Spatial variation in impacts of brushtail possums on two Loranthaceous mistletoe species

Peter J. Sweetapple
Landcare Research, PO Box 40, Lincoln 7640, New Zealand
(Email: sweetapplep@landcareresearch.co.nz)

Abstract: Browsing by introduced brushtail possums is linked to major declines in mistletoe abundance in New Zealand, yet in some areas mistletoes persist, apparently unaffected by the presence of possums. To determine the cause of this spatial variation in impact I investigated the abundance and condition (crown dieback and extent of possum browse cover) of two mistletoes (*Alepis flavida*, *Peraxilla tetrapetala*) and abundance and diet of possums in two mountain beech (*Nothofagus solandri* var. *cliffortioides*) forests in the central-eastern South Island of New Zealand. Mistletoe is common and there are long-established uncontrolled possum populations in both forests. Mistletoes were abundant (216–1359 per hectare) and important in possum diet (41–59% of total diet), but possum density was low (c. 2 per hectare) in both areas. Possum impacts were slight with low browse frequencies and intensities over much of the study sites. However, impacts were significantly greater at a forest margin, where possum abundance was highest, and at a high-altitude site where mistletoe density was lowest. Mistletoe crown dieback was inversely proportional to intensity of possum browsing. These results suggest that the persistence of abundant mistletoe populations at these sites is due to mistletoe productivity matching or exceeding consumption by possums in these forests of low possum-carrying capacity, rather than low possum preference for the local mistletoe populations.

Keywords: *Alepis flavida*; diet; mistletoe condition; *Peraxilla tetrapetala*; *Trichosurus vulpecula*

Introduction

The Australian brushtail possum (*Trichosurus vulpecula*) was introduced to New Zealand in the 1850s (Pracy 1974) and is now considered one of the most damaging of a suite of introduced herbivores in the country's indigenous forests (Cowan & Tyndale-Biscoe 1997). Possums modify indigenous forests by selectively browsing, and sometimes killing, mature trees of preferred species (Batcheler 1983; Payton 1987; Leutert 1988; Rose et al. 1992; Rogers & Leathwick 1997). The intensity of possum impacts varies between forest communities, largely due to inherent species differences in vulnerability to possums (Rose et al. 1992, 1993; Rogers & Leathwick 1997; Payton 2000). However, there is also marked spatial variation in possum impact on vulnerable species, within and among populations, both on local and regional scales (Batcheler 1983; Payton 2000).

These intraspecific spatial patterns in possum impacts are largely unexplained, although geomorphic processes appear to explain at least some of the regional variation in possum impacts in southern rātā–kāmahi (*Metrosideros umbellata – Weinmannia racemosa*) forests (Stewart & Rose 1988).[1] Provenance variation in palatability to possums has been proposed to explain regional differences in possum impacts on tree fuchsia (*Fuchsia excorticata*), but a test of this hypothesis (Sweetapple & Nugent 1999) failed to support it.

Loranthaceous mistletoes provide one of the best-documented New Zealand cases of spatial variation in possum impacts. These hemiparasitic plants were once widespread and abundant throughout much of New Zealand, particularly in *Nothofagus* (beech) dominated forests, but have undergone dramatic decline in many regions since European colonisation; one species, *Trilepidea adamsii*, is extinct (Norton 1991) and populations of the other five species have suffered local extinctions (Ogle & Wilson 1985; de Lange & Norton 1997; Bockett & Knightbridge 2004). Possums have been widely implicated as the causal agent of mistletoe decline, although much of the evidence is circumstantial (Ogle & Wilson 1985; Ogle 1997). A few quantitative studies have demonstrated high possum preferences for mistletoes at sites where mistletoes are rare (Sweetapple et al. 2002, 2004; Sweetapple 2003), or substantial possum impacts on mistletoes in some regions (Wilson 1984; Sessions

---

[1] Nomenclature follows Allan Herbarium (2000)

et al. 2001; Sweetapple et al. 2002). However, large and apparently vigorous mistletoe populations persist in the presence of long-established possum populations in some regions, particularly in eastern and central areas of the South Island (Owen 1993; Norton et al. 1997; Sessions & Kelly 2001). This regional variation in mistletoe populations in the presence of possums casts doubt over the role of possums in the national decline of these species, prompting studies of other factors such as the decline of indigenous avian pollinators and seed dispersers (Ladley & Kelly 1996; Robertson et al. 1999; Murphy & Kelly 2001) to explain widespread mistletoe decline.

I propose four potential hypotheses to explain regional variation in possum impacts on mistletoes. Regional possum impacts on mistletoe may vary due to (1) genotypic or phenotypic variation (in mistletoes or possums) in palatability of mistletoes to possums, (2) variation in preference (consumption relative to availability) for mistletoes by possums due to different possum food assemblages, (3) differences in mistletoe tolerance to possum browsing, and (4) differences in possum abundance relative to mistletoe abundance. Hypotheses 1 and 2 predict that possum dietary preference for mistletoe is low in low-impact regions, and (for hypothesis 2) is associated with high consumption of other strongly preferred foods. Hypotheses 3 and 4 predict that crown dieback is low relative to rate of possum browse, and possum abundance is low relative to mistletoe abundance, respectively, in low-impact regions.

This study tests hypotheses 1 and 2 by measuring possum preferences for mistletoes and other foods in two areas with apparently healthy populations of mistletoes and a long history of possum occupation, and comparing these with published preference data from other areas. Possum and mistletoe abundance and mistletoe condition are also measured to provide insight as to the merit of hypotheses 3 and 4.

Methods

Study areas

The study was undertaken in two areas of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest within the Waimakariri Catchment in the eastern South Island of New Zealand. One area is located on the eastern flank of the Craigieburn Range (43°08’S, 171°43’E), and the second on the north-eastern toe slope of Gray Hill (42°56’S, 172°01’E).

Two separate sites were studied at Craigieburn. Possum and mistletoe abundance, possum diet, and mistletoe condition were investigated in a 50-ha area at 1000–1100 m a.s.l. in the headwaters of the Broken River. Both *Alepis flavida* (yellow mistletoe) and *Peraxilla tetrapetala* (red mistletoe) were abundant at this site. These same parameters, but not possum diet, were also measured at a 10-ha site at Lyndon Saddle (1300 m a.s.l.) where *Peraxilla tetrapetala* was less common and *Alepis flavida* was rare. Both sites were located within a single block of forest totaling c. 2500 ha.

The Gray Hill area comprised a block, 500 × 900 m, at c. 800 m a.s.l. on the lower edge of extensive valley-side mountain beech forest. The lower 900-m boundary bordered unimproved pasture. Both *Peraxilla tetrapetala* and *Alepis flavida* were abundant throughout the study block area. The same parameters as for the lower site at Craigieburn were measured for the area as a whole, with the exception that separate measures of mistletoe condition were made for the forest–pasture margin (plants on pasture side of host trees on the boundary) and the forest interior (26–400 m away from the pasture margin).

The forests of both areas were similar, consisting of a monodominant canopy of mountain beech. Mountain beech was the host species for both mistletoe species in both study areas. Canopy height was c. 8 m at Lyndon Saddle and c. 20 m at the other two sites. Mountain beech also dominated the forest understoreys, often forming dense thickets of seedlings or saplings. Occasional small shrubs of *Coprosma* or *Pittosporum* species, the fern *Polystichum vestitum*, and scattered carpets of herbs, mosses, and filmy ferns (*Hymenophyllum* species) were the only other notable components of these forests.

In general these forests are regarded as having a low possum-carrying capacity, and possums have been present in both study areas for at least 50 years (Cowan 2005).

Mistletoe abundance and condition

Plots of 5-m radius were randomly located at Broken River (40 plots), Lyndon Saddle (20 plots) and Gray Hill (35 plots). The number of mistletoe plants found in each plot was recorded by species. For each mistletoe species present, the condition of the two individuals closest to the plot centre was recorded on each plot at Broken River and Gray Hill. Because mistletoes were less abundant at Lyndon Saddle, I assessed all suitable individuals encountered both on plots and while travelling between plots. Observable individuals were those that were clearly visible and had at least one branch longer than c. 20 cm. This gave totals of 64–80 plants of each species assessed at Gray Hill and Broken River, and 60 *Peraxilla tetrapetala* at Lyndon Saddle. Only three *Alepis flavida* were found at Lyndon Saddle. Subsequent possum-abundance assessment revealed that possums were more numerous at the forest margin than in the forest interior at Gray Hill. Therefore, an additional 74 *Alepis flavida* and 14 *Peraxilla tetrapetala* were sampled at the forest margin by measuring all observable mistletoes encountered along the 900-m pasture boundary within approximately 2 m of the pasture edge, a nearly complete census of this sub-group. This enabled mistletoe condition to be compared between two sites with different possum densities at Gray Hill.

Mistletoe condition was assessed using the foliar browse index (Payton et al. 1999). This included recording the amount of foliage browsed by possums on a 5-point scale (0 = no browse, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% browsed) and the amount of dead woody material (dieback) on a 5-point scale (0 = 0–5%, 1 = 6–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–99% of stems dead) for each assessed plant. Dead plants were noted but not scored. Percentages of browse and dieback were compared between species and sites within areas, using contingency tables. Error intervals given throughout the text are 95% Confidence Limits.

Possum abundance

Relative possum abundance was assessed at the three sites using the trap-catch method (NPCA 2004). In both areas Victor No. 1 leghold traps were laid at 20-m intervals on transects established along compass bearings. At Craigieburn, parallel traplines were set at 200-m intervals. There were three traplines of 20 traps at Broken River and two traplines of 10 traps at Lyndon Saddle, in November 2001. All traps were run for two fine nights. Trap-catch indices at Gray Hill were measured over three fine nights in July 2000 (A. Byrom, Landcare Research, Lincoln, unpubl. data). Six traplines were set parallel to the forest–pasture margin, one at the forest margin and the rest at 100-m intervals from the margin into the forests. Traplines were checked daily, captured possums killed, and sprung traps reset. At all sites, trap-catch rates were calculated as the number of possums caught expressed as a percent of the total trap-nights. Half a trap-night was subtracted for sprung-but-empty traps and non-target captures, but possum escapes (sprung traps containing possum fur) were treated as captures.

Possum diet and preference indices

Whole stomachs were taken from possums captured during possum density assessments and other collections at Broken River and Gray Hill. The percent dry weight of total stomach contents was determined for individual food items in each stomach using the layer separation technique (Sweetapple & Nugent 1998). A total of 46 stomachs were analysed from samples collected at Gray Hill in June 2000 (n = 25) and October 2001 (n = 21), and 38 stomachs were analysed from possums caught at Broken River in November 2001 (n = 10), March 2002 (n = 17) and July 2002 (n = 11). No distinction was made between the two mistletoe species during diet analysis because their foliage in stomach samples could not always be reliably separated. Mean percent dry weight of individual food items was calculated for each collection then averaged across all collections in each area to obtain percent-of-total-diet estimates.

The relative availability of forest plants can be estimated from percent cover data (Spurr & Warburton 1991; Owen & Norton 1995). Percent cover data were assessed on 35 and 40 randomly located, simplified Recce plots (Allen 1992) at Gray Hill and Broken River, respectively, with species cover scores given in each of three height tiers (0–2.0 m, 2.0–5.0 m, >5.0 m). Mistletoes were given a single cover score by species, regardless of position in the canopy, for each plot. Percent availability was then calculated for each species from percent cover data following Owen & Norton (1995) by weighting percent cover scores by the height interval of the tier in which the score was recorded, summing weighted scores, and dividing species totals by the total for all species. Mistletoes were assigned a height interval of 1.0 m, and mean top height of the canopy (Allen 1992) was recorded to calculate the height interval of the > 5.0-m tier.

Preference indices (PI) were then calculated for foliar foods using the method of Nugent (1990) as follows:

$$PI = \frac{\%diet - \%available}{\%diet + \%available}$$

where %diet = the percent of total foliar diet.

This produces values from −1.0 to 1.0. Negative or positive values indicate percent in diet is less than or greater than percent availability, respectively, while a value of zero indicates that percent in diet equals percent availability.

Results

Mistletoe abundance and condition

Mistletoes were abundant at both Broken River and the forest interior at Gray Hill, with densities of 1359 ± 226 and 840 ± 165 plants ha^{-1}, respectively. Mistletoes were present on 100% of plots at these two sites. *Alepis flavida* numerically dominated these populations, comprising 85% of Broken River and 81% of Gray Hill mistletoes. The 88 mistletoes recorded along 900 m of forest margin at Gray Hill equated to about 490 plants ha^{-1}. Mistletoes were less abundant at Lyndon Saddle (216 ± 80 plants ha^{-1}, present on 80% of plots) than at either Broken River or Gray Hill, but in contrast to the two latter sites, *Peraxilla tetrapetala* was the most common species (95% of mistletoes on plots). Although numerous, mistletoes contributed just 0.44% (Broken River and Gray Hill combined) to total estimated foliage biomass, as indexed by weighted percent cover scores.

Typical possum browse sign on both mistletoe species consisted of stems with many or all leaves reduced to just petioles, or totally defoliated live stems with the terminal buds missing. Often the youngest cohort of leaves was browsed while older leaves were left intact. Occasionally, recently dead stems, or whole dead plants, with heavy possum browse still evident were encountered at Lyndon

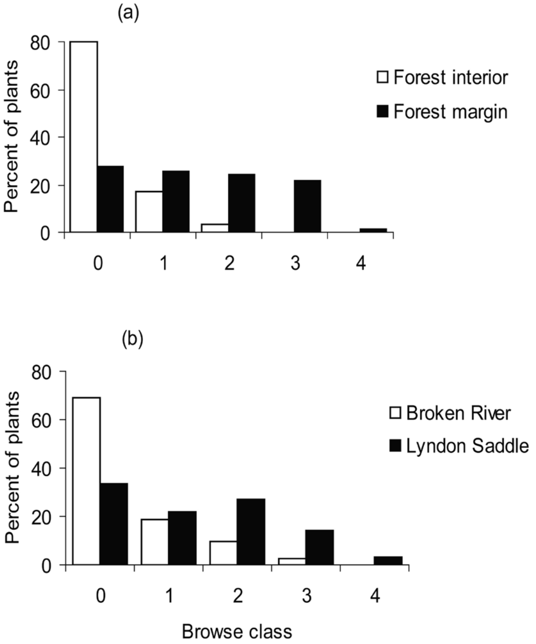

Figure 1. Frequency distribution of possum-browse-intensity classes for mistletoes (*Peraxilla tetrapetala* and *Alepis flavida* combined) at (a) Gray Hill and (b) Craigieburn. Browse classes are: 0 = no possum browse, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 75–100% of foliage browsed by possums.

Saddle and at the forest margin at Gray Hill.

Within the forest at Gray Hill 20% of mistletoes were browsed by possums with browse frequencies similar on both species (17% of *Alepis flavida* and 24% of *Peraxilla tetrapetala*, $\chi^2_1 = 0.8$, $P > 0.90$). No forest interior mistletoe had more than 50% of their foliage browsed. Possum-browse frequency was higher along the forest–pasture margin, where 70% of *Alepis flavida* and 100% of *Peraxilla tetrapetala* were browsed, than within the forest ($\chi^2_1 = 75.7$, $P < 0.001$). Browse intensity was also highest at the forest margin ($\chi^2_3 = 11.4$, $P < 0.01$) where 66% of possum-browsed plants had more than 25% of their foliage removed (browse classes 2, 3 and 4; Fig. 1a).

At Broken River 32% of all mistletoes were possum-browsed, and as in the forest interior at Gray Hill, frequencies were similar for both species ($\chi^2_1 = 1.4$, $P > 0.90$), with 28% of *Alepis flavida* and 36% of *Peraxilla tetrapetala* browsed. Browse frequencies were higher ($\chi^2_1 = 22.4$, $P < 0.001$), as was browse intensity on browsed plants ($\chi^2_3 = 33.7$, $P < 0.001$), in the sparser mistletoe population at Lyndon Saddle (Fig. 1b).

For all sites combined the frequency of dieback (> 5% of stems dead) on mistletoe plants increased significantly with increasing intensity of possum browse ($\chi^2_9 = 94.4$, $P < 0.001$; Fig. 2). Recorded dieback frequency increased from 31% of plants without observable possum browse to 94% of heavily browsed (> 50% of foliage) plants. Consequently, mistletoes at the two sites with the highest levels of possum browse (Lyndon Saddle and the forest margin at Gray Hill) carried significantly more dieback than those at the other two sites ($\chi^2_3 = 24.8$, $P < 0.001$).

Possum abundance and diet

Trap-catch rates were broadly similar at all sites. Mean trap-catch at Gray Hill was 8.3 ± 3.7%, but varied from 15.0% at the forest–pasture margin to a mean of 6.3 ± 1.8% 200–500 m within the forest (A. Byrom,

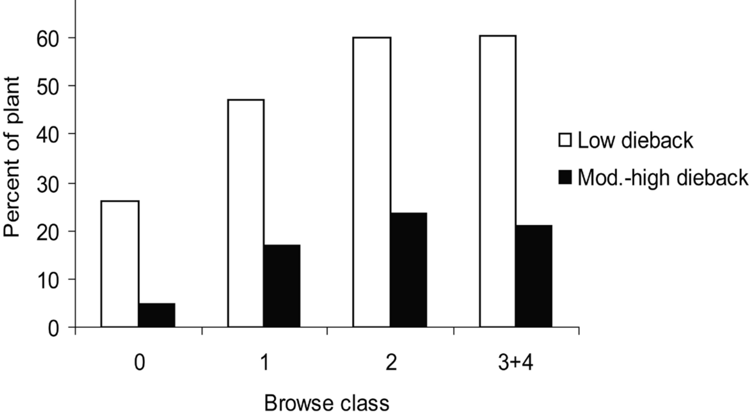

Figure 2. Frequency of low (6–25% stems dead) and moderate–high (26–99% stems dead) dieback recorded on mistletoe plants with different levels of possum browse (0 = no browse, 1 = 1–25%, 2 = 26–50%, 3+4 = 51–100% of foliage browsed) for all sites combined.

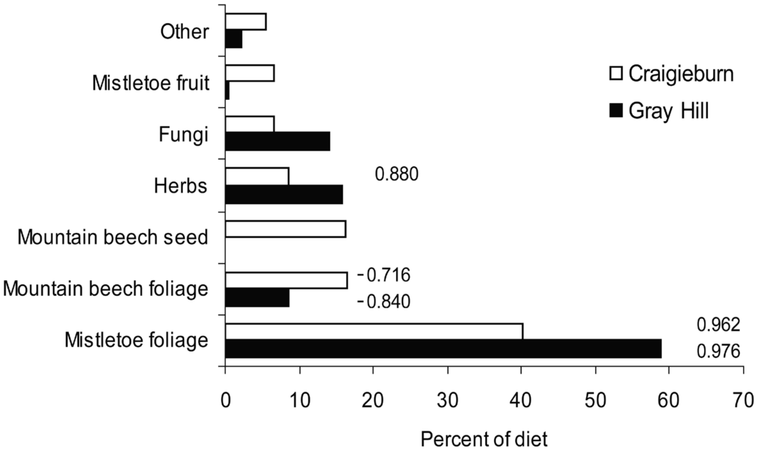

Figure 3. Possum diet at Gray Hill (forest margin and interior) and Craigieburn (Broken River site only) from June 2000 to July 2002. Preference indices, where available, are given at the right-hand end of columns.

Landcare Research, Lincoln, unpubl. data). Trap-catch rates at Craigieburn were 10.2 ± 4.0% and 10.0 ± 0.0% at Broken River and Lyndon Saddle, respectively.

The winter–spring possum diet at Gray Hill was dominated by mistletoe foliage, contributing 59% to total diet (Fig. 3). Pasture herbs, fungi and mountain beech foliage made up 93% of the remainder (Fig. 3). Mistletoe foliage was also the most commonly eaten food at Broken River at 40.1% of total diet (Fig. 3). Mountain beech seed and mistletoe fruit contributed 22.8% to total diet at Broken River, with the balance dominated by mountain beech foliage, herbs and fungi (Fig. 3). Mistletoe foliage was highly preferred by possums, with preference indices (both species combined) of 0.976 and 0.962 at Gray Hill and Broken River, respectively, close to their maximum possible value of 1.0.

Discussion

Mistletoe palatability

Foliage of red (*Peraxilla tetrapetala*) and yellow (*Alepis flavida*) mistletoes at both Craigieburn and Gray Hill was apparently very palatable to possums. Together they were the most commonly eaten food, and had very high preference indices (Fig. 3). Consumption of mistletoe foliage at both sites equalled or exceeded that of foliage from any single woody species in any previous New Zealand study of possum diet (Nugent et al. 2000). Similar levels of browse recorded for both species indicated that possums had similar preferences for both species, a result that is at variance with that of Sessions & Kelly (2001), who recorded that captive possums preferred *Alepis flavida* over *Peraxilla tetrapetala* foliage from Craigieburn.

Possum diet was only assessed in winter and spring at Gray Hill, and in winter, spring and autumn at Craigieburn. Had diet been assessed throughout the year, consumption of and preferences for mistletoe foliage might have differed from that recorded. However, even if possums ate no mistletoe foliage at all during the seasons not assessed, it would still have made up c. 30% of annual diet at both sites, giving high preference indices of 0.935–0.956.

Therefore, the abundant persistence of mistletoe in the presence of long-established possum populations at Gray Hill and Craigieburn cannot be ascribed to low possum preference for mistletoe foliage at these sites. Possums in both areas ate large quantities of, and had high preference for, mistletoe foliage.

Possums also exhibit strong preferences for Loranthaceous mistletoes elsewhere in New Zealand (Sweetapple et al. 2002, 2004; Sweetapple 2003). An exception was reported by Owen and Norton (1995), who recorded only a moderate possum preference for the beech mistletoe *Peraxilla colensoi* in the Haast Valley, South Westland. However, possums there were reported to have been colonising the site, and their diet was dominated by foliage of highly preferred seral species including tree fuchsia (*Fuchsia excorticata*), pōhuehue (*Muehlenbeckia australis*), and wineberry (*Aristotelia serrata*) (Owen & Norton 1995). Furthermore, Owen and Norton (1995) probably underestimated the contribution of mistletoe to possum diet in their study: stomach samples were washed through a 2-mm mesh and the larger fragments retained for analysis, leading to underestimates of the importance of thick-leaved species (e.g. *Peraxilla* spp.) relative to thin, soft-leaved species (e.g. tree fuchsia, pōhuehue, wineberry) in possum stomachs (Sweetapple & Nugent 1998). For example, in a small trial to quantify these biases, 2.0% and 28.8% of mistletoe and tree fuchsia foliage in possum stomachs, respectively, were retained after washing through a 2-mm mesh (n = 11 and n = 6, respectively) (unpubl. data).

These previous dietary studies cover four of the five extant New Zealand species of Loranthaceous mistletoe, with possum preference indices (Owen & Norton 1995, apart) all between 0.96 and 1.0. Therefore, I reject hypotheses 1 and 2 (variable possum preferences for mistletoe) as explanations for regional variation in possum impacts on mistletoes.

Abundance and condition of mistletoes

Which of the hypotheses best explains the persistence of large mistletoe populations in the study areas? As the preference data clearly refute the hypothesis that a low possum preference for mistletoe foliage is responsible, another explanation is required. The remaining hypotheses are that mistletoes in the study areas are unusually browse-tolerant (they survive despite high levels of possum browse; hypothesis 3) or that mistletoes, although vulnerable to possum browsing, are sufficiently abundant relative to low possum density in the study areas that their populations can sustain the current levels of possum browsing without annual mortality exceeding recruitment (hypothesis 4).

Browse tolerance can only be subjectively assessed with the data available, but high tolerance to possum browse does not appear to be an important factor in the study areas. Overall, possum browse pressure was low with ≤ 32% of plants browsed at Broken River and the forest interior at Gray Hill, with most of this browse in the lowest intensity category (Fig. 1). This compares with high browse frequencies (80–100% of plants) and frequent heavy browsing (> 50% of foliage removed) at Lyndon Saddle, the forest margin at Gray Hill (Fig. 1) and in some other areas (Wilson 1984; Sessions et al. 2001; Sweetapple 2003). Mistletoes in the current study areas that are heavily browsed do appear to be vulnerable to possum browse, because there was a strong relationship between browse intensity and dieback (Fig. 2). Field observations also indicate that heavy possum browsing was sometimes associated with mistletoe mortality.

Both mistletoe and possum abundance appear to be contributing factors to low possum impact in the study areas; mistletoes were abundant at both Gray Hill and Broken River, whereas possum densities were low in both areas. Trap-catch indices of about 10%, recorded in both areas, equate to a low density (about 2 possums ha^{-1}; Ramsey et al. 2005) compared with in other New Zealand indigenous forests (Efford 2000). Foliage production by the abundant mistletoe populations exceeding offtake by low-density possum populations is, therefore, a plausible explanation for the persistence of robust mistletoe populations in the study areas. This interpretation is supported by the increase in browse frequency and dieback where mistletoes were locally less common (Lyndon Saddle), or where possums were locally more abundant (forest margin at Gray Hill).

High-density and healthy mistletoe populations may still be at risk of possum-induced decline in the long term, due to edge effects. These populations are often of limited extent despite the lack of obvious habitat boundaries, and possum impacts are likely to be high at their population margins, because mistletoe abundance declines across the margins but possum abundance may not. The extent of high-density mistletoe populations may, therefore, be slowly reduced as possums continually degrade the population margins. At forest margins such as at pasture boundaries flower pollination and fruit set in mistletoe can be enhanced due to higher bird visitation rates (Kelly et al. 2000; Montgomery et al. 2003). However, the potential benefits from this may be offset by increased possum browsing at forest margins (Bach & Kelly 2004; this study).

Population dynamics and management

Population dynamics of consumers (e.g. possums) and their resources (e.g. mistletoe) are heavily dependent on whether the resource is a primary or secondary prey item. If primary prey, resource populations will be regulated by offtake by consumers and declines in resource abundance will trigger declines in consumer abundance (Holt 1977, 1984). Depending on time lags in resource or consumer population dynamics, this negative feedback mechanism provides potential for both the consumer and the resources to persist at equilibrium. If mistletoes are secondary prey, there will be no feedback mechanisms that drive possum abundance when resource abundance changes (Choquenot & Parkes 2001), therefore, resource populations can be reduced to low levels, or driven to extinction (type III or type II functional responses, respectively) by consumer offtake, or remain at high stable levels, depending on whether or not their initial density exceeds a level at which annual recruitment (e.g. foliage production) matches annual offtake by consumers (Schmitz & Sinclair 1997; Choquenot & Parkes 2001; Bayliss & Choquenot 2002).

Undisturbed possum abundance is broadly similar in all New Zealand simple beech forests, including the current study sites, regardless of mistletoe abundance (Clout & Gaze 1984; Wilson 1984; Owen & Norton 1995; Efford 2000; Sessions et al. 2001; Sweetapple 2003). Clearly possum populations have not markedly increased, relative to other simple beech forests, to fully utilise the abundance of mistletoe foliage at the current study sites. These observations suggest that mistletoe in these forests are secondary prey of possums. If so, the abundant, lightly browsed mistletoe populations at Broken River and lower Gray Hill probably represent stable equilibria, while the heavily browsed populations at Lyndon Saddle and the pasture margin at Gray Hill may represent unstable populations declining toward low-density equilibria or extinction.

Although the mistletoe populations at Broken River and the forest interior at Gray Hill are apparently healthy and probably stable, they may not remain so indefinitely. External perturbations that increase consumer (possum) abundance or decrease resource recruitment (mistletoe foliage production) can destabilise formerly high density equilibria driving resource populations to low densities or extinction (Choquenot & Parkes 2001). Management of mistletoe populations reduced by possums requires intensive possum control (Wilson 1984; Sweetapple 2003) to initiate population recovery. This control effort is likely to be required in perpetuity – or at least long term – until these slow-growing populations exceed levels at which annual production will exceed annual offtake by uncontrolled possum populations. Regular monitoring of high-density stable mistletoe populations would be prudent to ascertain that they remain stable.

That an abundant, highly preferred food (mistletoe foliage) in these food-poor simple beech forests is probably secondary prey of possums raises the question of what regulates possum abundance in these forests? If food-regulated, then the absence of any other common highly preferred food seen in the study sites suggests a food available intermittently, but not readily available during the sampling periods. The most likely candidate fitting this description is a flower, fruit or seed, possibly from beech which masts intermittently (Wardle 1984) and is consumed by possums in large quantities when available (Sweetapple 2003). The observations in this study and those of Sweetapple (2003) support the thesis of Nugent et al (2000, 2001) that foliage provides forest-dwelling possums with a subsistence diet only, and that their populations are largely regulated by the availability of high-energy, easily digested, non-foliar foods.

Acknowledgements

I thank G. Nugent for many informal discussions on possum dynamics and impacts over many years that have helped formulate ideas expressed in this paper. I also gratefully acknowledge A. Byrom for generously providing the June 2000 possum diet data from Gray Hill. Thanks also to C. O'Connor, G. Nugent, J. Parkes, R, Pech, G. Rogers, A. Robertson, and C. Bezar for comments on the draft manuscript. This work was funded in part by the New Zealand Foundation for Research, Science and Technology.

References

Allan Herbarium 2000. Ngā Tipu Aotearoa – New Zealand Plant Names Database. New Zealand, Landcare Research. Available http://nzflora.landcareresearch.co.nz (accessed April 2008).

Allen RB 1992. RECCE – an inventory method for describing New Zealand vegetation. FRI Bulletin No. 176. Christchurch, Forest Research Institute.

Bach CE, Kelly D 2004. Effects of forest edges on herbivory in a New Zealand mistletoe, *Alepis flavida*. New Zealand Journal of Ecology 28: 195–205.

Batcheler CL 1983. The possum and rata-kamahi dieback in New Zealand: a review. Pacific Science 37: 415–426.

Bayliss P, Choquenot D 2002. The numerical response: rate of increase and food limitation in herbivores and predators. Philosophical Transactions of the Royal Society London B 357: 1233–1248.

Bockett F, Knightbridge P 2004. South Westland: where the mistletoe are. Canterbury Botanical Society Journal 38: 33–39.

Choquenot D, Parkes J 2001. Setting thresholds for pest control: how does pest density affect resource viability? Biological Conservation 99: 29–46.

Clout MN, Gaze PD 1984. Brushtail possums (*Trichosurus vulpecula* Kerr) in a New Zealand beech (*Nothofagus*) forest. New Zealand Journal of Ecology 7: 147–155.

Cowan PE 2005. Brushtail possum. In*:* King CM ed. The handbook of New Zealand mammals. 2nd edn. Auckland, Oxford University Press. Pp. 56–98.

Cowan PE, Tyndale-Biscoe CH 1997. Australian and New Zealand mammal species considered to be pests or problems. Reproduction, Fertility, and Development 9: 27–36.

de Lange PJ, Norton DA 1997. New Zealand's loranthaceous mistletoes. Wellington, Department of Conservation.

Efford MG 2000. Population density, population structure, and dynamics. In: Montague TL ed. The brushtail possum: biology, impact, and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 47–61.

Holt RD 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12: 197–229.

Holt RD 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377–406.

Kelly D, Ladley JJ, Robertson AW, Norton DA 2000. Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe *Peraxilla tetrapetala* (Loranthaceae). In: Young A, Clarke G eds Genetics, demography, and viability of fragmented populations. Cambridge, Cambridge University Press. Pp. 241–252.

Ladley JJ, Kelly D 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): Dependence on birds. New Zealand Journal of Ecology 20: 69–79.

Leutert A 1988. Mortality, foliage loss, and possum browsing in southern rata (*Metrosideros umbellata*) in Westland, New Zealand. New Zealand Journal of Botany 26: 7–20.

Montgomery BR, Kelly D, Roberston AW, Ladley JJ

2003. Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Loranthaceous mistletoe. New Zealand Journal of Botany 41: 277–286.

Murphy DJ, Kelly D 2001. Scarce or distracted? Bellbird (*Anthornis melanura*) foraging and diet in an area of inadequate mistletoe pollination. New Zealand Journal of Ecology 25: 69–81.

Norton DA 1991. *Trilepidea adamsii*: an obituary for a species. Conservation Biology 5: 52–57.

Norton DA, Ladley JJ, Owen HJ 1997. Distribution and population structure of the loranthaceous mistletoes *Alepis flavida*, *Peraxilla colensoi*, and *Peraxilla tetrapetala* within two New Zealand *Nothofagus* forests. New Zealand Journal of Botany 35: 323–336.

NPCA 2004. Possum population monitoring using the trap-catch method. Wellington, National Possum Control Agencies.

Nugent G 1990. Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains, Otago. New Zealand Journal of Ecology 13*:* 83–95.

Nugent G, Sweetapple PJ, Coleman JD, Suisted PA 2000. Possum feeding patterns: Dietary tactics of a reluctant folivore. In: Montague TL ed. The brushtail possum: biology, impact, and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 10–23.

Nugent G, Fraser W, Sweetapple P 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. Biological Conservation 99: 65–79.

Ogle CC 1997. Evidence for the impacts of possums on mistletoes. In: de Lange PJ, Norton DA eds New Zealand's loranthaceous mistletoes. Wellington, Department of Conservation. Pp. 141–147.

Ogle C, Wilson P 1985. Where have all the mistletoes gone? Forest and Bird 16(3): 10–13.

Owen HJ 1993. Mistletoe and the brushtail possum in silver beech forest, South Westland, New Zealand. Unpublished MForSc thesis, University of Canterbury, Christchurch, New Zealand.

Owen HJ, Norton DA 1995. The diet of introduced brushtail possums *Trichosurus vulpecula* in a low-diversity New Zealand *Nothofagus* forest and possible implications for conservation management. Biological Conservation 71: 339–345.

Payton IJ 1987. Canopy dieback in the rata (*Metrosideros*) – kamahi (*Weinmannia*) forests of Westland, New Zealand. In*:* Fujimori T, Kimura M eds Human impacts and management of mountain forests. Proceedings of the 4th IUFRO Workshop P1.07-00, 1987. Ibaraki, Japan, Forestry and Forest Products Research Institute. Pp. 123–136.

Payton IJ 2000. Damage to native forests. In: Montague T ed. The brushtail possum: biology, impact, and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 111–125.

Payton IJ, Pekelharing CJ, Frampton CM 1999. Foliar Browse Index: A method for monitoring possum (*Trichosurus vulpecula*) damage to plant species and forest communities. Lincoln, Manaaki Whenua – Landcare Research.

Pracy LT 1974. Introduction and liberation of the opossum (*Trichosurus vulpecula*) into New Zealand. Wellington, New Zealand Forest Service.

Ramsey D, Efford M, Ball S, Nugent G 2005. The evaluation of indices of animal abundance using spatial simulation of animal trapping. Wildlife Research 32: 229–237.

Robertson AW, Kelly D, Ladley JJ, Sparrow AD 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conservation Biology 13: 499–508.

Rogers GM, Leathwick JR 1997. Factors predisposing forests to canopy collapse in the southern Ruahine Range, New Zealand. Biological Conservation 80: 325–338.

Rose AB, Pekelharing CJ, Platt KH 1992. Magnitude of canopy dieback and implications for conservation of southern rata-kamahi (*Metrosideros umbellata - Weinmannia racemosa*) forests, Central Westland, New Zealand. New Zealand Journal of Ecology 16: 23–32.

Rose AB, Pekelharing CJ, Platt KH, Woolmore CB 1993. Impact of invading brushtail possum populations on mixed beech-broadleaved forests, South Westland, New Zealand. New Zealand Journal of Ecology 17: 19–28.

Schmitz OJ, Sinclair ARE 1997. Rethinking the role of deer in forest ecosystem dynamics. In: McShea WS, Underwood HB, Rappole JH eds The science of overabundance. Deer ecology and population management. Washington, DC, and London, Smithsonian Institution Press. Pp. 201–223.

Sessions LA, Kelly D 2001. Heterogeneity in vertebrate and invertebrate herbivory and its consequences for New Zealand mistletoes. Austral Ecology 26: 571–581.

Sessions LA, Rance C, Grant A, Kelly D 2001. Possum (*Trichosurus vulpecula*) control benefits native beech mistletoes (Loranthaceae). New Zealand Journal of Ecology 25(2): 27–33.

Spurr EB, Warburton B 1991. Methods of measuring the proportions of plant species present in forest and their effect on estimates of bird preferences for plant species. New Zealand Journal of Ecology 15: 171–175.

Stewart GH, Rose AB 1988. Factors predisposing rata-kamahi (*Metrosideros umbellata-Weinmannia racemosa*) forest to canopy dieback, Westland, New

Zealand. GeoJournal 17: 217–223.

Sweetapple PJ 2003. Possum (*Trichosurus vulpecula*) diet in a mast and non-mast seed year in a New Zealand *Nothofagus* forest. New Zealand Journal of Ecology 27: 157–167.

Sweetapple PJ, Nugent G 1998. Comparison of two techniques for assessing possum (*Trichosurus vulpecula*) diet from stomach contents. New Zealand Journal of Ecology 22: 181–188.

Sweetapple P, Nugent G 1999. Provenance variation in fuchsia (*Fuchsia excorticata*) in relation to palatability to possums. New Zealand Journal of Ecology 23: 1–10.

Sweetapple PJ, Nugent G, Whitford J, Knightbridge PI 2002. Mistletoe (*Tupeia antarctica*) recovery and decline following possum control in a New Zealand forest. New Zealand Journal of Ecology 26: 61–71.

Sweetapple PJ, Fraser KW, Knightbridge PI 2004. Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand. New Zealand Journal of Ecology 28: 19–33.

Wardle JA 1984. The New Zealand beeches: ecology, utilisation, and management. Wellington, New Zealand Forest Service. 447 p.

Wilson PR 1984. The effects of possums on mistletoe on Mt Misery, Nelson Lakes National Park. In: Dingwall PR ed. Proceedings of the 15th Pacific Science Congress, section A4E, Dunedin, February 1983. Wellington, Department of Lands and Survey. Pp. 57–60.

Editorial Board member: Chris Lusk
Received 9 June 2008; accepted 11 August 2008