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DIET AND FOOD PREFERENCES OF WHITE-TAILED DEER IN NORTH-EASTERN STEWART ISLAND

Summary: The diet and food preferences of white-tailed deer *(Odocoileus virginianus)* on north-eastern Stewart Island are described from the analysis of 160 samples of rumen contents collected between 1979 and 1985, and vegetation surveys in 1975 and 1976. Deer browsed all the hardwood trees, but few shrubs, ferns, or podocarps. Woody plants comprised 85.1 % (dry weight) of annual diet. Broadleaf *(Griselinia littoralis;* 34.6%) and supplejack *(Ripogonum scandens;* 18.6%) were the most important foods, all other species comprising less than 5%. There were no differences in diet between the sexes and only small differences between areas. Fawns, however, ate more supplejack fruit and less shrubs, ferns, herbs, and grasses than older deer. All deer ate more supplejack fruit and foliage of subcanopy trees, and less broadleaf, shrubs, and ferns in winter than in other seasons. Food appeared scarcest in summer. Deer probably obtained most of their food as fallen leaves and fruit; this is discussed in the context of the long term trends in forest structure and deer carrying capacity that follow deer colonisation. We believe the main hardwood food trees will gradually die out, resulting in a substantial decline in the carrying capacity of the forest.

Keywords: White-tailed deer; Odocoileus virginianus; diets; feeding habits; food preference; Griselinia littoralis; Ripogonum scandens; Stewart Island.

Introduction

The diet of white-tailed deer *(Odocoileus virginianus)* was studied during a Forestry Research Centre (FRC) investigation of periodic dieback in the coastal forests of Stewart Island. Other studies included the impact of deer and brushtail possums *(Trichosurus vulpecula)* on the structure of the coastal forests (Veblen and Stewart, 1980) and forest regeneration when deer and possum densities were artificially reduced (New Zealand Forest Service, 1984).

The object of this study was to quantify deer diet according to season, area, age, and sex, and their food preferences. The rumen contents of shot deer were analysed, and forest plot data collected by the New Zealand Forest Service (NZFS) in 1975 and 1976 were reassessed~ The diet of deer on Stewart Island has not been described previously, although main food plants have been inferred from vegetation surveys (M.J. Williamson, unpubl.; A.D. Ross, unpubl.; Veblen and Stewart, 1980). We assess the accuracy of those inferences and relate our results to the changes in browse patterns, carrying capacity, and forest structure noted during the colonisation of New Zealand forests by deer.

Status and Habitat of Deer

Nine white-tailed deer from New Hampshire, U.S.A. were liberated in 1905 at Port Pegasus, near the southern end of Stewart Island (Thomson, 1922). They thrived, and by the late 1920's white-tailed deer had spread throughout the island (Harris, 1981). Little is known of their early history, but it is likely numbers increased quickly then declined as the deer depleted preferred food plants. Although hunted throughout the year, too few deer were shot to keep numbers much below carrying capacity, and the herd was in poor physical condition during our study (C.N. Challies, unpubl.).

On Stewart Island white-tailed deer prefer the coastal forests; their density declines inland and with increasing altitude, and they make little use of forest above 250 m a.s.l. (Harris, 1981). Density also varies from place to place along the coast, presumably because of differences in habitat quality (C.N. Challies, unpubl.).

The coastal forests of north-eastern Stewart Island have a mixed podocarp-hardwood canopy consisting mainly of rimu *(Dacrydium cupressinum)* and miro *(Podocarpus ferrugineus),* which are often emergent, southern rata *(Metrosideros umbellata),* and kamahi *(Weinmannia racemosa)* (Wilson, 1982). Beneath the canopy is an extensive subcanopy of hardwood trees such as broadleaf *(Griselinia littoralis), Pseudopanax simplex, P. crassifolius,* marbleleaf *(Carpodetus serratus),* and *Coprosma lucida,* and the tree.fern *Dicksonia squarrosa.* These sometimes form the canopy on wet sites where the climber, supplejack *(Ripogonum scandens),* is also common. The ground and shrub tiers are sparse, with few young hardwood trees. The only unforested coastal areas are small patches of dune and swamp vegetation, and patches of forest dieback where the fern *Histiopteris incisa* and sedges such as *Carex solandri* are usually dominant.

Methods

Assessment of diet

Between 1979 and 1985, samples of rumen contents were taken from 160 white-tailed deer shot by NZFS staff and recreational hunters between Toitoi Bay on the east coast and Little Hellfire Beach in the west; 72 deer were shot in the main FRC study area, 57 in the remainder of the east coast and 25 were taken from the north coast (Fig. 1; the location of the remaining six was not recorded). Most of the deer were killed within 0.5 km of the coast, and probably all within 3 km. At least five rumen samples were obtained for each month of the year.

The deer shot were grouped according to area (Fig. 1), sex (84 males, 76 females), age, and season. Three age classes were recognised: fawn (0-12 months; n = 50); yearling (13-24 months; n = 24); and adult (over 24 months; n = 43). The age of 43 was not determined. Forty deer were shot in summer (December to February), 59 in autumn (March to May), 29 in winter (June to August), and 36 in spring (September to November).

Samples of rumen contents were preserved in 10% formalin. Sub samples of about 500 g were later washed over a sieve with a 5.6 mm mesh and the retained material was sorted macroscopically as described by Nugent (1983). Trials with 2.0, 4.0, 5.6, and 8.0 mm meshes showed that the 5.6 mm mesh was most efficient. Nearly all the leaf and fruit material retained by this sieve could be identified, and the results were similar to those from more complete and time consuming analyses with smaller meshes. The sorted material, including the unidentified component, was then oven-dried to constant weight and weighed to the nearest milligram.

The percentage of the rumens in which each food was present (the frequency of occurrence) indicates how often each food was eaten. Contingency tables were used to test whether the frequencies of occurrence differed between age, sex, area, or season. Where necessary, data for rarely eaten foods were pooled to attain the minimum sample sizes required for these tests.

The percentage dry weight (% DW) of foods in each rumen was averaged for each of the age, sex, area, and season groupings of deer, and used to describe how much of each food was eaten. Differences in % DWs between groups were tested by one-way analysis of variance. Despite the data often being non-normal (Kolgomorov-Smimov test, $P < 0.05$), they were within the guidelines given for this test by Harris (1975).

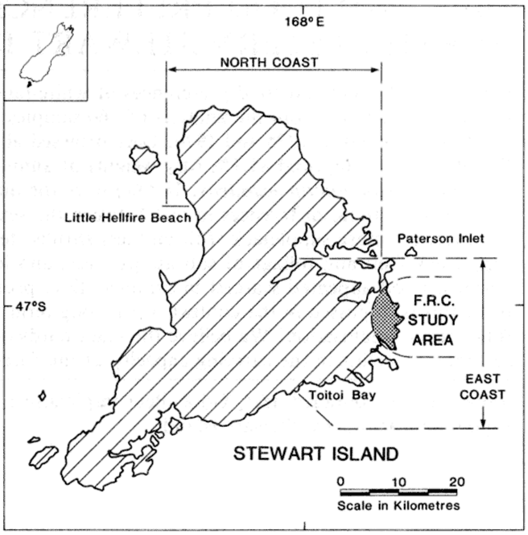

Figure 1: *Stewart Island showing the three areas from which deer were obtained. The Forestry Research Centre study area is treated separately from the remainder of the east coast because it was sampled more intensively.*

As more deer were shot in some seasons than in others, the annual diet was estimated by averaging the four seasonal estimates.

Assessment of food preferences

In the 1975 and 1976 NZFS surveys of Stewart Island, all vascular plant species present on 944 semi-randomly located reconnaissance plots were recorded, using Allen and McLennan's (1983) techniques. Data from the 321 plots within 3 km of the north and east coasts were reanalysed to obtain the frequency of occurrence of the 48 most common fern and woody species. To determine whether deer were selecting some plant species and avoiding others, the frequencies of occurrence on plots were compared with the frequencies of occurrence in the annual diet. Because the number of rumen samples collected in each season differed, the frequency of occurrence in the annual diet was obtained by averaging the four seasonal estimates, with the sample size adjusted to 116 (four times the smallest seasonal sample size of 29). A 48 x 2 contingency table was then used to test the null hypothesis that the ratio of occurrence in the diet to that in the forest was the same for all 48 species.

Presentation of results

The sampling error of estimates is presented as 95% confidence limits (95%CLs). Plant nomenclature follows Wilson (1982). Woody plants other than climbers are divided into shrubs, subcanopy, and canopy trees on the basis of stature (Wardle, 1984). The term shrub is used to describe those woody plants growing mainly in the browse tier (0-2 m); > 90% of the occurrences of each shrub species were confined to the browse tier on the 321 reanalysed vegetation plots.

Results

Annual diet

A total of 104 food items were identified to species (80) or genus (24) (0.9% DW of the sorted material could not be assigned to a major food category in Table 1 and was excluded from the analysis). The 31 species or genera comprising more than 0.1 % DW of the annual diet are listed in Table 1, the remainder in Appendix I.

Overall, woody plants comprised 85.1 % DW of annual diet (identified tree species 53.1 ±3.3% DW, climbers 19.0 ±3.4% DW, and shrubs 7.3 ±1.4% DW). Apart from the stems and fruit of supplejack, nearly all the identified woody plant material was foliage. The unidentified woody plant material, however, consisted mainly of debarked twigs. Microscopic examination of some of these indicated most were from *Coprosma* shrubs.

Only nine plant species comprised more than 1 % DW of the annual diet (5 trees, 1 shrub, 1 climber, and 2 ferns). Although, as categories, seaweeds, grasses, herbs, and fungi each made up more than 1% DW of diet, no species in these groups comprised more than 0.5% DW of the total.

Broadleaf and supplejack were the two most important foods, together making up 53.2 ±3.9% DW of annual diet. The supplejack consisted mainly of ripe fruit, with smaller amounts of leaf and the soft tips of young stems (11.3 ±3.4, 4.6 ±1.0, and 2.7 ±0.8% DW respectively). The broadleaf material in 22 samples (including some from each season) was re-sorted to determine how it had been obtained by deer. Three-quarters of the broadleaf in these samples consisted of wholly or partially yellowed mature leaves, with most of the remainder being mature green leaves (21.1 ±7.9, 6.1 ±4.1 % DW respectively). Very little (0.5 ±0.5% DW) was made up of small thin apical or seedling leaves. As the proportion of yellowed leaves in .the rumens far exceeded that on broadleaf trees, and fallen leaves are often green, most of the broadleaf foliage eaten probably consisted of cast leaves.

On average, there were 18 foods in each rumen (range 3-34) of which two or three usually formed 60-70% DW of the contents. The dominant food in each rumen comprised 44.8 ±2.6% DW (range 18.6-97.9). It was nearly always one of the overall 'main food plants, although other foods were occasionally eaten in quantity. Seaweed, for example, occurred in only 14 samples, but was dominant in two. Mosses, in comparison, were present in many samples but never comprised more than 1% DW of any sample, which suggests they were eaten accidentally.

Seasonal differences in diet

Deer appeared to eat each food with similar frequency throughout the year since the frequencies of occurrence of the 28 most commonly eaten food groups did not differ significantly between seasons. However the relative importance of some foods did vary seasonally (Table 2). The importance of the two main foods varied inversely, with broadleaf the most important food in autumn and supplejack in spring. Since supplejack fruit ripens mainly in autumn (Leathwick, 1984), its peak use in winter and spring indicates most of this food was also obtained after it had fallen to the ground.

There were two main patterns of seasonal change in the use of minor foods, and these appeared to be related to stature (Table 2). Vascular plants growing mainly in the browse tier (shrubs, ferns, herbs, and grasses) formed a higher proportion of diet in summer than in winter. In contrast, most of the minor tree species tended to predominate in winter, with the exception of fuchsia *(Fuchsia excorticata)* which is deciduous and so not available in winter (Table 2). These patterns were independent of the seasonal use of broadleaf and supplejack, as they did not disappear when the percentage dry weights were recalculated excluding these foods.

Differences in diet between ages and sexes of deer

The diets of males and females, and of fawns, yearlings, and adults were similar, except that fawns

Table 1: *The annual diet of white-tailed deer on north-eastern Stewart Island, showing the frequencies of occurrence and average percentage dry weight for nine major categories of foods (capitals) and for those species or groups of indistinguishable species comprising more that 0.1% DW of annual diets (italics).*

	Freq. Occ. (%) ± 95%CL		% Dry Weight ± 95%CL	
WOODY PLANTS		100.00 ± 0.7		85.1 ± 2.3
Canopy trees				
Weinmannia racemosa	94.6 ± 4.1		3.3 ± 0.7	
Metrosideros umbellata	58.4 ± 8.3		3.1 ± 1.1	
Podocarpus ferrugineus	30.6 ± 7.8		0.7 ± 0.4	
Subcanopy trees				
Griselinia littoralis	99.4 ± 1.6		34.6 ± 2.6	
Carpodetus serratus	91.8 ± 5.0		4.4 ± 1.1	
Pseudopanax crassifolius	49.0 ± 8.6		2.4 ± 0.9	
Pittosporum spp.	33.2 ± 8.0		1.1 ± 0.5	
Fuchsia excorticata	23.7 ± 7.2		0.8 ± 0.8	
Pseudopanax simplex	25.4 ± 7.5		0.6 ± 0.2	
Pseudopanax edgerleyi	10.0 ± 5.6		0.6 ± 0.5	
Myrsine australis	45.3 ± 8.5		0.4 ± 0.2	
Aristotelia serrata	10.0 ± 5.4		0.4 ± 0.4	
Pseudopanax colensoi	11.6 ± 5.4		0.3 ± 0.4	
Schefflera digitata	9.1 ± 5.4		0.2 ± 0.2	
Elaeocarpus hookerianus	4.0 ± 3.8		0.1 ± 0.2	
Shrubs				
Coprosma foetidissima	78.9 ± 7.2		4.0 ± 1.0	
Coprosma lucida	34.2 ± 8.2		0.6 ± 0.4	
Olearia colensoi	0.8 ± 2.0		0.3 ± 0.5	
Senecio reinoldii	9.7 ± 5.5		0.2 ± 0.2	
Coprosma areolata	18.5 ± 6.5		0.2 ± 0.1	
Climbers				
Ripogonum scandens	93.6 ± 4.4		18.6 ± 3.4	
Metrosideros diffusa	21.2 ± 6.9		0.1 ± 0.1	
Unidentified woody material				
stem	89.2 ± 5.4		4.2 ± 0.7	
leaf	45.5 ± 8.5		0.3 ± 0.1	
fruit	18.9 ± 6.9		0.3 ± 0.2	
FERNS		98.7 ± 2.1		7.9 ± 1.3
Unidentified	56.9 ± 8.3		2.2 ± 0.7	
Dicksonia squarrosa	57.5 ± 8.3		2.1 ± 0.4	
Blechnum fluviatile	34.0 ± 8.0		1.4 ± 0.7	
Phymatosorus diversifolium	51.5 ± 8.3		0.4 ± 0.2	
Blechnum capense	3.4 ± 3.6		0.4 ± 0.6	
Asplenium flaccidum	29.7 ± 7.5		0.2 ± 0.1	
Polystichum vestitum	5.5 ± 4.0		0.1 ± 0.1	

GRASSES		77.2 ± 7.3		2.6 ±0.9
SEA WEED		9.3 ± 5.3		1.3 ±1.0
Durvillea antarctica	1.8 ± 2.6		0.4 ±0.7	
HERBS		62.6 ±8.3		1.2 ±0.8
Phormium sp.	0.6 ± 1.6		0.3 ±0.5	
Nertera depressa	24.0 ± 7.3		0.2 ±0.1	
FUNGI				
LICHENS		39.0 ±8.2		1.1 ±0.7
ANIMAL MATERIAL		34.0 ±8.2		0.4 ±0.2
MOSSES AND		29.9 ±7.5		0.2 ±0.2
LIVERWORTS		38.7 ±8.2		0.1 ±0.1

Table 2: *Significant seasonal variation in the use of foods. a. Species* or *small groups of species. b. Two groups of minor vascular species. The group of species growing to more than 2m tall consists of all the trees except broadleaf and fuchsia, while the group seldom exceeding 2m contains all the shrubs, ferns, herbs and grasses.*

Food Item	Seasonal % DW				
	Autumn	Winter	Spring	Summer	P (Anova) 3 & 155 df
a.					
Griselinia littoralis	43.9	35.3	23.4	35.7	<0.001
Fuchsia excorticata	0.2	0.0	0.2	2.9	<0.05
All other subcanopy trees	9.8	14.3	13.5	11.4	<0.01
Ripogonum scandens - fruit	4.8	17.8	20.8	2.0	<0.001
leaf	4.1	4.4	6.9	2.8	<0.05
Coprosma foetidissima	4.4	1.7	2.8	7.3	<0.01
Other *Coprosma* shrubs	1.5	0.7	2.6	2.9	<0.05
Dicksonia squarrosa	3.9	0.4	1.4	2.6	<0.01
All other ferns	3.6	2.1	3.0	5.4	<0.05
b.					
Minor species> 2m	16.8	24.1	22.3	17.2	<0.01
Minor species < 2m	18.9	7.8	17.6	26.4	<0.001

Table 3: *Comparison of the frequencies of occurrence of the 48 most common fern and woody species present on vegetation plots with those observed in the diet. The preference index is the ratio of the number of observed and expected occurrences in the diet, based on a 48x2 contingency table.* [1] ^{2} *values are the row totals for each species, and measure the likelihood that the ratio of occurrences in the diet and in the forest is the same as the overall average ratio for all 48 species.*

	Frequency of Occurrence (%) in Diet	in Forest	χ^2 (1)	Index of Preference
A. OBSERVED USE > EXPECTED ($p<0.05$)				
Canopy trees				
Weinmannia racemosa	94.7	94.4	10.9	1.3
Subcanopy trees				
Griselinia lit/oralis	99.4	82.2	24.5	1.5
Pseudopanax crassifolius	49.0	38.0	15.3	1.6
Carpodetus serratus	91.8	37.7	101.8	2.3
Myrsine australis	45.3	21.2	42.3	2.2
Pseudopanax colensoi	11.6	6.9	7.7	1.9
Pittosporum spp.	33.2	6.5	66.3	3.1
Fuchsia excorticata	23.7	2.2	73.4	3.9
Pseudopanax edgerleyi	10.0	0.9	33.5	4.0
Schefflera digitata	9.1	0.9	26.5	3.8
Aristotelia serrata	10.0	0.9	33.5	4.0
Climbers				
Ripogonum scandens	93.6	39.6	99.7	2.3
Metrosideros diffusa	21.2	14.6	8.3	1.7
Shrubs				
Coprosma foetidissima	79.0	92.2	5.0	1.2
Coprosma lucida	34.2	20.6	20.5	1.9
Senecio spp.	36.2	21.5	21.7	1.9
Ferns				
Phymatosorus diversifolius	51.6	39.9	19.0	1.6
Blechnum fluviatile	34.0	6.9	69.2	3.0
Polystichum vestitum	5.5	1.2	9.0	2.0
B. OBSERVED USE = EXPECTED ($p>0.05$)				
Canopy trees				
Metrosideros umbellata	58.4	79.4	0.1	1.0
Podocarpus spicatus	0.0	3.7	3.0	0.0
Subcanopy trees				
Elaeocarpus hookerianus	4.0	1.9	0.5	2.0
Climbers				
Rubus spp.	18.6	31.2	0.4	0.9
Shrubs				
Gaultheria spp.	4.3	4.0	0.6	1.4

Ferns				
Dicksonia squarrosa	57.5	80.7	0.0	1.0
Hymenophyllum spp.	39.7	73.2	2.4	0.8
Asplenium flaccidum	29.7	31.8	2.0	1.2
Asplenium bulbiferum	18.1	29.6	0.1	0.9
Histiopteris incisa	6.0	9.0	0.0	1.0
C. OBSERVED USE < EXPECTED (p<0.05)				
Canopy trees				
Dacrydium cupressinum	6.0	88.5	56.8	0.1
Podocarpus ferrugineus	30.6	70.7	7.5	0.7
Podocarpus hallii	1.7	57.0	36.2	0.1
Subcanopy trees				
Pseudopanax simplex	25.7	81.6	17.7	0.5
Shrubs				
Small-leaved *Coprosma* spp.	24.1	63.2	9.3	0.6
Pseudowintera colorata	0.8	42.7	29.8	0.0
Cyathodes juniperina	0.0	41.4	25.4	0.0
Dracophyllum longifolium	1.7	39.3	27.3	0.1
Neomyrtus pedunculata	0.0	30.8	24.3	0.0
Leptospermum scoparium	0.0	28.0	22.7	0.0
Myrsine divaricata	1.7	24.0	7.3	0.4
Olearia spp.	1.7	11.2	5.1	0.3
Ferns				
Blechnum discolor	0.0	92.8	75.1	0.0
Grammitis spp.	15.5	57.3	15.9	0.4
Blechnum capense	3.4	57.0	22.3	0.3
Cyathea smithii	15.5	41.1	6.1	0.6
Tmesipteris spp.	1.7	19.0	10.4	0.2
Rumohra spp.	0.9	14.6	9.7	0.1

ate significantly more supplejack fruit than yearlings and adults (19.0, 10.5, and 5.5% DW respectively, 3 & 113 df, p<0.005). Yearlings and adults ate proportionately more shrub and non-woody species than fawns.

Geographic differences in diet

The frequencies of occurrence of foods did not differ significantly in the three areas shown in Fig. I, but the amount eaten differed for five foods. Deer along the northern coast ate significantly more kamahi and herbs and less rata, *Pittosporum* spp., and *Senecio* spp. than those in the two east coast areas (2 & 150 df, p<0.05), but the differences were slight. The estimate of annual diet in Table 1 is unlikely to be biased by the different sampling intensities in the three areas.

Deer food preferences

Deer clearly preferred some plant species to others (Table 3; $X^2 = 1116.5$, 47 df, p< 0.0001). As all chi-square values are positive, a preference index (PI: the ratio of observed to expected occurrences in the diet) was derived to indicate whether plants were eaten more or less often than expected. Twenty species were eaten more often (preferred; PI> 1) and 18 less often (less preferred; PI < 1) than expected at the 95% level of probability (Table 3). Only seven of the 48 common species present on plots were not eaten at all (PI = 0). The less preferred species tended to be more common on plots than preferred species (mean number of occurrences of 144 and 91 respectively), and species with the highest preference indices were among the rarest plants in the forest. This is consistent with evidence that deer are preventing regeneration of the preferred species (Veblen and Stewart, 1980).

None of the less preferred species comprised more than 1% DW of the annual diet, whereas the preferred species made up 90% DW of the identified fern and woody plant material.

Subcanopy trees were the most consistently preferred plants, only *Pseudopanax simplex* being less common in the diet than expected (even though it was present in 26% of the rumens). The remainder were eaten at least 1.5 times more frequently than expected. Podocarps were generally avoided, only miro occurring in more than 10% of the rumens. The other main canopy trees were often eaten, but not highly preferred.

Except for *Coprosma* and *Senecio* spp., the most common shrubs were seldom or never eaten. In contrast, only one of the common ferns *(Blechnum discolor)* was totally avoided, the others being eaten although not usually preferred.

Discussion

White-tailed deer on Stewart Island have clear food preferences, favouring the subcanopy hardwood trees. Possums also eat many of the same species, although broadleaf, the main deer food, is not generally regarded as preferred by possums (Leathwick, Hay, and Fitzgerald, 1983; Coleman, Green and Polson, 1985). In addition, the only two hardwood trees not actually preferred by deer (rata and *Pseudopanax simplex)* are preferred by possums. All the hardwood trees thus appear to be preferred by at least one introduced mammal.

The fern and woody plant species preferred by white-tailed deer on Stewart Island are also frequently browsed by other deer species and goats *(Capra hircus)* elsewhere in New Zealand (Wardle, 1984; Leathwick *et al.,* 1983; Mitchell, Fordham, and John, 1987). The few other studies of deer diet in New Zealand forests based on rumen or faecal analyses show the same dependence on subcanopy hardwoods (Lavers *et al.,* 1983; Mason, 1966; G.Nugent, unpubl.; C.N. Challies, unpubl.). However, where deer have access to grassland, grass and herb species tend to dominate (Lavers, 1978; Gibb and Flux, 1973; Kelton and Skipworth, 1987). Although Hoffman (1985) suggests the small rumen volume to body size ratio of white-tailed deer indicates they may be more selective feeders than other deer, the similarities in the actual or inferred diets noted above suggest any differences in food preferences between ruminants are relatively minor. Differences in diet largely reflect differences in the local availability of plant species.

The relatively recent release of deer into New Zealand's forests has resulted in a marked variation in plant availability, depending on the time since liberation. Wardle (1984) described changes in deer diet during their colonisation of Fiordland. Initially deer focused on the most preferred foods, such as the sub-canopy hardwoods, but as these were eaten out and deer densities began to decline, less preferred species became more important. Based on browse patterns on plants growing within the browse tier, Wardle estimated that the generally less preferred shrubs, ferns, herbs, and grasses comprised only 30% of pre-peak diet, but 70% of post-peak diet. By the late 1970's the white-tailed deer population on Stewart Island was clearly past peak density, and browse patterns there were consistent with post-peak status. Estimates of the percentage of total browse on vascular species attributable to shrubs, ferns, herbs and grasses, using the methods in Wardle, Hayward and Herbert (1971) were 65% (M.J. Williamson, unpubl.), 57% (A.D. Ross, unpubl.), and 60% (G.H. Stewart and L.E. Burrows, unpubl.). The actual diet (measured from rumen contents), however, more closely approximated Wardle's pre-peak diet, and showed heavy reliance on preferred overstorey species.

The ability of white-tailed deer to obtain so much of these preferred foods was initially puzzling. Although seedlings and saplings of the hardwood species' are common in the dense understorey on nearby Bench Island (where deer are absent), the coastal forest on Stewart Island itself has been substantially modifed by deer (Veblen and Stewart, 1980). It now contains very few saplings of subcanopy trees. The paucity of hardwood foods within the browse tier suggested that deer were somehow obtaining material from the canopy. The yellow colouring of most of the broadleaf leaves in the sampled rumens clearly indicated they were doing so by foraging on cast leaves and windbroken branches. As the greatest use of supplejack fruit did not occur until after the main peak of ripening in autumn it is likely this food also was being obtained mainly from the ground.

Foraging on fallen material, and, to a lesser extent, feeding on non-vascular plants, explains the difference between actual diet based on rumen analysis and dietary inferences based on browse observations noted above. The size of the discrepancy provides some indication of the proportion of diet obtained as fallen material. Nearly two-thirds of browse occurred on . shrubs, ferns, herbs, and grasses, but these foods comprised only 20% DW of annual diet. This suggests that the remaining third of browse observations made up only another 10% DW of annual diet, and, therefore, that all browsing contributed around 30% DW of annual diet. Non-vascular plants accounted for less than 10% DW of diet, and we infer that around 60% DW consisted of fallen leaves and fruit.

This inference is supported by the observations of hunters (Johnston, 1964), and also by evidence from deer exclosures (G.H. Stewart and L.E. Burrows, unpubl.). When deer were excluded from previously heavily browsed areas the greatest initial response was in the abundance and size of shrubs such as *Senecio reinoldii* and *Coprosma foetidissima* and the fern *Dicksonia squarrosa*. This indicated that most of the biomass produced within the browse tier previously removed by deer was comprised of these species, rather than the hardwoods that actually dominate in the diet.

The heavy reliance on fallen leaves and fruit helps explain the seasonal variation in diet. In summer deer ate nearly all the broadleaf made available to them, but left much uneaten for long periods in winter (C.N. Challies, unpubl.). This suggests a surplus of food in winter, presumably partly because supplejack fruit is available then. It is also likely that fallen leaves are more abundant in winter, as storms are more frequent and cast leaves and windbroken branches remain edible longer in cooler temperatures. A surplus would allow greater selectivity in the diet, and in winter deer did focus more on preferred tree species (other than broadleaf) and less on shrubs, ferns, herbs, and grasses. This is the opposite of what would be expected if deer were relying solely on plant material growing within the browse tier, when use of preferred species would tend to be greatest during the season of growth. The decrease in the use of broadleaf in winter probably reflected a lesser use of yellow leaves, as these appeared to be much less common in winter samples. Unfortunately this apparent difference was not adequately quantified.

The use of food produced above the browse tier has important consequences in the context of the eruptive fluctuation in ungulate numbers that follows colonisation of new areas. Based on earlier work (Holloway, 1950; Riney, 1964; Clarke, 1976; Caughley, 1970), Caughley (1980) describes the process as follows. Over the 20-30 year period following initial occupation, deer densities increase to a peak, then, with the food supply depleted, crash to lower levels. The decline is then followed by long-term adjustments of the vegetation to browsing, which Caughley (1980) depicts as relatively small fluctuations around a constant carrying capacity.

This interactive model assumes that browsing has an immediate effect on the productivity of all the palatable vegetation. On Stewart Island, however, deer have had no direct short-term impact on the composition (and productivity) of the forest overstorey (Veblen and Stewart, 1980), an important part of their food resource. We therefore speculate that the eruptive fluctuation there (and in other forests where deer rely on fallen food) is likely to have differed from Caughley's (1980) model. Following the population peak, when deer had depleted the plants growing within the browse tier, the continued availability of food produced in the canopy is likely to have decreased the size of the post-peak population crash. Since the crash, deer have prevented regeneration of most subcanopy hardwoods, so that the established food trees are slowly dying out and being replaced by less preferred species. The initial decline has probably been followed by a gradual decrease in carrying capacity that will continue well into the future, the rate of decline largely depending on the longevity of broadleaf and supplejack.

The ultimate carrying capacity will depend on the extent to which the food trees are replaced by less preferred forest species (such as podocarps and shrubs), rather than by dieback patches containing browse resistant grasses and herbs. If the availability of shrubs, ferns, herbs, and grasses does not change much in future, the low proportion of these foods in the annual diet (< 25 %) suggests that the carrying capacity when most of the food trees have died out will be only 20-30% of current deer densities.

Although very small hardwood seedlings remain common on Stewart Island, they are usually eaten at an early age (G.H. Stewart and L.E. Burrows, unpubl.). However, seedlings appeared to contribute little to the overall diet. The rapidity with which they are removed indicates they are highly preferred, and would probably continue to be eaten even if deer densities were artificially reduced below carrying capacity. As only 2% of all broadleaf eaten consisted of seedling-like material, its regeneration in areas accessible to deer may require the almost total removal of deer.

In summary, the gradual impoverishment of Stewart Island forest predicted by Veblen and Stewart (1980) will continue as long as deer remain near carrying capacity, and are largely sustained by food falling from the canopy. We suggest that there will be a substantial concurrent decline in carrying capacity, and that the trend toward an equilibrium with few hardwoods and few deer will only be disrupted by massive reductions in deer density.

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Appendix 1: *A list of species comprising less than 0.1% DW of annual diet. Most woody plant foliage was identified to species level, whereas much grass, and lower plant material could not be identified beyond category level.*

Canopy Trees:	*Dacrydium cupressinum, D. intermedium, Podocarpus spicatus, P. hallii.*
Subcanopy Trees:	nil.
Climbers:	*Clematis* spp., *Ileostylus micranthus, Muehlenbeckia australis, Rubus* spp.
Shrubs:	*Coprosma cheesemanii*, *C. ciliata, C. rotundifolia, Dracophyllum* spp., *Gaultheria* spp., *Hebe salicifolia, Myrsine divaricara, Olearia arborescens, Pseudowintera colorata.*
Ferns:	*Adiantum cunninghamii*, *Asplenium bulbiferum, A. hookerianum, A. obtusatum, Blechnum durum, B. minus, Cyathea smithii*, *Dicksonia fibrosa, Grammitis* spp., *Histiopteris incisa, Hymenophyllum bivalve, H. dilatatum, H. sanguinolentum, Hypolepis rufobarbata, Lastreopsis glabella, Pyrrosia serpens, Rumohra adiantiformis, Tmesipteris tannensis.*
Herbs:	*Acaena* spp., *Aciphylla* spp., *Australina pusilla, Bolobanthus* sp., *Celmisia* spp., *Cirsium* spp., *Crepis taraxacifolia, Gentiana saxosa, Haloragis erecta, Hydrocotyle americana, Hypochoeris radicata, Luzuriaga parviflora, Netera dichondraefolia,* Orchid sp., *Pernettya macrostigma, Pilosella aurantiaca, Plantago lanceolata, Pratia angulata, Pterostylus* spp., *Ranunculus acris, Rumex acetosa, Selliaria radicans, Sonchus* spp., *Trifolium* spp., *Urtica* spp.
Grasses:	*Carex appressa,* C. *coriacea, Juncus* spp., *Poa pratensis, Scirpus* spp., *Triglochin striatum, Uncinia* spp.
Moss/Liverworts:	*Bazzania* spp.
Fungi:	*Coriolus versicolor*
Lichens:	*Cladia aggregata, Pseudocyphellaria billardieri, Sticta* spp., *Usnea* spp.
Seaweed:	nil.