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A review of the damage caused by wild mammalian herbivores to primary production in New Zealand

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Manaaki Whenua – Landcare Research

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Summary

Project and Client

- Wild mammalian herbivores can compete with domestic livestock for forage and damage other production assets, including horticulture and silviculture. Environment Southland contracted Manaaki Whenua to review the damage caused by wild mammalian herbivores to primary production in New Zealand. The review was carried out between September 2017 and June 2018.

Findings

- With the exception of brushtail possums (*Trichosurus vulpecula*) and European rabbits (*Oryctolagus cuniculus*), there have been no direct quantitative assessments of pasture or crop depletion from wild mammalian herbivores on New Zealand farmland.
- Possums and rabbits can significantly deplete forage and reduce stocking rates of livestock.
- Based on indirect estimates using dry matter consumption by wild herbivores converted to stock unit equivalents, all species of wild herbivores that occur on New Zealand farmland have the potential to reduce stocking rates if they obtain a large amount of their food from forage and occur at moderate to high densities.
- There are only sparse quantitative data on the damage caused by wild herbivores to horticulture and silviculture in New Zealand.
- The process that farmers use to decide whether to control wild herbivores on their properties is complex. However, they do use available information to weigh up the expected costs and benefits of control. Less clear is how they respond to changes in forage availability following pest control: for example, do they alter their stocking rates of livestock to maximise marketable products?

Conclusions and Recommendations

- The lack of quantitative data on the impacts of wild herbivores on production assets is a significant knowledge gap. Even less is known about the impacts of these animals on production landscapes when multiple species occur sympatrically, as is often the case.
- A better quantitative understanding of damage in relation to pest density is needed for effective management, and we recommend this as a research priority for candidate species agreed upon by land owners, management agencies and research organisations.

1 Introduction

The primary resource for dry stock or dairy animals is pasture production (forage), and the main marketable products are beef, lamb, venison, milk, wool, and deer velvet. The economically astute farmer must optimise the use of forage to maximise these marketable products (Glimp 1988; Hunt et al. 2014), within acceptable environmental limits. Many farmers understand this optimisation challenge and are accomplished in its practice. They operate within the ebb and flow of seasonal forage availability to optimise their annual stocking rates and production from livestock (Macleod & Macintyre 1997; Matthews et al. 1999; Morris 2013). However, many farms around the world are shared by native or introduced wild herbivorous mammals, and these animals also consume forage and compete with livestock. If a large proportion of the available forage is eaten by wild herbivores, then the carrying capacity of livestock will, at least in theory, be reduced (Quinn 1968; Trdan & Vidrih 2008; Scroggie et al. 2012; Cooke et al. 2013; Davis et al. 2016). If the farmer does not place some value on the wild herbivores that are eating the available forage, such as for hunting or intrinsic reasons, they may be viewed as pests by the farmer, or legally defined as such by management authorities, and therefore controlled.

Despite the potential for wild herbivores to be pests, the relationship between the amount of forage consumed by wild herbivores and its effect on stocking rates remains poorly understood (Spurr & Jolly 1981; Cowan 2007; Davis et al. 2016), particularly when multiple wild species occur sympatrically on the same property (e.g. Parkes 2001; Mutze et al. 2016; Lush et al. 2017). Similarly, the costs and benefits of controlling wild herbivores to reduce their consumption of the available forage have not been well quantified (Norbury & Reddiex 2005), especially in relation to the decisions farmers make about adjusting their stocking rates following control, or as pest numbers increase.

Starting in the late 18th century and continuing until the early 20th century, a wide variety of wild herbivorous mammals were introduced into New Zealand for utility (a source of wild meat) and sport hunting (King 2005; Latham & Nugent 2017b). Nine species occur at comparatively high densities across large tracts of agricultural New Zealand, including: dama (or tammar) wallaby (*Notamacropus eugenii*), Bennett's wallaby (*N. rufogriseus*), common brushtail possum (*Trichosurus vulpecula*), European rabbit (*Oryctolagus cuniculus*), European (or brown) hare (*Lepus europaeus*), fallow deer (*Dama dama*), red deer (*Cervus elaphus*), feral goat (*Capra hircus*), and feral pigs (*Sus scrofa*). All of these species have diets that overlap those of domestic livestock (Parkes et al. 1996; Norbury 2001; Sadleir & Warburton 2001; Cowan 2007; Latham & Nugent 2017b), and some are maintenance or spill-over hosts for important agricultural diseases, such as bovine tuberculosis (TB), which is caused by the bacterium *Mycobacterium bovis* (Coleman & Cooke 2001; Nugent et al. 2015).

In concert with their unwanted impacts on native vegetation and ecosystems (Veblen & Stewart 1982; Wardle et al. 2001; Latham et al. 2017), their actual or perceived competition with domestic livestock for forage has meant that their populations have been lethally controlled, primarily by shooting and poisoning, for around 100 years (Sadleir & Warburton 2001; Nugent et al. 2012; Warburton & Livingstone 2015; Latham & Nugent 2017b). Controlling wild herbivores on New Zealand farmland is predicted to become increasingly important for some species as they expand into previously unoccupied areas (or reinvade areas from which they were historically eradicated), increase in number, and potentially cause

more damage (Fraser et al. 2000; Latham, Latham & Warburton 2016; Latham & Nugent 2017a).

Despite the known spatial and dietary overlap between wild herbivores and livestock in New Zealand, there is a surprising dearth of quantitative data on the damage wild mammals cause to agricultural, horticultural and silvicultural systems. For example, despite 140 years of European rabbit control in New Zealand, few studies have quantified forage depletion by rabbits (Lough 2009), and those that have, have been short-term studies conducted exclusively in dry short-tussock grassland in the central South Island (Norbury & Norbury 1996; Norbury et al. 2002; Scroggie et al. 2012). Apart from limited data for possums (Spurr & Jolly 1981; Dodd et al. 2006), there are, to our knowledge, no direct quantitative assessments of pasture or crop depletion (i.e. using experimental exclosures) for the other species of wild mammalian herbivores on New Zealand farmland.

However, a number of studies have used qualitative or indirect methods to estimate the economic costs of forage depletion by these herbivores on New Zealand farmland (Warburton & Frampton 1991; Cowan 2007). Moreover, studies from other parts of the world have assessed damage to production assets for some species of wild mammalian herbivores (e.g. see reviews for wild deer in the United Kingdom: Gill 1992b and Putman et al. 2011), which may be relevant to production landscapes in New Zealand. These studies are generally limited by a lack of information about the actual abundance or density of the wild herbivore relative to the depletion of pasture biomass, or other production assets. Instead, indirect indices of herbivore abundance are often used (e.g. surveys of faecal accumulation, active burrow counts, or spotlight night counts) (Putman et al. 2011; Latham, Nugent et al. 2012; Forsyth et al. 2015). This results in an inability to determine per capita forage consumption from forage off-take studies, but it does permit pest density–impact functions (or damage functions) to be derived, and in some cases these may be useful for identifying relative abundance thresholds above which control could be triggered (Hone 2007; Putman et al. 2011; Norbury et al. 2015).

The aim of this paper is to review the literature, including relevant overseas evidence, to assess the impacts of wild herbivores on primary production, especially agriculture, in New Zealand. In the absence of studies directly measuring per capita forage off-take using experimental exclosures, we used an indirect method to estimate forage depletion by wild herbivores: dry matter (DM) consumption of forage per unit time, converted to ewe equivalents (Warburton & Frampton 1991), and compared it with the annual DM consumption (550 kg) of one New Zealand stock unit (i.e. a ewe) to estimate its potential effect on livestock carrying capacity (Cowan 2007; Morris 2013). This information permits density–impact functions to be estimated, assuming a linear relationship for forage depletion (Statham 1994; Fleming et al. 2002), and we present some examples of these.

We also assessed the extent to which the economic impacts predicted by qualitative and quantitative methods trigger farmers to control wild herbivores on their land, compared with behavioural factors such as self-identity and subjective norms, or regulatory frameworks within regional pest management plans.

Finally, we reviewed published and grey literature to determine whether farmers respond to changes in forage availability following pest control by altering their stocking rates of livestock to maximise marketable products.

2   Damage to primary production by wild herbivores

2.1   Arable crops

Damage to arable crops by wild herbivores in New Zealand is well known, although most evidence is anecdotal or qualitative (e.g. Warburton 1986; Butcher 2000; McIlroy 2005; Norbury & Flux 2005; NPCA 2012, 2015). Crop damage can be locally severe but is often concentrated at the edges of crops, nearest to cover such as forest or scrub (Wheeler & Nicholas 1987; Butcher 2000; Warburton 2005a; Trdan & Vidrih 2008). Nevertheless, the actual or perceived damage to crops and plantation forests (see below) was a key factor for many species being designated as pests, especially in the late 19th and early 20th centuries, and the ensuing control operations against them (Wodzicki 1950; Caughley 1983; Nugent & Fraser 1993). Control operations reduced their densities in many agricultural areas, and, although variable, control also alleviated much of the damage from wallabies (Catt 1975), rabbits (Gibb et al. 1978), and red deer (Caughley 1983; Batcheler 1986; Nugent 2005) on production assets. If the densities or distributions of wild herbivores are permitted to increase as a result of relaxed levels of pest control, or the effectiveness of biological control agents decreases (e.g. rabbit haemorrhagic disease virus [RHDV]), damage to arable crops may increase (Fraser et al. 2000; Lough 2009; Latham, Latham & Warburton 2016; Latham & Nugent 2017a).

Possums feed on cereal crops and fodder crops planted for livestock, such as oats, lucerne, chou moellier (*Brassica oleracea* var. *acephala*), swedes and turnips (Gilmore 1965; Butcher 2000). In an exclusion experiment, Spurr and Jolly (1981) reported losses caused by possums of up to 26% in a swede crop, and estimated that the lost yield from a 0.4 ha block over 3 months would have supported 336 ewe equivalents for one day. Possums also eat a wide variety of other fruits, vegetables and garden flowers (summarised in Butcher 2000).

Rabbits can cause significant damage to a wide variety of cereal and horticultural crops in some parts of the world, including Australia (Wheeler & Nicholas 1987) and Britain (Bell et al. 1998; Dendy et al. 2004). Robust data from exclosure experiments on crop damage caused by rabbits are lacking for New Zealand. However, palatability and acceptability trials to identify suitable baits for controlling rabbits in Australasia have shown that a number of arable crops are readily eaten, such as carrots, oats and barley (Rowley 1963a, b; Nugent et al. 2012), suggesting damage to some types of crops may occur and be at least locally severe. Damage to vegetables from rabbits in New Zealand gardens is well known but not quantified (NPCA 2012). Similarly, hares damage market garden crops (e.g. asparagus, cabbages, cauliflower and lettuces) and cereal crops (e.g. corn, wheat and maize) (NPCA 2015), but there are no estimates of the economic cost of this damage in New Zealand.

Damage to crops by deer in New Zealand is also well known, but evidence is anecdotal or qualitative. Complaints by farmers about damage to their crops began in the early 20th century as deer numbers increased following liberations in the mid to late 19th century (Caughley 1983). This led to the influential report by Perham (1922), in which he detailed the extensive damage deer caused to crops, pasture and silviculture, and this was the first attempt by the New Zealand Forest Service to wrestle control of deer management from the Department of Internal Affairs. It was a convincing report, showing photographs of deer damage to crops, but it lacked quantitative data about the magnitude of the damage, per

capita consumption, and effects on stocking rates. Nearly one century later little new knowledge has been gained about deer damage to crops (and pasture) in New Zealand. Many documents report that deer damage crops (e.g. Caughley 1983; Fraser et al. 2000; Nugent 2005; Latham & Nugent 2017b), but rarely are the types of crops itemised and, to our knowledge, the magnitude of the damage is not quantified. Damage to swede crops has been reported by farmers from Southland, with about 44% of farmers in that region being concerned about the level of damage deer cause to crops and pasture (Latham, Craddock-Henry, et al. 2012). Sika deer (*Cervus nippon*) also feed on swede crops in central North Island (Davidson 1979).

The economic damage caused by red deer and Eurasian wild pigs to crops, especially wheat, maize and sunflower, averaged about NZ\$3.4–5.3/km^2 per year in the least affected counties in Hungary (Bleier et al. 2012). For the Hungarian counties most affected by deer and pigs, damage estimates were much higher (NZ\$500.65/km^2 per year; Bleier et al. 2012). Crop damage in Hungary was positively correlated with the relative abundance (based on hunting bag data) of red deer and wild pigs (Figure 1). Assuming that hunting effort and hunter success were equal across counties, an assumption often violated (Mysterud et al. 2007; Pettorelli et al. 2007), the figure shows that damage increases exponentially as harvest reaches about 0.8 deer/km^2. The relationship for pigs is not as strong and is primarily driven by one high observation corresponding to a harvest of 1.75 pigs/km^2. If this information is put into the context of a pest density–impact function, the trend lines best represent the 'resistant' or 'moderately resistant' relationships presented in Norbury et al. 2015. This means that crops are comparatively resistant to damage caused by, particularly, deer up to a threshold of c. >0.8 deer harvested/km^2 or >1 pig harvested/km^2. The patterns are indicative of the damage these two species might cause to crops in New Zealand.

Presumably damage by deer in New Zealand is most severe around the edges of crop fields, as has been shown elsewhere (Trdan & Vidrih 2008; Putman et al. 2011). However, if wild deer are sufficiently abundant and undisturbed by humans, damage may be more severe and occur further from crop edges. As some species of deer (e.g. fallow deer and red deer) have increasingly expanded into farmland via natural dispersal, farm escapes and human-assisted liberations (Fraser et al. 2000; Latham & Nugent 2017a), damage to crops and increased potential for conflict between neighbouring land owners with different values towards wild deer may increase (Latham et al. 2017). In a similar vein, quantitative data on the damage caused by wallabies and goats to crops are sparse or absent (Warburton 1986; Parkes et al. 1996).

The lack of quantitative data on the impacts of wild herbivores on crops and pasture is a significant knowledge gap. It has major implications for control, raising questions such as is their feeding activity negatively affecting production assets, and if it is, what level of control is needed to mitigate this damage? Moreover, wildlife management agencies are increasingly required to justify their control operations in terms of animal welfare; i.e. how many pest animals need to be killed to reduce the damage they cause, and is there evidence the desired outcomes have been achieved following control?
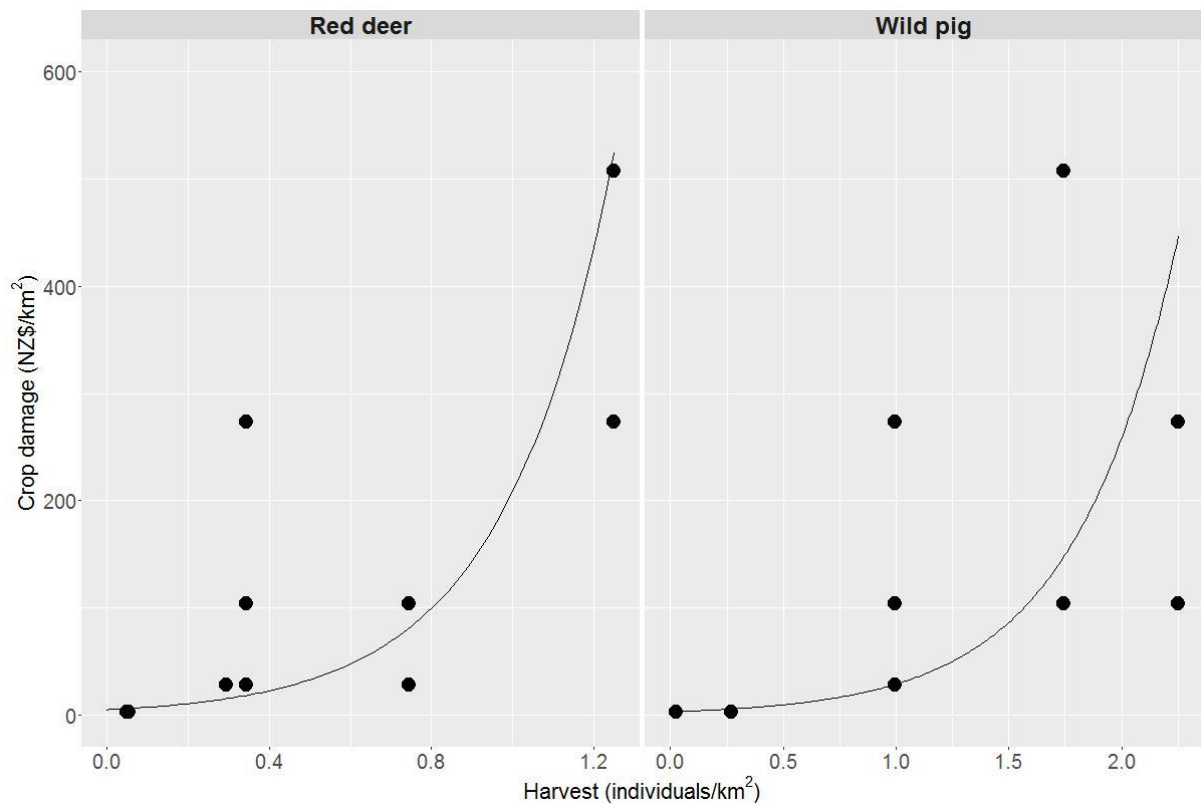
Figure 1: Economic damage to crops in 19 counties in Hungary (some points overlap) in relation to an index (hunter harvest) of wild red deer (*Cervus elaphus*) and Eurasian wild pig (*Sus scrofa*) abundance (data are from Bleier et al. 2012). Importantly, the x-axis does not represent absolute density, which is unknown.

2.2 Plantation forests

In New Zealand, damage by dama and Bennett's wallabies to young trees, particularly *Pinus radiata*, in newly planted production forests has been observed, but it is generally minor and restricted to 50–100 m from the forest edge (Warburton 2005a, b). The only quantitative measure of damage by wallabies to production forests in New Zealand comes from *P. radiata* in Waimate State Forest, South Island. Bennett's wallabies removed up to 20% of needles from seedlings near the forest edge, sometimes eating the entire apical buds and killing the seedlings (seedling survival ranged from 83–98% in the plots assessed) (Warburton 1986). Possum damage to plantation forests in New Zealand is generally low, with minor economic costs in most areas, but damage can be locally severe, with around 50% loss of 3-year-old seedlings at some sites (Warburton 1978; also see Clout 1977; Jacometti et al. 1997). The majority of possum damage involves needle clipping and damage to lateral branches, and it is negatively correlated with tree maturity (Jacometti et al. 1997). In Australia, local and seasonal damage by native wallabies and common brushtail possums to seedlings in native eucalypt and exotic pine plantations has been severe in some areas (McNally 1955; Wilkinson & Neilsen 1995; Di Stefano 2004).

Although not quantified, the damage caused by hares to plantation forests in New Zealand is considered significant (Norbury & Flux 2005). Hares eat the apical buds of pine seedlings and can strip the bark and lower branches from willow, poplar and citrus plantings (NPCA 2015).

In Europe, rabbits and hares can cause significant damage to tree plantations, particularly in winter when they are food limited (Gill 1992a). In Britain, rabbits have killed or damaged all seedlings within small forestry blocks days to weeks after planting (Lanier 1976), and hares have a characteristic habit of moving down a row of planted trees, browsing each in turn (Springthorpe & Myhill 1985). Damage by lagomorphs (hares and rabbits) to seedlings in larger forestry blocks is probably highest near forest edges (Gill 1992a).

Agroforestry research in New Zealand has shown that red deer and goats debark *P. radiata* until they are about 8 years old (Knowles 1991). Goats can be particularly detrimental to the survival of young pines (Hawke 1991). However, *P. radiata* are comparatively resilient to debarking, and provided the wound is less than one-third of the tree's circumference no significant loss of value occurs (Knowles 1991). Other plantation species, such as lodgepole pine (*Pinus contorta*), Scots pine (*P. sylvestris*) and Douglas fir (*Pseudotsuga menziesii*) are less resilient to bark-stripping and antler rubbing, and are more likely to be severely damaged or killed by these activities (Simberloff et al. 2003). Sika deer do little damage to pine trees in agroforestry environments in New Zealand (Knowles 1991), but they can cause severe damage to a variety of tree species in their native Japan by stripping bark to eat in summer (when food is most abundant), possibly to obtain essential minerals (Ando et al. 2004). Pine needles and bark made up 10% of the diet of sambar deer (*Rusa unicolor*) in coastal Manawatū, North Island (Stafford 1997).

Deer damage to plantation forests has been quantified in some temperate forest systems in the Northern Hemisphere (Gill 1992b). Red deer in Europe have little impact on young trees when they occur at low densities of c. 2 deer/km^2, but tree growth and survival decline quickly as the density of deer increases (starting at c. 3–4.5 deer/km^2) (Holloway 1967; Kraus 1987). At very high densities (25–50 red deer/km^2), young trees are killed and regeneration is prevented (Holloway 1967; Cummins & Miller 1982). Tree survival in Britain and Germany was unaffected by roe deer (*Capreolus capreolus*) at densities of 6–10 deer/km^2 (Holloway 1967; Stehle 1986), but browsing damage to conifers was strongly positively associated with an index (faecal pellet counts) of roe deer density (Ward et al. 2008). Fallow deer at very high densities (c. 100 deer/km^2) severely reduced tree survival in Britain (Putman et al. 1989). It is unlikely that fallow deer, or other deer species, in New Zealand would attain the density reported by Putman et al. (1989), although herds congregating in a plantation forest could theoretically cause similar damage if they were limited by a lack of other sources of food.

Feral pigs have been found to be capable of eating and killing large numbers of seedlings in plantation forests in the USA (Wood & Brenneman 1977).

2.3   Pasture depletion – evidence from exclosures

With the exception of possums and rabbits, there are no published studies that have directly assessed forage depletion by wild herbivores in New Zealand. To our knowledge, only two studies have quantified forage off-take by possums using an experimental exclosure approach (Spurr & Jolly 1981; Dodd et al. 2006). A field trial using wild, free-ranging possums in pasture–forest margins in Waikato, New Zealand, found that possums ate sufficient pasture to affect stocking rates (Dodd et al. 2006). They found that pasture yield was significantly greater inside exclosure plots compared with outside at sites where possums were not controlled (by c. 3 kg DM/ha/day in late winter and c. 7 kg DM/ha/day in late spring). In

comparison, there were no significant differences inside and outside exclosure plots at sites where possum control took place (Dodd et al. 2006). Conversely, Spurr and Jolly (1981) found no significant reduction of pasture yield that could be definitely attributable to possums. However, they suggest their results reflect the limitations of the trials (exclosures may have had a modified micro-climate and they only covered a small area) rather than a lack of significant possum damage.

European rabbits became established in New Zealand in the 1860s and spread rapidly in association with sheep farming (Wodzicki 1950). By the 1870s rabbits were considered a major agricultural pest in rabbit-prone areas, particularly in semi-arid Central Otago and the MacKenzie district, reducing forage otherwise available for livestock and causing erosion and soil loss at high densities (Kerr et al. 1983). Rabbit densities peaked in the 1940s, but control, particularly using sodium fluoroacetate (compound 1080), which was first used in New Zealand in the 1950s, greatly reduced their numbers and damage in many areas (Nugent et al. 2012). A report in 1978 stated that rabbits had not seriously affected farm production since about 1960, except in a few localities (Gibb et al. 1978). However, as no studies directly estimated forage depletion pre-1960, or until 1994 (Norbury & Norbury 1996), it is difficult to determine what effect rabbits have had on farm production (relative to other factors) over time. In addition to short-term direct forage depletion, it has also been predicted that stocking rates of livestock may be reduced if seed banks of palatable species are destroyed and do not recover once rabbits are reduced to low numbers (Leigh et al. 1989).

The three studies that have directly assessed forage depletion by rabbits in New Zealand span the introduction of RHDV, which was introduced in 1997, and therefore they also span a range of rabbit densities (Parkes et al. 2002). Norbury and Norbury (1996) reported that more pasture biomass accumulated where rabbits were prevented from grazing dry tussock grassland in Central Otago. They found that rabbits reduced yield by c. 84% in spring and c. 98% in summer. This work was done before the release of RHDV, and rabbit numbers ranged from 30–76 rabbits per spotlight kilometre (Norbury & Norbury 1996). Rabbit numbers declined to low numbers (3–6 rabbits per spotlight km) following the release of the original strain of RHDV, and this had a significant effect on pasture off-take (Norbury et al. 2002). Before the virus, about 74% of accumulated pasture biomass was removed by rabbits, compared with 34% after the virus had reduced rabbit numbers (Norbury et al. 2002). Rabbits had a detectable impact on pasture offtake 4–6 years after the release of the virus. Pasture grazed by rabbits and sheep on low productivity farms in Central Otago during 2001–2003 accumulated only when rabbit numbers were low (c. ≤ 10 rabbits per spotlight km) (Scroggie et al. 2012). If rabbit numbers increased to c. 20 or more per spotlight kilometre on these properties, pasture biomass did not accumulate in any season, and predicted stocking rates fell to zero in the most productive season, spring, at ≥ 10 rabbits per spotlight km (Scroggie et al. 2012).

On higher productivity farms (at which hares were also present), pasture biomass still accumulated when lagomorphs reached c. 50 per spotlight kilometre in spring and summer and 10–20 per spotlight kilometre in winter (Scroggie et al. 2012). Nevertheless, this had a noticeable effect on predicted stocking rates, with dry stock equivalents declining from 13 to 5 and from 6 to 0 in summer and winter (the primary food-limiting seasons for livestock in New Zealand; Dodd et al. 2006), respectively, when there were c. 30 lagomorphs per spotlight kilometre (Scroggie et al. 2012). Since these studies, rabbit numbers have increased to pre-

RHDV levels in some rabbit-prone areas (e.g. Lough 2009; Latham, Latham, Nugent et al. 2016) as immunity to the original RHDV strain has increased (Parkes et al. 2008). Presumably this has resulted in concomitant increases in pasture off-take by rabbits, but this has not been quantified.

In Australia, Short (1985) estimated from exclosure studies that 16 rabbits ate as much forage as one sheep, but noted that not all feed taken by rabbits would be eaten by sheep. Similarly, grazing pressure from rabbits at one site in South Australia was estimated at seven times the average maximum stocking rate in that area (Mutze 1991; also see Zaller 1986). At 'light to moderate' abundances, rabbits in Australia have been estimated to eat c. 10–47% of pasture biomass (Gooding 1955). At 'heavy' or 'very heavy' infestations they eat between 62 and 77%, and between 86 and 100%, respectively. Based on an interactive grazing model developed by Barlow (1987), the economic loss caused by rabbits in productive sheep grazing systems in New Zealand was estimated at $NZ1.1–2.1 per rabbit (1980s values, and assuming a gross margin per stock unit of $NZ21). Clearly this imposes significant costs on New Zealand agriculture. Attempts to estimate the average annual production loss due to rabbits (including control costs) in the 1990s ranged from $NZ22 million (c. $NZ34 million present value; Parkes 1995) to $NZ50 million (c. $NZ74 million present value; Hackwell & Bertram 1999).

Some species of deer, especially roe deer, fallow deer and red deer, are overabundant in parts of Britain and Europe (Apollonio et al. 2010). Here they can reduce pasture biomass (Rutter & Langbein 2005; Trdan & Vidrih 2008), but their damage is usually localised (Putman et al. 2011). Moreover, damage caused by deer to agriculture accounted for comparatively few of the total number of reported cases of damage to agriculture by any species of wildlife (e.g. c. 1% in Britain in the 1990s; Putman & Moore 1998), and most of these reports were related to damage to arable crops like barley, wheat, maize and sugar beet (e.g. Putman & Kjellander 2003).

As for New Zealand, few studies have directly estimated forage depletion by wild deer in Europe, and there are few objective data available for estimating the national economic significance of the damage caused by deer to agriculture. Red deer reduced forage grown for hay and silage near a forest border in Slovenia by an average 50% DW yield on plots not protected from their grazing compared with protected plots (Trdan & Vidrih 2008). On some of the most heavily affected sites, DW yield was reduced by 80%, but these were located immediately adjacent to forests that provided deer with cover (Trdan & Vidrih 2008; also see Putman et al. 2011). To our knowledge nothing is known about the effect of forage depletion by wild deer on stocking rates or livestock production in Europe (Putman & Moore 1998; Putman et al. 2011). Theoretically, however, such large reductions in pasture yield as reported from Slovenia (Trdan & Vidrih 2008) should negatively affect stocking rates, or in the case of hay and silage, force farmers to obtain additional winter feed from other sources. In North America, damage caused by native deer to agriculture is considered a major problem, but this also appears to be primarily to crops like corn, rather than pasture (Côté et al. 2004). Similarly, the distribution of introduced wild deer in Australia overlaps with livestock and may affect stocking rates, but this has not been quantified (Davis et al. 2016).

We are unaware of any overseas studies that have directly assessed forage depletion by other species of wild herbivores present in New Zealand (e.g. macropods). However, some studies

may be indicative of the damage these species might have on New Zealand pastures. Grazing by red kangaroos (*Osphranter rufus*) significantly impeded the accumulation of annual and perennial grass biomass, but not the biomass of forbs, in an exclusion experiment in destocked open shrubland in Western Australia (Norbury et al. 1993). Although red kangaroos primarily graze the pasture layer, whereas dama and Bennett's wallabies also browse woody species, it is likely that the damage caused by wallabies at high densities in New Zealand does not differ greatly from that reported by Norbury et al. (1993) (also see Warburton 2005a, b). We acknowledge, however, that this comparison may be affected by different mechanisms driving the arid Australian system versus the New Zealand system (Caughley 1987; Choquenot & Parkes 2001).

Feral goats in Australia have caused significant economic losses by eating pasture and competing with livestock, particularly sheep in semi-arid rangeland (Harrington 1982; Parkes et al. 1996). Henzell (1989) estimated a net average cost per feral goat to sheep graziers in Australia of NZ$14.7 (present value) per goat (this cost accounts for profits farmers can make from mustering and selling feral goats). The total average annual loss to sheep production due to feral goats in Australia in the early 1990s was estimated to be c. NZ$32.5 million (present value) (Parkes et al. 1996). Feral goats in New Zealand are most common in rocky habitats such as cliffs along river gorges and in some forest and shrub systems, and therefore tend to overlap pasture used by domestic livestock less than in the rangelands of Australia (Parkes 2005). Thus, the net average cost per feral goat to sheep farmers in New Zealand would probably be substantially less than in Australia.

Although omnivorous, feral pigs primarily consume plant matter (McIlroy 2005). Where they overlap agriculture, feeding and rooting by feral pigs can cause significant damage to pasture and crops (e.g. Gong et al. 2009; Bengsen et al. 2014; Gentle et al. 2015). Although feral pig populations are limited by pasture availability in some areas (e.g. the rangelands of Australia), they have little influence on variation in pasture biomass in those areas (Choquenot 1998). Choquenot (1998) stated that because pigs are inefficient grazers and usually occur at low average densities relative to other domestic and wild herbivores, competition with domestic livestock for pasture is probably negligible in most areas. However, an economic analysis of the economic damage caused by vertebrate pests in Australia found that feral pigs contributed significantly to annual economic losses for grain producers and the sheep industry (c. NZ$9 million present value) (see Table 3.13 in Gong et al. 2009). Feral pigs can also directly affect domestic livestock, particularly sheep, via predation of new-born lambs (Pavlov & Hone 1982; Choquenot et al. 1997; McIlroy 2005; Latham, Craddock-Henry et al. 2012). In New Zealand, loss of lambs to pigs is rare and localised, except in back-country farms close to native forest (McIlroy 2005). Also, pigs can indirectly affect livestock by maintaining and transmitting TB (Nugent et al. 2015).

2.4   Forage depletion – indirect estimates

Much of the information about DM consumption of forage by wild herbivores has not been directly quantified. An alternative method is to derive estimates of DM consumption using foraging studies from their domesticated counterparts and multiply these estimates by the density of the wild herbivore population. This approach has a number of limitations. For example, the proportion of daily DM intake from forage compared to other food sources (e.g.

browse) will be different between domestic and wild herbivores (e.g. red deer, Nugent 2005; pigs, Lincoln College 1972; Gentle et al. 2015). Although this proportion can be quantified from dietary analysis, these techniques are not without bias, particularly when diet includes a variety of plants with different digestibility or decomposition rates (Barker 1986).

Moreover, the amount of food wild herbivores obtain from pasture will be spatially and temporally variable. For some species, such as possums (Butcher 2000) and deer (Bleier et al. 2016), it will vary depending on their proximity to the forest–agricultural edge, and pasture in the diet may be more important in some seasons than in others. For example, in some areas feral pigs increase their use of crops and pastures in summer compared to the rest of the year (McIlroy 1989). Daily food intake requirements also vary with the animal's age and seasonal changes in the nutritional quality of the forage (Hudson & White 1985). These factors have been quantified for domestic livestock (e.g. https://deernz.org; https://beeflambnz.com; accessed 15 May 2018), but not for wild herbivores.

Estimated stock unit equivalents for each species of wild herbivore in agricultural New Zealand are presented in Table 1. Values vary from 105 possums consuming the equivalent of one SU, to 0.4 and 0.56 for red deer and fallow deer, respectively. For red deer, for example, this means that one mature deer consumes the same amount of DM forage as 2.5 sheep. These values need to be used cautiously, however, as they can vary greatly within a species, primarily because the amount of forage eaten by individuals is influenced by a number of location- and season-specific factors. These include the physiological condition of the animal, nutritional and digestibility characteristics of the forage, and climatic conditions (Crawley 1983).

For example, Rayner (2010) estimated a maximum daily intake rate of c. 151 g kg$^{-0.75}$ for rabbits in improved semi-arid pasture in Central Otago (equivalent to 7.3 rabbits equalling one SU; Table 1), but up to c. 223 g kg$^{-0.75}$ in semi-improved pastures (equivalent to five rabbits equalling one SU). Moreover, both of these estimates are substantially higher than those estimated by Short (1985) and Cooke (2014) in semi-arid chenopod shrublands in Australia (i.e. 16.5 rabbits to one SU; Table 1). They are also higher than estimates (74–80 g per rabbit per day) derived using allometric relationships (Nagy et al. 1990). Rayner (2010) attributed differences between studies to the physical and nutritional characteristics of the vegetation, its availability to rabbits, and competition among wild and domestic herbivores (which were excluded in the Rayner 2010 experiments).

Table 1: Daily dry matter (DM) forage consumption and stock unit (SU) equivalents for the common species of wild herbivores present in agricultural areas of New Zealand. SU equivalents were calculated as the number of individuals of a given species required to consume the annual DM eaten (550 kg) by one New Zealand SU (i.e. one ewe)

Species	Weight[a]	Total daily consumption (kg DM/head)	Description of total daily consumption assumption	Reference for total daily consumption	Proportion of pasture in diet	Daily forage consumption (kg pasture DM/head)	1 SU equivalent[b]
Brushtail possum	–	0.0478		Cowan 2007	30%	0.0144	105
	–	0.080		Dodd et al. 2006[c]	25% (winter)	0.0200 (winter)	45[c]
Fallow deer	–	2.71	1–2.1 SU depending on size, 3-year average = 1.8 (but consumption varies depending on age and season)	Deer Industry NZ[d]	100%	2.71	0.56
Red deer	–	3.77	1.5–3.5 SU depending on size, 3-year average = 2.5 (but consumption varies depending on age and season)	Deer Industry NZ[d]	100%	3.77	0.40
Feral goat	–	1.05	Meat goat (40 kg) consumes 1.2 kg DM/head/day; fibre goat (30 kg) consumes 0.9 kg DM/head/day	Meat and Wool New Zealand 2008; Parker 1998	Meat goats consume 30% pasture, fibre goats consume 50% pasture	1.05	1.43
Feral pig	–	1.25	500 meal units (MU) per year for a pig to reach a live weight of 91 kg by 6 months = 1.37 MU per day. 1 MU = 0.91 kg DM pasture	Gentle et al. 2015	24% (16% of diet biomass from grasses + 8% from forage sorghum in Queensland)	0.3	5
		1.25		Lincoln College 1972, based on 90 kg domestic pig	100%	1.25	1.2
Dama wallaby	4.4 kg	0.151	g DM/day = 0.20 * (g body mass$^{0.79}$) (Nagy et al. 1990)	Warburton & Frampton 1991	100%	0.151	10
Bennett's wallaby	13 kg	0.356			100%	0.356	4.2

Species	Weight[a]	Total daily consumption (kg DM/head)	Description of total daily consumption assumption	Reference for total daily consumption	Proportion of pasture in diet	Daily forage consumption (kg pasture DM/head)	1 SU equivalent[b]
European rabbit	1.5 kg	0.092	g DM/day = 68 / (kg body mass$^{0.75}$)	Cooke 2014; Short 1985	100%.	0.092	16.5
	1.5 kg	0.205	151 g DM / kg body mass$^{0.75}$ (in improved semi-arid pastures)	Rayner 2010	100%	0.205	7.3
European hare	3–4 kg, but up to 5 kg. Assumed 4 kg	0.215	g DM/day = 0.235 * g body mass$^{0.822}$	Nagy 1987	100%	0.215	7
	–	0.132	0.132 kg DM/day (in New Zealand tall tussock grasslands)	Perry & Robertson 2012	100%	0.132	11.4

[a] Weights included only for those species for which allometric relationships were used to derive daily food intake (weights obtained from King 2005)

[b] Assumes 1 SU consumes 550 kg DM per year

[c] Assumes 1 SU consumes 328.5 kg DM per year (based on winter consumption of 900 g per day)

[d] https://deernz.org; accessed 15 May 2018

Choquenot (1998) estimated that the daily DM intake rate of pasture by feral pigs in Australia's rangeland could vary from 0 to 1.4 kg for an 85 kg pig and was primarily related to available pasture biomass. Although these estimates are similar to those presented in Table 1, they are substantially less than those estimated for slightly larger Iberian pigs (c. 110 kg) grazing in natural pasture in southern Spain (3.6–4.0 kg per pig, Rodríguez-Estévez et al. 2008). All of these estimates are based on pigs obtaining food exclusively from pasture, and this produces an SU equivalent of 1.2 pigs to one ewe. However, if feral pigs include a smaller proportion of pasture in their diet (as shown by Gentle et al. 2015), the SU equivalents can be as much as five pigs to one ewe.

Most estimates of pasture consumption are derived from large domestic or semi-domesticated pigs (c. 100 kg or more). Weights of feral pigs in New Zealand vary widely but are likely to be more like 40 kg on average (King 2005). This means that per capita consumption by feral pigs in New Zealand will be less than reported above, and the ratio of pigs to SU equivalents will be higher. Therefore, unless the density of feral pigs is high, they are unlikely to have a noticeable impact on stocking rates, although they do destroy pasture with their rooting (McIlroy 2005). The results from Table 1 (if not corrected for the average weight of feral pigs in New Zealand) may be more relevant for the damage caused by larger-bodied feral pigs in North America and Eurasian wild pigs in Europe (weight range 44–320 kg, Seward et al. 2004; Meijaard et al. 2011).

Hypothetical density–impact functions, assuming a linear relationship between forage depletion and pest density (Statham 1994; Fleming et al. 2002) are shown for fallow deer and red deer in Figure 2, and Bennett's wallaby and dama wallaby in Figure 3. To create these, we used the classification of Morris (2013) to acknowledge that different grassland types in agricultural New Zealand have different carrying capacities of livestock per hectare and will therefore be affected differently by the damage caused by wild herbivores. The three grassland types included flat to rolling pasture, hill country pasture, and high-country pasture (Table 1 in Morris 2013). For each of these grassland types we estimated the reduction in SUs as a function of wild herbivore density (assuming the amount of pasture consumed per individual remains constant as pest density increases) using the SU equivalents in Table 1 above. For both species of deer, the SU equivalent in Table 1 assumes that their diet comprises 100% pasture. However, Nugent (2005) reports that around forest margins, only 70–80% of deer diet comprises grasses and herbs, with the remainder taken as browse. Accordingly, we also present reductions in SUs assuming deer diet is composed of a lesser amount of pasture (75%, the average from Nugent 2005, and a hypothetical average of 50%) (Figure 2). The SU equivalent for wallabies in Table 1 assumes their diet comprises 100% pasture; however, for illustrative purposes, we also present SU reductions assuming wallaby diet is composed of 75% and 50% pasture (Figure 3).

Fallow deer at high densities (0.3/ha) could reduce stocking rates per hectare by 1.9–3.9% in flat to rolling country and 3.6–7.2% in hill country (Figure 2). For an average farm in North Island hill country (530 ha, Morris 2013), this would represent a loss of between NZ$17,600 and NZ$35,000 per year (Table 2). In the high country, stocking rates would be reduced by 38–77% at high densities of fallow deer. Red deer at high densities (0.3/ha) could reduce stocking rates per hectare by 2.7–5.4% in flat to rolling country and by 5–10% in hill country (Figure 2). For an average farm in hill country, this would represent a loss of between NZ$24,500 and NZ$49,000 per year (Table 2). In the high country, stocking rates would be

reduced to nil at red deer densities of c. 0.28/ha. In reality, the densities of both these species is likely to be substantially lower than 0.3/ha (Latham & Nugent 2017b), and therefore the economic damage they cause will be substantially less than that estimated above. Nevertheless, deer in parts of the USA and Europe can occur at densities comparable to or higher than 0.3/ha (Côté et al. 2004; Putman et al. 2011), and historically they were in parts of New Zealand (Forsyth et al. 2010). If permitted to increase in density on production landscapes, our estimates are indicative of the economic damage deer have the potential to cause.

Dama wallaby at high densities (6/ha) could reduce stocking rates per hectare by 2.2–4.3% in flat to rolling country and 4–8% in hill country (Figure 3). For an average farm in hill country, this would represent a loss of NZ$19,500–$39 000 per year (Table 2). At intermediate densities (3/ha) stocking rates per hectare would be reduced by 1.1–2.2% in flat to rolling country and 2–4% in hill country (Figure 3). In the high country, stocking rates would be reduced by 43–86% at high densities of dama wallabies. Bennett's wallaby at high densities (6/ha) could reduce stocking rates per hectare by 5–10% in flat to rolling country and 9.5–18.9% in hill country (Figure 3). For an average farm in hill country, this would represent a loss of NZ$46,000–$92,500 per year (Table 2). In the high country, stocking rates would be reduced to zero at densities of ≥3/ha, but only if Bennett's wallabies obtained 100% of their diet from pasture.

We do not know if it is appropriate to use a density of 6/ha. Warburton (2005a) reports an absolute density of >2–3 Bennett's wallaby per hectare as comparatively high, but this estimate was qualitative and came from a population being controlled. Therefore, we do not know what the absolute density would be for an uncontrolled population in good habitat. The absolute density for dama wallaby is also unknown, but given their smaller size we assume that their densities in good habitat would be higher than for Bennett's wallaby. In contrast, the carrying capacity of Bennett's wallaby has been estimated at 0.14/ha based on an allometric relationship between body mass and density (Choquenot & Warburton 2006). This is substantially lower than the estimates we used, but it is also lower than some estimates for larger-bodied macropods; e.g. 0.11–0.17 per hectare for eastern grey kangaroos (*Macropus giganteus*; 19–90 kg for males; 17–42 kg for females) (Hill et al. 1998), and 0.45 per hectare for western grey kangaroos (*M. fuliginosus*; 18–72 kg for males; 17–39 kg for females) (Cheal 1986). The lack of robust data on absolute density is a significant knowledge gap.

Table 2: Stocking units of livestock with and without wild mammalian herbivores present on an average-sized (530 ha) hill country farm in New Zealand. Estimated monetary losses from reduced stock units are calculated assuming an average price of NZ$123 per ewe. Source: http://www.ird.govt.nz/technical-tax/determinations/livestock/national-averages/livestock-nationalavemarketvalues-2018.html

Species	Pest density per hectare	Percent pasture in diet	SU per hectare without pest	SU per hectare with pest	Monetary loss (NZ$)
Fallow deer	0.15	100%	7.5	7.230	17,586
		50%	7.5	7.37	8,793
	0.3	100%	7.5	6.96	35,172
		50%	7.5	7.23	17,586
Red deer	0.15	100%	7.5	7.12	24,464
		50%	7.5	7.31	12,232
	0.3	100%	7.5	6.75	48,929
		50%	7.5	7.12	24,464
Dama wallaby	3	100%	7.5	7.20	19,597
		50%	7.5	7.35	9,798
	6	100%	7.5	6.90	39,195
		50%	7.5	7.20	19,597
Bennett's wallaby	3	100%	7.5	6.79	46,204
		50%	7.5	7.15	23,102
	6	100%	7.5	6.08	92,408
		50%	7.5	6.79	46,204
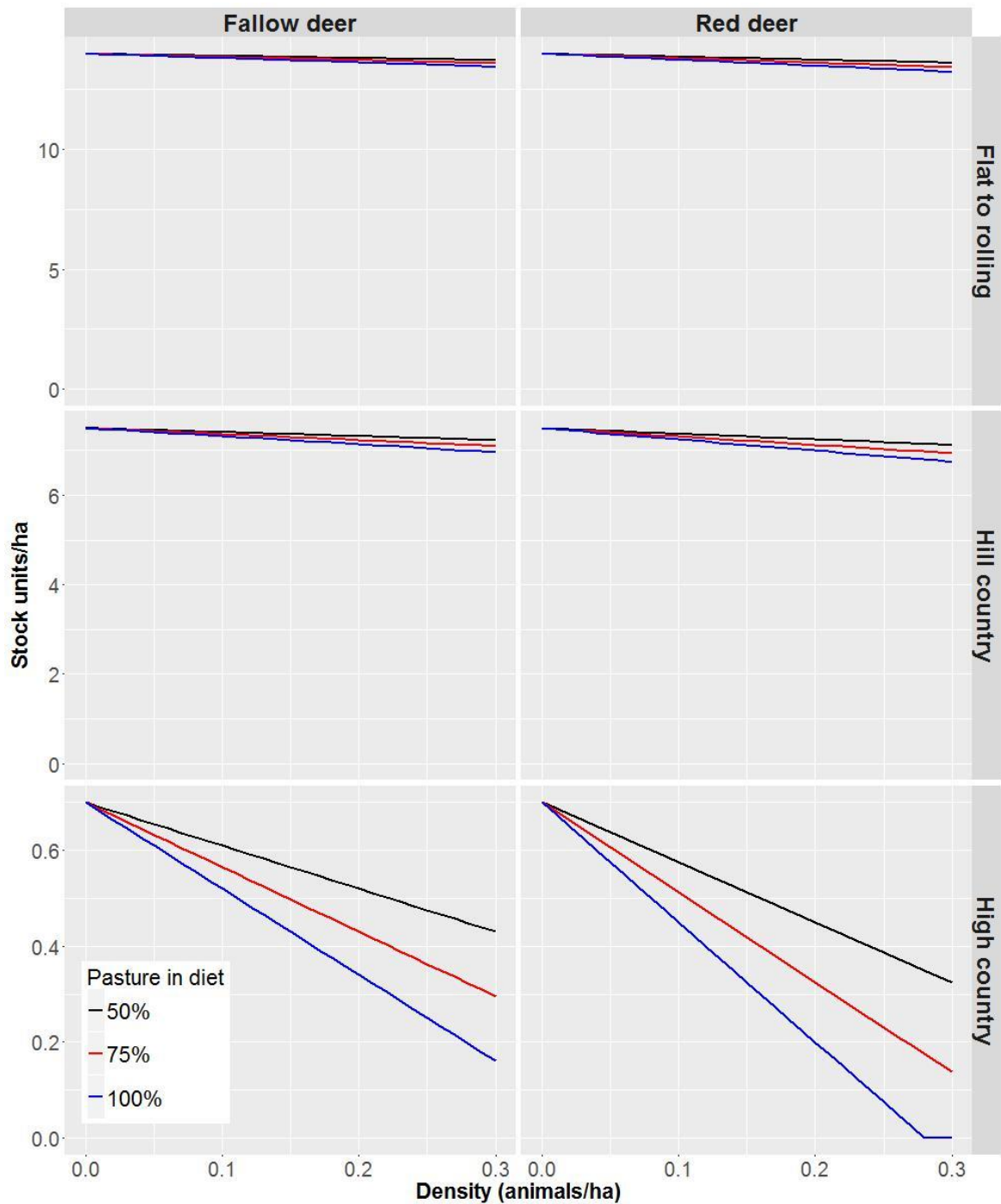
Figure 2: Inferred reduction in stock units (SU) per hectare in the presence of increasing densities of fallow deer (Dama dama) and red deer (Cervus elaphus). Reductions in SUs are presented for three different grassland types in New Zealand, each with a different SU capacity per hectare (flat to rolling: 14 SUs; hill country: 7.5 SUs; high-country: 0.7 SUs). Reductions in SU per hectare are also shown, assuming that wild deer include different proportions of pasture in their diets.
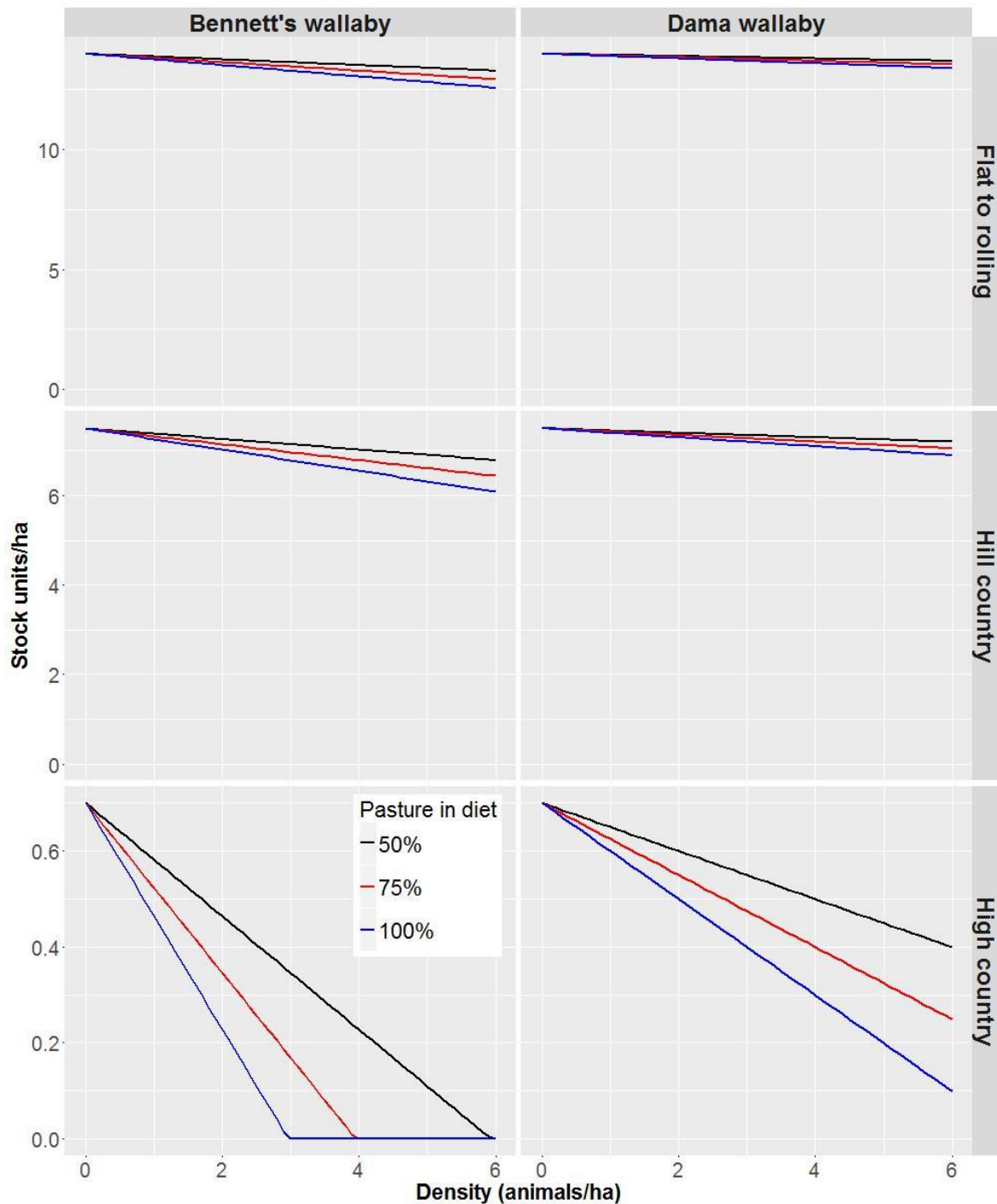
Figure 3: Inferred reduction in stock units (SU) per hectare in the presence of increasing densities of Bennett's wallaby (Notamacropus rufogriseus) and dama wallaby (N. eugenii). Reductions in SUs are presented for three different grassland types in New Zealand, each with a different SU capacity per hectare (flat to rolling: 14 SU; hill country: 7.5 SU; high-country: 0.7 SU). Reductions in SU per hectare are also shown assuming that wallabies include different proportions of pasture in their diets.

2.5 Separating the effects of multiple wild herbivore species

So far this review has focused on the impacts of single species of wild mammalian herbivores on New Zealand agricultural lands. However, most of these exotic species do not occur on farmland or forest in isolation, and therefore their combined impacts should be assessed (Rogers & Leathwick 1997). In these cases, disentangling the species-specific impacts of sympatric grazing mammals is difficult (Hone 2007; Mutze et al. 2016). Also, it is often unclear which wild herbivores must be managed to reduce the damage, and the level to which their populations must be reduced. In New Zealand most of the studies that have assessed damage by a species of wild herbivore have not attempted to separate the damage they cause from that of other sympatric herbivores, including domestic livestock and waterfowl. For example, Dodd et al. (2006) quantified the impacts of possums grazing on pasture accumulation rates, but they were unable to discard the potential contribution of other grazing herbivores, such as hares and rabbits, which were also present in the study area but at lower densities. Likewise, Scroggie et al. (2012) could not disentangle the contributions of hares and rabbits on forage depletion in semi-arid grassland in Central Otago. Thus, although hares were often most common in areas where rabbit densities were low (Scroggie et al. 2012), the authors assessed stocking rates of sheep in relation to total lagomorph density.

In New Zealand semi-arid grasslands, rabbits are considered to have a larger effect on stocking rates than sympatric hares and possums, primarily because of the exceedingly high densities they can attain (e.g. 300 rabbits/ha, versus around 2 hares/ha and up to about 25 possums/ha in forest–pasture margins; Douglas 1970; Flux 2001; Cowan 2005; Norbury & Flux 2005; Scroggie et al. 2012). Conversely, in other habitats elsewhere in the country (e.g. South Island high country and montane grassland, central North Island), hares can be the main mammalian grazer (Wong & Hickling 1999). In grassland reserves established on former sheep-grazing lands in Australia, over-abundant large macropods have been shown to impede the recovery of degraded native pastures (e.g. Norbury et al. 1993; de Preu 2006), whereas other studies have found sympatric rabbit populations to be the main factors preventing recovery (Leigh et al. 1989; Mutze 2006). More recently, Mutze et al. (2016) found significant competition for food between rabbits and large macropods in Australian native pastures. Regardless of contemporary kangaroo grazing pressure, the severely degraded state of the pastures was perpetuated by rabbits, suggesting that historical damage by rabbits was more severe than that caused by macropod grazing. Similarly, Dawson and Ellis (1994) found marked competition between red kangaroos, rabbits and sheep in Australian rangelands, with dietary overlap between sheep and kangaroos becoming more severe when pasture conditions deteriorated during periods of droughts.

In Africa, competition for forage between cattle and grazing wildlife has been documented (Prins 1992; Voeten & Prins 1999). However, Prins (2000) argues that this competition is largely asymmetrical, with cattle competitively excluding wildlife species but not vice versa. In contrast, Young et al. (2005) found that cattle grazed the grass cover to the same low levels in plots with and without other grazing herbivores (primarily African bush elephant, *Loxodonta africana*, and Burchell's zebra, *Equus burchelli*), suggesting that cattle compensated for the absence of competitors by increasing their food intake. This was supported by observations that cattle feed significantly less in plots with elephants than in plots without them (Young et al. 2005). The implications of this for New Zealand agricultural systems might be that cattle, for example, can outcompete deer for forage and that deer

change their feeding behaviour to include a greater proportion of browse. Alternatively, deer may spatially separate from cattle and graze paddocks not stocked with cattle or other livestock. Moreover, similar relationships may exist for species of sympatric wild herbivores; for example, Bennett's wallaby may outcompete deer (or vice versa) and cause a shift in the proportional intake of forage to browse eaten by deer. Alternatively, at least at low to moderate densities, they might not competitively exclude one another and their damage to pasture may be additive.

An additional complexity is that coexisting species of wild herbivores might utilise available forage differently (i.e. there might be some level of niche partitioning). For example, although sheep and feral goats can eat similar pasture species in Australian rangelands (Landsberg & Stol 1996), more than half the diet of domestic goats in New Zealand can be weed species that are not eaten by coexisting domestic livestock (Meat and Wool New Zealand 2008). Similarly, hares in New Zealand have been shown to eat proportionally fewer grass species in pasture than rabbits (e.g. Blay 1989).

To shed further light on the relative contributions to damage caused by sympatric wild herbivores, methods are needed to tease apart species-specific impacts. This can be done qualitatively based on the evidence of different feeding behaviours. For example, domestic and wild ungulates in New Zealand high country more often pull forage species out by their roots compared with hares, and are more likely to erode soil with their hooves (Flux 1967). These observations have been used to infer that ungulates do more damage to vegetation than hares. Although this method can indicate which species causes the most damage, it does not allow DM consumption per unit time to be estimated, and therefore potential impacts on stocking rates.

Exclosure experiments are ideal. For example, Knowlton and Panapa (1982) erected three permanent 20 m × 20 m plots in the Okataina Scenic Reserve, North Island, to assess the damage to native forest by dama wallaby and red deer. One plot excluded only dama wallaby, one plot excluded red deer and dama wallaby, and one plot was left open to both mammalian herbivores as a control. This approach enabled the authors to determine that plant species diversity was 57% higher where dama wallabies were excluded and 142% higher where both species were excluded. Accordingly, they concluded that both species, but particularly red deer, need to be removed or reduced to low levels to permit the recovery of plant species diversity (also see Wright 2017). We recommend that a similar methodology be used on agricultural land containing multiple species of sympatric wild herbivores to tease apart their relative impacts.

3 Factors influencing decisions about herbivore control

Why do some farmers control wild herbivores on their properties and others do not? A farmer's decision-making process for controlling wild herbivores is influenced by many complex behavioural and sociological factors (Parminter & Wilson 2003). Many of these factors seem intuitive, despite being largely unquantified.

One method that has been used to help quantify these complex decision-making processes is the Theory of Reasoned Action (a theory of human behaviour) (Fishbein & Ajzen 1975;

Ajzen & Fishbein 1980). Parminter and Wilson (2003) used this method to help understand the influence of a number of factors and attitudes on the likelihood that New Zealand farmers would act to control possums on their properties. Using this theory, they categorised the factors that might influence farmer decision-making. The main ones were:

- weighing up the expected costs and benefits of doing control (instrumental attitudes)
- the image the farmer wants to portray with regard to pest control (self-identity)
- the recreational aspect of doing control in the form of hunting or trapping (affective attitudes)
- how farmers perceive the views of others towards the issue (subjective norms)
- the belief that they as the land owner are able to effectively manage the pest for successful outcomes (behavioural control and self-efficacy).

The main factors influencing intentions for possum control were, in declining order: instrumental attitudes, self-identity, affective attitudes, subjective norms, and behavioural control (Parminter & Wilson 2003). Instrumental attitudes were driven by the belief that the economic benefits accrued from reducing possum numbers, and therefore health problems in farmed livestock (particularly TB), and damage to orchards and gardens would outweigh the costs of control.

The economic benefits for farmers of controlling possum populations to reduce the prevalence of TB have been widely reported (Coleman & Livingstone 2000). Therefore, the finding that farmers weighed up the expected costs (or risks) and benefits of doing control (Parminter & Wilson 2003) is not surprising. To our knowledge, similar studies have not been done for other wild herbivores in New Zealand, but a similar prediction could be made for farmer decision-making in relation to rabbit control. Research in New Zealand and overseas has shown that rabbits can cause extensive damage to pasture and reduce stocking rates (Norbury & Reddiex 2005; Scroggie et al. 2012), at least at moderate to high infestations (Gooding 1955). Therefore, instrumental attitudes are likely to be key drivers for many farmers deciding whether to control rabbits on their properties. Nevertheless, some farmers choose not to control their rabbit populations, despite the economic damage they cause. This may be because (1) in some rabbit-prone areas the costs of control can exceed the income gained from the land, (2) land owners may be against the primary method (poisoning using 1080) of reducing high rabbit numbers, or (3) they might consider that the periodic effects of RHDV are sufficient for economic relief from high rabbit numbers (e.g. Jarvis et al. 1993; Green & Rohan 2012 Cooke et al. 2013).

Where land owners do not control rabbits they may be inspected by regional councils and issued 'notices of compliance' if rabbit numbers on their properties are found to be too high using the modified McLean scale, an index based on faecal pellet density and sign and sightings (NPCA 2012). If they fail to manage rabbits in accordance with the rules laid out in regional pest management plans, they can be subject to legal action under the New Zealand Biosecurity Act 1993. In this instance, their decision-making process could be to do nothing until found to be non-compliant.

The decision-making process on whether to control other species of wild herbivores in New Zealand is likely to be similar to that for possums and rabbits, despite the lack of quantitative

data about the economic damage they cause. For example, a survey of farmers in Southland showed that they weighed up the expected costs and benefits of deer, pig and goat control (i.e. they used instrumental attitudes), but in the absence of quantitative data they used observations of damage from their own properties or anecdotal reports from other farmers (Latham, Craddock-Henry et al. 2012). This survey also highlighted the different values held by land owners, with about half the respondents viewing deer and pigs as a resource and half seeing them as an economic liability. The recreational aspect of control in the form of hunting (i.e. affective attitudes) was also important for these species, with 31% of respondents preferring control by recreational hunters (versus 52% by professional hunters, and 15% by poisoning) (Latham, Craddock-Henry et al. 2012).

Complex behavioural and sociological factors have been shown to influence decision-making by farmers elsewhere. For example, goats significantly reduce maize yield in Uganda, but subsistence farmers tolerate such losses because they perceive that the benefits provided by goats (milk, meat, manure and, ultimately, financial security) outweigh their costs (decreased maize yield, increased conflict between neighbours, and building and maintaining fences) (Webber 2010). Similarly, sheep graziers in the Australian rangeland can profit from mustering and selling feral goats on their properties, but the goats also compete with sheep for pasture (Parkes et al. 1996). When farm gate prices are high for feral goats, it makes economic sense to retain the population and harvest it for profit. However, as the farm gate price for goats can fluctuate widely and quickly, the farmer is taking a risk by maintaining high goat numbers if the farm gate price drops, or if pasture biomass declines and increases competition between sheep and goats for food. In contrast, the stocking rates of sheep can be managed through both fluctuations with greater flexibility (Parkes et al. 1996).

In summary, a number of complex behavioural and sociological factors affect farmer decision-making about the management of wild herbivore populations on their properties. Formal or informal cost–benefit analyses (instrumental attitudes) seem to feature prominently among these. However, confidence in these analyses is only possible if reliable data are available for assessing the costs and benefits of control. With the exception of possums and rabbits, few data are available, making the results from cost–benefit analyses tenuous (e.g. Latham, Latham & Warburton 2016).

4   Post-control stocking rate decisions

There is sparse information about how farmers alter their stocking rates following control of wild herbivores on their properties. Quinn (1968) reported that a farmer in the Wanganui area, North Island, was able to increase the winter stocking rate by 15% following possum control (although this assumes there was real competition between possums and livestock). Similarly, Dodd et al. (2006) found the potential winter consumption rate by possums on Waikato farmland was 3 kg DM/ha/day. They state that regaining this level of pasture availability for livestock would enable an increase in winter stocking rate of about three SUs per hectare, but there is no indication that farmers responded to this. Moreover, at a gross margin of c. NZ$21 per SU at the time of publishing, the increase in available forage (assuming it was utilised) would almost have covered the cost of the land owner's possum control (Dodd et al. 2006).

Even if stocking rates are not altered, farmers can still increase productivity if weight gain yields of existing livestock increase with reduced competition for pasture. For example, an additional 30–40 kg live weight per head of bull cattle was reported by one farmer following regional possum control in Waikato (Dodd et al. 2006).

It is worth noting that although many farmers are trying to optimise the use of the available forage produced by their land to maximise marketable products, little information is available about how they do this in relation to the control of wild herbivores on their properties. If farmers do not explicitly increase their stocking rates, we speculate that they presume productivity will increase post-control via increased weight gain yields from existing livestock. Alternatively, they may be happy to incur some economic losses if they value the competing wild herbivore as a resource; for example, for hunting (Nugent & Fraser 1993; Latham, Craddock-Henry et al. 2012).

In the absence of quantitative demonstrations of the impact of wild herbivores on productive assets (as for possums and rabbits) or native biota in productive landscapes, their inclusion in regional pest management plans could be seen as questionable. However, if population control produces favourable outcomes for productive assets, it seems legitimate to keep wild herbivores at low levels (and prevent them from spreading) to minimise future economic damage (e.g. Latham, Latham & Warburton 2016; Parkes et al. 2017). Therein lies a second problem: not only is there a lack of quantitative data about damage, but rarely are control operations monitored to determine if the density of the pest is reduced, and whether the asset being protected responds positively (Norbury et al. 2015). For some species, such as feral pigs, other factors, including rooting and the potential for disease transmission, may be sufficient justification for their control.

5 Conclusions and research priorities

There is a lack of data on wild herbivore damage to productive assets relative to their abundance, especially in New Zealand. Based on the indirect method of assessing annual DM consumption by wild herbivores and its theoretical effect on stocking rates, it is both intuitive and tempting to assume that any reduction in a wild herbivore population will have a corresponding reduction in the damage they cause. This assumption does not always hold, as density–impact functions are often non-linear. Numerous authors have advocated the use of experimental exclosures for determining the relationship between pest herbivore density and damage. This has remained a key knowledge gap for most species in New Zealand for over a century, but it is critical for reliable cost–benefit analyses and for ethical justification of killing animals (Littin et al. 2004).

The implications of this review for land owners and for regional councils tasked with managing these species under the Biosecurity Act 1993 is that, with the exception of possums and rabbits, very little is known about the economic damage caused by wild herbivores to productive assets in New Zealand. Moreover, estimates of relative abundance and absolute density are generally lacking, meaning that pest density–impact functions and per capita consumption of forage by wild herbivores cannot be derived.

We recommend that quantitative data on the damage caused by these pests and their relative abundance or absolute density be collected. However, we acknowledge this is likely to be expensive and therefore recommend candidate species for research be agreed upon by land owners, management agencies and research organisations. Without a quantitative understanding of the economic damage caused by wild herbivores, their inclusion in regional pest management plans appears to be based on anecdotal reports of damage, their potential for damage at high densities, and 'good neighbour' rules aimed at reducing spill-over damage from a property that does not regularly control wild herbivores (note that little is known about the dispersal of pests between properties).

Many of the potentially problematic wild herbivore species (e.g. Bennett's wallaby, brown hare, fallow deer and red deer in South Canterbury) occur on the same properties, and their populations appear to be expanding (Latham & Nugent 2017a). Currently we do not understand the effect of potential competitive interactions between sympatric wild herbivores on the consumption of forage or crops. An understanding of this may help to guide control. For example, all species of sympatric wild herbivores on a property might compete with one another and livestock for the available forage, and therefore all wild herbivores will need to be controlled to produce favourable outcomes for the asset. Alternatively, some species may compete with livestock for forage, whereas others do not (or may have a negligible effect). In this instance, removing the greatest competitor for forage is likely to produce the most favourable outcome for production. Importantly, however, species' diets are not fixed, and controlling or eradicating a significant consumer of forage may result in a second wild herbivore species that had primarily been a browser switching to foraging following the removal of the first pest herbivore.

As a final research priority, we recommend gaining a better understanding of the seasonal effect of wild herbivores on stocking rates, and whether herbivore control will enable annual stocking rates to be increased, particularly in food-limiting seasons. Further, at what point does an increase in pest numbers following control begin to affect stocking rates or weight gains of livestock? Identifying thresholds related to these factors would enable cost–benefit analyses, perhaps using some form of decision support system (e.g. as for deer–forest systems in the Northern Hemisphere, Tremblay et al. 2004), to optimise the timing and intensity of pest control operations.

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