Biological Conservation **49** (1989) 275–293

The Impact of White-tailed Deer *Odocoileus virginianus* on Regeneration in the Coastal Forests of Stewart Island, New Zealand

G. H. Stewart & L. E. Burrows

Forestry Research Centre, Forest Research Institute,
PO Box 31-011, Christchurch, New Zealand

(Received 3 December 1988; accepted 4 February 1989)

ABSTRACT

The impact of white-tailed deer Odocoileus virginianus *Zimmermann on regeneration patterns in the coastal conifer-broadleaved hardwood forests of Stewart Island was monitored for 6 years. Permanent 20 × 20 m quadrats, established in 1979 on deer-free Bench Island, inside deer exclosures on Stewart Island, and in an area subject to deer browsing on Stewart Island, were remeasured in 1985. In the absence of deer (Bench Island) seedlings of deer-preferred hardwood trees and shrubs were abundant on the forest floor and on the trunks of treeferns that colonised canopy openings and areas of dieback. On Stewart Island, after deer exclusion, numbers of treeferns and tall seedlings of hardwoods increased, especially in treefall gaps and areas of partial canopy dieback. Under the influence of deer, tall seedlings of hardwood trees and shrubs were rare and were being eliminated.*

The effects of deer will become more severe unless numbers are reduced, especially in forest types where the canopy hardwood tree species are preferred deer foods. In these types the maintenance of a forest canopy is endangered, and in others species of low preference could replace deer-preferred species in the canopy.

INTRODUCTION

The ecological consequences of introducing non-indigenous wild animals into an unadapted ecosystem are exemplified by the vegetation of New

Zealand. Thirty-two species of mammals are now widely accepted as part of the New Zealand fauna (Wodzicki & Wright, 1984), although before settlement by Polynesians toward the end of the first millenium AD no terrestrial mammals were present except for two species of bat (Bull & Whittaker, 1975). Few areas of New Zealand have escaped the influences of introduced browsing mammals, and the forests of Stewart Island are no exception. North American white-tailed deer *Odocoileus virginianus* Zimmermann were liberated in the south of Stewart Island in 1905 and by the late 1920s had spread throughout the island (Harris, 1981). Present deer numbers are high, especially in the preferred coastal forests (C. N. Challies, pers. comm.).

The coastal forests are primarily conifer-broadleaved hardwood forests dominated by the conifers *Dacrydium cupressinum* and *Podocarpus ferrugineus*, and the hardwoods *Metrosideros umbellata* (southern rata) and *Weinmannia racemosa* (kamahi) (Wilson, 1987). Subcanopy hardwood trees include *Griselinia littoralis*, *Carpodetus serratus*, several species of *Pseudopanax*, and the treefern *Dicksonia squarrosa*. Adjacent to the sea, low forest and scrub communities contain species such as *Fuchsia excorticata*, *Schefflera digitata*, *Senecio reinoldii* (muttonbird scrub), *Coprosma areolata*, and *Dracophyllum longifolium*. Species nomenclature follows Wilson (1987).

Forest dieback was noticed on the coast of Stewart Island in the 1950s and by the mid to late 1970s was extensive along the north and eastern coastlines (Purey-Cust & McClymont, 1979). The most likely explanation for this dieback was that it was initiated by exposure to salt-laden winds, although browsing by the introduced Australian brushtail possum *Trichosurus vulpecula* Kerr was also implicated (A. D. Ross, pers. comm.; Veblen & Stewart, 1980). Similar dieback has occurred in the absence of possums (and deer) on neighbouring Bench Island (Veblen & Stewart, 1980) and on the Auckland Islands (Campbell & Rudge, 1984). Forest regeneration in both the dieback zone and intact forests further inland was generally inhibited by browsing by white-tailed deer (Veblen & Stewart, 1980). Concern about poor forest health prompted a series of scientific investigations in the late 1970s and early 1980s.

This study compared plant regeneration processes on Bench Island, which had no history of deer browsing, with those in two areas on the east coast of Stewart Island; Chew Tobacco Bay and Port Adventure (Fig. 1). In the Stewart Island areas two types of sites were investigated: non-excluded sites where deer numbers had been reduced by a poisoning operation in 1981 (New Zealand Forest Service, 1984) but were now expanding again, and fenced exclosures from which deer had been excluded since 1979. Particular emphasis was placed on determining the effects of deer in different vegetation types and at different stages of forest dieback.

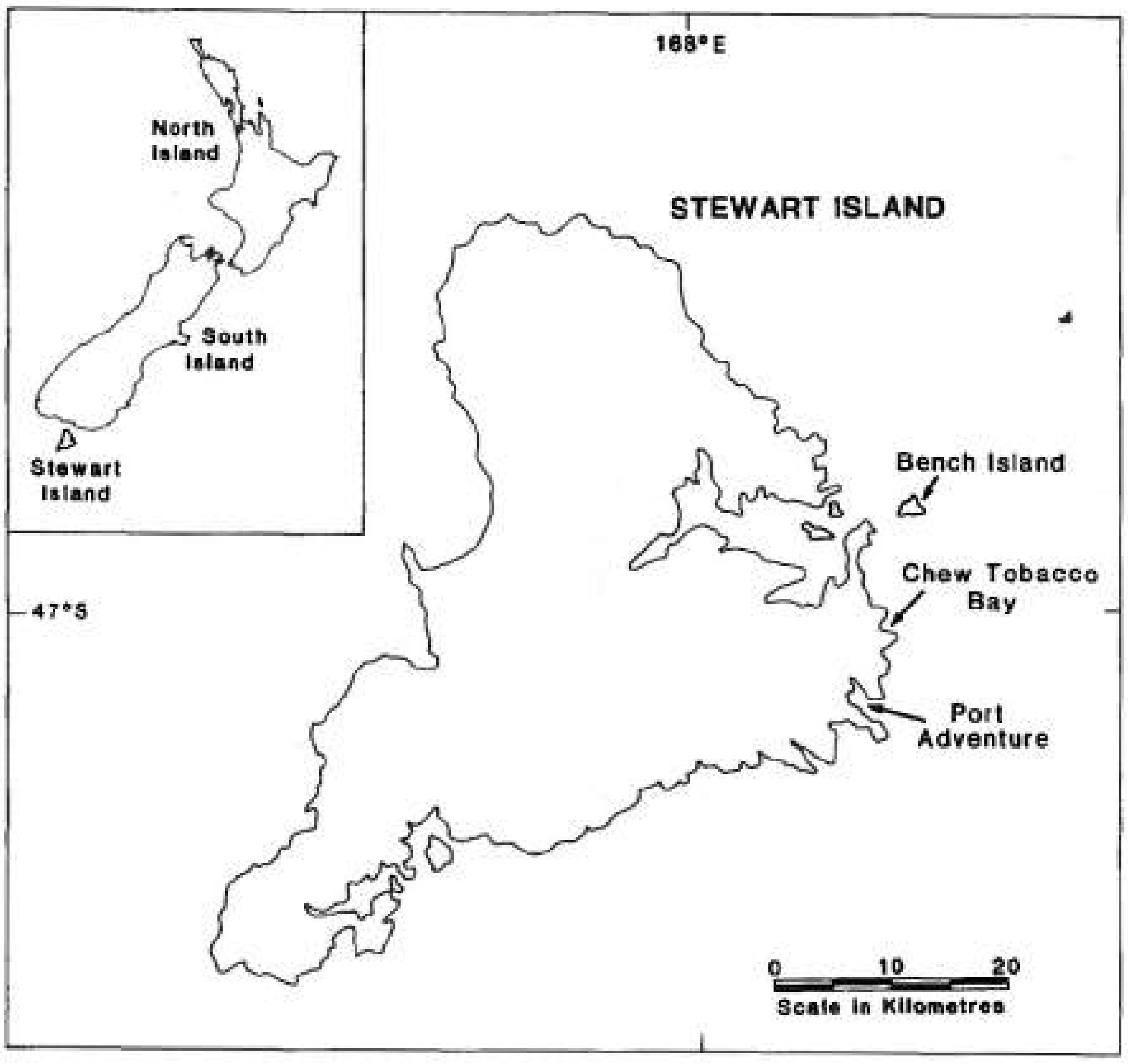

Fig. 1. Study site location.

METHODS

Plot location

Permanent 20 × 20 m quadrats (Allen & McLennan, 1983) were established and measured in all three areas in 1979 and remeasured in 1985. For Stewart Island permanent quadrats, understorey plots were also remeasured in 1981 (see Plot Methodology).

Nine permanent exclosure quadrats and 22–24 non-exclosed quadrats were subjectively located in each Stewart Island area to include the seven major vegetation types and different stages of dieback. Another two permanent quadrats, one in each area, were located in open muttonbird scrubland (see Table 1 for names of vegetation types and dieback stages). Five non-exclosed quadrats were established on Bench Island.

TABLE 1
Number of Non-exclosed Quadrats and Exclosures in Different Vegetation Types on Stewart and Bench Islands

Vegetation type	*Non-exclosed quadrats*			*Exclosures*	
	Chew Tobacco Bay	*Port Adventure*	*Bench Island*	*Chew Tobacco Bay*	*Port Adventure*
Tall forest-*Blechnum* fernland	3	2	1	1	1
Open canopy-depleted treefern thicket	2	2	1	2	
Canopy gap-*Cyathodes* shrubland	5	4	1	1	2
Partial rata-kamahi dieback forest	4	4	2	2	2
Open *Fuchsia* low forest	1	3		1	1
Dense short herbfield	2	4		1	2
Total dieback-grassland and sedgeland	6	2		1	1
Open muttonbird scrubland	1	1			
All plots	24	22	5	9	9

The degree of canopy dieback follows a general sequence from least at the top of the table to greatest at the bottom.

Plot methodology

The total number of species and the number of species present in the browse height tier (0·3–2 m) were recorded on 'recce' plots (Allen & McLennan, 1983) located in each permanent quadrat or inside each exclosure. Browsed plant species and intensity of browsing were recorded on the Stewart Island plots. Browse indices (Wardle *et al.*, 1971; Rose & Burrows, 1985) were calculated to assess changes in the feeding patterns of deer from 1979 to 1985.

Each 20 × 20 m permanent quadrat was divided into 5 × 5 m subplots. The diameters of all trees (stems > 2·5 cm dbh) in each subplot were measured and tagged, and the numbers of saplings (< 2·5 cm dbh but > 1·35 m tall) were counted. The numbers of treeferns (primarily *Dicksonia squarrosa*) in the subplots were recorded in height classes (height taken to highest point of the crown) of 0·3–2·0, 2–5 and 5–12 m.

The frequency of small seedlings (≤ 15 cm tall) and the numbers of tall seedlings (16–135 cm) and saplings were recorded in 24 systematically located and permanently marked $0{\cdot}75\,m^2$ understorey plots (Allen & McLennan, 1983). In each understorey plot 40 top point-intercept counts were made at fixed distances along eight equally spaced radii from the understorey plot centre. The species of woody plants, non-woody plants, and ferns, and bare ground/litter, or moss/lichens were recorded.

The two treeferns > 2 m tall nearest to each understorey plot were tagged. Seedlings on their trunks were measured as in the understorey plots (treefern plots). If two treeferns were not present one or none was sampled. Plant heights were taken as their length from the surface of the treefern trunk.

RESULTS

Natural regeneration patterns—Bench Island

Understorey cover 1979–1985

The amount of bare ground/litter increased in all plots from 40% in 1979 to 54% in 1985. This was balanced by a decline in treefern cover from 54 to 40%, indicating that *Dicksonia squarrosa* which had established in canopy gaps and in areas of dieback in the 1970s was now collapsing. Understorey cover of woody and non-woody vegetation and lichen/moss remained at $<5\%$ during this period.

Regeneration on the forest floor 1979–1985

All quadrats contained a total of 20–30 species in both years. The number of species in the browse tier was high (10–15 spp.) in 1979 and remained high in 1985 (12–15 spp.).

Many shrub hardwoods highly preferred by deer were abundant as tall seedlings and saplings, e.g. *Pseudopanax simplex*, *Coprosma foetidissima*, and *Pseudopanax colensoi* (Table 2). The only seedlings and saplings of main canopy trees were those of *Weinmannia racemosa*, which were present in only three quadrats. The number of tall seedlings of most species generally increased from 1979 to 1985 although these increases were not statistically significant. There were slight increases in the numbers of saplings of most species. Some species not present as seedlings in 1979 appeared in some plots by 1985, e.g. *Griselinia littoralis*, *Pseudopanax crassifolius*, and *Coprosma lucida*.

Regeneration on treefern trunks 1979–1985

The number of seedlings on treefern trunks remained similar or increased slightly between 1979 and 1985 (Table 2). Saplings were rare on treefern

TABLE 2
Numbers of Tall Seedlings on Treefern Trunks and Mean Number of Tall Seedlings and Saplings (±SE) on the Forest Floor per Quadrat (0·04 ha) on Bench Island in 1979 and 1985

Species[a]	Understorey plots						Treefern plots	
	Seedlings			*Saplings*			*Seedlings*	
	n^b	*1979*	*1985*	n^b	*1979*	*1985*	*1979*	*1985*
Griselinia littoralis				3	1·3 (1·3)	5·7 (1·9)	6·2[c]	5·5
Myrsine australis				5	0·4 (0·2)	1·2 (0·5)	6·9	6·7
Pseudopanax colensoi				3	1·7 (1·7)	6·3 (4·4)	3·6	6·4
Pseudopanax crassifolius				4	3·5 (2·9)	4·8 (2·8)	2·6	2·9
Coprosma foetidissima	3	22·2 (38·4)	28·9 (7·3)	5	15·8 (12·1)	16·2 (10·5)	2·6	3·5
Coprosma lucida				3	4·3 (2·9)	—	2·0	2·0
Weinmannia racemosa							3·3	5·2
Pseudopanax simplex	4	44·4 (37·3)	95·5 (44·8)	5	18·4 (11·9)	16·4 (9·4)	4·2	4·4
Senecio reinoldii				4	1·5 (0·9)	3·0 (1·2)	—	—
No. treefern plots per quadrat				5	35·4 (5·5)	29·8 (4·1)		

[a] Only species with seedlings or saplings on the forest floor that occurred in ≥3 quadrats in either year were included.
[b] *n* is number of quadrats that contained seedlings or saplings of each species in either 1979 or 1985.
[c] Estimates based on the mean no. seedlings per treefern × mean no. treeferns > 2 m tall per quadrat.

trunks in both years. Many treeferns had collapsed by 1985, and the seedlings and saplings present on their trunks were re-establishing on the forest floor.

Seedlings of some species were more abundant on treefern trunks than on the forest floor, e.g. *Myrsine australis, Griselinia littoralis,* and *Pseudopanax crassifolius.*

Treefern population dynamics

The number of treeferns per quadrat declined from about 200 to 130 from 1979 to 1985, and all height classes were affected (also see Table 2). The proportion of treeferns in the 0·3–2 m height class declined by about 5% and this was compensated for by a similar increase in the 2–5 m class. These patterns reflect the death of treeferns that had proliferated after canopy collapse in the 1970s.

Responses to the exclusion of deer—exclosures on Stewart Island

Understorey cover 1979–1985

When deer were excluded, the amount of bare ground/litter declined in all vegetation types, coinciding in each with a marked increase in fern cover (primarily *Dicksonia squarrosa*, Table 3). The cover of woody species did not change significantly in vegetation types where the canopy had been severely depleted by dieback, e.g. total dieback-grassland and sedgeland, or under intact forest canopies of types such as tall forest-*Blechnum* fernland. Woody species cover increased only where partial canopy breakdown had occurred, such as in the partial rata-kamahi dieback type and often was in the form of dense thickets of *Senecio reinoldii*.

The cover of non-woody species was higher (> 40%) in coastal types than inland types, and generally declined from 1979 to 1985 (Table 3). Lichen/moss cover changed little over this period.

Regeneration on the forest floor 1979–1985

The mean number of species in the browse tier in exclosures increased significantly from six in 1979 to nearly 14 in 1985. The number of species in the browse tier doubled in open *Fuchsia* low forest (12 to 24) and almost trebled in dense short herbfield exclosures (5 to 14). Many species present only as seedlings ≤ 15 cm tall in 1979 had grown into the browse tier after the exclusion of deer.

Numbers of most tall woody seedlings (16–135 cm) and saplings were extremely low in 1979, and highly preferred species such as *Griselinia littoralis* were not represented (Table 4). Numbers of seedlings and saplings in exclosures increased markedly from 1979 to 1985, especially those of *Pseudopanax simplex*, *Coprosma foetidissima*, *C. areolata*, and *Senecio reinoldii*. Seedlings of some deer-preferred species absent in 1979 were present in 1985 (e.g. *Griselinia littoralis*), and saplings of several species (e.g. *Carpodetus serratus* and *Senecio reinoldii*) were recorded for the first time (Table 4).

Different species showed increases in exclosures in different vegetation types. *Pseudopanax simplex*, although present in the overstorey of most forest types, was virtually absent in the understorey in 1979 (Fig. 2), but appeared or increased in the understoreys of tall forest types by 1985, as did *Weinmannia racemosa* (not illustrated). Most of the increase in *Coprosma*

TABLE 3

Mean Percent Frequency of Understorey Cover Categories in 1979 and 1985 for Exclosures and Non-Exclosed Quadrats in the Seven Major Vegetation Types, and in Muttonbird Scrubland for Non-Exclosed Quadrats

		Vegetation type[a]							
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Exclosures									
Bare ground/litter	1979	45	80	64	77	36	40	20	na[b]
	1985	34	50	40	27*	12	21*	16	na
Woody species	1979	2	6	10	8	4	9	1	na
	1985	3	6	25	34*	16	18	2	na
Non-woody species	1979	+[c]	2	6	5	40	45	63	na
	1985	—	+	2	1	27	40	35	na
Fern	1979	45	8	6	4	18	5	16	na
	1985	54	36	20*	33*	44	20	47	na
Lichen/moss	1979	8	4	14	6	2	1	+	na
	1985	9	6	13	+*	1	+	+	na
Non-exclosed quadrats									
Bare ground/litter	1979	37	76	61	79	39	43	20	48
	1985	37	51	53	40*	30	34	18	21
Woody species	1979	5	6	11	7	6	8	3	12
	1985	4	12*	12	32*	4	5	5	36
Non-woody species	1979	+	2	4	4	32	42	64	36
	1985	+	3	3	+*	30	47	55	29
Fern	1979	47	8	7	6	21	4	13	4
	1985	49	27	12	27*	33	11	22	14
Lichen/moss	1979	11	7	18	3	2	3	+	+
	1985	10	7	20	+	3	2	+	+

[a] Vegetation types are: 1, Tall forest-*Blechnum* fernland; 2, Open canopy-depleted treefern thicket; 3, Canopy gap-*Cyathodes* shrubland; 4, Partial rata-kamahi dieback forest; 5, Open *Fuchsia* low forest; 6, Dense short herbfield; 7, Total dieback-grassland and sedgeland; 8, Open muttonbird scrubland.

[b] na = not available.

[c] + = <1%.

* = significant difference between years at $P < 0{\cdot}05$ according to a t-test.

foetidissima also occurred under open canopies of tall vegetation types, but it also increased markedly in partial rata-kamahi dieback forest (Fig. 2). *Dicksonia squarrosa* showed a similar pattern (not illustrated), but also appeared in dense short herbfield. Many *Dicksonia squarrosa* measured in 1979 were browsed sprouts, and the increased numbers in 1985 were probably the result of suckering from adventitious rhizomes after the removal of browsing pressure. *Senecio reinoldii* was uncommon in 1979 but

TABLE 4
Mean Number of Tall Seedlings and Saplings per Quadrat (0·04 ha) in the Exclosures and Non-exclosed Quadrats

Species[a]	Exclosures				Non-exclosed Quadrats			
	n^b	*1979*	*1985*	P <	n^b	*1979*	*1985*	P <
Seedlings (16–135 cm)								
Highly preferred species[d]								
Griselinia littoralis	7	—	75·5	0·05[c]		—	—	
Carpodetus serratus	8	8·9	62·2	NS	5	—	26·6	
Coprosma foetidissima	15	28·9	752·6	0·001	26	11·1	301·9	0·001
Moderately preferred species								
Weinmannia racemosa	7	2·2	51·1	0·05	5	—	66·6	
Pseudopanax simplex	6	6·7	306·4	0·05	7	6·7	28·9	0·05
Coprosma areolata	8	17·8	543·9	NS	17	31·1	102·1	0·05
Senecio reinoldii	10	113·2	435·1	NS	18	33·3	1 332	0·001
Least preferred species								
Podocarpus ferrugineus	4	—	22·2		11	17·8	77·7	0·05
Myrsine divaricata		—	—		5	40·0	97·7	
Leptospermum scoparium		—	—		5	177·6	71·1	
Cyathodes juniperina	3	133·2	199·8		8	173·2	217·6	NS
Dracophyllum longifolium	3	6·7	237·5		15	4·4	250·9	0·001
Saplings								
Highly preferred species								
Coprosma foetidissima	6	2·0	66·3	NS	16	1·9	1·3	NS
Moderately preferred species								
Weinmannia racemosa	4	5·8	5·5		11	1·3	0·8	NS
Senecio reinoldii	8	—	552·3	0·01	14	0·2	251·6	0·001
Least preferred species								
Cyathodes juniperina	2	1·0	9·0		7	29·3	36·7	NS
Dracophyllum longifolium	1	1·0	8·0		7	5·3	11·3	NS
Podocarpus hallii	1	1·0	—		5	1·8	1·6	

[a] Only species with seedlings or saplings that occurred in ≥ 5 quadrats in either treatment or year were included.
[b] n is number of quadrats that contained seedlings or saplings of each species in either 1979 or 1985.
[c] Differences between years were subjected to a Wilcoxon signed-ranks test for $n \geq 6$ quadrats.
[d] Browse preference categories based on browse records and Nugent & Challies (1988).
NS = not significant.

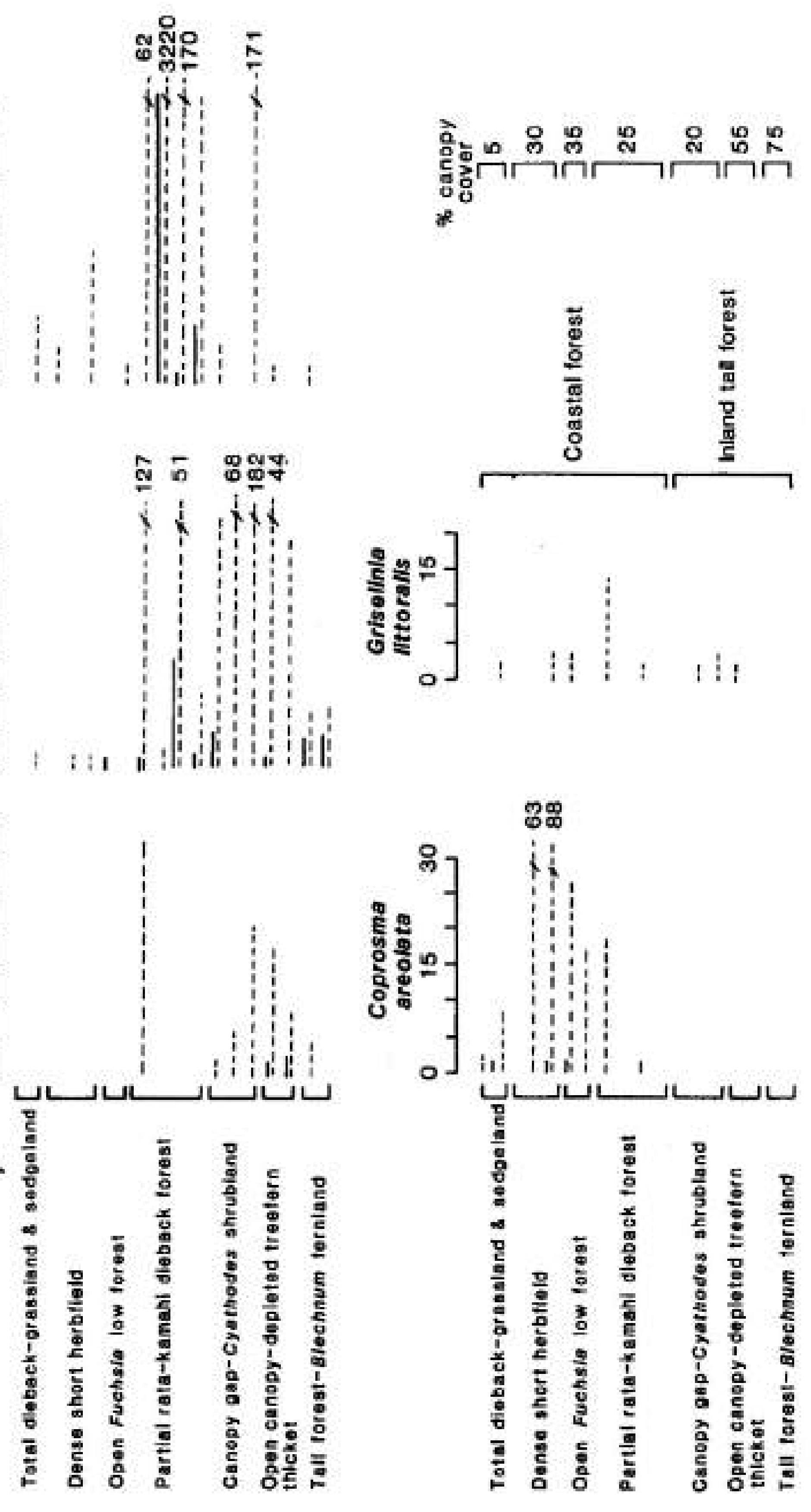

Fig. 2. Numbers of tall seedlings (16–135 cm) and saplings in exclosures in different forest types on Stewart Island in 1979 (——) and 1985 (- - -).

occurred in almost all types in 1985, with the greatest increases being in types affected by partial canopy dieback (Fig. 2). *Coprosma areolata* was almost absent in 1979 but increased significantly in types affected by almost total dieback by 1985 (Fig. 2). *Griselinia littoralis*, absent in all quadrats in 1979, had established in almost all vegetation types by 1985, reflecting the removal of browsing pressure.

Numbers of seedlings and saplings of the least preferred species *Cyathodes juniperina* changed little, but those of another, *Dracophyllum longifolium*, increased markedly in some types with open canopies or partial dieback.

Regeneration on treefern trunks 1979–1985

Seedlings 16–135 cm tall on treefern trunks generally occurred above the browse zone of deer in 1979 and were often as common as on the forest floor (Tables 4 and 5). Some deer-preferred species that were rare or absent on the forest floor in 1979, e.g. *Pseudopanax simplex*, *Griselinia littoralis* and *Myrsine australis* seedlings and *P. simplex* and *G. littoralis* saplings, were present on treefern trunks (Tables 4 and 5).

Frequency of small seedlings and numbers of tall seedlings on treefern trunks changed little from 1979 to 1985 for some species, e.g. *Coprosma foetidissima* (Table 5). Seedlings of others, such as *P. simplex* declined. This decline is related to the 13% decline in the number of treefern substrates over the 6-year period (Table 5). Although treeferns declined, the more open conditions appear to have favoured establishment of *Weinmannia racemosa* seedlings, which increased in tall forest-*Blechnum* fernland and canopy gap-*Cyathodes* shrubland exclosures.

Treefern population dynamics

The number of treeferns in exclosures in all vegetation types increased about 135% from 1979 to 1985 (Table 6), but proportions in different height classes changed. In 1979 most were 2–5 m tall, but by 1985 most were in the 0·3–2 m height class, reflecting the proliferation of suckers after the removal of browsing and trampling pressure. The number of treeferns 2–5 m declined markedly from 1979 to 1985, and many had collapsed and died (also see Table 5). The largest increases in numbers of treeferns occurred under depleted canopies.

The effects of deer browsing—non-exclosed quadrats on Stewart Island

Understorey cover 1979–1985

Although the amount of bare ground/litter declined in all vegetation types in response to reduced deer numbers after the 1981 poisoning (Table 3), in

TABLE 5

Estimated Number of Tall Seedlings (16–135 cm) per Quadrat (0·04 ha) on Treefern Trunks in Exclosures and Non-exclosed Quadrats on Stewart Island

Seedlings[a]		*Exclosures*			*Non-exclosed quadrats*		
		Tall forest- Blechnum *fernland*	*Canopy gap-* Cyathodes *shrubland*	*Open canopy-depleted tree fern thicket*	*Tall forest-* Blechnum *fernland*	*Canopy gap-* Cyathodes *shrubland*	*Open canopy-depleted tree fern thicket*
Highly preferred species							
Griselinia littoralis	1979	—	11·0[b]	—	6·3	5·6	3·9
	1985	1·0	10·2	—	4·9	5·1	2·9
Myrsine australis	1979	1·7	2·5	5·7	2·0	2·0	3·9
	1985	—	1·3	6·6	1·2	1·4	2·9
Coprosma foetidissima	1979	4·3	28·5	4·1	5·6	22·3	4·2
	1985	5·9	26·0	4·2	3·4	23·4	5·1
Moderately preferred species							
Weinmannia racemosa	1979	3·8	10·0	26·0	13·5	19·2	1·3
	1985	18·6	17·9	14·1	10·1	20·7	—
Pseudopanax simplex	1979	2·6	8·5	8·1	5·6	7·6	1·0
	1985	1·0	7·7	4·2	4·7	8·7	1·1
No. treefern	1979	48	98	72	156	318	130
plots	1985	45	86	59	143	278	103

[a] Only vegetation types with > 1 seedling per quadrat in either treatment or year were included.

[b] Estimates based on the mean no. seedlings per treefern for each vegetation type × mean no. treeferns > 2 m tall per quadrat.

TABLE 6
Mean Number of Treeferns per Quadrat (0·04 ha) in Exclosures and Non-exclosed Quadrats by Vegetation Type and by Height Class

Vegetation type	Exclosures				Non-exclosed quadrats			
	n^a	*1979*	*1985*	P<	n^a	*1979*	*1985*	P<
Tall forest-*Blechnum* fernland	2	44·5	59·5		5	43·8	47·8	
Open canopy-depleted treefern thicket	2	80·5	114·0		4	48·3	65·0	
Canopy gap-*Cyathodes* shrubland	3	39·3	79·7		9	64·9	74·8	NS[b]
Partial rata-kamahi dieback forest	4	15·3	100·3		8	17·6	65·5	0·05
Open *Fuchsia* low forest	2	5·5	46·5		4	6·5	7·0	
Dense short herbfield	3	6·3	25·7		5	8·2	8·4	
Total dieback-grassland and sedgeland	1	1·0	7·0		4	2·5	15·8	
All types	17	29·3	68·8	0·01	39	31·2	46·7	0·01
Treefern height classes (all quadrats)								
0·3–2 m	14	7·4	63·0	0·01	34	4·7	28·8	0·001
2–5 m	17	21·9	14·5	0·01	39	23·7	19·7	0·001
>5 m	12	1·8	3·4	NS	26	4·3	2·2	NS

[a] *n* is number of quadrats that contained treeferns in either 1979 or 1985.
[b] Differences between years were subjected to a Wilcoxon signed-ranks test for vegetation types with ≥6 quadrats.
NS = not significant.

general, the decrease was not as great as that in response to total removal of deer by the exclosures. The cover of woody species remained similar in all vegetation types, except in open-canopied types such as open canopy-depleted treefern thicket and partial rata-kamahi dieback forest, where it increased significantly. The lack of an increase in woody species cover in exposed open-canopied coastal forest types such as open *Fuchsia* low forest and dense short herbfield contrasts sharply with the response in exclosures in these types.

The cover of non-woody species was similar in most types from 1979 to 1985, although the species composition changed in many plots (Table 3).

Regeneration on the forest floor 1979–1985

As in the exclosures, the mean number of species in the browse tier increased significantly, from about eight in 1979 to over 10 in 1985, but these numbers were generally lower than in the exclosures. Although many species entered the browse tier after the initial reduction in deer numbers, increased browsing pressure by 1985 resulted in their subsequent removal. Also, much of the increase in species richness in the browse tier could be attributed to natural regeneration after canopy breakdown, e.g. species of low preference as deer food such as *Dracophyllum longifolium* that were rare or absent in the browse tier in 1979 had established in many quadrats by 1985 (Table 4).

Seedlings and saplings of many woody species were rare or absent in all non-exclosed quadrats in 1979 (Table 4). By 1985, tall seedlings of some species had increased, but not as markedly as in the exclosures. Seedlings of highly preferred species that had appeared in the exclosures (e.g. *Griselinia littoralis* and *Coprosma lucida*) were still rare or absent. There were very few seedlings and saplings of preferred subcanopy hardwoods such as *Pseudopanax simplex* and *Carpodetus serratus*. Even though some seedlings were establishing they were being impeded from further height growth by browsing.

Seedling regeneration patterns for the different species were related to vegetation type, as described for the exclosures. *Weinmannia racemosa* and *Pseudopanax simplex* changed little in tall forest types, where they were the most abundant. Numbers of *Coprosma foetidissima* seedlings increased primarily in tall forest types. *Dicksonia squarrosa* also increased in these types, but not as much as in the exclosures.

As in the exclosures, *Senecio reinoldii* increased the most in partial rata-kamahi dieback forest, but the two non-exclosed quadrats in muttonbird scrubland also showed large increases in seedlings and saplings. Similarly, *Coprosma areolata* increased in the same types as for the exclosures (i.e. open *Fuchsia* low forest and dense short herbfield). In contrast to the exclosures, however, several highly preferred deer food species did not respond in non-exclosed quadrats in any type, e.g. *Carpodetus serratus* and *Griselinia littoralis*. Non-preferred *Dracophyllum longifolium* increased in canopy gap-*Cyathodes* shrubland, partial rata-kamahi dieback forest, and muttonbird scrubland. Other species of low preference such as *Cyathodes juniperina*, *Podocarpus ferrugineus*, and *Myrsine divaricata* increased slightly in the one type in which they primarily occurred, canopy gap-*Cyathodes* shrubland.

Regeneration on treefern trunks 1979–1985

As in the exclosures, numerous woody seedlings and saplings were present on treefern trunks in 1979 (Table 5). By 1985, the numbers of seedlings and saplings of species such as *Pseudopanax simplex* and *Coprosma foetidissima* on treefern trunks had changed little, although *Griselinia littoralis* and *Myrsine australis* seedlings had declined and saplings of these two species had all but disappeared. In contrast to the exclosures, the numbers of *Weinmannia racemosa* seedlings did not increase markedly in any vegetation type.

The number of treefern plots had declined by about 13%, a similar rate of decline to that in the exclosures. It is likely that as the treeferns continue to collapse, the seedlings and saplings rooted on their trunks will be browsed by deer.

Treefern population dynamics

The number of treeferns in all vegetation types increased by about 50% from 1979 to 1985, a lesser increase than in the exclosures (Table 6). Changes in the proportions of treeferns in different height classes were similar to those in the exclosures (also see Table 5), but fewer entered the 0·3–2 m tier because of increasing browsing and trampling pressure after the initial poisoning operation.

Changes in deer diet 1979–1985

The intensity of browsing in Chew Tobacco Bay and Port Adventure in 1985 was as great as, or greater than, in 1979 (Table 7). This reflects the resurgence

TABLE 7

Changes in the Feeding Patterns of Deer between 1979 and 1985 in Chew Tobacco Bay and Port Adventure

Species[a]	*Chew Tobacco Bay*		*Port Adventure*	
	1979 ($n = 31$)	*1985* ($n = 24$)	*1979* ($n = 30$)	*1985* ($n = 22$)
Dicksonia squarrosa	22[b]	27	30	19
Griselinia littoralis	10	10	21	—
Coprosma foetidissima	11	15	—	11
Coprosma areolata	—	12	—	11
Fuchsia excorticata	—	—	—	13
Senecio reinoldii[c]	2	3	2	3
Mean Browse Index[d] (MBI)	7·5	6·5	5·5	8·7

[a] Only species represented in > 10% diet in any 1 year were included.
[b] The apparent composition of the diet, as determined from browse indices, is given as percentages.
[c] Included for comparison.
[d] Calculated after Rose & Burrows (1985).

in deer numbers and browsing pressure since the poisoning in early 1981 initially reduced the influence of deer (New Zealand Forest Service, 1984).

Dicksonia squarrosa was a feature of deer diet in both years, and several species not browsed in 1979 (e.g. *Coprosma areolata* and *Fuchsia excorticata*) were browsed in 1985. In contrast, some species such as *Senecio reinoldii* were rarely browsed. Many of the browse records for the species listed in Table 7 (except *Senecio reinoldii*) were for epicormic sprouts or adventitious suckers (*Dicksonia squarrosa*) that proliferated after the removal of deer in 1981.

DISCUSSION

The natural regeneration patterns that occur in the absence of deer browsing (Bench Island) show that treeferns and seedlings of subcanopy shrub hardwoods colonise treefall gaps and coastal areas that have suffered canopy dieback. As treeferns collapse and die, seedlings of subcanopy hardwoods that had rooted on treefern stems also establish on the forest floor. Under the influence of deer browsing on Stewart Island, however, this regeneration pattern is disrupted. In treefall gaps and dieback areas deer rapidly remove small seedlings on the forest floor as they grow into the browse zone. They also reduce woody seedling regeneration by impeding the establishment of treeferns. The continued death of treeferns caused by opening up of the forest by deer browsing and trampling will eventually remove most of the remaining safe sites for seedling establishment.

The largest increases in treeferns and woody seedlings and saplings on Stewart Island occurred in treefall gaps or where the forest canopy had partially collapsed after dieback. These vegetation types were partial rata-kamahi dieback forest, open canopy-depleted treefern thicket, and canopy gap-*Cyathodes* shrubland. These vegetation types also appear to be preferred habitat for white-tailed deer. After deer exclusion many seedlings in these areas were of deer-preferred species such as *Griselinia littoralis*, *Weinmannia racemosa*, *Pseudopanax simplex*, and *Coprosma foetidissima*. In contrast, lesser increases in treeferns and woody seedlings occurred on non-exclosed quadrats in these areas, and many were of non-preferred species such as *Dracophyllum longifolium* and *Cyathodes juniperina*. Highly preferred food species such as *Griselinia littoralis*, *Pseudopanax crassifolius*, and *Myrsine australis* were rare or absent.

As preferred food plants have become rare in the understorey, white-tailed deer have changed their feeding patterns. Cockayne (1909*b*) noted the abundance of deer-preferred subcanopy hardwoods, shrubs, herbs and ferns in the understorey a few years after deer liberation, and Traill (1965) recorded their gradual removal from early this century to the present day. In a recent diet study, Nugent & Challies (1988) found that white-tailed deer obtained *c.* 60% of their food from scavenging fallen leaves and fruit and that browsing of seedlings or epicormics in the understorey now constituted only *c.* 40% of diet.

On Stewart and Bench Islands, the dominant main canopy tree species, *Metrosideros umbellata* and *Weinmannia racemosa*, regenerate intermittently in treefall gaps or after large-scale blowdown (Veblen & Stewart, 1980). *Metrosideros umbellata* also frequently regenerates vegetatively by layering (Cockayne, 1909*a*; Veblen & Stewart, 1980). Thus, a lack of saplings and small stems of *Metrosideros* on Stewart Island does not necessarily mean that its regeneration is endangered. The impact of deer browsing on *Weinmannia* regeneration is less clear. Seedlings of *Weinmannia* were present in the non-exclosed quadrats in 1985 and saplings were present in areas inaccessible to deer such as *Senecio reinoldii/Rubus* thickets in the dieback zone (Stewart, G. H. & Burrows, L. E., unpublished). Some regeneration of *Weinmannia* therefore appears likely even under continued browsing pressure. Because deer have removed dense competing understoreys on Stewart Island, regeneration of *Weinmannia* is now more likely if deer numbers were to be reduced. Tall seedlings of *Weinmannia racemosa* were already abundant in the exclosures after 6 years of deer exclusion.

The general food preference of white-tailed deer for subcanopy hardwoods (this study; Nugent & Challies, 1988) is similar to that of other deer species and goats elsewhere in New Zealand (Veblen & Stewart, 1982; Wardle, 1984). In the initial stages of colonisation red deer *Cervus elaphus scoticus* Lonnberg preferentially browse hardwoods such as *Griselinia littoralis*, *Fuchsia excorticata*, *Carpodetus serratus*, *Coprosma lucida*, *Pseudopanax colensoi* and *P. simplex* (Johnson, 1972; Mark & Baylis, 1975; Wardle, 1984). Many of these species frequently occur in seral communities on soils of high nutrient status (Wardle, 1984; Rose & Burrows, 1985; Stewart & Harrison, 1987) or in areas of broken forest canopy such as treefall gaps (Stewart, 1986). For red deer these sites are preferred deer habitat (Stewart & Harrison, 1987; Nugent *et al.*, 1987; Stewart *et al.*, 1987).

Because many of the deer-preferred hardwoods form the canopy in some vegetation types on Stewart Island (e.g. *Carpodetus serratus*, *Myrsine australis*, and *Fuchsia excorticata* in dense short herbfield), the maintenance of a canopy in these types is endangered. As the adult canopy individuals of these hardwood tree species die, species richness will diminish because there are few seedlings and saplings to replace them, as predicted by Veblen & Stewart (1980). In many areas this will cause a change in the composition of the forests, with a shift to more browse-tolerant species or those less preferred by deer. Other areas now covered by forest may degrade to shrubland, grassland, or, as has already occurred in north-eastern Stewart Island, to dense fernland dominated by *Histiopteris incisa* or *Carex* sedgeland.

At present, woody seedlings ≤15 cm tall of most subcanopy and canopy tree species are abundant on the forest floor on Stewart Island. Although deer browsing prevents their height growth, as long as canopy individuals remain small seedlings will continue to be recruited. As canopy trees die and the available seed source declines the present deterioration in forest health will continue. Deer numbers would have to be reduced drastically and maintained at low levels to slow or arrest this trend.

ACKNOWLEDGEMENTS

Special thanks are due to John Wardle and Rob Allen for many aspects of the study and to Ron Tindal and his staff on Stewart Island for logistical support. Thanks are also extended to numerous staff of the Forestry Research Centre for field assistance, to Drs Peter Wardle and Hugh Wilson for comments on the manuscript, and to Joanna Orwin for valuable editorial comments. This study was partially funded by the New Zealand Department of Conservation.

REFERENCES

Allen, R. B. & McLennan, M. J. (1983). Indigenous forest survey manual: two inventory methods. New Zealand Forest Service, *FRI Bull.*, **48**.

Bull, P. C. & Whittaker, A. H. (1975). The amphibians, reptiles, birds, and mammals. In *Biogeography and Ecology of New Zealand*, ed. G. Kuschel & W. Junk, The Hague, pp. 231–76.

Campbell, D. J. & Rudge, M. R. (1984). Vegetation changes induced over 10 years by goats and pigs at Port Ross, Auckland Islands (Subantarctic). *N.Z. J. Ecol.*, **7**, 103–18.

Cockayne, L. (1909*a*). The ecological botany of the subantarctic islands of New Zealand. In *Subantarctic Islands of New Zealand, Vol. 1*, ed. C. Chilton. Philosophical Institute of Canterbury, Wellington, pp. 182–235.

Cockayne, L. (1909*b*). *Report on a Botanical Survey of Stewart Island.* Department of Lands, Government Printer, Wellington.

Harris, L. H. (1981). White-tailed deer in New Zealand. Supplement to *New Zealand Wildlife*, **8**, Issue 63.

Johnson, P. N. (1972). Applied ecological studies of shoreline vegetation at Lakes Manapouri and Te Anau, Fiordland, Part 1. Vegetation of Lake Manapouri shoreline. *Proc. N.Z. Ecol. Soc.*, **19**, 102–19.

Mark, A. F. & Baylis, G. T. S. (1975). Impact of deer on Secretary Island, Fiordland, New Zealand. *Proc. N.Z. Ecol. Soc.*, **22**, 19–24.

New Zealand Forest Service (1984). Deer control and vegetation response on Stewart Island. *What's New in Forest Research*, **126**. Forest Research Institute, Rotorua, New Zealand.

Nugent, G. & Challies, C. N. (1988). Diet and food preferences of white-tailed deer in north-eastern Stewart Island. *N.Z. J. Ecol.*, **11**, 61–71.

Nugent, G., Parkes, J. P. & Tustin, K. G. (1987). Changes in the density and distribution of red deer and wapiti in northern Fiordland. *N.Z. J. Ecol.*, **10**, 11–21.

Purey-Cust, J. R. & McClymont, R. B. (1979). *Stewart Island: Land Management Study*. New Zealand Forest Service and Department of Lands and Survey, Wellington, New Zealand.

Rose, A. B. & Burrows. L. E. (1985). The impact of ungulates on the vegetation. In *Report on a Survey of the Proposed Wapiti Area, West Nelson*, ed. M. R. Davis & J. Orwin, New Zealand Forest Service, *FRI Bull.*, **84**, 210–34.

Stewart, G. H. (1986). Forest dynamics and disturbance in a beech/hardwood forest, Fiordland, New Zealand. *Vegetatio*, **68**, 115–26.

Stewart, G. H. & Harrison, J. B. J. (1987). Physical influences on forest types and deer habitat, northern Fiordland, New Zealand. *N.Z. J. Ecol.*, **10**, 1–10.

Stewart, G. H., Wardle, J. A. & Burrows, L. E. (1987). Forest understorey changes after reduction in deer numbers, northern Fiordland, New Zealand. *N.Z. J. Ecol.*, **10**, 35–42.

Traill, R. (1965). Notes on Stewart Island by Mr R. Traill, 1959. *Protection Forestry Newsletter*, **3**, 2–4.

Veblen, T. T. & Stewart, G. H. (1980). Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. *N.Z. J. Ecol.*, **3**, 50–68.

Veblen, T. T. & Stewart, G. H. (1982). The effects of introduced wild animals on New Zealand forests. *Ann. Assoc. Amer. Geog.*, **72**, 372–97.

Wardle, J. A. (1984). *The New Zealand Beeches—Ecology Utilization and Management*. New Zealand Forest Service, Caxton Press, Christchurch, New Zealand.

Wardle, J., Hayward, J. & Herbert, J. (1971). Forests and scrublands of northern Fiordland. *N.Z. J. For. Sci.*, **1**, 80–115.

Wilson, H. D. (1987). Vegetation of Stewart Island (New Zealand). Supplement to *N.Z. J. Bot.*, 1987, 1–131.

Wodzicki, K. & Wright, S. (1984). Introduced birds and mammals in New Zealand and their effect on the environment. *Tuatara*, **27**, 77–104.

ASSESSMENT OF ANIMAL EFFECTS

ON FOREST REGENERATION

IN STEWART ISLAND

FGE 4.2.1.1
FGE 4.2.2.2
FGE 4.2.1.3
FGE 4.2.1.4

G.H. Stewart and L.E. Burrows

Forest and Grassland Ecology Section
Forestry Research Centre
Forest Research Institute
P.O. Box 31-011, Christchurch

PREPARED FOR:
Director, Science and Research
Conservation Sciences Centre
Department of Conservation

DATE: March 1988

Note: This appears to be full paper
Deer section only
printed & attached

CONTENTS

PAGE

1. OVERVIEW SUMMARY 3

2. COMPARISON OF FOREST STRUCTURE AND REGENERATION ON BENCH AND STEWART ISLANDS (Project 4.2.1.1) 5
   - 2.1 Summary 5
   - 2.2 Background 6
   - 2.3 Objectives 6
   - 2.4 Methods 6
   - 2.5 Results 6
     - 2.5.1 Forest structure 6
     - 2.5.2 Forest regeneration 6
     - 2.5.3 Regeneration after disturbance 7
   - 2.6 Conclusions 7

3. THE INFLUENCE OF DEER ON REGENERATION PATTERNS (Project 4.2.1.2) 8
   - 3.1 Summary 8
   - 3.2 Background 9
   - 3.3 Objective 9
   - 3.4 Methods 9
     - 3.4.1 Study area 9
     - 3.4.2 Plot location 9
     - 3.4.3 Plot methodology 10
   - 3.5 Results 11
     - 3.5.1 Natural regeneration patterns - Bench Island 11
     - 3.5.2 Responses to the exclusion of deer - exclosures 12
     - 3.5.3 The effects of deer browsing - permanent quadrats 14
     - 3.5.4 Changes in deer diet 1979-1985 14
   - 3.6 Conclusions 15
   - 3.7 Recommendations 15

4. BRUSH-TAILED POSSUM EXCLOSURE PLOTS (Project 4.2.1.3) 17
   - 4.1 Summary 17
   - 4.2 Background 18
   - 4.3 Objectives 18
   - 4.4 Methods 18
   - 4.5 Results 18
   - 4.6 Conclusions 20
   - 4.7 Recommendation 20

5. ECOTONE TRANSECTS (Project 4.2.1.4) 21
   - 5.1 Summary 21
   - 5.2 Background 22
   - 5.3 Objectives 22
   - 5.4 Methods 22
     - 5.4.1 Transect location 22
     - 5.4.2 Transect methodology 22

5.4.3 Crown condition on permanent quadrats 23
5.5 **Results** 23
5.5.1 Changes in crown condition 1982-1985 23
5.5.2 Changes in crown condition on permanent quadrats 1979-1985 23
5.5.3 Tree mortality 1982-1985 24
5.5.4 Recruitment of new saplings 1982-1985 24
5.6 **Conclusions** 25
5.7 **Recommendation** 25

6. **ACKNOWLEDGEMENTS** 26

7. **REFERENCES** 26

8. **APPENDICES** 27