Framework for assessing the susceptibility of management areas to deer impacts

SCIENCE FOR CONSERVATION 213

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ABSTRACT

We reviewed the impacts of deer on New Zealand's forest flora and developed some guidelines for estimating the intensities of deer control required for achieving three representative management goals for forest ecosystems: (i) maintaining an intact forest canopy, (ii) maintaining an intact mature sub-canopy, and (iii) maintaining all forest species. We used the results of a recent study classifying common plant species as either 'preferred', 'not preferred and not avoided', or 'avoided' by deer. This three-way classification was translated into a relative density of deer (low, medium and high) likely to help achieve the above management goals. The guidelines successfully predicted observed changes inside and outside of exclosures for preferred and avoided species. However, sufficient data were available for only the most common species, and more data are required in order to predict the consequences of deer control for other species. Because the long-term and relative roles of deer and biophysical factors on forest dynamics are unknown, the uncertainty surrounding the predicted outcomes of deer control is large. Controlling deer to low densities will not necessarily 'reverse' the historical changes caused by deer, but rather should be seen as a prerequisite for allowing the regeneration of some highly preferred species provided that other abiotic and biotic conditions are present.

Keywords: Browsing, deer impacts, exclosures, forest dynamics, herbivory, impacts, National Vegetation Survey, ungulates

1. Introduction

The Department of Conservation (DOC) has a statutory obligation to protect the 'intrinsic values' of natural resources, for example by ensuring 'that deer are controlled to levels which maintain and enhance forest health and ecosystem processes, thereby protecting indigenous diversity' (DOC 1997). Since most deer populations cannot be eradicated with current technology, DOC is forced to manage the impacts of deer in perpetuity. Management options for deer can either be passive, where the impacts of deer are accepted in the absence of intervention, or active, by which DOC defines and attempts to achieve realistic objectives.

To make informed decisions about deer control, DOC managers need to know (i) the susceptibility of different ecosystems to the impacts of deer, and (ii) the likely response of ecosystems to different intensities of deer control. Landcare Research was contracted by DOC to summarise available information on these subjects. We focus primarily on forest systems, because deer are now rarely found in areas without forest cover.

We here develop a set of guidelines and criteria to enable managers to assess, for specific management areas, the potential for deer to adversely affect the conservation values within those areas.

2. Sources of information

2.1   ECOLOGY AND IMPACTS OF DEER: THEORETICAL AND EMPIRICAL MODELS

We briefly reviewed published and unpublished literature on deer ecology and impacts, especially: (i) work relating deer impacts and density to biophysical factors, and (ii) models for predicting the impacts of deer and the response of these impacts to deer control.

2.2   DIET PREFERENCES

Diet preferences are assessed by comparing the relative frequency of plant species ingested by the animal with what is available in the study area. Various statistical techniques can then be used to divide species into three classes (Manly et al. 1993):

(i)   *Preferred species*: those eaten more than expected from their availability;

(ii)   *Neither preferred nor avoided:* those eaten in proportion to their availability;

(iii)   *Avoided*: those eaten less than expected based on their availability.

Forsyth et al. (2002) collated published and unpublished information on the diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. Since diet preferences have been described in only a few New Zealand habitats (Forsyth et al. 2002), we also used 'browse index' data from vegetation studies in other habitats to classify additional plant species. The browse index involves subjectively scoring plants for browse (e.g. light = 1, moderate = 2 and heavy = 3) and calculating indices from these (e.g. Wardle et al. 1971; Allen & McLennan 1983; Rose & Burrows 1985). Although other herbivores can also damage seedlings (Jane & Pracy 1974), Rose & Burrows (1985) reviewed eight studies and showed a strong linear relationship (r^2 = 98%) between the mean browse index and estimated deer density within mixed beech forests. In addition, when we compared preference ratings for the species which appeared in both diet-preference indices, we found that they were largely in agreement. We therefore use browse indices for rating species that were not recorded by other techniques. The studies we reviewed were Wardle & Hayward (1970); Wardle et al. (1971, 1973); Rose & Burrows (1985); and Stewart & Burrows (1989).

Plant nomenclature in this report follows Allan (1961); Moore & Edgar (1970); Alison & Child (1975); Raven & Raven (1976); Galloway (1985); Connor & Edgar (1987); Webb et al. (1988); Brownsey & Smith-Dodsworth (1989); Beever et al. (1992); Large et al. (1992); Stevenson (1994); Heenan (1996, 1998); Mitchell et al. (1997); and Edgar & Connor (2000).

2.3 FOREST TYPES MOST AFFECTED BY DEER

We used permanent-plot data to quantify the availability of species in the three preference classes (preferred, avoided and not preferred/not avoided) in different forest types, recognising that food availability is a function of three components which, at this stage, are difficult to disentangle: (i) climatic and edaphic factors that determine (in part) the distribution of plant species, (ii) forest successional stage, and (iii) history of deer in an area. Data were collated from a total of 3348 permanent forest plots (each of 0.04 ha) that were mostly surveyed around 1980, and are now stored in the National Vegetation Survey database (S. Wiser et al., Landcare Research, unpubl. data). The plots were established using a standard protocol, and were randomised at the catchment scale (Allen 1993). In each plot, the following measurements were available:

- Counts of saplings, by species. Saplings are defined as woody species greater than 1.4 m in height but less than 2.5 cm in diameter at breast height (dbh).
- Diameters of all trees, from which the summed basal areas by species were calculated. Trees are defined as having dbh > 2.5 cm.

These data were then merged with the deer-preference indices to obtain, for each plot:

- Basal areas of preferred, not-preferred and avoided species. A fourth category of unclassified species was introduced.
- Counts of saplings, in each preference class.

Finally, the Vegetation Cover Map of Newsome (1987) was used to type the vegetation of each plot (using the grid conversion software provided by R. Pickard, DOC, Wellington). The number of plots in each vegetation type are listed in Table 1. We then obtained average numbers of saplings and basal area of trees in each of these types.

TABLE 1.   NUMBER OF PLOTS LOCATED IN THE SEVEN FOREST TYPES DEFINED BY NEWSOME (1987).

VEGETATION COVER MAP FOREST TYPES	NUMBER OF PLOTS
Beech	2168
Subalpine (includes shrubland)	692
Lowland podocarp–broadleaf–beech	690
Lowland podocarp–broadleaf	293
Broadleaf	277
Highland podocarp–broadleaf–beech	134
Beech–broadleaf	91

2.4   GUIDELINES FOR DEER MANAGEMENT

The information on the diet preferences of deer was rearranged to provide guidelines on how managing densities of deer might influence the regeneration of plant species. Sufficient data were available only for forest ecosystems, so the three management goals we used were:

• To maintain an intact mature forest canopy

• To maintain an intact forest sub-canopy

• To maintain all species

There was evidence that preferred species became less abundant in the presence of deer (see below). The corollary is that the abundance of such species *might* only be maintained by controlling deer to low densities; we termed these 'low-threshold' species. Species avoided by deer were expected to become generally more abundant at high densities of deer due to the suppression of interspecific competition. These species would be more abundant at high densities and thus were termed 'high-threshold' species. We believed that trends in the abundance of species not preferred and not avoided by deer would be more variable, but that their abundance might be maintained by medium or low densities of deer ('medium-threshold' species). The implications of these classifications for managers are described in the Discussion.

We used the results of five long-term (≥10 years) exclosure studies to validate and adjust our guidelines. These exclosures were fences erected to prevent entry by ungulates. Exclosures have been located throughout New Zealand's forests, and the abundances of plant species inside and outside have been periodically re-measured. Although none of the studies estimated the densities of deer present outside the exclosure, the response inside the exclosure indicates likely trends in abundance when deer are reduced to very low densities.

For the five studies, we summarised trends (increased, decreased or no change) in the abundance of species inside and outside the exclosures. For each species we then compared the observed trend with that expected from our classification.

3. Main findings

3.1 ECOLOGY OF DEER IN NEW ZEALAND

Nugent & Fraser (1993) estimated the breeding population of wild deer in New Zealand to be c. 250 000, roughly equivalent to 4 deer/km^2 of forested range. Seven taxa of deer currently live on New Zealand's conservation lands (Table 2). Of these, the red deer (*Cervus elaphus scoticus*) is by far the most widespread and abundant species (Challies 1990; G. Nugent, unpubl. data; Fraser et al. 2000). Almost all New Zealand ecosystems are occupied by deer, although sambar deer (*C. unicolor unicolor*), white-tailed deer (*Odocoileus virginianus*) and rusa deer (*C. timoriensis*) do not use either subalpine shrub-land or alpine grassland (Table 2).

TABLE 2.   RANGE SIZES AND USE (0 FOR NOT USED, 1 FOR USED) OF FOUR ECOSYSTEM TYPES BY THE SEVEN SPECIES OF WILD DEER IN NEW ZEALAND. RANGE SIZE IS FROM FRASER ET AL. (2000); HABITAT USE IS FROM FORSYTH & DUNCAN (2001).

SPECIES	RANGE SIZE (km^2)	ECOSYSTEM TYPE			
		BEECH FOREST	PODOCARP– BROADLEAF FOREST	SUBALPINE SHRUBLAND	ALPINE GRASSLAND
Red deer	120575	1	1	1	1
Sika deer	6008	1	1	1	1
Fallow deer	4995	1	1	1	1
Sambar deer	5346	1	1	0	0
Wapiti	2045	1	1	1	1
White-tailed deer	2013	1	1	0	0
Rusa deer	469	1	1	0	0

Deer are large herbivores (≥30 kg) with large home ranges. The size of the home range varies between species, sexes, habitats, and seasons. For red deer, wapiti (*C. e. nelsoni*) and white-tailed deer, home ranges of non-migratory females are likely to be in the order of 150–300 ha, compared with about half that for fallow deer (*Dama dama dama*) (G. Nugent, unpubl. data).

The limited data for sambar, rusa and sika (*C. nippon*) suggest that their home ranges would be of intermediate size. Migratory populations can have much larger ranges, as can deer living in unforested patchy habitats. These data indicate that the minimum scale for deer management will usually be at least 1000 ha (i.e. deer

impacts and management must be considered at the landscape scale rather than at the community or individual-stand scale).

Deer are opportunistic and adaptable ruminants, but unlike possums (*Trichosurus vulpecula*) which are arboreal and can reach most forest tiers, a key constraint is that deer can feed only within about 2 m of ground level (the 'browse-tier'). Deer also have a more sophisticated digestive system than possums, enabling them to consume almost all of the foliage of preferred native species (Nugent et al. 2001).

Densities of deer are now largely determined by harvesting (Challies 1985, 1990; G. Nugent, unpubl. data; Nugent & Fraser 1993). Pellet data from three catchments in *Nothofagus* forest in South Westland show the effects of colonisation stage and hunting on habitat use by red deer. During colonisation, the highest pellet frequencies were in the alpine grasslands well above timberline, but at post-peak densities (c. 20–30 years later) pellet frequencies were more evenly distributed throughout the forest, shrublands and grasslands (Tustin 1973 in Wardle 1984). In the catchment subject to intensive aerial and ground hunting, deer were virtually absent above timberline and were most common in mid-altitude forest (see also Nugent et al. 1987). Deer have thus been eliminated, or nearly so, from most alpine and lowland grasslands, and densities reduced in most forest types by commercial hunting. A national-scale summary of faecal-pellet surveys indicated that the abundance of deer declined by at least 75% between 1960 and 1980, but suggested that densities may have increased from 1980 to 1990 (Nugent & Fraser 1993). Trends in deer abundance since 1990 are largely unknown, but, given the ongoing commercial harvesting, deer densities are probably stable (K. Fraser & L. Burrows, Landcare Research, unpubl. data).

3.2 MATHEMATICAL AND CONCEPTUAL MODELS OF PLANT–UNGULATE INTERACTIONS

We present six models of plant–ungulate interactions to indicate how deer could modify ecosystems. It is important to note that the models are not necessarily 'competing', but rather relate to different components and/or timescales.

3.2.1 Density-dependence of animal populations

Under this construct, population dynamics are regulated by competition among animals for food. When an animal colonises an area, the food supply far exceeds consumption and the population increases. Eventually the animal population reaches a density at which animals compete among one another for food, with negative consequences on demographic parameters such as survival of young (Caughley & Sinclair 1994). The population dynamics of the animal can hypothetically vary from stable equilibrium, through population cycling to chaotic behaviour, depending on the nature of the competitive response of animals to food supply, and plants to herbivory (Schmitz & Sinclair 1997).

3.2.2 Annual variation in food availability

The growth of vegetation depends upon climatic conditions, which can vary greatly from year to year. Responses of animal populations to this environmental variation obscure the density-dependent regulation of populations. Choquenot (1998) proposes that a continuum exists between systems dominated by 'intrinsic' sources of variation in food availability (i.e. driven by numbers of animals) and 'extrinsic' sources of variation (i.e. driven by environmental variation). New Zealand forests, in which the *supply* of a major food of deer (i.e. litterfall) is independent of the density of deer, will be at the extrinsic end of the continuum (Nugent et al. 2001; D. Choquenot, Landcare Research, pers. comm.).

3.2.3 Annual variation in survival, independent of food availability

The population densities of ungulates vary as a consequence of disease (Jorgenson et al. 1997), harvesting (Nugent et al. 1987), top-down effects of natural predators (Messier 1994), and climate (Saether 1997; Post & Stenseth 1998). This again obscures the effects of density dependence driven by food supply.

The emphasis of these models is on the dynamics of the deer, but from a conservation management perspective the impacts of deer on flora (and other components of the ecosystem) are important. No mathematical models effectively deal with this issue, so we move on to conceptual models derived from field observations.

3.2.4 Declining quantity and quality of food following colonisation

Deer have strong food preferences (see below), and thus there appears to have been a consistent sequence of removal of plant species following colonisation of an area by deer (e.g. Wardle 1984). Deer initially feed on the most preferred foods only, but apparently become far less selective as the most preferred species are removed (Wardle 1984). However, the pattern of modification depends on the interaction between browsing intensity (itself a function of deer preference and deer density) and browse tolerance. Long-lived canopy and sub-canopy species may be highly preferred, such that all leaves within the browse tier are removed, but since most photosynthetic material is above the browse tier, the tree survives for many years (Allen et al. 1984). Nugent & Challies (1988) and Nugent (1990) noted that litterfall from such species can provide 40% of the diet of deer. Thus, long-lived palatable species like *Griselinia littoralis* are expected to greatly diminish in abundance from the sub-canopy or canopy due to an absence of terrestrial recruitment (i.e. all seedlings are killed by browsing), but this would take several hundred years (Nugent & Challies 1988; Nugent 1990). Conversely, cohorts of seedlings from unpalatable species that establish due to suppression of competition during periods of high deer density may remain for hundreds of years (e.g. *Podocarpus hallii* at Waihaha; Nugent et al. 2001). We note, however, that the long-term effects of deer on canopy species are unclear (Veblen & Stewart 1982).

### 3.2.5 Quantity and quality of food in post-irruptive forests

Most of New Zealand's forested conservation lands have been colonised by deer for > 70 years. Nugent et al. (2001) partitioned species in these 'post-irruptive' forests into three main categories:

- Browse-intolerant. Epicormic regrowth and seedlings of highly-preferred species that continue to be used by deer at very low densities. The annual production of this resource is relatively small and tightly regulated by deer. An example of such a species that is widespread in New Zealand forests is *Fuchsia excorticata*.

- Fallen leaves. The availability of this resource is seasonally constant, but over longer time periods, highly preferred species will decline in abundance due to the predation of seedlings by deer. An example of such a species is *Griselinia littoralis*.

- Browse-tolerant. Unpalatable or browse-tolerant species that are relatively abundant. Not eaten when more preferred foods are abundant, but, when preferred foods are scarce and ungulate densities are high, this component is affected by deer. Examples are *Prumnopitys taxifolia, P. ferruginea* and *Nothofagus menziesii*.

3.2.6 Recovery of forests following deer control

Nugent et al. (2001) developed a conceptual model on the principle that, all else being equal, the impacts of deer on regeneration patterns of some forest species are dependent upon the density of deer (Fig. 1). One of the central premises of their model is that the transition toward browse intolerance induced by deer is reversed once pests are reduced to sufficiently low densities. The abundance of the most palatable and browse-intolerant species is strongly reduced at all but the lowest densities of deer. In contrast, the least palatable and most browse-tolerant species benefit from reduced competition at moderate and high deer densities, and increase in abundance. The response of plant species to deer control is assumed to be non-linear, with deer causing major changes in the distribution and abundance of browse-intolerant species even at low densities.

Figure 1. Conceptual model of deer impacts on selected species at Waihaha. K is the 'equilibrium density' of deer. Note that equilibrium density ('K') refers to deer density only, and the ecosystems deer inhabit are continuing to change and are therefore not in a state of equilibrium. Source: Nugent et al. (2001).
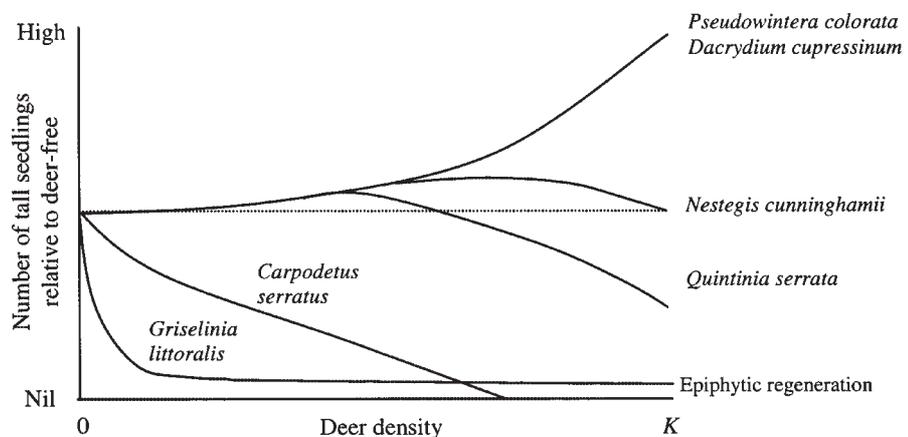
One of the most comprehensive studies of the diet of deer in New Zealand was conducted by Nugent et al. (1997) in podocarp-hardwood forest in the Waihaha catchment, central North Island. The annual diet of red deer there was composed of woody plants (70%), ferns (17%) and grasses (10%). Most woody-plant foliage was obtained as litterfall (Nugent et al. 1997). For the most deer-preferred tree species, deer consumed virtually all of the small amounts of foliage produced within the browse tier, and therefore apparently prevented ground-level regeneration of some of their preferred species (Nugent et al. 1997) but did not affect survival of adult trees. There is thus likely to be a strong influence of historical deer densities, as well as current deer densities, on food preferences and impacts.

3.3 DIET PREFERENCES OF UNGULATES IN NEW ZEALAND

A total of 185 indigenous plant genera (379 species) was recorded as eaten in 19 diet studies by Forsyth et al. (2002). The plant species commonly reported in the diet were generally consistent across different ungulate species from similar forest habitats. However, some forest types (e.g. kauri *Agathis australis*) were not represented.

Five of the 19 studies assessed diet preferences by four ungulate species. The studies were of feral goats on Mount Egmont (Mitchell et al. 1987) and on Isolated Hill (Cochrane 1994), white-tailed deer on Stewart Island (Nugent & Challies 1988), fallow deer in the Blue Mountains (Nugent 1990), and red deer at Waihaha (Nugent et al. 1997). Based on the classifications in each of these five studies and on the authors' expert knowledge, Forsyth et al. (2002) classified each of the common species as 'preferred', 'neither preferred nor avoided', and 'avoided'.

Estimates of diet preference were available for 119 species (107 genera; Forsyth et al. 2002). There did not seem to be any obvious differences in the preferences of feral goats and the three deer species. Of the 60 plant species or genera present in two or more studies, 8 were always preferred (eaten more than expected from their availability) and 15 were always avoided (proportion-ately less eaten than was available); most others were not selected (eaten in proportion to their availability).

Five species were always preferred where present; *Griselinia littoralis, Melicytus ramiflorus, Pseudopanax arboreus, Schefflera digitata* and *Weinmannia racemosa*. Ten species were always avoided where present: *Alseuosmia turneri, Blechnum capense, Leptospermum scoparium, Leptopteris superba, Microlaena avenacea, Neomyrtus pedunculata, Nestegis cunninghamii, Prumnopitys ferruginea, Pseudowintera colorata,* and *Trichomanes reniforme*, as were the genus *Uncinia* and 'small-leaved *Coprosma* species'. Preferences for remaining species were more variable among studies.

By combining the indicators of preference from diet and browse studies, we have assigned woody plants and ferns to one of three preference classes (Table 3).

TABLE 3.   A THREE-WAY CLASSIFICATION OF THE PREFERENCES OF
UNGULATES FOR COMMONLY OCCURRING FOREST SPECIES IN NEW ZEALAND.
(1) denotes deduced from both preference and browse index data; (2) deduced only from preference
data; (3) deduced only from browse index data. The preference classifications were from Forsyth et
al. (2002).

| | DEER PREFERENCE CLASS | |
PREFERRED	NOT PREFERRED/NOT AVOIDED	AVOIDED
Trees		
Aristotelia serrata (1)	*Elaeocarpus hookerianus* (1)	*Dacrydium cupressinum* (1)
Carpodetus serratus (1)	*Hedycarya arborea* (1)	*Lepidothamnus intermedius* (1)
Fuchsia excorticata (1)	*Metrosideros umbellata* (1)	*Neomyrtus pedunculata* (1)
Griselinia littoralis (1)	*Pennantia corymbosa* (1)	*Nothofagus fusca* (1)
Melicytus ramiflorus (1)	*Raukaua simplex* (1)	*Nothofagus menziesii* (1)
Melicytus lanceolatus (2)	*Elaeocarpus dentatus* (2)	*Nothofagus solandri* var. *cliffortioides* (1)
Myrsine australis (1)	*Metrosideros robusta* (2)	*Prumnopitys ferruginea* (1)
Pseudopanax arboreus (1)	*Sophora microphylla* (2)	*Prumnopitys taxifolia* (2)
Pseudopanax colensoi (1)	*Myrsine salicina* (2)	*Podocarpus hallii* (1)
Pseudopanax crassifolius (1)	*Pittosporum tenuifolium* var. *colensoi* (3)	*Pseudowintera colorata* (1)
Raukaua edgerleyi (1)		*Beilschmiedia tawa* (2)
Schefflera digitata (1)		*Nestegis cunninghamii* (2)
Weinmannia racemosa (1)		*Nestegis lanceolata* (2)
Cordyline australis (2)		*Phyllocladus trichomanoides* (2)
Cordyline indivisa (2)		*Phyllocladus alpinus* (3)
Hoheria glabrata (3)		*Dacrycarpus dacrydioides* (3)
		Quintinia acutifolia (3)
		Metrosideros fulgens (2)
Shrubs		
Coprosma lucida (1)	*Coprosma foetidissima* (1)	*Myoporum laetum* (2)
Carmichaelia egmontiana (2)	*Coprosma propinqua* (1)	*Dracophyllum menziesii* (1)
Brachyglottis rotundifolia (2)	*Coprosma rhamnoides* (1)	*Leptospermum scoparium* (1)
Carmichaelia grandiflora (3)	*Myrsine divaricata* (1)	*Kunzea ericoides* (4)
Large-leaved *Coprosma* spp.	*Alseuosmia pusilla* (2)	*Cyathodes juniperina* (1)
(incl. *C. grandifolia*,	*Corokia cotoneaster* (2)	*Dracophyllum longifolium* (1)
C. tenuifolia) (1)	*Geniostoma rupestre* (2)	*Gaultheria antipoda* (1)
	Lophomyrtus obcordata (2)	*Hebe stricta* (2)
	Pseudopanax lineare (3)	*Quintinia serrata* (2)
	Coprosma cuneata (3)	*Alseuosmia macrophylla* (2)
	Coprosma ciliata (3)	*Alseuosmia turneri* (2)
	Coprosma colensoi/C. banksii (3)	*Leucopogon fasciculatus* (2)
	Coprosma parviflora (3)	*Olearia ilicifolia* (2)
	Coprosma pseudocuneata (3)	*Melicope simplex* (2)
	Coprosma rotundifolia (3)	*Rhabdothamnus solandri* (2)
	Coprosma rugosa (3)	*Aristotelia fruticosa* (3)
	Coriaria sarmentosa (3)	*Pittosporum crassicaule* (3)
	Olearia lacunosa (3)	*Pittosporum divaricatum* (3)
	Brachyglottis buchananii (3)	*Archeria traversii* (3)
	Coprosma microcarpa (3)	*Raukaua anomalus* (3)
		Dracophyllum traversii (3)
		Dracophyllum uniflorum (3)
		Olearia arborescens (3)
		Olearia colensoi (3)
		Olearia nummularifolia (3)
		Podocarpus nivalis (3)

| | DEER PREFERENCE CLASS | |
PREFERRED	NOT PREFERRED/NOT AVOIDED	AVOIDED
Climbers		
Ripogonum scandens (2)	*Clematis* spp. (2)	*Parsonsia* spp. (2)
	Metrosideros diffusa (2)	
	Rubus spp. (1)	
	Muehlenbeckia australis (2)	
Ferns		
Asplenium bulbiferum (1)	*Leptopteris superba* (1)	*Blechnum capense* (1)
Asplenium flaccidum (2)	*Dicksonia squarrosa* (1)	*Blechnum discolor* (1)
Phymatosaurus pustulatus (2)	*Polystichum vestitum* (1)	*Cyathea smithii* (1)
	Asplenium oblongifolium (2)	*Cyathea dealbata* (2)
	Asplenium polyodon (2)	*Histiopteris incisa* (1)
	Blechnum fluviatile (2)	*Asplenium hookerianum* (2)
	Blechnum penna-marina (2)	*Blechnum chambersii* (2)
	Blechnum procerum (2)	*Blechnum colensoi* (2)
	Cardiomanes reniforme (2)	*Ctenopteris heterophylla* (2)
	Rumohra adiantiformis (2)	*Grammitis rigida* (2)
	Tmesipteris spp. (2)	*Hypolepis* spp. (2)
	Cyathea colensoi (3)	*Leptopteris* spp.
		Pteridium esculentum (2)
		Grammitis spp. (2)
		Hymenophyllum spp. (2)

3.4 VEGETATION TYPES MOST AFFECTED BY DEER

In the absence of harvesting, habitat use by deer in New Zealand appears to be determined largely by the availability and quality of preferred foods. Understanding the key biophysical factors influencing the distribution and abundance of preferred food species is therefore crucial to managing the impacts of deer.

3.4.1 Forests

At the catchment level, several studies show that the abundance of palatable species is closely related to soil fertility, with the most deer-preferred species occurring on nutrient-rich sites, and the least-preferred species on nutrient-poor sites. The fertility of a site depends not only on soil type, but also on how recently the site was disturbed. Forests containing the most food species preferred by deer occur on high-fertility sites subject to frequent disturbance (Rose & Burrows 1985 and references therein). In *Nothofagus* forests in West Nelson, browsing, as estimated by the Mean Browse Index, was highest on sites of highest fertility; these sites were characterised by high plant-species richness, many of which were apparently 'preferred' by deer (Rose & Burrows 1985). Stewart & Harrison (1987) ranked *Nothofagus* forests in Fiordland according to the proportion of deer-preferred foods, and showed that this order was positively correlated with landform stability. Landforms associated with high proportions of preferred species were debris cones and colluvial sideslopes; in contrast, stable bedrock sideslopes, benches and ridges supported few preferred species (Stewart & Harrison 1987). Mountain beech forests with the fewest preferred species occur on the most stable but poorly drained sites (Wardle 1984)

We also need to know which vegetation types are most affected by browsing. This is not necessarily correlated with deer numbers, because some plants may be better able to tolerate browsing. For example, if deer prefer early successional vegetation, but the species associated with early succession tend to be least affected by browsing (in terms of growth and survival), then it is unclear whether the impact of deer is greatest in early- or late-successional vegetation. Questions of this sort require careful experimentation, but some insights can be gained from permanent-plot data. National Vegetation Survey (NVS) data provide representative samples of forests at a catchment scale, including stands at all stages of development, so they provide a useful starting point.

We ranked forest types in order of the basal area of deer-preferred tree species in the forest canopy (Fig. 2; see Appendix for species lists). Predictably, beech forests contain few deer-preferred tree species, while around one-third of the basal area in broadleaved forest consists of deer-preferred species. We then related the number of saplings of preferred species to basal areas, and found a positive correlation ($r = 0.79$, $P < 0.05$).
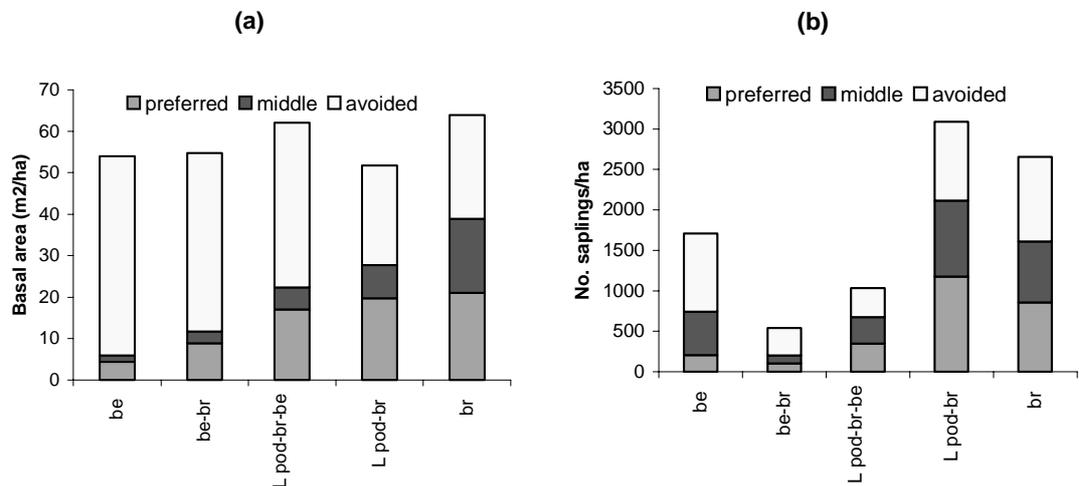
Figure 2. (a) Mean basal area, in five forest types, of trees in three deer preference classes (highly preferred, neither preferred nor avoided, and avoided), (b) mean number of saplings in the understorey of these plots. Abbreviations: be = beech, pod = podocarp, br = broadleaved, L = lowland.

This broad-scale information suggests that ungulate impacts may, in relative terms, be greatest in forest types with the fewest preferred species. Nonetheless, the data also strongly suggest that, as a broad class, preferred species are still regenerating in all forest types despite the now almost universal presence of ungulates. It is important to note that we are unable to easily determine and compare ungulate abundance and density in these habitats at the time the measurements were made. Even in areas where deer numbers are high, preferred species can regenerate on raised surfaces (e.g. fallen logs and tree ferns; Stewart & Burrows 1989). The range of preferred species present in beech forests may differ in relative abundance from those in broadleaved forests and have different sapling to basal area ratios. This is suggested by the pattern for individual species such as *Griselinia littoralis* (Fig. 3).

Griselinia littoralis

Pseudowintera colorata
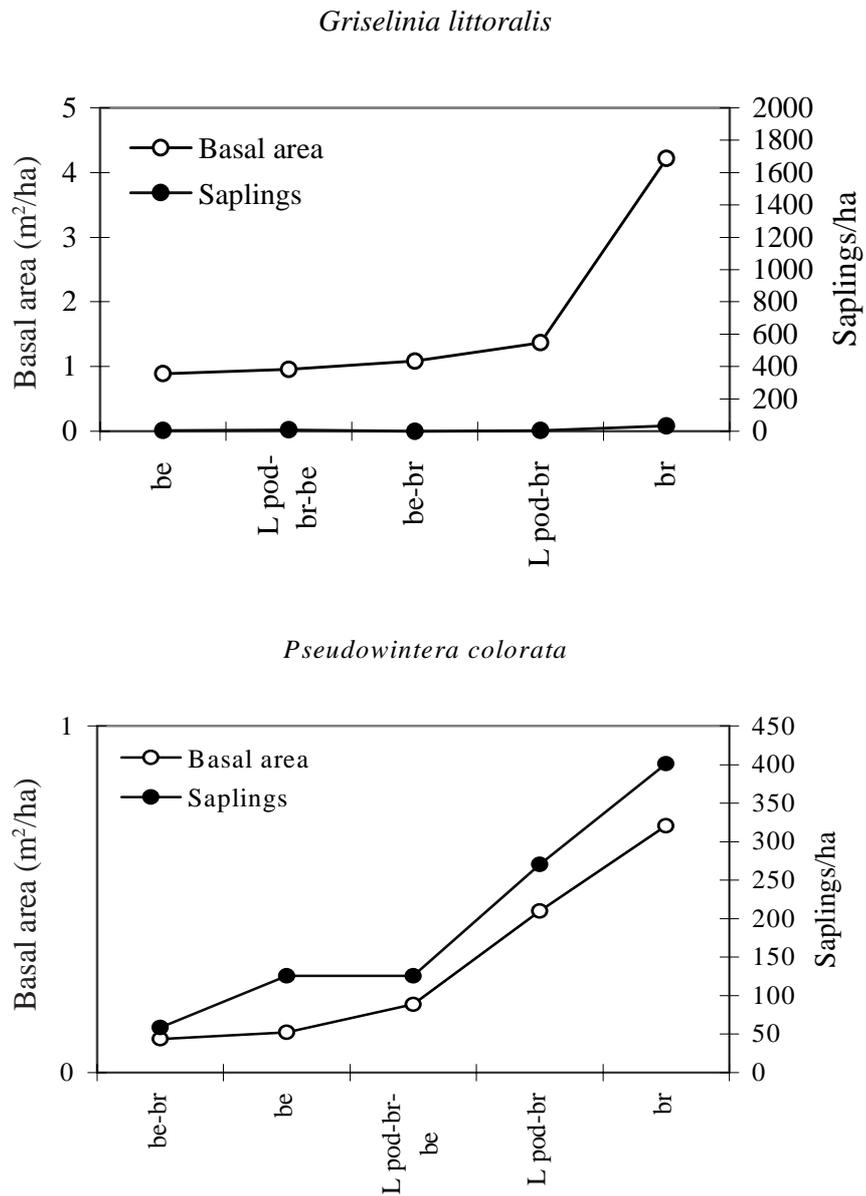
Factors other than deer abundance may be important in determining the balance of deer-preferred and avoided species in the browse layer. Notice that there were more saplings of the 'preferred' species than of the 'avoided' species in some forest types (Fig. 2), a result that indicates herbivory is not regulating regeneration. A reason for these observations is that the dominant species in the 'avoided' category are the beeches, totara and rimu (collectively contributing 91% of basal area in this category), and these species do not typically regenerate strongly in deep shade. Hence, the shade tolerance of species in relation to forest structure primarily dictates the balance of species in the understorey (Wardle & Guest 1977; Veblen & Stewart 1982). Forest structure, the spatial array of species, will therefore be an important determinant of susceptibility to deer.

We note that our results would possibly have been different if NVS contained more North Island plots, because several canopy dominants are shade tolerant and avoided by deer (e.g. *Beilschmiedia tawa*). An important development of

the ideas expressed by Nugent et al. (2001) will be a consideration of how deer-density and seedling-abundance relationships vary along environmental and disturbance gradients.

The highly preferred *Griselinia littoralis* contributed 2–7% of the basal area of the stands, but only 0–2% of sapling regeneration. The species is failing to regenerate in all forest types except some broadleaved forests, and even there it is likely that the level of regeneration is inadequate to maintain present abundance of the species. This pattern is likely to be true for other highly-preferred tree species with low browse tolerance. By contrast, the highly avoided *Pseudowintera colorata* constitutes a smaller component of the canopy basal area (0.2–1.3%) but a larger component of the sapling layer (9–13%), and the correlation between sapling numbers and basal area is very close.

3.4.2 Alpine grasslands and shrublands

Red deer made intensive use of alpine grasslands and subalpine shrublands prior to the advent of helicopter-based hunting, but are now largely absent from this ecosystem (Nugent et al. 1987). 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 habitat preferences of deer in this ecosystem type appear to also reflect soil fertility, with the most preferred habitats associated with recent high-nutrient soils (Rose & Platt 1987). Direct observations of Himalayan thar have indicated that lower-altitude fertile sites are preferred, when available, but that preferences change seasonally, presumably in response to the altitudinal cascade in growing season (Tustin & Parkes 1988), and there is no reason to suppose that the behaviour of deer would be different.

The factors governing habitat use by deer in subalpine shrubland are unknown. However, we presume that soil fertility is also important in this ecosystem type because preferred food species grow on sites with high nutrient status.

From the NVS dataset, subalpine forest/shrublands are among the few places where *G. littoralis* can still reach high sapling densities (mean of 477 plots is 193 saplings/ha). This may be attributable to effective helicopter hunting of deer, perhaps combined with the impenetrability or inaccessibility of some stands.

3.5 GUIDELINES FOR ASSESSING SUSCEPTIBILITY TO DEER

3.5.1 General approach

Overall, the direct impacts of deer are primarily a consequence of their feeding and the effects that has on forest composition. Although there can be indirect or flow-on effects from that for soil processes and for other components of the ecosystem, the direction and strength of those indirect effects are idiosyncratic (Wardle et al. 2001). In attempting to develop a framework that managers can use to help make assessments of the likely susceptibility of a particular forest

area to deer in the absence of deer control, we have focused on the likelihood, nature, and magnitude of deer-induced changes in vegetation composition.

We considered first using biophysical predictors of vegetation composition. Factors such as climate, substrate type, and disturbance regime are all significant determinants of vegetation type, and it is clear that the species most highly preferred (and therefore most likely to be strongly affected) by deer are most common and abundant on the most fertile and frequently disturbed sites. Intuitively, management units with a predominance of fertile sites and/or frequent disturbance are likely to have the greatest potential for absolute change in vegetation composition if deer force a transition toward browse-tolerant species. Biophysical parameters have been used with some success to predict what forest types should occur where, but such predictions remain one step removed from the vegetation that is actually present, and (as discussed later) there is little certainty that the vegetation now present would revert to what was originally present even if all anthropogenic impacts could be completely removed. We therefore considered it best to develop a framework based directly on species composition of the extant vegetation.

Allen et al. (1988) suggested that three factors determine the extent of deer impacts on flora: (i) history of deer colonisation and control; (ii) biophysical and climatic factors affecting the distribution and abundance of both deer and flora, and (iii) the structure of the vegetation. We agree that these three factors are important, but consider that insufficient data are available to create a more explicitly multi-dimensional guideline. Managers need to consider all available information when attempting to assess susceptibility for sites. It is beyond the scope of this review to document and characterise the vegetation in every management unit in New Zealand. We also rejected the option of some sort of generic ranking of forest or ecosystem types according to their susceptibility to deer as originally proposed, primarily because our results (Fig. 3) highlight the point that deer effects can be both relative as well as absolute. Loss of the relatively few sub-canopy broadleaved species present in simple high-altitude *Nothofagus* forest, for example, may have greater flow-on implications for the avifauna than loss of far greater numbers of the same species in broadleaved forest. Thus, the vegetation management goals for each area are likely to differ widely. In the absence of any widely accepted yardstick for measuring the importance of biological changes, it is simply not possible to separate susceptibility from the management goal. In other words, deer browsing will induce some changes in all but the few very simple vegetation types composed solely of avoided species, but the relative importance of those changes is a human value judgement that we cannot resolve in this review. Susceptibility is a measure of the potential for important change, so it is also basically a value judgement. In some instances the goal might be to protect the forest type as a whole, in its own right, whereas in other instances the goal might be to protect a rare plant species that might or might not be preferred by deer, and in yet other cases the goal might be to maintain key attributes of the vegetation that are crucial to the survival of a threatened animal. Protection of the fern *Hypolepis millifolium* as a winter food source for takahē in the Murchison Mountains, Fiordland, is an example of the last named.

3.5.2 The guidelines

Our guidelines basically consist of three groups of indicator species that are widespread and often quite common components of a large number of ecosystems. We have designated the three groups as low-, medium- and high-threshold species, with these designations aligning against the three representative management goals that span the 'required intensity of deer control' continuum (Table 4). It is important to note that the species listed come from a range of habitats, and differ markedly in their shade tolerances. Consequently, it should not be assumed that effective deer control will bring about the return of all (or any) of the species listed. For example, *Cordyline australis* is only found in large canopy gaps, and would not regenerate under closed forest in the absence of deer.

TABLE 4. DEER DENSITIES FOR ACHIEVING THREE FOREST MANAGEMENT GOALS FOR SELECTED SPECIES. SUB-CANOPY SPECIES ARE DEFINED AS > 2 m BUT NOT ATTAINING CANOPY CLOSURE. SPECIES ARE ARRANGED ALPHABETICALLY WITHIN CLASSES.

MANAGEMENT GOALS	THRESHOLD DEER DENSITY		
	LOW	MEDIUM	HIGH
Maintain intact mature forest canopy	*Weinmannia racemosa*	*Metrosideros robusta*	*Beilschmiedia tawa*
		Metrosideros umbellata	*Dacrycarpus dacrydioides*
			Dacrydium cupressinum
			Nestegis cunninghamii
			Nestegis lanceolata
			Nothofagus spp.
			Phyllocladus trichomanoides
			Podocarpus hallii
			Prumnopitys ferruginea
			Prumnopitys taxifolia
			Quintinia serrata
Maintain intact sub-canopy	*Aristotelia serrata*	*Coprosma foetidissima*	*Coriaria arborea*
	Brachyglottis rotundifolia	*Coprosma parviflora*	*Cyathea dealbata*
	Carmichaelia spp.	*Coprosma propinqua*	*Cyathea smithii*
	Carpodetus serratus	*Coprosma rhamnoides*	*Dracophyllum* spp.
	Coprosma grandifolia	*Coprosma rotundifolia*	*Kunzea ericoides*
	Coprosma lucida	*Corokia cotoneaster*	*Leptospermum scoparium*
	Coprosma tenuifolia	*Cyathea colensoi*	*Leucopogon fasciculatus*
	Cordyline australis	*Dicksonia squarrosa*	*Melicope simplex*
	Cordyline indivisa	*Elaeocarpus dentatus*	*Myoporum laetum*
	Fuchsia excorticate	*Elaeocarpus hookerianus*	*Neomyrtus pedunculata*
	Geniostoma rupestre	*Hedycarya arborea*	*Olearia arborescens*
	Griselinia littoralis	*Lophomyrtus obcordata*	*Olearia ilicifolia*
	Hoheria glabrata	*Myrsine salicina*	*Phyllocladus alpinus*
	Melicytus lanceolatus	*Olearia lacunose*	*Pseudowintera colorata*
	Melicytus ramiflorus	*Pennantia corymbosa*	*Pittosporum crassicaule*
	Myrsine australis	*Pittosporum* spp.	*Pittosporum divaricatum*
	Myrsine divaricata	*Pseudopanax lineare*	*Quintinia acutifolia*
	Pseudopanax arboreus	*Raukaua simplex*	*Quintinia serrata*
	Pseudopanax colensoi	*Sophora microphylla*	
	Pseudopanax crassifolius		
	Raukaua edgerleyi		
	Schefflera digitata		

| | THRESHOLD DEER DENSITY | | |
MANAGEMENT GOALS	LOW	MEDIUM	HIGH
Maintain all forest species	*Asplenium bulbiferum*	*Alseuosmia pusilla*	*Alseuosmia macrophylla*
	Asplenium flaccidum	*Asplenium oblongifolium*	*Alseuosmia turneri*
	Phormium tenax	*Asplenium polyodon*	*Archeria traversii*
	Astelia solandri	*Astelia cockaynei*	*Aristotelia fruticosa*
	Phymatosaurus pustulatus	*Blechnum fluviatile*	*Asplenium hookerianum*
	Ripogonum scandens	*Blechnum penna-marina*	*Blechnum capense*
		Blechnum procerum	*Blechnum chambersii*
		Cardiomanes reniforme	*Blechnum colensoi*
		Clematis spp.	*Blechnum discolor*
		Coprosma ciliate	*Ctenopteris heterophylla*
		Coprosma colensoi (incl. *C. banksii*)	*Cyathodes juniperina*
		Coprosma microcarpa	*Dawsonia superba*
		Coprosma pseudocuneata	*Gahnia procera*
		Coprosma rugosa	*Gaultheria antipoda*
		Coriaria sarmentosa	*Geniostoma rupestre*
		Geniostoma ligustrifolium	*Grammitis rigida*
		Leptopteris superba	*Grammitis* spp.
		Metrosideros diffusa	*Hebe stricta*
		Muehlenbeckia australis	*Histiopteris incisa*
		Polystichum vestitum	*Hymenophyllum* spp.
		Rubus spp.	*Hypolepis* spp.
		Rumohra adiantiformis	*Leptopteris* spp.
		Tmesipteris spp.	*Metrosideros fulgens*
			Microlaena avenacea
			Olearia colensoi
			Olearia nummularifolia
			Urtica spp.
			Parsonsia spp.
			Podocarpus nivalis
			Pratia angulata
			Pteridium esculentum
			Raukaua anomalus
			Rhabdothamnus solandri
			Uncinia uncinata
			Urtica incisa

The low-threshold indicators also represent the other highly preferred plants species listed in Table 3. Where these species are (or once were) abundant or for some other reason are deemed an important element of the vegetation, deer have the potential to cause major or important changes in that vegetation type, and in many forests that potential has already been at least partially realised. In such areas, preventing further undesirable change and establishing at least the potential for reversion of changes that have already occurred, will generally require that deer numbers be reduced to low levels. Such deer management will obviously also protect the less preferred medium- and high-threshold species.

The high-threshold species represent species that will generally only be affected by deer when their densities are sustained near equilibrium density for extended periods. Where these species are the predominant or otherwise important component of the ecosystem that for management reasons must be

protected from further deer-induced changes, but no other ecosystem components require protection from deer, then low-intensity deer control should provide adequate protection.

The medium-threshold species are species that require an intermediate intensity of deer control for protection.

Table 4 should be interpreted as follows. To maintain an intact mature forest canopy, where that canopy is *Weinmannia racemosa*, deer would need to be controlled to low densities. Of the canopy species most common in New Zealand forests, only *W. racemosa* is classified as a low-threshold species, and even it is probably closer to medium-threshold status than most of the sub-canopy or smaller tree species that typify the low-threshold group. At Waihaha, there were some tall *W. racemosa* seedlings present at sites with the lowest deer densities recorded, but still no tall seedlings for most of the other highly preferred species (Nugent et al. 1997); this may have been due to factors other than deer. Maintaining *Metrosideros robusta* and *M. umbellata* in the canopy would require control of deer to medium densities, but remaining canopy species can be expected to persist in the presence of high deer densities.

If the goal is to maintain an intact sub-canopy, deer should be controlled to low densities for the 22 genera/species listed in the 'Low' column for that management goal, as well as for *W. racemosa*. Then, if the goal is persistence of all forest species, deer should be controlled to relatively low densities for the six species in the 'Maintain all forest species' × 'Low' cell as well as for the 22 species in the 'Maintain sub-canopy' × 'Low' cell, as well as for *W. racemosa*. The management goals within Table 4 are therefore nested, such that the increasingly complex management goals (down the Table) must also include the information presented for simpler management goals.

We are unable to define what low, medium or high deer densities are with respect to the management goals (i.e. the number of deer per unit area), but this is expected to be the subject of further research (see below). The low, medium and high densities of deer should therefore be considered as *relative* differences in density.

We note that forest structure and perhaps the species of deer present may also affect the susceptibility of management areas to deer impacts. These points are elaborated on in Section 4.1.

Overall, we envisage that managers will use these guidelines to assess both the susceptibility to deer of the vegetation in an area, and the intensity of deer control needed to prevent intolerable changes in the vegetation by first identifying the components of the vegetation that have the highest conservation value. Tables 3 and 4 can then be used to identify which (if any) of those critical components are most threatened by deer (i.e. if one or more of the vegetation components deemed crucial consists of mainly low-threshold species, then the threat is high).

3.5.3 A partial test of the guidelines using exclosure data

The guidelines are consistent with the simple conceptual models relating deer density to their impacts on seedling height growth developed by Nugent et al. (1997), but we lack the comprehensive mechanistic understanding of how such

effects modify, or are modified by, the other drivers of regenerative processes (see Discussion) that also determine the direction and long-term outcomes of compositional changes in the vegetation. Exclosure studies provide a source of data on medium-term outcomes but have several limitations.

The first limitation is that exclosures have typically been located subjectively, rather than randomly, often at sites where people expected the greatest changes to occur (L. Burrows et al., Landcare Research, unpubl. data), and, because of the cost, are usually poorly replicated (numbers of exclosures in five published studies range from 2 to 17). Furthermore, exclosures in which there was no obvious response to deer were often not maintained (R. Allen, Landcare Research, pers. comm.). The second limitation is that exclosures only exclude deer and other large animals, but not other herbivores such as possums and rats, so the lack of a response either inside or outside an exclosure does not necessarily signal a deer effect. These two limitations mean that observed responses can only tentatively be generalised and extrapolated to larger scales. The third main limitation is that exclosures can only show the responses that follow total deer removal (which is seldom an economically affordable management option), and they provide little insight into the graduations in response following the partial removals of deer.

Despite these limitations, exclosure studies still provide the best available data for testing our guidleines. We predict that, provided deer remain present in at least moderate numbers outside exclosures, the low-threshold species will usually be present only inside exclosures, whereas high-threshold species will usually be equally abundant inside and out, or more common outside. We expect the responses of medium-threshold species to be more variable, depending on deer density and the responses of the other groups of species.

The location of the five published studies used for our validation are shown in Fig. 4.

(i) Podocarp–hardwood forest, Urewera Ranges (Allen et al. 1984)

A total of 17 exclosures were established during 1961–68 and remeasured in 1980–81. Red deer densities were initially high but had been reduced to moderate levels by the early 1980s (Beadel 1988). Pigs were present at all sites (R. Allen, Landcare Research, pers. comm.).

Of the eight canopy species with saplings present, only two were not in our guidelines. Although present at only one site, the low-threshold *Weinmannia racemosa* was absent outside the exclosure, as predicted. The high-threshold *Beilschmiedia tawa* and *Dacrycarpus dacrydioides* were both more common outside relative to inside exclosures, also as we predicted. The high-threshold *Nothofagus menziesii* was more abundant outside the one exclosure, whereas *N. truncata* was more abundant inside exclosures. The high-threshold *Quintinia acutifolia* was similarly abundant inside and outside exclosures.

Of the 36 sub-canopy species, seven were not in our guidelines. Of the 13 'low-threshold' species, only *Carpodetus serratus*, *Melicytus ramiflorus* and *Myrsine australis* had trees (dbh at 1.4 m ≥ 2.0 cm) and/or saplings present outside the exclosures. For the remaining nine species (*Aristotelia serrata*, *Coprosma grandifolia*, *C. lucida*, *C. tenuifolia*, *Cordyline australis*, *Griselinia*

Figure 4. Locations of
four of the five published
exclosure studies used to
validate our management
guidelines. The fifth study
used to validate our
guidelines (Wardle et al.
2001) is not shown
because it used 30
exclosures located
throughout New Zealand.

Allen et al. 1984
Mixed forest and red deer
exclosures

Jane & Pracy 1974
Nothofagus forest and red deer
exclosures

Burrows et al. unpubl. 1999
Nothofagus forest and red deer
exclosures

Stewart & Burrows 1989
Podocarp–hardwood forest and white-tailed deer
exclosures
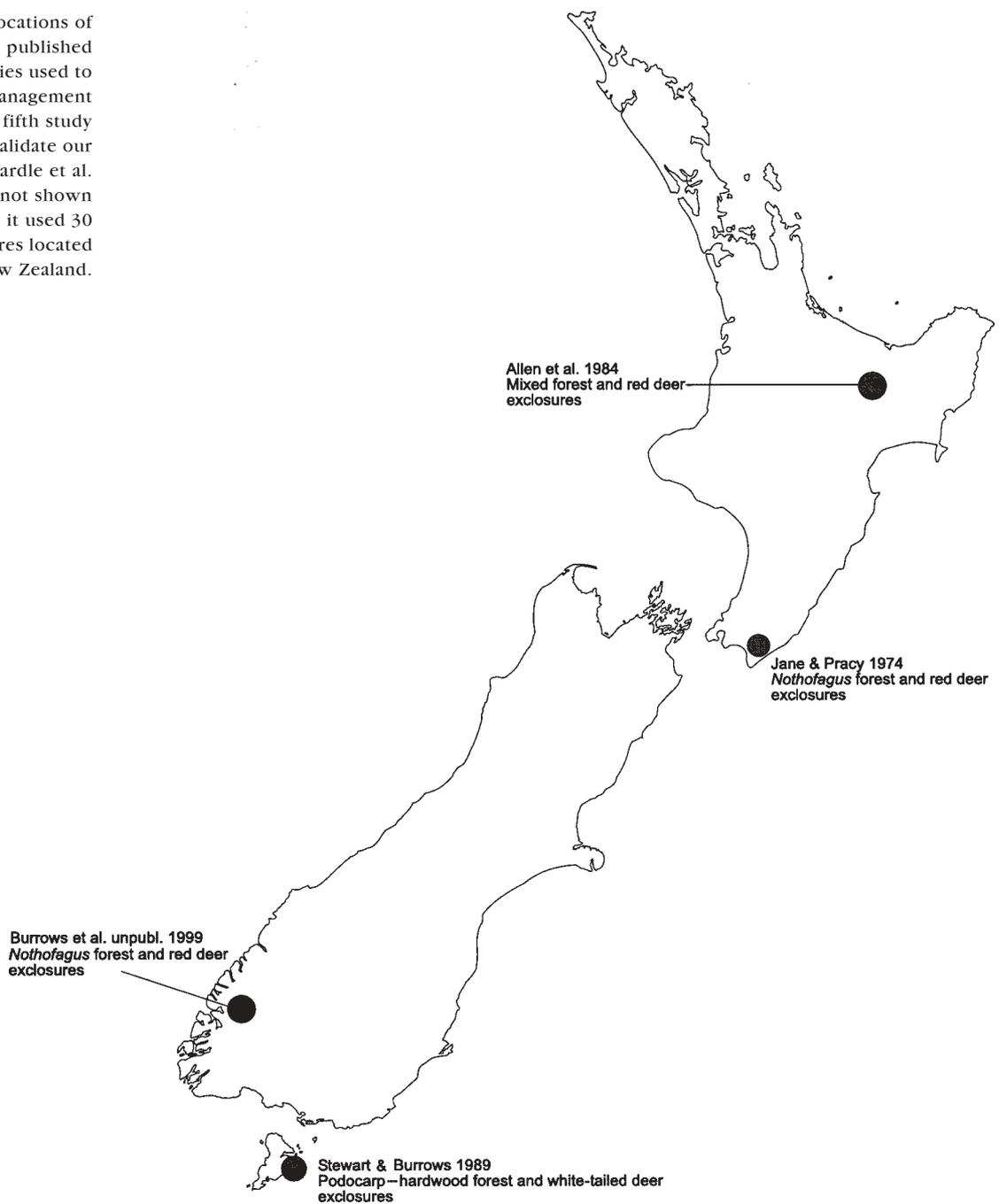
littoralis, *Pseudopanax arboreus*, *P. crassifolius*, and *Schefflera digitata*), both trees and saplings were absent outside exclosures. Seedlings (15–140 cm high) of *P. crassifolius* and *Schefflera digitata* were observed outside exclosures, but were more common inside. *Geniostoma rupestre* was absent as trees outside three exclosures and significantly less abundant (almost absent) as saplings outside eight exclosures.

The nine medium-threshold sub-canopy species were usually present initially at fewer sites than the low-threshold species, so inferences about the effects of deer on these species are weaker. *Coprosma ciliata*, *C. foetidissima*, *C. rhamnoides*, *C. rotundifolia*, and *Raukaua simplex* were at lower sapling densities outside the exclosure at the one site each was observed at. *Hedycarya arborea* and *Pittosporum tenuifolium* were both present as adults outside the

exclosure ($n = 1$ site each) but not as saplings ($n = 1$ and 4 sites, respectively). *Myrsine divaricata* and *Pennantia corymbosa* were both more abundant as saplings relative to the exclosures.

Of the seven high-threshold sub-canopy species, four (*Kunzea ericoides*, *Melicope simplex*, *Raukaua anomalus* and *Pseudowintera colorata*) matched the prediction that they would be similarly, or more, abundant outside the exclosures. *Leucopogon fasciculatus* and *Cyathodes juniperina* were abundant inside and outside the exclosures, but more so inside. *Alseuosmia macrophylla* was absent outside the one exclosure it was recorded in.

The responses of the three understorey species matched our predictions. Densities of the two low-threshold ferns (*Asplenium bulberiferum* and *A. flaccidum*) and the climber *Ripogonum scandens* both increased markedly within the exclosures. The high-threshold *Uncinia* spp. were more abundant outside the exclosures.

Herbivory by red deer had pronounced and seemingly predictable effects on the abundance of canopy and sub-canopy species. Despite the small number of sites and the lack of statistical significance for many of the differences for inside and outside the exclosures, we believe that the observations of Allen et al. (1984) generally support our predictions for low-threshold and high-threshold species.

(ii) Nothofagus forest and red deer, Haurangi Range (Jane & Pracy 1974)

Two exclosures were established in 1951 in *Nothofagus* forest, Haurangi Range, and remeasured periodically to 1971. Red deer were initially present at high densities but apparently had declined to moderate densities by 1971.

Within 2–3 years of establishment, there was a rapid growth of four low-threshold species (*Coprosma grandifolia*, *C. lucida*, *Schefflera digitata* and *Geniostoma rupestre*) inside both exclosures. By 1971 the number of species in the exclosures declined (the low-threshold *C. lucida* and *Carpodetus serratus*, and the medium-threshold *Pittosporum eugenioides*). The low-threshold *Melicytus ramiflorus* and *Myrsine australis* continued to increase within the exclosures, and the high-threshold sub-canopy species (especially *Leucopogon fasciculatus* and *Uncinia uncinata*) and the ferns *Cyathea dealbata* and *C. smithii* increased outside the exclosures.

This study represents the longest ungulate exclusion so far published in New Zealand. The initial pattern within the exclosures of an irruption of some low-threshold sub-canopy species followed by a decline, presumably due to shading, emphasises how changes in the abundance of species also affect the regeneration of species.

(iii) Podocarp–hardwood forest and white-tailed deer, Stewart Island (Stewart & Burrows 1989)

Exclosures and control plots established at two sites on Stewart Island in 1979 were remeasured in 1984. In 1979 the deer density was high, but was reduced to low densities by a poisoning campaign in 1981; thereafter the population recovered rapidly (Forest Research Institute 1984; Stewart & Burrows 1989).

Numbers of most tall woody seedlings (16–135 cm) and saplings were very low in 1979, and low-threshold species such as *Griselinia littoralis* were absent.

Following establishment of the exclosures, seedlings and saplings increased over the study period. For tall seedlings there was a strong effect of exclosures for both low-threshold and medium-threshold species (Table 4 in Stewart & Burrows 1989). Three of the five low-threshold species (*G. littoralis*, *Carpodetus serratus*, and *Myrsine divaricata*) were more abundant inside the exclosures relative to outside, *Weinmannia racemosa* was similarly abundant, and *Brachyglottis rotundifolia* was much more common outside. The two medium-threshold species, *Coprosma foetidissima* and *Raukaua simplex* were also much more common inside the exclosures, but were both also present outside. The four high-threshold species, *Prumnopitys ferruginea*, *Leptospermum scoparium*, *Cyathodes juniperina*, and *Dracophyllum longifolium* were either similarly or more abundant outside the exclosures. It was noted that outside the exclosures the seedlings of some low- and medium-threshold species were impeded from becoming saplings by deer browsing.

For saplings (< 2.5 cm dbh and > 1.35 m tall), the low-threshold *W. racemosa* and *B. rotundifolia* were much more abundant inside exclosures. The medium-threshold *C. foetidissima* was almost eliminated from outside the exclosures but was common inside. The saplings of the high-threshold species *C. juniperina*, *D. longifolium*, and *Podocarpus hallii* were all considerably more abundant outside than inside exclosures. Hence, the observed patterns matched the predictions of our guidelines.

Stewart & Burrows (1989) noted that the responses of species to exclosures varied according to vegetation type. For example, the high-threshold *W. racemosa* was absent from the understorey in 1985 but had increased in tall forest understorey by 1985.

(iv) Nothofagus forest and red deer, Murchison Mountains (L. Burrows et al., Landcare Research, unpubl. data)

Five exclosures and eight adjacent plots in mixed *Nothofagus* forest in Fiordland were remeasured in 1998. The exclosures had been established between 1960 and 1965. Densities of red and wapiti-type deer (*Cervus elaphus*) were high in the 1960s but had been heavily reduced by government-funded control since 1975 (G. Nugent, unpubl. data).

The species not appearing as saplings outside the exclosures were all in our low-threshold class (*Aristotelia serrata*, *Carpodetus serratus*, *Griselinia littoralis*, *Hoheria glabra*, and *Myrsine australis*). The number of saplings of medium-threshold and high-threshold species was unaffected by the exclosures, suggesting that intensive and sustained deer control in that area had been sufficient to maintain all but the low-threshold species.

The number of seedlings (15–135 cm high) and seedling species richness was significantly less in exclosures than in adjacent control plots, presumably because the higher density of saplings produced a deeply shaded understorey that inhibited seedlings. These dynamics contrast with those observed by Allen et al. (1984), and were probably a consequence of competitive suppression mediated by deer, with similar results reported for some grasses and herbs by Jane & Pracy (1974) and Stewart & Burrows (1989).

L. Burrows et al. (Landcare Research, unpubl. data) also measured changes in forest composition in 39 permanent plots and 74 'recce' plots. When separated

by forest type, the response to reduced deer densities was variable. In *Nothofagus menziesii-Hoheria glabrata-Polystichum vestitum* (seral) and *N. fusca/Blechnum discolor* forests there were large increases in low-threshold and medium-threshold species. Low-threshold species were absent from the *N. solandri* var. *cliffortioides–N. menziesii* forest type in 1975 and there had been no recolonisation. One possibility is that the species had never been present in that forest type.

L. Burrows et al. (Landcare Research, unpubl. data) showed that forest type and slope had significant effects on seedling density. Because no estimates of deer density were available, the effects of landform, vegetation processes and deer herbivory could not be partitioned.

(v) National patterns inside and outside exclosures (Wardle et al. 2001)

Plant community composition was measured at 30 exclosures and adjacent control plots located in forest throughout New Zealand (not shown) during 1997–99. The exclosures were at least 13 years old, and the principal excluded ungulate was red deer, although other ungulates were also present at some sites. The densities of deer relative to equilibrium density were not known, but are likely to have been highly variable.

Plant density in the browse layer (0–2 m) was usually greater within the exclosures than the adjacent controls. However, ground-layer vegetation (0–10 cm) was sometimes greater outside than inside the exclosure. At several locations, large-leaved species were abundant inside the exclosure but absent outside. Species considered to be 'severely reduced' by browsing were those classified by us as low-threshold (*Griselinia littoralis*, *Coprosma grandifolia*, *Geniostoma rupestre*, and some *Astelia* spp.). Species considered 'promoted by browsing' were mostly high-threshold species (*Leucopogon fasciculatus*, *Uncinia* spp., *Microlaena avenacea*, *Hymenophyllum* spp., and some *Blechnum* spp.) and also a medium-threshold species, *Polystichum vestitum*. These results support the observations from the four sites described above.

(vi) Summary

We consider that our predictions were generally supported by the five studies for the low- and high-threshold species. Patterns were more variable both within and among studies for the medium-threshold species, which suggests that our classification for these species was about right. In other words, the densities of deer at which the abundance of medium-threshold species will increase appears to be somewhere between that for low- and high-threshold species. That our initial guideline classification based on diet preference indices seemed generally consistent with the trends observed inside and outside exclosures suggests that our guidelines will be useful for the other species.

4. Discussion

4.1 NON-REVERSIBILITY OF DEER IMPACTS

Conservation of New Zealand's native flora appears to be largely predicated on the assumption that the anthropogenic alterations in vegetation structure, composition and functioning since human colonisation are reversible to some unmodified state if the agents of change (primarily pests and weeds) are controlled (e.g. DOC 1997). For deer, that assumption is a logical inference from simple models (e.g. Nugent et al. 1997; McShea et al. 1997; Fig. 1) relating deer density (and deer density alone) to regeneration indices for various plant species; the apparent implication for forest managers is that they need only alter deer density to achieve the desired level of regenerative response in palatable species. Exclosure evidence showing that seedlings and saplings of preferred species do tend to return after deer are excluded (Section 3.5.3) provide a measure of support for that simplistic view, as do studies showing increases in abundance of deer-preferred species after a large reduction in deer density (Stewart et al. 1987; Rose & Platt 1987). However, the drivers of resilience in relation to deer impacts are far more complex than any simple correlation with deer density alone.

Coomes et al. (in press) give several examples of situations in which deer impacts may not be reversible, and describe at least seven factors responsible for the lack of a response to deer control. We summarise those seven factors below because they need to be considered by managers when contemplating the benefits of deer control at a site.

4.1.1 Diet switching

Deer appear to switch to eating litter and less preferred species when they lack more nutritious forage. Control may reduce the number of deer browsing on some species, but the benefits of this reduction may be counteracted by increased *per capita* intake of those species resulting from deer switching their diet away from less preferred litter and leaves. The conceptual model in Fig. 1 depicts such shifts in functional responses by a highly non-linear relationship between deer density and seedling regeneration of *Griselinia littoralis*, a species highly preferred by deer (Forsyth et al. 2002).

4.1.2 Expanded niche occupation by species that deer avoid eating

The removal of highly preferred species can enable the spread of less-preferred forest species as a result of reduced interspecific competition. Once these less-preferred species occupy space, they may effectively prevent the re-establishment of the preferred species following deer control. For example, there is evidence that browsing of woody saplings has promoted the spread of the avoided ground ferns *Blechnum discolor* and *Blechnum procerum* (Wardle 1984; Wardle et al. 2001), which provide a barrier against further regeneration of woody species (Wardle 1984). The expansion of avoided shrubs such as *Pseudowintera colorata* and *Neomyrtus pedunculata* may have similar consequences (Allen et al. 1984). Many of these compositional shifts caused by deer

browsing are poorly understood, limiting our ability to predict the consequences of deer control.

4.1.3 Changes to successional pathways

Herbivores can accelerate, slow or fundamentally alter the course of succession, depending on which species they choose to eat. For example, the small myrtaceous trees *Kunzea ericoides* and *Leptospermum scoparium* often dominate early successional shrublands following abandonment of agricultural land or burning in New Zealand. These species have small tough leaves that are avoided by deer but act as nurse plants facilitating the recruitment of other species such as the small, broadleaved trees *Melicytus ramiflorus* and *Myrsine australis* (Wardle 1991), both of which are preferred by deer. Smale et al. (1995) showed that the exclusion of fallow deer from stands of *Kunzea ericoides* led to the increased establishment of *Melicytus* and *Myrsine* and that they began to replace *Kunzea* 10 years after the exclusion of deer. In contrast, where deer had not been excluded the vegetation remained dominated by *Kunzea* and *Leptospermum*. In this example it is unclear whether deer are arresting or causing an irreversible shift in the successional pathway.

4.1.4 Lack of seeds required to re-establish populations

Browsing by deer may eventually result in the total elimination of species from patches of forest, and without local seed sources such species may be unable to re-establish. Seed limitation may be exacerbated in New Zealand by the loss of native pollinators and seed dispersers as a consequence of predation by introduced feral cats (*Felis catus*), stoats (*Mustela erminea*), possums, rodents (e.g. *Rattus rattus*) and wasps (e.g. *Vespula germanica*) (Clout & Hay 1989) and by a lack of long-lived seeds in the soil (Enright & Cameron 1988). The role of seed limitation is illustrated in the southern Ruahine Range, North Island, where extensive canopy dieback of *Metrosideros robusta* and *Weinmannia racemosa* occurred over large areas in the mid-twentieth century (Rogers & Leathwick 1997). In such areas there is now no regeneration of these tree species. Browsing by deer apparently promoted a competitive sward of non-preferred species at the time of canopy dieback (Rogers & Leathwick 1997). Reduced deer numbers alone will not now allow the canopy species to re-establish because their propagules are unlikely to be found in the seed rain. Whether or not plants will rapidly re-establish following pest control is difficult to generalise because it depends on the presence of suitable refugia to provide seed sources and the mode of dispersal of the species; for example, fleshy-fruited seeds may be carried long distances by birds (Dungan et al. 2001).

4.1.5 Long-term alteration of ecosystem properties

A recent comparison of below-ground assemblages inside and outside 30 exclosures spread throughout New Zealand has drawn attention to the effects of browsing on litter quality, soil microbial properties, and microarthropod and macrofaunal groups, although it appears that these effects vary rather unpredictably from location to location (Wardle et al. 2001). The idiosyncratic responses among sites may reflect the multiple pathways by which herbivores exert influence. For example, because the foliage of avoided species tends to be low in nutrients and high in lignin (Forsyth et al. 2002; Wardle et al. in press),

litter may be relatively slow to decompose, so the selective removal of preferred species may result in a reduction in decomposition rates and a consequent slowing of nutrient cycling.

Deer may also alter below-ground processes by consuming fallen leaves (sometimes in very large quantities; Nugent et al. 1997) and by causing compaction of soils by trampling. It appears there are marked differences among sites as to which of these below-ground processes are most affected by deer; thus simple generalisations are not yet possible (Wardle et al. 2001), although we might speculate that altered below-ground pathways could influence tree regeneration, in which case they could have century-level consequences.

4.1.6 Interactions among multiple herbivore pest species

The arrival of deer in New Zealand coincided with the successful introduction of many other mammalian herbivores (King 1990). Of the other introducd herbivores, feral pigs (*Sus scrofa*) and brushtail possums are common throughout New Zealand forests and, like deer, appear to be most abundant on low-elevation fertile sites. There is much debate within New Zealand (e.g. Forsyth et al. 2000) about the benefits of single-species management. In particular, it is often unclear which species is the primary driver of change: hence there is uncertainty as to whether reducing the density of one species will have conservation benefit. It is possible that the effects of the controlled species will be replaced by another pest species. For example, the abundance of red deer declined in the Kaweka mountains, partly as a result of hunting, but the abundance of sika deer increased (Davidson & Fraser 1991).

4.1.7 Re-establishment of trees in areas invaded by exotic plants

The number of introduced plant species far exceeds native plants in New Zealand, with sward-forming grasses now naturalised over extensive areas. These species may strongly impede regeneration of native species (e.g. Widyatmoko & Norton 1997), with herbivory taking a relatively minor role. For example, a fire in 1981 caused the death of adult trees in around 300 ha of mountain beech forest in the dry eastern foothills of the Southern Alps, and long-term monitoring indicates that mountain beech largely fails to regenerate on burnt areas because introduced browntop grass (*Agrostis capillaris*) rapidly became dominant (Wiser et al. 1997). Seeding experiments on the freshly burned forest floor suggest that between 1981 and 1986 mountain beech seeds germinated and grew when sown with other native woody species but failed to grow when sown with pasture grasses including browntop (Ministry of Forestry 1987). Red deer commonly browse the open areas dominated by browntop, but they are unlikely to be the primary cause of regeneration failure because seedlings also fail to establish in browntop turf when deer are excluded with exclosures (Ministry of Forestry 1987). Even with deer control, other factors, in this case invasive grasses, are still going to restrict the re-establishment of forest. Browsing/grazing may even facilitate the re-establishment of native species if the exotic plants are preferentially browsed. The introduced grass *Dactylis glomerata* greatly slows the establishment of native early successional species such as *Kunzea ericoides*, unless browsed (Wilson 1994). Conversely,

Zavaleta et al. (2001) provide several examples of invasive plants that increase in abundance following the eradication of invasive herbivores.

In summary, there are many possible explanations of why deer control can fail to provide long-term conservation benefits, and conservation managers will need to identify which of these issues are relevant to each management area.

4.2   SUSCEPTIBILITY FRAMEWORK

4.2.1   Defining management goals

The above reasons highlight why deer control or removal is highly unlikely to result in a full and rapid return of ecosystems to the pre-deer state. A consequence of this is that it requires that managers explicitly define their goals. Managers cannot simply assume that deer control will result in a reversal of deer-induced impacts, but must take into account whether other prerequisites for recovery are also in place. If rapid recovery is not achievable, the management goal may instead be to at least reduce the severity on ongoing deer-induced changes. Alternatively, the goal may simply be to allow the return of browse-intolerant species even if they differ from those originally present.

As already noted (Section 3.5.1), susceptibility cannot therefore be assessed in isolation from the management goal. Nor can it be assessed solely in terms of what was initially present, but must also take into account the current state of the ecosystem, whether the other drivers of regeneration are likely to permit any recovery, and the time frame over which any opportunity for recovery is likely to occur. We therefore consider that the simple guidelines presented in this report provide a flexible first step for assessing susceptibility, but only a first step.

4.2.2   Information needs

Our guidelines should be regarded as provisional, in that they are based largely on diet preference data mostly derived from studies in which the ungulates were at densities well below a likely equilibrium density. Preference indices will vary depending on how close to equilibrium density the populations are. At very low densities, far from any equilibrium density, only a few species are eaten in greater proportions than their abundance in the vegetation, but that number could be expected to increase as deer densities increase. We lack studies that would enable us to separate species that would be eaten in quantity if the deer were near starvation, from those that would not, so our high-threshold species list includes species that may in fact never be seriously affected by deer.

That information gap aside, the guidelines suggest that most of the main canopy species can be expected to persist in the presence of at least moderate densities of deer. Recent work in the Kaweka Range, central North Island, suggests that high densities of red and sika deer have slowed, but not prevented, the recovery of mountain beech (*Nothofagus solandri* var. *cliffortioides*) (Allan 1997). However, at a few sites regeneration was considered insufficient to maintain a complete forest canopy, an effect attributed to deer browsing (Allen & Allan

1997). In mixed podocarp forests, regeneration dynamics are more complex and the spatial and temporal scales of observation provided by the exclosure studies are insufficient to make inference about the dynamics of canopy species (see Bellingham et al. 1999).

The responses of sub-canopy species seem more predictable than for canopy species. Sub-canopy species have shorter lifespans and a greater proportion of their photosynthetic material available to deer compared to canopy species. However, although some sub-canopy species consistently decline in abundance in the presence of sustained herbivory (e.g. *Griselinia littoralis*), others increase (e.g. *Pseudowintera colorata*). This is a common phenomenon (Augustine & McNaughton 1998). The implication for managers is that planning deer control requires consideration of both increases and declines in the abundance of species.

It is unclear how our three thresholds translate into actual deer densities. Unfortunately, faecal pellet data are not commonly collected, and most such historical data have not been collated. This has proved a major barrier to our attempts to translate deer impacts into an index of deer density, and must be remedied if our understanding of the impacts of deer on forest dynamics is to improve.

There is limited anecdotal information suggesting how low deer densities should be to maintain sub-canopy species. At Waihaha, there were few significant relationships between the mean height of small seedlings (< 50 cm) and deer (or possum) density (Nugent et al. 1997). Seedlings of the deer-preferred species were small (< 5 cm) and independent of deer density, except in natural 'exclosures' where deer were absent. This suggests that either the biophysical environment was unsuitable, and/or the density of deer was too high for these seedlings to increase in height. The exception was *Weinmannia racemosa*, the seedlings of which increased in height with decreasing deer density. Moreover, significantly more deer-preferred species (10 of 12) had negative regression coefficients than species not preferred by deer (8 of 20), suggesting that seedling height is inversely related to deer density for most low-threshold species, but that the size of the effect is small. In other words, deer densities would have to be reduced lower than present at Waihaha (i.e. < 6/km^2) to increase the height of deer-preferred species. Bellingham et al. (1999) considered that deer densities had been lowered sufficiently to enable the regeneration of *Griselinia littoralis*, probably the species most preferred by deer, in the Kokatahi and Copland catchments, central Westland, during the 1970s–90s. No quantitative estimates of deer density are available, but commercial helicopter-based hunters indicate densities are low (S. Cross, Department of Conservation, pers. comm.).

4.2.3   Indicator species

'Indicator' species may be useful for managers to monitor the impacts of deer. The term 'indicator' implies that trends in that species are representative of other species, but for deer this is unknown. However, a reasonable assumption may be that, if a highly-preferred species is abundant in the understorey, other preferred species with similar regeneration strategies may also be similarly 'protected'. Of the widespread and common preferred sub-canopy species, *Griselinia littoralis* is the most preferred. If *G. littoralis* can regenerate, it is

likely that the other low-threshold species can also regenerate. However, indicator species may be inappropriate for canopy species due to different modes of regeneration, which are still not well understood (Bellingham et al. 1999).

5. Conclusions

Deer have clear diet preferences, with native plants varying widely in their preferences, and therefore susceptibility, to deer.

The susceptibility of the vegetation of particular management units also varies widely, with deer-preferred species tending to be most abundant in fertile and frequently disturbed areas. These biophysical characteristics are, however, too general and imprecise to provide useful indicators of susceptibility.

Broad-scale comparison of different forest types indicates that, although some highly preferred species are failing to regenerate in nearly all forest types, other preferred species continue to establish in all forest types, and there was no strong evidence that these effects differed between forest types.

Because the importance of any change in abundance of a particular plant or group of plants within an ecosystem depends on the human valuation of that change, susceptibility can only be judged in the context of area-specific management goals, and so general rules for the susceptiblity of forest types cannot be promulgated.

Predictions based on deer feeding preferences were consistent with the available data from exclosures on the outcomes of deer removal, and with studies of the vegetation responses to deer control. In general, retention of native forest canopies is likely to require far less stringent control than protection of the sub-canopy trees or of all species affected by deer.

Deer control is seldom likely to result in the rapid and full return of the ecosystem to its pre-deer state because many of the changes induced by deer have long-term effects on forest composition and functioning, and because there are many other drivers of the regenerative processes needed for recovery. Assessment of susceptibility and of the likely response to deer control cannot be based solely in terms of what was initially present, but must also take into account the current state of the ecosystem, whether the other drivers of regeneration are likely to permit any recovery, and the likely time frame over which any opportunity for recovery is likely to occur.

Assessment of susceptibility based on our guidelines would be treated as management hypotheses to be empirically tested in an adaptive management framework. There is also an urgent need to gather better and far more comprehensive information relating quantitative indices of deer density to their impacts, and to overall forest condition, than is presently available.

We recommend that historical information on the densities of deer should be collated and used to investigate, from NVS, relationships between the long-term

abundance of plant species and deer, and other biophysical factors. All studies assessing the impacts of deer on vegetation should use a standardised monitoring protocol to index the abundance of deer. This includes plots associated with exclosures. A standardised monitoring protocol needs to be developed and validated.

6. Acknowledgements

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Appendix

The proportion of total basal area of forests classified by the Vegetation Cover Map (Newsome 1987), with number of NVS plots given in brackets. All species that contribute at least 0.1 % of the total basal area of a forest type are shown.

Podocarp forest (27)

Dacrydium cupressinum	0.616
Weinmannia racemosa	0.165
Quintinia acutifolia	0.096
Prumnopitys ferruginea	0.045
Metrosideros umbellata	0.040
Phyllocladus aspleniifolius var. *alpinus*	0.009
Lagarostrobus colensoi	0.008
Podocarpus hallii	0.006
Elaeocarpus hookerianus	0.003
Myrsine australis	0.002
Pseudopanax ferox	0.002

Lowland podocarp–broadleaf forest (262)

Weinmannia racemosa	0.329
Dacrydium cupressinum	0.193
Beilschmiedia tawa	0.127
Metrosideros umbellata	0.064
Melicytus ramiflorus subsp. *ramiflorus*	0.054
Prumnopitys ferruginea	0.039
Griselinia littoralis	0.033
Podocarpus hallii	0.033
Nothofagus fusca	0.021
Prumnopitys taxifolia	0.021
Knightia excelsa	0.016
Elaeocarpus dentatus	0.015
Dicksonia squarrosa	0.015
Carpodetus serratus	0.014
Quintinia serrata	0.014
Coprosma foetidissima	0.013

Lowland podocarp–broadleaf–beech forest (697)

Nothofagus menziesii	0.230
Weinmannia racemosa	0.216
Nothofagus truncata	0.121
Nothofagus fusca	0.092
Dacrydium cupressinum	0.062
Metrosideros umbellata	0.047
Nothofagus solandri var. *cliffortioides*	0.033
Melicytus ramiflorus subsp. *ramiflorus*	0.026
Prumnopitys ferruginea	0.022
Podocarpus hallii	0.022

Nothofagus solandri var. *solandri*	0.017
Griselinia littoralis	0.015
Prumnopitys taxifolia	0.013
Beilschmiedia tawa	0.011
Metrosideros robusta	0.006
Carpodetus serratus	0.005
Kunzea ericoides	0.005
Hedycarya arborea	0.005
Cyathea dealbata	0.004
Myrsine salicina	0.003
Elaeocarpus dentatus	0.003
Pseudowintera colorata	0.003
Knightia excelsa	0.003
Cyathea smithii	0.003
Elaeocarpus hookerianus	0.002
Myrsine australis	0.002
Pseudowintera axillaris	0.002
Raukaua simplex	0.002
Quintinia acutifolia	0.002
Pseudopanax crassifolius	0.001
Coprosma foetidissima	0.001
Laurelia novaezelandiae	0.001
Dacrycarpus dacrydioides	0.001
Ixerba brexioides	0.001

Beech forest (1905)

Nothofagus solandri var. *cliffortioides*	0.386
Nothofagus menziesii	0.315
Nothofagus fusca	0.143
Weinmannia racemosa	0.048
Nothofagus truncata	0.016
Griselinia littoralis	0.015
Metrosideros umbellata	0.012
Podocarpus hallii	0.009
Quintinia acutifolia	0.006
Dacrydium cupressinum	0.006
Phyllocladus aspleniifolius var. *alpinus*	0.004
Carpodetus serratus	0.003
Prumnopitys ferruginea	0.003
Nothofagus solandri var. *solandri*	0.002
Raukaua simplex	0.002
Hoheria glabrata	0.002

Pseudowintera colorata	0.002	*Raukaua simplex*	0.004
Elaeocarpus hookerianus	0.002	*Prumnopitys ferruginea*	0.004
Archeria traversii	0.002	*Coprosma linariifolia*	0.004
Melicytus ramiflorus subsp. *ramiflorus*	0.002	*Melicytus ramiflorus* subsp. *ramiflorus*	0.002
Fuchsia excorticata	0.002	*Kunzea ericoides*	0.002
Myrsine divaricata	0.001	*Podocarpus totara*	0.002
Pseudopanax crassifolius	0.001	*Pseudowintera colorata*	0.002
Elaeocarpus dentatus	0.001	*Olearia rani*	0.002
		Myrsine divaricata	0.002
Beech–broadleaf (91)		*Elaeocarpus hookerianus*	0.002
Nothofagus menziesii	0.296	*Nothofagus solandri* var. *solandri*	0.001
Nothofagus solandri var. *cliffortioides*	0.236		
Nothofagus fusca	0.175	Broadleaf forest (228)	
Weinmannia racemosa	0.132	*Metrosideros umbellata*	0.300
Metrosideros umbellata	0.036	*Weinmannia racemosa*	0.241
Nothofagus truncata	0.021	*Podocarpus hallii*	0.238
Griselinia littoralis	0.020	*Griselinia littoralis*	0.078
Podocarpus hallii	0.014	*Quintinia acutifolia*	0.066
Dacrydium cupressinum	0.010	*Libocedrus bidwillii*	0.032
Leptospermum scoparium	0.008	*Beilschmiedia tawa*	0.019
Halocarpus biformis	0.008	*Prumnopitys ferruginea*	0.016
Carpodetus serratus	0.005	*Pseudowintera colorata*	0.014
Archeria traversii	0.004		