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THE ECOLOGY OF THE DAMA WALLABY (MACROPUS EUGENII,
DESMAREST) IN FORESTS AT ROTORUA, WITH
SPECIAL REFERENCE TO DIET

BY

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A B S T R A C T

The dama wallaby (*Macropus eugenii*, Desmarest, 1817), tamar or Kangaroo Island wallaby is present in high numbers throughout the Okataina Scenic Reserve and common elsewhere in the Rotorua Lakes region. Little is known of the animals' ecology in the area although its present status is that of a pastoral and forest pest. Major aims of the present study were to investigate feeding habits and general ecology of the dama.

Between November 1983 and March 1985 1076 wallabies were shot and autopsied; results have confirmed that the dama is a preferential grazer and where there is access to managed pasture, upwards of 70% of identifiable stomach material is likely to consist of pasture species. However wallabies also live and successfully breed within indigenous forest of the Okataina Scenic Reserve, with access to meagre amounts of grass. Here preferred foods include foliage of *Meliccytus ramiflorus*, *Weinmannia racemosa*, *Geniostoma rupustre*, *Coprosma* spp., *Hedycarya arborea* and *Leptospermum* spp.

Some seasonal variation in plant species selected is evident, as are some minor differences in diet between adults and juveniles; however there are no significant differences in foods eaten between males and females.

Wallabies in exotic forest consume largely grass and weed species but relatively little *Pinus radiata*.

Molar indexing appears to be an excellent method of aging *M. eugenii* up until at least three years of age.

Wallabies in general attain the largest size where they have access to managed pasture and it is suggested that a pasture/forest margin is very suitable wallaby habitat. This is supported by kidney fat assessment, which shows that male and female wallabies with access to pasture are in better condition than those in nutritionally

poorer areas. Breeding data suggests that yearling wallabies from pasture margins may be more fecund than those from other areas.

Kidney fat reserves of males drop considerably during the rut and take several months to reach previous levels. Whereas for females considerable stress is imposed during the late spring when energy demands of the pouch young are greatest.

In general female damas breed in their first year and as in Australia the breeding season is very short; however in New Zealand it is marginally earlier.

Sex ratios of pouch young, with one exception were found to be not significantly different from 1:1. Nevertheless there was a significant and consistent bias towards males in shot samples. It is suggested that this is a result of males being more active within their home-range.

Rhodamine trials revealed that wallabies may travel at least 500m from within the forest to pasture margins, presumably to feed.

Evidence is presented which suggests that wallabies are detrimentally influencing the structure of forests within the Okataina Scenic Reserve, however it is also held that there is considerable doubt as to how much blame is directly attributable to wallabies.

CHAPTER ONE

INTRODUCTION

1.1 General

The dama wallaby (*Macropus eugenii*); known in Australia as the tammar or Kangaroo Island wallaby, was liberated in the Rotorua region about 1912 (Wodzicki and Flux, 1967). Their rate of dispersal has been slow (Kean, 1959, see Fig. 1.1) but they are now regarded as a local pest and have reached high numbers in the Okataina Scenic Reserve (Knowlton and Panapa, 1982). Knowlton and Panapa conclude that "There seems little doubt that wallabies are having a considerable effect on the vegetation of the Okataina Scenic Reserve." This reserve (4388 ha) is locally a valuable asset, but as well as alleged forest damage in this immediate area, the potential impact of wallabies in adjacent forests must be considered. That is, unlike the insular situation of Kawau Island where the dama has also been reported to be damaging indigenous vegetation (V. Vujcich, 1979) the Rotorua Lakes region is bordered by the Mamaku and Urewera State Forests. The potential impact of wallabies in these forests is an important consideration.

In addition to being a threat to indigenous forest the dama is considered to be a pasture pest on rateable land and large numbers have been shot by the Central Bay of Plenty Pest Destruction Board (D.S. Moore, personal communication). Although this shooting has been ongoing for many years and the present status of the animal is that of a pastoral and forest pest, the research work available to reach such a conclusion is very scant.

Plate 1: Dama wallaby in kamahi forest
(mid-afternoon).

Plate 2: Immature wallaby from the Makatiti Dome.
When photographed this animal was
grazing the vegetation seen here, that
is predominantly *Leucopogon fraseri*,
Epilobium spp. and *Raoulia glabra*.
(Photograph by Chris Cheesman.)

Plate 3: For a short period during the study 2
immature wallabies (male and female)
were kept in captivity - male is seen
in the foreground.



1.2 Present Distribution of *Macropus eugenii*

M. eugenii was once widely distributed through south-west Western Australia, and was common in South Australia (Hume, 1982). It is now largely confined to mainland Western Australia and several islands off Western and Southern Australia (Tyndale-Biscoe, 1973). Among the latter is Kangaroo Island which according to Inns (1980) is the only area in Australia *M. eugenii* can presently be found in abundance.

In New Zealand the dama is found on Kawau Island "...where it was presumably introduced by Sir George Grey about 1870" (Wodzicki and Flux, 1967) and in the Rotorua Lakes region. Wodzicki and Flux reported that the origin of the Rotorua wallabies is obscure, although they may have been released by the late M.H.R. Benn near Lake Okareka. The area occupied by the Rotorua dama has been steadily increasing albeit slowly. Fig. 1.1 is the most recently available map of wallaby distribution in the Rotorua region and is largely the result of a 1983/84 animal survey by the New Zealand Forest Service, combined with confirmed sightings in outlying areas (Llewellyn, 1985a). Llewellyn notes that "While the spread of wallabies has been slow in comparison to red deer, they have now colonised a large area of the central Bay of Plenty and continue to occupy new territory."

Fig. 1.1: Dama wallaby distribution 1983/84.
From Llewellyn (1985a).

1.3 Previous Research

Some aspects of dama biology have been extensively studied by Australian researchers. For example nutritional physiology and metabolism, and morphology of the digestive system have, in relation to other aspects of the animals biology, been well documented. This is evident in the unpublished bibliography by Knowlton (1982).

Publications regarding ecology and behaviour of *M. eugenii* are not well represented in the literature. As summed up by Hume (1982) "*Macropus eugenii* has been the subject of numerous laboratory investigations, but only comparatively recently has its field ecology received any great attention." In this latter regard, Hume may have been referring to the unpublished Ph.D thesis of Inns (1980) who investigated the ecology of *M. eugenii* on Kangaroo Island.

There has only been a paltry amount of New Zealand research on the dama. Knowlton in his 1982 bibliography noted that "...there are only six known published documentations containing information on the species in the New Zealand situation."

There are no detailed studies of *M. eugenii* in the Rotorua region.

The only New Zealand work on the diet of this animal has been carried out on Kawau Island. There, generalities of the feeding ecology were appraised by Kinloch (1973) and studied in more depth by V. Vujcich (1979). Some anecdotal information concerning dama diet is scattered through the literature (eg. Kean, 1959; Wodzicki and Flux, 1967; Andrewartha and Barker, 1969).

The social behaviour of *M. eugenii* on Kawau has been studied by M. Vujcich (1979).

1.4 Aims of the Study

1.4.1 Diet

1.4.1.1 Diet in Relation to Habitat, Season, Sex and Age

It was an important aim to identify preferred foods of wallabies living in the Okataina Scenic Reserve. It was held that this information would help to suggest the extent to which forest damage being sustained in this reserve can be attributed to wallabies. Such information could be used to predict what impact the dama may have on the Urewera and Kaimai State Forests which are on the outskirts of the animals present distribution.

Identification of highly palatable plant species could be of assistance should natural vegetation poisoning such as that used on red-necked wallabies (*Macropus rufogrisea*) in the South Island (Warburton, 1983) ever be considered as an appropriate means of control.

To identify preferred foods it was considered necessary to examine not only wallabies living exclusively within the reserve, but also those frequenting adjoining farmland. That is, if such animals are making full use of pasture as a food source they may be consuming little or no forest vegetation.

It was also hoped to confirm or refute the claim that wallabies consume large amounts of pasture and therefore to determine whether the extensive shooting of wallabies which has been carried out on rateable land is justified.

A further aim of the diet study was to ascertain whether exotic forest (namely *Pinus radiata*) is at all palatable to wallabies.

It was deemed necessary to investigate the variation in usage of plant species with season, sex and age. Such information would be particularly relevant when considering the likely success of a natural vegetation poisoning campaign.

1.4.1.2 Wallaby Impact in Forests

Knowing the diet per se of an animal is of limited use in isolating its impact on the forest; it is also necessary to have information on spatial and temporal changes in forest structure which can then be related to the animals diet.

At the time this study commenced, the New Zealand Forest Service had begun a vegetation survey of the Okataina Scenic Reserve. For this reason it was considered superfluous to examine forest structure in this study. In addition to the vegetation survey the Forest Service also established exclosure plots within the reserve. These were erected early in this study in the hope that it would be possible to incorporate results into the diet analysis work.

1.4.2 Population Biology

It was considered essential to look at as many aspects of population biology as possible.

1.4.2.1 Age Structure

By aging all animals shot it was hoped to get an indication of age structures of the populations in each habitat sampled. The most obvious use for such information is to assess the effectiveness of present control techniques (ie. night shooting). Also as stated by Odum (1971) "... the ratio of the various age groups in a population determines the current reproductive status of the population and indicates what might be expected in the future."

1.4.2.2 Animal Size

Another major aim was to ascertain whether there exist any significant differences in animal size between habitats. Such differences might be attributable to nutrition (Challies, 1973) and thus it may be possible to get some indication of the most optimal wallaby habitat. Such information might be useful when predicting the likely spread of wallabies into surrounding areas.

A further reason for examining the size of wallabies in the Rotorua area was to investigate the rumour that there may be a second species there, as suggested by Wodzicki and Flux (1967) and Jane (1979).

1.4.2.3 Wallaby Condition

"The level of fat reserves provides a useful indication of a populations general well-being because it reflects changes in environmental favourability over short periods of time." (Caughley, 1970). Thus it was hoped to examine fat reserves to measure differences in "general well-being" with habitat, season, sex and age. Such data might be useful when designing poisoning campaigns, as well as supporting data on size differences to indicate ideal wallaby habitats.

1.4.2.4 Breeding

It was intended to investigate the age at which damas first breed and also to determine the proportion of females that successfully breed, for both yearlings and adults. In addition to this it might be possible to establish whether wallabies confined to the forest interior have significantly lower breeding success than those with access to pasture, also to discover whether New Zealand damas are any more or less fecund than Australian animals. A further aim was to establish the season of births and relate this to Australian studies (eg. Inns, 1980). Such data might also be useful for deciding on the most appropriate time to poison should it be necessary.

1.4.2.5 Sex Ratios

Coleman and Green (1984) described four geographically separated populations of brush-tailed possums (*Trichosurus vulpecula*) which showed biases in sampling toward males. They suggested this resulted from males being more mobile than females. It was decided in the present study to compare sex ratios of pouch young with adults in shot samples for each habitat and season. This might provide information on wallaby movements and/or real biases in sex ratio.

1.4.3 Wallaby Movements

Because of time constraints on this study it was decided that relatively little attention could be spent investigating wallaby movements. However the distinct paucity of information available on this subject led to the conclusion that any investigation no matter how limited might yield useful data. Therefore studies were initiated to ascertain:

1. The distances wallabies travel to reach pasture. Such data would be valuable for estimating likely kills from poison laid along marginal areas. It was also hoped to discover any differential pasture usage with sex and age.
2. Long term dispersal habits of wallabies.

1.4.4 Summary of Aims

1. To identify preferred foods.
2. To establish possible food preferences in relation to habitat, season, sex and age.
3. To quantify wallaby impact on forests.
4. To ascertain the age structure of each habitat.
5. To compare animal size for each habitat.
6. To describe variation in short-term condition with habitat, season, sex and age.
7. To investigate breeding success and season of births.
8. To investigate differences in sex ratios for pouch young and adults and describe any variation with habitat.
9. To collect information on wallaby movements.

CHAPTER TWO

STUDY AREAS AND GENERAL SAMPLING TECHNIQUE

2.1 General Description of the Lake Okataina Region

2.1.1 Soils and Climate

Ballance (1980, Chapman, ed.) noted that "All the rocks and landforms of the Rotorua Lakes area are volcanic. They are also very young, less than 40,000 years in most areas." The Okataina Scenic Reserve - and all areas used in this study - is included in what Ballance described as the Okataina Volcanic Centre which consists of a large number of rhyolite domes, most of which are covered by bush. The major soils of the Rotorua Lakes district are of volcanic origin and can be broadly divided into two groups: airfall tephra (erupted from volcanic sources) and water-sorted tephra (deposited as erosion products from slopes, rivers or lakes) (Rijkse, 1980, Chapman, ed.). The most recent of these deposits are important soil components in the Okataina region and originated in the eruption of Mount Tarawera. That is, on June 10th 1886, Tarawera erupted and "...spread a thin sheet of dark coloured basaltic ash over much of the Rotorua Lakes area." (Ballance, 1980, Chapman, ed.). Tarawera Ash is described by Rijkse (1980, Chapman, ed.) as being coarse textured with a low nutrient status. The other important material deposited during the Tarawera eruption is Rotomahana Mud (formed when large amounts of mud were eroded off the surrounding hills) (Kennedy and Pullar, 1980, Chapman, ed.). As noted by Rijkse, soils from Rotomahana mud have a high nutrient status but shallow top soils and weakly developed soil structure.

Climate of the Rotorua Lakes region is generally warm with a moderate rainfall. The following is a summary of rainfall data collected by the New Zealand Meteorological Service (at Rotorua airport) during the present study.

Month	1983		1984				
	N	D	J	F	M	A	M
Total Rainfall (mm)	53.4	141.3	129.9	124.2	190.1	29.1	57.4
Days with Rain	12	13	11	13	18	7	8

Month	1984						
	J	J	A	S	O	N	D
Total Rainfall (mm)	90.6	145.2	97.4	118.8	16.7	108.2	201.9
Days with Rain	11	16	16	17	9	9	15

Mean monthly temperatures calculated from data collected between 1963 and 1980 are summarised below, (from New Zealand Meteorological Service data).

Month	J	F	M	A	M	J
Mean Temp. (°C)	17.6	17.8	16.5	13.6	10.4	8.0

Month	J	A	S	O	N	D
Mean Temp. (°C)	7.5	8.7	10.2	12.0	14.0	16.0

2.1.2 Vegetation

Forest structure of the Okataina Scenic Reserve is described in detail in section 2.3 and the following is a brief overview of the Okataina and surrounding area.

As noted by Nicholls (1980, ed. Chapman) the Rotorua district has only a remnant of the "great original forest". Nicholls attributes much of the blame for this reduction to repeated burning by Maoris and suggests that the area of forest cleared since European settlement is "proportionately very small". Nevertheless most remaining indigenous forest around the lakes district has at some time been logged. Rather than logging *per se*, much recent clearing of indigenous forest has been for farmland or conversion to exotic forests (Jane, 1979). This trend is evident on the borders of the Okataina Scenic Reserve; that is west of the reserve is farmland whereas immediately east is exotic forest.

Much of the forest within the reserve is "second-growth", probably either because of logging in accessible areas, or abandoning of Maori villages and cultivations on lakeside terraces (Nicholls, in Chapman, 1980). The only virgin bush in the reserve is that bordering the road to the lake.

Forest types of the surrounding lakes region were examined by Jane (1979) in a survey which extended from Lake Rotoma to the immediate east of Lake Rotorua and south to Lake Tarawera. Jane found tawa (*Beilschmiedia tawa*) to be the predominant forest type throughout the survey region. Table 2.1 (from Jane, 1979) summarises the proportions of various forest types.

Table 2.1: Forest types of the survey area from
Lake Rotoma to the immediate east of
Lake Rotorua and south to Lake
Tarawera (from Jane, 1979).
(See Appendix III for specific and
generic names.)

TABLE 2.1:

Forest Type	Proportion
Tawa	23.6
Tawa/Mahoe	9.6
Tawa/Kamaha	6.7
Tawa/Ponga	31.1
Tawari	7.3
Mahoe	2.9
Kamaha	15.3
Kanuka	3.6

2.1.3 Other Animals Present

Introduced mammals, other than wallabies, present within Okataina Scenic Reserve include:

Red deer (*Cervus elaphus*), which were liberated in the region between 1907 and 1921 (Logan and Harris, 1967); Knowlton and Panapa (1982) described the density of deer in the reserve as being low (see Table 2.2).

Pigs (*Sus scrofa*) are present but as with deer, in low numbers and are mainly found in the south-western sector of the Reserve (Knowlton and Panapa, 1982). Llewelyn (1985b) noted that pig hunting in the district serves to keep numbers in check.

Possoms (*Trichosurus vulpecula*) were "...liberated at a number of points around the Rotorua basin between 1905 and 1906 (Okataina, Rotoiti, Rotorua)..." (Jane, 1979). Knowlton and Panapa (1982) found possum numbers within the reserve to be low.

Table 2.2 shows animal pellet frequencies for the various forest types within the Okataina Scenic Reserve as identified by Knowlton and Panapa (1982) (note the high frequency of wallaby pellets relative to other animals).

Table 2.2: Animal pellet frequencies for the various forest types within the Okataina Scenic Reserve. Note the high frequency of wallaby pellets relative to other animals. (From Knowlton and Panapa, 1982.)

TABLE 2.2:

Forest Type	Pellet Frequency			
	Wallaby	Deer	Possum	Pig
Kamahi	38.5	1.7	1.1	-
Kanuka	58.3	-	-	-
Podocarp/Tawa	22.8	2.5	2.5	-
Tree fern	23.8	-	-	9.5
Mixed hardwood	47.7	0.7	3.5	0.7
Bracken	46.7	1.3	4.0	2.7

2.2 Rationale for Choosing Areas

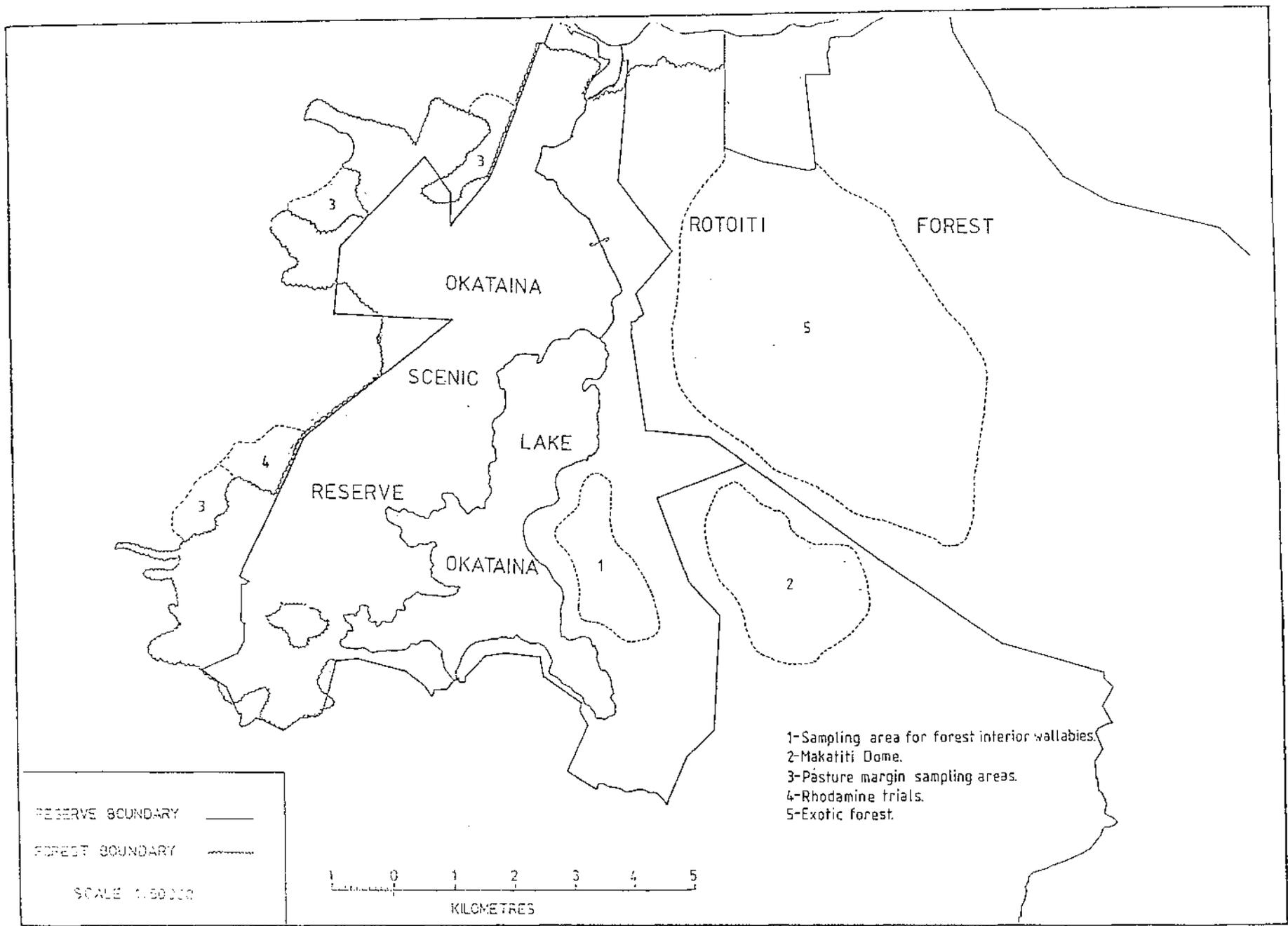
It was decided that for a comprehensive diet study wallabies must be sampled from two major habitat types:

- (a) indigenous forest
- (b) pasture/forest margin (see section 1.4.1)

(Some information was also collected from exotic forest.)

- (a) Initially the area chosen as indigenous forest habitat was mixed hardwood forest east of Lake Okataina, an area known locally as the Makatiti Dome. An attractive feature of this study area was the presence of bush tracks through the forest, enabling animals to be shot from a motorbike. However the presence of these tracks meant that a small amount of introduced weeds and grasses were available to wallabies, but in volumes very small in comparison to a situation where animals have access to managed pasture. Therefore, it was considered likely that forest species would be utilised to some extent as a food source by wallabies on the Makatiti Dome. This was subsequently found to be true. For this reason and also because of apparently higher numbers of wallabies than in the bush proper, the Makatiti Dome was sampled through the entire study. Because fringe areas ruled out the Makatiti Dome as strictly a forest habitat an attempt was made to collect animals from within the forest proper. An area of forest within the reserve as far as possible from any verge was chosen and is shown in Fig. 2.1.
- (b) Pasture/forest margin is largely confined to the western side of Lake Okataina. The following criteria were used for selecting a study area:
 - (1) Ease of access; ie. it had to be possible to shoot animals from a motorbike.
 - (2) Sufficient numbers of animals, which did not prove to be a problem as all farms bordering the reserve were carrying high numbers of wallabies.

Fig. 2.1: Map of Lake Okataina showing location
of study areas.



The exotic forest study area chosen was Rotoiti Forest, east of Lake Okataina. There were good reasons for this selection:

- (1) The Pest Destruction Board on several occasions shot large numbers of wallabies, most of which were for a DSIR Ecology Division study, and excess animals were made available to me.
- (2) The plantation consists primarily of young trees and therefore is more likely to be sustaining wallaby damage.
- (3) Rotoiti Forest is the only exotic plantation near to Lake Okataina that has a large population of wallabies.

2.3 Descriptions of Study Areas

2.3.1 Forest (see Fig. 2.1 and Plate 4)

This was an area of forest spanning the south-eastern half of Lake Okataina; that is between Kaiwaka Bay and Oruaroa Point. It is predominantly kamahi* (*Weinmannia racemosa*) with some areas of mixed hardwood and kanuka (*Leptospermum ericoides*) forest types (Knowlton and Panapa, 1982; Llewelyn, 1985b). Altitude ranges from 320 m to 540 m.

When describing this kamahi forest type, Knowlton and Panapa (1982) noted that

"The kamahi appears to be even-aged forest. It is interspersed throughout with scattered emergent rewarewa. The understorey is generally open although patches of mangeao and rewarewa do occur, along with occasional mamakus."

As noted by Llewellyn (1985b) silver fern (*Cyathea dealbata*), wheki ponga (*Dicksonia squarrosa*) and rangiora (*Brachyglottis repanda*) are also common understorey species. Dominant forest floor vegetation being moss spp. with *Uncinia* spp. and some filmy ferns (*Hymenophyllum* spp.) Llewellyn described this kamahi forest as representing an early successional stage, after much burning in the past.

Knowlton and Panapa (1982) noted that there are patches of kanuka forest amongst the kamahi. This kanuka forest is dominated by kanuka with mahoe (*Meliccytus ramiflorus*), kamahi, rewarewa (*Knightia excelsa*) and mamaku (*Cyathea medullaris*) locally sub-dominant (Llewellyn, 1985b). Mingimingi (*Leucopogon fasciculatus*), mangeao (*Litsea calicaris*), silver fern and rangiora are common in the understorey. Mangeao is the only common tree seedling, however ferns and mosses are widespread (Llewellyn, 1985b).

Plate 4: A view across the southwest of Lake Okataina showing kanuka forest (in the foreground) with kamahi forest behind. The former supports a relatively high concentration of wallabies (see Knowlton and Panapa, 1982).

Plate 5: In some areas of the Lake Okataina Scenic Reserve there are small beaches many of which are regularly used by wallabies - they appear to graze in particular weed near the water line (as shown in the lower right of the photograph). The photograph is taken at the southern end of the Lake - note the kanuka forest in the top right.



During sampling several forest-living wallabies were shot in mixed hardwood forest adjacent to the transition zone between kamahi and mixed hardwood. Knowlton and Panapa (1982) described rewarewa, mangeao, kamahi, kanuka, tawa (*Beilschmiedia tawa*) and rata (*Metrosideros robusta*) as all being components of the mixed hardwood type overstorey. He also noted that the understorey varies from being open through to being dense, where thickets of mangeao and rewarewa exist.

* The first time a plant species is referred to in this text the proper name and the common name are used. In the interests of brevity common names where they exist, are thereafter used in preference to proper names. A full nomenclature appears in Appendix III.

2.3.2 Makatiti Dome (see Plate 7)

The forest type is predominantly mixed hardwood (see 2.3.1). The Makatiti Dome is higher above Lake Okataina than that area of forest described in 2.3.1 (that is, altitude ranges from 720 - 900 m). Dominant canopy species of mixed hardwood were described in 2.3.1, however as noted by Llewelyn (1985b) there is some change in mixed hardwood forest with altitude, ie tawari (*Ixerba brexiodes*) becomes a dominant canopy in localised areas, particularly on the Dome itself. Llewellyn listed common mixed hardwood species in association with tawa and kamahi as being pigeonwood (*Hedycarya arborea*), mahoe, black maire (*Nestegis cunninghamii*), hinau (*Eleaocarpus dentatus*), rewarewa and lemonwood (*Pittosporum eugenioides*). Toro (*Myrsine salicina*) and pepperwood (*Pseudowintera colorata*) are common understorey species; putaputaweta (*Carpodetus serratus*), *Coprosma* spp., red matipo (*Myrsine australis*), Hall's totara (*Podocarpus hallii*), supplejack (*Ripogonum scandens*), wheki ponga and silver fern are locally common. The understorey is relatively dense in places and the forest floor is open (Llewelyn, 1985b).

As previously mentioned (section 2.2), the Makatiti Dome is not a forest environment per se, that is bulldozed tracks have resulted in many verge areas. Such areas support a number of colonising species, many of which were later found to be important in the diet of wallabies. Table 2.3 includes many if not most of the common verge species found on the Dome.

Plate 6: A view across to the north western side of Lake Okataina where there is an altitudinal gradient of mixed hardwood forest near the shore, kamahi in the mid-altitudes, and tawa/podocarp forest on the skyline (Knowlton and Panapa, 1982; Llewellyn, 1985). Note the steep terrain. The lower left of the photograph shows kamahi forest with emergent rewarewa, and pohutokawa (*Metrosideros excelsa*) near the shore, on the eastern side of the lake.

Plate 7: A typical section of track on the Makatiti Dome (mixed hardwood forest); note the verge area, which is used extensively by wallabies.

Plate 8: A section of pasture forest margin on the western boundary of the Lake Okataina Scenic Reserve, where the forest type is largely tawa/podocarp (Knowlton and Panapa, 1982; Llewellyn, 1985). Note the fenced boundary, with rank grass on the reserve side.



Table 2.3: Common verge species found on the
Makatiti Dome.

TABLE 2.3

Herbaceous Dicotyledons

Acaena spp.
Cirsium spp.
Leucopogon fraseri
Epilobium spp.
Hydrocotyle spp.
Plantago spp.
Raoulia glabra
Taraxacum spp.

Monocotyledons

Carex spp.
Cortaderia spp.
Deyeuxia avenoides
Juncus spp.
Poa caespitosa
Uncinia spp.

Others

Blechnum spp.
 Rangiora
 Putaputaweta
Coprosma spp.
 Tutu (*Coriaria arborea*)
Erica lustricana
 Broadleaf (*Grisilinia* spp.)
Hebe stricta
 Tawari
Leptospermum spp.
 Moss spp.
 Toro
Pittosporum tenuifolium
 Horopito (*Pseudowintera colorata*)

2.3.3 Pasture/Forest Margin (see Plate 8)

Because of the nature of the reserve, the only suitable pasture margin areas are on the western side of Lake Okataina. Therefore during the study three different farm properties on this side of the reserve were utilised. It became necessary to sample from more than one property because of a difficulty in maintaining high sample numbers throughout the year.

It is realised a possible element of error is introduced when treating all three wallaby samples as a single entity, but the farms are all relatively close together on the same margin of the reserve with similar aspects (westwards facing) and altitudes (425 - 485 m). Also all properties share a common adjacent forest type (Knowlton and Panapa, 1982; Llewellyn 1985b). I consider a more likely error to stem from differential "management" of the wallaby populations on each property. That is, hunting pressure and available food may vary between farms. Nevertheless the assumption was made that between-farm variation was significantly less than that between study areas. In hindsight this assumption appears valid.

The dominant forest type adjacent to the farm properties used for sampling is tawa/podocarp (Llewellyn, 1985). As noted by Knowlton and Panapa (1982) podocarps, particularly rimu (*Dacrydium cupressinum*) are scarce and the overstorey is predominantly tawa. With rewarewa, mangeao, hinau and pukatea (*Laurelia novae-zelandiae*) being locally sub-dominant (Llewellyn 1985b). Mahoe, pigeonwood, tawa, mangeao, rangiora, putaputaweta, kawakawa (*Macropiper excelsum*), supplejack and wheki ponga are all common understorey species. In the seedling tier, tawa, pukatea, rewarewa, pigeonwood, ferns and sedges are all common (Llewellyn 1985b).

On all properties used, the reserve boundary is fenced. There is commonly a thin strip of rank grass on the reserve side of the fence (see Plate 8), although wallabies prefer to use the rateable side and are often found at distances greater than 500 metres out onto pasture.

Commonly occurring pasture species are listed in Appendix III.

2.3.4 Exotic Forest (see Plate 9)

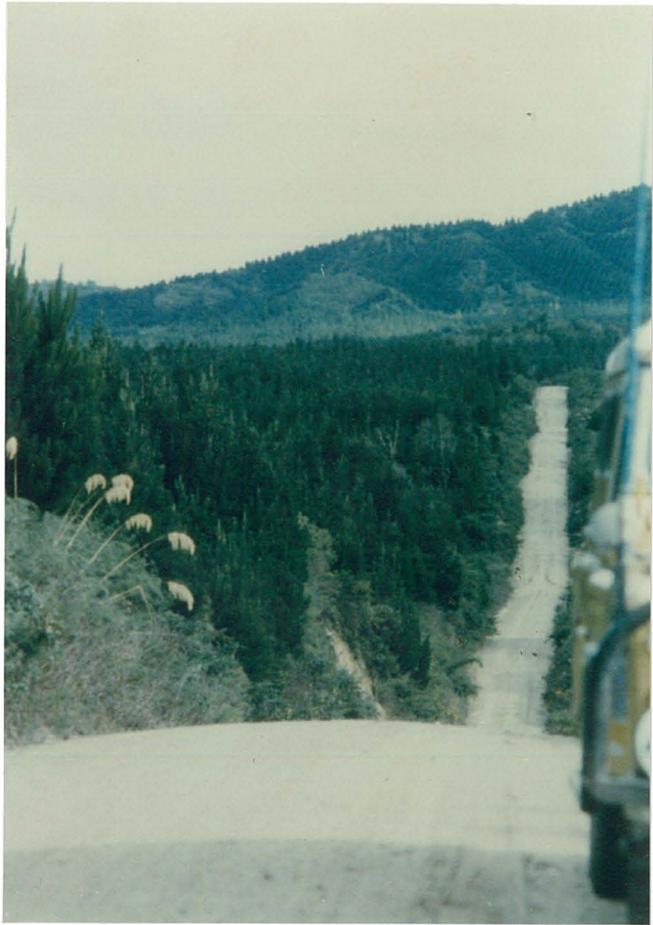
Rotoiti Forest is situated north-east of Lake Okataina, and the area utilised in this study is planted in immature *Pinus radiata*. Altitude ranges from approximately 150 to 757 metres.

Growing within the pines is an abundance of seral vegetation, much of which is indigenous, eg. wineberry (*Aristotelia serrata*), tutu, *Pittosporum* and *Coprosma* spp. There is also a wealth of herbaceous dicotyledons and grasses.

Wallabies are very abundant and can be seen at night in large numbers on the private roads which service the forest. Access into Rotoiti Forest is restricted although there is undoubtedly frequent poaching by hunters spotlighting for animals, in particular wallabies. This is assumed from the number of carcasses seen during sampling for this study, and also from communication with those people regularly in the area. Therefore this study area is probably the one subject to the heaviest hunting pressure.

Plate 9: A view across Rotoiti Forest showing
immature *Pinus radiata*; note also
the seral plant species present.

Plate 10: The farm property used for rhodamine
trials (see Chapter 9).



2.4 General Sampling Technique

Sampling was carried out by spotlight shooting, either from motorbike, four-wheel drive vehicle or in the case of forest animals from on foot. In all sampling a head mounted spotlight (12 volt "Life-Lite") and .22 calibre rifle were used.

Almost all animals were shot between 2000 and 0100 hours. Autopsies were performed as soon as possible after shooting and all were done by me personally.

Sampling was as near as practicable to the end of each month. An attempt was made to collect 30 wallabies of mixed sex and age per month from each of the pasture/forest margin and Makatiti Dome study areas. However sampling from the forest interior was much more difficult. This was not only because of the more obvious problems associated with shooting in forest compared with open margin areas, but also because it appeared that the density of wallabies was much less than at the forest margins. Therefore it was hoped to collect 10 animals per month from within the forest interior, but this goal was not always reached.

Animals were visually appraised as mature or immature. Males were deemed mature if the prostate gland was obviously enlarged and therefore by inference active. This is useful for assessing whether possums (*Trichosurus vulpecula*) are mature (J.D. Coleman, personal communication).

Skulls of all animals were collected and these later provided a means of checking classification by prostate evaluation. That is, using cleaned skulls, a molar index reading was calculated for each animal. Molar indexing was found to give results consistent with visual appraisal of age (viz; whether adult or juvenile).

It is also noteworthy that size alone is a useful indicator of whether a wallaby is an adult or a juvenile because that cohort consisting of immature animals from the previous year is of distinctive size.

Females were assessed as mature if there was evidence of a pouch young or lactation.

Stomach samples were collected as described in section 3.1.1. Material was also removed from the mouths of wallabies to give a subjective assessment to food types being eaten.

CHAPTER THREE

DIET ANALYSIS

3.1 Methods

3.1.1 Cuticle Analysis

There is still much controversy surrounding acceptable methodology for studying the diet of mammalian herbivores. However since there have recently been several adequate summaries of this controversy (for example Kelton, 1981; Nugent, 1983; and Scotcher, 1979) my discussion on the subject is confined to Appendix I; which also outlines why the following methodology was chosen:

Cuticle analysis methods: A sample of approximately 10mls was removed from each of three stomach regions; these being the sacciform forestomach, tubiform forestomach and hindstomach (see Hume, 1982 for comprehensive descriptions of these regions). This sample was then placed in an Agee jar and topped up with formalin-acetic-alcohol (85 parts 70% alcohol, 10 parts 40% formaldehyde, and 5 parts glacial acetic acid) (FAA).

For the pasture/forest margin and Makatiti Dome study areas, samples were bulked together to form a total sample from 3 animals, a similar methodology to Warburton (1978), where 30 possum stomachs collected each month were bulked into 5 groups of six. Grouping in this present study was according to sex and age ie animals were classed as immature or mature (see section 2.4). Bulking was seen in the present study as a means of processing the large amounts of stomachs within the limited time available. It was only used for those samples from the Makatiti Dome, pasture/forest margin and exotic forest. Samples from the forest interior were analysed individually.

Before removing subsamples for analysis, storage jars were vigorously stirred. This was to ensure adequate mixing in case of layering from either differential settling of particles or insufficient mixing of the individual animal samples.

A subsample of approximately 30ml was then removed and this was further mixed in a Waring blender for 30 seconds. Fitzgerald (1976) has pointed out that as well as mixing effects, the action of the blender also serves to reduce plant fragments to a more even size. The resulting mixture was washed through a 210um mesh sieve (Fitzgerald, 1976) then placed in sodium hypochlorite bleach for 45 minutes. After the subsample had been again washed in the 210um sieve approximately 5ml was finally removed and stored in glycerol.

When analysing samples 2 to 4 drops of the glycerol mixture were put on a microscope slide and a coverslip placed on top. Four slides were prepared per sample. For samples from the Makatiti Dome and pasture/forest margin study areas 25 abaxial (Fitzgerald, 1976) fragments were identified per slide, making a total of 100 fragments identified per 3 animals. Whereas for samples from wallabies shot in the forest interior 50 fragments were identified per slide, making a total of 200 fragments per animal.

Random transects across the microscope slide were used, and all fragments encountered were identified. A point on the eyepiece lens was used to determine whether or not a fragment was on the transect line. With the aid of an eyepiece micrometer the length and width of every particle encountered was measured in arbitrary units. Length multiplied by width was used as a measure of fragment area. Area measurements for each species were later summed to give a measure of total cuticle area per sample.

It was decided to identify abaxial cuticle only, (Fitzgerald and Wardle, 1979). This is because many dicotyledon species do not have sufficient identifiable characteristics on their adaxial surfaces. However when dealing with grasses it is often not possible to differentiate between abaxial and adaxial surfaces. Therefore the procedure adopted by Fitzgerald (personal communication) is to divide the frequency of grasses by half. However this introduces a source of error, particularly evident in this study, when animals are consuming large amounts of grass (ie. those animals from the pasture/margin and Makatiti Dome). That is, dividing the frequency of grasses by half means that the actual number of abaxial fragments identified in each sample is not always consistent; the extent of this inconsistency depending on the number and variance of grass fragments in the diet. When the number of grass fragments is low the amount of variation in the actual number of abaxial fragments identified will be small. This is true for forest living animals in this study, where 200 abaxial fragments were identified per animal and the proportion of grass species was seldom more than 3% of total identifiable stomach contents. However it is realised that an element of variance is introduced when considering the percentage occurrence (see section 3.2.1) data for wallabies from the Makatiti Dome and pasture/forest margin. That is although 100 cuticle fragments were identified per sample, this may not represent exactly the same number of abaxial fragments for each sample. However it should be noted that there were not large between sample variances in the number of grass fragments in samples (ie. pasture/margin mean number of grass fragments being 71.8 with a standard deviation of 11.3) and this factor will tend to reduce the actual variance in number of abaxial fragments identified.

For the purpose of presenting percentage occurrence results for Makatiti Dome and pasture/forest margin samples (see sections 3.2.2 and 3.2.3) data was corrected to represent 100 abaxial fragments for all samples. In hindsight this is not an ideal procedure and instead, every second grass fragment should have been recorded rather than halving the final number.

Stomach samples from 50 exotic forest wallabies of each sex, were collected during a wallaby shoot carried out by the Pest Destruction Board on the 27th and 28th of February, 1984. Approximately equal amounts of stomach material were removed from autopsied animals and bulked together to comprise a single sample for each sex. Stomach material was preserved with F.A.A and stored in Agee jars. Preparation of microscope slides was exactly as described previously for other habitats except that 20 slides were prepared from each of the two bulk samples.

One thousand cuticle fragments were examined (50 per slide) for each sex and the frequency of *Pinus radiata* noted - no attempt was made to identify to species level other plant fragments present.

3.1.2 Reference Collection

A collection was made of 120 plant species commonly occurring in the study areas (see Appendix III for a complete list of species). This collection included not only species from within the forest interior but also from on the forest margin.

Reference slides were prepared by first cutting leaves into 5mm squares then crushing on a flat surface, to separate cuticle from mesophyll cells. The resulting material was then placed in bleach for an approximately similar length of time as that used in preparation of stomach material, (ie. 45 minutes). When dealing with plants that have relatively thick leaves a longer period was needed to produce clean sections of cuticle (sometimes up to several hours). It is realised that there is a potential source of error in that where 45 minutes is used for stomach samples, sometimes longer is needed to clear reference material. Thus in stomach material some cuticle fragments may not have enough time to clear and therefore be labelled as unidentifiable. However I assume this to be a minimal source of error because by the time stomach material reaches the microscope slide it has been more thoroughly macerated than the 5mm square sections of reference cuticle. That is, macropodidae chew food very thoroughly (Storr, 1961) also the plant material has been subjected to some microbial and enzymatic action in the stomach. Moreover the stomach sample is placed in a Waring blender for 30 seconds.

Reference slides not only contained fragments of leaf cuticle but also trichomes, prickle-hairs and any other leaf appendages, as well as cuticle from petioles and buds.

When reference slides had been prepared micro-photographs (mostly black and white) were taken of all abaxial and many adaxial surfaces. Index cards as suggested by Nugent (1983) were also constructed. Micro-photographs proved to be invaluable in identifying cuticle fragments and were used constantly right up until completion of the study. However while index cards were a useful tool in the initial stages of the project, they soon became redundant as too much time was involved in operating them.

Approximately 3 months in the early stages of the study were spent just compiling and becoming familiar with the reference collection. Even after this period much time was spent scanning stomach material to practise identifying fragments, before any data was collected. With the technique of cuticle analysis there will probably be serious errors involved if data collection is begun before a reasonable competence in identifying material is achieved. That is, in the early stages a fragment type may be labelled as unidentified whereas with an improvement in skill the fragment identity is realised and therefore while being initially recorded as absent the particular species will make a sudden appearance into the diet of the animal.

To further guard against such error, samples were not analysed in the order collected.

3.2 Results

3.2.1 Diet of True Forest-Living Wallabies

Several methods are used routinely for presenting diet analysis results. They have been reviewed by Nugent (1983). In this study results are expressed firstly by "frequency of occurrence" ie. the percentage of stomachs containing a particular food type. This "...qualitatively describes how commonly a food plant is used by the population, and also reflects differences in availability or palatability (or both) of food species." (Nugent, 1983). However as noted by Nugent, frequency of occurrence "...does not always rank the food types in the correct order of proportional composition in the diet." So food items eaten less frequently tend to be over represented in the diet while those more common items tend to be under represented.

A commonly used method of quantifying diet results is by expressing the relative proportions as a percentage of the total number of foods identified (Fitzgerald, 1976; Warburton, 1978) ie. by "percentage occurrence" (Nugent, 1983). Percentage occurrence by frequency per se does not take into account the variation in size of particles identified. Leaf fragments of thicker more robust leaves may survive maceration as larger particles, and therefore be underestimated when using number alone. This was evidenced in the present study by tawari (*Ixerba brexiodes*) which survived in samples as quite large fragments, relative to other plant species. However this problem is overcome by using percentage occurrence by area (Fitzgerald, 1976) as in Figs. 3.1, 3.2, and 3.3.

In this study absolute area of cuticle in arbitrary units is also given, this is intended to display sample variance (Fig. 3.4).

Fig. 3.1: Diet results for forest living wallabies.

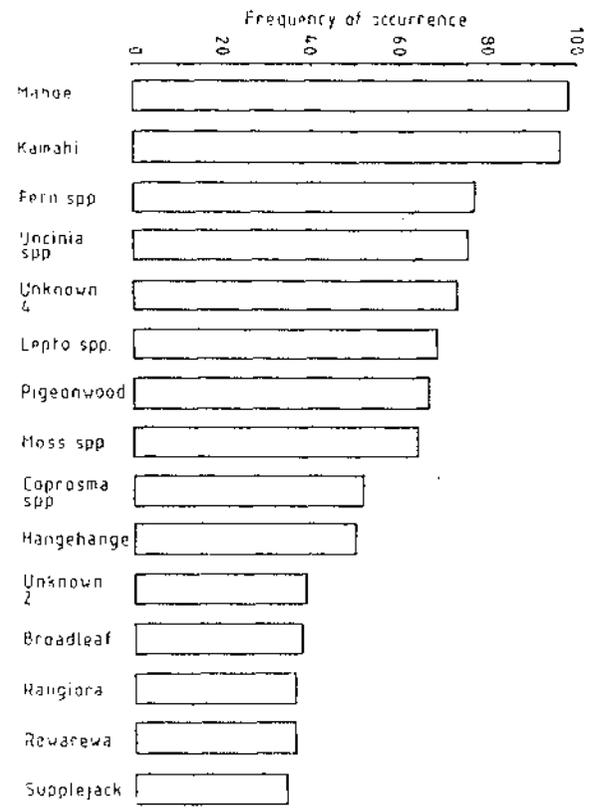
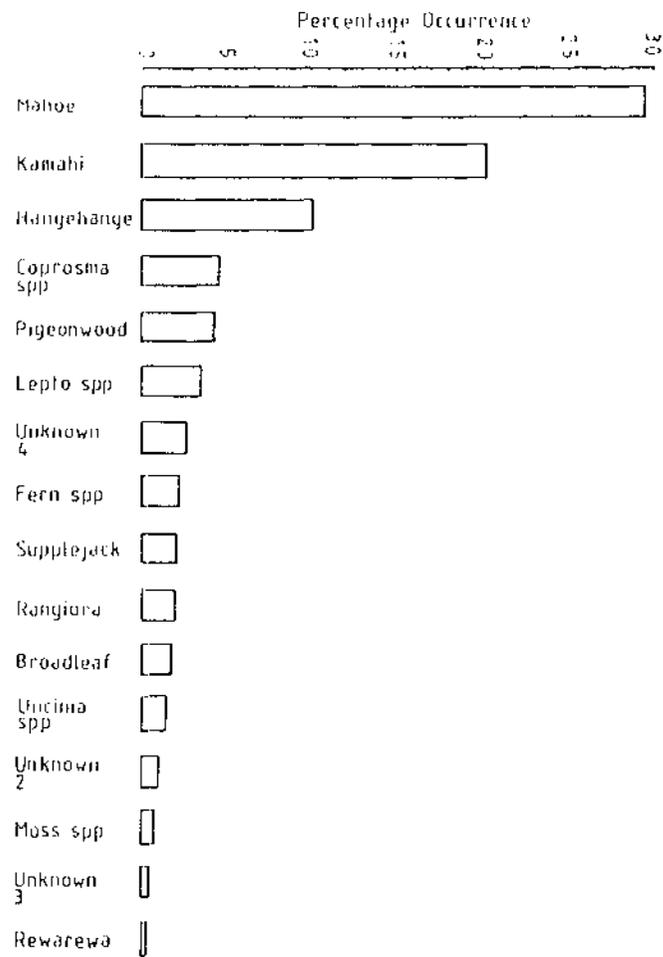


Fig. 3.2: Diet results for wallabies from the
Makatiti Dome.

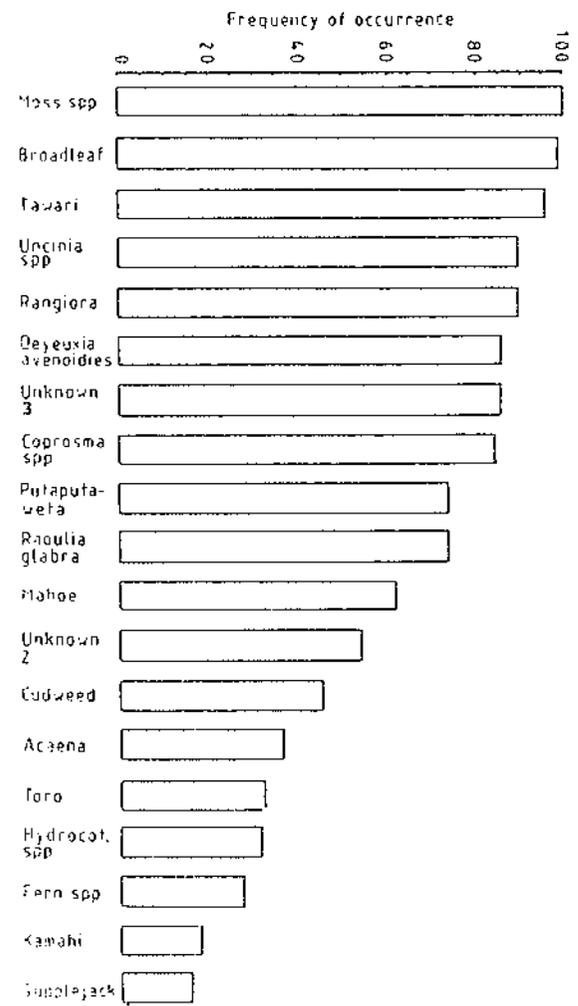
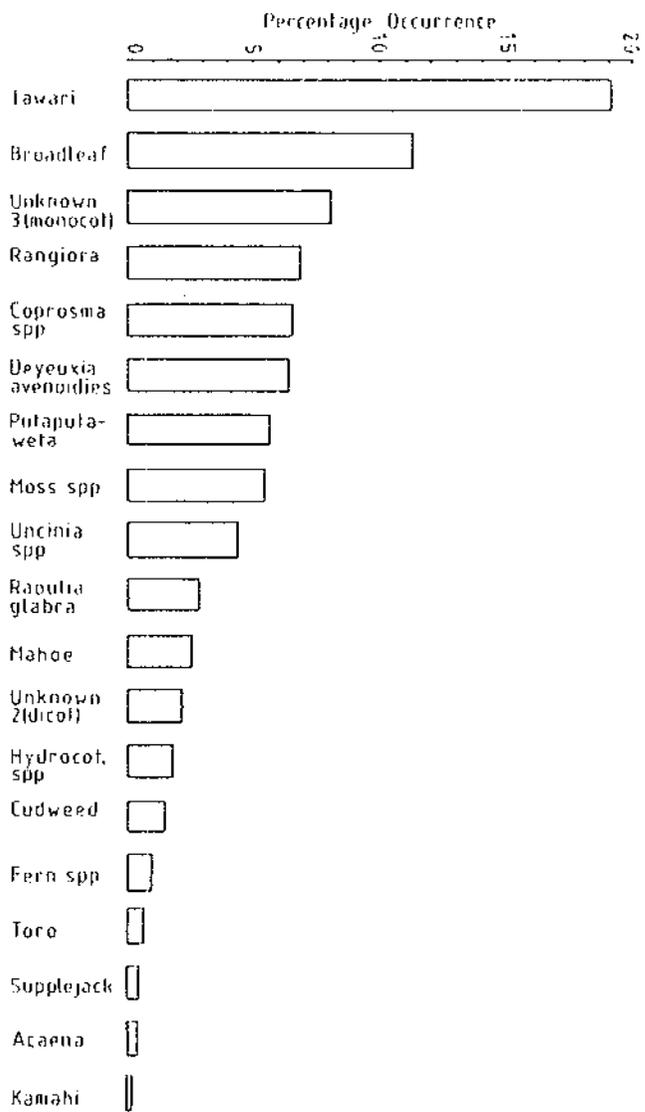


Fig. 3.3: Diet results for pasture/forest margin wallabies.

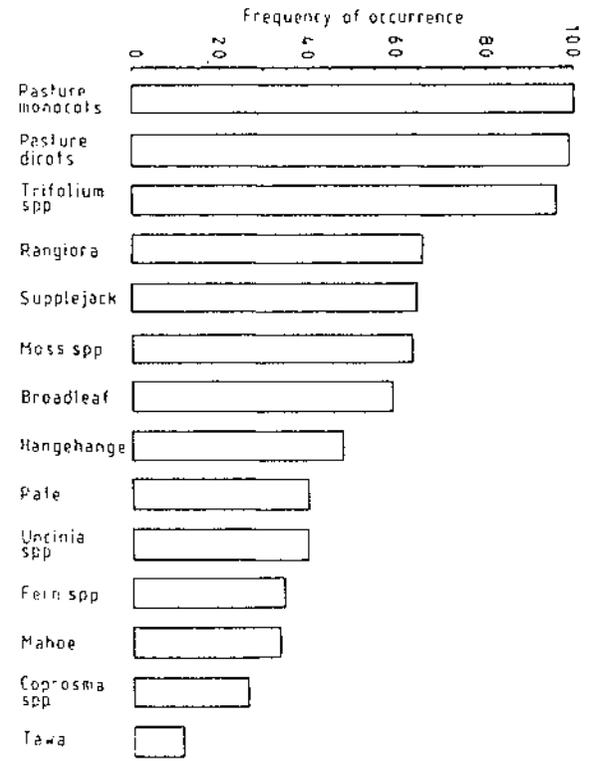
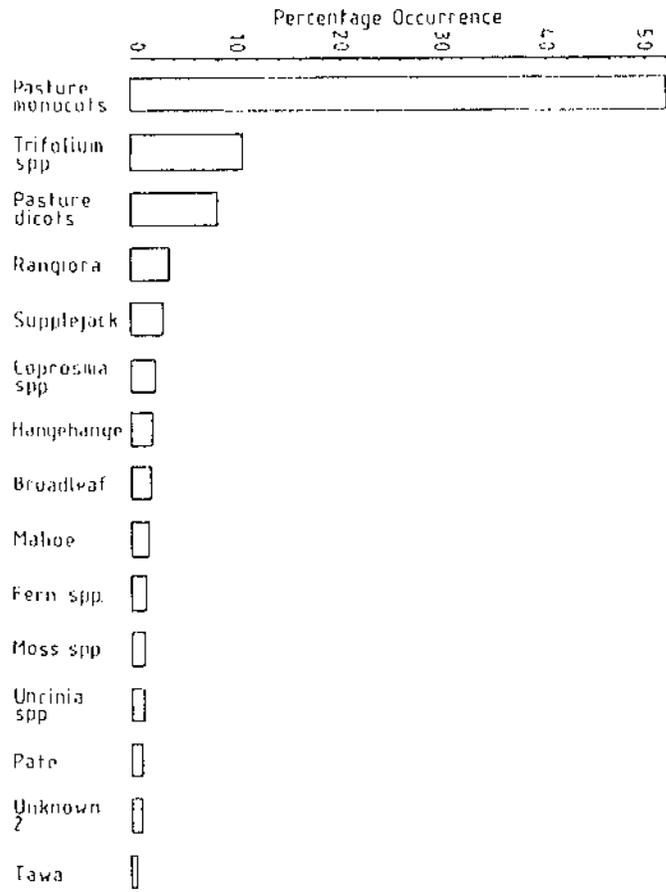


Fig. 3.4: Absolute mean area of cuticle for all habitats.

(a) Forest interior.

(b) Makatiti Dome

(c) Pasture/forest margin

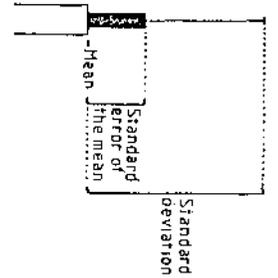
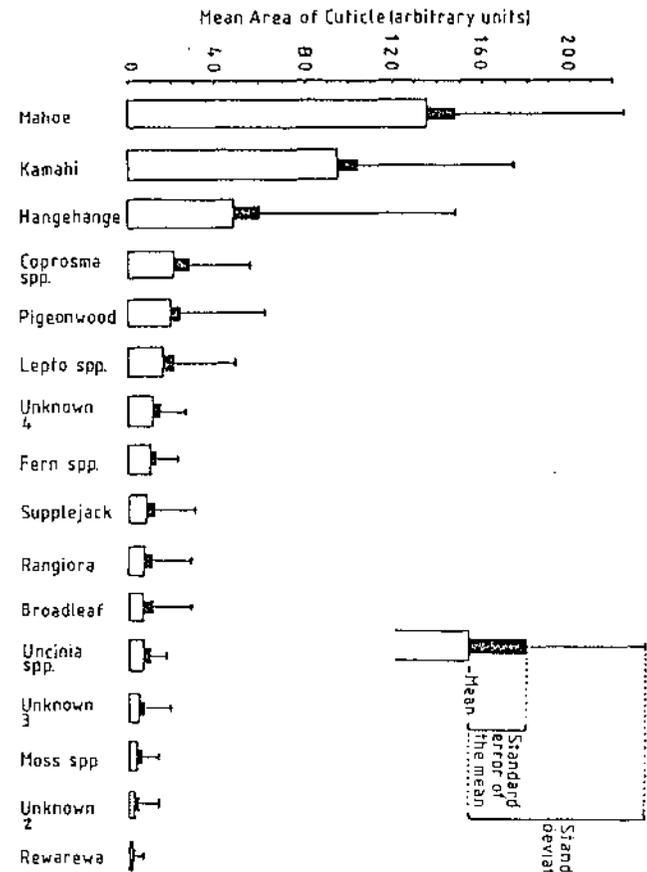
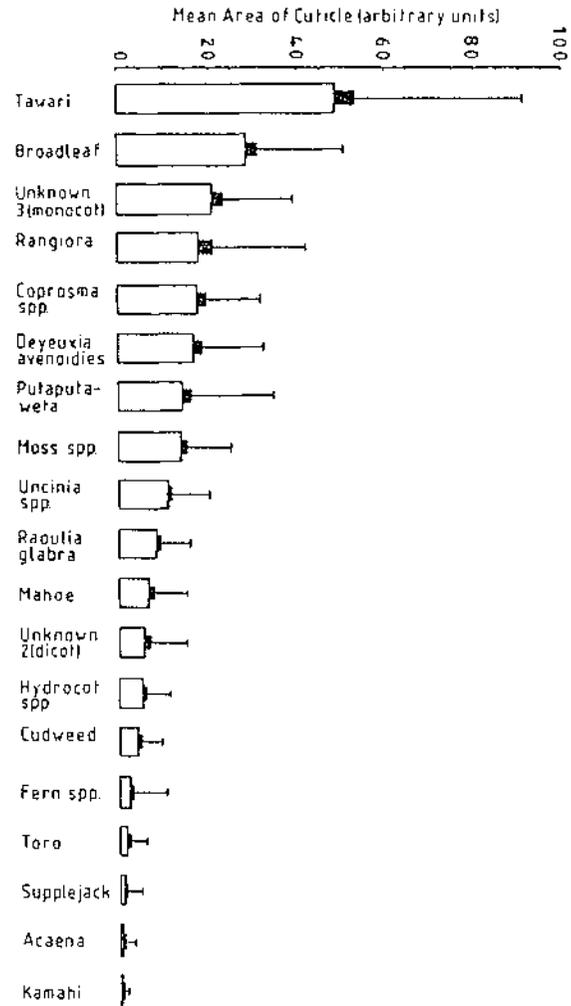
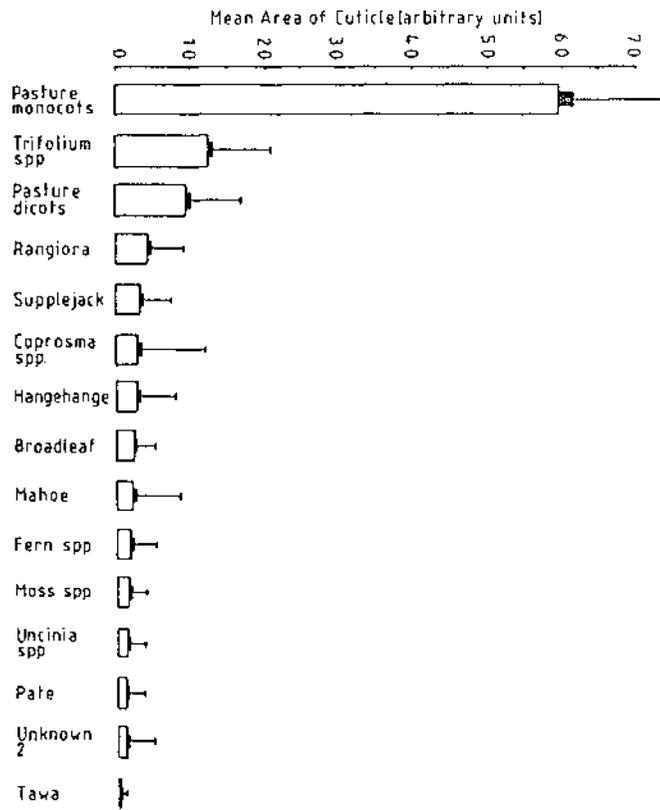
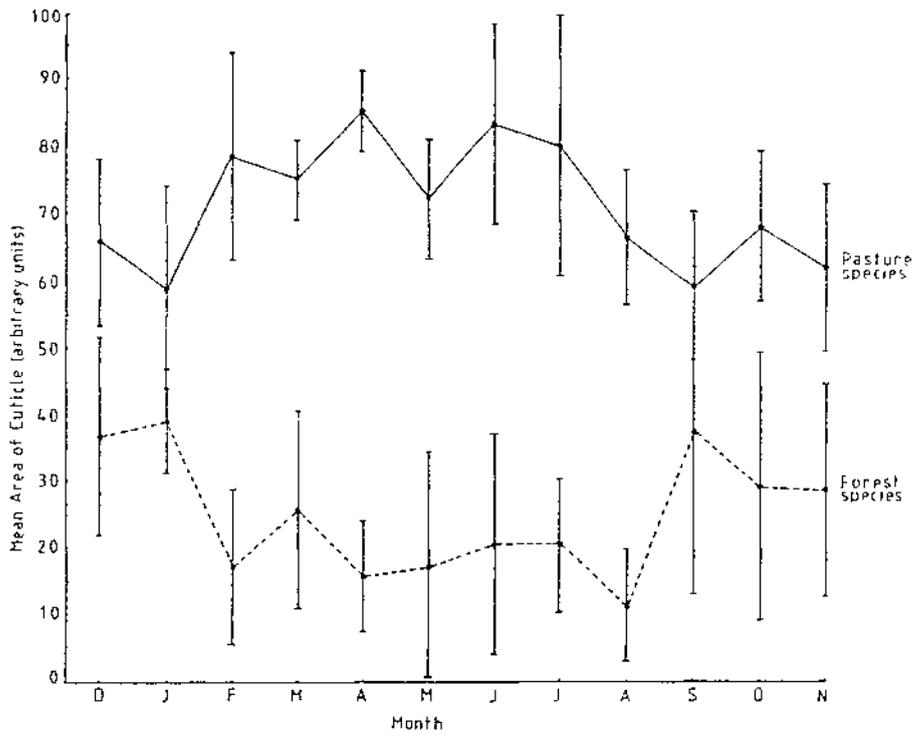
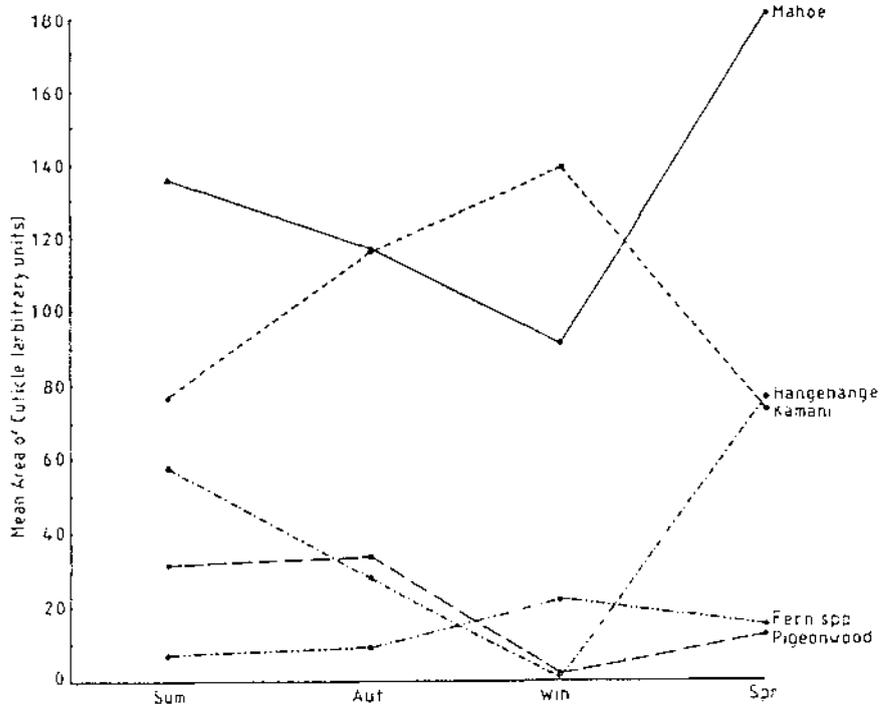


Fig. 3.5: Seasonal trends in major food types.

(a) Forest interior.

(b) Pasture/forest margin
Vertical lines indicate standard deviation.



Figures 3.1 and 3.4 summarise the diet analysis results from a sample of 57 wallabies shot within the forest proper. Frequency of occurrence results show that mahoe and kamahi are very highly preferred foods, being found in 98 and 96% of stomachs respectively. In quantitative terms (Fig. 3.1) more mahoe is eaten than kamahi (20.6% versus 29.3%). These two species alone contributed to on average 49.9% of identifiable material in the stomach; while 70% can be accounted for by mahoe, kamahi, hangehange (*Geniostoma rupestre*), *Coprosma* spp., pigeonwood and *Leptospermum* spp. (kanuka and manuka).

The cuticles from three commonly eaten plant species eluded identification. The most commonly occurring (Unknown 4) was from a dicotyledon and was not greatly dissimilar in form to mahoe. I believe Unknown 4 is likely to have been cuticle from some part of a plant included in the reference collection rather than a separate species, although there is no evidence to support this. Unknown 4 contributed on average to 2.8% of the total stomach contents. It was found in stomachs all year round and was not confined to any particular sex or age group.

Unknown 2 contributed to 1.2% of the stomach contents, was from a dicotyledon and was also found in stomachs from the Makatiti Dome and pasture/forest margin (see sections 3.2.2 and 3.2.3).

Unknown 3 was from an unidentified monocotyledon and was also found in the stomachs of animals from the Makatiti Dome. It contributed on average to 0.6% of stomach contents from forest dwelling wallabies.

Other identifiable fragments not included in Figs. 3.1 and 3.4 contributed on average to only 3.1% of identifiable stomach contents and are listed in Table 3.1 along with respective frequencies of occurrence.

Table 3.1: Minor food items in the diet of
forest living wallabies.

TABLE 3.1:

Food Item	Frequency of Occurrence
Unidentified seed fragments	17.5
Fivefinger (<i>Pseudopanax arboreum</i>)	14.0
Fragments of fruit or pith	12.3
Insect fragments	12.3
Toro	8.8
Pate (<i>Schefflera digitata</i>)	5.3
Tawa	5.3
Kohuhu (<i>Pittosporum tenuifolium</i>)	3.5
Mingimingi	3.5
Fuchsia (<i>Fuchsia excoaticata</i>)	3.5
Tawari	3.5
Bark fragments	3.5
<i>Oleria rani</i>	1.7
Tutu	1.7
Pukatea	1.7
Totara (<i>Podocarpus totara</i> or <i>P. hallii</i>)	1.7

On average 9% (by area) of stomach material was unable to be identified, with 8.2% being from dicotyledons and 0.8% from monocotyledons.

Monocotyledons contributed on average to only 3% of identifiable stomach material.

The number of different plant species found in each stomach was on average 12 (maximum = 17; minimum = 6; standard deviation = 2.3)

3.2.2 Diet of Makatiti Dome Wallabies

Stomach samples were taken from 282 wallabies and the results are summarised in Figs. 3.2 and 3.4.

Frequency of occurrence data (Fig. 3.2) show that all samples examined (each sample representing 3 animals) contained fragments of moss. Broadleaf and tawari were the next two most widely utilised food sources (99 and 96% respectively). However in more quantitative terms it is evident that tawari makes up the greatest proportion of identifiable stomach material (19.1%, with broadleaf making up 11.4%).

Monocotyledons (primarily Unknown 3, *Deyeuxia avenoides* and *Uncinia* spp.) accounted for 21.3% of identifiable cuticle area.

Access to a forest verge must provide a greater range of foods to choose from. Thus while more than 70% by area of identifiable plant material in the diet of forest wallabies can be accounted for by only 5 food types, it takes 9 plant species to make up the same fraction for Makatiti Dome animals.

Other identifiable foods not represented in Figs. 3.2 and 3.4 made up approximately 4.2% and the major of these are listed in Table 3.2 with respective frequencies of occurrence.

The proportion of unidentified cuticle in each sample was approximately 7%; 5% being from dicotyledons and 3% from monocotyledons.

Table 3.2: Minor food items in the diet of wallabies from the Makatiti Dome.

TABLE 3.2:

Food Item	Frequency of Occurrence
Fragments of unidentified seeds	19.0
<i>Ranunculus</i> spp.	18.0
<i>Epilobium</i> spp.	17.0
<i>Taraxacum</i> spp.	16.0
Pigeonwood	10.6
Pate	9.6
<i>Leptospermum</i> spp.	6.4
<i>Poa caespitosa</i>	6.4
<i>Leucopogon fraseri</i>	5.3
Fivefinger	5.3
Thistles (<i>Cirsium</i> spp.)	3.2
Wineberry	2.1
Toetoe (<i>Cortaderia</i> spp.)	2.1
<i>Erica lustricana</i>	2.1
Fragments of fruit or pith	2.1
<i>Oleria rani</i>	2.1
Ragwort (<i>Senecio jacobaea</i>)	2.1
Pepperwood	1.1
Tawa	1.1
Rewarewa	1.1

3.2.3 Diet of Pasture/Forest Margin Wallabies

Stomach samples were taken from 240 wallabies shot on pasture/forest margins, the results are summarised in Figs. 3.3 and 3.4.

Fig. 3.3 shows that all samples collected contained pasture grasses; 99% contained one or more pasture weed species; whereas clover (*Trifolium* spp.) had a 96% frequency of occurrence.

While there was a wide usage of some forest plants, primarily rangiora (66%), supplejack (65%), moss (64%) and broadleaf (59%), Fig. 3.3 shows that quantitatively there were considerably more pasture species consumed than forest species, with pasture grass making up 51.9% by area of identifiable fragments. The next most important food items were clover (10.4%) and pasture weeds (7.8%); thus 70.1% of identifiable stomach material consisted of pasture species whereas 18.5% was attributable to forest species. A further 4.3% of identifiable plant foods was not clearly attributable to either pasture or forest habitats; that is, these food items were found in both areas, for example *Uncinia* spp., moss and fern species.

The remaining 7.1% of stomach contents was unidentified.

As an adjunct, stomachs of a number of wallabies shot on pasture were weighed and the mean stomach weight of adult males was 0.6 kilos (standard deviation = 0.133; number weighed = 25) (see Chapter 10).

3.2.4 Diet of Exotic Forest Wallabies

Stomach material from exotic forest wallabies was found to consist almost entirely of various grass and weed species. The percentage occurrence for *Pinus radiata* foliage was 2.4% for males and 1.6% for females. That is, *P. radiata* was consumed in relatively small amounts. However it is important to note that samples collected here will not reflect any seasonal differential usage of *P. radiata*.

3.2.5 Diet in Relation to Season, Sex and Age

One-way analysis of variance was used to test for significant differences with season, sex and age. Multiple analysis of variance was not used because data was not sufficiently balanced, that is a large amount of data would by necessity have been omitted. The major reason for unbalanced data was the influx of yearlings into the samples during summer months (as they left the pouch).

One-way analysis of variance assumes a random sample from each population, equal variance and a normal distribution (Ryan *et al*, 1976). These authors noted that the most important of these assumptions is that of a random sample. The sampling techniques for diet analysis in this study are assumed to be random (see Appendix I).

The "equal variance assumption is not important if the sample sizes for the different samples are about the same,..." (Ryan *et al*, 1976). Sample sizes in this study for each season and for each sex are approximately equal, however in some data sets age is imbalanced. Note will be made where there is a likelihood of a type 1 error being made through violating the assumption of equal variance.

Ryan *et al* (1976) stated that "In practise the normality assumption is not too important...". Histograms of data used in this study gave no reason to assume the data was not approximately normal.

3.2.5.1 Diet in Relation to Season

Wallabies from the forest proper did show some variation in food preference with season (see Fig. 3.5). However the only significant difference was

in supplejack which was eaten more during winter months ($F = 3.82$; D.F. = 3/53; $P < 0.01$). There were apparent but non-significant differences in consumption of the two highly preferred species mahoe and kamahi ($F = 2.3$ and 2.2 respectively; D.F. = 3/53), the former being eaten more in spring whereas more of the latter was eaten during winter and autumn.

Wallabies from the Makatiti Dome showed significantly greater proportions of broadleaf in their diet during autumn ($F = 4.65$; D.F. = 3/90; $P < 0.01$), rangiora during winter ($F = 4.92$; $P < 0.01$), putaputaweta during winter ($F = 8.65$; $P < 0.01$), and *Uncinia* species during spring and summer ($F = 4.54$; $P < 0.01$).

Pasture/forest margin animals showed a significant difference in the proportion of pasture grasses with season ($F = 10.1$; D.F. = 3/76; $P < 0.01$) (see Fig. 3.5). Relatively more grass and more pasture plants ($F = 6.22$; D.F. = 3/76; $P < 0.01$) were consumed during autumn and winter, whereas significantly more forest species were eaten during summer and spring ($F = 2.82$; D.F. = 3/76; $P < 0.05$).

3.2.5.2 Diet in Relation to Sex

There were no significant differences in selectivity of food types between males and females for any of the habitats examined.

3.2.5.3 Diet in Relation to Age

Immature wallabies shot from within the forest were found to be eating significantly more moss than adults ($F = 8.99$; D.F. = 1/55; $P < 0.01$). However it should be noted that sample sizes were 17 for yearlings and 40 for adults; this difference in sample size may increase the likelihood of a type 1 error (see section 3.2.5.1).

Adults from the Makatiti Dome showed significantly more puatputaweta in their diet than juveniles ($F = 7.7$, D.F. = 1/92; $P < 0.01$) whereas juveniles showed a greater proportion of the grass *Deyeuxia avenoides* ($F = 13.16$; D.F. = 1/92; $P < 0.01$) and the herb *Raoulia glabra* ($F = 6.11$; D.F. = 1/92; $P < 0.05$) although once again it must be noted that sample sizes were markedly different (adults = 73, juveniles = 21).

There were no significant differences in the diet of adults and juveniles from pasture/forest margin habitat.

3.3 Discussion

3.3.1 Diet in Relation to Habitat

Sanson (1978) classified macropodine genera on the basis of dental morphology into 3 grades - browsing, grazing and intermediate. All members of the genus *Macropus* examined were classified as grazers. Hume (1982) when reviewing the work of Sanson noted that molar progression (which occurs in all *Macropus* species) is more characteristic of grazers than browsers and is a useful adaptation to the problem of tooth wear as a result of grazing. (Sanson defined graze as abrasive siliceous grasses often of high fibre content while browse was defined as soft unabrasive, low fibre herbage.) V. Vujcich (1979) reviewed literature and also concluded that in macropods the general feeding habit is that of grazing rather than browsing.

Inns (1980) and Hume (1982) described *M. eugenii* as a pastoral pest on Kangaroo Island. There are also other short anecdotes throughout published literature which reiterate the suggestion that the dama is a preferential grazer (eg. Andrewartha and Barker, 1969; Wodzicki and Flux, 1967; Kean, 1959). This suggestion has been confirmed by the few existing studies on diet.

Christensen (1980) for example examined the stomachs of 4 tammars (*M. eugenii*) from Boyicup (Western Australia); 3 had large amounts of monocotyledonous material (95, 90 and 50%) while only 1 stomach examined had no monocotyledonous material, with 95% being dicotyledonous with also a little fungal material. V. Vujcich (1979) examined faeces from 8 dama on Kawau Island and found grass to "...make up about half of the diet". The remainder comprised *Leptospermum scoparium* (28.4% of faecal material), weed species (4%) and an unidentifiable portion (17%). Kinloch (1973) also examined faecal pellets of damas on Kawau Island although

in less depth than V. Vujcich; that is the study was, by Kinlochs own admission "...restricted to an exploratory trial of the techniques". He examined 6 microscope slides from 2 samples of dama pellets and noted that identifiable cuticle fragments were "...almost entirely remnants of various species of grasses".

In summary then, *M. eugenii* appears well adapted to a grazing mode of life and available literature shows grass is a preferred food type.

While the above conclusion was also true for most wallabies examined in this study, it was apparent early that animals living within the Okataina Scenic Reserve were surviving in a habitat with a paucity of grasses. Results of diet analysis for this population are summarised in Figs. 3.1 and 3.4. It is noteworthy that monocotyledonous species makeup only a small proportion (3%) of stomach material.

At the time of writing there were no other known studies of wallaby diet within a true forest habitat and therefore nothing with which to make a direct comparison on palatabilities. It is useful to examine New Zealand diet studies of the possum (*Trichosurus vulpecula*), although similarities between damas and possums could extend little further than both being marsupials of a comparable size. Table 3 is a summary extracted from reputable sources indicating food taken by possums in mixed broadleaf forest. Most of these, kamahi and mahoe in particular, are favoured also by wallabies. Therefore it would seem that any damage caused by wallabies within indigenous forest might be comparable with that resulting from possums. (Fitzgerald (1976), and Meads (1978) have documented forest damage by possums.)

Wallabies from the Makatiti Dome consumed a much wider range of foods (see section 3.2.2), with a significant portion of these coming from track verges.

TABLE 3.3:

Author	Species Found Palatable By Both Possums and Forest-Living Wallabies
Mason (1958)	Kamahi, rangiora, supplejack, <i>Coprosma</i> spp., fivefinger, pigeonwood, <i>Leptospermum</i> spp.
Kean and Pracy (1949)	Kamahi, rangiora.
Gilmore (1966)	Mahoe, broadleaf (<i>Grislinia littoralis</i>) kanuka (<i>Leptospermum ericoides</i>).
Fitzgerald (1976)	Kamahi, mahoe, supplejack, hangehange.
Fitzgerald and Wardle (1979)	Kamahi, mahoe, supplejack, fern spp. pate (<i>Schefflera digitata</i>).
Leathwick <i>et al</i> (1983)	Kamahi, mahoe, rangiora, hangehange, fern spp., <i>Coprosma</i> spp.
Coleman <i>et al</i> (in press)	Kamahi, mahoe.

Table 3.3: Plants commonly eaten by both possums
and wallabies.

Therefore animals in this habitat approach more closely a grazing lifestyle. However grass species still constitute only a little over 21% of identifiable stomach material.

Most plant species eaten by true forest living wallabies were also represented in the diet of animals from the Makatiti Dome (eg. mahoe, kamahi, *Coprosma* spp., *Leptospermum* spp., fern spp., supplejack, rangiora, broadleaf, *Uncinia* spp., and moss spp.). However they differ in both proportion and amount. A probable reason for the former is that the availability of species differs because of a dissimilar forest type on the Makatiti Dome (see section 2.3). Whereas the lesser amounts of forest species represented in the diet probably reflect a wider selection of food types and preferential selection of verge species.

Diet analysis of pasture/forest margin wallabies largely confirms previous findings; given access to a wide selection of grass species, wallabies are preferential grazers (ie. 70% of the identifiable cuticle in stomach material examined consisted of species found on pasture).

Coleman *et al* (in press) find that pasture foods comprise 12% of the foliage eaten by possums living within 300m of the forest interface, with 90% of this being clover and grasses. However some caution is required when comparing my results with those of Coleman *et al*. These researchers examined faecal pellets which may represent diet over a wider time period than the stomach analysis used in this study, moreover the two areas are geographically widely separated. Stomach samples from wallabies were taken from animals shot on pasture (some of Coleman *et al*'s possums were also trapped on pasture) and therefore may under-represent forest species consumed during other feeding periods. (As noted in Appendix II stomachs are unlikely to contain

material from greater than 12 - 15 hours previous.) Nevertheless it is pertinent to note that faecal analysis combined with the particular acid maceration techniques used by Coleman *et al* may under-represent the frequency of grass and clover species. With this caveat in mind, evidence here suggests that wallabies living on a pasture/forest margin rely more heavily on pasture foods than possums in a comparable situation. Such an hypothesis is credible when the arboreal habits of the possum and the wider range of food types such a lifestyle must offer are considered.

Although pasture margin wallabies were found to consume largely pasture species, several forest species were also represented in the diet. Most of these were also consumed in both the Makatiti Dome and true forest habitats; ie. rangiora, supplejack, *Coprosma* spp. broadleaf, mahoe, fern spp., moss, *Uncinia* spp., and tawa (the latter being consumed in only exiguous proportions in all habitats). Importantly the presence of such foods suggests that feeding is not restricted to the time spent out on pasture. This is supported by observations on three separate occasions when wallabies were seen browsing during daylight hours. V. Vujcich (1979) when referring to *M. eugenii* and *M. parma* on Kawau Island stated that "There is a restricted amount of feeding by both species throughout the day." But as noted by Inns (1980) and V. Vujcich (1979) and also as supported by observation in this study the major feeding activity is from late afternoon to early morning.

Jane (1979) when discussing the dama in Rotorua noted that "Wallabies pose some problems in exotic forest establishment...". Wodzicki and Flux (1967) when referring to *M. eugenii* reported that "They are blamed for damage to newly planted pines on Kawau and as many as 3,000 were shot and poisoned in one year by local land-owners."

In the exotic forest examined during the present study wallabies were found to be eating primarily weeds, grasses and only a small percentage of *Pinus radiata*. However as noted in section 3.2.4 samples examined were from within a single season. Therefore wallabies may consume more or less *P. radiata* in other seasons. It is perhaps noteworthy that Warburton (1978) found possums to consume a greater proportion of pine needles during winter than spring or autumn, whereas needles were not found in stomachs at all during summer. Nevertheless the relatively low percentage of pine foliage in wallaby stomachs is not altogether surprising when the nature of Rotoiti Forest is considered. As noted in section 2.3.4 in addition to *P. radiata* there is an abundance of weeds, grasses and other seral vegetation. As noted by McNally (1955) when discussing the black-tailed wallaby (*Wallabia bicolor*) it seems probable that wallabies only attack pines when normal foods are in short supply, such as subsequent to clearing of the forest prior to planting. In the present study usual foods for *M. eugenii* in marginal situations were found to be grasses and herbaceous dicotyledons (see sections 3.2.2 and 3.2.3). Thus such foods are likely to be in short supply following burning or other clearing practises during the initial establishment of exotic plantations. At such times browsing pressure on *P. radiata* may become significant.

In summary, investigation here shows that *P. radiata* is palatable to wallabies but also suggests that at present in Rotoiti Forest, it is being consumed in relatively meagre amounts.

3.3.2 Diet in Relation to Season, Sex and Age

Variation in diet with season has been documented for possums by Warburton (1978), Fitzgerald and Wardle (1979) and Coleman *et al* (in press), the latter authors having additionally demonstrated that some differences are dependent on altitude and sex. V. Vujcich (1979) found that "Faeces from *M. parma* showed no radical seasonal changes in diet".

With forest living wallabies in the present study only supplejack showed a statistically significant variation in amount eaten with season (most was eaten during autumn). Yet it should be noted that this difference could be more an aberration of the data rather than a true seasonal preference. That is, supplejack showed a low frequency of occurrence (see Fig. 3.1) and percentage occurrence (see also Fig. 3.1) relative to other foods.

Amounts of mahoe and kamahi (the two most preferred food types for the forest habitat) fell just short of being statistically different for each season. This variation with season is shown in Fig. 3.5.

Fig. 3.5 supports the hypothesis presented in this study (see Chapter 9) that wallabies get much of their food from leaf litter on the forest floor. Within the kamahi forest types, the frequency of kamahi and mahoe seedlings within browse height was found to be almost nil (Llewellyn, 1985b; Chapter 9) although these species still feature prominently in the diet.

Cowan *et al* (1985) examined seasonal leaf-fall in a podocarp/broadleaf forest in the Orongorongo Valley. It is realised that any correlation between leaf-fall and peak of consumption in the diet of wallabies may be purely coincidental and further it may not be fair to

compare leaf-fall in such geographically isolated areas. Nevertheless, there is evidence to suggest leaf-fall is utilised by wallabies and a comparison may have some relevance. Cowan *et al* showed that the maximum leaf-fall for mahoe was in spring and summer, which coincides with peaks of mahoe in the diet of wallabies (Fig. 3.5). The peaks of consumption of kamahi do not however match up with leaf-fall data as well as for mahoe, with Cowan *et al* recording maximum leaf-fall in summer and autumn, whereas wallabies were found to eat most kamahi in autumn and winter. The other species noted by Cowan *et al* which was also consumed by wallabies was pigeonwood, leaf-fall being greatest in summer and least in winter. This is similar to seasonal proportions in wallaby diet.

I do not think diet could realistically be expected to reflect exactly leaf-fall data, because wallabies are in all likelihood browsing seedlings as well as leaf litter, and also may actively search out certain palatable species at times when their concentration in leaf litter is low. In addition to this, certain leaves may be unpalatable at some times of the year regardless of their concentration in the litter layer. Nevertheless the leaf-fall data of Cowan *et al* appears to support the hypothesis that wallabies browse leaf litter.

Makatiti Dome animals showed some significant differences in seasonal food preference. Rangiora and putaputaweta were winter foods whereas broadleaf was eaten more during autumn and *Uncinia* spp. during summer and spring. Such information is useful should natural vegetation poisoning such as suggested by Warburton (1983) be considered as a means of control. However it should also be noted that wallabies on the Makatiti Dome show considerable preference for grazing small verge species, and the effectiveness of using large leaved dicots as vectors for 1080 gel may be reduced, compared to potential kills for strictly forest animals.

Pasture/forest margin wallabies ate proportionately more pasture plants and less forest species during autumn and winter (see Fig. 3.5). Possible reasons for this difference may be that longer days during summer and spring lead to less time being spent out on pasture. Also there may be a drop in the rate of growth and therefore quality of pasture grass during summer. This was suggested by V. Vujcich (1979) as a reason for the apparent drop in grass species found in faeces of *Macropus parma* during summer.

That no significant difference in diet between the sexes was found is not altogether surprising, considering the sociality of the dama. M. Vujcich (1979) made several references to strong grouping behaviour by damas. Also Christensen (1980) noted that *M. eugenii* appears to be "group-territorial" and also found that, "Family units comprising a male, a female and a sub-adult were occasionally caught together in the traps". Inns (1980) found no significant differences in mean home range size between male and female Kangaroo Island wallabies in either summer or winter. Therefore male and female wallabies will encounter largely the same food types during feeding periods.

Results from the present study suggest that there are no markedly different nutritional demands between the sexes, or at least that these are catered for within the same range of food types.

Although there is some doubt about the validity of statistical tests for variation in diet between adults and immature animals, the data implies that immature animals might consume more "graze" and less "browse". That is more moss, grass (*Deyeuxia avenoides*) and the herb *Raoulia glabra* and less of the shrub putaputaweta.

3.4 Summary

Investigation of available literature suggests that the dama wallaby is a preferential grazer and this conclusion is supported by results from the present study. Grass species will be represented in the diet in proportion to their availability; that is with wallabies shot on pasture/forest margins in this study more than 70% of identifiable stomach material consisted of pasture species. However diet analysis also showed that wallabies are able to survive in forest situations without access to pasture, in such areas examined here monocotyledonous plant species only constituted 3% of stomach contents. Kamahi and mahoe were found to be highly preferred foods, comprising on average almost 50% of identifiable stomach material; these two species along with hangehange, *Coprosma* spp., pigeonwood and *Leptospermum* spp. (kanuka and manuka) made up 70%. The average number of plant species found in the stomachs of forest living wallabies was 12.

Diet was also examined for wallabies from a habitat considered to be intermediate in terms of availability of grasses and verge species between pasture margin and forest interior. Here over 19% of identifiable stomach material consisted of tawari which is a common canopy species, while more than 11% was accountable to broadleaf. Monocotyledonous species comprised over 21% which is an intermediate percentage between the other two habitats and must reflect availability.

The present study also suggests that wallabies in forest situations may rely upon leaf-fall to supply some foods, in particular kamahi and mahoe.

A brief review of literature shows that dama wallabies in forest situations consume many plant species also preferred by New Zealand's most ubiquitous

marsupial, the possum. Thus an important consideration is the potential for combined effects of both these animals on forest ecosystems.

Wallabies were found to show some seasonal preference for certain foods, that is, pasture species were eaten more during winter and autumn relative to forest species. For wallabies from the Makatiti Dome rangiora and putaputaweta were found to be winter foods, with more broadleaf eaten in autumn, and *Uncinia* spp. preferred in spring and summer. For forest animals apparent but non-significant differences were found in consumption of the two highly preferred food types, that is mahoe was eaten more in spring, whereas kamahi was preferred in winter and autumn.

No significant difference was found between plant species eaten by males and females, although there is some evidence that juvenile animals consume less browse than adults.

Pinus radiata was shown to be palatable to wallabies living in young exotic forest but was only eaten in relatively meagre amounts. The suggestion that wallabies are only likely to present problems to exotic forest early in establishment when alternative foods are not available is reiterated here.

Plate 11: An open understorey beneath a kamahikanuka canopy. Note the presence of largely unpalatable seedlings (rewarewa and mangeao).

Plate 12: Probable wallaby browse on *Uncinia* spp.



CHAPTER FOUR

AGE STRUCTURE

4.1 Aging

Heads from shot animals were removed, skinned and a numbered metal tag wired through one orbit. The skulls were then either stored in formaldehyde or frozen.

Skulls were cleaned by boiling in a large vat. The exact time of boiling was not consistent for all skulls. That is, whereas frozen skulls from immature animals were clean after only four hours, those skulls stored in formaldehyde and from mature animals required overnight boiling. After boiling the skulls were picked clean of flesh and the lower jaw removed.

The method of aging followed that of Kirkpatrick (1964) and utilised the device invented by Knowlton (1984). Briefly, skulls were held in palatal view by Knowlton's device and a sighting taken across the anterior rim of the orbits. From this sighting line it is then possible to numerically describe forward progression of the molar row. This "molar index" is directly related to age (Kirkpatrick 1964).

Aging technique was standardised with that used by DSIR Ecology Division.

4.2 Results

Inns (1982) noted that "...it would seem that molar progression still remains the best method of aging macropods beyond the stage of full tooth eruption". In the same publication Inns stated that "Molar progression in the Kangaroo Island wallaby was linearly related to log age and could be used to age animals up to about 14 years."

Dudzinski *et al* (1977) in a study on agile wallabies, *Macropus agilis*, concluded that molar progression is more accurate than molar eruption for determining age, because it is objective and has narrower confidence limits. Kirkpatrick (1965) stated that "Molar index can be relied on into old age." However as noted by Sharman *et al* (1964) "Unfortunately the forward movement of the molar row in the jaw slows down with advancing age". Therefore older animals will show relatively smaller increments in molar index for each year than young animals. Thus I think variability in molar row movement between animals, observer error, and differences in exact date of birth (note the spread in Fig. 7.1) are all likely to become more significant when dealing with older animals. This is apparent in Fig. 4.1 which collectively shows molar index readings for all animals aged during this study*. The first year cohort (leaving the pouch about December) is very obvious and the increase in molar index over the year is clearly seen. The cohort of the previous year is also visible as a peak (particularly in the July month where N is largest) although after the third year, individual cohorts are not so easily recognised. Although this is probably in part a result of less available data for older animals.

Regression equations used by other workers to convert molar index to absolute age tend to rely on small samples of known age animals (Kirkpatrick (1964)

used 26 grey kangaroos) and describe different populations to the one in this study. Because of these factors and in the light of the possible variances encountered when dealing with older animals it was not considered appropriate here to attempt to convert molar index results to absolute age.

However because molar index does appear to separate yearly cohorts until at least the third year it was decided that for the purposes of constructing age pyramids (Fig. 4.2) molar index results would be separated into age classes approximating these yearly cohorts. Age classes were chosen using the regression equation of Inns (1980) calculated from known age *M. eugenii* on Kangaroo Island. Inns used the age classes 1-2, 2-3, 3-4, 4-5 and older than 5 years. These will be used in this study, and the corresponding molar index will also be given.

* Females from the month of July were aged by J. Whyte of DSIR Ecology Division, and I am grateful to R. Sadleir for making these results available for use in this thesis. This data is also used in Fig. 4.2 (females from exotic forest).

Fig. 4.1: Cumulative age distribution.

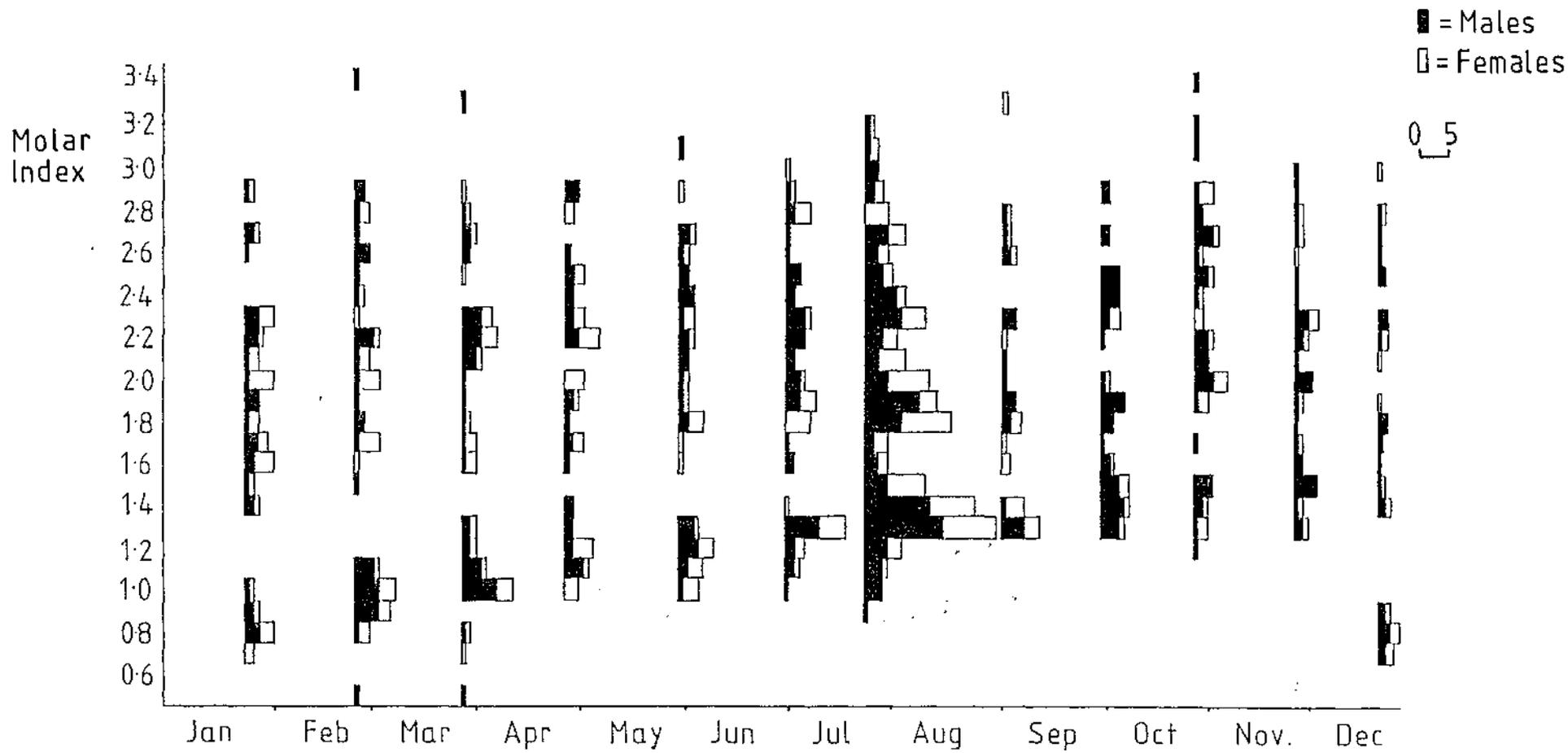


Fig. 4.2: Age pyramids for all habitats.

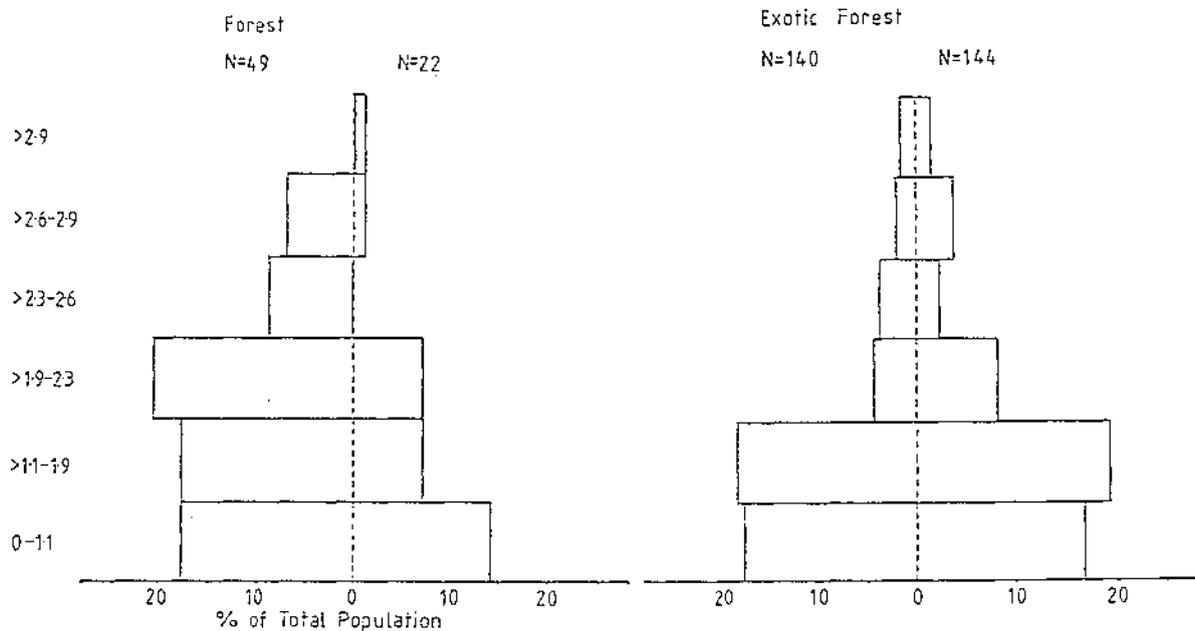
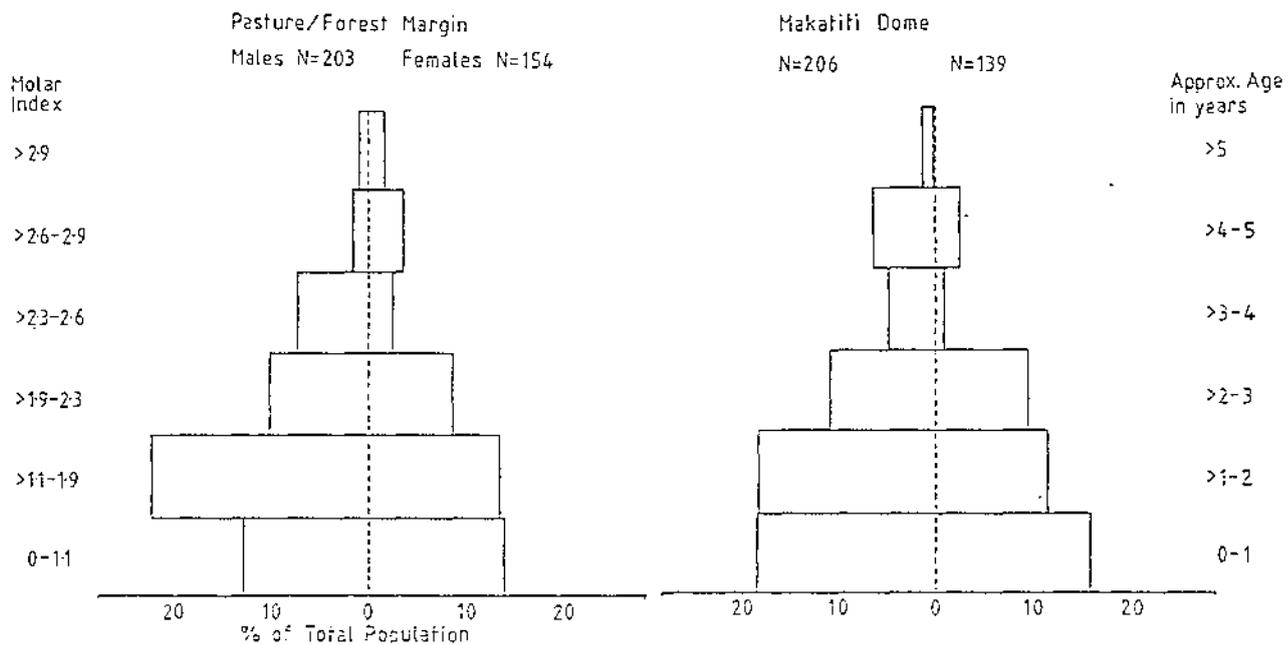


Table 4.1: Age structure for Kangaroo Island wallabies caught between 1975-78 (from Inns, 1982).

4.3 Discussion

Table 4.1 is part of a table reproduced from Inns (1980) and represents a useful comparison with age data from the present study. It is noteworthy that the sample of Inns showed a much larger proportion of older animals than samples from Rotorua, particularly in the "older than 5" age class (see Fig. 4.2). Such a discrepancy is likely to result from either different sampling techniques or actual differences in age structures. Kangaroo Island wallabies were captured by driving into "fence-traps" then caught with hand nets. I see no reason why older wallabies should be caught by this method yet escape being shot in the samples collected during the present study. Thus I think it credible to suggest that Rotorua animals on average do not attain similar ages to those in the population studied by Inns (1980). Inns noted that predation is unlikely to be a major factor in the mortality of Kangaroo Island wallabies as the only large predator is the wedge-tailed eagle (*Aquila audax*). Whereas in Rotorua, wallabies are routinely shot for sport and because of pest status. This hunting pressure which does not exist in the "... large undisturbed population in Flinders Chase National Park,..." (Inns, 1980) could be a factor in reducing the proportion of older animals in the Rotorua population.

Age pyramids for populations in this study indicate fairly even mortality throughout the age classes, a characteristic also found by M. Vujcich (1979) for dama on Kawau Island. A similar age distribution to that of the present study was also found by Maynes (1977) for a sample of 33 *M. eugenii* also from Kawau.

Fig. 4.2 shows similar age distribution for all habitats. Although the sample from exotic forest appears to contain a greater proportion of younger animals, this may reflect greater hunting pressure (which might reduce

5.1 Methods

Body measurements were used as follows:

1. Skull length and width (also equivalent to basal length and width, (Wodzicki and Flux, 1967)). Points on the skull used to read off these measurements were standardised against DSIR Ecology Division (A.J. Whyte, personal communication). Skull length was taken from the anterior edge of the foramen magnum to the anterior tip of the palate. That is, between the two foremost incisors, which usually had to be removed. Skull width was measured at the widest point of the zygomatic arches. Vernier calipers were used to read both length and width.
2. Total body length (TBL). Here a flexible nylon tape measure was placed along the centre of the animals back and a reading taken from the tip of the tail to the tip of the nose.
3. Tail length (TL). Again using a nylon tape measure this was recorded as that distance from the posterior tip of the tail to the base of the tail on the ventral side.
4. Hindfoot length (HFL). This was measured from the heel of the foot to the tip of the central toenail.
5. Weight. Wallabies were weighed using one of several Salter spring balances (each balance catering for a different range of weight); the animals were not eviscerated before weighing.

TBL, TL AND HFL were all standardised against DSIR Ecology Division (R. Sadleir, personal communication).

5.2 Results

Body measurements were collected from 1076 wallabies and the results are summarised in Appendix.V.

There is a very noticeable difference in animal size between habitats. That is, the largest animals were collected from pasture/forest margin, and in order of decreasing size were those from exotic forest, Makatiti Dome, and the forest proper.

Discriminant function analysis was used statistically to distinguish between habitats in order of size. That is by utilising all discriminating variables (body measurements) the groups (habitats) were made to be as statistically significant as possible. Discriminant analysis does this by using one or more linear combinations of the discriminating variables. These "discriminant functions" are formed in a way which maximises the separation of the groups (Nie *et al*, 1975).

SPSS-X (Statistical Package for the Social Sciences) was used for discriminant analyses. The program has two selection methods available for the analysis; namely Stepwise and Direct. The former uses the discriminating power of each variable to choose the set of variables which best discriminates between the groups. The Direct method which was used here creates discriminant functions directly from the entire set of independent variables (Nie *et al*, 1975).

Tables 5.1 and 5.2 summarise the results of discriminant analysis. Eigen values and associated canonical correlations describe the relative ability of each function to separate the groups. For example the third discriminant function for male adults has an eigen value of 0.02664 which indicates that there is still some discriminating power in this function although not as much as the first or second.

Wilks Lambda and associated chi-squared tests of statistical significance describe how much discriminating power remains as each function is removed. The larger lambda, the less discriminating power present. Thus, from Table 5.1 it is evident that although Wilks Lambda after removing functions 1 and 2 is 0.974, there is still significant discriminating power at 0.05 ($\chi^2 = 10.594$; D.F. = 4).

The separation between the groups can also be shown visually by using the discriminant functions as axes and plotting mean discriminant scores for each group. Using only 2 discriminant functions gives a visual representation as in Figs. 5.1 and 5.2. The group centroids are shown as asterisks. Figs. 5.1 and 5.2 show that although there is a significant separation between the groups there is still a large overlap.

Discriminant analysis was also used to examine data for immature animals, however the only significant function derived was that describing a significant size difference between immature males from exotic forest and the other three habitats. However this difference is almost certainly a result of a biased (all juveniles from exotic forest were collected during one sampling period) and small (N = 15) sample. The discriminant functions for immature females were not significant.

Table 5.1: Discriminant analysis results for male
adult wallabies.

TABLE 5.1:

Function	Eigenvalue	Percent of Variance	Canonical Correlation	Wilks Lambda	Chi-squared	D.F.	Significance
1	0.33867	64.49	0.50298	0.6273	187.910	18	0.0000
2	0.15987	30.44	0.37126	0.8398	70.362	10	0.0000
3	0.02664	5.07	0.16108	0.9740	10.594	4	0.0315

TABLE 5.1 (Continued):

Standardised Canonical Discriminant Function Coefficients

	Function 1	Function 2	Function 3
Weight	1.132	1.725	-0.414
TBL	0.335	-0.180	1.554
TL	-0.046	-0.542	-0.082
HFL	0.904	-0.025	-0.800
Basal length	-1.184	-0.055	-0.132
Basal width	-0.442	0.114	0.382

Canonical Discriminant Functions Evaluated at Group Means

Group	Function 1	Function 2	Function 3
Forest	-0.795	-1.144	0.076
Makatiti Dome	-0.664	0.345	-0.029
Pasture/forest	0.469	0.050	0.164
Margin			
Exotic forest	0.505	-0.134	-0.268

Table 5.2: Discriminant analysis results for female adult wallabies.

TABLE 5.2:

Function	Eigenvalue	Percent of Variance	Canonical Correlation	Wilks Lambda	Chi-squared	D.F	Significance
1	0.520	78.12	0.5848	0.574	94.51	12	0.0000
2	0.146	21.88	0.3564	0.873	254.76	5	0.0002

TABLE 5.2 (Continued):

Standardised Canonical Discriminant Function Coefficients

	Function 1	Function 2
Weight	0.3440	0.898
TBL	0.2120	-0.254
TL	0.4850	-0.018
HFL	0.6760	0.161
Basal length	-0.9110	-0.030
Basal width	0.0695	0.655

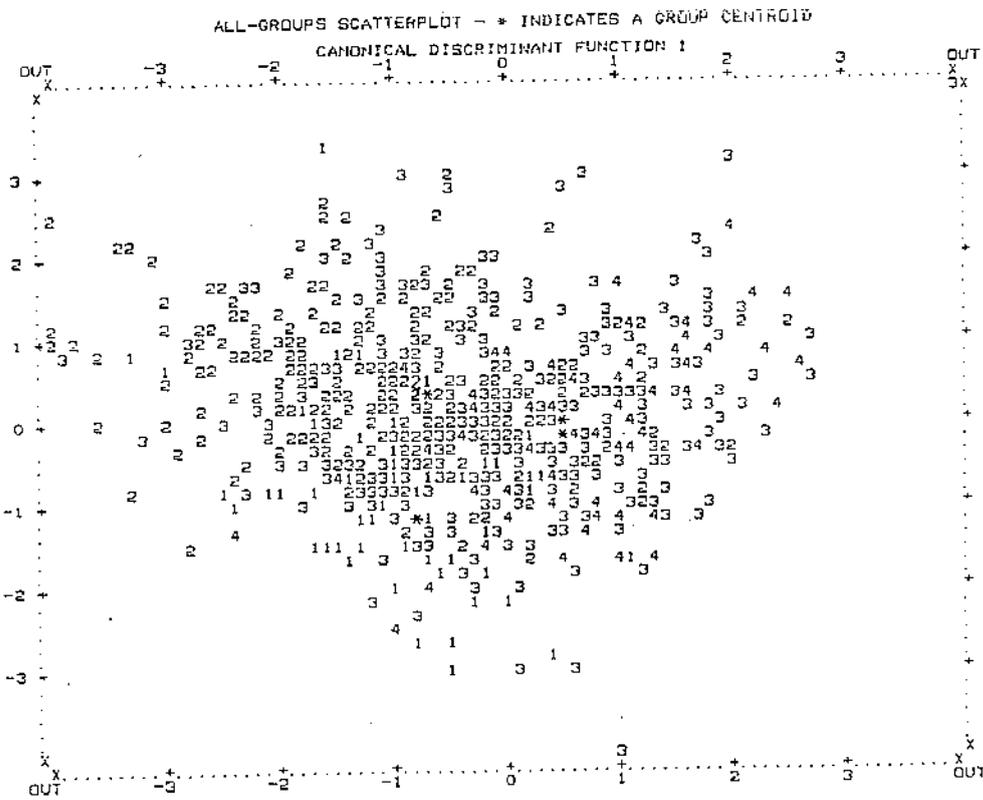
Canonical Discriminant Functions Evaluated at Group Means

Group	Function 1	Function 2
Forest	-0.462	-1.467
Makatiti Dome	-0.955	0.182
Pasture/forest	0.567	0.048
Margin		

Fig. 5.1: All groups scatterplot of canonical discriminant functions for male adults.

Group 1 = Forest interior
2 = Makatiti Dome
3 = Pasture/forest margin
4 = Exotic forest

Fig. 5.2: All groups scatterplot for female adults.



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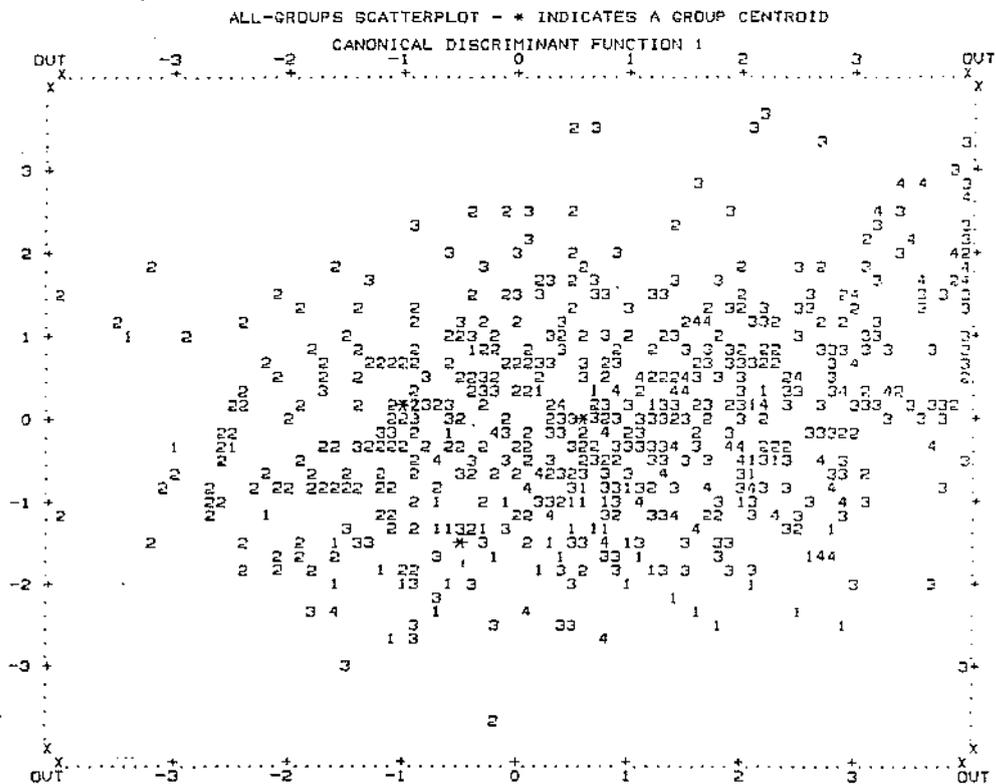
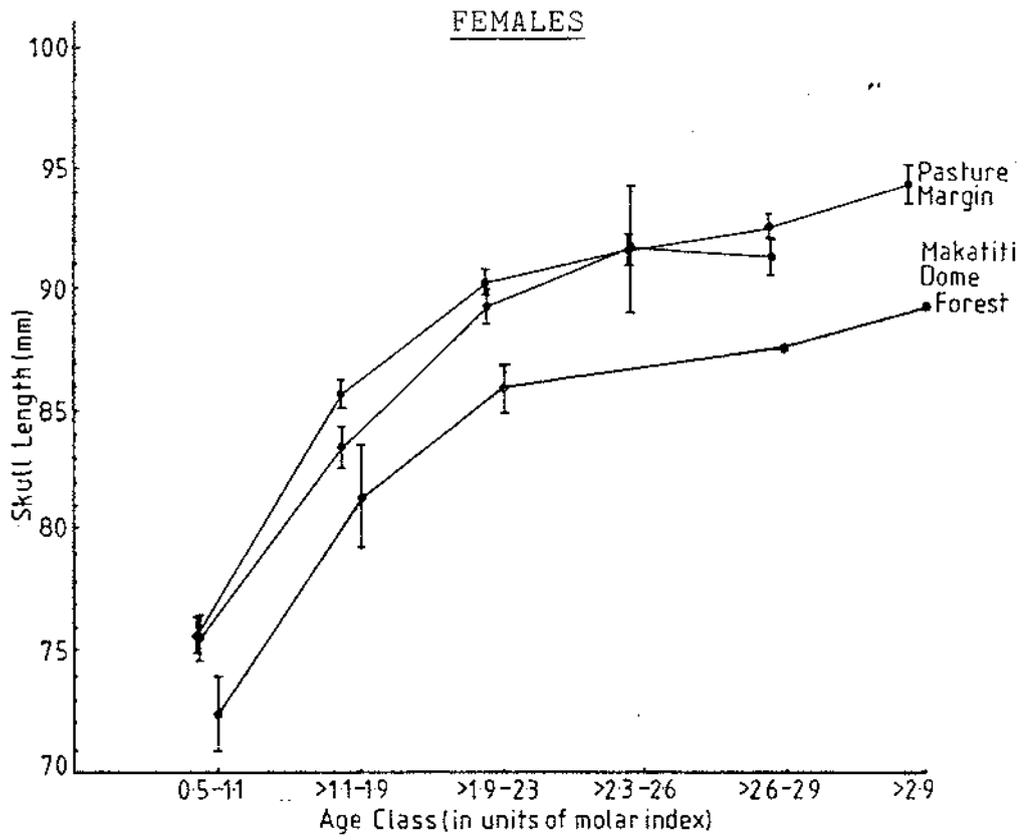
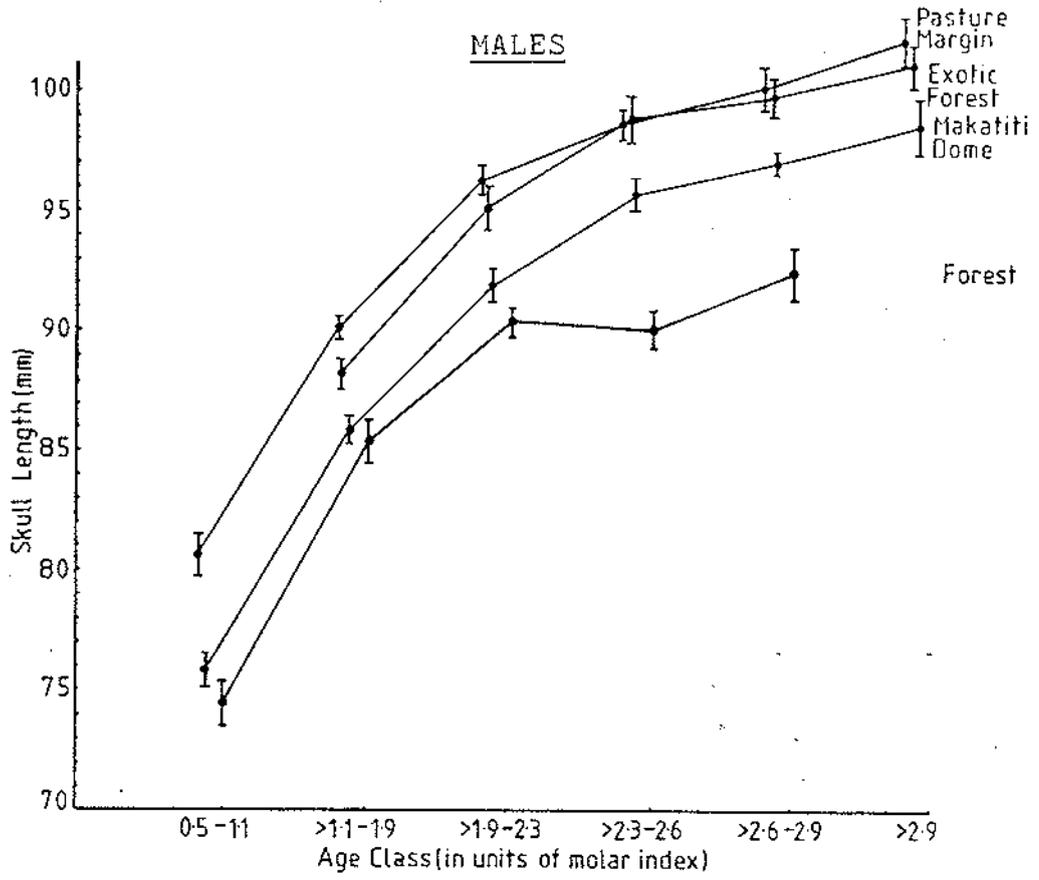
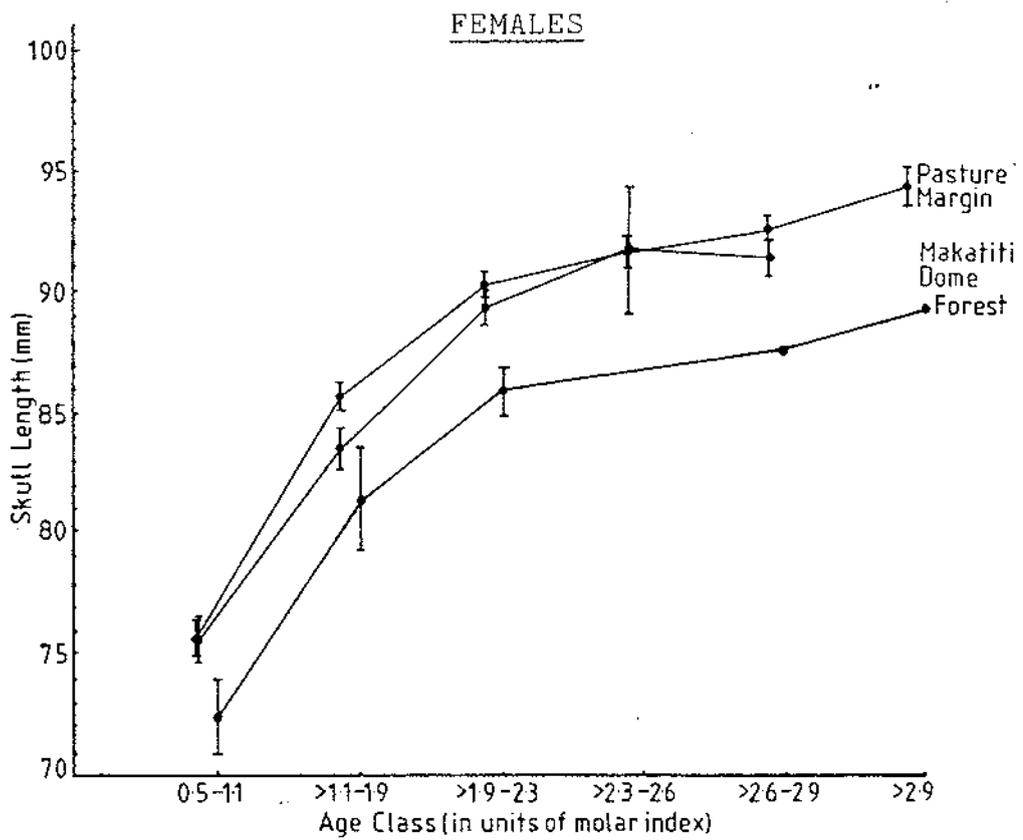
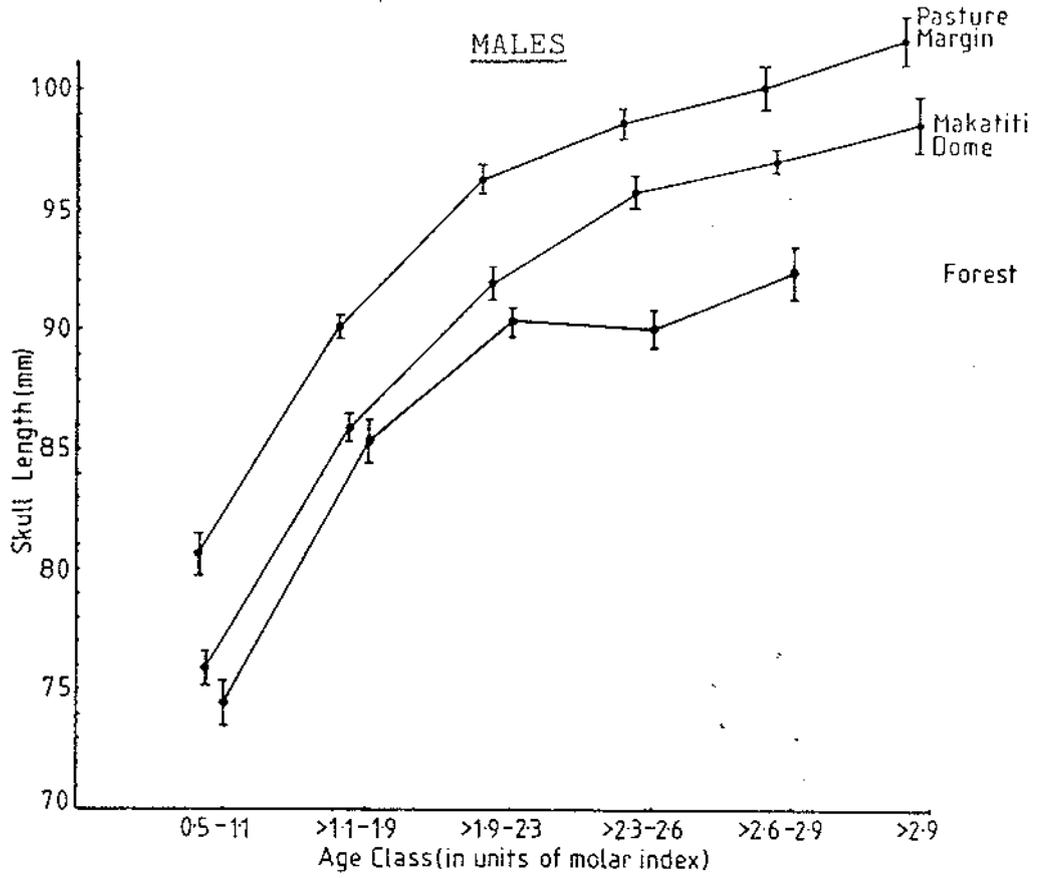
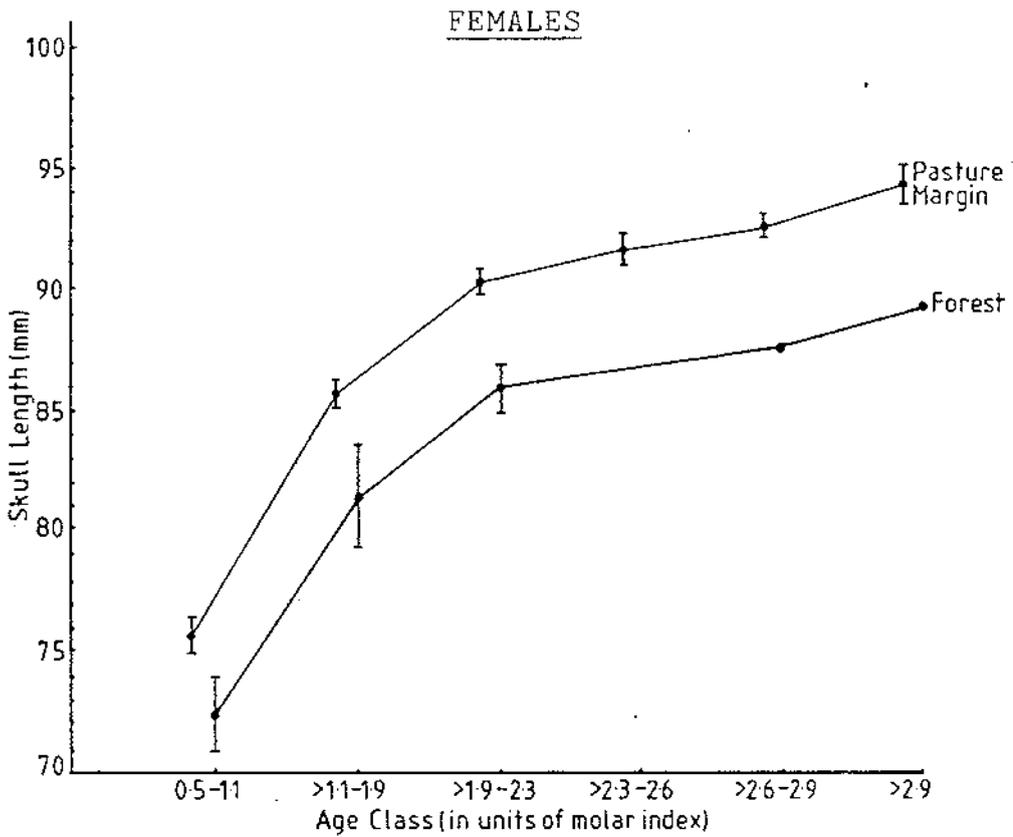
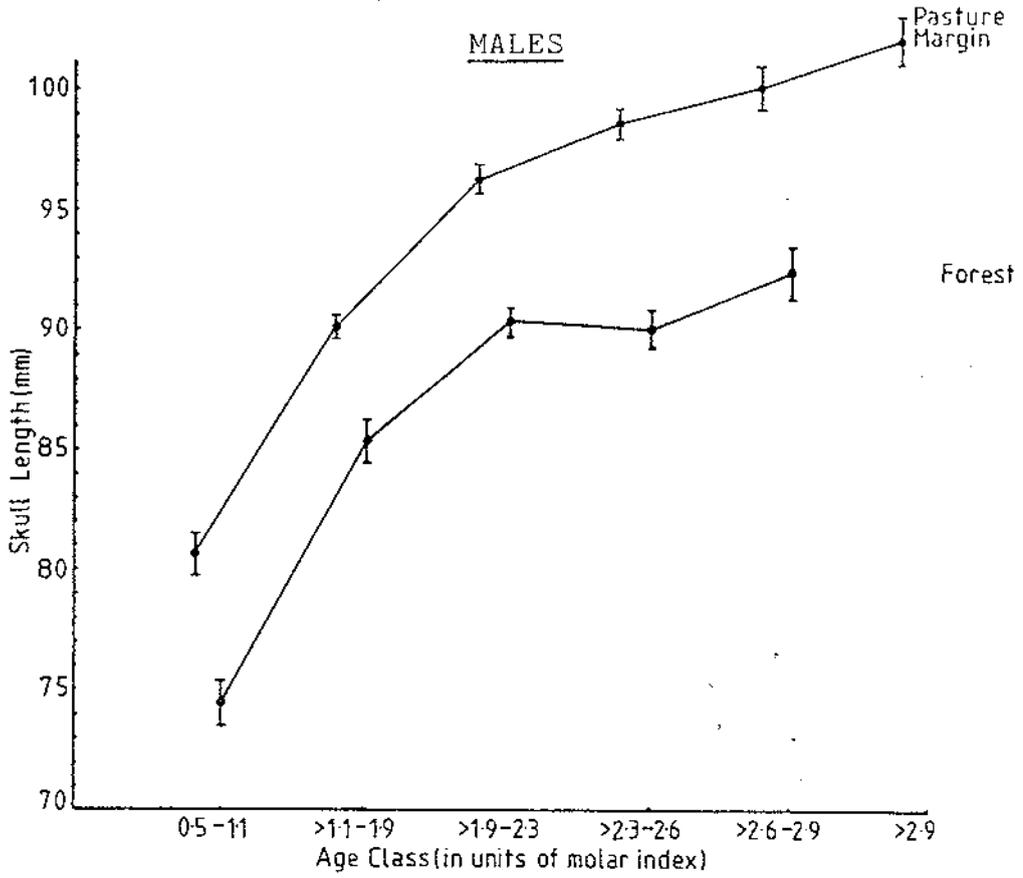
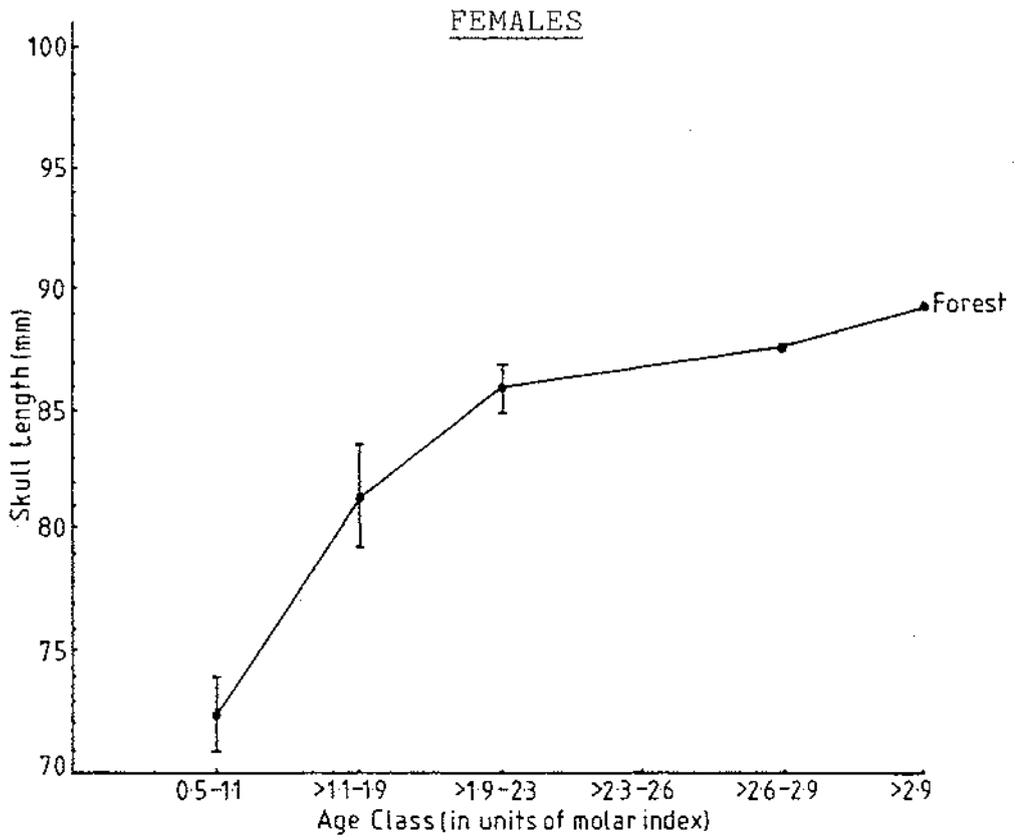
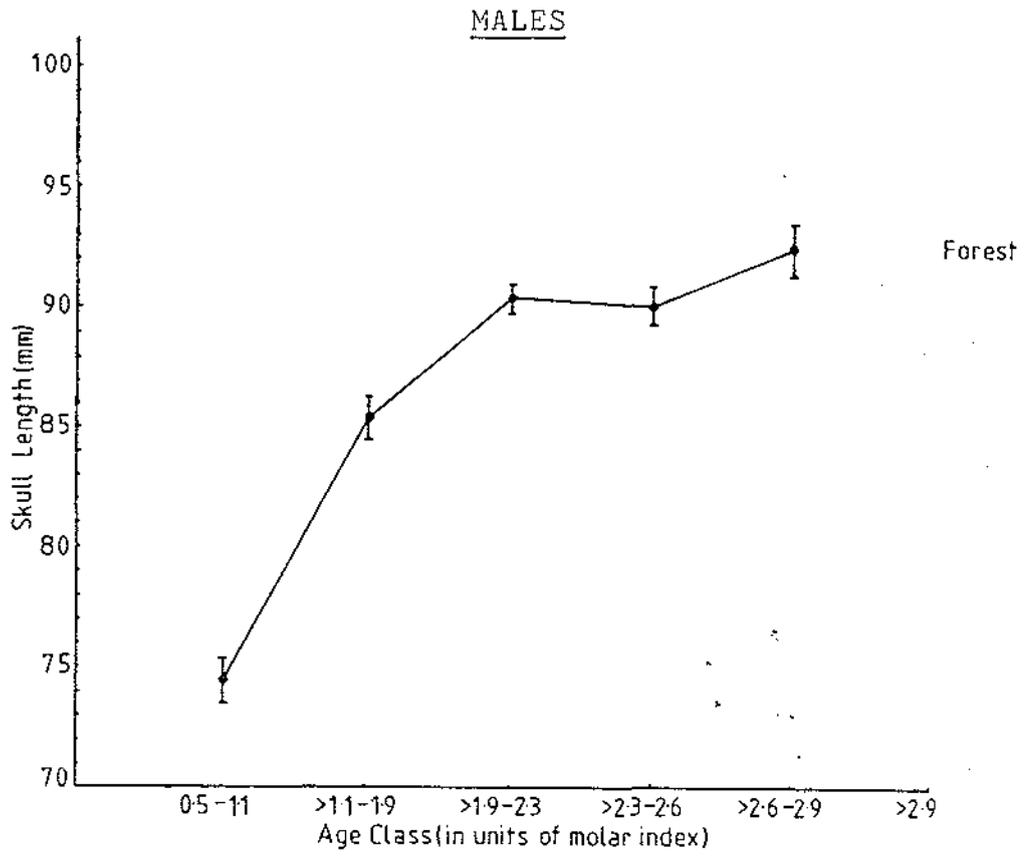


Fig. 5.3: Skull length measurements versus age class for all habitats. (Vertical lines represent standard error of the mean.)









5.3 Discussion

Challies (1973) concluded that a reduction in deer numbers since the advent of helicopter shooting led to an increase in the amount of food available to surviving deer and that this in turn led to an increase in average jaw length.

In the present study wallabies with access to pasture were larger than in other areas, while forest interior animals were generally smallest. It could be argued that this size difference is a result of differing age distributions for each habitat, however Fig. 5.3 shows consistent size disparity throughout all age classes. A further explanation for size differences could be that wallabies living in a pasture/margin habitat may sustain heavier hunting pressure than in other areas, such as the forest interior. This hunting pressure might act to artificially suppress population numbers and therefore result in more food being available to less wallabies. Such animals might attain larger sizes than forest wallabies which must compete vigorously for food. To test such an hypothesis would require accurate assessment of numbers throughout all habitats. However general observation while sampling indicated much higher numbers of wallabies on pasture/forest margins than in the forest interior. Therefore I suggest that rather than size differences being a result of a disparity in numbers such differences can be more easily explained in terms of habitat quality per se. That is, food quality is likely to be better in areas with access to managed pasture than in the forest interior. This hypothesis is further supported by evidence presented in Chapters 3, 6, and 7.

Size data (and general observation during autopsies) revealed no evidence of a second wallaby species (Wodzicki and Flux, 1967; Jane, 1979) in the areas sampled.

CHAPTER SIX

WALLABY CONDITION

6.1 Methods

This involved a subjective estimate of the amount of fat around and covering the kidneys. The method was based on that used by the NZFS (FRI) for possums (Green and Coleman, 1984) and Inns (1980) for *M. eugenii*. Amount of fat was graded using a numerical scale of 1 - 5, which corresponded to the visual estimations of nil, poor, average, good and excellent. As noted in section 2.4 all recordings were carried out by one observer, which could have assisted in restricting the variance of such a subjective technique.

Even when the subjectivity of visual estimation was considered it was decided against using weight of kidney fat because of the time involved and also because the technique is not without criticism (Batchelor and Clark, 1970; Bamford, 1970).

Weight of wallabies (see section 5.1) was also used to investigate short-term condition.

Kidney fat data was not available for wallabies shot in exotic forest.

6.2 Results

Fig. 6.1 summarises mean monthly kidney fat indices for each habitat. Indices are expressed by season for forest animals because of insufficient data. Fig. 6.1 shows that even with large variances in the data, there are recognisable trends in kidney fat index throughout the year.

For several reasons non-parametric statistical tests were used to analyse kidney fat data. First as recommended by Mendenhall and Ott (1980) ordinal data should be described with non-parametric statistics. Second, histograms of kidney fat data showed skewed curves, indicating something other than a normal distribution, and non-parametric statistics do not assume normality (Mendenhall and Ott, 1980).

Mann-Whitney two-sample rank test was used to test for significant differences in kidney fat index with sex, age and habitat. Results are summarised in Table 6.1. An asterisk denotes significance at the 0.01 level and where the null hypothesis can be rejected at 0.05 but not 0.01, the level of significance is included. All immature animals from each habitat had median kidney fat indices of 0.000.

Table 6.1 shows that kidney fat indices for pasture/forest margin females were significantly greater than females and males from other habitats. Females from the Makatiti Dome and forest habitats did not show significantly different kidney fat indices.

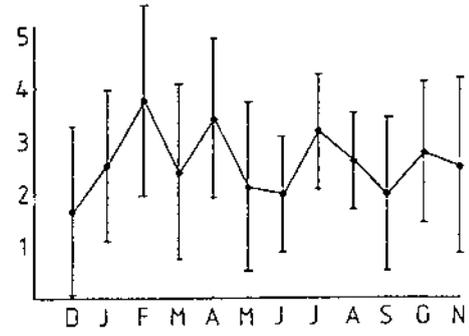
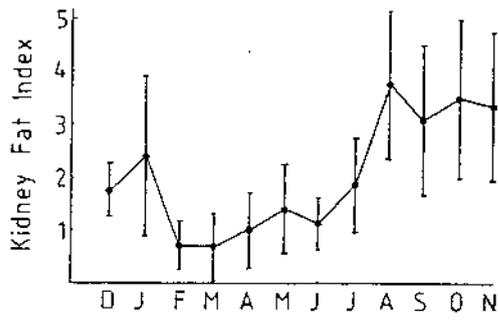
Males from the pasture/forest margin had better kidney fat than both Makatiti Dome and forest males. Makatiti Dome males showed better kidney fat deposits than forest males, however this difference was not significant at $P < 0.01$, (ie. $P = 0.028$).

Fig. 6.1: Annual variation in kidney fat index.
(Vertical lines represent standard
deviations.)

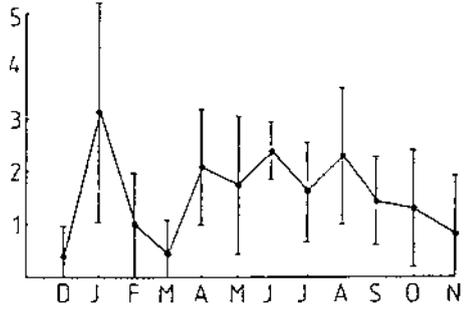
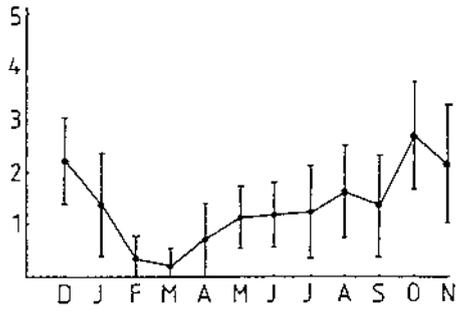
MALES

FEMALES

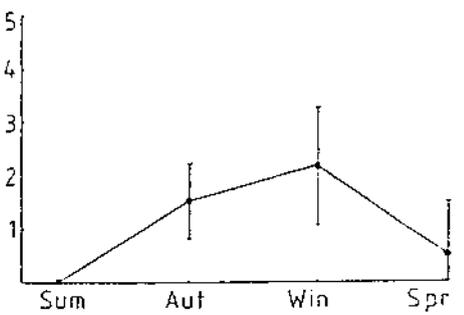
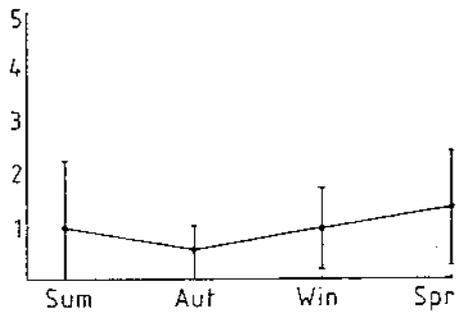
Pasture/Forest Margin



Makatiti Dome



Forest



A Kruskal-Wallis test was used to examine differences in kidney fat throughout the year, for each sex and habitat. Kruskal-Wallis is a non-parametric alternative to one-way analysis of variance and assumes independent random samples from continuous distributions all having the same shape (Ryan, Joiner and Ryan, 1982). The distribution of the test statistic H can be approximated by a chi-square distribution with $k - 1$ degrees of freedom.

Table 6.2 summarises results of Kruskal-Wallis tests for significant differences in kidney fat with season. It is noteworthy that those differences shown in Table 6.2 were also found to be significant when Kruskal-Wallis tests were performed using month rather than season.

Table 6.1: Results of Mann-Whitney tests for significant differences in kidney fat with sex and habitat.

TABLE 6.1:

	Forest Males	Dome Males	Pasture Males	Forest Females	Dome Females	Pasture Females
Forest Males						
Makatiti Dome Males	0.028					
Pasture Males	*	*				
Forest Females	NS	NS	NS			
Makatiti Dome Females	0.025	NS	*	NS		
Pasture Females	*	*	*	*	*	

Table 6.2: Results of Kruskal Wallis tests for significant differences in kidney fat with season.

TABLE 6.2

	H	DF	Significance level
Forest males	1.32	3	NS
Makatiti Dome males	30.40	3	0.001
Pasture/forest males	51.69	3	0.001
Forest females	6.77	3	0.1
Makatiti Dome females	14.37	3	0.005
Pasture/forest females	0.48	3	NS

6.3 Discussion

Although there has been some conjecture over the reliability and usefulness of kidney fat assessment (Batchelor and Clarke, 1970) the technique is still in use (eg. Green and Coleman, 1984). It appears to provide a useful relative measure of "well-being" of mammal populations (Caughley, 1970). However the subjectivity of the technique must be realised, and also as noted by Caughley (1970) when discussing the methods reliability, "Individuals vary greatly, even within a single combination of season, sex and age; accurate means come only from large samples." Such variability was observed in this study (see standard deviations presented in Fig. 6.1), but because of the large sample numbers involved, kidney fat assessment did produce useful and statistically significant differences in habitat, season, sex and age.

Adult female wallabies with access to pasture were found to be in better condition* all year round than any other group. Males with access to pasture were also in better condition than males from the Makatiti Dome and forest interior. It is not unreasonable to assume this difference is related to nutrition. This is supported by data on animal size, (see section 5.3) which showed pasture-margin animals to be larger than wallabies in the other habitats. Thus kidney fat results imply pasture/forest margin animals are less affected by the seasonal stresses faced by all wallabies (rutting, rearing young and climatic extremes). At the same time it should be noted that males with access to pasture showed a statistically significant drop in fat reserves during the rut (February-March). This was supported by general observation during autopsies in that males showed signs of fighting and general ill thrift.

Inns (1980) used a visual assessment of fat present in the gut cavity of Kangaroo Island wallabies (*M. eugenii*) and showed a similar trend to that seen in this study. That is that males were in relatively good "condition" in September-November, whereas in March fat reserves were at their lowest. Inns noted that stress could occur during the breeding season when males are competing for oestrous females.

Males from the Makatiti Dome also showed significant declines in kidney fat levels during the rut, and were unable to recover to levels reached by pasture/forest margin wallabies. It is suggested that this slow recovery is a result of the nutritionally poorer habitat, and further support for such an hypothesis comes from forest interior males which showed very low kidney fat reserves all year round with a drop (although not statistically significant) during late summer and autumn.

Females from the Makatiti Dome showed significant decreases in kidney fat during February and March, this coincides with the rut and entry of young into the pouch, and although there is no evidence to support these as being major causes of this decline, it appears quite probable. These females also show a decrease in kidney fat through spring, reaching a low in December. At this time the young leave the pouch, so energy demands are likely to be high just prior to that event.

Although forest females showed no significant differences in kidney fat with season, the basic trend of being highest during autumn and winter agrees with females from the Makatiti Dome.

Immature animals invariably had almost no kidney fat. This was true for all habitats, with no significant differences in kidney fat between habitats, Thus it may be that stresses imposed on immature animals are such that fat reserves cannot be accumulated.

Such stresses may arise from:

1. Being weaned.
2. Rapid growth inherent in all young animals.
3. Social pressures associated with being subordinate (see M. Vujcich, 1979).

Batchelor *et al* (1967) when discussing possums noted that fat reserves may influence relative acceptance of poisoned baits. This was also noted by Bamford and Martin (1971) in a study of poison campaigns for possums when they concluded that "...sufficiently close correlations have been obtained to identify a definite relationship between fat reserves and percent kill."

Should this be true for wallabies, then the greatest bait acceptance and therefore percent kill will be achieved with animals living in the forest interior or with access to limited verges. It is noteworthy that these are the animals having the greatest impact upon indigenous forest (see Chapter 9).

Kidney fat results also imply that the best time of the year for bait drops is just after the rut (April-May). (During the rut is probably not ideal because increased activity may mean shorter feeding periods.)

Mean seasonal weights for each sex were calculated and one-way analysis of variance was used to test whether the mean weight of adult wallabies varied with season. It is however conceded that any such differences may be a phenomenon of sampling rather than representing any overall change in weight. Nevertheless it was considered worthy of investigation and it is pertinent to note that Catt (1981) found significant differences in weight with season for Bennetts wallaby, as did Inns (1980) for *M. eugenii* on Kangaroo Island. However in this study no significant differences were found in weight of animals with season.

* Note that "condition" is used in this context to describe a single measurable factor, namely kidney fat reserves. As noted by Bamford (1970) "...the term "condition" implies a great deal more than quality of fat reserves." Although it is fair to assume that if an animal is generally in poor health and under stress, this will be reflected in fat reserves.

CHAPTER SEVEN

BREEDING AND SEX RATIOS

7.1 Methods

Pouch condition was assessed and presence or absence of pouch young was noted. If the female was lactating this was considered evidence of a pouch young; because often, particularly in November-December, the pouch young are mobile enough to escape when the female is shot.

Pouch young were sexed, weighed with a Salter spring balance and headlength was measured using Vernier calipers.

7.2 Results

7.2.1 Breeding Success of Yearlings

Table 7.1 summarises pouch condition for female yearlings, ie. wallabies born in the previous season. Data from after the end of August is not used because it is unlikely that females will replace young lost from the pouch after this date (Sadlier, personal communication; data from this study). That is, females examined after August which bred during the season but have since lost their pouch young and have not replaced it will be recorded as non-breeders and therefore the true proportion of breeding females may be underestimated.

Animals were judged in the field to be yearlings on the basis of size, and this was later checked with molar index; all data in Table 7.1 is from wallabies with a molar index of less than 1.4 (see Chapter 4).

Seventy-two percent of yearlings examined were either carrying a pouch young or were lactating. This proportion varied significantly (although at $P < 0.05$) with habitat; a greater proportion of yearlings from the pasture margin habitat were breeding than for yearlings from the Makatiti Dome ($\chi^2 = 4.818$; D.F. = 1; $P < 0.05$).

Table 7.1: Breeding success of yearling females.

Table 7.2: Breeding success of females two years
or older.

TABLE 7.1:

Habitat	Number Examined	Number with Pouch Young	Proportion
Forest	4	2	0.50
Makatiti Dome	22	13	0.59
Pasture/Forest Margin	24	21	0.88
TOTAL	50	36	0.72

TABLE 7.2:

Habitat	Number Examined	Number with Pouch Young	Proportion
Forest	5	5	1.00
Makatiti Dome	50	45	0.90
Pasture/Forest Margin	40	34	0.85
TOTAL	95	84	0.88

7.2.2 Breeding Success of Females Two Years of Age or Older

Table 7.2 summarises comparable data as in Table 7.1 but for female wallabies with a molar index of greater than 1.4 (that is, approximately 2 years or older).

The total proportion of these females either carrying a pouch young or lactating is significantly greater than that for yearlings ($\chi^2 = 6.15$; D.F. = 1; $P < 0.025$). There is no significant difference in this proportion between habitats but it should be noted that more females greater than 2 years of age were breeding on the Makatiti Dome than yearlings from the same habitat ($\chi^2 = 9.3$; D.F. = 1; $P < 0.025$).

Table 7.3: Cumulative monthly results for proportion of females either carrying young or lactating.

TABLE 7.3:

Month	Total Number Examined	Total Number With Pouch Young	Proportion
January	11	3	0.27
February	17	10	0.59
March	21	21	1.00
April	22	19	0.86
May	21	20	0.95
June	23	22	0.96
July	22	18	0.82
August	21	19	0.90
September	19	16	0.84
October	28	24	0.86
November	20	16	0.80
December	17	7	0.41

7.2.3 Season of Births

Dates of birth for pouch young were estimated using growth curves produced by Murphy and Smith (1970) and are shown in Fig. 7.1. Murphy and Smith measured growth rates of captive pouch young and found "Size was fairly closely correlated with age until the young were 320 days old but thereafter it had little value for age determination". They also examined the reliability of using regressions to determine age and found the largest error between estimated and actual age was about 5%.

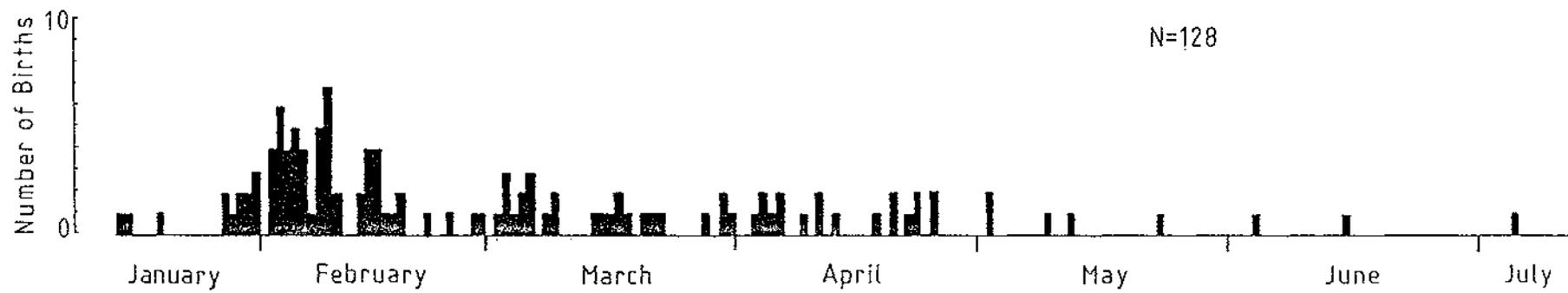
A major assumption necessary when using regressions from captive animals to estimate the age of field animals is that the growth rate of the two groups is the same. To test this assumption Murphy and Smith compared growth proportions of captive and field reared young, and found them to be similar until the young were about 350 days old.

Inns (1982) found that during a long dry summer on Kangaroo Island the growth rates of pouch young may be retarded and thus there may be some error when aging such animals using growth curves for captive wallabies. However Inns concluded that "...in normal years it seems that estimation of the age of pouch young in the field from data on captive animals is quite accurate."

In the present study the major assumption made when calculating birth dates is that the growth rates of dama pouch young in New Zealand are similar to that of captive Australian animals.

Fig. 7.1 shows that approximately 50% of the births of Rotorua animals occurred within the last week of January and the first two weeks of February. There was a steady tail off in births through March and April, with over 90% of births having taken place by the end of April. The latest estimated birth was July 13th.

Fig. 7.1: Season of births.



7.2.4 Pouch Young Sex Ratios

Table 7.4 summarises the sex ratio data for pouch young. The only significant deviation from a 1:1 ratio was seen in the exotic forest habitat and was significant at $P < 0.05$. However all other habitats, and cumulative results show no significant difference between numbers of males and females.

Also there were no significant differences in sex ratios between habitats ($\chi^2 = 5.36$; D.F. = 3).

Table 7.4: Pouch young sex ratios.

TABLE 7.4:

Habitat	No. of Females	No. of Males	pf	χ^2	Level of Sig.
Forest	4	3	0.57	2.57	NS
Makatiti Dome	38	33	0.50	0.352	NS
Pasture/Forest Margin	32	27	0.54	0.420	NS
Exotic Forest	20	36	0.36	4.570	0.05
TOTAL	94	99	0.487	0.130	NS

7.2.5 Sex Ratios of Shot Samples

Table 7.5 summarises the sex ratios for shot samples. All habitats except exotic forest showed a significant bias towards males; this bias was significant in all seasons except in summer when the difference was significant only at $P < 0.1$. However there was no significant difference in sex ratio between seasons or habitat, or between seasons for individual habitats.

Table 7.5: Sex ratios of shot samples.

TABLE 7.5:

Season	Habitat	No. of Females	No. of Males	pf	χ^2	Level of Sig.
Summer	Forest	5	21	.19	9.85	0.005
	Makatiti Dome	39	49	.44	1.14	NS
	Pasture/Margin	44	41	.52	1.06	NS
	Exotic Forest	89	103	.46	1.02	NS
	TOTAL	177	214	.45	3.50	0.1
Autumn	Forest	4	13	.24	4.77	0.05
	Makatiti Dome	37	50	.43	1.94	NS
	Pasture/Margin	31	50	.38	4.46	0.05
	TOTAL	72	113	.39	9.09	0.005
Winter	Forest	5	3	.42	0.33	NS
	Makatiti Dome	34	46	.43	1.80	NS
	Pasture/Margin	28	51	.35	6.70	0.01
	Exotic Forest	66	75	.47	0.57	NS
	TOTAL	133	179	.43	6.78	0.01
Spring	Forest	5	10	.33	1.67	NS
	Makatiti Dome	28	54	.34	8.24	0.005
	Pasture/Margin	39	53	.42	2.13	NS
	TOTAL	72	117	.38	10.70	0.005
All Seasons	Forest	19	51	.27	14.63	0.005
	Makatiti Dome	138	199	.41	11.04	0.005
	Pasture/Margin	142	195	.42	8.34	0.005
	Exotic Forest	155	178	.47	1.59	NS
	TOTAL	454	623	.42	26.52	0.005

7.3 Discussion

7.3.1 Breeding

Andrewartha and Barker (1969), Kinloch (1973), M. Vujcich (1979), Inns (1980) and Sadleir (personal communication) all found female *M. eugenii* to be breeding by about 1 year of age, and in fact Inns (1980) stated that "Kangaroo Island wallabies become sexually mature at 9 months of age, just after leaving the pouch." The youngest female recorded by Andrewartha and Barker (1969) breeding was also 9 months of age "at her first fertile mating."

In the present study most females were also found to be breeding in their first year. However there were some differences in numbers breeding between juveniles and adults ($\chi^2 = 6.15$; $P < 0.025$), and also between habitats for juveniles ($\chi^2 = 4.818$; $P < 0.05$).

Inns (1980) found that for *M. eugenii* on Kangaroo Island "There was a high fecundity for adults in all years while the fecundity of juveniles fluctuated from year to year." Inns noted that the birth rate for juveniles appeared to drop immediately following a long dry summer in 1978.

Maynes (1977) listed 5 examples of workers who have to various degrees implicated nutrition as being responsible for delays in sexual maturity of marsupials. Maynes went on to conclude that poor conditions on Kawau Island were responsible for a delay in the sexual maturity of female parmas (*Macropus parma*).

In the present study a greater percentage of juveniles from the pasture margin habitat were found to be breeding than on the Makatiti Dome. Although sample numbers are small and significance level not great ($P < 0.05$) such a

difference is consistent with the hypothesis that poor nutrition can delay the onset of breeding. (Evidence suggesting that the Makatiti Dome is nutritionally poorer than the pasture/forest margin is presented in Chapters 2, 5 and 6.

The percentage of adults found to be breeding was similar for each habitat, which is consistent with the findings of Inns (1980), that fecundity of adults was not affected by poor conditions as it was for juveniles. (Inns recorded the proportion of females greater than 2 years of age carrying a pouch young for 4 years running as 0.95, 0.85, 0.93, 0.84.)

It is worthwhile noting that although the fecundity of yearlings from the Makatiti Dome was significantly less than those 2 years or over from the same habitat, this difference was not mirrored in the pasture/forest habitat. That is, in the nutritionally richer habitat, the fecundity of yearlings is not significantly different from females two years or over.

To summarise, in this study there is some evidence to suggest that juvenile fecundity, defined as "the number of offspring produced over an interval of time" (Inns, 1980) is affected by habitat quality, but this is not true for older animals.

7.3.2 Season of Births

The dama wallaby is one of that free-standing group of animals exhibiting embryonic diapause (Tyndale-Biscoe, 1973). That is, within 24 hours after birth the female mates again and development of the embryo is arrested at the blastocyst stage and this resulting blastocyst remains in a quiescent state for 11 months. However should the pouch young be lost at some stage, reactivation of the blastocyst will occur and the former pouch young will be replaced (Sadleir, personal communication). If the original pouch young completes development and vacates the pouch about December as is normal, then the dormant blastocyst will not reactivate until after the summer solstice around the end of December (Renfree and Tyndale-Biscoe, 1973). (Sadleir and Tyndale-Biscoe (1977) suggested "...that the time of reactivation of development is related to the time of full moon relative to the summer solstice.")

The gestation period for *M. eugenii* is 27 days (Sadleir and Tyndale-Biscoe, 1977) and the peak of the breeding season on Kangaroo Island is at the end of January (Inns, 1980). However it has been noted by Sadleir (personal communication) and seen in the present study that the breeding peak for Rotorua wallabies is about 10 days later. In this study and that of the DSIR Ecology Division (Sadleir, personal communication) the peak of births was during the last week of January and the first 2 weeks of February.

It is likely that some if not many of the births outside the main peak are due to termination of embryonic diapause as a result of young being lost from the pouch. This is particularly probable for births as late as June and July and may be the cause of the small peak of births in early March (Fig. 7.1). However it also seems possible that some late births may result from young females born

the previous year being themselves late births. Therefore such females may not be recruited into the breeding population until after January-February.

7.3.3 Pouch Young Sex Ratios

Caughley and Kean (1964) examined available literature on 7 marsupial species and concluded that only one (*Macropus kanguru*) showed a real disparity in sex ratio at birth.

No examined studies of *M. eugenii* describe significant deviations in a 1:1 sex ratio for pouch young. Inns (1980) in a study between 1975 - 1978 found no significant disparity; he also cited unpublished data for the period 1966 - 1969 which also showed no differences from a 1:1 ratio. M. Vujcich (1979) in a small sample of *M. eugenii* from Kawau Island reported a sex ratio of 5 male and 4 female. Andrewartha and Barker (1969) found that for 246 pouch young 128 were males and 118 were females, which is close to unity.

In the present study pouch young sex ratios were very even and only one sample (from exotic forest) showed a significant disparity ($P < 0.05$). Overall sex ratios were consistent with a 1:1 ratio.

7.3.4 Sex Ratios of Shot Samples

In a shot sample of *M. eugenii* from Kawau Island Maynes (1977) demonstrated no bias in sex ratio, although the sample was very small (11 male, 11 female).

Andrewartha and Barker (1969) noted that for Kangaroo Island wallabies, "During the early winter until green feed becomes scarce in the cleared areas, female wallabies are more abundant than males. During the summer months, males outnumber females..."

In the present study there was a consistent and significant bias towards more males in shot samples. This difference was evident throughout all seasons and habitats, with no significant difference between seasons or habitats.

With possums Coleman and Green (1984) noted that "Any imbalance in sex ratios apparent within free-ranging populations is probably because of either differential mortality during some postnatal life stage - perhaps resulting from previous trapping or control activities - or the sampling procedure employed."

In this study there was no imbalance in pouch young sex ratio, (except in one sample and at $P < 0.05$) (see section 7.2.4) thus implying that any differential mortality between males and females must be post-natal.

The bias towards males was consistent throughout all habitats, which might not be expected if imbalanced sex ratio was a result of "previous trapping or control activities"; this was one of the possibilities suggested by Coleman and Green. In Rotorua, forest interior animals are possibly not subjected to hunting pressures similar to those in more accessible habitats. (Jane (1979) stated that wallabies "...are subject to intensive

control on the margins of the forest") therefore sex ratios might not reflect the trends of pasture/forest margin, exotic forest or Makatiti Dome populations.

The bias towards males was also consistent throughout all age classes (see Figs. 4.1 and 4.2) with no significant difference in proportion of females between age classes.

Thus there is either greater mortality of females throughout all age classes and habitats or the bias towards males results from sampling procedure.

By trapping a possum population to extinction Coleman and Green established that an imbalance towards males shown in live trapping results did not represent the true sex ratio of the population, which was nearly 1:1. They concluded that for possums, "As males are more mobile than females of similar age, the former are generally taken more frequently."

I believe that the imbalance in sex ratios of shot samples in this study is also a result of behavioural differences between males and females. This hypothesis is supported in a study by Christensen (1980) who trapped a greater proportion of *M. eugenii* males than females. The conclusion reached by Christensen was that "Disparity in numbers between the sexes appears to reflect a higher male capture rate than any real differences."

M. Vujcich (1979) suggested that male darvas (sic) may range over a wider area than females. However Vujcich qualifies this as only being a suggestion and later recommends more work to establish if it is true. This suggestion by Vujcich was not supported by data of Inns (1980) who in a detailed movement study using radio telemetry found that "There was no significant difference in the mean size of the home-range between males and females in either summer or winter."

Thus it may be that while there is little difference between home-range of males and females the former is more active within the home-range.

CHAPTER EIGHT

WALLABY MOVEMENTS

8.1 Methods

8.1.1 Live Captures

Twenty-five wallabies were captured in Rotoiti Forest during January and February of 1984. The procedure for catching these animals involved firstly confusing them with several spotlight beams then pursuing them on foot. The animal was caught either by "bulldogging" or with the use of a net constructed similarly to a butterfly net. Wallabies were then put into a sack to aid in handling. They were weighed and measured (as in section 5.1) then tagged with sheep ear tags ("Rototag" brand) which carried an animal number as well as a contact address and phone number. Both ears were tagged, thus if one tag was lost the animal could still be identified.

A collar was also fitted around the animal's neck. These were constructed from "hospital arm bands" following Kinloch (1973) with "Scotchlite" reflective tape fixed in a unique sequence of colours for each animal. This was in the hope that marked wallabies could be identified at a distance with a spotlight. Dunnet (1956) has noted that "Scotchlite" tape greatly increased the conspicuousness of quokkas in a spotlight.

It was hoped to recover, or identify without shooting, some of these marked animals during further visits into the area. Also it was known at the time of marking that extensive sampling of wallabies in Rotoiti Forest by the Pest Destruction Board for DSIR research purposes, was to be carried out over the following months, and this was intended to lead to recovery of some of the marked population.

8.1.2 Rhodamine Trials

A farm property (see Plate 10) was chosen on the western border of the Lake Okataina Scenic Reserve. This property was adjoining one of those used for the diet and population study (see section 2.3.3 for a description of the area).

Two hundred kilograms of "Mapoua" possum pellets (manufactured by Mintec, Nelson) were obtained and impregnated with rhodamine dye. They were used because in trials conducted by Murray Llewellyn of NZFS, they were shown to be very attractive to wallabies. The pellets were then layed out on a line within the forest, parallel with the pasture/forest margin. A compass and a NZFS "hip chain" were used to ensure that the line was always at a consistent distance from the pasture.

Approximately 0.25 kilos of pellets was thrown out as evenly as possible every 10 metres along the line. Two such lines were put out, the first being 500 metres from the forest margin and 840 metres long. Approximately 37 kilos of pellets were distributed along the line. They were left for two nights and on the third night shooting was commenced on the adjoining pasture.

The alimentary tracts of all shot wallabies were opened and examined under an ultraviolet light for traces of rhodamine.

The second line almost two months later, was layed 400 metres from the forest margin, and was 1000 metres long, with 50 kilos of bait used. As with the first line, shooting commenced on the third night after laying of the line.

8.2 Results

8.2.1 Live Captures

At the time of writing only one tagged animal had been recovered. This was a female (estimated to be approximately 1 year old when tagged) and was shot by private hunters 10 months after the original capture. The wallaby was shot approximately 1.5 kilometres away from the capture point. Although both tags were still in place the collar had been lost.

8.2.2.1 Trial 1 (A rhodamine line 500 metres from the pasture margin.)

Nineteen animals (12 male, 7 female) were shot on pasture within the limits of the rhodamine line. Two animals (both male) were collected just outside the end of the line. The hindgut of one of these animals (a yearling male shot approximately 70 metres along the boundary fence from the end of the line) showed traces of rhodamine present and a second of similar age from within the boundary of the line contained large amounts of rhodamine pellets through the entire stomach.

None of the other wallabies shot showed any traces of rhodamine.

8.2.2.2 Trial 2 (Rhodamine 400 metres from the pasture margin.)

Nine wallabies (5 male, 4 female) were shot within the confines of the rhodamine line. Of these

only one mature male and two mature females, both with pouch young, showed no traces of rhodamine. The remaining 6 wallabies were all rhodamine positive. The specifics of these are presented in Table 8.1. (Three mature males and one female (with pouch young) were shot just outside the rhodamine boundary, and none of these showed traces of rhodamine.)

Table 8.1: Results of rhodamine trial 2.

TABLE 8.1:

Animal Status	Concentration of Rhodamine
Mature Male	Minute traces in the stomach.
Mature Male	Stomach saturated, with only small amounts of green material in the fore-stomach. Rhodamine was also found in mid- and hind-gut, but not in faeces.
Immature Male	Scattered traces through mid-stomach, whereas hind-gut, intestine and newly formed faeces saturated.
Immature Male	Entire digestive tract heavily stained with rhodamine; stomach full of pellets with very little other material present, however a small amount of green material was present near the oesophageal opening.
Mature Female With Pouch Young	Rhodamine present in the hind-gut and faeces.
Mature Female With Pouch Young	Entire digestive tract stained, except for fore-stomach which contained fresh green material.

8.3 Discussion

It is estimated that in the 17 months since the 25 wallabies were tagged in Rotoiti Forest, approximately 400 wallabies have been known to have been shot from within, and immediately surrounding the capture area. Almost all of these were shot by the Central Bay of Plenty Pest Destruction Board and all animals were inspected for the presence of tags. The remainder were shot by myself. It was not known how many wallabies had been shot by private hunters during this period, although the number is likely to be substantial.

Although only 25 wallabies were tagged it might be expected that more than 1 should be recovered. While the loss of the collars was to some degree expected (Kinloch, 1973) it is unlikely that the animals were able to remove both ear tags. However another possible reason for the low recovery rate of animals is that the trauma involved with tagging led to these wallabies becoming very wary for some time afterwards. It is also likely that some tagged animals were shot by private hunters and the tags not returned. There was no monetary reward for returning the tags and also many private shooters may be hunting in the area illegally and not wish to reveal this.

I think it unlikely that the tagged animals have moved out of the area. This hypothesis is supported with research on movements of *M. eugenii* on Kangaroo Island by Inns (1980). Inns found that "None of the animals that were radio-tracked were ever observed to move completely away from the Main Study Area or to permanently change the location of their home-range."

There may well be a reluctance among damas to move into a territory already occupied by another social group. Christensen (1980) found that there was a "degree of hostility" between members of different *M. eugenii* groups.

Christensen was studying the movements of *M. eugenii* after their habitat was destroyed by fire and also noted that "A few individuals appear to settle in with other colonies, others occupy what seems to be sub-optimal habitat on the fringes of other colonies."

Therefore it seems likely that wallabies marked in this study have either been shot by private hunters and not handed in or are still in the area and have not yet been recovered, possibly in part because of a "waryness" installed into them after being tagged.

Rhodamine trials. Inns (1980) using radio telemetry, established the mean home-range size for *M. eugenii* on Kangaroo Island to be 42.4 ± 17.6 hectares (1 ha = 0.01km²) during summer, and 15.9 ± 8.1 ha during winter. Although much caution is necessary when drawing comparisons with such a geographically and climactically removed habitat as Kangaroo Island it is pertinent to mention the results of the research which may give some indication as to possible range sizes for Rotorua populations.

Green and Coleman (1980) in a telemetry study of possums on Mt Bryan O'Lynn showed that "...possums may move as much as 1 - 2 kms from den sites to feed on pasture..." It is reasonable to assume wallabies are capable of moving through forest as quickly and with similar energy expenditure as possums. Therefore it would not be surprising to discover that wallabies move similar distances as possums to reach pasture. Also, motivation to reach pasture may be greater for wallabies than possums, that is wallabies do not have access to food sources in the forest canopy. This is perhaps evidenced by the fact that Coleman *et al* (in press) found that for possums on Mt Bryan O'Lynn "Pasture foods comprised 12% of the foliage eaten by possums living within 300 m of the forest interface." In the present study pasture foods were found to comprise 70% of foliage eaten by wallabies shot on the pasture/forest margin.

Further evidence indicating the attractiveness of pasture to wallabies comes from M. Vujcich (1979) who suggested that open grassland areas assist in maintenance of social structure; and he also noted that "Data from the present study suggest the darma (sic) has one of the most highly developed social systems in the *Macropodidae*."

Rhodamine trial 1 showed that 2 immature males (out of a sample of 21 wallabies) had at some time travelled at least 0.5 kms back from the pasture margin. This supports the suggestion (section 7.3.4) that males are more mobile than females, as do results from the second trial when out of 9 animals shot 6 had travelled up to 400 metres from the pasture margin and 4 of these were males.

Because sample sizes were small little else can be concluded except that data is consistent with the hypothesis that pasture areas are important to wallabies, whether it be for food (see section 3.2.3), socialisation (M. Vujcich, 1979) or both. Also this limited investigation suggests that a more detailed study of wallaby movements may show these animals are moving substantial distances to reach pasture. In the case of the Okataina Reserve where a relatively thin belt of forest surrounds the lake (this is particularly true of the western side), it may be possible to achieve high kills by poisoning only farm boundaries.

CHAPTER NINE

DISCUSSION OF WALLABY IMPACT IN FORESTS

This discussion combines the results of the present diet study with NZFS information on the vegetation of the Okataina Scenic Reserve (their survey was carried out during 1983-84) and attempts to evaluate the impact of wallabies on forest in the reserve. To examine the potential impact of wallabies in areas outside the Rotorua Lakes region my results are combined with the information of Jane (1979).

9.1 Impact in the Okataina Scenic Reserve

The NZFS has identified four forest types as occupying 95.5% of the area of the reserve (Llewellyn, 1985b). These are kamahi, tawa*, mixed hardwood and kanuka. Llewellyn (and Chapter 2 in this thesis) describes other species present in each forest type. Wallabies shot from forest interior during this study were primarily from kamahi forest interspersed with some kanuka. Makatiti Dome wallabies were from mixed hardwood forest while pasture margin wallabies were shot on properties adjacent to tawa/podocarp.

Table 9.1 and Figs. 9.1 - 9.4 summarise the results of the 1983-84 vegetation survey and are reproduced from Llewellyn (1985b). Procedure for the survey entailed the establishment of 39 20m² vegetation plots, 15 in kamahi, 10 in tawa/podocarp, 7 in mixed hardwood and 7 in kanuka. Table 9.1 and Fig. 9.1 show that although in kamahi forest kamahi is by far the most common tree species there is a distinct lack of regenerating kamahi. No kamahi in the seedling or shrub tiers was recorded in any of the 20m² plots. My diet analysis (Chapter 3) revealed that kamahi is an especially preferred food of wallabies and there is an initial temptation to assume that wallabies are responsible for suppressing kamahi regeneration. However there are other aspects to be considered including the probability that wallabies rely

Table 9.1: Dominant species by forest type for the
Okataina Scenic Reserve (reproduced from
Llewellyn, 1985b).

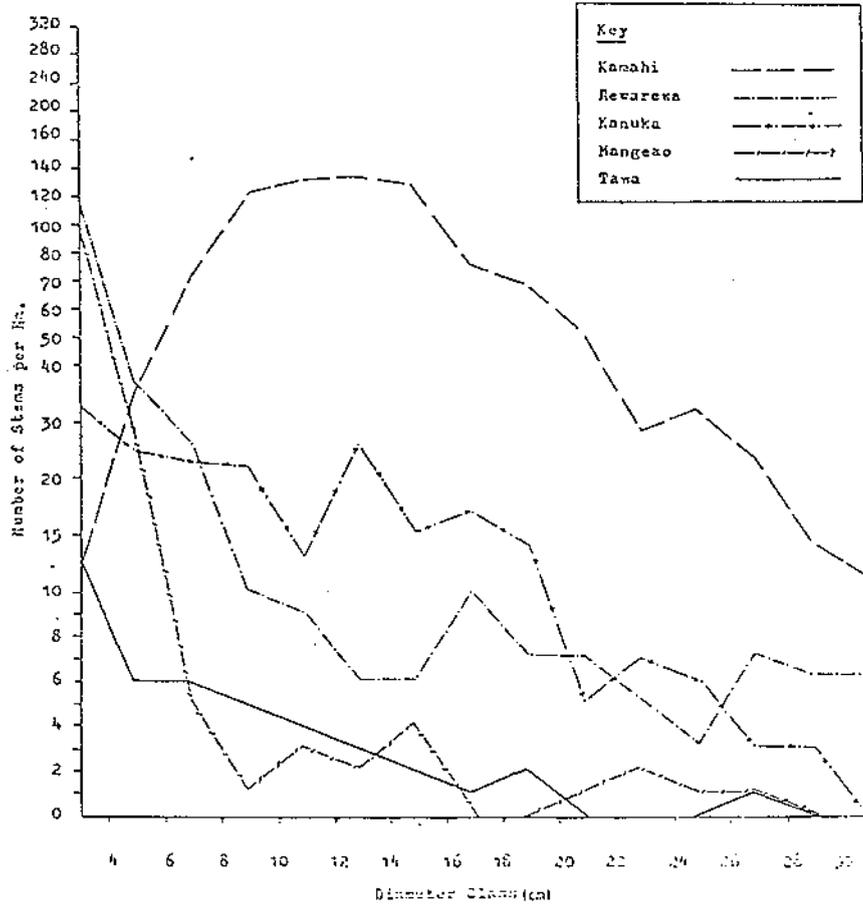
STOCKINGS OF DOMINANT SPECIES
(by height and diameter class, cm)

FOREST TYPE (B/Area)	SPECIES	SEEDLING ≤ 45ht < 2 diam	SHRUB ≥46 ≤ 135ht < 2 diam	POLE ≥ 136ht < 2 diam	TREE ≥ 136ht ≥ 2 diam
KAMAHI (58.22)	WEI RAC	0	0	5	1560
	KNI EXC	1694	1399	554	481
	LEP ERI	0	0	50	368
	LIT CAL	589	147	437	233
	BEI TAW	184	37	9	75
KANUKA (27.7)	LEP ERI	0			
	KNI EXC	0	0	50	160
	LIT CAL	158	0	357	292
	MEL RAM	0	0	0	96
	WEI RAC	0	0	0	39
TAWA- (47.2)	BEI TAW	1436	1657	742	992
	MEL RAM	276	0	17	392
	LIT CAL	331	55	60	207
	KNI EXC	939	717	170	150
	HED ARB	497	220	30	150
	LAU NOV	1326	331	55	12
MIXED HARDWOOD (55.5)	WEI RAC	395	158	21	460
	IXE BRE	79	0	4	196
	BEI TAW	789	395	150	390
	MYR SAL	789	158	14	188
	PSE COL	1657	1105	329	681

Fig. 9.1: Stem diameter distribution for kamahi forest (Figs. 9.1 - 9.4 are from Llewellyn, 1985b).

Fig. 9.2: Stem diameter distribution for mixed hardwood forest.

STEM DIAMETER DISTRIBUTION
KAHAKI FOREST.



STEM DIAMETER DISTRIBUTION
MIXED HARDWOOD FOREST.

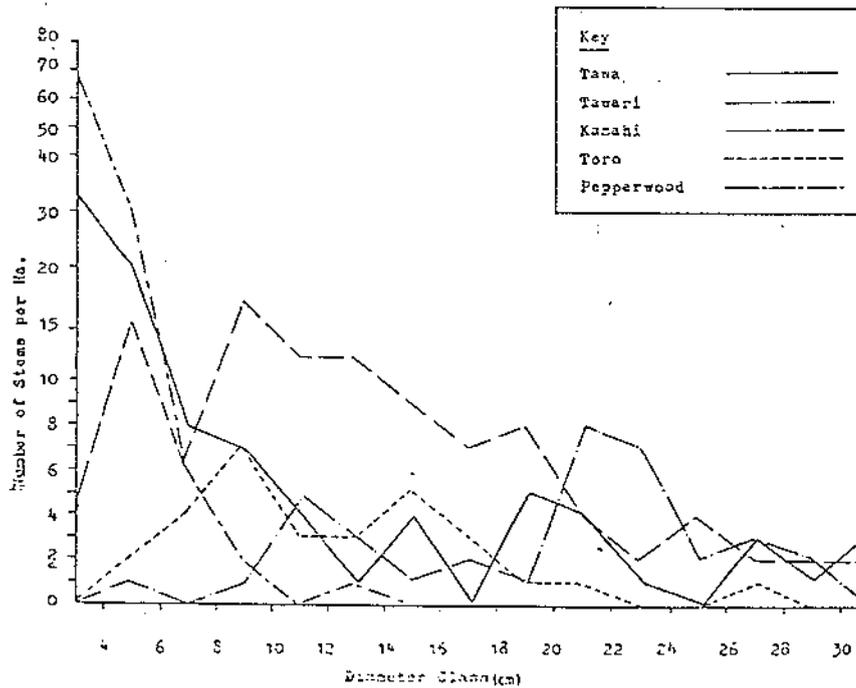
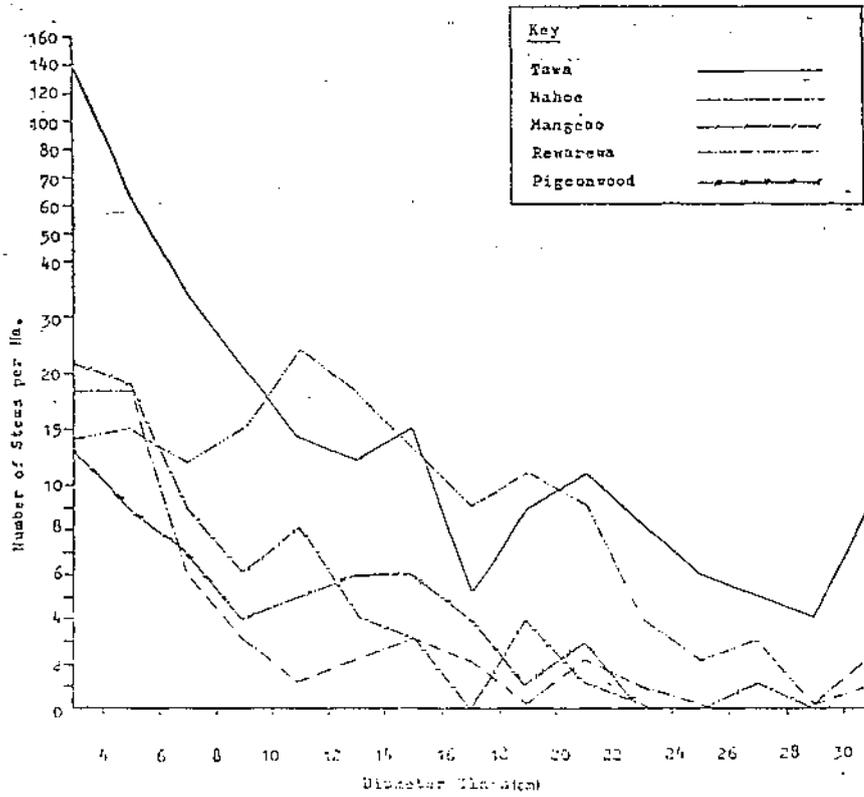


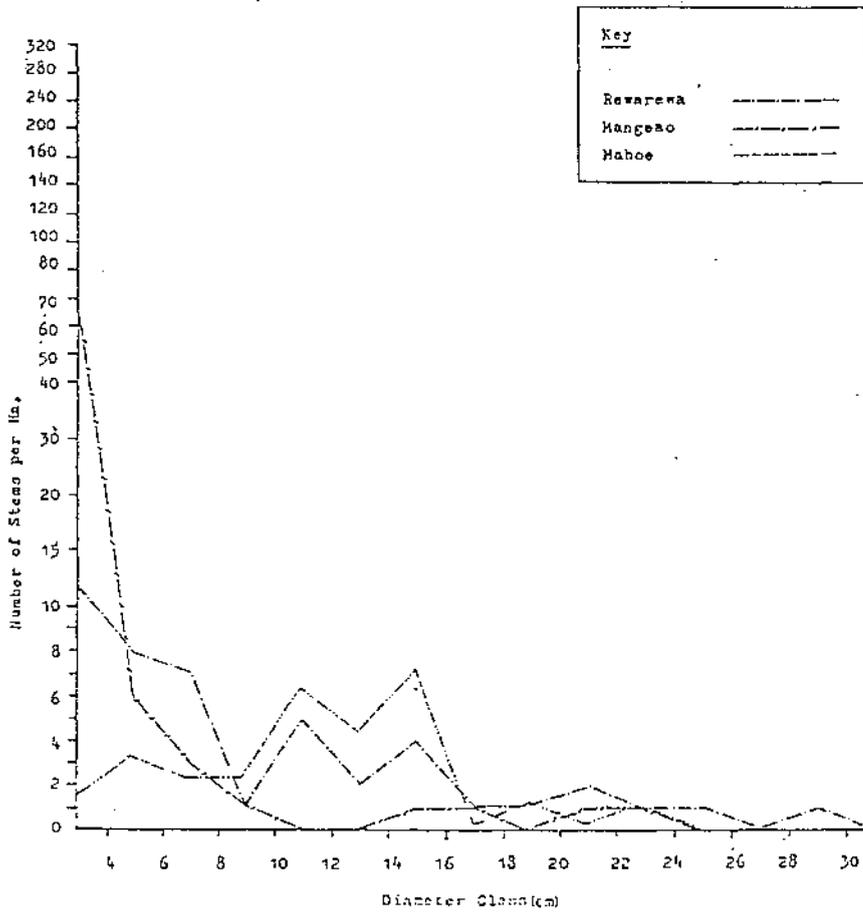
Fig. 9.3: Stem diameter distribution for tawa-
podocarp forest.

Fig. 9.4: Stem diameter distribution for kanuka.
(Unfortunately kanuka is not graphed
because of suspected mis-identification
by the 1983/84 survey party (Llewellyn,
1985b).)

STEM DIAMETER DISTRIBUTION
TAWA FOREST. (= TAWA-PODOCARP)



STEM DIAMETER DISTRIBUTION
KANUKA FOREST.



to a degree on leaf-litter to supply many species, particularly kamahi (see section 3.3.3)

When discussing surveys in general, particularly those of the NZFS, Stewart and Veblen (1982) have stated that "The tendency in interpreting the data from surveys has been to assume that introduced browsing animals are wholly responsible for the observed variations in forest structure and composition." Their explanation for structural abnormalities relates more to natural disturbances such as earthquakes and storms. Irrespective of the absolute validity of their suggestions they do raise serious questions which imply that caution is necessary before attributing damage unequivocally to animals. As mentioned by Llewellyn (1985b) the survey was a "one-off" describing the present state of the forest rather than accounting for change over time. It must also be realised that when using diet and vegetation survey data to demonstrate the degree of wallaby impact there is no suitable control area available which is free of wallabies, although exclosures do offer a partial solution.

Kamahi forest within the Okataina Scenic Reserve consists largely of even aged stands (Knowlton and Panapa, 1982) and as noted by Allen *et al* (1984) kamahi does not readily regenerate under such stands. It could therefore be argued that although wallabies utilise kamahi as a food source, they may not be responsible for suppressing its regeneration, but that rather it is an artifact of stand dynamics. Yet it is also fair to assume that because kamahi is a favoured food, were the existing canopy to be partially or wholly removed (for example as a result of wind or drought), high numbers of wallabies are likely to prove a destructive influence on kamahi regeneration.

A further complication to assessing wallaby impact is that not all palatable plants are equally and adversely affected by animal browsing. Mahoe is very palatable to damas (see Chapter 3) yet as noted by Fitzgerald and Wardle (1979) "...*Meliccytus ramiflorus* eaten in any season appears to be able to produce new growth almost immediately." It will not therefore be possible to measure the degree of decline in palatable plants until the second NZFS vegetation survey is undertaken.

Table 9.1 and Figs. 9.1 - 9.4 show that tawa is a common seedling present in large numbers within three of the four major forest types. Tawa was also found to be largely unpalatable to wallabies, but to suggest that wallabies must be responsible for this abundance of tawa seedlings may be unreasonable. Knowles and Beveridge (1982) described tawa as being shade tolerant and that it may "regenerate continuously." Within Okataina Scenic Reserve abundant tawa regeneration may be a result of its ability to regenerate in conditions unsuitable to other species rather than the sole explanation being lack of browsing. A similar situation may be reflected in the abundant regeneration of mangeao (see Table 9.1 and Figs. 9.1 - 9.4). Nevertheless I believe that whilst other factors may be involved, freedom from the browsing to which palatables are subjected, must place the unpalatables at an advantage. Where shade has been removed, as in areas of wind damage, then the presence of wallabies may lead to the establishment of tawa, rewarewa, mangeao, pukatea and pepperwood ahead of more palatable species such as kamahi, mahoe, pigeonwood, tawari, kanuka and manuka, despite the fact that the latter group tends to contain seral species better suited to such conditions.

Wallabies may also be affecting the forest through interaction with other browsing animals. The situation could be similar to that described by Fitzgerald and

Wardle (1979) where browsing ungulates eat seedlings and young plants within their reach, thereby opening the understorey and allowing possums easier access to canopy trees.

The diet of wallabies in other situations was also examined during this study. Makatiti Dome wallabies were found to be eating largely verge species but clearly they are also browsing mixed hardwood forest. Tawari is a preferred food type and Table 9.1 and Fig. 9.2 indicate that this species is under-represented in the seedling class. It is quite possible that wallabies are to some degree responsible. Yet kamahi is relatively well represented in the seedling class. An explanation could be that tawari may be more palatable and in the presence of verge species browsing pressure may not be as great on the Makatiti Dome as in the interior of the reserve. That is, wallabies with access to verges may not place such heavy browsing pressure on adjacent forest. This hypothesis is particularly credible when considering the diet of wallabies shot on pasture bordering tawa/podocarp. Here wallabies were found to obtain approximately 70% of their diet from pasture; although stomachs examined probably did not represent a 24 hour period (see Appendix II). It is clear from Table 9.1 and Fig. 9.3 that the palatable species mahoe and pigeonwood are quite well represented in the seedling tier of tawa/podocarp forest and that even in their presence pasture species are preferred.

As mentioned in Chapter 1 exclosures were installed by the NZFS in January 1983 and at the time of writing they had shown little measureable change. Nevertheless whilst NZFS procedure deems it too early for quantitative reassessment, general observation shows that many small identifiable seedlings have recently germinated. Among the species evidently germinating well are mahoe, rewarewa, *Uncinia* spp., *Asplenium* spp. and *Cirsium* spp.

All of these have been shown to be palatable to wallabies (Chapter 3) although rewarewa less so than the other species. Thus it seems probable that exclosures will eventually show an increase in palatable species implying that browsing animals are suppressing regeneration in the immediate area.

To summarise, it is reasonable to suspect that wallabies are influencing the structure of the forests in the Okataina Scenic Reserve. Results of the recent vegetation survey indicate that palatable species are poorly represented in the seedling tier and my analysis suggests that wallabies are to some degree responsible. Even so stand dynamics and several other factors will also need to be considered as more information becomes available.

Long term wallaby damage is likely to be most substantial in kamahi forest and least in tawa/podocarp where seedlings of canopy species are largely unpalatable. It is further suggested that those forests near to areas which support grass and other verge species (pasture margins or even old skid roads) may sustain the least wallaby damage.

* The tawa/podocarp forest type originally identified by Knowlton and Panapa (1982) is referred to simply as tawa forest by Llewellyn. This is because of its relatively small podocarp component, however for the purposes of this thesis, tawa/podocarp is retained.

9.2 Potential for Impact in Forests Outside Rotorua

Wallaby distribution has been steadily increasing since their introduction to the Rotorua region (Wodzicki and Flux, 1967; Fig. 1.1) and consideration needs to be given to the potential impact of wallabies in forests which are on the outskirts of their present distribution. Jane (1979) in a comprehensive NZFS report, described the dominant forest types of the Rotorua Lakes, Mamaku, Oropi and Horohoro regions. The latter 3 are just outside the area presently occupied by wallabies. Table 9.2 shows the proportions of forest types for each of these regions.

Jane noted that tawa forest predominates throughout the regions and that kamahi and mahoe (favoured foods of forest living wallabies) are very common species in all regions. Jane described the regional forests as being open in places with seral scrub and areas of grass; from my evidence I contend that this is very suitable habitat for wallabies. When discussing the Oropi region, Jane noted that "Forest condition is generally very good with coprosmas, privet and pate forming a dense shrub storey and there is a dense cover of ferns on the ground." All these species are palatable to wallabies. A similar general description was given for Mamaku forests.

Forests of Horohoro, Mamaku and Oropi all contain similar forest types to those areas already occupied by Rotorua wallabies (see Table 2.1) and there seems no reason why given access to these areas, wallabies should not colonise them in a similar fashion to the Lake Okataina Scenic Reserve.

When discussing potential increases in wallaby distribution, the Urewera National Park must also be considered. McKelvey (1973) described vegetation of the Ureweras and noted that there is a transition from conifer/mixed hardwood forest on the lowlands to conifer/mixed hardwood/beech and conifer beech at middle

altitudes and pure beech forest on the upper slopes. I suspect conifer and probably also beech forest would be less suitable for wallabies, although lower altitude forest where kamahi and mahoe are important species could well come under threat. Should wallabies be allowed to establish in the Urewera National Park then because of the large area of forest involved, control would surely prove difficult.

If wallabies do colonise in large numbers any of the Mamaku, Oropi, Horohoro or Urewera forests then they might well produce a decline in forest quality which would add to damage presently attributed to other introduced animals. It must however be noted that the Rotorua population of damas is to an extent surrounded by extensive tracts of cleared land, and rapid colonisation of new areas would not be anticipated. Even so, close monitoring of population levels and distribution changes is important to the continued confining of the population to the Rotorua area. Any control measures therefore should be designed so as to discourage dispersal. Poisoning for example would probably be preferable to shooting.

Table 9.2: Proportion of forest types by regions
(January, 1979).

TABLE 9.2:

Forest Type	Region		
	Horohoro	Mamaku	Oropi
Tawa	24.6	19.7	18.3
Kohekohe	-	-	20.0
Tawa/Mahoe	4.6	16.8	28.3
Tawa/Kamahi	11.7	9.9	4.6
Tawa/Tanekaha	-	1.6	3.3
Tawa/Ponga	7.7	5.9	1.7
Beeches	-	-	7.4
Tawari	16.0	32.2	10.7
Wineberry	14.4	7.9	2.0
Mahoe	3.0	3.2	-
Kamahi	12.3	1.1	3.8
Kanuka	2.4	-	-
Open	3.3	1.7	-

CHAPTER TEN

GENERAL SUMMARY AND RECOMMENDATIONS

The present study has reiterated previous suggestions that the dama wallaby is a preferential grazer - grasses will be represented in the diet in proportion to their availability. Where wallabies have access to pasture, upwards of 70% of identifiable stomach material is likely to consist of pasture species. A very crude calculation based on stomach weights (section 3.2.3) suggests that an adult male wallaby may consume in the vicinity of 0.42 kilos of fresh pasture material in a night. This tends to confirm the status of the dama as a pasture pest.

However wallabies are also able to survive well in the forests of Okataina Scenic Reserve where there is only meagre amounts of grass. In these situations leaf matter from forest plants makes up the bulk of the diet. Kamahi and mahoe are the most commonly eaten foods, while hangehange, *Coprosma* spp., pigeonwood and *Leptospermum* spp. are also highly preferred. This suggests natural vegetation poisoning using large leaved dicotyledonous species painted with 1080 gel might be a useful means of control, and there is a wide range of plant species which would be suitable. However seasonal variation in species usage as discussed in Chapter 3 should be considered before such an operation. Also natural vegetation poisoning as above may not produce successful results in areas where wallabies have access to verges.

An examination of wallabies living in exotic forest revealed that *Pinus radiata* is palatable but eaten in very small amounts and wallabies are probably likely to cause economic damage only to newly planted areas where grass and herbaceous graze is not available.

Wallabies were aged using the molar indexing method of Kirkpatrick (1964) and it appears that this method is very accurate up to at least 3 years of age. A comparison of Rotorua data with a population from Kangaroo Island suggests that the latter contains a larger proportion of older animals. It is suggested

that the populations sampled in Rotorua do not reach similar ages because of hunting pressure not experienced on Kangaroo Island. However it does not necessarily follow that hunting pressure is suppressing numbers, rather it may simply be altering the age structure of the populations sampled.

Mortality of Rotorua wallabies appears to be fairly even through the age classes, with no obvious difference between males and females.

My information suggests that the most suitable wallaby habitat is a pasture/forest margin, wallabies shot here were found to attain larger size than in the other habitats, whereas the smallest animals were shot from the forest interior. Presumably the latter is nutritionally a poorer environment. The hypothesis that pasture forest margin is the most suitable habitat for wallabies was supported by a study of wallaby condition using kidney fat assessment. Male and female wallabies with access to pasture have more kidney fat than those from either the Makatiti Dome or forest interior. Data on wallaby breeding also suggests that yearlings from pasture margins may be more fecund than those from other areas.

Kidney fat data showed that the fat reserves of males in all habitats drops significantly during the rut, when males are competing vigorously for females (Inns, 1980). It takes a longer period for males in poor habitats to replace these lost reserves. The greatest stress imposed on females is during late spring culminating in December, the period when the energy demands of pouch young are greatest. There is also some decline in fat reserves coinciding with the rut and entry of young into the pouch. Young wallabies are not able to accumulate significant fat reserves during their first year.

Changes in kidney fat deposits suggest that the greatest bait acceptance (Bamford and Martin, 1971) will be with wallabies living in the forest interior and that the most appropriate time for poisoning is following the rut in April-May.

As a rule female damas breed in their first year although this may be affected by habitat quality, yet adult fecundity does not appear to be adversely affected in poorer habitats. Thus the difference in breeding success between more and less suitable environments would be expected to be slight. Any difference that might arise would be from earlier breeding yearlings in nutritionally richer areas. Breeding success of Rotorua *M. eugenii* appears to be similar to that of the Australian population studied by Inns (1980). As in Australia the breeding season is quite short, although the peak of births is approximately 10 days later in New Zealand (ie. during the last week of January and the first 2 weeks of February). There is an attenuation of births through March and April - many of these may be a result of the termination of embryonic diapause when recently born young are lost from the pouch.

Sex ratios of pouch young were found to be almost 1:1 but there was a consistent and significant bias towards males in shot samples. It is suggested that this is a result of behavioural differences, with males being more active within their home range.

Because of limited time and resources the mark-recapture experiment was not particularly successful. Good results should however be obtainable by marking a larger number of wallabies and using a less traumatic capture technique.

Rhodamine trials suggested that wallabies will travel considerable distances to reach pasture and that males may

be more mobile than females.

It must be noted that there is a very real paucity of knowledge concerning wallaby movements. Research is needed to ascertain,

1. Daily home ranges
2. Seasonal variation in home range
3. Long term dispersal patterns.

Considering the results from the present diet study along with those from the recent NZFS vegetation survey produced the strong suggestion that wallabies are having a detrimental impact on the forest structure and species diversity of the Okataina Scenic Reserve. At the same time it is realised that the situation may be more complex than a direct cause and effect relationship between wallabies and forest species, although it would be unwise not to attempt some control of wallaby numbers within the reserve. If wallabies in this particular forest are left to reach an equilibrium, it is likely at best to result in a substantially impoverished forest which may or may not have a stable canopy structure.

It is also felt that consideration must be given to the continuing spread of wallabies within the Bay of Plenty. The Rotorua Lakes region is surrounded by forests which provide many suitable wallaby habitats. Some form of monitoring of numbers and distribution is desirable; regular pellet counts of regional forests are an obvious possibility.

Recommendations

1. Continued monitoring of numbers and distribution is necessary.
2. Some control measures aimed at reducing numbers, particularly in the kamahi forests of the Okataina Scenic Reserve are desirable. Aerial or natural vegetation poisoning during the late autumn and winter may be the most successful techniques.
3. Continued investigation into wallaby impact within the Okataina Reserve, through successive vegetation surveys should along with the results from exclosure plots, help to elucidate the true extent of wallaby influence.
4. More research to fill the extensive gaps in knowledge concerning wallaby movements is required. Daily home range, seasonal variation in home range and long term dispersal patterns all need to be ascertained.

Within animal control organisations there has been a trend towards management and monitoring of populations, rather than extermination.

The Rotorua Lakes wallaby population although quite dense, is at present restricted to a small area. It is probably comparable to Nelson red deer (Clarke, 1971) or sika (Davidson, 1973) 30 - 40 years after their initial liberation, and if the option of extermination is to be considered, a decision to that effect would need to be taken very soon. On the other hand in mainland Australia distribution of *M. eugenii* is now very restricted and it may be that the Rotorua population represents an undiscovered resource with a financial potential. This could include a fur trade, live export to zoos, tourist attraction, meat

for animal or even human consumption and safari hunting. Thus it may be an option to reduce the population to a level where forest and pasture damage is economically and asthetically acceptable while at the same time developing the wallaby as a resource. Although much more information of a fundamental nature is required, these are questions the addressing of which may be timely.

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APPENDIX I

Choosing a Methodology for Diet Analysis

When deciding on the most suitable technique for a study of wallaby diet, it was first necessary to select from the following broad methodologies.

Direct Observation

This involves identifying the plant species being eaten and using bite counts and feeding duration to estimate the proportions consumed (Holchek *et al*, 1982). This technique was not considered viable for wallabies because of the difficulties inherent in such observations, ie. they were often hidden from view, nocturnal, easily distracted and such a method be time consuming.

Utilisation Techniques (Holchek *et al*, 1982)

The most promising involves evaluating differences between grazed and ungrazed areas such as the erecting of exclosure plots as was done for wallabies by Kinloch (1973). It was decided to use exclosures in this study.

Another utilisation technique is that described by Jensen and Urness (1981) which uses measurements of twig diameter to determine the length and weight of twigs browsed. This was not suitable here because of the presence of other animals in the study area (see section 2.1.3).

Macrohistological Analysis (reviewed by Nugent, 1983)

This involves estimates of diet by "measuring the relative amounts of each food type that can be identified in a sample of rumen contents without the use of high-power microscopy." (Nugent, 1983). Material for analysis can be collected either by sacrificing animals and sampling from stomachs (Mitchell, 1985) or by using

fistulated animals (Holchek *et al*, 1982). Nugent (1983) noted that there are two techniques for analysing samples: sorting (physical separation of food types) or point analysis (systematic sub-sampling).

Prior to the present study several entire stomachs were obtained from wallabies within Rotoiti forest, and the possibility of macrohistological analysis was examined. It was found that stomach material was too finely ground to be identified from macroscopic features. Extensive chewing has been noted in other macropods, eg. Griffiths and Barker (1966) found that kangaroos grind food much more than do sheep.

Microhistological Analysis

This was the most appropriate technique for a study of wallaby diet. Microhistological analysis makes use of the fact that "...the cuticle layer of plant foliage has a species-specific pattern that persists throughout the digestive process and can be used for identification" (Nugent, 1983). There are many epidermal and cuticular features that can be used for identification, as have been described by Baumgartner and Martin (1939), Martin (1955), Croker (1959), Hercus (1960), Storr (1961), Gilmore (1966), Griffiths and Barker (1966), Zyznar and Urness (1969), and for a wide perspective of monocotyledons, Metcalfe (1960), dicotyledons, Metcalfe and Chalk (1979), and for grasses in particular Stewart (1965).

Having decided to use cuticle analysis it was then necessary to decide on a specific methodology - that is there are many different methods described in the literature and no general consensus as to which method is subject to the least errors. The following is a brief review of cuticle analysis techniques.

The earliest description of the microhistological technique must be that of Baumgartner and Martin (1939) where stomach material (from squirrels) was rinsed in water then mounted on a slide in a mixture of HCl, glycerine, and chloral hydrate crystals (Herwigs solution). The finished product was then compared to reference slides "of various plant tissues anticipated in stomachs."

Mason (1958) used epidermal structures when analysing the stomach contents of possums (*Trichosurus vulpecula*) in a broad qualitative fashion; and she compared "...scraps of leaf, about 4mm square or larger..." found in the stomachs, with herbarium specimens.

In a widely cited study of sheep diet, Croker (1959) used faecal samples which were simply diluted with an "...equivalent volume of water and spread between two slides." She then compared fragments of cuticle with a reference collection.

Chippendale (1962) used stomach samples of kangaroos and cattle which were washed in a fine sieve, dried in the sun, sorted and examined using a binocular microscope after which a visual estimate of species percentages was made.

The methods described so far are purely qualitative, that is particle size is not taken into account and plant species are just recorded as percent particles identified. Storr (1961) produced a method which he claimed was both qualitative and quantitative. The method was quantitative because Storr assumed there is a "...determinable relation in each species of plant between the surface area and dry weight of its foliage." Faeces were digested in vitro using 10% nitric and chromic acid, when mounted the area of each epidermal fragment was estimated with a graduated eyepiece. Storr's method depended on the important assumption that the "digestibility of epidermis

is approximately the same in all perennial plants." This has been criticised by Griffiths and Barker (1966), when Storr's "in vitro" acid digestion was shown to produce anomalies. "Digestion of two samples of the one plant with the recommended strength of nitric acid-chromic acid mixture would result sometimes in the complete disappearance of one sample after 10 minutes of treatment, whereas its digest-mate would survive 30 minutes." (Griffiths and Barker, 1966). More recently Vavra and Holchek (1980) have also noted that in vitro digestion (using different compounds to Storr) can result in a difference between estimated and actual means of plant species.

As well as in vitro digestion, differential digestion of plant species in vivo must also be considered and has been observed by many workers (eg. Dunnet *et al*, 1973; Dawson and Ellis, 1979; Fitzgerald and Waddington, 1979).

Griffiths and Barker (1966) used a method which they claimed destroyed no part of the plant by chemical agents. Stomach samples of kangaroos and sheep were "ground fine in a Wylie mill", differentially sieved so that "...particles could pass a sieve with a mesh of 60 to the inch but not one of 120 to the inch." The relative proportions of plants were estimated by counting along randomly selected transects of the slides (for a discussion of line intercept procedures see Seber and Pemberton, 1979). Counting gave a direct measure of relative volume because sieving led to all particles being of a similar size.

Even though Griffiths and Barker used stomach samples rather than faecal, they had major problems identifying particles. In many samples a large proportion could not be identified even to dicotyledon or monocotyledon; the percentage unidentifiable ranged from 29% to 70%. The most obvious explanation for this would seem to be

grinding in the Wylie mill, however Vavra and Holchek (1980) found that grinding in a Wiley (sic) mill followed by soaking in a dilute solution of sodium hydroxide "...increased the number of identifiable particles."

It is interesting to note that Griffiths and Barker supplemented the stomach analysis with plant samples taken from the mouth of animals immediately after being shot. This was also done by Bailey *et al* (1971), who used Griffiths and Barker's analysis technique. Clearly mouth sampling could be valuable, as the plant species would be relatively simple to identify and could provide the investigator with a valuable beginning to deciding what is in the animals gut.

Faecal and stomach analysis - using plant cuticle to identify species - has been used extensively in New Zealand, primarily in possum studies. Examples of workers using faecal analysis are: Gilmore (1967), Dunnet *et al* (1973), Fitzgerald (1976), Fitzgerald and Wardle (1979), Fitzgerald and Waddington (1979), and for stomach analysis Gilmore (1965), Warburton (1978), Harvie (1973).

The pros and cons of faecal versus stomach analysis were reviewed by Holchek *et al* (1982). The major advantage of faecal analysis is that it does not in any way interfere with the animal. The disadvantages are: plants in the faeces are not always in a similar proportion to that ingested, and particle identification can be difficult, with large amounts of unknown material.

Slater and Jones (1971) issued a warning that faecal analysis may be satisfactory for robust plants found in arid and semi-arid environments but may not produce valid results where there are softer species involved. This warning might seem especially applicable to the New Zealand situation.

By feeding known amounts of plant material to possums, Fitzgerald and Waddington (1979) found that it was necessary to apply an index of digestion to frequency of occurrence results to get them to fall within 10% of the expected value. The conclusion of Fitzgerald and Waddington was that a "correction factor" is needed to allow for the differential loss of cuticle during natural digestion or preparation for examination. The need for correction factors can be largely overcome by using stomach rather than faecal material and also by selecting an *in vitro* technique which is not likely to produce large differential losses of cuticle.

In summary, stomach analysis is subject to less variability of results than faecal analysis and should be used where ever possible. Whether faecal or stomach samples are used, an attempt should be made to determine quantitatively, amounts of food ingested; either by measuring area of particles (as in Fitzgerald, 1976) or by differential sieving and using relative number of particles as a measure of volume ingested (Griffiths and Barker, 1966). Also whatever microhistological procedure is finally decided upon there are a number of sources of error to be considered. These are (based on Westaby *et al*, 1976):

1. Differential loss of cuticle through *in vivo* and *in vitro* digestion for various plant species.
2. Plant species may contain different proportions of unidentifiable particles.
3. It is easier to identify material from some species than from others.
4. Material may be identified wrongly.
 - i. The wrong name may be given to all particles of some identifiable material.
 - ii. The analyst may attempt and fail to name material which was not reliably identifiable.

5. If a plant species is subject to underestimation, the species which occur with it will tend to be overestimated and vice versa.
6. A problem which is separate from the above, but probably more important, is extrapolation from a sample of stomach contents to the diet of the population.

For this study it was decided that stomach analysis would be used because it is subject to less error than faecal analysis.

When preparing material for identification (see Appendix II for a discussion of how digesta was sampled from stomachs) it was initially decided to follow the technique of Fitzgerald (1976). However there were subsequently found to be several problems with using acid maceration. Cuticle of mosses and clovers (*Trifolium* spp.) do not readily survive, a point noted by Kelton (1981); using acid maceration for preparing actual stomach material would surely result in underrepresentation or complete disappearance of at least these two types.

It was suggested (Fitzgerald, personal communication) that bleaching with sodium hypochlorite ("Janola") may provide better results. This was subsequently used and found to be very successful. Clover and mosses readily survived long periods of bleaching. Even being left overnight in concentrated bleach did not result in any overt loss of cuticular material. (H. Outred (personal communication) states that most mosses do have a cuticle although it is chemically different from that of higher plants. Dick (1985) used bleach, when investigating the diet of rats on Kapiti Island.

I believe that when preparing samples with bleach the only major source of error may arise when fragments of plants with particularly robust leaves pass through

bleaching without their cuticles clearing sufficiently for identification. Thus these plants may be labelled as unidentifiable (see section 3.1.2 for a further discussion). However in this study the proportion of unidentifiable material in samples was not excessive, compared for example, with Griffiths and Barker (1966) where unidentifiable material was sometimes as much as 70%. Therefore it is argued that if many plant fragments were labelled as unidentifiable as a result of insufficient clearing, their absence would not greatly affect final proportions.

The method of processing samples as outlined in section 3.1.1 is based on that used by Fitzgerald (1976), that is, a Waring blender was used to mix samples and to reduce fragments to a uniform size. The sieve size (210 μ m) used for rinsing samples, and also to remove dirt and very small fragments, was as that used by Fitzgerald (1976) for possums.

As to the number of cuticle fragments to be identified Scotcher (1979) recommended that 100 fragments per sample were adequate, whereas Stevens (1977) used 200 identifications. Nugent (1983) suggested that "The most appropriate number of identifications for any one particular study will have to be decided by considering the level of precision required, the amount of time and labour available, and the effect of operator efficiency on precision." For the present study it was decided that 100 fragments per sample would be identified for wallabies from the Makatiti Dome and pasture/forest margin. Whereas with wallabies from forest interior a greater "level of precision" was desirable because (a) these wallabies were considered to be the most important in terms of aims of the study (see section 1.4), and (b) the sample size of wallabies from forest interior was smaller than that for other areas. Therefore it was decided to identify 200 fragments per sample as in Stevens (1977).

Sparks and Malechek (1968) prepared 5 slides for each sample, but Casebeer and Koss (1970) used only 2 microscope slides. It was decided here to prepare 4 slides.

Seber and Pemberton (1979) using simulation experiments recommended the "line intercept method" to be the best way of treating slide identifications, they also noted that it holds for all shaped particles. Therefore this method was used in this study and fragments were thus identified on random transects across the slides.

APPENDIX II

Passage of Ingested Material Through the Gut of *M. eugenii*

As mentioned in Chapter 1 the morphology and physiology of the digestive system has been well documented for *M. eugenii* in Australia. Some of this work is relevant to this study; in particular flow of material through the alimentary tract.

As noted in a recent review by Hume (1982) the macropodine digestive system is quite different to that of ruminants. In particular "their gastric morphology leads to tubular flow of digesta through the stomach and to shorter passage times of food residues through the gut...(than for ruminants)" (Hume, 1982). A significant portion of the work reviewed by Hume was carried out by Dellow (1982). Dellow used the markers $^{51}\text{CrEDTA}$ and ^{103}RuP to examine digesta flow in 4 macropodine marsupials, one of which was *M. eugenii*. He found that the pattern of digesta flow in macropodines differed markedly from sheep and attributed this "...solely to the mode of transport through the elongated stomach." That is, as reviewed by Hume (1982), in ruminants larger food particles have a longer retention time in the reticulorumen (the forestomach) than do small particles. Whereas in macropodines this does not appear to be so. Thus in sheep, food entering the ruminoreticulum is mixed with a digesta pool which contains material from previous feedings (Reid *et al*, 1977). However Dellow (1982) found that "in the macropodines it was apparent that total mixing of forestomach contents did not occur; rather, digesta flowed slowly along the tubiform forestomach." Hume (1984) has recently reviewed the work of Barker *et al* (1973) and reiterates that macropodines do not ruminate, a process which would serve to mix material in the forestomach.

I believe tubular flow was demonstrated to a very small extent in the present study in that animals shot during rhodamine trials (Chapter 9) showed definite boundaries within the stomach between rhodamine stained and unstained material.

Recognition of tubular flow in macropods is relevant to the present study because it implies that samples of digesta taken from various regions of the digestive tract may largely represent food consumed within a defined period. For ruminants it must be more difficult to establish the time period over which rumen material was consumed.

Dellow (1982) also examined retention times of material within the alimentary tract of *M. eugenii* and Table 1 shows the results of one such experiment. Values are mean retention times for dry matter \pm standard errors. The table shows a cumulative mean retention time for dry matter in the stomach of 15.6 hours. Warner (1981) found a mean retention time of 11.4 hours for a particulate marker in the stomach of *M. eugenii* and Dellow (1982) in another experiment determined a "50% excretion time" for a particulate marker (103RuP) through the entire digestive system of 23.6 \pm 3.5 hours. In a third experiment 50% excretion time (ET) was found to be 25.9 \pm 1.5 with a 50% ET for the intestinal system per se of 12.7 \pm 2.1.

Extrapolating from the above research it would seem that material in the stomachs of damas could possibly consist of plant matter from up to approximately 12 - 15 hours previous to being shot. Although in practice it is likely to represent foods consumed within a much shorter period and if the animal has eaten little for the previous 12 hours, all material may be from the present feeding period. In this study it was decided that the most appropriate way to sample

Table 1: Retention times for dry matter within the
alimentary tract of *M. eugenii* (from Dellow,
1982).

TABLE 1:

	Mean Retention Time (hr)
Sacciform forestomach	3.3 \pm 0.6
Tubiform forestomach	10.3 \pm 2.3
Hindstomach	2.0 \pm 0.4
Caecum-proximal colon	3.3 \pm 0.3
Distal colon	5.1 \pm 2.3

stomachs would be to take equal portions of digesta from several regions along the entire length of the stomach. Thus food would be collected from over as great a time span as possible. It is also realised that to achieve a sample from the previous 24 hours it would be necessary to sample along the entire length of the digestive tract and it was decided that the advantages of doing so were outweighed by the fact that samples would then be liable for those criticisms applicable to faecal analysis (see Appendix I). Thus in this study an equal portion of digesta was removed from the sacciform forestomach, hindstomach and the curve of the tubiform forestomach which is between these two.

APPENDIX III

Common and Botanical Names for Plant Species Included in
the Reference Collection.

Nomenclature for indigenous species follows; Flora of New Zealand, Volumes 1 (Allen 1961), 2 (Moore and Edgar, 1970) and 3 (Healy and Edgar, 1980); for introduced weeds and grasses Healy (1982) and Lambrechtsen (1981).

<u>Botanical Name</u>	<u>Common Name</u>
<i>Acaena</i> spp.	Bidi bidi
<i>Achillea millefolium</i>	Yarrow
<i>Agropyron cristatum</i>	
<i>Agrotyis tenuis</i>	
<i>Alectryon excelsus</i>	Titoki
<i>Alseuosmia</i> spp.	
<i>Anthoxanthum odoratum</i>	Sweet vernal
<i>Aristotelia serrata</i>	Wineberry
<i>Asplenium bulbiferum</i>	Hen and Chickens fern
<i>Asplenium falcatum</i>	
<i>Asplenium flaccidum</i>	Hanging spleenwort
<i>Asplenium lucidum</i>	Shining spleenwort
<i>Beilschmiedia tawa</i>	Tawa
<i>Blechnum capense</i>	Kiokio
<i>Blechnum discolor</i>	Crown fern
<i>Blechnum fluviatile</i>	
<i>Brachyglottis reparda</i>	Rangiora
<i>Bromus cathensis</i>	
<i>Bromus inermis</i>	
<i>Bromus mollis</i>	
<i>Bryopsida</i>	Moss spp.

<u>Botanical Name</u>	<u>Common Name</u>
<i>Carex</i> spp.	
<i>Carpodetus serratus</i>	Putaputaweta
<i>Cirsium arvense</i>	Californian thistle
<i>Cirsium vulgare</i>	
<i>Coprosma australis</i>	Raurekau
<i>Coprosma foetidissima</i>	Stinkwood
<i>Coprosma robusta</i>	Karamu
<i>Coprosma tenuifolia</i>	
<i>Coniaria arborea</i>	Tutu
<i>Cortaderia</i> spp.	
<i>Corynocarpus laevigatus</i>	Karaka
<i>Cyathea dealbata</i>	Ponga, silver fern
<i>Cyathea medularis</i>	Black mamaku
<i>Cyperus ustulatus</i>	
<i>Dacrydium cupressinum</i>	Rimu
<i>Dactylis glomerata</i>	Cocksfoot
<i>Deyeuxia avenoides</i>	
<i>Dicksonia squarrosa</i>	Wheki ponga
<i>Elaeocarpus dentatus</i>	Hinau
<i>Epilobium glabellum</i>	
<i>Epilobium rummulariifolium</i>	
<i>Erica luscicana</i>	Heather
<i>Erigeron floribundus</i>	
<i>Festuca arundinacea</i>	
<i>Fuchsia excorticata</i>	Fuchsia, Konini
<i>Galium aparine</i>	Cleavers
<i>Gaultheria antipoda</i>	
<i>Geniostoma rupustre</i> *	Privet, Hangehange
<i>Griselinia littoralis</i>	Broadleaf
<i>Griselinia lucida</i>	Broadleaf

<u>Botanical Name</u>	<u>Common Name</u>
<i>Hebe stricta</i>	
<i>Hedycarya arborea</i>	Pigeonwood
<i>Histiopteris incisa</i>	Water fern
<i>Hoheria angustifolia</i>	Lacebark
<i>Holcus lanatus</i>	Yorkshire fog
<i>Hydrocotyle microphylla</i>	
<i>Ixerba brexioides</i>	Tawari
<i>Juncus gregiflorus</i>	
<i>Juncus tenuis</i>	
<i>Knightsia excelsa</i>	Rewarewa
<i>Laurelia novae-zealandiae</i>	Pukatea
<i>Leontodon taraxacoides</i>	
<i>Leptospermum ericoides</i>	Kanuka
<i>Leptospermum scoparium</i>	Manuka
<i>Leucopogon fasciculatus</i> [†]	Mingimingi
<i>Leucopogon fraseri</i> [†]	
<i>Litsea calicularis</i>	Mangeao
<i>Lolium multiflorum</i>	
<i>Lolium perenne</i>	
<i>Lotus pedunculatus</i>	
<i>Macropiper excelsum</i>	Kawakawa
<i>Meliccytus ramiflorus</i>	Mahoe
<i>Metrosideros excelsa</i>	Pohutokawa
<i>Metrosideros perforata</i>	
<i>Metrosideros robusta</i>	Northern rata
<i>Microlaena avenacea</i>	Oatgrass
<i>Myrsine australis</i>	Mapou, red matipo
<i>Myrsine salicina</i>	Toro
<i>Olearia rani</i>	
<i>Oxalis</i> spp.	

<u>Botanical Name</u>	<u>Common Name</u>
<i>Paesia scaberula</i>	
<i>Paspalum notatum</i>	Paspalum
<i>Persoonia toru</i>	
<i>Phleum pratense</i>	Timothy
<i>Phymatosorus deversifolius</i>	
<i>Pimelea prostrata</i>	
<i>Pinus radiata</i>	
<i>Pittosporum eugenioides</i>	Tarata, Lemonwood
<i>Pittosporum tenuifolium</i>	Kohuhu
<i>Plantago lanceolata</i>	
<i>Plantago major</i>	
<i>Pneumatosorus penninger</i>	
<i>Poa caespitosa</i>	
<i>Poa pratensis</i>	
<i>Podocarpus halli</i>	Totara
<i>Podocarpus totara</i>	Totara
<i>Polygonum persicaria</i>	Willowweed
<i>Polystichum richardii</i>	
<i>Pseudopanax arboreum</i>	Fivefinger
<i>Pseudowintera colorata</i>	Horopito
<i>Pseudowintera axillaris</i>	Pepperwood
<i>Pteridium aquilinum</i>	Bracken fern
<i>Pteris comans</i>	
<i>Pteris tremula</i>	
<i>Ranunculus repens</i>	
<i>Raoulia glabra</i>	
<i>Ripogonum scandens</i>	Supplejack
<i>Rubis cissoides</i>	Bush lawyer
<i>Rubis fruticosus</i>	Blackberry
<i>Rumex spp.</i>	Dock
<i>Schefflera digitata</i>	Pate
<i>Senecio jacobaea</i>	Ragwort
<i>Stellaria media</i>	Chickweed

<u>Botanical Name</u>	<u>Common Name</u>
<i>Taraxacum officinale</i>	Dandelion
<i>Trifolium pratense</i>	Red clover
<i>Trifolium repens</i>	White clover
<i>Ulex europaeus</i>	Gorse
<i>Uncinia</i> spp.	Hookgrass
<i>Urtica incisa</i>	Stinging nettle
<i>Weinmannia racemosa</i>	Kamahi

* Recent name change.

APPENDIX IV

A Note on Classification of *M. eugenii*

The dama wallaby (*Macropus eugenii*) (Desmarest, 1817) is known in Australia as the tamarin or Kangaroo Island wallaby.

The species has not always been included in the genus *Macropus*; in chronological order the genera that have been used are *Macropus*, *Thylogale*, *Protemnodon*, *Macropus* (as reviewed by Kinloch, 1973).

Sharman (1961) in a study of marsupial chromosomes suggested a return to using *Macropus*, and most workers have done so. Exceptions include Andrewartha and Barker (1969), Barker *et al* (1970) and Jones *et al* (1966) where in each case *Protemnodon eugenii* has been used.

APPENDIX V

Summary of wallaby numbers shot and body statistics.

Status	Number	Percent
Male adult	525	48.7
Female adult	395	36.9
Male immature	99	9.2
Female immature	57	5.3

Area	Number	Percent
Makatiti Dome	337	31.2
Exotic forest*	336	31.1
Pasture margin	335	31.0
Forest	71	6.6

* Shot during two sampling periods only, ie. February and July 1984.

Male Adults

Habitat	Weight (kg)	TBL (cm)	TL (cm)	HFL (cm)	Skull length (mm)	Skull width (mm)
Pasture Margin	$\bar{x} = 5.57$ SD = 1.23 N = 170	100.0 7.23 170	41.36 3.5 170	15.90 0.68 170	92.7 5.2 154	53.86 2.29 157
Exotic Forest	$\bar{x} = 4.9$ SD = 1.39 N = 163	96.29 8.14 163	40.77 3.59 163	15.76 0.67 163	91.13 5.78 94	53.20 2.56 94
Makatiti Dome	$\bar{x} = 4.86$ SD = 1.08 N = 150	94.4 7.63 150	38.73 3.8 150	15.28 0.83 149	90.55 5.17 133	53.14 2.42 134
Forest Interior	$\bar{x} = 4.269$ SD = 0.701 N = 42	93.89 6.57 42	39.96 3.40 42	15.2 0.61 42	88.94 3.44 37	52.37 1.64 36

Female Adults

Pasture Margin	$\bar{x} = 4.34$ SD = 0.77 N = 119	91.11 5.9 119	37.6 2.9 119	15.1 0.69 119	87.7 4.79 112	52.51 2.25 112
Exotic Forest	$\bar{x} = 4.02$ SD = 0.7 N = 148	90.1 5.44 148	37.9 2.4 148	14.96 0.57 148	- - -	- - -
Makatiti Dome	$\bar{x} = 3.7$ SD = 0.65 N = 114	86.81 5.87 114	35.13 3.38 114	14.54 3.03 114	86.4 4.68 63	51.86 2.14 63
Forest	$\bar{x} = 3.26$ SD = 0.54 N = 14	87.25 5.91 14	36.62 2.40 14	14.41 0.66 14	84.31 4.77 13	50.57 2.21 13

Immature Males

Habitat	Weight (kg)	TBL (cm)	TL (cm)	HFL (cm)	Skull length	Skull width
Pasture	$\bar{x} = 2.465$	78.77	32.96	14.67	78.79	48.32
Margin	SD = 0.675	7.19	2.55	0.85	3.41	1.85
	N = 26	26	26	26	15	15
Exotic	$\bar{x} = 2.57$	82.6	36.0	14.67	81.0	47.9
Forest	SD = 0.2	2.72	1.2	0.49	4.3	3.2
	N = 15	15	15	15	15	15
Makatiti	$\bar{x} = 2.33$	74.8	29.88	13.67	76.76	48.8
Dome	SD = 0.535	6.19	2.42	0.79	4.87	7.0
	N = 49	49	49	49	37	37
Forest	$\bar{x} = 1.91$	73.44	30.89	13.67	74.34	46.55
Interior	SD = 0.375	2.46	0.35	0.35	1.69	1.19
	N = 9	9	9	9	5	8

Immature Females

Pasture	$\bar{x} = 1.91$	72.45	30.45	13.63	73.11	46.03
Margin	SD = 0.469	4.79	1.43	0.63	3.14	2.30
	N = 20	20	20	20	9	9
Exotic	$\bar{x} = 2.22$	79.0	34.1	13.94	-	-
Forest	SD = 0.32	4.03	1.55	0.32	-	-
	N = 8	8	8	8	-	-
Makatiti	$\bar{x} = 2.05$	71.76	29.33	13.28	74.49	46.41
Dome	SD = 0.39	5.35	2.27	0.75	2.84	1.18
	N = 23	23	23	23	16	16
Forest	$\bar{x} = 1.92$	73.42	30.83	13.17	73.67	45.84
Interior	SD = 0.465	6.28	3.06	0.75	5.35	1.5
	N = 6	6	6	6	3	5