

special issue:

# Feathers to Fur

The ecological transformation of Aotearoa/New Zealand



## Impacts of introduced deer and extinct moa on New Zealand ecosystems

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**Abstract:** There has been considerable ongoing debate about the extent to which the impacts of introduced deer on native vegetation have replaced those of moa, and since the 1980s there have been major changes in thinking about the impacts of deer and ratites on ecosystems. Although it has long been known that deer caused a predictable sequence of changes in forest understorey composition, recent work has shown that the foliage of species preferred by deer contains lower concentrations of fibre – and decomposes faster – than avoided species. Analyses of long-term permanent plot data suggest that some preferred species are failing to regenerate in forest types where deer are present. As well as likely altering the long-term biogeochemistry of forest ecosystems, deer have a strong negative effect on the abundance of litter-dwelling macrofauna (most likely through trampling). Estimating the impacts of extinct taxa on an ecosystem has much uncertainty, but recent experiments have shown that extant ratites and deer may have more similar feeding preferences than previously believed. It is likely that moa were important seed dispersers, but this has not been studied for deer in New Zealand. Although collectively the various taxa of deer in New Zealand use all of the habitats utilised by moa, and there is partial overlap in the diets of deer and moa, deer can attain densities and biomasses 100-fold greater than reasonably surmised for moa. We believe that the impacts of introduced deer on ecosystems are markedly different from those of moa. One way to compare the impacts of moa and deer is to use pollen to reconstruct the vegetation at a forested site in recent millennia and evaluate vegetation dynamics during the moa period, following the extinction of moa but prior to the arrival of deer (i.e. the moa gap), and following the arrival of deer. We illustrate the potential of this approach with a soil core from Chester Burn, Murchison Mountains in Fiordland. Five other areas that deserve further research are also identified.

**Keywords:** biomass; browsing; carbon; exclosures; forest; grazing; moa gap; pollen; population dynamics; red deer; seed dispersal; trampling; ungulates

### Introduction

There has been considerable ongoing debate about the extent to which the impacts of introduced deer on native vegetation were similar to those of moa. Batcheler (1989: 57) concluded: "... on easier low altitude country, their [moa] feeding pressure would have been equivalent to that exerted by the introduced mammals". In contrast, Atkinson and Greenwood (1989: 92) thought: "introduced browsing mammals are acting as a new influence on vegetation". Caughley (1988) considered New Zealand plant communities that now contained deer were more similar to those containing moa than during the 'moa gap' (when both were absent), but that 'moas would not have had the same effect as deer' (Caughley 1989: 8). Craine et al. (2006: 172) thought the New Zealand flora had "few defenses

against... herbivorous mammals". The objectives of this paper are to review current thinking about the impacts of introduced deer on New Zealand vegetation and to then contrast those with the likely impacts of moa. In doing so, we identify areas that deserve further research.

### What is known about the impacts of deer?

#### Diversity, distribution and dynamics

The introduction of deer to New Zealand has been well documented (e.g. Thomson 1922; Donne 1924). Introductions were made between c. 1851 and 1926; thereafter the importation of deer to New Zealand ceased, although animals captured from established herds are still being released in new range

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(King 1990; Fraser et al. 2000). Not all introductions were successful, with the number of individuals being an important determinant of success (Forsyth & Duncan 2001). Seven deer taxa (six species, one with two subspecies) are extant in New Zealand (King 2005): red deer (*Cervus elaphus scoticus*), wapiti (*C. elaphus nelsoni*), white-tailed deer (*Odocoileus virginianus*), sambar deer (*C. unicolor*), sika deer (*C. nippon*), rusa deer (*C. timorensis*), and fallow deer (*Dama dama*). It is uncertain whether moose (*Alces alces andersoni*) remain in Fiordland and they are not considered further here.

The seven taxa vary in adult female/male body mass from 40/54 kg (white-tailed deer on Stewart Island; Nugent 2005) to 157/245 kg (sambar deer; Fraser & Nugent 2005). There is considerable variation in age-sex-specific body masses between and within populations (e.g. Challies 1985), depending on per capita food availability. Deer use nearly all vegetated habitats in New Zealand, including coastal dunes (white-tailed deer, sambar deer and red deer) and lowland swamps (sambar deer and red deer), forest (red deer, wapiti, sambar deer, sika deer, rusa deer, fallow deer and white-tailed deer), and alpine grasslands (red deer and wapiti). Grassland habitats at all elevations tend to be used less in winter relative to other seasons (e.g. sika deer; Davidson 1973). Although deer do not form strong social bonds, other than between a mother and unweaned offspring, in high-density populations large (>50) groups may form around favoured feeding areas (e.g. grasslands in spring and summer) and during rut. The sexes of most species appear to be segregated (i.e. they seldom mix and often utilise different habitats) outside of the mating season (e.g. Clutton-Brock & Albon 1989). Male and female red deer live to a maximum of 14 and 20 years, respectively, and females usually give birth at 24 months, with one offspring per annum the norm (Challies 1990).

Holloway (1950) gave the first description of the sequence of events that followed the colonisation of new range by deer in New Zealand. Holloway proposed that the forest initially provided a maximum amount of browse, such that the herbivore population increases most rapidly at first. The deer population eventually “overtakes ... available food supply”: many animals starve and the population density declines. It was thought the population would eventually achieve a static (“equilibrium”) density that depended upon the renewal rate of food plants (e.g. Caughley 1976). The dynamic outlined by Holloway (1950) was seemingly a common occurrence for ungulate populations that established in New Zealand and non-native ranges elsewhere, and is termed an “irruption” (Riney 1964; Caughley 1970; Forsyth & Caley 2006). Importantly, the post-decline density is lower than the initial peak because the availability of forage has been modified (Riney 1964; Caughley 1970). Based on estimates of faecal pellet abundance, and deposition and decay rates, peak densities of red deer have been estimated to be 30–50 deer km<sup>-2</sup> in forests where deer have access to productive grasslands (Nugent & Fraser 2005).

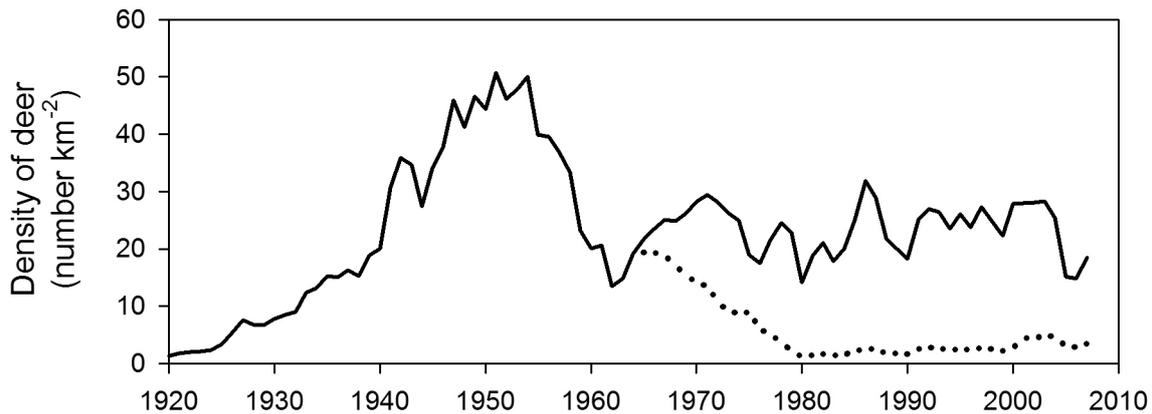
The likely dynamics of a deer population that established in 1920 are shown in Fig. 1. If a mean body mass of 70 kg is assumed for a population of red deer at peak density (based on data in Nugent & Fraser (2005)), then the peak biomass would have been 2100–3500 kg km<sup>-2</sup>. It is difficult to estimate the food intake of wild deer empirically. Pinned male red deer (2–3 years old; 138–153 kg) consumed 1–3 kg of dry matter per day depending on season (Fennessy 1981; Kay 1985), but wild red deer living in New Zealand forests would have smaller masses and would therefore consume less (Nugent & Fraser 2005).

Deer feed on different species during the irruption (e.g. Wardle 1984; Challies 1990). During the early years after establishment, deer feed on only a few species that often grow on the most fertile parts of the landscape (e.g. *Griselinia littoralis*, *Schefflera digitata* and *Asplenium bulbiferum*; plant nomenclature follows Allan Herbarium (2000)). As the deer population increases, these plant species become much less abundant per capita in accessible areas and deer feed on other species such as *Coprosma foetidissima* and the fern *Polystichum vestitum*. Accounts of forests at the peak of deer abundance and during the ‘decline’ phase indicate that all plants within the browse tier were being browsed (Challies 1990). The pattern of modification probably depends on the interaction between browsing intensity (itself a function of deer taxa and deer density; see below) and the ‘tolerance’ of the species to browse (Allen et al. 1988; Augustine & McNaughton 1998). Studies of deer in the post-decline phase (e.g. white-tailed deer on Stewart Island; Nugent & Challies 1988) show that the diet is dominated by contributions from canopy trees, such as epicormic shoots of *Weinmannia racemosa* and fallen leaves of *G. littoralis*. Hence, impacts vary depending upon how long deer have been present at the site.

Humans are the only predators of deer in New Zealand and the establishment of commercial markets for deer products led to a reduction in the abundance of deer from the late 1960s, particularly in non-forest habitats (Parkes et al. 1978; Challies 1985; Nugent & Fraser 1993). Estimating the absolute abundance of deer in forests is problematic, but Nugent and Fraser (2005) estimated that hunting reduced national densities of red deer in forested habitats to c. 3–4 deer km<sup>-2</sup>. The dynamics of deer in most New Zealand forests have thus been strongly modified by harvesting, with abundances often reduced >90% below what otherwise would have been since the mid-1960s (Nugent & Fraser 2005; Fig. 1). When considering recent studies on the impacts of deer in New Zealand, it should be noted that commercial hunters have not targeted all deer taxa in all areas equally, for reasons of access and differential vulnerability/profitability of deer.

Smaller-bodied deer taxa often attain higher densities than larger-bodied taxa in New Zealand forests, and the former normally out-compete the latter (Nugent & Fraser 2005). For example, fallow deer have attained post-peak densities of 40 deer km<sup>-2</sup> in parts of the Blue Mountains, Otago (Nugent & Asher 2005), much higher than would be achieved by red deer at the equivalent stage of the irruption (Fig. 1). The various deer taxa appear to have broadly similar diets (Forsyth et al. 2002; Nugent & Fraser 2005), although differences have been demonstrated for sympatric red and sika deer in the central North Island: sika deer ate more beech (*Nothofagus* spp.) and ferns than did red deer (Nugent et al. 2001a), and the rumen morphology of sika appears better for digesting fibrous foliage than that of red deer (Fraser 1996). Mountain beech (*Nothofagus solandri* var. *cliffortioides*) seedlings (15–135 cm tall) were much less abundant in the central North Island, where sika were abundant, than in three similar forests in the South Island, where only red deer were present (Husheer et al. 2006). Hence, the impacts of deer will vary according to the deer species present.

Nugent et al. (2001b) proposed that in Waihaha (at Pureora, central North Island) relationships between deer density and the abundance of tall seedlings were strongly non-linear for all species. The most preferred species were thought to be greatly reduced in abundance, even at very low deer density. The least preferred and most browse tolerant



**Figure 1.** Hypothesised dynamics of a red deer population that established in 1920. The figure illustrates how the population would undergo an irruption and then decline to lower densities. Commercial hunting since c. 1964 (Challies 1985; Nugent & Fraser 1993) reduced the population to much lower densities (dotted line) than otherwise would have occurred (solid line post-1964). There are no long-term data with which to test this hypothesis so the figure is schematic.

shrub and tree species were thought to benefit from reduced competition at moderate and high deer densities, but at very high deer densities even some of these species were thought to be negatively affected. However, there is no evidence that deer have caused the extinction of any plant species on the North, South or Stewart islands. Although deer have greatly reduced the abundances of seedlings and saplings of some species, all of these species do recruit in areas inaccessible to deer (e.g. cliffs, windthrows and as epiphytes). In south-eastern Fiordland, red deer browsing was evident on many seedlings growing on fallen tree ferns ( $49 \pm 3\%$ ) and on standing tree ferns up to 2 m ( $35 \pm 7\%$ ), but seedlings growing above 2 m were not browsed ( $0 \pm 0\%$ ; Gaxiola et al. 2008). Epiphytic regeneration can be important for the dynamics of some tree species at some sites (e.g. *Weinmannia racemosa* on fertile terraces in south-eastern Fiordland; Coomes et al. 2005), and the impacts of deer might be less important for these species.

In summary, the impacts of deer at a site vary according to the deer taxa present, how long the population has been established (i.e. the phase of the irruption), and the effect of hunting on the population.

### Diet selection

Plant-defence theory suggests that plants have evolved two strategies for reducing the impact of herbivory; they either avoid damage by investing heavily in anti-herbivore defences or they tolerate damage by investing in traits associated with fast growth and rapid recovery (Coley et al. 1985). Although the theory has attracted much criticism for its simplistic assumptions, it has received some support from empirical studies and was the basis for McGlone and Clarkson's (1993) conjecture that subcanopy angiosperm tree species in New Zealand that are preferred by deer tend to invest more in growing fast and have fewer defences than other tree species. A simulated browsing experiment on saplings of 12 tree species showed that the fastest-growing species would be the quickest to recover from the clipping of branches in terms of shoot length but not diameter (Bee et al. 2007). Interestingly, saplings of the three conifer species in the sample (species which are nearly always avoided by deer) often died at 100% clipping, perhaps because conifers lack parenchyma cells in the xylem and thus cannot store as much starch as angiosperms, reducing their ability to survive defoliation.

A major advance has been the estimation of diet selection indices (Manly et al. 2002) for forest species by white-tailed deer (Nugent & Challies 1988), fallow deer (Nugent 1990) and red deer (Nugent et al. 1997; Forsyth et al. 2005). Diet was estimated from the rumen contents of shot animals. The frequency of occurrence and/or the relative dry weight of each plant group was compared with an estimate of that group's availability within the study area, which was estimated by sampling the forage considered to be within the deer's reach ( $\leq 200$  cm according to deer species). The statistical comparison of what is eaten with what is considered available enables plant species to be classified into one of three groups: (1) preferred: those eaten more than expected from their availability; (2) not selected: those eaten in proportion to their availability, and; (3) avoided: those eaten less than expected based on their availability. Although the ungulate taxa, time since colonisation, history of harvesting and forest composition varied, selection indices were remarkably similar for many plant species (review in Forsyth et al. 2002).

There is not yet a consensus on the plant traits that most influence diet selection by deer. Coomes et al. (2003) concluded that the mean foliar lignin concentration of 'preferred' species was significantly lower than that of 'intermediate' and 'avoided' species; these results were based on chemical trait data collected from a wide variety of locations, years and seasons, and estimates of diet selection from a synthesis of six studies, including two of feral goats (*Capra hircus*) (Forsyth et al. 2002). Forsyth et al. (2005) tested 13 a priori predictions about the role of seven chemical traits and one morphological trait in determining red deer diet selection in a lowland forest. Diet selection was estimated by identifying the rumen contents of 24 deer that fed in the summer on alluvial river terraces and neighbouring forests in south-eastern Fiordland. The alluvial sites in southern Fiordland exhibit wide variation in plant traits; e.g. they still retain soft-leaved deer-preferred species, such as *Fuchsia excorticata*, alongside which grow sclerophyllous species such as *Dacrydium cupressinum*. Within this context, Forsyth et al. (2005) found that the best predictor of whether a forest species was preferred, not selected or avoided by red deer was the concentration of foliar fibre; preferred species usually had less foliar fibre than avoided species. The results of Forsyth et al. (2005) fit Hofmann's (1989) suggestion that red deer select diets to minimise the intake of fibre. Bee et al.

(in press) examined the rumen contents of 426 deer shot within the Murchison Mountains, Fiordland, in 1976–78. This dataset was different in several respects to that analysed by Forsyth et al. (2005). First, the deer were shot over a larger area that included more habitats, including extensive beech forests and alpine grasslands. Very little of the study area comprised fertile alluvial habitats in which deer-preferred species are relatively plentiful. Second, the deer were shot in all seasons rather than only summer. Deer fed mostly on grass in the spring, summer and autumn, and selected woody species that were low in phenolic content during these periods (Bee et al. in press). None of the other traits examined were significantly related to diet selection by deer. In winter, when access to grass was limited, deer consumed species with high phenolic and fibre concentrations (e.g. *Weinmannia racemosa*) and preference was unrelated to any of the measured traits. One reason why foliar fibre was unrelated to diet selection is that soft-leaved species were uncommon in the study area. Both Forsyth et al. (2005) and Bee et al. (in press) show that ferns are seldom eaten, despite having moderate fibre and phenolic concentrations. We suspect that chemical compounds that are not included in coarse measures such as ‘total phenolic content’ are responsible for deer avoiding these plants.

In *Nothofagus* forests in western Nelson, browsing by red deer (as measured by the Mean Browse Index) was greatest on the highest fertility sites that had the highest plant species richness (Rose & Burrows 1985). Using data collected in plots (10 × 10 m) in the Murchison Mountains (Fiordland) during 1980–1981, Bee et al. (2009) showed that the probability of six forest species (*Coprosma ciliata*, *C. foetidissima*, *Polystichum vestitum*, *Weinmannia racemosa*, *Pseudopanax lineare* and *P. simplex*) being browsed by red deer increased significantly if the plot contained high abundances of frequently browsed species and/or low abundances of rarely browsed species. Hanley (1997) emphasised the difficulty of understanding diet selection by deer due to interactions between physical and behavioural constraints and objectives, and the extreme heterogeneity of available food.

Cafeteria trials with captive red deer and goats and a different suite of plant species suggest that consumption of species was low because of structural traits (in particular the divaricating growth form) rather than chemical plant traits (Pollock et al. 2007). These structural traits were included in the analyses of Bee et al. (in press), but were found to be unrelated to deer diet selection. Further controlled studies with a wider range of both plant and deer taxa are required to tease apart the relative roles of chemical versus morphological traits in determining diet selection.

### Composition, structure and ecosystem processes

No studies have evaluated the impacts of deer on primary succession following disturbance in New Zealand, but theory suggests deer will have a strong influence above a threshold biomass (Oksanen & Oksanen 2000). Deer alter the growth and survival rates of plants by removing material from that plant and/or neighbouring plants, and may accelerate succession in low-productivity ecosystems of low soil fertility (Bardgett & Wardle 2003) (which is most of New Zealand) through the replacement of preferred, browse-intolerant plant species by less preferred or avoided species, a phenomenon termed ‘apparent competition’ (Connell 1990). There is evidence that browsing has promoted the spread of the avoided ground ferns *Blechnum discolor* and *B. procerum* (Wardle 1984; Wardle et al. 2001), and the expansion of avoided shrubs such as

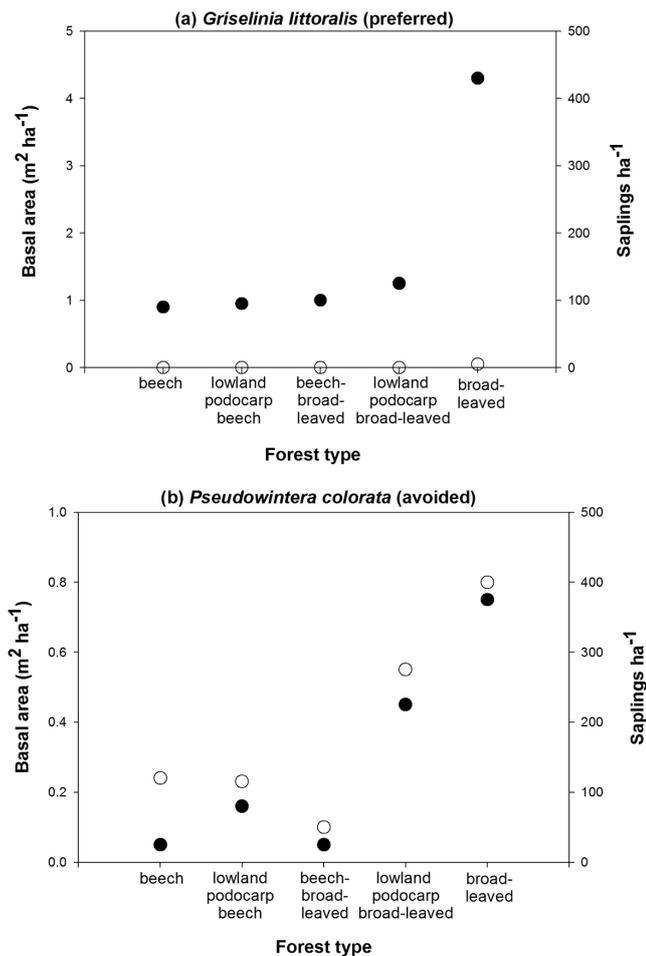
*Pseudowintera colorata* and *Neomyrtus pedunculata* (e.g. McKelvey 1973; Allen et al. 1984). Although taller saplings and trees are killed by ring-barking (e.g. *Pseudopanax colensoi* var. *ternatus* by invading red deer on Secretary Island, Fiordland; Mark & Baylis 1975, 1982) this seems to be currently infrequent in New Zealand forests. Rather, the main impact of deer is thought to be on the growth and survival rates of seedlings and saplings up to 200 cm tall, with the dynamics of canopy tree species affected through deer-induced changes in recruitment rates.

Deer may have strong influences on secondary succession that may not be reversed once a particular phase of the succession has been completed (Payton et al. 1984; Coomes et al. 2003). The small myrtaceous trees *Kunzea ericoides* and *Leptospermum scoparium* are avoided by fallow deer (Nugent 1990) and often dominate early successional vegetation following burning or the abandonment of agricultural land. Smale et al. (1995) recorded changes over 10 years inside and outside exclosures established in early successional stands of *K. ericoides* inhabited by fallow deer. Within exclosures, preferred broad-leaved species such as *Melicactus ramiflorus* and *Myrsine australis* established and were starting to replace *K. ericoides*, but *K. ericoides* remained dominant outside and was able to reach sufficient height to establish for a further generation (80–100 years). Browsing by red deer on seedlings of the canopy tree *Weinmannia racemosa* was proposed as the reason for the failure of this species to replace *L. scoparium* in fire-affected northern Urewera forests (Payton et al. 1984).

The National Vegetation Survey databank (NVS; Wiser et al. 2001) contains repeated measurements of permanent plot data from throughout New Zealand forests. Although estimates of deer abundances are unavailable for most plots, these data nevertheless provide an opportunity to evaluate large-scale patterns in forest composition. Forsyth et al. (2003) showed that the highly preferred *Griselinia littoralis* contributed 2–7% of the basal area of NVS stands nationally, but only 0–2% of sapling numbers, with low abundances of saplings in all forest types except some broad-leaved forests (Fig. 2). In contrast, the avoided species *Pseudowintera colorata* comprises a smaller component of the canopy basal area (0.2–1.3%), but a large component of the sapling layer (9–13%), and the correlation between sapling numbers and basal area is strong (Fig. 2). Although data from deer-free areas were unavailable, the observed patterns suggest positive and negative effects of deer on the abundance of saplings of some forest species.

The type, scale and frequency of disturbance (particularly earthquakes, volcanism, cyclones and drought) have a strong influence on successional stage and hence forest composition (Wardle 1991). Deer show strongest preferences for fast-growing and shade-intolerant angiosperms that characterise low-elevation, relatively fertile landforms and typically regenerate after disturbance (Wardle et al. 1971; Stewart & Harrison 1987; Nugent et al. 2001a; Coomes et al. 2003). In northern Fiordland, red deer and wapiti have had the greatest impact in areas of vegetation on recent, relatively more-fertile soils, particularly those on landslides (Wardle et al. 1971; Stewart & Harrison 1987).

The prediction that deer would reduce forest cover (Perham 1922) is not supported by available data, although this could simply be because the time since colonisation by deer is short compared with the lifespan of many trees. At the national scale, Bellingham et al. (1999) reported that canopy tree (defined as >10 cm in diameter at breast height (dbh)) mortality rates were approximately balanced by recruitment



**Figure 2.** Sapling abundance (open circles, right axis) for a species preferred by deer (*G. littoralis*) and a species avoided by deer (*P. colorata*), compared with the basal area of canopy trees (filled circles, left axis) of that species (after Forsyth et al. 2003) in different forest types.

rates (c. 1% per year). In contrast, Coomes et al. (2003) reported a dramatic decrease in the number of small trees (particularly 3–5 cm dbh) within forests nationally, equating to about 20% loss over 16 years. Subsequent work has found that deer-preferred species account for most of these losses (D. Wright, University of Cambridge, unpubl. data). However, brushtail possums *Trichosurus vulpecula* (present in nearly all forest in the North, South and Stewart islands; Cowan 2005) and feral goats (present in some North and South island forests; Fraser et al. 2000) may be partly responsible for the observed declines. Importantly, adult New Zealand trees have low annual mortality rates (e.g. Kunstler et al. 2009) and, even in the case of preferred subcanopy tree species like *Griselinia littoralis*, it is expected that populations will take several centuries to diminish (Nugent & Challies 1988; Nugent 1990).

There is strong evidence that deer have affected browse-layer composition (e.g. Wardle et al. 2001), but the demographic consequences for canopy trees has yet to be demonstrated (Veblen & Stewart 1982). Because of the very low mortality rates of adult trees, models are required to investigate the century- and millennia-level impacts of deer on canopy composition. In the central North Island, the growth rates of mountain beech seedlings inside deer exclosures were

substantially higher than those outside the exclosures (by factors of 1.2–1.4 times in the high culling-intensity area, 2.3–14.4 times with medium culling and >1.74 times with low culling), an impact attributed to sika deer (Husheer & Robertson 2003). Subsequent modelling indicates that these growth rates translate into a faster time to canopy closure in the parts of the forest subject to high-intensity helicopter-based shooting of deer or fencing (R Duncan, W Ruscoe, S Richardson, R Allen 2006 Landcare Research unpubl. report LC0607/021), but those results were based only on seedling data and did not account for compensatory growth of adults. A national-scale consequence of deer for a canopy species has not been demonstrated. Models parameterised for seedlings, saplings and adults, and the effects of neighbours on growth and survival rates, are required (e.g. Pacala et al. 1996).

There has been far less work on the impacts of deer in grasslands compared with impacts in forests, partly because deer have almost been eliminated from grasslands as a result of helicopter-based hunting. Red deer made intensive use of alpine grasslands and subalpine shrublands prior to the advent of helicopter-based hunting (Challies 1990). In alpine grasslands, deer preferred the well-drained and fertile sites containing the highest diversity and biomass of preferred food plants (principally the grasses *Chionochloa pallens* and *C. flavescens* and the herbs *Anisotome haastii* and *Celmisia verbascifolia*) (Lavers 1978; Rose & Platt 1987). The effects of deer on individual grassland plants may persist for decades. Lee et al. (2000) showed that 20 years after simulated deer browsing, *C. pallens* tiller weights, lengths and basal diameters were 30% less than for unbrowsed plants.

Bardgett and Wardle (2003) suggested three ways that above-ground herbivores such as deer might influence below-ground processes. First, how herbivores regulate the return of organic matter to the soil can influence biomass production and resource allocation. Recent comparisons of above- and below-ground properties inside and outside ungulate exclosures showed how deer can modify the composition of the litter layer and hence the rate of litter decomposition (Wardle et al. 2001, 2002), but the flow-on effects for biomass production and resource allocation have not been investigated. Second, deer alter the quality of resource inputs to decomposers through the return of faeces and urine. Forsyth et al. (2005) showed that red deer at Waitutu (south-eastern Fiordland) did much of their feeding on small, fertile, alluvial terraces but rested on the larger and relatively infertile marine terraces. Hence, it is likely that deer were moving organic material from more fertile to less fertile parts of the landscape. Similarly, white-tailed deer on Stewart Island may, through the consumption of seaweed, move marine nutrients inland. The consequences of plant materials being returned to the soil as faeces and urine, rather than litterfall, has not been investigated in New Zealand. Third, over long timescales, deer may alter the quality and quantity of litter returned to the soil, and hence its decomposability. Wardle et al. (2002) found, for 30 forest sites throughout New Zealand, that the rate of litter decomposition declined as the effect of browsing mammals on vegetation density increased. Mixing-experiments showed that litters produced by the plant species that were reduced in abundance by browsers tended to promote the decomposition of other litters (Wardle et al. 2002). Wardle et al. (2002) also measured the rate of decomposition, irrespective of browsers. Results are listed here from fastest rate of decomposition to slowest: large-leaved dicots, small-leaved dicots, *Nothofagus* spp., ferns, and monocots. All macrofaunal, and nearly all mesofaunal, litter-dwelling groups were consistently reduced in abundance by browsing mammals,

an outcome attributed more to trampling by ungulates than to changes in above-ground vegetation composition and density (Wardle et al. 2001). Indeed, there was no relationship between the magnitude of the ungulate effects on browse layer vegetation density or composition and the magnitude of the effect of ungulates on the abundance of any group of soil biota. Another possible explanation for reduced abundance of litter-dwelling biota is that the more open understorey outside the exclosures facilitated predation by birds and rodents. Herbivory can also have positive (Ashkannehad & Horton 2006) or negative effects on mycorrhizal associations (Gehring & Whitham 1994), but no study has investigated the links between deer and mycorrhizal associations in New Zealand.

Managers of New Zealand's natural ecosystems have recently begun to consider how mammalian herbivore management impacts on carbon sequestration (Morrison 2008), but no New Zealand study has investigated the ecosystem-level impacts of deer (or any other ungulate) on carbon. The major carbon pools in natural ecosystems are live biomass, detritus and soil carbon, consumers and decomposers (Schlesinger 1997). Deer directly affect carbon by consuming foliage (i.e. they are consumers) and indirectly through plant–soil feedbacks (Bardgett & Wardle 2003). Wardle et al. (2001) found that soil carbon storage responded idiosyncratically to the exclusion of ungulates at 30 New Zealand sites (cf. Pastor et al. 1993). Resolution of such idiosyncratic responses requires further understanding of how deer impact on forest succession and mediate soil processes. Given that live biomass in forests is a large carbon pool, the most profound effect of deer on carbon storage in New Zealand is likely to be where herbivory slows the succession of grassland to forest. Whether, and if so, when, deer cause gains or losses in ecosystem carbon stocks is a question to be resolved (Peltzer et al. 2009).

We have identified a wide variety of factors that can potentially influence the impacts of deer on an ecosystem in space and time. Other introduced herbivores may also be present at sites used by deer and often the impacts of deer cannot be partitioned from those of other species. It is therefore unsurprising that Wardle et al. (2001) found the effects of browsing mammals on many of the measured ecosystem properties at the 20 × 20 m scale to be idiosyncratic, with about equal numbers of the 30 sites showing strong positive and strong negative effects. However, above-ground effects were less variable than below-ground effects, and the effects of browsing mammals on some attributes (e.g. vegetation density and richness and litter macrofauna abundance) were consistently strong (Wardle et al. 2001). The idiosyncratic responses among sites may reflect initial conditions (e.g. an absence of vegetation in the browse layer due to low light or soil fertility), the availability or otherwise of seeds of some eliminated species and/or the dynamics and population status of the browsing mammals that are present (e.g. deer may have been harvested to very low densities at that site). Most studies of the impacts of deer in New Zealand have been conducted over small spatial and short temporal scales; the oldest of the exclosures examined by Wardle et al. (2001) was 36 years. Key unanswered questions centre on the long-term effects of deer on canopy and subcanopy tree composition and the flow-on effects of any associated changes in litter quality and quantity for both above-ground and below-ground ecosystem properties and processes.

Finally, we note that work outside New Zealand has shown that deer can reduce the diversity and abundance of birds, particularly those that utilise the understorey (e.g. Côté et al.

2004; Allombert et al. 2005). Leathwick et al. (1983) thought that red deer and feral goats had contributed to the decline of kōkako (*Callaeas cinerea wilsoni*) through the removal of preferred feeding plants, but predation by possums seems to be a much more important agent of decline than the removal of food trees (Innes et al. 1999) and it has recently been argued that food limitation is rarely important for New Zealand forest birds (Innes et al. 2010).

Wardle et al. (2001) observed lower vegetation density in the browse tier outside compared with inside ungulate exclosures at 25 of the 30 sites they sampled. In addition to deer modifying food availability, reduced vegetation density in the browse tier may change nesting opportunities and/or success (e.g. by increasing nest predation rates by introduced rodents and brushtail possums). The reduced abundance of litter-dwelling macrofauna (Wardle et al. 2001) could also have important consequences for some bird species.

## What is known about the impacts of moa?

### Diversity, distribution and dynamics

Moa and their ancestors have been present in New Zealand since its geological split from Australia/Antarctica about 82–85 million years ago (Cooper et al. 2001). There are ten currently accepted Holocene moa species (Worthy & Holdaway 2002, with revisions by Bunce et al. 2003; Huynen et al. 2003; Worthy 2005); Tennyson and Martinson (2006) and Tennyson (2010) accept nine, combining the two *Euryapteryx* spp., but until that revision is published we use ten (see also Lee et al. 2010). The ten species lived in three main habitats (Worthy 1990; Worthy & Holdaway 2002): upland, lowland wet forest, and lowland dry climate. The upland habitat was the grassland area above treeline and the most common species here was upland moa (*Megalapteryx didinus*; 14–63 kg). However, three other species – crested moa (*Pachyornis australis*; 44–90 kg), North Island giant moa (*Dinornis novaeseelandiae*; females 76–242 kg; males 34–85 kg) and South Island giant moa (*D. robustus*; females 76–242 kg; males 34–85 kg) – were also present. Snow would have covered most of the upland habitat for three or four months of the year. The lowland wet forests were in areas of rainfall >1200 mm (i.e. western and northern main islands and Stewart Island) and were characterised by tall forest with a continuous canopy. The little bush moa (*Anomalopteryx didiformis*; 19–73 kg) was the most common species in lowland wet forest, but South Island giant moa and eastern moa (*Emeus crassus*; 36–79 kg) were also present in the South Island, and North Island giant moa in the North Island. The lowland dry climate habitats, mosaics of shrubland, grassland and open-canopy forest, were in the low-rainfall areas in the east of both main islands. The South Island lowland dry climate habitats were occupied by stout-legged moa (*Euryapteryx gravis*; females 49–105 kg; males 12–34 kg), heavy-footed moa (*Pachyornis elephantopus*; 44–90 kg), and South Island giant moa. In the North Island, Mantell's moa (*Pachyornis geranoides*; 17–36 kg), coastal moa (*Euryapteryx curtus*; females 49–105 kg; males 12–34 kg) and North Island giant moa were common. The dominant species of moa within the lowland dry climate habitats varied depending on elevation, topography and climate (Worthy & Holdaway 2002).

The ten species of moa varied considerably in body mass (Worthy & Holdaway 2002). Sexes were dimorphic, with females up to 150% of the male's size and 280% of their

body mass (Bunce et al. 2003). Within a species, skeletal size and body mass varied with epoch (Worthy & Holdaway 2002) and habitat: for example, the larger *Dinornis* occurred in more open vegetation, at lower altitude, with lower rainfall (Bunce et al. 2003).

It is generally agreed that all species of moa in New Zealand went extinct after the earliest evidence of prehistoric human colonisation, and that these extinctions were caused by human-hunting and loss of habitat (Anderson 1989a, b). However, there is some debate about the speed of these extinctions following initial human arrival c. 1280 AD (Wilmshurst et al. 2008), with estimates ranging from <50 years after arrival (Holdaway & Jacomb 2000) to c. 1400 AD (Anderson 2002). The period between the extinction of moa and the arrival of deer from the late 1800s is termed the 'moa gap'. Avian herbivores other than moa also went extinct, including the North Island goose (*Cnemiornis gracilis*), South Island goose (*C. calcitrans*), Hodgens' waterhen (*Gallinula hodgenorum*), New Zealand coot (*Fulica prisca*) and Finsch's duck (*Chenonetta finschi*) (Worthy & Holdaway 2002; Tennyson & Martin 2006; Lee et al. 2010). The distributions and abundances of many other terrestrial plant-eating birds would also have been changed by habitat loss and predation (Lee et al. 2010). Hence, the 'moa gap' includes changes in many more species than the ten moa.

In contrast with moa, present in New Zealand for millions of years, deer have only been present in New Zealand for a maximum of c. 150 years and, in most places, much less than that. Hence, there was a potential for coevolution between moa and plants (see below), but less so for deer and plants. However, it remains difficult to determine how much the vegetation present when Europeans arrived had been shaped by moa versus the other factors such as climate, glaciation, large-scale disturbances and colonisation events (Wardle 1991) and how much it has changed since the widespread extinction of the avian megaherbivores c. 600 years ago.

The largest moa could have browsed to a height of c. 3 m (Worthy & Holdaway 2002), about 1 m higher than for deer. Although moa possessed a more simple stomach than deer, they possessed gizzards in which food was crushed between stones (Worthy & Holdaway 2002). The deer taxa present in New Zealand are medium-sized ruminants that continually mix their foods in their multi-chambered stomachs and through remastication (Hofmann 1989). Worthy & Holdaway (2002: 209) stated that deer, goats and moa are all browsers; however, feral goats and the deer taxa present in New Zealand are classified as 'opportunistic mixed feeders' that avoid fibre as much as possible (Hofmann 1989). Although most published studies of the diet of deer in New Zealand have been conducted in forest habitats, native and/or introduced grasses are known to be a very important seasonal food source for most deer in New Zealand (Nugent & Fraser 2005).

In the absence of hunting, deer occupy all habitats from coastal dunes and forest through montane forest to subalpine grasslands (see above). Like the upland moa probably did, red deer make use of the subalpine grasslands in all seasons, but much less so in winter. Hence, deer now use most of the habitats used by moa. The smallest geographic range of a deer taxon in New Zealand is c. 469 km<sup>2</sup> (rusa deer; Fraser et al. 2000). In contrast, Worthy and Holdaway (2002) thought that the smallest geographic range of a moa species, crested moa, was c. 40% of the South Island (i.e. c. 60,000 km<sup>2</sup>).

Whereas the dynamics of deer populations in New Zealand are well described (see above), relatively little is known about

the population dynamics of moa. Moa probably lived either in pairs or in small family groups (cf. Caughley 1989) and were hunted by avian predators (Worthy & Holdaway 2002). Haast's eagle (*Harpogornis moorei*), the remains of which have been found only in the South Island, killed adults of even the largest moa species (Worthy & Holdaway 2002). Pairs of moa produced one or two eggs per clutch, but adults may have lived for  $\geq 50$  years (Worthy & Holdaway 2002; Turvey & Holdaway 2005). Estimating the abundance of a long-extinct species is problematic. Anderson (1989a) thought the biomass of moa at the time of human settlement would have been 2–10 times that of emu (*Dromaius novaehollandiae*), and would have declined with increasing forest cover. Based on published estimates of emu abundance and assumed emu and moa masses of 35 kg and 75 kg, respectively, Anderson (1989a) estimated that there were 70 500 moa in New Zealand, with 44 000 of those in the South Island. Holdaway & Jacomb (2000: 2251) estimated there were 158 000 moa at the time of human settlement "from a regional analysis of distribution and abundance", with no other details provided. Gemmell et al. (2004) estimated the prehuman abundance of moa to be c. 3–12 million, based on mitochondrial DNA; however, the estimate is based on small sample sizes ( $n = 21$  and 36 *Dinornis* on the North and South islands, respectively) that lived from c. 1000 to 6000 years ago. We think that Gemmell et al.'s estimate is unreasonably high and do not consider it further here. If we assume that moa lived in all habitats except alpine herbfields, rock, scree and ice, then based on values in Blaschke et al. (1981) and using the estimates of Anderson (1989a) and Holdaway & Jacomb (2000), moa density was c. 0.3 or 0.6 individuals km<sup>-2</sup> at the time of human settlement. These estimates are in broad agreement with robust estimates of extant ratite abundance. Using aerial surveys, Giordano et al. (2008) estimated the maximum density of greater rhea (*Rhea americana*; c. 25 kg) in a semi-natural grassland in the Argentine pampas to be  $0.86 \pm 0.24$  individuals km<sup>-2</sup>. Barri et al. (2008) estimated the densities of lesser rhea (*Rhea pennata pennatai*; c. 15 kg) sympatric with livestock on grasslands in the Patagonia steppe to be  $<1.65 \pm 0.26$  individuals km<sup>-2</sup>. The abundances of emus inside and outside the dingo fence in South Australia were estimated at  $\leq 2.0$  and  $\leq 0.8$  individuals km<sup>-2</sup>, respectively, using aerial survey (Pople et al. 2000).

Emus (c. 60 kg) eat a variety of fruits, seeds, flowers and the green herbage of annual and perennial plants (Davies 1978). They need to consume c. 1 kg of dry matter per day (O'Malley 1995). Ostriches (*Struthio camelus*; c. 130 kg) eat annual grasses and forbs, leaves, flowers and fruits from both succulent and woody plants and need at least 1.5–2.0 kg of dry matter per day (Milton et al. 1994). When corrected for body mass with an allometric scaling exponent of 0.75 (West et al. 1997), the intake rates of dry matter required by red deer (Fennessy 1981; Nugent & Fraser 2005) and extant ratites are broadly similar.

Given the inter- and intra-specific variation in the body masses and geographic ranges of moas (Worthy & Holdaway 2002), it is difficult to estimate a mean body mass. However, if we use the 60 kg used by Caughley (1989), then the average moa biomass would have been 18–36 kg km<sup>-2</sup>. Caughley (1989) estimated the biomass of moa to be 2000 kg km<sup>-2</sup> (33 moa km<sup>-2</sup>) using a published relationship between the abundance of vertebrates and rainfall, soils and vegetation (grass or forest) in part of Africa. Of course, local moa densities would have been more variable than the simple averages presented here, but even a 10-fold increase in abundance (6 individuals km<sup>-2</sup>)

gives a biomass (360 kg km<sup>-2</sup>) an order of magnitude less than for red deer at peak abundance.

### Diet selection

Table 1 (a summary of Appendix 1) lists the species recorded in the gizzards and coprolites (dried droppings) of moa. Recent studies of gizzard contents (Wood 2007) and especially coprolites (Horrocks et al. 2004; Wood et al. 2008) have shown the moa taxa to have a much broader diet than previously thought (Lee et al. 2010). In particular, coprolites (attributed to upland moa) from Takahē Valley, Fiordland, show that tussocks and lake-edge herbs could be an important component of moa diets. Coprolites from central and west Otago and identified by DNA as from South Island giant moa, heavy-footed moa and upland moa contained at least 30 taxa with a predominance of herbs and low shrubs, and showed that the different moa species ate a similar range of plant species at those sites (Wood et al. 2008). Current thinking, based on skull morphology and the analysis of gizzards and coprolites, is that *Dinornis*, *Anomalopteryx*, *Megalapteryx* and *Pachyornis* were principally coarse-fibre feeders and *Emeus* and *Eurapteryx* preferred soft-fibre foods, but that *D. robustus*, *M. didinus*, *P. elephantopus* and *Emeus crassus* had a browser–grazer diet (Wood et al. 2008; Lee et al. 2010). Wood et al. (2008: 2600) considered *M. didinus* to be “predominantly a herb grazer”. It seems that moa were generalist herbivores but, like deer, diet varied greatly depending upon vegetation type and season. Further studies of coprolites from throughout New Zealand can be expected to broaden the list of items in the diets of each moa species.

Table 1 and Appendix 1 list whether or not plant species recorded in the diets of moa have been recorded in the rumens or faecal pellets of deer in New Zealand. The majority (c. 73%) of taxa recorded in the diet of moa have been recorded in the rumens or faecal pellets of deer, a result also obtained by Lee et al. (2010). Conversely, at least 186 taxa comprising trees, shrubs, climbers, ferns and allies, grasses, Liliaceae, herbs, fungi, lichens, liverworts and orchids have been recorded in the diet of deer but not moa (cf. Table 1 with Forsyth et al. 2002). Hence, the majority of taxa recorded in the diet of deer have not yet been recorded in the diet of moa. Note, our comparison only includes deer, not other introduced ungulates.

Leaves of *Prumnopitys taxifolia*, *Myrsine divaricata* and *Rubus* were common in the gizzards of the South Island giant moa (Burrows 1980; Burrows et al. 1981). Although deer will eat conifers, they have not been preferred in any of the New

Zealand diet selection studies (Forsyth et al. 2002, 2005). For example, *P. taxifolia* was avoided by red deer at Waihaha (Nugent et al. 1997) and constituted <0.1% of the diet of white-tailed deer on Stewart Island (Nugent & Challies 1988). *M. divaricata* is an angiosperm tree common in the diet of moa, but is eaten in approximate proportion to its availability by fallow deer in the Blue Mountains (Nugent 1990) and avoided by white-tailed deer on Stewart Island (Nugent & Challies 1988) and red deer in Waihaha (Nugent et al. 1997). Although it is often difficult to identify ingested fragments to species, *Rubus* was eaten in approximate proportion to its availability by white-tailed deer on Stewart Island and fallow deer in the Blue Mountains. It is more difficult to make inferences about other items because of uncertainty about the species present in the diet of moa and/or deer (e.g. selection for *Coprosma* spp. by deer varies greatly; Appendix 1). Wood et al. (2008: 2601) considered that their data “strongly refute the idea that ... deer ... might act as browsing surrogates for moa” because moa in Otago ate a high proportion of taxa that are avoided by deer. We note that there has not been a study of diet selection by any deer taxa in the vegetation that characterised the semi-arid Central Otago sites analysed by Wood et al. (2008). Interestingly, several subcanopy tree species that are strongly preferred by deer (*Griselinia littoralis*, *Fuchsia excorticata* and *Schefflera digitata*; Forsyth et al. 2002, 2005) have not yet been recorded in the diet of moa. Further studies of moa diet from locations at which those plant species were present are needed to determine whether they were eaten by moa.

High proportions of seeds and fruits (particularly *Coprosma* spp.) have been recorded in moa gizzards and coprolites, but have seldom been recorded in the rumens of deer (Appendix 1). Some exceptions are noted: Ripe *Ripogonum scandens* fruit formed 18 and 21% of the diet (by dry weight) of white-tailed deer on Stewart Island during winter and spring, but <5% in summer and autumn; *Ripogonum* leaves formed <7% of the diet in all seasons (Nugent & Challies 1988). *Griselinia littoralis* fruits are occasionally observed in red deer rumens, but these were most likely incidentally ingested with foliage from windfall branches (P. Sweetapple, Landcare Research, pers. comm.). Grass seeds are occasionally present in the rumens of wild deer in New Zealand (G. Nugent, Landcare Research, pers. comm.).

The only site where there are data on the diets of both moa and deer is in Fiordland. Analysis of moa coprolites (most likely of upland moa) deposited c. 2500 years ago in eastern Fiordland showed that the animal had been browsing branchlets

**Table 1.** Summary of plant taxa recorded in the diets of only moa and both moa and deer. For sources see Appendix 1.

Eaten only by moa	<i>Baumea arthropophylla</i> / <i>Lepidosperma australe</i> , <i>Calystegia sepium</i> , <i>Carex secta</i> , <i>Centrolepis</i> / <i>Gaimardia</i> sp., <i>Ceratocephalus pungens</i> , <i>Coprosma petriei</i> , <i>C. wallii</i> , <i>Cordyline australis</i> , <i>Einadia allanii</i> , <i>E. triandra</i> , <i>Eleocharis</i> sp., <i>Lophomyrtus obcordata</i> , <i>Muehlenbeckia axillaris</i> , <i>M. complexa</i> , <i>Myosurus minimus</i> subsp. <i>novae-zelandiae</i> , <i>Passiflora tetrandra</i> , <i>Pimelea</i> sp., <i>Rytidosperma setifolium</i> , <i>Teucrium parvifolium</i>
Eaten by moa and deer	<i>Aristolelia</i> spp., <i>Carex</i> spp., <i>Carmichaelia</i> spp., <i>Carpodetus serratus</i> , <i>Clematis</i> spp., <i>Colobanthus</i> spp., <i>Coprosma</i> spp., <i>Coprosma cuneata</i> , <i>C. microcarpa</i> , <i>C. rhamnoides</i> , <i>C. rotundifolia</i> , <i>Coriaria plumosa</i> , <i>Corokia cotoneaster</i> , <i>Dacrycarpus dacrydioides</i> , <i>Elaeocarpus hookerianus</i> , <i>Euphrasia</i> spp., <i>Gaultheria crassa</i> , <i>Gonocarpus aggregatus</i> , <i>Hebe</i> spp., <i>Hoheria</i> spp., <i>Juncus</i> spp., <i>Lagenifera pumila</i> , <i>Leptospermum scoparium</i> , <i>Leucopogon fraseri</i> , <i>Lobelia angulata</i> , <i>Melicope simplex</i> , <i>Meliccytus</i> spp., <i>Muehlenbeckia australis</i> , <i>Myosotis pygmaea</i> , <i>Myrsine divaricata</i> , <i>Nertera</i> spp., <i>Nothofagus menziesii</i> , <i>N. solandri</i> var. <i>cliffortioides</i> , <i>Olearia</i> spp., <i>Oxalis exilis</i> , <i>Pennantia corymbosa</i> , <i>Phormium tenax</i> , <i>Phyllocladus alpinus</i> , <i>Pittosporum</i> spp., <i>Plagianthus regius</i> , <i>Poa</i> spp., <i>Podocarpus hallii</i> , <i>Polystichum vestitum</i> , <i>Prumnopitys taxifolia</i> , <i>Pseudopanax</i> spp., <i>Ranunculus</i> sp., <i>Raukawa anomalus</i> , <i>Rubus</i> spp., unidentified mosses, <i>Urtica incisa</i> , <i>Wahlenbergia pygmaea</i>

of *Nothofagus menziesii* and *N. solandri* var. *cliffortioides*, and had been grazing on tussocks (Poaceae/Cyperaceae) and lake-edge herbs (*Isoetes*) (Horrocks et al. 2004). The absence of fruit in these coprolites suggests that fruit was a resource exploited seasonally by moa. Lavers (1978) estimated the diet of 174 red deer shot in the Murchison Mountains during 1976–1978. Although many of the deer were shot in grassland rather than forest, *N. menziesii* and *N. solandri* var. *cliffortioides* were present in 39 (22%) and 15 (9%) rumens, respectively. *Nothofagus menziesii* was preferred, and *N. solandri* var. *cliffortioides* avoided, by red deer in south-eastern Fiordland (Appendix 1). Hence, there is evidence that moa and deer both ate the same species at the same site.

Some of the species recorded in Table 1 and Appendix 1 were present only as traces in both deer and moa diets, and it is possible that these species were ingested accidentally. Moreover, estimates of food abundance need to be paired with estimates of diet to make inferences about diet selection, and this is obviously difficult to do for extinct moa. Wood et al. (2008) used seed assemblages in the coprolite-bearing soils in three Central Otago rockshelters as a proxy for vegetation composition; when compared with the abundance of seeds in coprolites, there was a non-significant preference for low shrubs and herbs and a non-significant avoidance of trees and tall shrubs.

As noted above, there has been much speculation about the degree to which the divaricate growth form has evolved in response to moa browsing (Greenwood & Atkinson 1977; Atkinson & Greenwood 1989; cf. McGlone & Webb 1981; McGlone & Clarkson 1993). Bond et al. (2004) examined the feeding behaviour and intake rates of extant ratites (ostriches *Struthio camelus* and emus) on two tree species with divaricate and non-divaricate juvenile and adult growth forms, respectively. The divaricate growth forms had 30–70% less biomass removed compared with the adult growth forms. In a further contrast, a single goat removed four times more biomass than the ratites. Further trials with emus, red deer and goats presented with 14 indigenous shrubs that varied in architecture and phytochemistry showed that all three herbivores ate less of species with small leaves, and that consumption was reduced more by divarication than by chemical traits (Pollock et al. 2007). Moreover, some of the plants recorded by Wardle et al. (2001) as increasing in the presence of deer had heterophyllic or divaricate growth forms. Hence, the prediction (Bond et al. 2004) that the ratite-resistant structures confer little resistance against introduced browsing mammals is not wholly supported by data.

## Composition, structure and ecosystem processes

The large numbers of fruits and seeds of some genera in the diet of moa (Appendix 1) suggest that moa may have been important dispersers (see also Lee et al. 2010). Cassowaries (*Casuaris* spp.) are crucial dispersers of large-fruited plant species (e.g. Mack 1995; Webber & Woodrow 2004), although in contrast to moa they lack gizzards. We are unaware of anyone investigating an analogous role for deer in New Zealand (see also Kelly et al. 2010) but introduced hog deer (*Axis porcinus*) have recently been shown to disperse the seeds of twenty exotic and 22 native species in south-eastern Australia (Davis et al. 2009).

If moa–plant coevolution was significant, then the extinction of moa might be expected to have had a strong

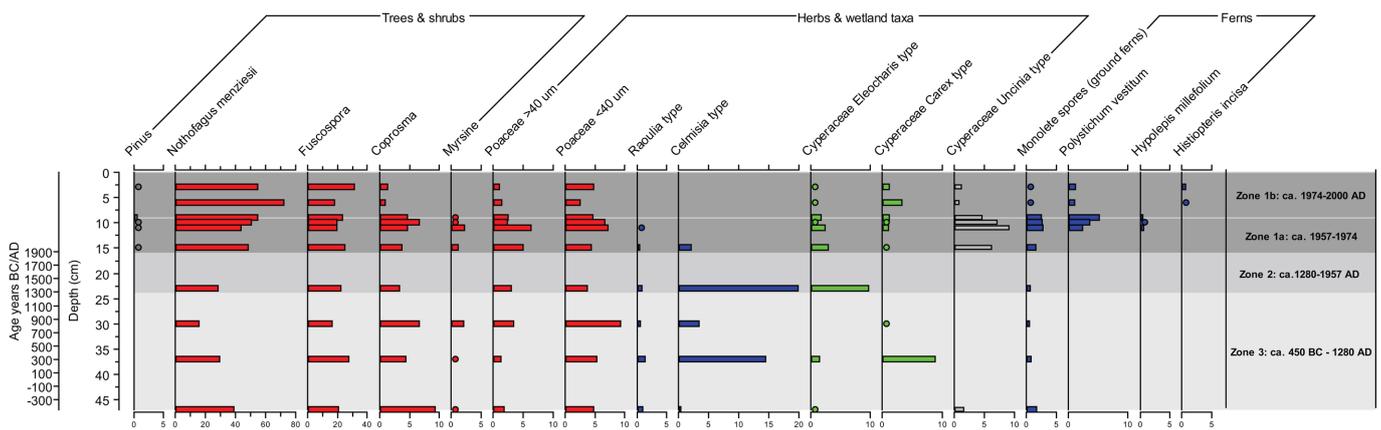
effect on New Zealand plants (Cooper et al. 1993). H. W. Wellman (cited in Fleming 1977) suggested that regeneration failure in native conifers may have followed the extinction of moa as a consequence of increased competition from plants previously eaten. Although the ‘regeneration gap’ for conifers is the subject of ongoing debate, its causes seem unrelated to moa. In particular, widespread regeneration of podocarps in the lowland forests of the west coast of the South Island occurs following catastrophic earthquakes; we agree with the conclusion of Wells et al. (2001) that the large-scale absence of regeneration simply reflects an absence of such disturbances in the last 300 years.

Wardle et al. (2001) attributed the reduced abundance of litter macrofauna outside compared with inside ungulate exclosures to trampling rather than to ungulate-mediated differences in litter. Interestingly, Duncan and Holdaway (1989) showed that the foot pressures of red deer, goats and Himalayan tahr (*Hemitragus jemlahicus*) were double those of moa, and that those of moa were similar to emu. Ungulate hooves cut into soft ground, but moa feet had relatively little impact. Horn (1989) suggested that moa tracks were still visible in the landscape. We agree that moa would have used the same pathways to move between preferred parts of the landscape and this would have created tracks, but we suspect such tracks would be difficult to distinguish c. 600 years after the extinction of moa, due to ongoing movement of soil and other perturbations. We believe trampling caused by deer living at higher densities than moa (at least prior to helicopter-based hunting) is an important new impact in New Zealand forests.

One way to compare the impacts of moa and deer is to use pollen to reconstruct the vegetation at a forested site in recent millenia. Wilmshurst (2003) used pollen analyses of 50-cm organic soil cores from clearings in *Nothofagus menziesii* forest in the Chester Burn catchment, Murchison Mountains, to evaluate understorey changes over the last 2000 years (Fig. 3). A pollen record covering this time period could be used to evaluate forest understorey composition during three periods: (1) when moa and other avian megaherbivores were present, (2) when moa and other avian megaherbivores were extinct, but before the arrival of deer (i.e. the moa gap), and (3) following colonisation by red deer. Moa and other avian megaherbivores were likely extinct by c. 1400 AD and red deer colonised the Murchison Mountains in the 1930s (Parkes et al. 1978).

One of the pollen records from Chester Burn has been radiocarbon-dated to help pinpoint the arrival of humans and deer (Fig. 3). A radiocarbon date at the base of the core (47 cm) returned an age of  $2452 \pm 45$  years BP (i.e. before 1950 AD; lab code NZA 15756), which calibrates (using the software CALIB v5.0.1 (Stuiver & Reimer 1993) with the Southern Hemisphere Calibration dataset SHCal04 (McCormac et al. 2004)) to c. 450 calendar years BC. *Sphagnum* fragments from 15 cm were also radiocarbon-dated, returning an age of c. 1957 AD (Radiocarbon laboratory code WK 14535;  $105.2 \pm 0.5\%$  modern; calibrated to calendar years using CALIBomb Radiocarbon Calibration Program; Reimer et al. 2004).

The pollen record (Fig. 3) shows a distinct Pinaceae pollen horizon at 15 cm that pinpoints the establishment of major *Pinus* plantations in the wider Southland region. Pine pollen provides a chronomarker for European plantations. The low levels represented throughout the Chester Burn core are similar to those recorded in modern surface samples taken from the same catchment at the time of coring (Wilmshurst 2003). Although pines were planted as shelter belts elsewhere in New Zealand from the late 1800s, the early planting of pines



**Figure 3.** Relative percentage pollen diagram for core X00/4 from c. 990 m a.s.l., Chester Burn, Murchison Mountains, showing selected taxa (see Wilmschurst 2003 for full taxa). Dots represent values <1% of the total pollen. Total pollen consists of all terrestrial taxa except ferns. The four zones are described in the text. Red indicates taxa eaten by deer and moa (*Nothofagus* to *Poaceae*), green indicates taxa eaten only by moa (*Eleocharis* and *Carex*), blue indicates taxa eaten only by deer, and grey indicates taxa not recorded in the diets of deer or moa (*Pinus*, *Uncinia*). Avian megaherbivores were likely extirpated from this area c. 1400 AD and the earliest pollen records are dated at c. 2450 years BP.

in Southland began c. 150 km to the south-east of Chester Burn during 1920–1935 (Roche 1990). However, we believe that the beginning of the pine horizon in Fig. 3 represents the second major phase of extensive plantation forestry in Southland from 1960–1975 onwards (Roche 1990), which is supported by our radiocarbon date of c. 1957 AD. On the basis of the pine pollen and radiocarbon dating, and the first evidence of *Pteridium* spores, which mark initial human arrival (see McGlone & Wilmschurst 1999), the pollen diagram (Fig. 3) has been divided into three zones: zone 3, avian megaherbivores present; zone 2, avian megaherbivores and deer absent (the moa gap), and zone 1 deer present. Zone 1 is further split into subzones 1a (1957–1974) and 1b (1974–2000) because deer abundance was much reduced in the latter period by commercial and official hunting (KW Fraser, G Nugent 2003. Landcare Research unpubl. report LC0203/178). The 1974 age at 9 cm was derived by linear interpolation.

There are several changes in relatively short-lived taxa in zone 1 (Fig. 3) that are unprecedented in the previous 2000 years of the profile. These are likely to have been caused by deer. In particular, there is a decrease of *Celmisia* and an increase of ground ferns (probably *Blechnum* spp., but represented by unidentifiable monolete fern spores), *Polystichum vestitum* and the sedge *Uncinia* (avoided by deer), which was not recorded in the core before pine pollen occurs. *Uncinia* and ground ferns including *P. vestitum* may have increased in abundance after peak deer densities following release from interspecific competition (Allen et al. 1984; Wardle et al. 2001). The relative abundance of preferred tree species such as *Griselinia littoralis*, *Schefflera digitata* and *Weinmannia racemosa* did not change in the pollen record following the arrival of deer (see Wilmschurst 2003). However, these species are long-lived and even if all seedlings and saplings were killed by deer, trees with flowers above the height of deer would continue to contribute pollen to the soils for many decades or centuries until those adults died. In zone 1b there were declines in *Poaceae* (particularly grains >40  $\mu\text{m}$ , which includes *Chionochloa* type), *Eleocharis* type (all *Eleocharis* spp. except *E. sphacelata*; Moar & Wilmschurst 2003) and *Uncinia* type. The decline in *Poaceae* following a reduction in deer abundance is surprising because these taxa are eaten by deer in Fiordland (Lavers 1978; Rose & Platt 1987).

Caughley (1989), Bond et al. (2004) and Bellingham & Lee (2006) all proposed that the extinction of moa would have resulted in a change in vegetation composition. Caughley (1989: 7) made the specific prediction that “decreaser species” (i.e. those favoured by moa) would have “outcompeted the increaser species”, and Bond et al. (2004) elaborated on this by suggesting that broad-leaved plant species would have increased because they outcompeted the ratite-resistant species (i.e. those that are heterophyllic or strongly divaricate). The upland moa was the most abundant moa species in this area, although some other South Island species probably also used the area (Duff 1952; Worthy & Holdaway 2002). From the pollen record, only *Eleocharis* type, which has been recorded in moa diets from coprolite studies (Wood 2007), appears to show an increase during the moa gap.

Finally, herbivore conversions may have consequences on components other than vegetation. There appear to be major differences between moa and deer in greenhouse gas production. Methane ( $\text{CH}_4$ ), an important greenhouse gas, is produced by anaerobic bacteria in the stomachs of deer (and all other ruminants), but apparently not in emu, cassowary or kiwi (*Apteryx* spp.; review in Hackstein & van Alen 1996). Although there is debate about the amount of methane produced by ostriches and rheas, given the taxonomic relationships reported in Bunce et al. (2003) it is unlikely that moa were methane producers. Hollinger and Hunt (1990), assuming annual production of 14 kg  $\text{CH}_4$  per deer, estimated that the then wild deer population (thought, at that time, to be c. 250 000; Nugent & Fraser 1993) produced 3000 tonnes of  $\text{CH}_4$  carbon annually. Although that is a very small value relative to other ‘natural’ and anthropogenic sources (Hollinger & Hunt 1990), it is nevertheless more than would have been produced by moa.

## Future research

In conducting this review we have identified many questions that warrant investigation. Below we list six of the most important areas for further research.

### Deer and seed dispersal

It is likely that moa were important dispersers of the seeds of some species. Although fruits and seeds of forest species are seldom eaten by deer, except for *Ripogonum scandens* on Stewart Island (Nugent & Challies 1988), Kelly et al. (2010) emphasise that even rare long-distance dispersal events can be important for plant populations. The role of deer in dispersing native grasses and fungi has also not been addressed. This topic should be seen within the wider question of how deer redistribute biomass around the landscape, with flow-on effects for both above- and below-ground communities and processes (Bardgett & Wardle 2003).

### Impact of deer on canopy trees

The long-standing question of how deer impact on canopy trees (Perham 1922; Veblen & Stewart 1982) needs to be evaluated with appropriate enumeration of all canopy tree life-history stages (e.g. Pacala et al. 1996). The impacts of deer on the composition and structure of canopy trees need to be evaluated for tree species at different sites with different species of deer.

### Do deer constrain grassland to forest succession?

We believe the most profound effect of deer on carbon storage in New Zealand is likely to be where herbivory slows the succession of grassland to forest. Understanding how deer affect succession of grassland to forest requires knowledge of how deer affect seedling establishment, growth and mortality (LE Burrows, DA Peltzer, PJ Bellingham, RB Allen 2008. Landcare Research unpubl. report LC008/087). Such effects will be at least partly determined by the traits of the individual woody species in the succession.

### Long-term effects of deer on below-ground ecosystems

There has been little work on the long-term effects of deer on below-ground communities and processes. Litter is a key link between above- and below-ground communities and processes (Wardle 2002). The selective foraging of deer is

expected to lead to a litter with higher concentrations of foliar fibre, making it slower to decompose (Wardle et al. 2001, 2002; Forsyth et al. 2005). Such an impact is likely to have flow-on effects for other components of the below-ground ecosystem (Bardgett & Wardle 2003). Although Wardle et al. (2001) found the effects of browsing mammals on litter to be idiosyncratic among the 30 sites, the longer term consequences of deer for forest composition, and hence litter quality and quantity, deserve further investigation. It is also unknown how defoliation of individual seedlings and saplings influences their below-ground communities.

### Effect of deer on forest birds

Given that work outside New Zealand has shown that introduced deer can reduce the diversity and abundance of understorey birds (e.g. Allombert et al. 2005), we believe the effects of deer on New Zealand forest bird populations and communities deserve investigation. Although Innes et al. (2010) believe that food availability is seldom likely to be limiting for New Zealand forest birds, the effects of deer-induced reductions in understorey density (Wardle et al. 2001) on nesting success – perhaps via altered predation risk – may be particularly important.

### Further use of pollen analysis to assess herbivore effects

The use of pollen from cores to reconstruct the vegetation histories at multiple sites with a range of deer colonisation and harvesting histories is the most obvious way to evaluate the relative impacts of deer and moa on vegetation (Wilmshurst 2003; Fig. 3). One caveat on interpreting vegetation changes during, and subsequent to, the decline of moa is the strong influence of Polynesian fire on vegetation at some sites (e.g. McGlone 1989; McGlone & Wilmshurst 1999): hence, currently forested landscapes, such as in the Chester Burn example (Wilmshurst 2003), would be the most appropriate sites for such work. Preliminary data from the Chester Burn revealed limitations to the detection of vegetation change associated with moa and/or deer, and further work to detect

**Table 2.** Similarities and differences in factors determining deer and moa impacts in New Zealand ecosystems.

Factor	Similarities	Differences
Diversity, distribution and dynamics of herbivore	Seven deer taxa (and red deer alone) utilise all of the habitats previously occupied by moa taxa.	Deer attain densities and biomasses that are at least an order of magnitude greater than reasonably surmised for moa. Moa probably lived in small family groups whereas deer form large groups in favoured feeding areas. Deer are ruminants, whereas moa possess more simple stomachs and gizzards.
Diet selection of herbivore	Deer exhibit considerable overlap in diet with moa, although several subcanopy tree species highly preferred by deer have not yet been recorded in the diet of moa. Divarication apparently confers resistance to biomass removal by deer and a ratite surrogate for moa. The diet of moa, like deer, varied greatly among vegetation types and probably also with season.	The potential for coevolution between moa and plants is greater than for deer and plants. Moa were important seed dispersers and this appears to be generally not so for deer. Palatable forest understorey plants dispersed by moa were markedly reduced by deer through foliage consumption and bark stripping.
Composition, structure and ecosystem processes	Deer consume seedlings of some of the same tall forest tree species utilised by moa, but the subsequent effects on canopy dominance need to be understood within a context of disturbance-mediated dynamics.	During the moa era New Zealand was largely forested, whereas during the deer era forests only dominate in wet and high-elevation parts of the country. Deer impacts have been relatively short-term compared with moa and this is particularly significant for long-lived tree species. Foot pressure is greater of deer than moa and together with the higher densities of deer could mean trampling is an important new impact of deer.

the impact of avian extinctions and introduced deer on the vegetation composition should target sites in fertile clearings with numerous and relatively short-lived taxa. In such clearings the pollen rain would be less dominated by tall long-lived forest trees that might obscure the detection of browsing impacts in the subcanopy. Finally, radiocarbon dating of the soil profiles would not only identify points within each core when Polynesians arrived and when moa likely went extinct, but help to establish a robust age–depth model and guide the core-sampling resolution. A high temporal resolution (e.g. one sample per decade) would increase the chances of detecting change in short-lived taxa.

## Conclusion

Our key findings concerning the similarities and differences of the impacts of deer and moa are summarised in Table 2. We do not think the evidence supports Batcheler's (1989: 57) statement: "on easier low altitude country, moa feeding pressure would have been equivalent to that exerted by the introduced mammals". Although deer have occupied all habitats utilised by moa and have a partially overlapping diet (Table 1, Appendix 1), at peak density red deer were probably several orders of magnitude more abundant (in terms of density and biomass) than moa. There is evidence of widespread understorey/grassland compositional change caused by deer. It is likely moa played an important role in the dispersal of some plants, but this has not been studied for deer. Trampling is likely a major new impact of deer. We believe that the impacts of introduced deer on ecosystems have been markedly different from those of moa (see also Worthy & Holdaway 2002; Wood et al. 2008) and beyond the likely differences in species preferences of the two groups suggested by Caughley (1989).

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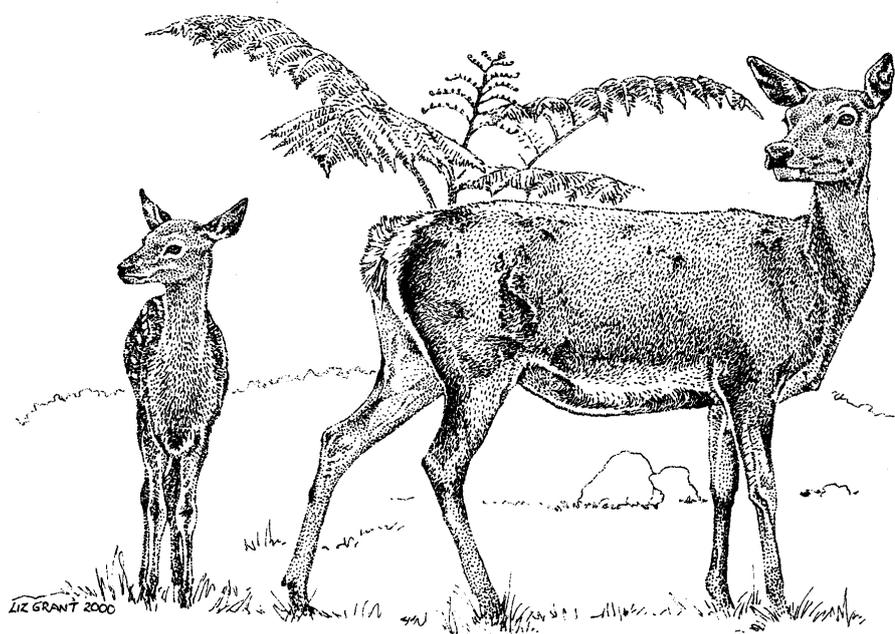
**Appendix 1.** Plant taxa eaten by moa and whether or not they have been recorded in the rumens or faecal pellets of deer. Diet selection by deer is indicated by + for preferred, zero for neutral, and – for avoided (Forsyth et al. 2002). Plant nomenclature follows Allan Herbarium (2000). We did not list the plants that were: (a) poorly identified (e.g. ‘cf. *Cyathodes empetrifolia*’; Wood 2007) or (b) identified by only pollen/spores in Horrocks et al. (2004), as these were probably accidentally ingested. Locations of deer diet studies are shown in Forsyth et al. (2002). For data sources see table footnote.

Plant taxa	Moa: seeds, fruits, capsules	Moa: wood, leaves, petioles	Deer: Selection indices	Deer: Eaten
<b>Trees – Angiosperms</b>				
<i>Aristolelia</i> spp.	-	?8	<i>A. serrata</i> , + (26, 27), 0 (29)	<i>A. serrata</i> , 23, 24, 25, 26, 27, 29; <i>A. fruticosa</i> , 30, 31
<i>Carpodetus serratus</i>	7, 9	-	0 (26, 27, 29), + (34)	7, 24, 25, 26, 27, 29, 30, 32, 34
<i>Cordyline australis</i>	6, 7, 9	-	-	-
<i>Elaeocarpus hookerianus</i>	6, 7, 9, 10, 11, 12	-	0 (26), + (29)	7, 24, 25, 26, 29, 31, 34
<i>Hoheria/Plagianthus</i>		14		<i>H. glabrata</i> , 30, 31, 32; <i>P. regius</i> , 27
<i>Melicytus</i> spp.	19, 22		<i>M. lanceolatus</i> , + (29); <i>M. ramiflorus</i> , + (29)	<i>M. lanceolatus</i> , 23, 24, 27, 29; <i>M. ramiflorus</i> , 23, 24, 29, 33
<i>Myoporum laetum</i>	1		-	-
<i>Nothofagus menziesii</i>		8, 15, 18	- (27), + (34)	8, 25, 27, 30, 31, 32
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>		8	- (34)	8, 25, 30, 31, 32
<i>Pennantia corymbosa</i>	6, 7, 9, 11, 12		+ (29)	8, 29, 32
<i>Phyllocladus alpinus</i>		6, 8		8
<i>Pittosporum</i> sp.	3, 12		+ (26, 29), 0 (27)	7, 24, 26, 27, 29
<i>Plagianthus regius</i>	6, 7	6		27
<i>Pseudopanax</i> spp.	6, 7		<i>P. arboreus</i> , + (29); <i>P. colensoi</i> , + (26); <i>P. crassifolius</i> , + (26, 27, 29, 34); <i>Raukaua simplex</i> , + (34)	<i>Pseudopanax</i> sp., 23, 25, 30; <i>P. arboreus</i> , 29; <i>P. colensoi</i> , 26, 27, 31; <i>P. crassifolius</i> , 23, 24, 25, 26, 27, 29, 31, 34; <i>P. linearis</i> , 30
<i>Pseudopanax ferox</i>	6		-	<i>Pseudopanax</i> sp., 23, 25, 30
<i>Raukaua anomalus</i>		?8	- (29)	31
<b>Trees – Gymnosperms</b>				
<i>Dacrycarpus dacrydioides</i>		7, 10, 11, 12	- (29)	29
<i>Podocarpus hallii</i>		7	0 (26, 27), - (29, 34)	26, 27, 29, 31, 34
<i>P. totara</i>		10	-	23, 24
<i>Prumnopitys taxifolia</i>	1,3, 4, 5, 6, 7, 9, 11, 12	4, 5, 6, 9, 10, 12	0 (26), - (29)	8, 26, 29

Plant taxa	Moa: seeds, fruits, capsules	Moa: wood, leaves, petioles	Deer: Selection indices	Deer: Eaten
<b>Shrubs</b>				
<i>Carmichaelia</i> sp.	?1, 18	5	-	24, 31
<i>Coprosma</i> sp.	3, 5, 6, 7, 9, 11, 12, 13, 15, 16, 17, 18, 19, 22	8, 18, ?19, ?21, ?22	<i>C. foetidissima</i> , 0 (29), + (26, 27, 34); <i>C. lucida</i> , + (26); <i>Coprosma</i> spp., 0 (27); <i>Coprosma</i> spp. (large-leaved), + (29); <i>Coprosma</i> spp. (small-leaved), - (26, 29).	<i>C. areolata</i> , 26; <i>C. cheesemaniae</i> , 24, 26, 27; <i>C. ciliata</i> , 26, 27, 30; <i>C. colensoi</i> , 24; <i>C. crassifolia</i> , 27; <i>C. cuneata</i> , 30, 31; <i>C. foetidissima</i> , 23, 24, 25, 26, 27, 29, 30, 31, 32, 34; <i>C. grandifolia</i> , 23, 24, 29, 34; <i>C. linariifolia</i> , 24, 27; <i>C. lucida</i> , 23, 25, 26, 29; <i>C. macrocarpa</i> , 24; <i>C. propinqua</i> , 27; <i>C. pseudocuneata</i> , 24, 27, 30; <i>C. rhamnoides</i> , 24, 27; <i>C. rotundifolia</i> , 23, 26, 27; <i>C. rugosa</i> , 27; <i>C. serrulata</i> , 30, 31; <i>C. tenuifolia</i> , 23, 24; <i>Coprosma</i> spp., 23, 25, 27, 29, 30, 31, 33; <i>Coprosma</i> spp. (large-leaved), 23, 29; <i>Coprosma</i> spp. (small-leaved), 29, 34
<i>C. cuneata</i>	9	-	-	30, 31
<i>C. microcarpa</i>	10	-	-	24
<i>C. petriei</i>	15, 16, 17, 18	-	-	-
<i>C. rhamnoides</i>	2, 6	?2	-	8, 27
<i>C. rotundifolia</i>	3, 6, 7	-	-	7, 26, 27
<i>C. wallii</i>	12	-	-	-
<i>Coriaria plumosa</i>	15, 17, 18	-	-	30
<i>Corokia cotoneaster</i>	6, 7, 9, 10, 11, 12	-	0 (27)	27
<i>Gaultheria crassa</i>	15, 17, 18	-	-	30
<i>Hebe</i> sp.	21	-	-	<i>H. hectorii</i> , 30; <i>H. odora</i> , 30; <i>H. salicifolia</i> , 26, 27; <i>H. stricta</i> , 24, 29; <i>Hebe</i> spp., 24, 25, 29, 30, 31
<i>Hebe</i> sp. cf. <i>pimeleoides</i>	-	10, 11, 12, 13	- (29)	24, 25, 26, 27, 29, 30, 31
<i>Leptospermum scoparium</i>	6, 7, 10, 11, 12	6, 7	- (26, 27)	7, 24, 26, 27
<i>Leucopogon fraseri</i>	15, 16, 17, 18, 22	15, 16, 17, 18	-	24, 32
<i>Lophomyrtus obcordata</i>	6	-	-	-
<i>Melicope simplex</i>	6, 7	6, 7	- (29)	8
<i>Myrsine divaricata</i>	6	6, 12	0 (27), - (26, 29)	8, 25, 26, 27, 29, 30, 31, 32, 34
<i>Olearia</i> sp. / <i>O. virgata</i>	7, 21	6, 7, 10, 11, 12, 14, ?19, ?21, ?22	<i>Olearia</i> spp., - (26), 0 (27), + (29)	<i>Olearia</i> spp., 24, 26, 27, 29, 30
<i>Pimelea</i> sp.	7	-	-	-
<i>Teucrium parvifolium</i>	6	-	-	-
<b>Vines</b>				
<i>Calystegia sepium</i>	12	-	-	-
<i>Clematis</i> sp.	6	-	0 (29)	<i>C. paniculata</i> , 24, 27; <i>C. quadribracteolata</i> , 24; <i>Clematis</i> spp., 23, 24, 26, 29
<i>Muehlenbeckia australis</i>	5, 5, 6, 7	-	- (29)	8, 26, 27, 30
<i>M. axillaris</i>	15, 17, 18, 19, 22	-	-	-
<i>M. complexa</i>	6	-	-	-
<i>Passiflora tetrandra</i>	6	-	-	-
<i>Rubus</i> sp.	5, 6, 8, 5, 9, 11, 12, 13, 14, 22	5, 6, 7, 22	0 (26, 27), - (27, 29)	<i>R. australis</i> , 27, 29; <i>R. cissoides</i> , 24, 29, 31, 33, 34; <i>R. schmidelioides</i> , 29, 32, 34; <i>Rubus</i> spp., 23, 24, 25, 26, 27, 29
<b>Graminoids</b>				
<i>Baumea arthropphylla</i> or <i>Lepidosperma australe</i> (formerly <i>Cladium</i> sp.)	4	-	-	-
<i>Carex</i> spp.	?8, 10, 11, 12, 13, 15, 16, 17, 18, 22	-	<i>Carex coriacea</i> , - (29); <i>Carex</i> sp., - (29)	<i>Carex appressa</i> , 26; <i>C. coriacea</i> , 26; <i>Carex</i> spp., 29, 31
<i>C. secta</i>	6, 7, 9	-	-	-
<i>Centrolepis/Gaimardia</i> sp.	?1	-	-	-
<i>Eleocharis</i> sp. cf. <i>acuta</i>	10, 11, 12, 13	-	-	-
<i>Juncus</i> spp.	16, 18, 22	-	- (29)	26, 27, 29, 33, 34
<i>Phormium tenax</i>	6, 7	7, 13	+ (29)	28, 29, 33
Poaceae/Cyperaceae	6, 7, 19, 22	8*	<i>Carex coriacea</i> , - (29); <i>Carex</i> sp., - (29); <i>Microlaena avenacea</i> , - (29); <i>Uncinia</i> spp., - (27, 29)	<i>Carex appressa</i> , 26; <i>C. coriacea</i> , 26; <i>Carex</i> spp., 29, 31; <i>Uncinia</i> spp., 23, 24, 26, 27, 29, 31, 34; <i>Chionochloa</i> spp., 24, 30, 31; <i>Microlaena avenacea</i> , 24, 29, 31; <i>Poa colensoi</i> , 24; <i>Zotovia thomsonii</i> , 31
<i>Rytidosperma setifolium</i>	-	8*	-	-
<b>Herbs</b>				
<i>Ceratocephalus pungens</i>	19, 22	-	-	-
<i>Colobanthus</i> spp.	12, 22	-	-	26
<i>Einadia allanii</i>	6, 7, 9, ?22	-	-	-

Plant taxa	Moa: seeds, fruits, capsules	Moa: wood, leaves, petioles	Deer: Selection indices	Deer: Eaten
<i>Einadia triandra</i>	19, 22		-	-
<i>Euphrasia</i> spp.		?8	-	<i>E. cuneata</i> , 24, 29
<i>Gonocarpus aggregatus</i>	15, 16, 17, 18		-	27
<i>Lagenifera pumila</i>	15, 16, 17, 18		-	29
<i>Lobelia angulata</i>	15, 17, 18		– (29)	24, 26, 27, 29, 30
<i>Myosotis pygmaea</i>	22		-	<i>Myosotis</i> spp., 27, 33
<i>Myosurus minimus</i> subsp. <i>novae-zelandiae</i>	22		-	-
<i>Nertera</i> sp.	1		+ (27), – (29)	<i>N. ciliata</i> , 27, 34; <i>N. depressa</i> , 24, 26, 27, 30, 34; <i>N. dichondrifolia</i> , 24, 25, 26, 27; <i>Nertera</i> spp., 24, 27
<i>Oxalis exilis</i>	22		<i>Oxalis</i> spp. – (29)	<i>Oxalis</i> spp., 24, 27
<i>Ranunculus</i> spp.	15, 16, 17, 18, 20		<i>Ranunculus</i> spp. + (29)	24, 25, 26, 27, 29, 30, 33, 34
<i>Ranunculus gracilipes</i>	10, 11, 12, 15, 16, 17, 18		-	<i>Ranunculus</i> sp., 24, 25, 26, 27, 29, 30, 33, 34
<i>Urtica incisa</i>	15, 16, 17, 18		– (29)	24, 27
<i>Wahlenbergia pygmaea</i>	15, 17, 18		-	24
Ferns				
<i>Polystichum vestitum</i>		12, 13	+ (26), – (27, 29)	24, 26, 27, 29, 30, 32, 34
Mosses				
Unidentified moss		8, 10, 11, 12, 13	<i>Dawsonia superba</i> – (29)	<i>Hypnodendron</i> sp., 27; Unidentified, 23, 24, 25, 26, 32, 33, 34

\* From phytoliths only and assumed to be leaf material (see Horrocks et al. 2004); ? denotes ‘identified with uncertainty’. Data sources: 1, *Emeus crassus* gizzard (XV1b), Pyramid Valley (Falla 1941); 2, *Dinornis robustus* gizzard (XXIIk), Pyramid Valley (Falla 1941); 3, *Emeus crassus* gizzard (CM AV20,119), Pyramid Valley (Gregg 1972); 4, *Euryapteryx gravis* gizzard (CM AV20,113), Pyramid Valley (Gregg 1972); 5, *Dinornis robustus* gizzard (CM AV20,118), Pyramid Valley (Gregg 1972); 6, *Dinornis robustus* gizzards ( $n = 11$ ), Pyramid Valley (Burrows 1980; Burrows et al. 1981); 7, ?*Dinornis robustus* gizzards ( $n = 3$ ), Scaifes Lagoon (Burrows et al. 1981); 8, subalpine moa (most likely *Megalapteryx didinus*) coprolites, Takahē Valley (Horrocks et al. 2004); 9, *Dinornis robustus* gizzard (OM Av3647), Scaifes Lagoon (Wood 2007); 10, *Emeus crassus* gizzard (CM M2/4), Treasure Downs (Wood 2007); 11, *Emeus crassus* gizzard (CM 88/23), Treasure Downs (Wood 2007); 12, *Pachyornis elephantopus* gizzard (CM M2/2), Treasure Downs (Wood 2007); 13, *Pachyornis elephantopus* gizzard (CM M2/2), Treasure Downs (Wood 2007); 14, Unidentified gizzard (OM Av10790), Styx Mire (Wood 2007); 15, *Dinornis robustus* coprolites ( $n = 13$ ), Dart River Valley (Wood et al. 2008); 16, *Pachyornis elephantopus* coprolites ( $n = 3$ ), Dart River Valley (Wood et al. 2008); 17, *Megalapteryx didinus* coprolites ( $n = 4$ ), Dart River Valley (Wood et al. 2008); 18, Unidentified coprolites ( $n = 61$ ), Dart River Valley (Wood et al. 2008); 19, *Pachyornis elephantopus* coprolites ( $n = 2$ ), Central Otago (Wood et al. 2008); 20, *Megalapteryx didinus* coprolites ( $n = 1$ ), Central Otago (Wood et al. 2008); 21, *Euryapteryx gravis* coprolites ( $n = 1$ ), Central Otago (Wood et al. 2008); 22, unidentified coprolites ( $n = 31$ ), Central Otago (Wood et al. 2008); 23, rusa deer, Galatea (Nugent 1993; G. Nugent, pers. comm.); 24, sika deer and red deer, Kaimanawa (Fraser 1991; K.W. Fraser pers. comm.); 25, red deer, north-west Nelson (C. Thomson, Landcare Research, pers. comm.); 26, white-tailed deer, Stewart Island (Nugent & Challies 1988); 27, fallow deer, Blue Mountains (Nugent 1990); 28, sambar deer, Manuwatu (Kelton & Skipworth 1987); 29, red deer, Waihaha (Nugent et al. 1997); 30, red deer, Murchison Mountains (Lavers 1978; R. Lavers and W.G. Lee pers. comm.); 31, red deer, Fiordland (Mason 1951); 32, fallow deer, Caples/Greenstone (Golding 2000); 33, sambar deer, Manawatu (Stafford 1997); 34, red deer, south-eastern Fiordland (Forsyth et al. 2005; D.M. Forsyth, unpubl. data).



Red deer, from drawing by Liz Grant (<http://www.artbyliz.co.nz/>) for the cover of NZ J Ecology 24(1), 2000.