorded on haumakaroa and southern rātā after control, despite these species having moderate to high mean scores before control.

At the poisoned sites in the Matemateaonga Range, the mean browse score on kāmahi (Fig. 8A) and the other broadleaved indicators (Fig. 8G) fell to low levels and remained low for 4 years before increasing, whereas browse on Hall's tōtara did not fall as far (Fig. 8D). In the unpoisoned areas, browse levels also fell, but not as much, before again increasing (Fig. 8A, D & G). There was a marked difference between poisoned and unpoisoned blocks, with kāmahi being browsed heavily in the latter, but only lightly in the former (Fig. 8A).

In the Ikawhenua Range, browse at poisoned sites fell over the 2 years after control for all species, and then fell further over the next 2 years before increasing by the sixth year (Fig. 8B, E & H). In the unpoisoned area (Otere), browse on all species other than Hall's tōtara also fell to near zero 2 years after control, mostly remained low 4 years after control but then increased for some species (Fig. 8B, E, H). This initial decline in browse was not coincident with a decline in TCI.

Sites in the Richmond Range showed a similar pattern, with very little browse recorded on most species in the poisoned blocks 2 and 4 years after control, but with continued browse on Hall's tōtara and an increase in browse (mainly on red mistletoe and māhoe) after 6 years (Fig. 8C, F & I). Again, in the unpoisoned block (Pine Valley), little browse was evident on kāmahi over the 6 years after control (Fig. 8C), but there was some browse recorded on other species (mainly Hall's tōtara and wineberry) 2 and 6 years after control (Fig. 8F & I).

As possum numbers increased after control, the renewed browse tended to occur mainly on trees that were being browsed at the time of the pre-control survey. In the Matemateaonga Range, for example, two-thirds of broadleaved indicator trees that had initially been heavily browsed were again being browsed 8 years after control, compared with only 20% of those with no browse recorded at the time of the first survey ($\chi^2 = 162.8$, $P < 0.001$; Fig. 9A). The difference was initially less marked for Hall's tōtara (Fig. 9B), possibly reflecting technical problems in distinguishing low levels of current-year browse from the hedged appearance of some tōtara resulting from browse in previous years.

Taking account of the nesting of trap lines within sites within areas, linear mixed-effect models of the percentage of all of the indicator-species trees on each trapline indicated that at unpoisoned sites the TCI recorded on each trapline at the same time as the browse was recorded was not a significant predictor of browse levels (slope = 0.00, $t = 0.001$, $df = 261$, $P = 0.99$), and there was no improvement when TCI was expressed as a percentage of the maximum TCI recorded on a trapline in any of the surveys (slope = -0.12, $t = 0.86$, $df = 261$, $P = 0.38$). At the poisoned sites, however, browse levels were positively and additively (i.e. in a single model) related to TCI (slope = 0.23, $t = 2.14$, $df = 261$, $P = 0.033$) and even more strongly related to the closeness to maximum TCI (slope = 0.15, $t = 2.76$, $df = 261$, $P = 0.006$). These two variables accounted for only about 20% of the variation in the percentage of indicators browsed, mainly because when TCIs were high and/or close to maximum levels, browse levels could be either high or low. When TCIs were well below maximum levels, however, it was rare to record high browse levels on a trap line (Fig. 10).

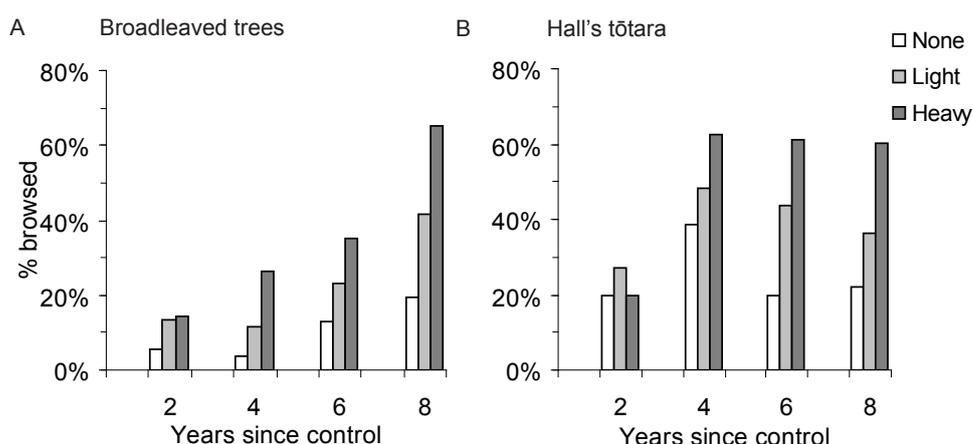
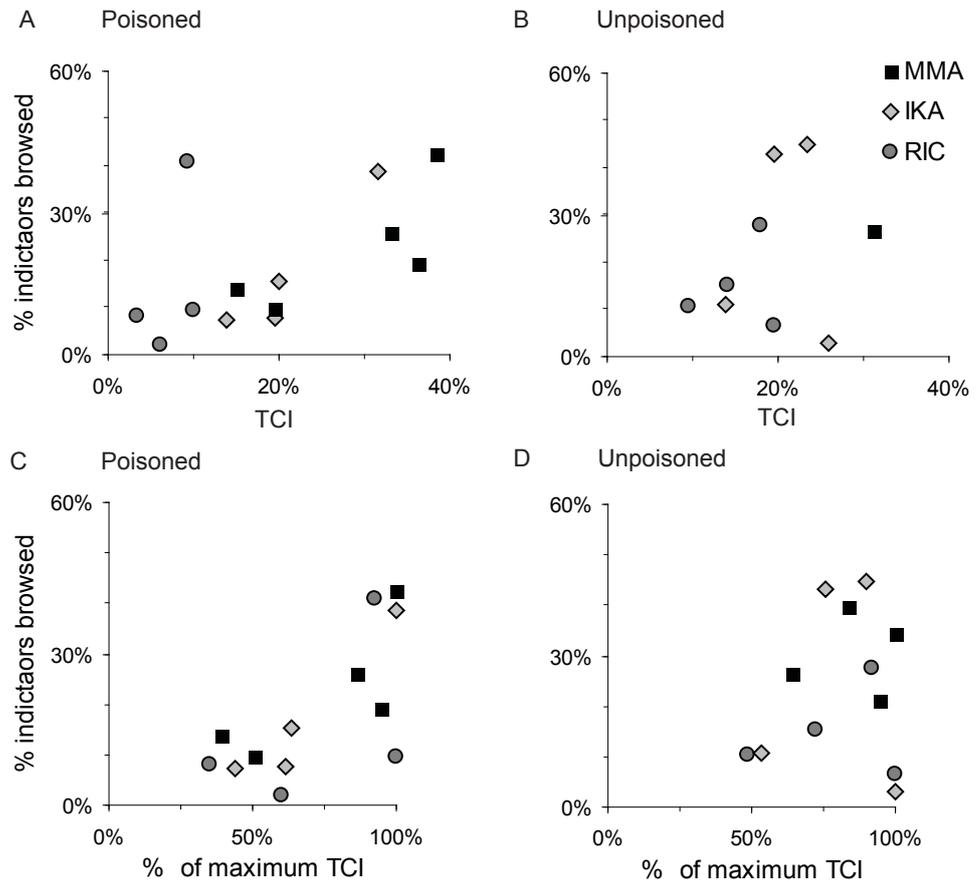


Figure 9. Percentage of A. the most common broadleaved indicator species, and B. Hall's tōtara (*Podocarpus ballii*) at the poisoned sites in the Matemateaonga Range that were recorded as browsed during each post-control survey in relation to their initial, pre-control browse score ('none' = 0% browse, 'light' = 1-25%, 'heavy' = >25%). The common broadleaved indicators are tawa (*Beilschmiedia tawa*), māhoe (*Melicytus ramifloris*), heketara (*Olearia rani*), toro (*Myrsine salicina*) and kāmahi (*Weinmannia racemosa*).

Figure 10. Relationship between trap catch index (TCI) and the percentage of all possum-preferred indicators that were browsed for each area and each remeasurement for poisoned (A and C) and unpoisoned (B and D) sites. In the upper graphs, TCI is expressed as the actual value while in the lower graphs it is presented as a % of the maximum recorded. The data are the averages of the site means, which in turn are the averages of the values for each trapline.
 MMA = Matemateonga Range, IKA = Ikawhenua Range and RIC = Richmond Range



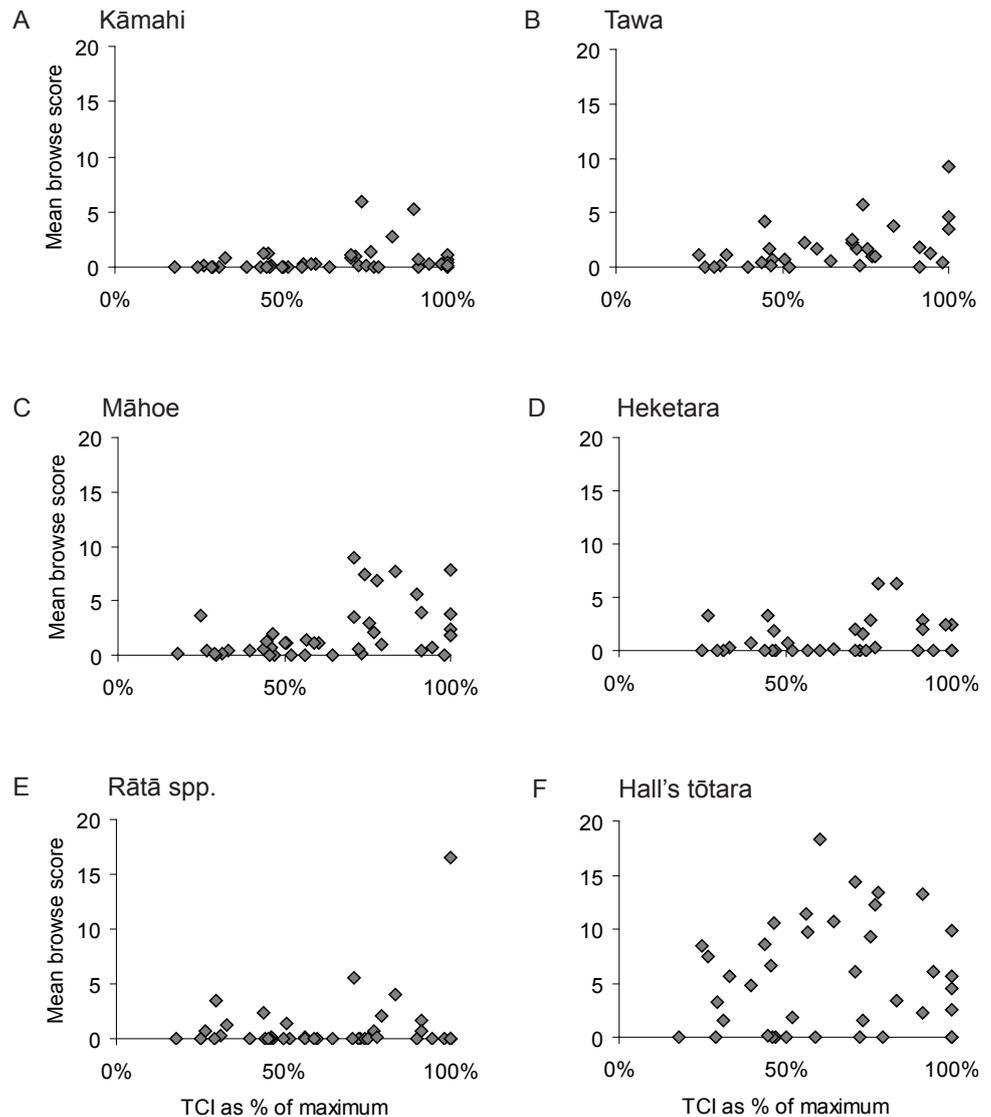
This pattern of wide variation in browse pressure relative to possum abundance, but with the heaviest browse occurring only when possums were near maximum levels, was consistent across all the common broadleaved indicator species. However, it was not apparent for Hall's tōtara, where high browse scores were sometimes recorded, even when TCIs were well below maximum levels (Fig. 11).

To test the hypothesis that closeness to maximum TCI determined the maximum level of browse that could occur, the whole-site TCIs from each survey (poisoned and unpoisoned) were ranked according to closeness to the maximum TCI, and the sample was arbitrarily split into eight equal-sized groups. The maximum mean browse score within each of these groups was closely correlated with closeness to the maximum TCI ($r = 0.88$, $df = 6$, $P < 0.05$).

4.4 CHANGES IN FOLIAR COVER

The overall all-species all-years all-areas mean FCI of the marked trees was $57.1 \pm 0.1\%$. For those trees that remained alive throughout the study, there was no change in mean FCI for all species and areas combined at unpoisoned sites (Table 2), but a small increase of 4.8% (i.e. 2.7 FCI percentage points) 6 years after control at poisoned sites (Table 2). Including the trees that died (and assigning them an FCI score of zero), the mean FCI declined by 8.5% (4.8 FCI percentage points) at unpoisoned sites, but was unchanged at poisoned sites. For individual species, the pattern was much more variable, but the species most frequently browsed during the study tended to have the largest increases in FCI, at least at the poisoned sites (Table 2).

Figure 11. Relationship between closeness to maximum trap catch index (TCI) and mean browse score for the six most common and widespread indicator species (kāmahi (*Weinmannia racemosa*), tawa (*Beilschmiedia tawa*), mähoe (*Melicytus ramifloris*), heketara (*Olearia rant*), rātā (*Meterosideros* spp. and Hall's tōtara (*Podocarpus ballii*). Separate values are shown for each site and each remeasurement. Only data from post-control surveys of poisoned sites are included.



The patterns of change in FCI over time varied widely between sites (Figs 12–14). At all 12 poisoned sites, the mean FCI of the main indicator trees that were browsed at some time during the study was higher at the end of the study than at the start, whereas it was lower at three of the four unpoisoned sites (Figs 12–14). In the two broadleaved-conifer forest areas, there were no significant changes in mean FCI of the main indicator trees relative to trees that were never browsed at the three unpoisoned sites (Figs 12 & 13). In contrast, statistically significant increases ($P < 0.05$) were recorded at five of the nine poisoned sites. At seven of the nine poisoned sites a concave-downward trend line (quadratic) provided a better fit than did a linear trend line, indicating that the initial increases in FCI had ceased by the end of the study, and had apparently begun to decline at three of these sites (Mangamako, Tahupo North and Tahupo East) (Figs 12 & 13). In the beech forest of the Richmond Range, mean FCI increased at all three poisoned sites, but also at the unpoisoned site (Fig. 14), so some of the increases in the former may have occurred even without possum control.

The best of the various models of the rate of change of FCI in relation to possum abundance included species, site and trapline as important random effects (Table 3). It used the average closeness to maximum observed TCI (Av%MaxTCI)

TABLE 2. CHANGES IN THE REPEATED MEASURES MEANS OF THE FOLIAGE COVER INDICES (FCIS) (\pm SE) OF THE MARKED TREES OVER THE 6 YEARS BETWEEN THE FIRST AND FOURTH SURVEYS FOR SITES WITH AND WITHOUT POSSUM (*Trichosurus vulpecula*) CONTROL.

Note: All poisoned/unpoisoned sites in all three areas have been combined. Only trees recorded alive in both surveys are included, and species are ranked in order of the percentage of trees of that species that were browsed on at least one occasion during the study. See Appendix 1 for scientific names.

	% BROWSED	UNPOISONED				POISONED			
		FCI 1996-97	FCI 2002-03	% CHANGE	<i>n</i>	FCI 1996-97	FCI 2002-03	% CHANGE	<i>n</i>
Silver beech	0.0	63.7 \pm 1.9	67.2 \pm 1.3	5.5%	47	67.8 \pm 0.8	70.0 \pm 0.8	3.4%	145
Fuchsia	10.0	64.0 \pm 3.6	59.0 \pm 3.2	-8.1%	10				
Pigeonwood	10.8	68.6 \pm 0.8	67.2 \pm 0.7	-2.2%	138	67.9 \pm 0.5	66.1 \pm 0.5	-2.7%	415
Hinau	27.5	61.3 \pm 2.1	58.7 \pm 1.5	-4.3%	19	64.7 \pm 1.6	58.1 \pm 2.2	-10.2%	32
Pökākā	37.5	55.7 \pm 2.1	62.0 \pm 1.6	11.3%	42	58.8 \pm 1.3	63.8 \pm 1.2	9.2%	94
Southern rātā	41.2					58.4 \pm 1.2	64.5 \pm 0.9	10.6%	136
Kāmahi	47.9	59.8 \pm 0.9	59.9 \pm 0.9	0.3%	190	58.1 \pm 0.4	59.6 \pm 0.4	2.8%	812
Lancewood	52.3	51.5 \pm 1.4	53.2 \pm 1.6	3.4%	65	47.7 \pm 1.1	55.2 \pm 1.0	16.5%	151
Northern rātā	57.0	56.7 \pm 2.5	56.4 \pm 2.0	-1.7%	29	54.6 \pm 1.0	53.3 \pm 1.0	-2.7%	201
Wineberry	67.7	42.9 \pm 2.5	43.8 \pm 2.3	2.1%	39	50.7 \pm 2.1	55.3 \pm 1.8	7.8%	54
Heketara	71.5	65.2 \pm 1.4	64.3 \pm 1.5	-1.4%	49	53.0 \pm 1.3	58.5 \pm 1.1	10.0%	158
Māhoe	76.3	58.8 \pm 1.0	59.8 \pm 1.0	1.4%	166	57.4 \pm 0.7	59.4 \pm 0.6	3.6%	487
Tawa	80.0	66.5 \pm 1.0	65.9 \pm 0.7	-0.9%	155	62.9 \pm 0.8	67.0 \pm 0.5	6.4%	466
Mistletoe	81.5					64.3 \pm 2.3	27.6 \pm 4.1	-57.1%	27
Hall's tōtara	86.6	48.5 \pm 2.1	50.6 \pm 1.7	5.1%	60	38.3 \pm 0.7	44.1 \pm 0.7	15.0%	447
Toro	89.2	55.0 \pm 8.2	58.3 \pm 2.7	6.1%	3	42.9 \pm 1.4	54.6 \pm 1.4	27.2%	127
Haumakaroa	96.7					41.7 \pm 2.6	52.3 \pm 2.2	28.9%	30
All-species total	56.7	60.5 \pm 0.4	60.6 \pm 0.4	0.3%	1012	56.1 \pm 0.3	58.8 \pm 0.2	4.8%	3782

over the 2 years preceding each survey as the index of possum abundance and considerably outperformed models using any of the other three possum abundance indices that explored abundance (Table 3: Model 6 v. Models 11, 13, 14). Including absolute TCI as well as closeness to maximum observed TCI did not improve the model fit for either current, transformed current or average possum abundance indices (Table 3: Models 17, 18, 21 respectively).

There was no indication that including treatment (poisoned or unpoisoned) improved the model (Table 3: Model 15). This is most likely because the index for possum abundance implicitly takes into account the effect of control. Likewise, the best model did not require an area factor within the random-effects structure (Table 3: Model 5 v. Model 6), indicating either that the variation in area-wide forest structure was minor relative to the variation between sites within areas, or that area-wide differences are accounted for implicitly in the use of the Av%MaxTCI index.

Standard deviations of the random effects showed that the effect of possum abundance varied more between years (standard deviation (SD) = 0.021) than between species (SD = 0.014). Between-site variation in response of rate of change of FCI to increasing possum abundance was small (SD = 0.005); however, within-site (line) variation was large (SD = 0.095). The residual variation not explained by the model was large (SD = 0.12), suggesting high variability between individual tree responses.

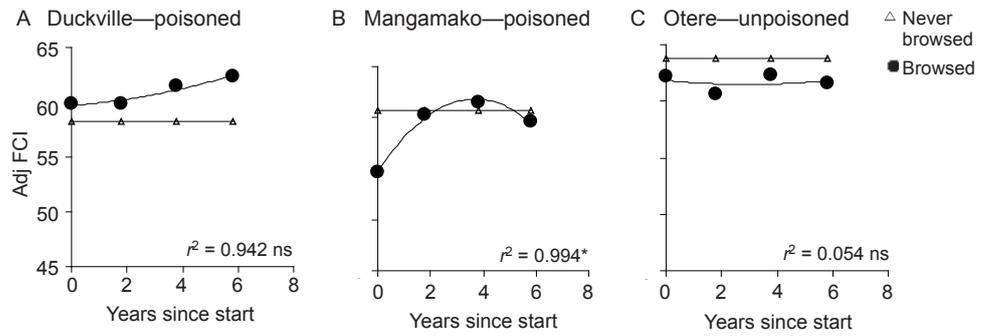


Figure 12. Trends over time in the mean adjusted FCI at the three Ikawhenua sites. Only the subset of trees from the main indicator species (those present at more than one treatment site and at least one non-treatment site) are included. The solid trend lines and r^2 values are for quadratic equations with 1 df (ns = not significant, * = $P < 0.05$). The flat trend line represents the mean adjusted FCI for the main indicator trees that were never browsed during the study.

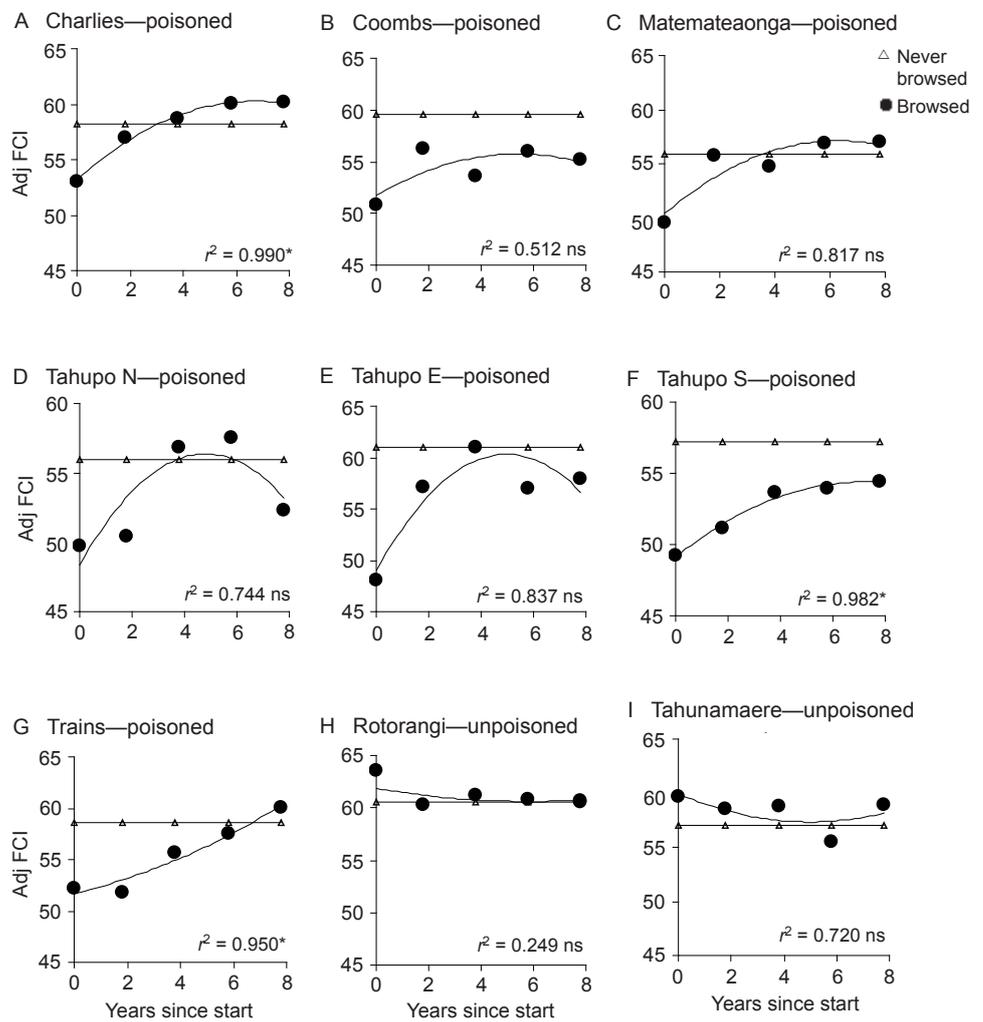


Figure 13. Trends over time in the mean adjusted FCI at the nine Matemateaonga sites. Only the subset of trees from the main indicator species (those present at more than one treatment site and at least one non-treatment site) are included. The solid trend lines and r^2 values are for quadratic equations with 2 df (ns = not significant, * = $P < 0.05$). The flat trend line represents the mean adjusted FCI for the main indicator trees that were never browsed during the study.

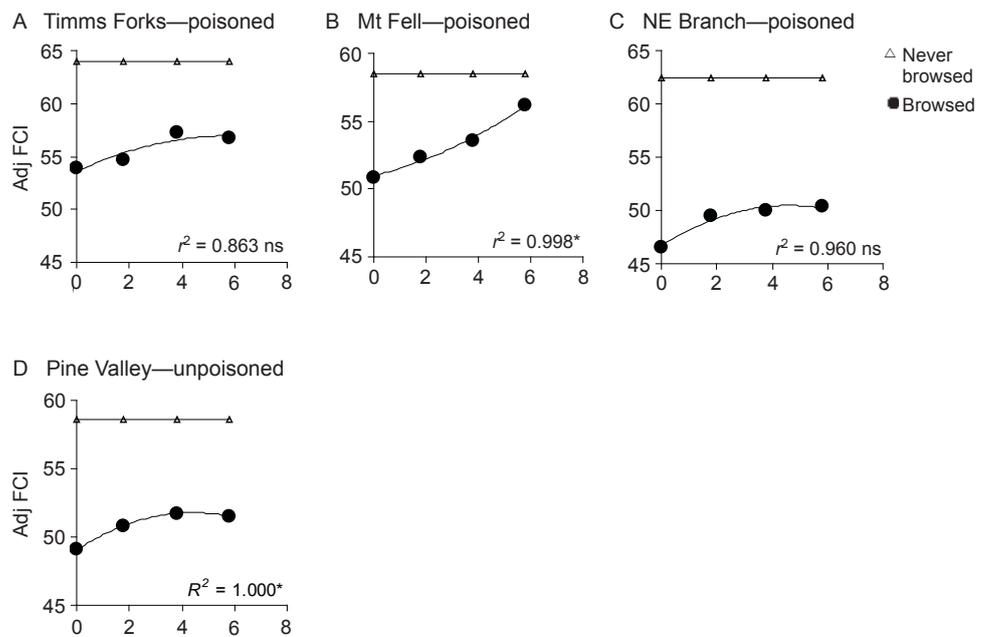


Figure 14. Trends over time in the mean adjusted FCI at the four Richmond sites. Only the subset of trees from the main indicator species (those present at more than one treatment site and at least one non-treatment site) are included. The solid trend lines and r^2 values are for quadratic equations with 1 df (ns = not significant, * = $P < 0.05$). The flat trend line represents the mean adjusted FCI for the main indicator trees that were never browsed during the study.

Estimated parameters for the best model are shown in Table 4. For the main indicators that were never browsed, possum abundance had no significant effect (95% CI for the slope of dF/dt relative to $Av\%MaxTCI$ includes zero). For those that were browsed at some time during the study, however, overall FCI was negatively affected by increased possum abundance (slope negative and 95% CI does not include zero; Table 4).

The effect of increased possum abundance is most easily depicted by the predicted 'steady-state' equilibrium values of FCI relative to possum abundance (Fig. 15). For most of the main indicator species the slopes are negative, with tawa appearing the most responsive to changing possum abundance. However, Hall's tōtara, wineberry, and northern rātā appeared little affected, on average. This indicates either continued impacts of possums even when possum numbers were low relative to maximum TCIs, or that any effect of current possum abundance was minor compared with historical or other non-possum effects.

The large t -value for the 'starting FCI' parameter (i.e. the FCI at the previous assessment) in Table 4 indicates that this was the most important predictor of the rate of change in FCI. For trees with a high starting FCI, the average rate of change of foliage was predicted and observed to be generally negative (Fig. 16). This was observed for both browsed and unbrowsed trees, and may in part be an artefact of sampling, in that trees with the maximum possible FCI score recorded at the time of first survey often had lower scores in later surveys, but few trees with lower first-survey scores ever increased to the maximum score.

Trees with starting FCIs below 55% and that survived till the end of the study were predicted to have a positive rate of change of foliar cover at any possum abundance (Fig. 16B). However, in some site-year combinations this was not

TABLE 3. AKAIKE INFORMATION CRITERION (AIC) VALUES AND WEIGHTS FOR 21 MODELS FITTED TO THE DATASET. THE BEST MODEL (LOWEST AIC) IS SHOWN IN BOLD.

The AIC weight can be interpreted as the proportion of instances where a model chosen randomly from this set would be the best predictor of the data. The random effects structure X|a/b/c indicates that the effects of c are nested within b within a, with X = 1 indicating intercept only, X = 0 + P indicating random slope on P only, and X = P indicating a random intercept and a random slope with respect to possum abundance index P.

MODEL	POSSUM INDEX	RANDOM EFFECTS STRUCTURE	AIC	ΔAIC	WEIGHTS
6	Av%MaxTCI	(AvC%MaxTCI species/year/site/line)	-18476	0	0.96
14	%MaxTCI	(%MaxTCI species/year/site/line)	-18467	9	0.01
11	TCI	(TCI species/year/site/line)	-18465	11	0
13	AvTCI	(AvTCI species/year/site/line)	-18463	13	0
17	Av%MaxTCI*TCI	(AvC%MaxTCI species/year/site/line)	-18455	21	0
18	Av%MaxTCI*TCItrans	(AvC%MaxTCI species/year/site/line)	-18452	24	0
21	AvCLMax*Av TCI	(AvC%MaxTCI species/year/site/line)	-18455	21	0
15	Av%Max*factor(treatment)	(AvC%MaxTCI species/year/site/line)	-18443	33	0
5	Av%MaxTCI	(AvC%MaxTCI species/year/area/site/line)	-18468	8	0.02
20	Av%MaxTCI	(1 species/year/site/line)	-18464	12	0
12	TCItrans	(TCItrans species/year/site/line)	-18462	14	0
16 ^a	Av%MaxTCI	(AvC%MaxTCI species/year/site/line)	-18390	86	0
10	Av%MaxTCI	(AvC%MaxTCI species/year/line)	-18355	121	0
3	Av%MaxTCI	(AvC%MaxTCI line) + (1 AvC%MaxTCI/year/area/site)	-18318	158	0
4	Av%MaxTCI	(AvC%MaxTCI line) + (1 species/year/site)	-18315	161	0
2	Av%MaxTCI	(TCI line) + (1 species/year/area/site)	-18278	198	0
1	TCI	(TCI line) + (1 species/year/area/site)	-18264	212	0
7	Av%MaxTCI	(AvC%MaxTCI species/year/site)	-18171	305	0
19	Av%Max	(0 + AvC%MaxTCI species/year/site/line)	-17821	655	0
9	Av%MaxTCI	(AvC%MaxTCI year/site/line)	-17635	841	0
8	Av%MaxTCI	(AvC%MaxTCI species/site/line)	-17551	925	0

^a This model also included a fixed effect of species on intrinsic recovery rate of FCI (b).

TABLE 4. FIXED-EFFECTS PARAMETER ESTIMATES FOR THE BEST LINEAR MODEL IN TABLE 3 (MODEL 6) DESCRIBING THE RELATIONSHIP BETWEEN POSSUM ABUNDANCE P (THE AVERAGE CLOSENESS TO MAXIMUM TCI) AND THE RATE OF CHANGE IN FCI (dF/dt) FOR THE MAIN INDICATOR TREE SPECIES, WITH SEPARATE SLOPE AND INTERCEPT ESTIMATE FOR TREES THAT WERE NEVER BROWSED DURING THE STUDY AND THOSE THAT WERE.

MODEL PARAMETER	ESTIMATE	SE	t-VALUE	95% CI	
				LOWER	UPPER
Starting FCI	-0.159	0.004	-44.87	-0.166	-0.152
Unbrowsed, dF/dt intercept	-0.109	0.012	-8.77	-0.133	-0.084
Unbrowsed, slope wrt P	0.013	0.012	1.10	-0.010	0.036
Browsed, dF/dt intercept	-0.089	0.006	3.36	-0.100	-0.077
Browsed, slope wrt P	-0.021	0.010	-3.46	-0.040	-0.002

Figure 15. Predicted average equilibrium foliar cover for main indicators with respect to possum abundance, as measured by average closeness to the maximum observed trap catch index. See Appendix 1 for scientific names.

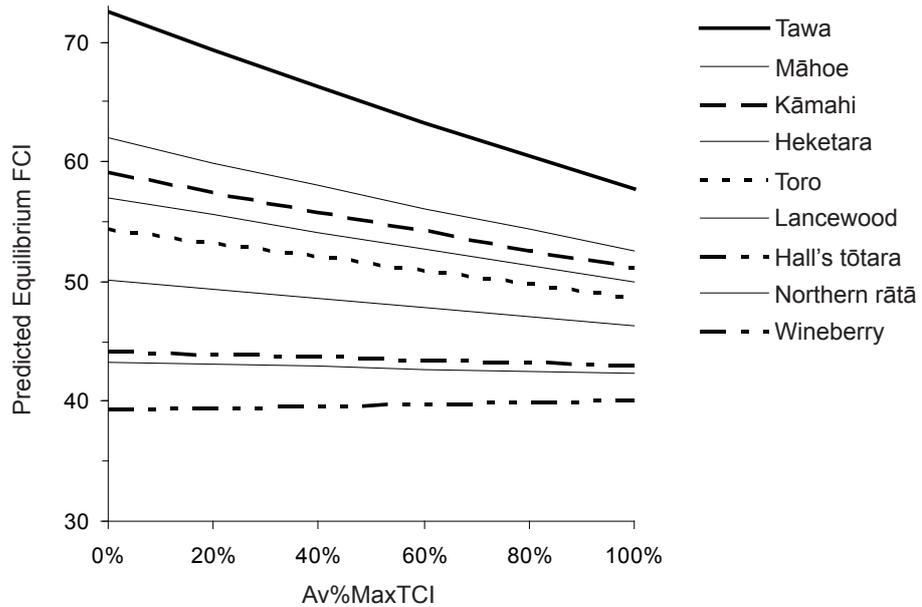
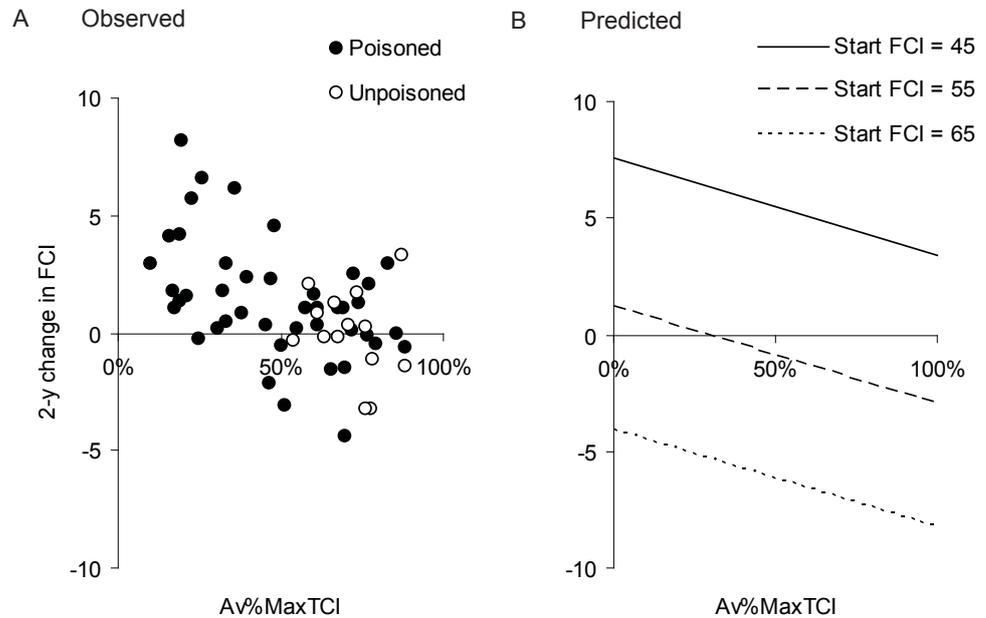


Figure 16. Change in foliar cover between biennial surveys in relation to possum abundance (average closeness to maximum TCI) for all main indicator trees combined that were browsed during the study. A. Observed changes—data points are the means for each site, with poisoned and unpoisoned sites shown separately and with a separate point for each survey. B. Changes predicted by the best-fitting model in Table 3 for each of the three most common FCI scores recorded for browsed trees.



observed, indicating that in some instances some heavily defoliated trees were unable to recover. This dichotomous effect could not be easily accommodated within the linear models explored here (i.e. simply added to the error term in the model).

The observed patterns of change for all browsed main indicator trees combined indicated that where TCIs were below about half of the maximum levels recorded, the mean FCI usually increased (Fig. 16A). In line with that, the overall average FCI of browsed main indicators at the beginning of all observation intervals in the study was 54%, and the best fitting model predicted that foliage recovery (i.e. positive rate of change in FCI) of browsed trees would occur, on average, when possum abundance is below 40% of maximum levels (Fig. 16B).

For the minor indicator species, the most striking pattern was for red mistletoe, which was recorded only on a supplementary line at Mt Fell in the Richmond Ranges. Most (60%) of the 33 extant plants tagged during the first survey were browsed (pre-poison TCI = 4.0% for the whole site), but the species appeared to be coping with that browse pressure, as the mean FCI was 64%. Two years after poisoning (site TCI = 2.5%), only 6% of plants were browsed, and most plants still had good foliar cover (mean FCI = 56%). By 6 years after poisoning, however, TCI had increased to 8.6% (double the pre-poison index), 55% of plants were browsed, and FCI had plummeted to 23%, with 18% (6/33) of the plants apparently dead. That outcome indicated that red mistletoe was heavily affected even at low TCIs where those low TCIs were close to the maximum for the site.

4.5 MORTALITY

4.5.1 Observed patterns in the marked trees

A total of 5291 trees were accounted for during each of the four or five surveys in each area. Of these, 497 (9.4%) had died by the end of the study (Appendix 4). This slightly underestimates mortality rates, as some trees were not relocated during the final surveys and were therefore deleted from the dataset used to analyse mortality patterns, and these are likely to have included a higher than average proportion of dead trees. Overall, only 27 (3.5%) of the 772 unpalatable control species (pigeonwood and silver beech) died during the study. In contrast, 470 (10.4%) of the 4510 designated indicator species died (Yates $\chi^2 = 36.3$, $df = 1$, $P < 0.0001$).

Across all indicator tree species combined, similar overall mortality was recorded in each of the three areas, but with higher mortality in the unpoisoned areas than in the poisoned areas (Fig. 17, Appendix 4). The difference between treatments did not appear to decrease with time since control even though the possum populations were increasing rapidly; if anything, the Ikawhenua data suggest a 2-year lag in the reduction in mortality after control.

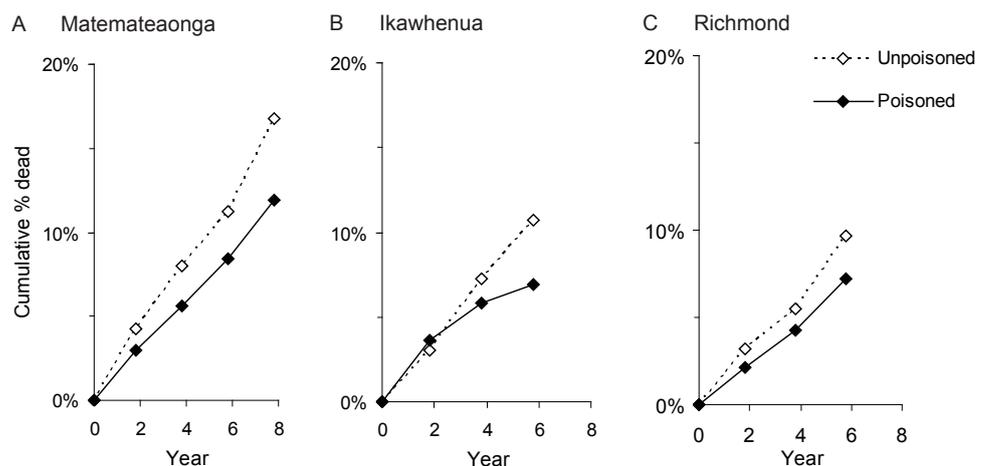


Figure 17. The cumulative percentage of trees dead 0–8 years after initial survey at poisoned and unpoisoned sites in A. Matemateaonga Range, B. Ikawhenua Range and C. Richmond Range. Only possum-preferred indicator species and trees that were accounted for in every survey are included.

The overall pattern of greater mortality at unpoisoned sites was not always evident at the species level (Appendix 4). Some of this variability in mortality patterns reflected localised events unrelated to possums. One example of this was the sudden death in 1999 of several large tawa in two of the highest-elevation possum-control blocks in the Matemateaonga Range, apparently due to a severe frost event; in contrast, no tawa died in the two non-treatment blocks (which were at much lower elevations) during that measurement period. Another factor was the difference between sites at the time of the pre-control survey. A smaller percentage of heketara trees died at the unpoisoned sites in the Matemateaonga Range than at poisoned sites (Appendix 4), because many of the trees (23%) at poisoned sites were heavily defoliated (FCI < 20) in 1996 compared with very few (3%) at the unpoisoned sites. Within the initial FCI classes, greater percentages of trees died at the unpoisoned sites, but the sample sizes were too small for statistical testing. Similarly, for māhoe, there was a greater percentage (42%) of very small diameter (< 5 cm) trees monitored at poisoned sites than at unpoisoned sites (25%), so because almost half the māhoe that died were in this size class, the mortality at poisoned sites appeared higher.

Mortality rates differed widely between species (Appendix 4). There was weak evidence of a correlation between the mean initial browse score for each species and the overall percentage mortality for that species ($r^2 = 0.33$, $df = 14$, $P = 0.09$). In broad terms, mortality rates were highest (3–5% per annum (p.a.)) for mistletoe and the shrubbier subcanopy or seral species (haumakaroa, heketara and wineberry; Appendix 4). Intermediate rates of 1–2% p.a. were recorded for the group composed mainly of species that are widely used as indicators of possum impacts (northern rātā, lancewood, toro, māhoe, kāmahi, tawa and Hall’s tōtara). Rates of < 1% p.a. were recorded for the two unpalatable control species (silver beech and pigeonwood), and hinau and pōkākā (which were also seldom browsed), as well as for southern rātā.

For all species combined, mortality rates were much higher for trees with high levels of possum browse during the first surveys (Table 5). However, the patterns varied between areas.

TABLE 5. PERCENTAGE OF TREES THAT DIED DURING STUDY, BY INITIAL BROWSE CLASS AND TREATMENT.

INITIAL BROWSE SCORE	POISONED		UNPOISONED	
	% DEAD	<i>n</i>	% DEAD	<i>n</i>
0	6.3	2257	7.8	614
1	10.2	1377	10.8	406
2	14.1	326	21.1	71
3	15.9	138	44.1	34
4	29.5	44	55.6	18
All trees	8.8	4142	11.6	1143

In the Matemateaonga Range, only about 1% of the trees that were never browsed died each year and mortality of lightly browsed trees was only slightly higher, with no differences in either mortality or browse-pressure trends between poisoned and unpoisoned areas (Fig. 18). In contrast, mortality and browse pressure were higher in the unpoisoned areas for trees that were frequently or heavily browsed during the study.

In the Ikawhenua Range, mortality of unbrowsed trees was again similar between poisoned and unpoisoned areas, but browsed trees had higher mortality in the unpoisoned blocks than in the poisoned blocks, despite similar browse pressure (Fig. 19).

In the beech forests of the Richmond Range, unbrowsed trees had higher mortality in the unpoisoned than the poisoned areas (Fig. 20). This difference reflected high mortality of apparently unbrowsed wineberry, fuchsia and lancewood, which represented 30% of the unbrowsed trees in the unpoisoned block but only 13% of those in the poisoned blocks. Mortality of browsed trees in the unpoisoned blocks was similar to that in the poisoned blocks, despite the higher browsing pressure.

Tree mortality also varied strongly with initial canopy condition. The few trees that had low foliar cover (<30%) when first surveyed seldom survived the study in areas where possums were not controlled (Fig. 21). For the two conifer-broadleaved forest areas (Matemateaonga and Ikawhenua), higher possum mortality was recorded in these low-cover classes in the unpoisoned areas than in the poisoned areas. In the Richmond Range beech forests, no difference was apparent between treatments.

4.5.2 Effect of possum control

The observed patterns above suggested that mortality patterns varied between areas, species and time periods, as well as with initial foliar cover and the extent of possum browse. Initial model-fitting analyses showed substantial support for a link between initial FCI and the (biennial) probability of mortality, taking into account location, year and species effects (Model 3, Table 6). Overall, the most heavily defoliated trees suffered about 40% mortality by the time of the first remeasurement, whereas trees with greater than 50% foliage cover had very low mortality rates (Fig. 22A). A comparison of actual mortality rates with the values predicted by Model 3 in Table 6 indicated this model fitted the data well. This is illustrated using the observed data and model predictions for three common species at Matemateaonga in 1998 as examples (Fig. 22B–D).

Using the best model in Table 6 as a base, eight further models were constructed and compared using AIC (Table 7). Two of the models (Models 5 and 8; Table 7) were strongly supported by the data (low AIC values). These two models are nearly identical, differing only in the way the 'possum treatment' variable is represented. The remaining models were poorly supported. Thus, in addition to the effects of species, location, year and initial foliage condition, the best fitting model indicates treatment (i.e. possum control) is also an important effect, which differs among species (treatment × species interaction), and whereby larger trees are more prone to mortality.

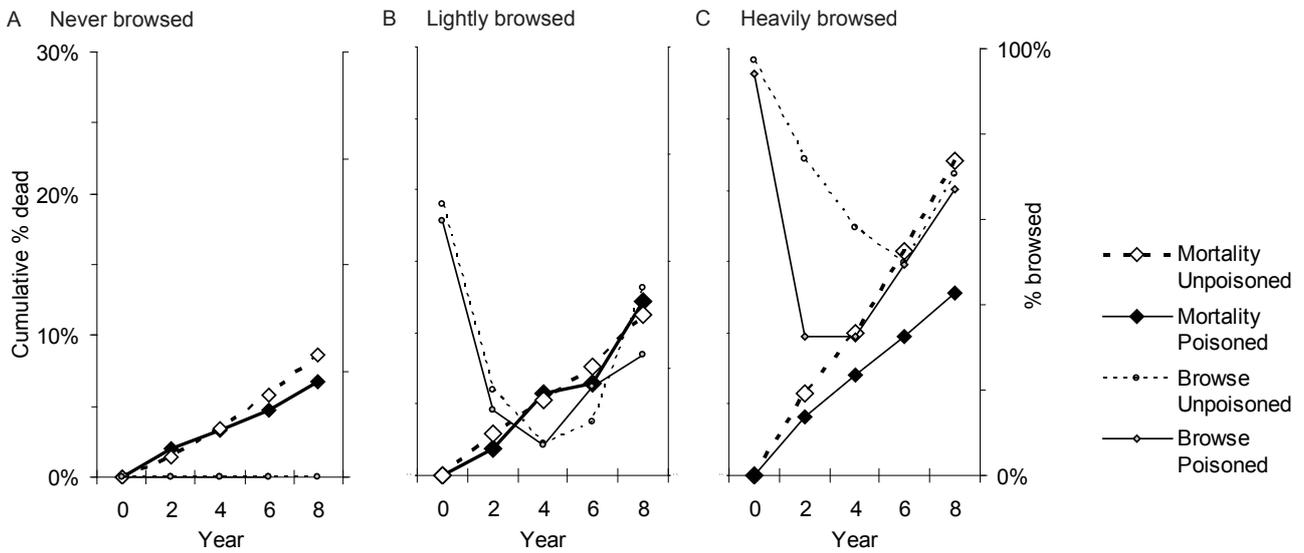


Figure 18. Comparison of cumulative mortality (large diamonds, left axis) and browse pressure (small circles, right axis) between poisoned and unpoisoned sites in the Matemateaonga Range, for trees that were A. never browsed ($n = 1055$), B. lightly browsed on only one or two occasions during the study ($n = 921$), and C. heavily browsed ($n = 844$). Browse pressure is represented as the percentage of trees having at least some browse observed during each survey.

Figure 19. Comparison of cumulative mortality rates (large diamonds, left axis) and browse pressure (small circles, right axis) between poisoned and unpoisoned sites in the Ikawheneha Range, for trees that were A. never browsed ($n = 425$) and B. browsed on at least one occasion during the study ($n = 584$). There were too few heavily browsed trees to create a separate class for them. Browse pressure is represented as the percentage of trees having at least some browse observed during each survey.

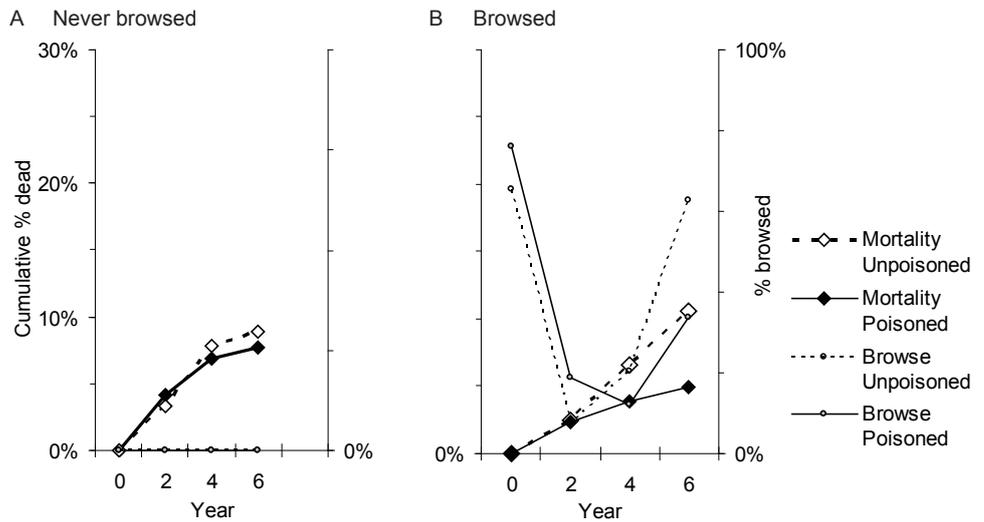


Figure 20. Comparison of cumulative mortality rates (large diamonds, left axis) and browse pressure (small circles, right axis) between poisoned and unpoisoned sites in the Richmond Range, for trees that were A. never browsed ($n = 753$) and B. browsed on at least one occasion during the study ($n = 709$). There were too few heavily browsed trees to create a separate class for them. Browse pressure is represented as the percentage of trees having at least some browse observed during each survey.

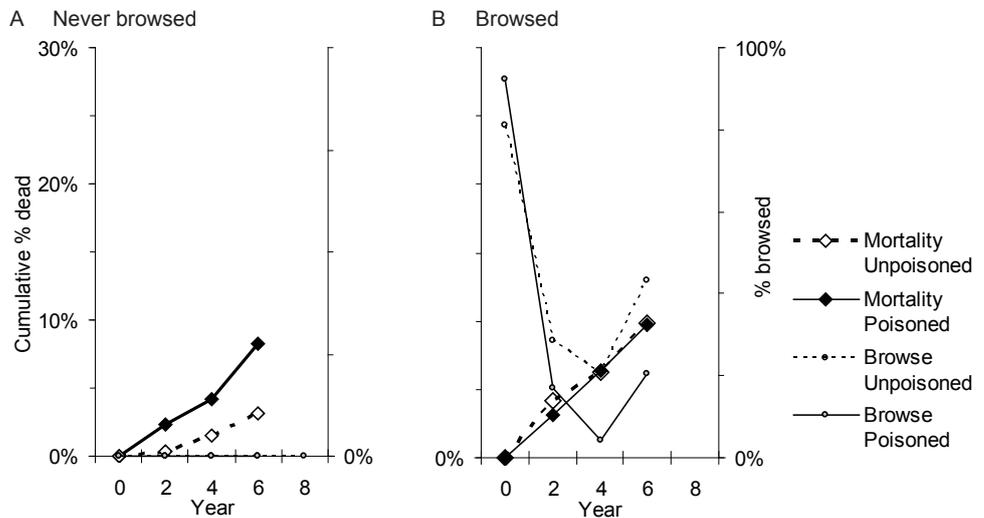


Figure 21. Comparison of the relationship between tree foliar cover index (FCI) when first surveyed and total mortality during the study at poisoned and unpoisoned sites in A. Matemateonga Range (8 y), B. Ikawhenua Range (6 y), and C. Richmond Range (6 y).

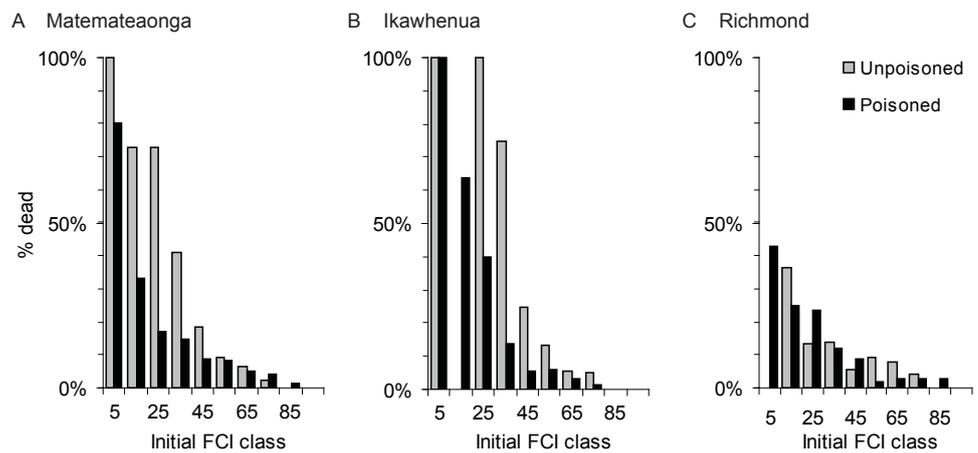
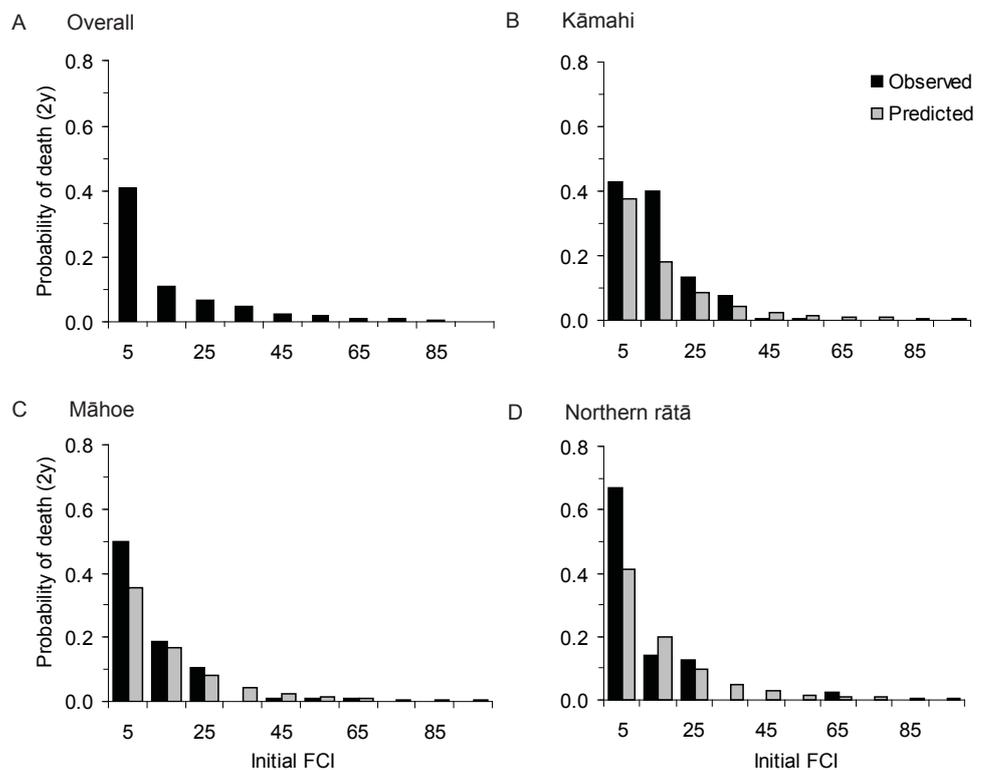


TABLE 6. COMPARISON OF THE FIT OF DISCRETE-TIME FAILURE ANALYSIS MODELS FOR THE RELATIONSHIP BETWEEN THE (BIENNIAL) PROBABILITY OF MORTALITY AND THE INITIAL FOLIAR COVER INDEX (IFCI) OF TREES.

Note: For each model, the columns show the factors included as explanatory variables, the log-likelihood of the fitted model, the number of parameters estimated, the AIC of the fitted model, Δ AIC (the difference in AIC between the model and the best fitting model in the candidate set, with the best fitting model having Δ AIC = 0), and the AIC weights, which give the approximate probability that a model is the best fitting model in the set. The best fitting model (Model 3, bolded) includes a squared term for IFCI, implying a non-linear relationship between IFCI and probability of mortality (see Fig. 22) after accounting for location (Area | Site | Trapline), year and species effects.

MODEL	MAIN FACTORS	LOG LIKELIHOOD	<i>n</i> PARAMETERS	AIC	Δ AIC	AIC WEIGHTS
1	location, year, species	Δ 1726.2	18	3488.4	418.5	0.000
2	location, year, species, IFCI	Δ 1521.3	19	3080.6	10.6	0.005
3	location, year, species, IFCI, IFCI²	Δ1515	20	3069.9	0.0	0.995

Figure 22. Observed tree mortality rate as a function of initial foliar cover index (IFCI) across A. all species, locations and years, and B. kāmahi (*Weinmannia racemosa*), C. māhoe (*Melicactus ramiflorus*) and D. northern rātā (*Metrosideros robusta*) in Matemateonga Range in 1998. The grey bars represent the mortality rate predicted by the best supported model in Table 8 (Model 3).



The effect of possum control and how that effect differs between species is illustrated using the predictions for a single site (Matemateaonga) and year (1998) (Fig. 23). For six species, predicted biennial mortality was higher at unpoisoned sites, sometimes substantially so. However, for three species with the lowest overall mortality, the opposite was the case. However, since the latter three had very few or no trees monitored at the unpoisoned sites (Appendix 4), this result may in part reflect sampling error. The zero mortality of 51 Hall's tōtara in the unpoisoned site in the Richmond Range (Pine Valley) seems anomalous, however, possibly reflecting a much higher mean initial FCI at that site ($46.5 \pm 1.1\%$) than at the nearby poisoned sites ($38.6 \pm 0.6\%$).

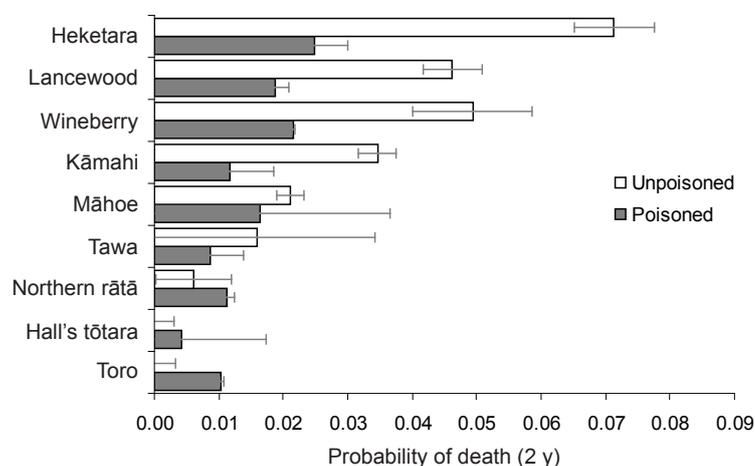
Excluding the trees on the supplementary transects (for which there was no TCI) and using the TCI collected immediately after control (PostTCI) as the treatment effect, we found similar relationships between initial foliar cover and mortality to those found in the previous analysis, which used the full data. Three further models were added to the set shown in Table 7, by substituting PCtrl in Models 4–6 with PostTCI. Of the 11 models considered, three received substantial support ($\Delta AIC < 4.0$). A model identical to Model 5 (PCtrl) in Table 7 was again the best fitting model (AIC weight = 0.77), and the other two well-supported models were again nearly identical apart from having the treatment effect measured

TABLE 7. COMPARISON OF THE FIT OF DISCRETE-TIME FAILURE ANALYSIS MODELS FOR THE RELATIONSHIPS BETWEEN THE BIENNIAL PROBABILITY OF MORTALITY AND FACTORS REFLECTING DIFFERENT LEVELS OF EITHER POSSUM CONTROL (PCtrl; A BINARY YES/NO VARIABLE) OR CUMULATIVE POSSUM BROWSE SCORE (PBrows).

Note: The best fitting model from Table 6 was used as the base model (BM). See Table 6 for an explanation of the column headings. BM = location, year, species, IFCI (= initial foliar cover index), IFCI² (= IFCI squared); TD = tree diameter.

MODEL	MAIN FACTORS	LOG LIKELIHOOD	n PARAMETERS	AIC	ΔAIC	AIC WEIGHTS
1	BM	-1515	20	3069.9	47.2	0.000
2	BM, TD	-1507.1	21	3056.1	33.4	0.000
3	BM, PCtrl	-1498.1	21	3038.2	15.5	0.000
4	BM, PCtrl, PCtrl × species	-1489.2	29	3036.4	13.6	0.001
5	BM, PCtrl, PCtrl × species, TD	-1481.4	30	3022.8	0.0	0.850
6	BM, PBrows	-1510.8	21	3063.5	40.8	0.000
7	BM, PBrows, PBrows × species	-1490.8	29	3039.6	16.8	0.000
8	BM, PBrows, PBrows × species, TD	-1483.1	30	3026.3	3.5	0.148

Figure 23. Predicted mean (biennial) probability of mortality (\pm SEM) for each species at poisoned and unpoisoned sites, with the site variable set to Matemateaonga Range, remeasurement year to 1998, initial foliar cover to 55%, and diameter at breast height (DBH) to 20 cm. See Appendix 1 for scientific names.



in a different way, either in term of browse pressure (PBrows) or post control possum abundance (PostTCI). Using the PostTCI model, the predicted biennial probability of mortality was low for post-control TCIs of <10%, but began to increase at TCIs above this for five species (heketara, lancewood, kāmahi, māhoe and tawa), although the predicted increase was small for tawa (Fig. 24).

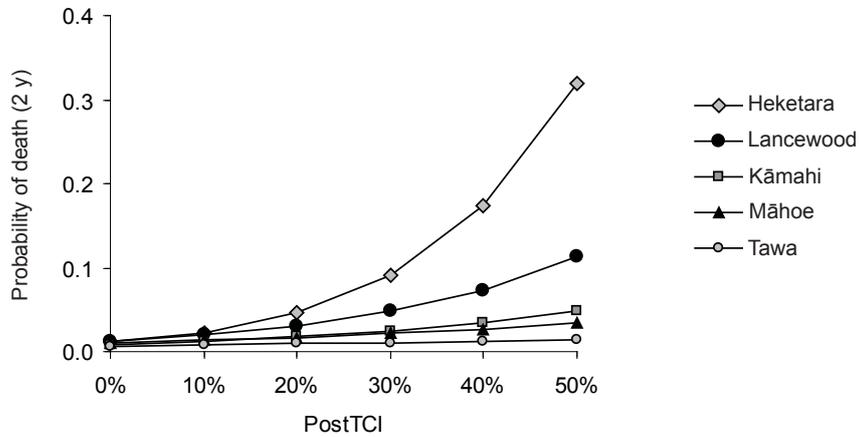


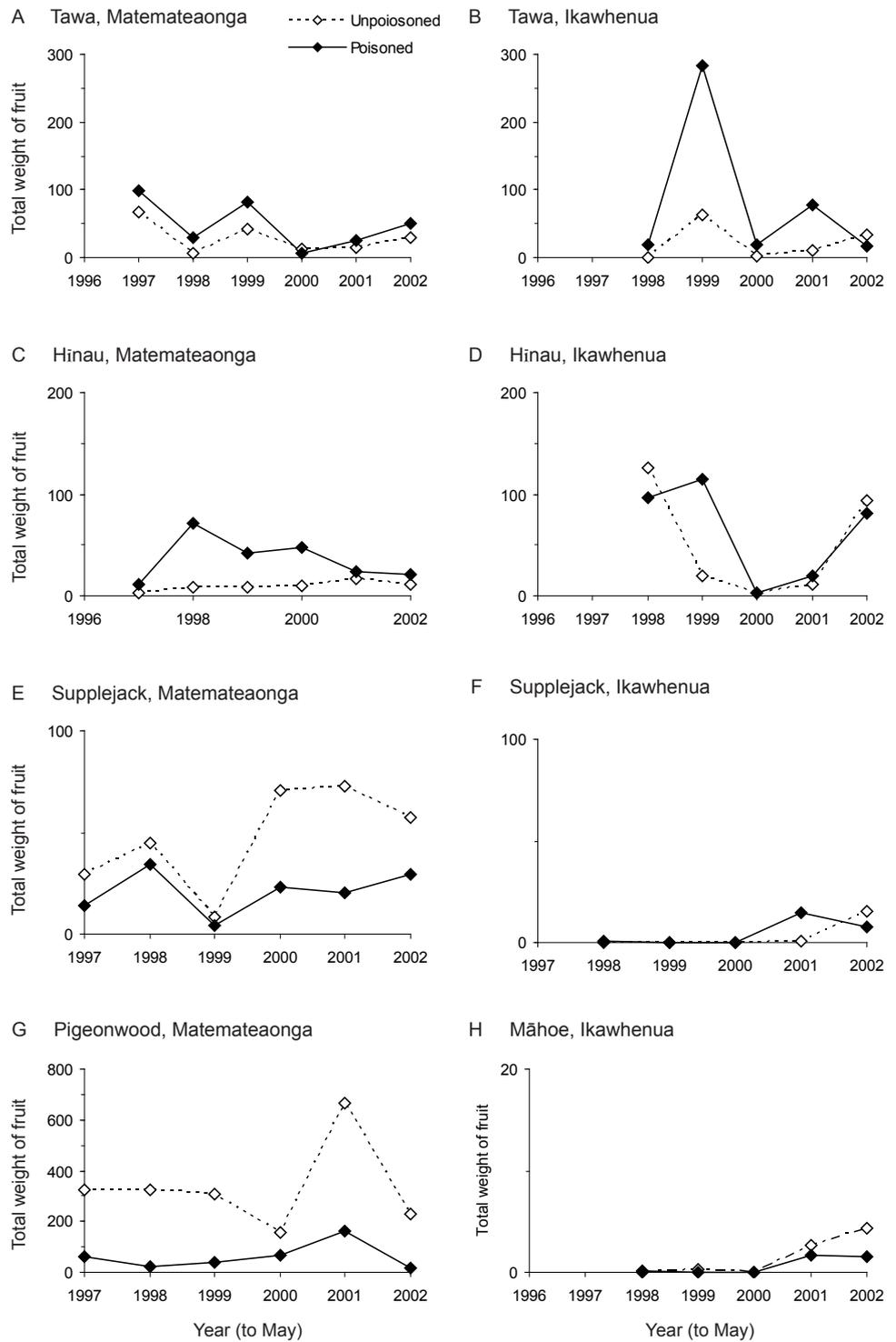
Figure 24. Predicted mean (biennial) probability of mortality for heketara (*Olearia rani*), lancewood (*Pseudopanax crassifolius*), kāmahi (*Weinmannia racemosa*), māhoe (*Melicytus ramiflorus*) and tawa (*Beilschmiedia tawa*) given various levels of post-control trap catch index (PostTCI), with the site variable set to Matemateaonga Range, remeasurement year to 1998, initial foliar cover index (FCI) to 55% and diameter at breast height (DBH) to 20 cm. PostTCI is the trap catch recorded in 1996 or 1997 immediately after control in the treatment block or at the equivalent time in non-treatment blocks.

4.6 FRUITFALL

There were too many gaps in the fruitfall data from the Richmond Range to permit any meaningful analysis. For the two North Island areas, fruitfall varied hugely between years, but few of the changes were consistent within or between areas (Fig. 25). A general linear mixed-effects model with area, site and trapline included as random effects, and with species, year and treatment as fixed main effects, along with species \times year and species \times treatment interactions indicated significant variation between years ($F = 12.0$, $df = 5$, 594 , $P < 0.0001$) and species ($F = 20.0$, $df = 3$, 123 , $P < 0.0001$). The variation between species was not consistent between years, shown by the significant interaction between year and species ($F = 3.93$, $df = 15$, 599 , $P < 0.0001$). Overall, fruitfall was no higher in the poisoned areas than in the unpoisoned areas ($F = 1.2$, $df = 1$, 123 , $P = 0.28$), but there was a highly significant interaction between treatment, area, and species ($F = 16.40$, $df = 3$, 123 , $P < 0.0001$), reflecting the higher fruitfall of tawa but lower fruitfall of pigeonwood in poisoned areas. For tawa, we infer that this reflected reduced consumption of developing fruit by possums, but that inference is necessarily weak because of the contrasting outcome for pigeonwood.

There was weak synchrony between areas in the yearly variation for tawa, with peaks in 1999 in both the Ikawhenua and Matemateaonga Ranges (Fig. 25). For the Ikawhenua Range, the 1999 peak coincided with the very low levels of browse on broadleaved species recorded at the unpoisoned site that year (Fig. 8H). In the Matemateaonga Range, the monitored tawa produced almost no fruit at all in 2000 (Fig. 25), coinciding with the period 2–4 years after control when rates of possum increase were lower than in the following period (Fig. 5A).

Figure 25. Total weight (g) of fruit collected annually in a fixed array of litter traps placed under specific trees of four species (tawa (*Beilschmiedia tawa*), hinau (*Elaeocarpus dentatus*), pigeonwood (*Hedycarya arborea*) and māhoe (*Melicytus ramiflorus*)) and one climber (supplejack (*Ripogonum scandens*)), at poisoned and unpoisoned sites in autumn 1996 (Matemateaonga Range) or 1997 (Ikawhenua Range).



4.7 PREDICTORS OF POSSUM CARRYING CAPACITY

The simpler beech-kāmahi forest of the Richmond Range had lower possum carrying capacity than the more varied broadleaved-conifer forests in the North Island areas. Pre-control and final TCIs were particularly low at the high-altitude Mt Fell site (4% and 8%, respectively), even though two preferred indicators (kāmahi and Hall's tōtara) comprised 22% and 6% respectively of the total amount of cover recorded at that site.

At the level of individual trap lines (ignoring area and site effects), there was no evidence of a positive relationship between the maximum TCI recorded on each line and the index of relative abundance of kāmahi, māhoe, Hall's tōtara, beech species and rātā species, with the trend lines for all these species being near zero or negative (Fig. 26). The same was true for all widespread unpalatable species that comprised only a small percentage of total cover. For tawa, however, there was a positive trend line. Wherever tawa was common, the TCI recorded was always at least moderate if not high, although high TCIs were sometimes also recorded where the species was rare. The patterns recorded for *Elaeocarpus* species (hīnau and pōkākā combined) and for pigeonwood were similar.

Using the 16 most common tree or tree fern species, a multiple linear regression model using the % of total cover scores contributed by each species as a predictor accounted for about 56% of the variation in maximum TCI between trap lines. Using forward selection, a simpler model that included just seven species accounted for almost as much of the variation (51%). Ranking these in order of greatest effect on TCI per unit change in the index of relative abundance (Table 8), the three species that appeared to have the greatest influence on TCI (hīnau/pōkākā, rewarewa and pigeonwood) were all species whose foliage is not considered to be highly palatable to possums, but whose flowers and/or fruit are eaten by possums. Tawa, another major source of fruit for possums, ranked fourth. Fruiting species therefore appeared to be more important predictors of maximum possum abundance than species that are largely foliar foods, such as kāmahi and māhoe.

TABLE 8. RESULTS OF A MULTIPLE LINEAR REGRESSION RELATING POSSUM CARRYING CAPACITY (AS MEASURED BY THE MAXIMUM TRAP CATCH INDICES (TCIs) RECORDED DURING THE STUDY) TO THE RELATIVE ABUNDANCE OF TREE SPECIES ON INDIVIDUAL TRAPLINES, IGNORING AREA AND SITE EFFECTS.

Note: The regression constant was set to zero, and the change in TCI per unit change in the mean % of total cover (Δ TCI) was calculated to show the size and direction of the effect for each species. See Appendix 1 for scientific names.

PARAMETER	MEAN % OF TOTAL COVER	REGRESSION COEFFICIENT	SEM	<i>t</i> (df = 78)	<i>P</i>	Δ TCI
<i>Elaeocarpus</i> spp.	2.1	0.025	0.007	3.67	< 0.001	1.19%
Pigeonwood	2.7	0.012	0.005	2.46	0.016	0.45%
Rewarewa	3.4	0.013	0.004	3.67	< 0.001	0.39%
Tawa	16.9	0.006	0.001	6.36	< 0.001	0.04%
Kāmahi	21.2	0.005	0.001	5.02	< 0.001	0.02%
Beech spp.	19.5	0.003	0.001	5.36	< 0.001	0.02%
Māhoe	2.8	-0.005	0.004	-1.51	0.13	-0.19%

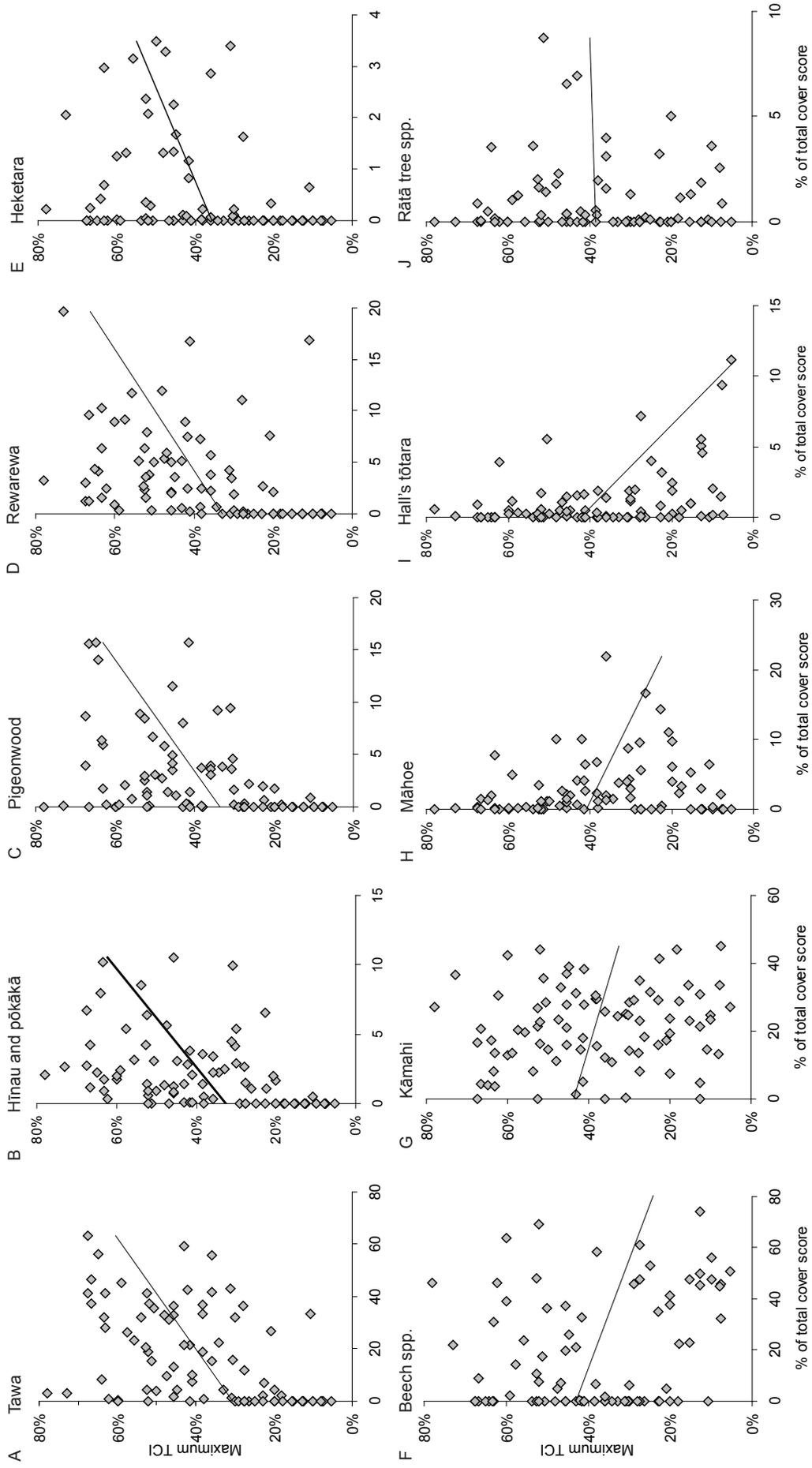


Figure 26. Relationships between the maximum trap catch index (TCI) recorded on each trampoline during the study and the relative abundance (% of total cover) of the species that were used as indicators or that were the most common and widespread species. The trend lines shown are not corrected for area and site effects, so are not statistically tested. See Appendix 1 for specific names.

5. Discussion

5.1 IMPACTS ON THE POSSUM POPULATION

It initially appeared that the three aerial poisoning operations monitored had successfully reduced possum numbers to satisfactorily low levels. Judged by the area-wide mean raised-set TCIs of 0.3–3.4% recorded immediately after control, reductions of 89–96% were achieved. However, it is now clear that those estimates of post-control TCI were biased in relation to the ground-set TCIs of 2% or 5% that are frequently set as operational targets. This bias partly reflects the 38% lower TCI recorded on raised sets. More importantly, it also appears to reflect a major downward bias in TCI measured immediately after control. This was first identified in the 1998 and 1999 resurveys and has since been observed in other control operations (GN, unpubl. data) and research projects (Forsyth et al. 2003; Monks & Ramsey 2005).

We now guess that only 70–80% of possums were killed in these three operations. This means that TCIs reached 35–40% of pre-control levels within 2 years of possum control, and were close to pre-control levels within 6 years. This study, therefore, documents responses to only a relatively modest reduction in possum numbers, with densities at most sites being held below half the pre-control level recorded for less than 3 years. Over the decade since these operations were conducted, aerial poisoning has become more efficient, with extremely high kills (>99%) now being recorded in some instances. As an example, a TCI of just 0.05% was recorded (eight possums captured from c. 15 000 trap nights) in 2005 after aerial poisoning of 88 000 ha of broadleaved-conifer forest in the Hauhungaroa Range, central North Island (Coleman et al. 2007). Even allowing for substantial bias in the post-control TCI, it seems clear that such operations will result in a more complete and longer term reduction in possum browse (and its consequent impacts) than was observed in this study.

The post-control bias in TCI precludes use of the increase in TCI over the first 2 years after control as a measure of possum population increase, but we assume that subsequent surveys were largely unbiased relative to the pre-control means.

The rate of increase r at all poisoned sites 2–4 years after control averaged 0.252 (± 0.037 SE, range 0.110–0.521), which was similar to the value of 0.260 (± 0.044 SE, range 0.000–0.491) calculated for the period 4–6 years after control. These averages exclude measurements known to be affected by unplanned trapping or by technical problems during trapping, but are still likely to be biased downward somewhat by suspected but unconfirmed possum kills by fur hunters in the Ikawhenua blocks, and by the killing of 16% of the possums caught during the biennial surveys.

These averages relate to periods when most TCIs were between 30% and 70% of the maximum TCI recorded at that site (mean = 0.47). By simplistically substituting the all-sites average data as parameter values in the theta logistic growth model used by Hickling & Pekarharing (1989), in which $r = r_m (1 - N/K^\theta)$, we calculate r_m (the intrinsic rate of maximum increase) as c. 0.52 assuming $\theta = 1$, 0.35 assuming $\theta = 2$, and 0.30 assuming $\theta = 3$. Aside from an estimate of 0.22–0.25 by Hickling

& Pekelharing (1989), which we question below, these three estimates span the range of reported values. Unfortunately, as a result of the bias in the post-control TCIs, it is not possible to use the data from the first 2 years after control to assess which estimate of θ is most appropriate. However, the maximum rates of increase recorded at the poisoned sites for the periods 2–4 and 4–6 years after control were 0.49 and 0.52, respectively, and the mean r for the period 4–6 years after control for the six untrapped poisoned blocks in the Matemateaonga Range was 0.386 ± 0.056 . Similarly large increases over short periods have been reported elsewhere (Thomas et al. 1993; Efford 2000; Efford & Cowan 2004), and the incidence of spring breeding (possibly resulting in some possums producing two young per year) is known to sometimes be high (Fletcher & Selwood 2000).

There are surprisingly few published data on the intrinsic exponential rate of increase (r_m) of possum populations. Keber (1985) provided an estimate based on maximum survival and fecundity rates of 0.59, but Clout & Barlow (1982) calculated a much lower value of 0.30 from birth and death rates. Hickling & Pekelharing (1989) calculated an even lower value (0.22–0.25) based on faecal pellet counts, which remains the only published estimate based on actual population recovery within a large area in which immigration was assumed to be a minor contributor to population growth. Their estimate is questionable, however, partly because the possum abundance index used (the density of faecal pellets) is imprecise due to high short-term variability in possum faecal output and the highly weather-dependent decay rate of pellets (D. Morgan, Landcare Research, unpubl. data). It is also uncertain whether the single pre-control estimate was an accurate estimate of the long-run average maximum.

We suggest pragmatically that for population modelling purposes r_m and θ could be assumed to be of the order of 0.45 and 1.5, respectively. This combination of parameters would allow for brief periods of rapid increase interspersed with similarly brief periods of much slower increase. Such modelling will facilitate long-term planning of (and budgeting for) periodic possum control by providing managers with conservative (i.e. short) estimates of the time required for a possum population to recover to any particular TCI threshold level.

5.2 IMPACT OF CONTROL ON BROWSE PRESSURE

At the poisoned sites, zero or near-zero mean browse scores in 1998–1999 for all species other than Hall's tōtara (Fig. 8) suggested that the possum control had been effective in protecting most trees from browsing. However, in the Ikawhenua and Richmond Ranges, browse pressure was also much reduced at the unpoisoned sites, despite the lack of possum control. Thus it appears likely that the moderate reductions in possum abundance coincided with natural changes in the amount of foliage needed by possums, so the more complex models were needed to determine the effect of control alone. Across all post-control surveys, total browse pressure was consistently only about 1.5–2.0 times higher at the unpoisoned sites than at the poisoned sites. It is therefore all the more striking that we were able to detect possum control effects on defoliation and mortality given this was only a relatively small difference in actual browse pressure given the >50% reductions in possum abundance.

The reductions in browse pressure in the unpoisoned blocks probably resulted from a combination of factors. These include possible observer error, the likelihood that the trapping in this study had some negative effect on possum abundance and, in at least one instance, the occurrence of unplanned possum hunting. However, the almost complete absence of browse at Ikawhenua in 1999, at a time when there was no decline in TCI, cannot be explained by these factors. Instead, we suggest the possibility that this was caused by the high fruitfall of tawa fruit in the preceding year (Fig. 25). Observations by one of us (PS) elsewhere in the central North Island have indicated that possums feed heavily on the kernels of tawa fruit while it is on the tree and also when it is available as ripe fruit on the ground, and possums consume far less foliage when non-foliar foods are abundant (Sweetapple 2003). Other research has shown that there can be a disjunction between browse levels and possum abundance. Cowan et al. (1997) found that browse on northern rātā in the Orongorongo Valley was very low in 1990, even though possums were at the highest levels there for 34 years. Browse then increased over the ensuing 4 years even though possum numbers fell somewhat, but remained above the long-term average. Their results imply that browse pressure is episodic and that high browse scores tend to develop incrementally over several years as high levels of browse are imposed on declining amounts of foliage.

More broadly, the >85% reduction in overall mean browse score for all of the broadleaved tree species at poisoned sites in 1998–1999, when possum densities were about 30–40% of pre-control levels, provides support for the hypothesis that the foliage of most of the tree species that persist long after possum invasion are ‘last-resort’ foods, which possums only eat in quantity when they are near or at carrying capacity (Nugent et al. 2000).

The browse pressure recorded on Hall’s tōtara was less responsive to possum control, partly reflecting technical problems in scoring browse on this species and partly reflecting the longer leaf retention time compared with the broadleaved species (Nugent et al. 1997: Appendix 10.8). Nonetheless, this species continued to be much more heavily browsed than most other species both 4 and 6 years after control. Hall’s tōtara is a favoured food of possums (Nugent et al. 1997, 2000) and is the one tree species that declined markedly during long-term monitoring of 14 sites throughout New Zealand (Bellingham et al. 1999a). That, coupled with the continuation of browse pressure after possum control in this study, indicates that sustained and intensive possum control is likely to be needed to protect this species from browsing.

Two other minor species in this study—toro and mistletoe—were again being heavily browsed at the end of the study, after having had some respite. The more common and widespread indicator species appeared to be moderately or heavily browsed only when TCIs were close to the maximum levels recorded.

Individual broadleaved trees that were heavily browsed before control were much more likely to be browsed after control than were trees not browsed before control (Fig. 9A), indicating some preference for these individuals by possums. That preference does not reflect unbroken habitual use, because these trees were often not browsed again until 4 or more years after control.

Notwithstanding that strong preference for previously browsed trees, about 20% of the trees browsed in the final surveys had not been browsed before control. Unless the attractiveness of these trees to possums somehow changed, this indicates that they comprised an untouched surplus of edible foliage that was available before control.

The hypothesis that the medium-term average density of uncontrolled possum populations can be predicted largely by the abundance of non-foliar foods fits well with the low TCIs recorded in the beech forest of the Richmond Range. Species with large fleshy fruits (such as tawa) were absent there, while predominantly foliar-food species such as kāmahi, Hall's tōtara and māhoe were relatively common. In line with that, the simple correlations between species abundance on individual trap lines and the maximum TCI recorded on that trapline were most strongly positive for species that were seldom browsed but which did produce flowers and fruit eaten by possums, while the correlations were generally zero or negative for browsed species whose fruits are rarely important in possum diet (Fig. 26). Because browse reflects the use of foliage but not fruit, the same hypothesis provides a plausible explanation for the lack of any strong correlation between TCI and browse levels (Fig. 10).

Regardless of the explanation, closeness to maximum TCI is a poor predictor of current browse levels (Fig. 10), but does appear to reflect the maximum browse risk. Where possums are well below maximum levels, there is little risk of high browse pressure, but there can also be little browse when possum levels are high. This appears to make any broad measure of browse pressure unreliable as a trigger for management action, whether it is the browse scores used in this study or some other technique (Forsyth & Parkes 2005). We suggest that despite the technical challenges it poses, scoring browse on Hall's tōtara where available is likely to provide the most reliable indicator of medium-term browse pressure.

5.3 RESPONSES IN CANOPY COVER

There were significant changes in FCI during the study which, although difficult to distinguish from the variation in FCI attributable to observer error and other non-possum sources of variation, clearly had a substantial impact on tree survival. The overall change in FCI was small, reflecting a tendency for possums to focus strongly on only a few trees. Most of the common indicators were either never browsed or only ever very lightly browsed, resulting in minimal defoliation of these individuals before control and therefore little potential for change in them.

For the total sample of trees marked, there was in fact no net change in FCI at poisoned sites, but this is because substantial increases in FCI for some of the trees that were initially almost completely defoliated but which survived and recovered were offset (and therefore obscured during the calculation of averages) by the decline to zero FCI of similarly defoliated trees that died during the study. At unpoisoned sites, fewer heavily defoliated trees survived, resulting in a net decline in mean FCI at those sites (Fig. 21).

Trees that were never browsed during the study effectively provided *in situ* controls. For the broadleaved indicator trees at the poisoned sites that survived, the mean FCI scores for browsed trees always shifted toward that of unbrowsed trees in the first few years after control (Figs 12–14). This provides direct evidence of a possum-control effect. Further, the initial increases for browsed trees appeared to have slowed and even reversed at most sites by the end of the study (Figs 12–14), suggesting that either recovery was complete or that renewed browse by possums was again causing defoliation. At unpoisoned sites, there was a smaller difference between the browsed and unbrowsed frequency distributions for surviving trees, largely because more of the defoliated trees that initially contributed to the difference had died.

For Hall's tōtara, northern rātā and wineberry there was little evidence of a consistent response to reduced possum numbers (Fig. 15). For Hall's tōtara, it is likely that this reflects continued possum impact throughout the study because many trees continued to be browsed even after possum control (Appendix 3). The condition of browsed northern rātā at Matemateonga appeared to worsen over the first 4 years after control before eventually improving, which is consistent with the suggestion that opening up of clumps of foliage on rātā trees tends to result in ongoing foliage loss even if further browsing is prevented (Payton 1988).

The direction of change in FCI was only weakly linked to actual TCI, but the relationship was stronger when TCI was expressed as a proportion of the maximum recorded at the site. Again, this suggests the hypothesis that use of foliage is not closely linked to the absolute numbers of possums, but rather to the per capita availability of all foods (foliar and non-foliar). Importantly, at sites where the TCI was less than half the maximum recorded at the site, there were few negative changes in the overall mean FCI of the browsed indicators (Fig. 16).

As it is possible that some of the most highly preferred and most vulnerable individuals within species could be affected even at very low densities, managers will rarely be able to afford to prevent all damage by reducing possum numbers to zero. Instead, they are forced to identify some level of possum abundance below which any damage is deemed to be tolerable. That level may be termed a protection 'threshold'. For common broadleaved indicators such as kāmahi, tawa and māhoe, the threshold appears to be quite high—we conclude that these species are at risk of defoliation severe enough to elevate whole-area mortality rates only when the possum density exceeds half the uncontrolled maximum level.

The threshold for Hall's tōtara is clearly lower than for the common broadleaved species, with some browsing being recorded on tōtara even at very low TCIs. However, occasionally only low browse levels were recorded at TCIs as high as 25%. This species has high resilience to possum browse and, importantly, most browse affects only the outermost sunlit foliage (Nugent et al. 1997), so that complete defoliation is rarely seen and mortality rates are low relative to browse pressure, which will offset the continued use of this species at low TCIs.

Mistletoe was recorded at only one site, Mt Fell, where the maximum TCI was lower than at any other site. This species was being heavily browsed again and FCI was declining 6 years after control, when TCI levels were twice as high as were recorded in the pre-control survey. These limited data are consistent with this species being particularly vulnerable to possums, as has been shown for other mistletoe species (Sessions et al. 2001; Sweetapple et al. 2001).

5.4 EFFECT ON TREE MORTALITY

Most tree mortality in this study followed defoliation. On average, only about 0.5% of trees with initial FCI scores of 65 or greater died during the study, mostly as a result of storm damage, landslip or (for some tawa) frost. In contrast, about 6.5% of trees with initial FCI scores below 20 died each year.

Possum browse was a major factor affecting mortality. About 1% of trees that were never browsed died each year, compared with 1.5% of trees that were browsed at any time during the study. On a species basis, the lightly or never browsed control species, silver beech and pigeonwood, had mortality rates of < 1% p.a., while at the other extreme, browse was recorded on 97% of haumakaroa trees, 6% of which died each year. Light browse affecting < 25% of leaves appeared to increase mortality rates by about 40%, whereas for trees that were heavily defoliated, even light browse doubled the already high mortality rate, with almost 10% of such trees dying annually in areas without possum control.

The relationships between possum abundance and foliar cover (Fig. 15) and between foliar cover and mortality (Fig. 21), and the reduction in mortality following possum control (Fig. 23) together provide strong evidence that possum browse resulted in elevated tree mortality at many of the study sites, and that a modest level of possum control was sufficient to reverse much of that impact. The equivalence in the goodness of fit of models of tree mortality, regardless of whether the possum effect was expressed directly in terms of browse pressure, less directly in terms of post-control TCI, or less directly still in terms of the presence or absence of possum control, indicates the looseness of those relationships, with post-control TCI being a very weak predictor of how quickly TCI increased, and TCI being a weak predictor of browse pressure. Notwithstanding this, however, the analysis does provide strong support for the intuitively obvious: possum control reduces possum numbers, resulting in reduced TCI and reduced browse pressure, which in turn leads to reduced defoliation and, eventually, reduced mortality.

For the sites with no possum control, the annual mortality rate across all of the species monitored was 1.6%, which is close to the long-run all-species average of 1.5% p.a. reported from a study of 14 New Zealand forests (Bellingham et al. 1999a, b). The lower rate of 1.2% p.a. at possum control sites suggests that the increase in the overall relative risk of annual mortality caused by uncontrolled possums is of the order of 25%. However, this risk will vary greatly depending on the composition of the forest, and is likely to be highest in forest where the possum-preferred species predominate, as in the Matemateaonga and Ikawhenua Ranges (Appendix 1). In the beech-dominated forests of the Richmond Range, however, the low densities of possums present had little effect on mortality of common species such as kāmahi and silver beech and thus on overall mortality rates. There was still evidence of possum impacts on minor species, however. For example, haumakaroa was only recorded at possum control sites, yet suffered the highest mortality (37% over 6 years) of any species, because at the time of the first survey most trees were being heavily browsed and many were heavily defoliated. Two-thirds of the trees of this species that died did so in the first 2 years, suggesting that most had already reached a point of non-recovery by the time possum control was imposed. This high mortality of haumakaroa is consistent with the 47% mortality observed over 37 months for this species in

beech forest in northern Westland (Pekelharing et al. 1998), and provides more evidence for the authors' contention that although the most common species in beech forest are not at risk, some of the minor species may be highly vulnerable to possums.

5.5 EFFECT OF POSSUM CONTROL ON FRUITFALL

The wide variation in fruitfall between years, with different patterns for different species, highlights the unreliability of this food source for possums. At the poisoned sites, fruitfall was consistently higher for tawa but lower for pigeonwood. The pattern for tawa makes sense given that possums feed on developing fruit (PS, pers. obs.) and there is evidence from elsewhere that possums can suppress fruit production in hinau (Cowan & Waddington 1990), kohekohe (*Dysoxylum spectabile*; Atkinson 1985, cited in Cowan & Waddington 1990), and nikau (*Rhopalostylis sapida*; Cowan 1991). Unfortunately, we lacked fruitfall data from before control, so although the size of the difference appeared to diminish as possum numbers increased at the poisoned site, this interpretation can only be regarded as speculative because treatment and area effects were confounded. That confounding effect may explain the lower fruitfall for pigeonwood at poisoned sites, but an alternative possibility is that ship rat (*Rattus rattus*) numbers are likely to have increased substantially after control (Sweetapple & Nugent 2007): ship rats can feed heavily on fruits (Sweetapple & Nugent 2007) but appear not to eat tawa fruit (Beveridge 1964).

5.6 METHODOLOGICAL ISSUES

5.6.1 Trap catch

This study provided some of the earliest indications of potential problems and biases affecting the trap catch index of possum abundance. The indication from this study that TCI was lower in winter than in summer or early autumn for two sites with high possum densities has since been strengthened by evidence of higher trappability in summer in native forest at Maungatautari, Waikato (Forsyth et al. 2005). Likewise, the short-term within-survey trap shyness we suspected was being induced by leghold trapping has also since been documented in a study in Southland that showed that most of the shyness abated after 3–5 days (Morgan et al. 2007).

This study also provided early evidence that raised (platform) sets catch fewer possums than ground sets. Although this appears to contrast with Thomson et al. (1996), who reported no statistically significant difference between raised- and ground-set traps, they did actually record lower catches (38% TCI on platforms compared with 46% for ground sets). Likewise, Thomas & Brown (2000) recorded lower but not significantly different catch rates on raised sets in several different trials, and Henderson et al. (1999) recorded reduced bait consumption from elevated bait stations. Collectively, these and other unpublished studies provide convincing evidence that raised sets are less effective than ground sets. The management implication is that raised sets will generally produce lower estimates of possum density, so any target densities set in terms of ground-set catch rates

would need to be adjusted accordingly. The 5% TCI level that has been widely used in a variety of conservation management contexts would translate to about 3% for raised sets using our protocol.

The increases in TCI over the <2-year period after control generally exceeded the maximum exponential rate of increase conceivably achievable by possums. Therefore, we conclude that immediate post-control estimates of trap catch substantially underestimated possum density. This conclusion, and operational reports of similarly impossible rates of apparent increase, prompted studies that demonstrated a plausible link between the probabilities of a possum surviving control and it then being difficult to detect during post-control trapping (Arthur et al. 2002; Monks & Ramsey 2005). Morgan et al. (2007) hypothesised that possums spend most of their time at ground level in a variable number of small activity centres near food trees or den sites, with the number and location of those centres changing seasonally. Those with the smallest number of activity centres are presumed to be most likely to survive a poison operation and, for the same reason, less likely than average to encounter a trap at that time. However, since activity centres change seasonally in location and number, the bias in trappability is presumed to largely disappear. These results and hypotheses suggest that any activity-based index of possum abundance is likely to be biased after control if there is any link at all between the likelihood of being killed during control and the likelihood of possum activity being detected during monitoring.

5.6.2 Foliar cover indices

As subjective assessments depend partly on the observer, their scoring position under the tree, the quality of light and other factors, and annual and/or seasonal variation in foliar cover (Pekelharing et al. 1998; Payton et al. 1999), FCI data are inherently variable and therefore require large sample sizes to show statistically significant differences. This is especially true where the indicator species are common and possum effects are light. Therefore, to filter out irrelevant variation, more sophisticated sampling designs, methods and analytical procedures are needed. In this study, the most useful and powerful insight was often provided by within-species or within-area contrasts of trees based on browse and/or defoliation history. This highlights the value of pre-control assessment, and suggests that efforts ideally should be made to rigorously pair browsed and unbrowsed trees wherever practically possible. We also recommend inclusion of more than one 'non-preferred' tree species as within-treatment controls, and the use of multiple observers (all trees scored by at least two observers on each occasion). The browse classes recommended by Payton et al. (1999) are too coarse for quantitatively assessing the small amount of browse present after possum control, in that almost all such browse affects much less than 5% of leaves. Therefore, it may be better to score browse as a continuous variable rather than as a categorical one, both in the field and during analysis.

5.7 HOW LONG BEFORE NEXT TIME?

5.7.1 Context

This study adds considerably and much more comprehensively to the evidence for forest recovery after possum control by documenting the ‘possum impact – possum density’ relationships in more detail and for a broader range of species, including those that are most frequently used as operational indicators of possum impacts. We found, not surprisingly, that possum density or, more precisely, closeness to carrying capacity is loosely linked to browse pressure, but with low predictability in the relationship. We also found that the severity of browse pressure is linked to foliar cover, and that partially defoliated trees can recover when browse pressure is reduced. Finally, we found that the severity of defoliation is closely linked to mortality, and that possum control reduces mortality. Although none of these findings are surprising, this study provides an important step toward evidence-based management of native forests.

However, the study also highlights the complexity of the interrelationships between possum density, browse pressure, defoliation and mortality. Outcomes for individual trees, groups of trees and species differ according to their local context and original conditions. This complexity, coupled with the small size of the overall response, is likely to have been a major contributor to the paucity of historical evidence of plant responses to possum control.

5.7.2 Possum–plant interactions

It seems that in uncontrolled populations, possum abundance is not closely linked to the abundance of their main foliar foods, but is more strongly related to the abundance and diversity of fruit-producing species. In line with this, possum rates of increase have previously been linked to hinau fruit production (Ramsey et al. 2002). However, it appears that for some species, the effect of possums on fruit and seed production is usually minor relative to the annual variability in fruiting effort, so there is no strong negative feedback between herbivore abundance and food production. For these species, the plant–herbivore relationship is perhaps best characterised as primarily a reactive but non-interactive system in the classification outlined by Caughley & Lawton (1976), with possums responding numerically (reacting) to food availability but having little short-term interactive impact on the availability of non-foliar foods that appear to be most important. However, Caughley & Lawton’s (1976) classification is simplistic, because possums do have an impact on foliage cover and mortality that appears strongest for species whose foliage is most highly preferred, such as mistletoe, kohekohe, tree fuchsia and tōtara, but which also applies to species such as kāmahi and tawa whose foliage is slightly less preferred. There is therefore some potential for negative feedback to affect possum abundance, but because it is mediated through gradual change in species composition as a result of differential mortality, any such feedback may be inconsequential in the short term. Consequently, we conclude that modelling of possum populations and their rate of recovery after control can generally be undertaken without reference to vegetation condition, provided some estimate of the medium-term average pre-control density is available, or can at least be inferred from forest composition.

5.7.3 Protection thresholds

This study suggests that management aimed primarily at conserving the possum-preferred canopy dominants in an area will generally need only to maintain possum numbers below a target of about 40% of uncontrolled levels, possibly even higher. For conifer-broadleaved forest (i.e. forests with a possum carrying capacity similar to that in Matemateaonga and Ikawhenua), that target will usually exceed 20% TCI for raised sets, or c. 30% TCI for ground sets. For beech forest, possums seldom threaten the canopy dominants or common broadleaved sub-dominants, but, conservatively, protection of minor broadleaved subcanopy species such as haumakaroa appears likely to be achieved by holding possum numbers below about 5% TCI for ground sets.

For red mistletoe at Mt Fell, heavy browse, defoliation and mortality occurred over the final 2 years of the study when raised-set TCIs were 4–8% (50–100% of the maximum of 8%), indicating that protection of this sensitive species is likely to require ground-set TCIs below 2%.

For Hall's tōtara, there is no clear indication from this study about the levels of control needed to prevent defoliation, but it is clear that the protection threshold is lower than for the broadleaved species. However, this species is also fairly browse resistant, with no mortality recorded in 51 trees at Pine Valley during the study, even though possums were uncontrolled and TCI always exceeded 9% at that site. We therefore suggest that maintaining possum abundance below a ground-set TCI of 10–15% should be sufficient to protect this species, depending on the local possum carrying capacity.

5.7.4 Triggers for repeat control

The strategy of intermittent control requires repeated control either at a set interval or when some indicator of risk exceeds a trigger level or protection threshold. The former is simplest for planning purposes but is likely to be inefficient or ineffective unless the interval consistently coincides with the time it takes possums to recover to threatening levels, which of course depends on the effectiveness of the previous control.

Potential indicators of risk include measures of mortality, foliar cover, browse levels or possum abundance:

- **Mortality index:** This would be difficult to measure, and would probably be untimely in that at least some trees would have to have been killed by possums before control was reimposed.
- **FCI score:** This will also be somewhat untimely because possums will again have to have substantially defoliated some trees before their effect can be reliably distinguished from the numerous other sources of FCI variability. That disadvantage could be minimised by contrasting trees known to have been heavily browsed previously with trees that were never browsed. Alternatively, where that is not practical because the pre-control browse status is not known, the species with lowest protection thresholds could be used. Protecting these species will automatically also protect less vulnerable species, but the difficulty is that such species are typically rare, having already been driven to near extinction, as is often the case with fuchsia, for example (Pekelharing et al. 1998). As noted above (section 5.7.3), Hall's tōtara appears likely to be one of the most useful species in this regard.

- **Browse score index:** This would provide earlier warning of increasing threat, but at any point in time is unreliable because of the rapidity with which browse levels can change. Although that unreliability could be mitigated by regular surveys, these would obviously be more expensive. Again, use of Hall's tōtara or some other vulnerable but resilient equivalent would also help.
- **TCI index:** This probably provides the best trigger in terms of simplicity, ease and speed of survey, and timeliness. Provided sufficient monitoring of vulnerable tree species is undertaken in the first few cycles of intermittent control to confirm that the protection thresholds suggested above are appropriate for the species of most concern in the management area, measurement of TCI 1-2 years after control will provide early prediction of the earliest time at which browse and defoliation is again likely to be occurring at threatening levels.

5.7.5 Optimising the strategy

In our opinion, the high protection thresholds for common indicator species we have identified in this study are good news for managers. Where possums have long been present, we suggest our results indicate that it should be relatively easy to prevent major ongoing change in forest canopy composition caused by possums. Although more intensive protection is likely to be needed to protect rarer and/or more vulnerable species such as mistletoe (Sweetapple et al. 2002), the forest superstructure seldom appears to be threatened by possum populations that are maintained even modestly below carrying capacity. A visual observation supporting this was the contrast between the predominantly greyish colour of the canopy of the northern Matemateaonga sites immediately before control in 1996 and the deeper green of the canopy in an adjacent block of privately owned land where the owner regularly killed possums for their fur. Two years later, the difference between the blocks was no longer apparent (GN, pers. obs).

Optimising the balance between the costs and benefits of intermittent possum control clearly depends not only on the relationship between percent kill and costs, but also on the trigger point. If, for example, the trigger point is set at 50% of maximum density, then an 80% kill will provide just 3 years of protection, whereas a 99% kill would provide 12 years of protection. If, for a highly vulnerable species, the protection threshold is set at just 10% of maximum density, then an 80% kill would provide no protection at all, while a 99% kill would provide 7 years of protection. Unfortunately, it is not easy to predict kill accurately, let alone the cost per marginal increment in percent kill, so more detailed bioeconomic modelling is of little practical value. Nonetheless, we suggest that halving possum survival is warranted wherever it can be achieved at less than double the cost. Further, we recommend maximising the reduction in possum numbers, both to increase the duration and completeness of protection and to reduce the follow-up survey effort required to time the next operation.

6. Recommendations

Where possum control is imposed to primarily prevent major changes in canopy composition, possum populations should be controlled to below about 40% of the uncontrolled maximum levels. If, however, the goal is to protect species that are more vulnerable to possum impacts, then the control target will often be much lower.

Where possum control is imposed periodically (rather than continuously), advance planning for repeat control should be based on the predicted time required for the possum population to reach the designated protection threshold. If the prediction is based on TCIs recorded immediately after control, a higher-than-usual rate of intrinsic increase ($r_m = 0.45$) should be assumed to allow for post-control bias in TCI.

The need for repeat control should be confirmed empirically 1–2 years prior to the predicted control-repeat time by measuring possum abundance and the status (FCI) of selected indicator trees species. Ideally, this should involve comparison of the mean FCIs of formerly browsed and unbrowsed individuals within species.

With periodic control, the reduction in possum numbers should be maximised wherever the marginal percentage increase in the cost of doing so is less than the additional percentage reduction in possum numbers. That will maximise the time between repeat control, and give at least some respite from possum impact to the most vulnerable species.

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Appendix 1

RELATIVE ABUNDANCE OF COMMON PLANTS IN EACH OF THE THREE STUDY AREAS

Aproximate relative abundance (% of total cover; see methods) of the most common species or species groups, by area, in order of decreasing overall abundance. The species used as indicators are shown in bold, along with their designation as either possum palatable (P) or unpalatable (UP). Three species used as possum-preferred indicator species that were too rare to be listed in the table were tree fuchsia (*Fuchsia excorticata*), haumakaroa (*Raukawa simplex*) and red mistletoe (*Peraxilla tetrapetala*). The composition of the species groups listed is as follows: (i) beech species—black beech (*Nothofagus solandri* var. *solandri*), red beech (*Nothofagus fusca*), silver beech (*Nothofagus menziesii*), hard beech (*Nothofagus truncata*), mountain beech (*Nothofagus cliffortioides*); (ii) tree ferns—kātote (*Cyathea smithii*), ponga (*Cyathea dealbata*), mamaku (*Cyathea medullaris*); (iii) rātā trees—northern rātā (*Metrosideros robusta*), southern rātā (*Metrosideros umbellata*); (iv) *Elaeocarpus* species—hīnau (*Elaeocarpus dentatus*), pōkākā (*Elaeocarpus bookerianus*).

SPECIES	AREA		
	IKAWHENUA	MATEMATEAONGA	RICHMOND
Kāmahi (P), <i>Weinmannia racemosa</i>	17.2	22.1	22.2
Beech (UP), <i>Nothofagus</i> spp.	6.0	12.5	47.2
Tawa (P), <i>Beilschmiedia tawa</i>	33.0	18.9	0.0
Tree ferns, <i>Cyathea</i> spp.	8.6	9.3	1.7
Rewarewa, <i>Knighitia excelsa</i>	6.9	3.7	0.0
Māhoe (P), <i>Meliclytus ramiflorus</i>	5.9	2.3	1.8
Pigeonwood (UP), <i>Hedycarya arboreus</i>	0.8	4.3	0.0
Elaeocarpus spp. (P) (hīnau, pōkākā)	1.6	3.1	0.0
Scarlet climbing rātā, <i>Metrosideros fulgens</i>	0.3	2.8	0.0
Rimu, <i>Dacrydium cupressinum</i>	1.7	0.7	3.6
Supplejack, <i>Ripogonum scandens</i>	2.5	1.6	0.0
Red matipo, <i>Myrsine australis</i>	1.5	1.2	1.2
Horopito, <i>Pseudowintera colorata</i>	0.0	1.6	1.1
Miro, <i>Prumnopitys ferruginea</i>	0.3	1.3	1.7
Hall's tōtara (P), <i>Podocarpus hallii</i>	0.3	0.2	3.0
Rātā (trees) (P), <i>Metrosideros</i> spp.	0.8	1.0	0.7
Broadleaf, <i>Griselinia littoralis</i>	0.0	0.3	2.3
Kānuka, <i>Kunzea ericoides</i>	1.4	0.0	1.7
Horopito, <i>Pseudowintera axillaris</i>	0.3	0.6	0.7
Marbleleaf, <i>Carpodetus serratus</i>	0.6	0.3	1.5
Mingimingi, <i>Leucopogon fasciculatus</i>	0.3	0.0	0.8
Heketara (P), <i>Olearia rani</i>	0.5	0.7	0.0
Black maire, <i>Nestegis cunninghamii</i>	0.0	0.8	0.0
Toro (P), <i>Myrsine salicina</i>	0.0	0.7	0.0
<i>Metrosideros diffusa</i>	0.7	0.4	0.0
White climbing rātā, <i>Metrosideros perforata</i>	0.3	0.5	0.0
Tōtara, <i>Podocarpus totara</i>	0.1	0.4	0.0

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SPECIES	AREA		
	IKAWHENUA	MATEMATEAONGA	RICHMOND
Wheki, <i>Dicksonia squarrosa</i>	0.8	0.3	0.0
Tāwari, <i>Ixerba brexioides</i>	1.1	0.0	0.0
Tānekaha, <i>Phyllocladus trichomanoides</i>	0.5	0.0	0.0
Lancewood (P), <i>Pseudopanax crassifolius</i>	0.1	0.1	0.6
<i>Coprosma microcarpa</i>	0.0	0.0	0.9
Matai, <i>Prumnopitys taxifolia</i>	0.6	0.0	0.0
Bush lawyer, <i>Rubus cissoides</i>	0.0	0.2	0.0
White maire, <i>Nestegis lanceolata</i>	0.0	0.1	0.0
Wineberry (P), <i>Aristotelia serrata</i>	0.1	0.0	0.2

Appendix 2

MEAN TRAP CATCH INDICES FOR EACH BLOCK AND AREA BY TREATMENT

Mean trap catch indices (TCIs) (% ± SE) for each block and area by treatment (P = Poisoned, UP = Unpoisoned), for each year surveyed, and percentage reduction in TCI after initial poisoning.

BLOCK	TREATMENT	PRE- 96-97	POST- 96-97	% REDUCTION	POST 98-99	POST 00-01	POST 02-03	POST 04-05
Matemateaonga								
Charlies CHA	P	31.9 ± 4.2	1.5 ± 0.9	95.3	12.2 ± 2.1	22.1 ± 2.5	36.8 ± 4.8	39.0 ± 3.2
Coombes CMB	P	21.1 ± 3.5	1.5 ± 0.9	92.9	10.1 ± 2.0	15.9 ± 0.8	21.9 ± 2.2	19.7 ± 1.7
Matemateaonga MMO	P	21.8 ± 4.5	4.0 ± 1.3	81.6	14.1 ± 2.4	11.1 ± 3.0*	19.9 ± 2.5	18.2 ± 2.3
Tahupo East THE	P	35.7 ± 3.2	5.5 ± 0.8	84.6	11.7 ± 1.6	19.1 ± 3.2	43.5 ± 4.2	39.7 ± 3.1
Tahupo North THN	P	42.6 ± 6.5	2.0 ± 0.8	95.3	12.6 ± 2.6	10.7 ± 3.0	31.6 ± 4.2	30.2 ± 5.4
Tahupo South THS	P	58.0 ± 5.0	3.5 ± 1.5	94.0	18.2 ± 4.9	23.0 ± 3.6	43.8 ± 3.2	45.1 ± 4.3
Trains TRN	P	57.8 ± 3.1	4.0 ± 1.8	93.1	25.8 ± 6.2	34.9 ± 4.0	56.8 ± 5.4	41.1 ± 2.0
Rotorangi ROT	UP		13.7 ± 4.2		45.2 ± 6.3	19.0 ± 8.2	33.6 ± 1.6	26.8 ± 3.5
Tahunamaere TAH	UP		29.8 ± 4.6		51.1 ± 3.9	43.1 ± 4.1	57.2 ± 4.4	53.7 ± 6.1
Waitotara WAI	UP					39.5 ± 4.2	27.9 ± 1.8	47.8 ± 2.6
Ikawhenua								
Duckville DVL	P	35.5 ± 5.1	4.8 ± 1.6	86.4	18.4 ± 0.6	26.0 ± 2.2	27.3 ± 6.6	
Mangamako MKO	P	27.7 ± 3.2	2.0 ± 0.9	92.9	9.2 ± 2.1	13.0 ± 2.2	12.8 ± 1.1	
Otere OTR	UP	23.4 ± 5.0			25.9 ± 5.1	13.8 ± 3.0	19.6 ± 1.7	
Richmond								
Timms Forks FRK	P	13.3 ± 4.0	0.0 ± 0.0	100.0	6.1 ± 1.2	7.5 ± 1.0	10.6 ± 3.7	
Mt Fell MFL	P	4.0 ± 1.1	1.0 ± 0.9	75.2	2.7 ± 0.7	5.1 ± 1.2	8.6 ± 1.8	
Northeast Branch NEB	P	10.6 ± 1.5	0.0 ± 0.0	100.0	2.0 ± 1.3	5.6 ± 1.5	11.1 ± 2.5	
Pine Valley PVA	UP	13.0 ± 3.1	18.0 ± 2.9		9.5 ± 1.6	19.6 ± 1.9	14.2 ± 7.5	
Area means								
Matemateaonga	P	38.4 ± 5.4	3.1 ± 0.5	91.8	14.9 ± 1.9	19.5 ± 2.9	36.3 ± 4.6	33.3 ± 3.8
Matemateaonga	UP		21.7 ± 5.7		48.1 ± 2.1	31.0 ± 8.5	45.4 ± 8.3	40.3 ± 9.5
Ikawhenua	P	31.6 ± 2.8	3.4 ± 1.0	89.2	13.8 ± 3.3	19.5 ± 4.6	20.1 ± 5.1	
Ikawhenua	UP	23.4 ± 5.0			25.9 ± 5.1	13.8 ± 3.0	19.6 ± 1.7	
Richmond	P	9.3 ± 2.3	0.3 ± 0.3	96.4	3.6 ± 1.0	6.0 ± 0.6	10.1 ± 0.6	
Richmond	UP	13.0 ± 3.1	18.0 ± 2.9		9.5 ± 1.6	19.6 ± 1.9	14.2 ± 7.5	

* Unscheduled trapping occurred at the MMO site in 2000.

Appendix 3

MEAN BROWSE SCORES BY SPECIES, AREA AND TREATMENT

Mean browse scores by species, area and treatment for the first assessment (y0) and for the first three post-control surveys combined (y2-6). Mean browse scores were calculated by assigning the midpoint value (12.5, 37.5, 62.5 and 87.5) to each non-zero browse score class (1-4 respectively). See Appendix 1 for scientific names.

	IKAWHENUA				MATEMATEAONGA				RICHMOND				TOTAL	
	UNPOISONED		POISONED		UNPOISONED		POISONED		UNPOISONED		POISONED		y0	y2-6
	y0	y2-6	y0	y2-6	y0	y2-6	y0	y2-6	y0	y2-6	y0	y2-6		
Mistletoe											8.3	9.7	8.3	9.7
Hall's tōtara			8.1	6.3			30.6	11.5	16.3	6.9	24.1	4.6	22.5	7.6
Matipo							27.1	3.7					27.1	3.7
Tawa	9.7	2.7	7.8	1.3	15.8	6.7	14.9	2.5					13.3	3.0
Māhoe	9.9	4.2	7.2	1.5	21.5	6.3	14.2	2.3	3.6	0.6	12.4	1.4	12.6	2.5
Northern rātā	0.7	6.3	4.9	0.8	9.6	5.7	6.1	2.1				5.7	2.3	
Heketara	11.3	1.9	9.4	1.6	9.1	2.1	15.9	2.7					12.9	2.2
Kāmahi	5.5	3.0	7.4	1.1	26.3	12.3	4.5	0.9	4.4	0.6	3.5	0.1	6.9	1.9
Wineberry									18.8	4.4	9.3	0.2	13.4	1.6
Lancewood			1.3	2.6	8.2	5.6	9.2	1.2	3.1	1.6	10.1	0.3	7.9	1.4
Hīnau	1.3	1.4	0.8	0.4			0.0	0.0					1.2	0.7
Haumakaroa											22.8	0.5	22.8	0.5
Pōkākā									3.0	0.2	5.4	0.4	5.0	0.3
Pigeonwood	0.0	0.0	0.2	0.3	0.0	0.0	0.1	0.5					0.1	0.3
Southern rātā											5.8	0.0	5.8	0.0
Fuchsia									0.8	0.0			0.8	0.0
Silver beech									0.0	0.0	0.0	0.0	0.0	0.0
Total	6.6	3.2	6.3	1.8	14.1	5.5	11.4	2.5	7.0	2.0	10.0	1.3	10.1	2.4

Appendix 4

PERCENTAGES OF EACH TREE SPECIES THAT DIED, BY AREA AND TREATMENT

The totals are not weighted to adjust for the difference in study duration between Matemateonga (8 years) and the other two areas (6 years). See Appendix 1 for scientific names.

SPECIES	MATEMATEAONGA				IKAWHENUA				RICHMOND				TOTAL	
	UNPOISONED		POISONED		UNPOISONED		POISONED		UNPOISONED		POISONED		TOTAL	
	% DEAD	<i>n</i>	% DEAD	<i>n</i>	% DEAD	<i>n</i>	% DEAD	<i>n</i>	% DEAD	<i>n</i>	% DEAD	<i>n</i>	%	<i>n</i>
Haumakaroa														
Heketara	15.2	33	25.5	137	32.3	31	20.0	70			37.5	48	37.5	48
Fuchsia									23.1	13			23.1	13
Wineberry									27.8	54	12.9	62	19.8	116
Mistletoe											18.2	33	18.2	33
Northern rātā	22.2	18	18.0	172	11.8	17	11.8	68					16.4	275
Lancewood	26.9	26	15.0	40			20.0	10	17.9	56	12.8	125	16.0	257
Matipo	0.0	2	14.9	148	0.0	1	0.0	1					14.5	152
Māhoe	7.9	76	14.7	334	12.9	62	7.0	115	4.5	44	3.1	98	10.4	729
Kāmahī	33.3	108	8.4	574	4.3	70	0.8	127	0.0	51	1.8	163	8.3	1093
Tawa	4.5	111	7.9	378	7.5	53	3.3	122					6.5	664
Hall's tōtara			7.7	194	0.0	9	6.5	93	0.0	51	6.2	193	6.1	540
Pigeonwood	6.7	120	3.5	346	3.7	27	1.2	82					3.8	575
Silver beech									4.1	49	2.0	148	2.5	197
Hīnau	0.0	1	0.0	1	5.3	19	0.0	31					1.9	52
Pōkākā			0.0	1			0.0	1	0.0	42	1.1	94	1.4	138
Southern rātā											1.4	138	1.4	138
Total	14.3	495	10.7	2325	10.0	289	6.3	720	8.9	360	6.5	1102	9.4	5291

Can the impact of individual possum control operations be quantified?

*How forests respond to possum (*Trichosurus vulpecula*) control is not well understood. This report documents how possum populations, and the tree species they feed on, responded over 6-8 years following single aerial 1080 poisoning operations. The study showed that although the interactions between the possums and their food supply were complex, possum control did reduce possum browse, and therefore tree defoliation and, ultimately, tree mortality. Importantly, the study indicated that reducing possum density by 60% was sufficient to protect most of the possum-preferred tree species studied.*

Nugent, G.; Whitford, J.; Sweetapple, P.; Duncan, R.; Holland, P. 2010: Effect of one-hit control on the density of possums (*Trichosurus vulpecula*) and their impacts on native forest. *Science for Conservation* 304. 64 p.