BIOLOGY OF SAMBAR DEER (*Cervus unicolor* Kerr, 1792) IN NEW ZEALAND WITH PARTICULAR REFERENCE TO DIET IN A MANAWATU FLAX SWAMP

A thesis presented in partial
fulfilment of the requirement for the degree
of Master of Science in Zoology at
Massey University

SIMON DOUGLAS KELTON

1981

SAMBAR HIND, MOUTOA
(L. Barnard)

ABSTRACT

This MSc. thesis is the first detailed account of the biology of sambar deer (Cervus unicolor Kerr, 1792) in New Zealand. Observations were made for fifteen months on approximately 35 animals inhabiting flax swamp at Moutoa, southern Manawatu.

Sambar are shy and cautious, mostly nocturnal and prefer dense cover. Methods used to overcome problems of direct observation of sambar are described and their relative effectivenesses are compared. Habitat requirements are also discussed.

Diet of Moutoa deer was determined by analysing monthly faecal samples supported by direct observation of feeding and examination of feeding evidence. A quantitative method of faecal analysis based on the area of plant cuticle present is described. Seasonal changes in diet composition are detailed. Flax and rank grasses comprise the greatest proportion of the diet, while ryegrass was present in low proportions and clover was absent from the faeces. Evidence is presented suggesting sambar deer do not compete with domestic stock for high quality forage.

The eight most frequent forage species found in faeces were sampled seasonally and analysed for Acid Detergent Fibre, energy, nitrogen (crude protein) and water content. There was no correlation between changes in forage quality throughout the year and seasonal changes in diet composition. Other factors involved in forage selection are discussed.

The Moutoa breeding population is viable and had an estimated average age structure of 36% adult males, 46% adult females and 18% juveniles.

In New Zealand sambar appear to breed throughout the year with two peaks of increased rutting activity in June, July and August, and in November.

Evidence is presented that the majority of stags shed their antlers annually, in contrast to the previously accepted belief that they hold antlers for two or more years. Antler cycle is closely associated with the breeding cycle, most sightings of stags in hard antler occurring from June to November. Examination of available information on breeding and antler cycles in Australian sambar revealed similar cycles to those in New Zealand, whereas in India it appears a single peak in rutting occurs from October to December, with a corresponding antler cycle.

Herds are loosely structured and generally comprise small family groups, commonly a hind, yearling and fawn. Young stags generally form groups of two to four individuals while old stags evidently lead solitary lives except in the breeding season when they were often observed with one or two hinds. Rutting stags are territorial with olfactory and visual cues apparently serving to exclude rivals. Roaring or fighting, apparently common in India during the rut, is rare in New Zealand.

Evidence is presented that some hybridisation with rusa deer (Cervus timorensis Blainville, 1822) occurs in the Bay of Plenty. A comparison of cranial characters between Manawatu and Bay of Plenty deer was inconclusive because of insufficient numbers of skulls. Sexually dimorphic cranial characters are given for animals from the Manawatu area. Sambar deer skulls were aged by counting the number of annuli in the cementum pad of molariform teeth.

ACKNOWLEDGEMENTS

My supervisor, Dr J.P. Skipworth, deserves my sincerest thanks for his constructive help during all of my research and thesis preparation.

Sincere thanks are also due to Mr and Mrs A.E. Hunter, who manage Moutoa. Without their enthusiastic help and kind hospitality this research would not have been possible.

The New Zealand Forest Service provided $500.00 towards my travel and often extended their generous help and advice for which I am grateful. In particular I appreciate the help and information given by Dr C. Challies, C.L. Batcheler and M. Douglas (Forest Research Institute, Islam), I. Logan, W. Simmons and J. Sutton (Forest Service, Palmerston North), and H. Vipond, Judy Gamble and J. Knowlton (Forest Service, Rotorua).

Considerable help was also given me by M. Daniel and Dr M. Rudge, (Ecology Division, D.S.I.R.) who gave me the benefit of their own field experience.

The following people also made their own unpublished data available to me : M. Daniel on Rotorua sambar ; Dr M. Draisma, (Deer Advisory Council of Victoria, Australia) on breeding and antler condition of Australian sambar ; J. Rudd (Deerstalkers' Association, Rotorua) on breeding and antler condition of Rotorua sambar.

I am indebted to Dr G. Arnold, D. Drummond, R. McCammon, P. McGregor, Dr E. Minot, Dr T. Moore (all of Massey University) and C.L. Batcheler for statistical assistance and advice on craniometric analysis. In addition Dr E. Minot kindly ran the "Genstat" program for analysing my nutrient data.

Thanks are also due to the following Massey staff : Dr A. Davey for allowing me the use of nutrient analysis equipment, and Mrs Y. Moore and J. Raven for showing me the use of this equipment ; Dr E. Kirk who provided a diamond saw for tooth sectioning ; J. Clouston and staff of the Central Photographic Unit for preparation of photographs ;

and the illustrator, K. Korndorffer, for the use of the Kroytype lettering machine.

I appreciate the invaluable information concerning practical experience with sambar given by C. Fergusson, J. Hargraves, A. Harnett, O. Maher, L. Rowe, R. Rowe, L. Shailer, M. Shailer, P. Smith and W. Wallace.

I also appreciate the help given me by Dr R.A. Fordham and I. McKelvey for the preparation of the skeleton shown in Plate 15 ; I. McKelvey for helping me erect the Massey hide ; L. Barnard for the use of his photographs shown in the frontispiece, Plate 4 and Plate 16 , and for helping erect and supplying material for the Coffin hide.

My thanks to N. Haack, P. Lo, Adrienne Pease, Mr and Mrs D.C. Pease, Moyra Roberts and my parents who assisted me in many ways and provided encouragement on innumerable occassions.

Some additional help with the preparation of the script was provided by Dr I. Stringer and Professor B.P. Springett.

Adrienne Pease and my parents helped by proof reading.

Lastly many thanks are due to Mrs J. Evans and Mrs F.S. Wicherts for the setting out and typing of this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

LIST OF PLATES

LIST OF PLATES

PLATE

Page

PART I - INTRODUCTION

CHAPTER 1

1.1 Introductory Description

The sambar (Cervus unicolor Kerr, 1792) is the third largest of the deer species imported into New Zealand; only moose and wapiti are larger.

New Zealand stags average between 180 to 225 kg in weight and stand nearly 150 cm high (Morrison and Harris, 1974) while hinds weigh approximately 150 kg and stand about 115 cm high (Harrison, 1979). Exceptional animals from India have been recorded as weighing up to 318 kg (Whitehead, 1972). Vaulted nasals, rhombiform to cruciform in shape and a flat to concave forehead give sambar a slightly "horse-like appearance" (Van Bemmel, 1949; Logan, 1965). Both sexes, but particularly the stag have well developed preorbital glands, which secrete a strong smelling waxy substance (Draisma, 1979). These glands are capable of being everted, presumably for display purposes, and caused the Chinese to name the sambar "four-eyes" (Cahalane, 1939). The ears are large, about half the length of the head (Lydekker, 1898; Draisma, 1979) and are very broad. Van Bemmel (1949) described the "rhinarium" (muzzle) as being "nearly bare, extending to the dorsal part of the face and forming a broadish rim below the nostrils ... covered with rather large warts, with some scattered hairs originating between them" (Plate 1). Pelage of both sexes is generally a uniform brown with underparts somewhat lighter in colour. The chin, between the buttocks (peroneum) and under the tail are pale brown. There is a considerable variation in colour between individuals from a very dark brown to a slate grey, stags in general being darker than hinds or young. Fawns have adult coat colouring (no white spots) with a dark dorsal strip that fades a few months after birth (Van Bemmel, 1949; Draisma, 1979). "Being a sub-tropical species the coat is coarse and bristle-like, lacking the fine under-fur of the European species.

Plate 1: Head of dead sambar hind

Note the following facial characteristics typical of sambar: Rhinarium which extends to the dorsal part of the face, forming a broadish rim below the nostrils and having a rather wart-like appearance with scattered hairs over its surface. A prominent nasal ridge gives sambar their horse like appearance. Ears are large.

This hind had been shot at Moutoa approximately three days earlier by poachers. Its age was later determined to be 9 years (see Section 5.6).

There is a distinct mane-like ruff around the upper part of the neck which along with the dorsal coat and tail hair is erectile" (Draisma). The tail is about 28 cm long and brushlike at the end (Logan, 1965). Small canines are present in the upper jaw of both sexes and "like most Cervidae" sambar have no upper incisors, but instead a horny dental pad (Draisma, 1979). Draisma has also found that, as in other ruminants, lower canines have become modified to form fourth incisors and lack alveoli. Upper molars are tall-crowned with a small additional column on the inner side (Lydekker, 1898). Draisma (1979) presented the following dental formula:

Deciduous teeth	Permanent teeth
$Io\ Co\ PM_3\ M_1$	$Io\ C_1\ PM_3\ M_3$
$I_4\quad PM_3\ M_1$	$I_4\quad PM_3\ M_3$

Adult stags normally possess a pair of rounded, three tined antlers. Lydekker (1898) found that in general, the rusine group is characterised by this antler form i.e. a brow-tine and beam simply forked at the extremity, bez and trez tines absent. The antler bone is denser (less porous) than that of red deer (Logan, 1965; Harris, 1966).

1.2 Taxonomy

The rusine deer have been variously assigned by some authors to the genus Cervus, subgenus Rusa e.g. Smith (1827), or by others to a separate genus, Rusa e.g. Loomis (1928).

Lydekker (1898) considered the simple antler form of rusine deer to be suggestive of a generalised group; "The original type would appear to be represented by the Indian spotted deer, or chital, in which the white spots are persistent at all ages and all seasons. A more advanced modification is displayed by the hog deer, in which the spots disappear in the adult during winter. But the most specialised form of all are the various kinds of sambar, in which the adult is uniformly coloured at all seasons, while even the fawn may have lost its dappling." He continued, "It is probable that the group reached the Oriental region at a comparatively early epoch (remains of fossil species occurring in the Pliocene strata of the Siwalik Hills), and that it has no connection with the ancestors of the [other] groups since the early part of the Pliocene epoch, when it may have branched off from sikine stock." However, Lydekker considered that the rusine deer belonged to the genus *Cervus* and used the specific name *unicolor* for sambar which had been revived by Blanford (1891). Until then the sambar was known as *Cervus aristotelis*. Blanford wrote - "This fine deer appears to have been first mentioned by Pennant, who described it as the middle-sized and greater axis (*Cervus axis unicolor* and *C. axis major* of Kerr). To these forms the names of *Cervus unicolor* and *C. albicornis* were applied by Bechstein. Cuvier, in the second edition of his *Ossemens Fossiles*, named different varieties *C. hippelaphus* and *C. equinus*, and two years afterwards added the names of *C. aristotelis* and *C. leschenaultii*, given to horns only. Why the name *C. aristotelis*, given to an abnormal horn, has been preferred for the Indian sambar is difficult to say. The name *C. unicolor*, employed by Hamilton Smith, is preferable on account of both priority and suitability, being an appropriate term for the only Indian deer with unspotted young."

In a lengthy taxonomic paper, Van Bemmel (1949) regarded the rusine group as belonging to a distinct genus, *Rusa*. His reasoning was - "*Rusa* is distinguished from *Cervus* L. mainly by the typical stature, the primitive build of the antlers, the more composed structure of dentition, the greater extention of the rhinarium and the longer more bushy tail. The genus *Rusa*, in its geographical distribution, forms a coherent group of tropical and sub-tropical deer. In my opinion this is a natural unity deserving generic value. The definition of the genus, as given above, is founded merely on the Indo-Australian species. Extra-limital material at my disposal was insufficient to do justice to every detail."

However, Whitehead (1972), fully cognisant of

Van Bemmel's work, classified sambar as Cervus unicolor Kerr, 1792; and rusa as Cervus timorensis Blainville, 1822; both belonging to the subgenus Rusa. His terminology is followed in this thesis.

Lydekker (1898) described 6 races of sambar, but Whitehead (1972) recognised 16 subspecies (Table I). Eight subspecies are found in the Philippines, although there is some confusion concerning their taxonomy because of lack of suitable specimens from the various islands in this archipelago.

1.3 Distribution

Sambar have an extremely wide geographical distribution (Fig. 1). Various races occur throughout most of South East Asia, including India, Sri Lanka, Burma, the Malay peninsula, Thailand, southern China, Borneo, Hainan, Taiwan and the Philippines.

In India sambar are recognised as being a forest hill country deer and have been found at an altitude of 2742 m a.s.l. in the Himalayan foothills (Whitehead, 1972). In Sri Lanka they are widely distributed and according to Whitehead, range from the coast up to altitudes of 2285 m a.s.l.

In the mid nineteenth century the species was introduced to Australia from India, Sri Lanka and Malaysia (Harrison, 1979). Bentley (1978) described sambar as the "dominant transplant" because they are the most firmly established and the largest of all deer species which exist in the wild in Australia.

It seems doubtful that records were made of all sambar liberations in New Zealand. This is indicated by the lack of continuity in the reports kept by acclimatization societies (Thomson, 1922). Perhaps the most comprehensive account of sambar liberations in this country was that given by Donne (1924). His findings are summarized as follows: The first liberation of sambar in New Zealand took place in June 1875 when a stag and hind from Sri Lanka were released on the Carnarvon

TABLE I

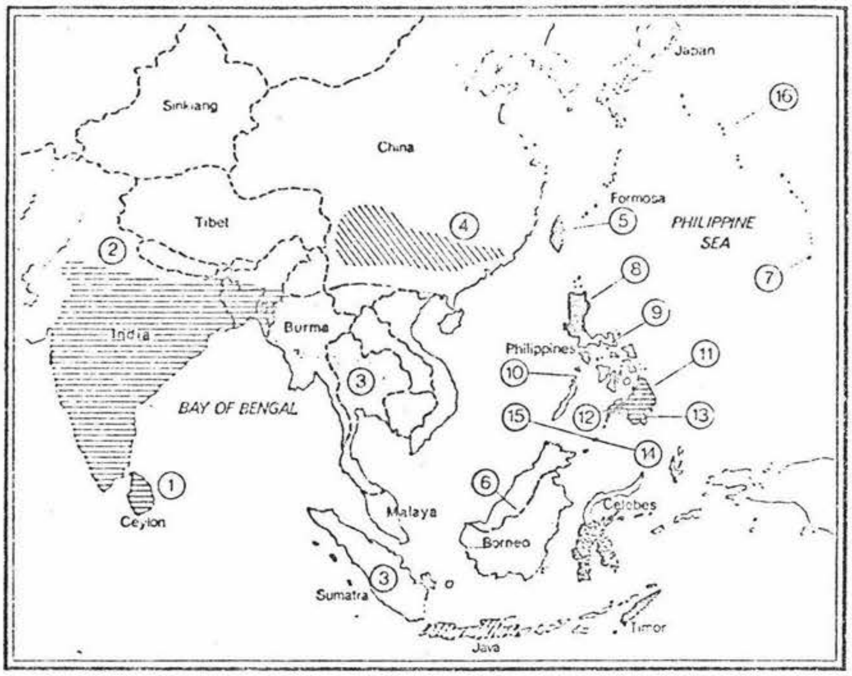
Classification of sambar deer according to Whitehead (1972)

FAMILY CERVIDAE
GENUS *CERVUS* Linnaeus, 1758
SUB GENUS *RUSA* H. Smith, 1827

One species *Cervus unicolor*,
sixteen subspecies

Cervus unicolor Kerr, 1792	Sambar
Cervus unicolor unicolor Kerr, 1792 Ceylon	
Cervus unicolor niger Blainville, 1816 Peninsula India	
Cervus unicolor mariannus Desmarest, 1822 Guam Island, Marianne Group	
Cervus unicolor equinus Cuvier, 1823 Sumatra, Malaya, Burma, China, etc	
Cervus unicolor philippinus H. Smith, 1827 Luzon, Philippine Group	Philippine deer
Cervus unicolor swinhoei Sclater, 1862 Formosa	Swinhoe's deer
Cervus unicolor alfredi Sclater, 1876 Central Philippine Islands	Prince Alfred's deer
Cervus unicolor nigricans Brooke, 1877 Basilan Island	Basilan or Blackish deer
Cervus unicolor brandanus (Heude), 1888 Mindoro Island, Philippines	
Cervus unicolor francianus (Heude), 1888 Mindanao Island, Philippines	
Cervus unicolor basilanensis (Heude), 1888 Basilan Island, Philippines	
Cervus unicolor brookei Hose, 1893 Sarawak, Borneo	
Cervus unicolor dejeani (Pousargues), 1896 South-west China	
Cervus unicolor boninensis Lydekker, 1905 Bonin Islands (extinct?)	
Cervus unicolor nigellus (Hollister), 1913 Mindanao Island, Philippines	
Cervus unicolor apoensis Sanborn, 1952 Mindanao Island, Philippines	

Figure 1: The world wide distribution of sambar as published by Whitehead (1972)



The range of Sambar *Cervus unicolor*

SAMBAR *Cervus unicolor*

1.	*Cervus unicolor unicolor*	Ceylon
2.	*C.u.niger*	India
3.	*C.u.equinus*	Burma, southern China, through to Sumatra
4.	*C.u.dejeoni*	South-west China
5.	*C.u.swinhoei*	Formosa
6.	*C.u.brookei*	Sarawak, Borneo
7.	*C.u.mariannus*	Guam Island, Marianne Group (probably extinct)
8.	*C.u.philippinus*	Luzon, Philippines
9.	*C.u.alfredi*	Central Philippines
10.	*C.u.barandanus*	Mindoro Island, Philippines
11.	*C.u.francianus*	Mindanao Island, Philippines
12.	*C.u.nigellus*	West Mindanao Island, Philippines
13.	*C.u.apoensis*	South-east Mindanao Island, Philippines
14.	*C.u.basilanensis*	Basilan Island, Philippines
15.	*C.u.nigricans*	Basilan Island, Philippines
16.	*C.u.boninensis*	Bonin Island (probably extinct)

Sambar have also been introduced to Australia and New Zealand.

Estate, Rangitikei River. The resulting herd established itself along the Manawatu coast. In 1876, a pair were presented to the Auckland Acclimatization Society. (These must have come from Sri Lanka, although Donne's account is ambiguous in this regard). The hind died, but a replacement was obtained from Sri Lanka and sent to Auckland. The pair were subsequently released near Morrinsville, Waikato, where they multiplied. In November, 1907, eight "sambar" were imported from New Caledonia, two by the Tourist Department and the other six by a Rotorua settler. These were all liberated in the Galatea district and bred successfully. It was Riney (1955) who recognised these to be Javan rusa deer rather than sambar. It appears that those who kept the records did not differentiate between the two species, and it is this population which may by interbreeding have had a genetic influence on the Rotorua sambar, which could render them different from those of the Manawatu. In 1915, seven sambar fawns, one male and six females, were captured in Foxton for the Government Tourist Department and liberated near Lake Rerewhakaitu, Hot Lakes district. In 1919 eight fawns were taken by the Tourist Department from Himitangi (near Carnarvon), reared until they could fend for themselves, then in 1920 released near Rotorua.

Thomson (1922) argued that if these documented accounts were in fact the only sambar liberations to have taken place in New Zealand, then the species would be closely interbred, having had only four animals contribute to the gene pool. He suggested therefore, that several other undocumented liberations must have occurred.

The Manawatu herd extends along a narrow coastal strip for approximately 170 km from the Waitotara River in the north to Paraparaumu in the south (Fig. 2). However, individuals have been seen or shot considerable distances from their normal range e.g. "Coal Creek (Western Ruahines), Waitatapia Stream (Western Tararuas), Reikorangi and Lismore State Forest" (Harris, 1966).

In the Bay of Plenty, sambar have spread considerably from their original liberation points (Fig. 3):

Figure 2: Distribution of sambar in the Manawatu

(from Harris,1966)

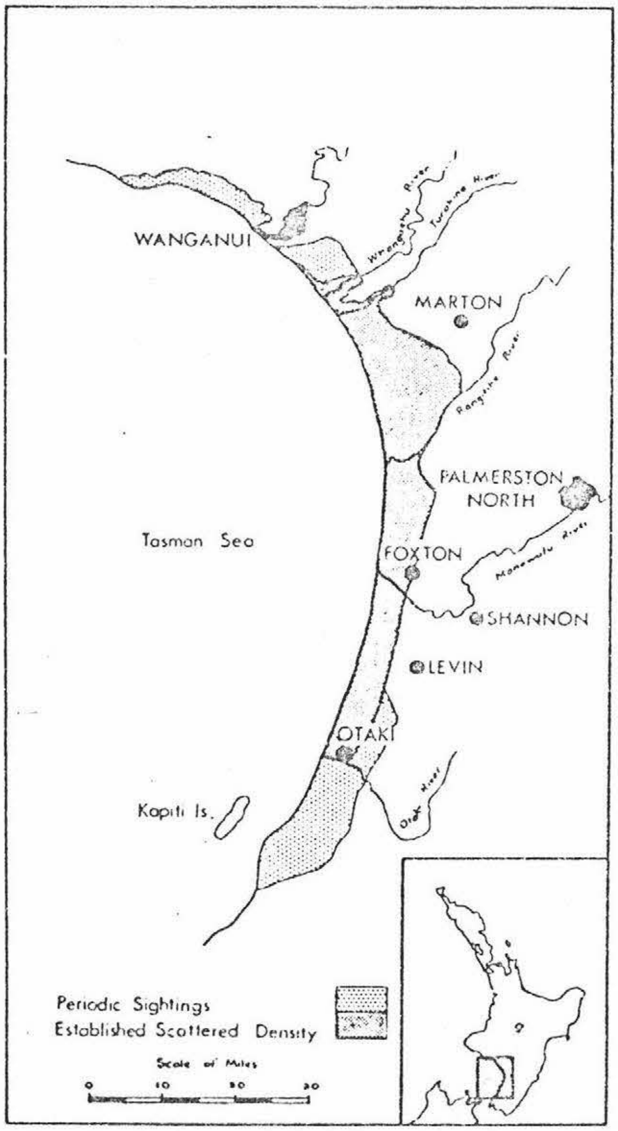
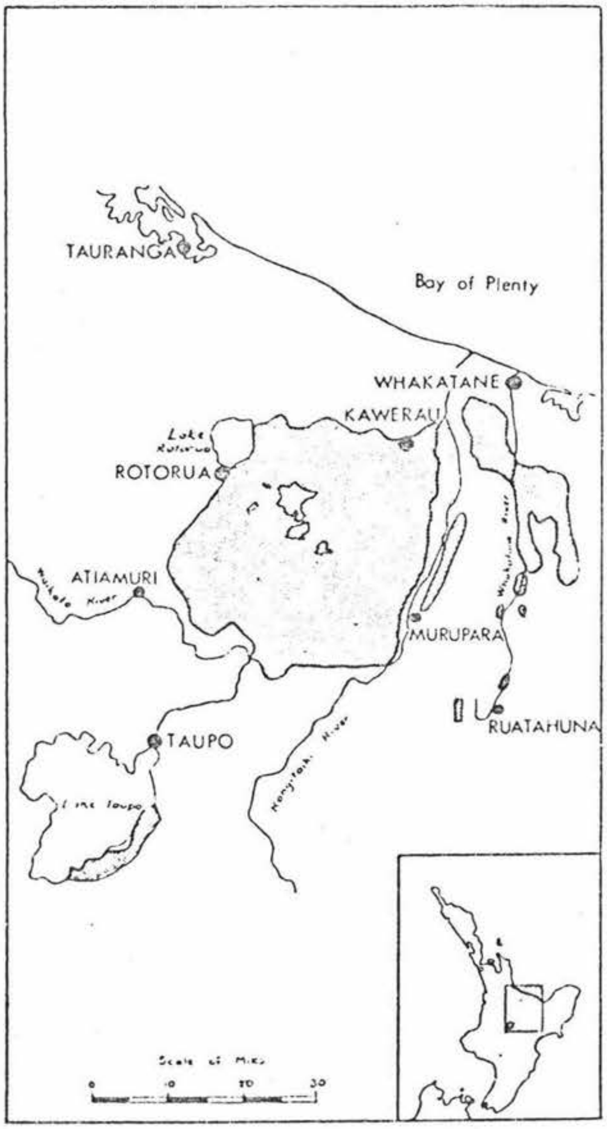


Figure 3: Distribution of sambar in the Bay of Plenty

(from Harris, 1966)



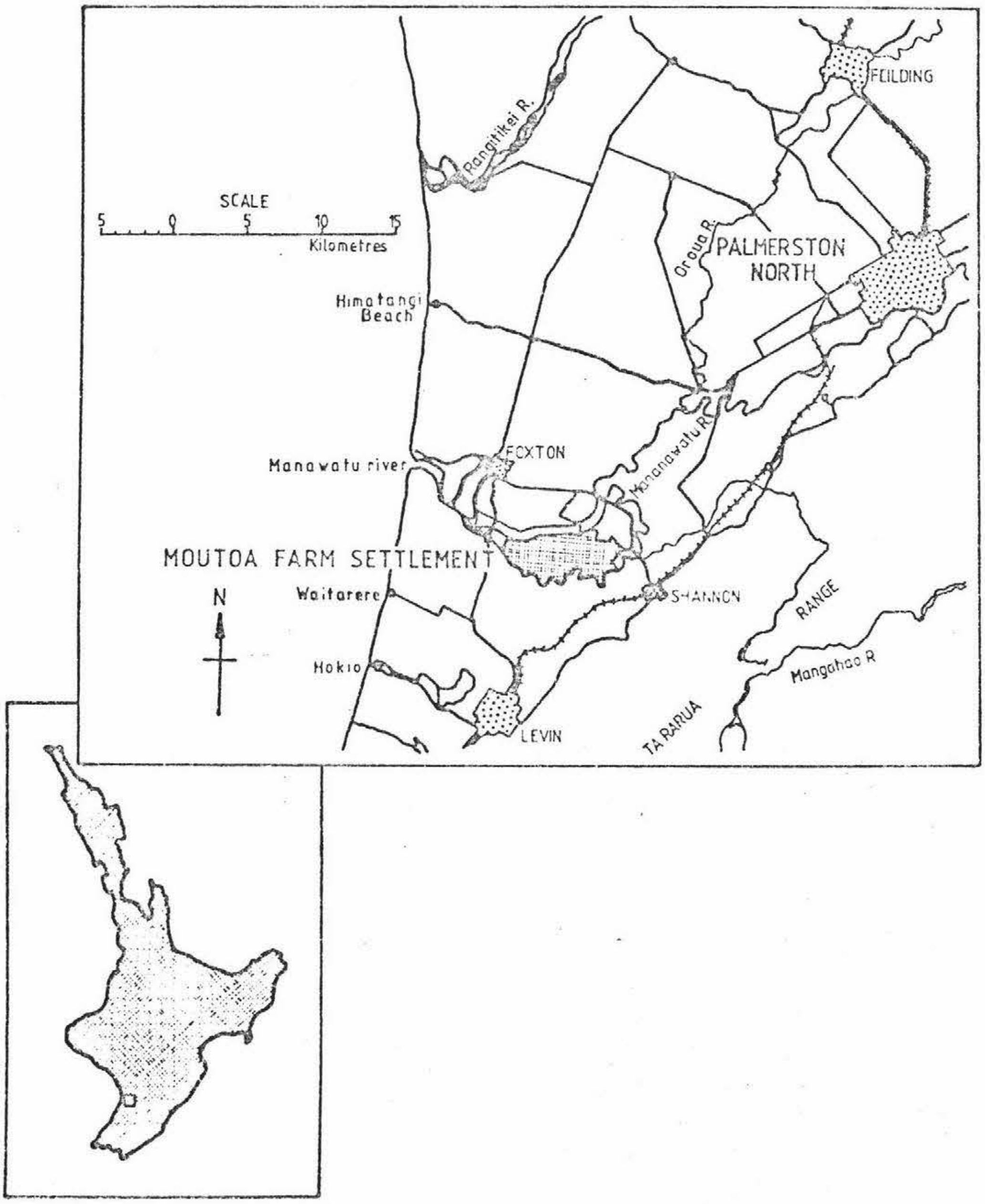
"North to the Rotorua-Whakatane Rd., eastwards to the Rangitaiki River and southward and westward to Murupara and Atiamuri. Further small breeding colonies, stemming from the Ruatoki liberations, extend southward up the Whakatane and Waimana Rivers, with isolated pockets appearing in the head waters of the Whakatane River as far south as the Rotorua-Waikaremoana Rd. Another small colony exists along the southern shores of Lake Taupo" (Harris). Again animals have been shot or sighted outside their normal range. Harris mentioned sambar being observed "at Waioeka Gorge, Ruatahuna Stream, Okahu, near Te Whaiti, and Patunamu State Forest, near Wairoa."

1.4 Moutoa

This project was conducted mainly in a flax reserve (N.Z.M.S. 1, N152, Ref. Area 825145) on the Moutoa Lands and Survey development block (Fig. 4). Moutoa (1982.1340 ha) lies 8 km west of Shannon. It is bounded in the south and east by the Manawatu River and in the west by a Manawatu Catchment Board floodway. The block was originally part of a large area of raupo* and flax "known to the Maori people as Hotuiti swamp" (Environmental Impact Report). This area contained numerous lagoons and although periodically flooded by the Manawatu River, was nevertheless used for sheep and cattle grazing as early as the 1890's. Following the gazettal of the land in the late 1930's for the flax milling industry, the Department of Agriculture, as it was then called, used Moutoa as a major source of supply of flax for the New Zealand Woolpack and Textiles Ltd's mill at Foxton. The Department of Lands and Survey joined in the undertaking by grazing the area with sheep and cattle from 1949 until present. With the phasing out of flax production by the government, the property was handed over to the Department of Lands and Survey for development and land settlement in September 1973 (Environmental Impact Report). The area is flat low lying land ranging from 0.3 to 2.5 metres above m.s.l., the higher land being adjacent

*Where possible common names will be used in the text throughout this thesis. For scientific names refer to Appendix 1.

Figure 4: Location of Moutoa



to the river and the lower near the floodway.

Management as a commercial proposition in recent years has resulted in the overall character of the land being changed. A substantial area of the block has been cultivated and replanted in improved strains of flax, mainly Siefferts Supreme, which has a higher fibre content but shorter life and less vigour than the wild type. Little evidence of the original vegetation now remains. Most of the soils are well supplied with major plant nutrients and only poor drainage has limited the intensive use of the area. "Original stands of good flax have been converted by cattle stocking to rough volunteer grazing on crushed flax" (Environmental Impact Report). Some reserve areas however, have been retained (Fig. 5).

1.5 The Flax Reserve (Main Study Area)

The study programme was focused in and around the largest (74.643 ha) reserve and adjacent River Loop Poplar Nursery (1.6 ha) as this combined area appeared to contain the greatest population of deer.

Approximately 60% (45 ha) of the reserve is in flax, 33% in rough unimproved pasture and the remaining 7% in improved pasture. (Estimated from Lands and Survey aerial photograph. Scale approximately 1:12300). Plates 2, 3 and 4 show types of cover present in the reserve.

The flax does not form a continuous block, but is dissected by about nine parallel tracks lying in a North-South direction and spaced between 43 to 55 m apart. These tracks, referred to as "fly lines" (A. Harnett, pers. comm.; A. Hunter, pers. comm.) were formed in the days of the flax milling industry so that harvesting machinery could gain access to the mature stands of flax. Several are now overgrown with flax, but others vary in width from 1.5 to 12 m (the 'main flyline'). A large drain 3 m across, parallel to the flylines, bisects the reserve (Fig. 6). The north and west boundaries of the reserve back onto improved pasture land grazed by stock, while the farm road and stopbank bounds the south and east.

Figure 5: Map of reserve areas at Moutoa

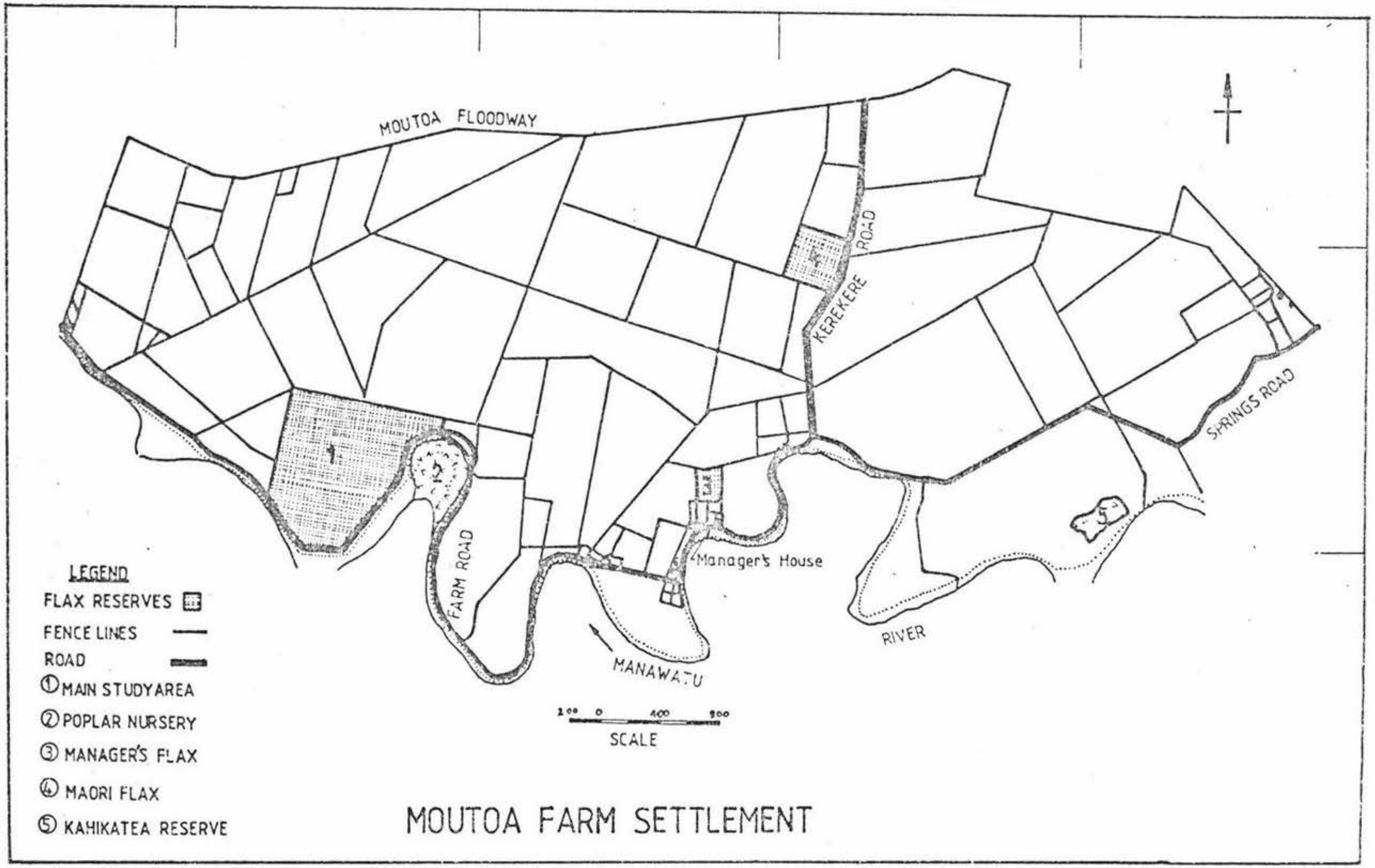


Plate 2: Area of medium density flax and unimproved pasture.

The photo was taken from Massey hide looking east. In the foreground tall fescue, reed canarygrass and floating sweet grass are interspersed with flax. The cabbage trees in the centre follow the large drain that bisects the reserve. Behind these is an area of rank pasture, predominantly tall fescue and floating sweet grass. Further back a tongue of flax screens the pasture from the farm road. The trees at the rear are growing in the poplar nursery. (November 1980)

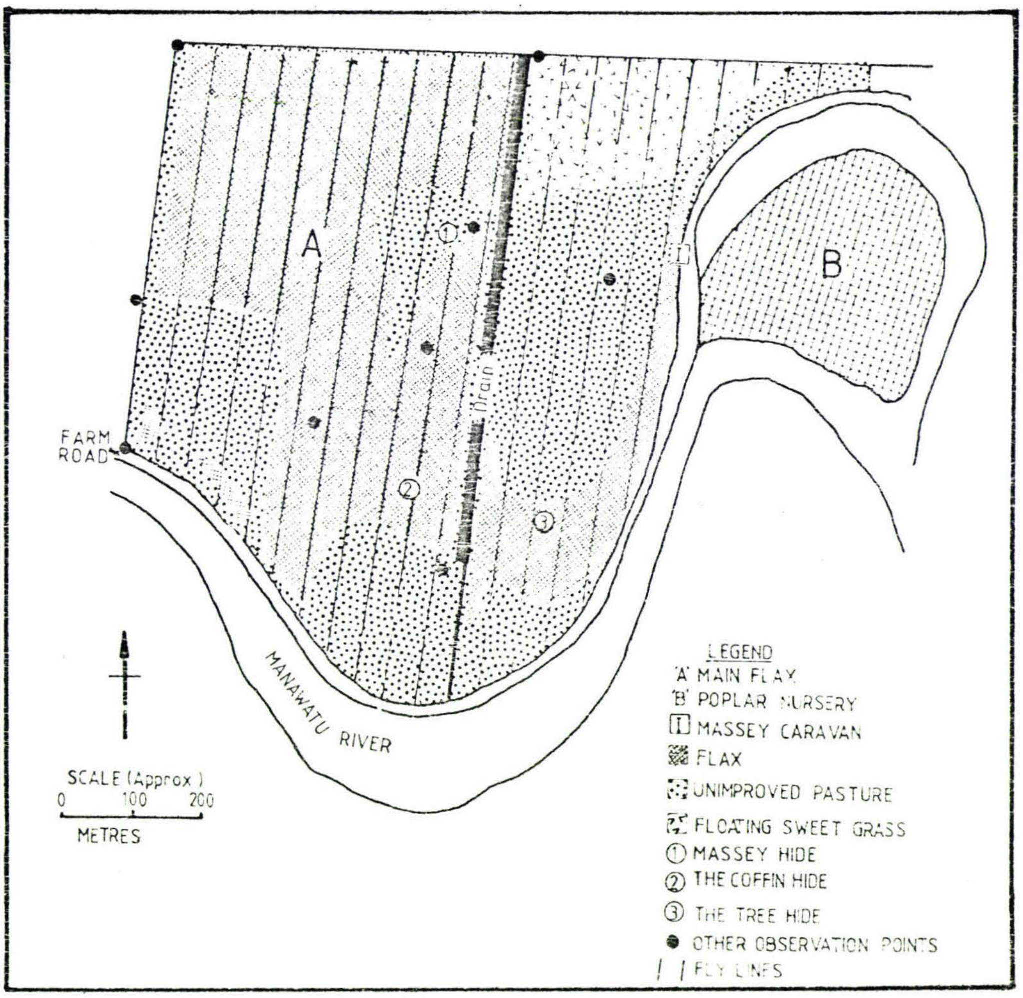
Plate 3: Area of high density flax.

The photograph was taken in August from the Massey hide looking north-west. The flax averages about 3 m high. In the foreground is an irregular patch of browned off tall fescue interspersed with green reed canarygrass and floating sweet grass. In the background is open pasture with trees.

Plate 4: Fully grown hind in dense flax cover.
(Photograph by L. Barnard)

Note the prominant ears and uniform colouration. This hind is about 1 m high at the shoulder and is standing in tall fescue. Compare the height of tall fescue shown in Plate 5 with this late spring growth.

Figure 6: The main study area



The reserve is surrounded by a conventional seven wire fence which keeps most stock out while the poplar nursery is fenced along its north, east and west sides, the south being open to the Manawatu River.

Although the study area contained a number of plant species, as described by Esler (1978), only a few of these were dominant viz., flax, tall fescue, reed canary grass, floating sweet grass, and to a lesser extent Yorkshire fog and ryegrass. A list of plants collected in the area is given in Appendix 1.

1.6 Climate

The prevailing north to north-west winds may be very strong at times and salt spray has been noted (A. Hunter, pers. comm.). The annual rainfall varies between 1000 to 1100 mm with the heaviest fall occurring over July through September. An average of 20 to 25 frosts per year may be experienced but these are generally light. Ground temperatures range up to 19°C during summer. (Environmental Impact Report, 1976). Temperature and humidity were recorded in the reserve over a 12 month period (Appendix 2) using a weekly thermohygrograph. This was done because it was thought the microclimate beneath the flax canopy would differ to that experienced in open pasture situations and so possibly affect animal activity.

PART II – DIET

CHAPTER 2 : OBSERVATION

2.1 Direct Observation

2.1.1 Introduction to Methods

Draisma (1979) found that sambar "were almost impossible to observe because of their extremely cautious habits and difficult habitat."

Sambar prefer heavy cover to open areas and are predominantly nocturnal feeders (Lydekker, 1898; Donne, 1924; Cahalane, 1939; Farmer, 1965; Logan, 1965; Harris, 1966; Schaller, 1967; Whitehead, 1972; Morrison and Harris, 1974; Harnett, 1979), particularly in disturbed areas (Draisma, 1979). This presented a number of problems as to what observation methods should be employed.

As would be expected of a cervid (Muller-Schwarze, 1971; Chaplin, 1977), senses of smell and hearing are acute and their ability to detect movement, even at long distances is also striking. However, a stationary observer may often remain undetected, especially if against a diffuse background. I found camouflaged clothing useful in this respect as it blended well with vegetation in the study area.

In winter the browning off of tall fescue and reed canarygrass in effect created clearings in the flax and opened up flylines. Over the summer months however, these species formed a dense two metre high cover (Plate 5). Thus winter was the most suitable time of year for observing animals.

The majority of my observations were made from hides set well above the vegetation. Hides were used for two reasons:

(a) A large area could be scanned without vegetation restricting the view.

(b) Human scent was carried above any animals in the vicinity.

In February 1980, 'Massey hide' was erected at the edge of a large grass clearing (see Fig. 6). This was a

Plate 5: Maximum height of tall fescue

This photo shows Dr J. Skipworth standing in mid summer growth of tall fescue.

free standing structure with an observation hut 4.5 m above its base (Plate 6). A second enclosed hide, 'the coffin', was built at a similar height in the fork of a large cabbage tree overlooking an area of low density flax and rough pasture (Plate 7). Materials for this hide were supplied by L. Barnard. In other trees which grew in suitable locations, fence battens were nailed as seats and these were used on occasions when the wind direction was unfavourable for approaching either of the enclosed hides (Plate 8).

2.1.2 Daytime Observations

Few animals were seen from the hides during the day. Most observations were of animals encountered as I walked along flylines or through the flax collecting faecal and/or vegetation samples. Sightings tended to be brief and many animals fled before they were seen. Others sensed my presence after sighting and moved off, while some, although undisturbed, were soon lost from view in the dense flax. On a few occasions I accidently walked to within 5 m of animals concealed in vegetation, before they ran off in alarm. Their ability to remain inconspicuous and not to break from cover at the approach of a human, until the last possible moment has been noted by many people (Logan, 1965; Harris, 1966; Schaller, 1967; Evans, 1976; and L. Barnard, A. Harnett, A. Hunter, L. Shailer, M. Shailer, P. Smith, J. Rudd and W. Wallace, all pers. comm.).

It was usually possible to identify the plants being fed upon once the animals had gone.

2.1.3 Night Observations

Observations using an Infrared Scope (Edmund Science Company) were unsuccessful because of its small field of view and short range. I found that a pair of 7 x 50 mm Nikon binoculars worked well on moonlit nights and animals could be watched up to 150 m away. On cloudy nights a 6V spotlight was used in conjunction with the binoculars. Logan (1965) and Harris (1966) noted that sambar were often hunted using a spotlight because they "held" well in the beam.

Plate 6: 'Massey Hide'

The weatherproof hut was built 4.5 m above the ground and offered a 360° view of surrounding vegetation. Massey hide was used for both night and day observations.

Plate 7: 'Coffin Hide'

The base of this hide is approximately 3 m above the vegetation and 5 m above the ground. This hide was effective for both day and night observations.

Plate 8: Tree 'Hide'
(Photograph by I. McKelvey)

This cabbage tree shows the author in his usual observation position. Despite the lack of obscuring vegetation this was an effective 'hide' at night provided no noise was made. Note the summer growth of tall fescue.

Over the first few months of the study, spotlighting was a useful technique as animals would often recommence feeding once the beam was off them. However, in late April 1980, after a spate of poaching in the study area, animals would no longer hold in the spotlight. From then on, the spotlight was only used to quickly scan an area for animals and then turned off.

Sambar eyes shine brightly in a spotlight beam and if binoculars are also used, they can be detected more than 200 m away. Counts of deer were made using this method.

In areas where cattle were also present, behavioural differences distinguished the two. While watching the light cattle tend to stare directly without moving, but sambar continually raise and lower their heads, eventually moving off if the beam is kept on them for too long.

It was often possible to determine where animals were in relation to various landmarks such as trees, gates, fences, water troughs and drains. Positions were noted and the areas visited in daylight to record those species that had evidently been eaten.

I normally spent from dusk until 0100 hrs watching animals but at each full moon the whole night was spent in the flax, either up one of the main hides or in an area that appeared to be heavily utilized by deer. Using the binoculars an hourly sweep of surrounding flax and pasture was made. If no animals were seen, the spotlight was used to locate any that may have been overlooked. The number of deer out and their type of activity were recorded.

2.2 Indirect Observation (Feeding Sign)

2.2.1 Flax

Flax was a major item in the diet. Individual leaves were grasped with the incisors and pulled until they snapped off at ground level. The succulent 15-20 cm basal portion was then eaten. This had been noticed by A. Harnett (pers. comm.) and I have observed it on several occasions. On a still night the sound of an animal feeding on flax carries a considerable distance. A dozen or more leaves may be removed from a single flax plant. Discarded leaves, minus basal portions are dropped where the animal stands (Plate 9). Sambar have also been observed by L. Barnard (pers. comm.) to eat flax flowers.

2.2.2 Poplar and Willow

Deer sometimes entered the Manawatu Catchment Board's nursery (Plate 10), where both poplar and willow trees were browsed. Deer activity was minimal in this area whenever cattle were present.

Bark biting occurred in March, June, July, August, September and October. In April there was considerable human activity in the area as shooters prepared their maimais for the coming duck shooting season. This is believed to be the explanation for the lack of deer activity in the nursery over April and May.

Sambar damage to *Pinus radiata* by bark stripping has been described by Farmer (1965), I. Logan (pers. comm.) and J. Sutton (pers. comm.). I. Logan (pers. comm.) noted that only young, smooth bark is attacked, before it becomes guttered and that trees about six years old are preferred. Damage occurs in spring and autumn according to I. Logan, and J. Sutton (*in lit.*) suggested that at this time of year, a single deer might attack up to 15 trees in one night.

Cattle as well as deer were found to strip and eat bark from trees in the study area. Sambar use their incisors to strip bark from ground level to head height, tearing it from there up until it comes free. Distinctive parallel groves made by the incisors, were often seen on trunks (Plate 11). If it was not apparent as to what species of animal had damaged a particular tree, hoof marks could usually be located beneath the undergrowth. Sambar have distinctive narrow foot prints, quite unlike those made by other deer species of a similar size (Plate 12).

Plate 9: Evidence of feeding on flax

Note that only the fleshy basal portions of the leaves have been eaten and that the discarded leaves are not scattered but dropped where the animal stood – characteristic of sambar feeding on flax.

Plate 10: Stag in poplar nursery

This stag was photographed lying down in the late afternoon.

Plate 11: Sambar damage to young poplar bark.

Note narrow ribbon stripped by incisors. This photograph was taken in the poplar nursery, and in the background is the Manawatu river stop bank behind which lies the main study flax reserve (refer to figure 6).

Plate 12: Sambar hoof print

Note the typically narrow hoof print. From its size it is probably a mature hind.

2.2.3 Grasses

In rough unimproved pasture, tall fescue clumps were often heavily cropped (Plate 13). Grazed regions were apparent in areas of floating sweet grass, Yorkshire fog and ryegrass. Faecal pellets or hoof prints could usually be found in these cases.

2.3 Feeding Habits

Donne (1924) wrote that sambar are grass eaters as well as browsers, feeding mostly at night, although like red deer, their appetites taper off after daylight. They lie down during most of the daytime, then rise to feed again before sundown.

My observations support this view. From late afternoon onwards, deer would be seen in areas of low density flax, but it was not until dark that they moved into surrounding unimproved pasture.

Animals would feed continuously for several hours, then lie down, presumably to ruminate. Feeding would be recommenced after an hour or more and continued till dawn, when the animals moved back into cover. An unusual feature of their behaviour is that they feed in one place for some time before moving on. Thus, at night, undisturbed animals could be watched for 15 minutes or more, in which time they would have only moved four or five metres from their original position. This habit has also been noticed in captive animals. L. Rowe and R. Rowe (pers. comm.) have found that sambar on improved pasture , crop areas much more heavily than do red deer.

Cover is apparently essential for sambar and even at night they were never seen far from it. This will be discussed further (see 8.1).

Clover was not abundant in or around the flax reserve and no clover cuticle appeared in any of the faecal samples examined (Chapter 3). However, the 4.015 ha stand of flax behind the manager's house, is bounded on one side by a 17.057 ha ryegrass/clover paddock that is shut up for hay each year. This piece of flax is inhabited by

Plate 13: Cropped clump of tall fescue

Note that the ends of the leaves have been eaten over the entire clump showing typical damage caused by sambar.

Nikon

four or five sambar (including one resident stag), as well as several horses and one or two other domestic animals. During December and January, before it was mown, the manager (A. Hunter) and his wife (pers. comm.) often watched deer of an evening out feeding in the hay paddock. In January 1981, I spent a number of nights observing animals in this area. The resident stag was usually the first to appear at the edge of the hay paddock (Plate 14). On most evenings he was out of the flax by dusk, but remained on the edge until dark when he moved into the paddock to feed. Later, up to four other animals would also enter the paddock and feed, returning to the flax between 0400 hours and 0700 hours. A. Hunter (pers. comm.) has however observed the stag returning later in the morning on several occasions.

From February to May deer frequently travelled at night to maize crops on neighbouring properties where they would remain unless disturbed. Not only do they consume considerable amounts of maize, but also sizeable areas are crushed as they wander through or bed down in the crop. (I. Easton pers. comm.)

Beet, turnip and swede crops as well as cereals are sought after by sambar (Farmer, 1965; Logan, 1965; J. Rudd, pers. comm.; and P. Smith, pers. comm.). P. Smith (pers. comm.) has noted that when in a vegetable crop such as beet, sambar often take just one bite from a single plant and then move onto the next. This habit apparently made sambar a pest in some market gardening areas during the 1920's as an entire crop could be destroyed overnight by two or three animals.

A total of 302 observations were made, deer being sighted on 83 out of 128 days spent in the field. (Appendix 3). Although many hours were spent in the field for relatively short periods of actual observation, it was a valuable technique for two reasons:

(a) It offered a subjective method of checking faecal analysis.

(b) Worthwhile information on feeding habits and other behaviour was gained.

Plate 14: Moutoa stag in the edge of clover/ryegrass paddock.

To the rear is a field of improved pasture with sheep grazing. This photograph was taken in rain at dusk. Note that not all tines of this six point stag are visible but the typically dark colour is evident.

CHAPTER 3 : FAECAL ANALYSIS

3.1 Introduction

Early studies of herbivore diet were largely qualitative but recently greater emphasis has been placed on quantative assessment. This has been achieved by direct observations on tame and/or wild animals, examination of ingesta from fistulated animals, vegetation analysis before and after utilization, the feeding of plant material on a free choice basis and measuring relative consumption, and microscopic stomach content or faecal analysis of the undigested or partly digested plant matter. These methods were evaluated by Skipworth (1972) and more recently by Scotcher (1979).

When studying a secretive or endangered species where observations and/or collections cannot be made, faecal analysis is the only feasible procedure to use for determing the diet (Anthony and Smith, 1974).

Three basic principles were stated by Hercus (1960):

"(a) Plant cuticle is a morphological entity, being a continuous layer on the outer surface of the shoots of green plants, formed by the polymerization of unsaturated fatty substances. When cell growth has ceased the cuticle has hardened to a solid film moulded to the contours of the underlying epidermal cells. The cell walls may also be impregnated, so that when the cuticle is separated from the leaf, either mechanically or chemically, it bears an imprint of, and sometimes part of the cells of the epidermis.

(b) The arrangement of the epidermal cells is characteristic of the plant group and family and often the species. Cell dimensions may differ considerably between individuals but the pattern of arrangement is characteristic. This specialization of the epidermis is well marked in the Gramineae.

(c) The cuticle is impermeable to water, and resistant to most chemicals and the action of

> microbial organisms. During digestion the cuticle is separated from the underlying leaf tissue and passes through the animal unchanged, apart from reduction in particle size due to mechanical action. The cuticle fragments in the faeces bear an outline of the epidermal cell pattern of the plants from which they derive."

Baumgartner and Martin (1939) analysed squirrel stomach contents by comparing material in the stomachs with permanent reference slides of stained leaf and stem epidermis from plants in the study area. Rumen samples from sheep were analysed in a similar way by Norris (1943). These techniques were later adapted by Dusi (1949, 1952) for faecal analysis of cottontail rabbits.

Adams (1957) examined snow shoe hare pellets and identified plant species eaten on the basis of leaf and stem fragments, which he termed "recognition items", but he did not attempt to identify any particles requiring microtechniques. Hegg, 1961 (in Ward, 1970) used the microtechnique of faecal analysis to examine faecal specimens from red deer, chamois, and roe deer from the Swiss National Park.

Since then the technique has been widely used in dietary studies of herbivorous animals and several reviews have been presented, viz. Zyznar and Urness, 1969; Ward, 1970; Scotcher, 1979. Table II lists some of the authors who have published papers on faecal or rumenal analysis techniques.

One major disadvantage of faecal analysis is that it is time consuming and its usefulness depends to some extent upon the species of herbivore in question, the nature of the diet, and the diversity of plants available for food (Anthony and Smith, 1974). Analysis of a highly diverse diet would be an excessively lengthy process because of the time required for identification of a large number of items. Another disadvantage is that the thickness of cuticle varies from species to species and some thin

TABLE II

Previous works on dietary analysis

Author	Subject	Animal
Adams (1957)	Faecal analysis	snowshoe hare
Adams *et al.* (1962)	Faecal analysis	snowshoe hare
Anthony and Smith (1974)	Comparison of rumen and faecal analysis	mule and white tailed deer
Baumgartner and Martin (1939)	Stomach content analysis	squirrel
Croker (1959)	Faecal analysis	sheep
Dearden *et al.* (1975)	Faecal analysis	reindeer, cattle and bison
Dunham (1980)	Faecal analysis	impala
Dunnet *et al.* (1973)	Faecal analysis	opossum
Dusi (1949)	Faecal analysis	cottontail rabbit
Dusi (1952)	Faecal analysis	cottontail rabbit
Dzieciolowski (1970)	Rumen analysis	red deer
Fitzgerald and Waddington (1979)	Comparison of two methods of faecal analysis	opossum
Fitzgerald and Wardle (1979)	Faecal analysis	opossum
Hansson (1970)	Stomach analysis	rodents
Hegg (1961)	Faecal analysis	red deer, roe deer, and chamois
Hercus (1960)	Faecal analysis	sheep
Hunt (1979)	Rumen analysis	wapiti
Jackson (1980)	Rumen analysis	roe deer
Kessler *et al.* (1981)	Comparison of rumen and faecal analysis	pronghorn antelope
Korschgen (1962)	Rumen analysis	white tailed deer
Medin (1970)	Stomach analysis	wild herbivores and birds
Norris (1943)	Stomach analysis	sheep
Puglisi *et al.* (1978)	Rumen analysis	white tailed deer
Reynolds *et al.* (1978)	Faecal analysis	bison
Robel and Watt (1970)	Comparison of volumetric and point analysis procedures in rumen analysis	white tailed deer
Rogerson *et al.* (1976)	Faecal analysis	sheep
Scotcher (1979)	Review of faecal analysis techniques	grazing herbivores
Scott (1941)	Faecal analysis	fox
Slater and Jones (1971)	Faecal analysis	sheep and cattle
Smith and Shandruk (1979)	Comparison of faecal, rumen and utilization methods for diet determination	pronghorn antelope
Stains (1976)	Evaluation of rumen analysis	red deer
Stewart (1967)	Faecal analysis	grazing herbivores
Stewart and Stewart (1970)	Faecal analysis	African plains ungulates
Storr (1961)	Faecal analysis	kangaroo and wallaby
Tilton and Willard (1981)	Faecal analysis	mountain sheep
Todd and Hansen (1973)	Faecal analysis	bighorn sheep
Vavra *et al.* (1978)	Comparison of faecal and oesophageal material	steer
Voth and Black (1973)	Faecal analysis	mountain beaver
Ward (1970)	Evaluation of faecal analysis and stomach content analysis methods	general
Williams (1969)	Faecal analysis	general
Zyznar and Urness (1969)	Faecal analysis	mule deer

cuticles may not survive digestion or may be destroyed by the chemical maceration process. Slater and Jones (1971) warned that clover, having a thin cuticle was destroyed in this manner; however, clover cuticle was seen by Hercus (1960). Anthony and Smith (1974) noted that different maceration techniques gave different percentages of recognisable epidermal fragments and that maceration time was critical, if disintegration of the thinner cuticles were to be avoided.

Although not as precise as some other methods e.g. fistulation, faecal analysis is ideal for such a study as this because:

(a) There is little, if any disturbance to the animals.

(b) It allows sampling under natural conditions of a number of different animals.

(c) The faeces themselves are more representative of food eaten at different times and over different parts of the animals' range.

(d) The presence of other species of animals feeding in the same environs will not affect analysis of the diet (Scotcher, 1979).

Where possible the faecal analysis work was supported by direct observation of sambar feeding. Observations provided a subjective check as to which species could be expected to appear in the faeces.

3.2 Methods

3.2.1 Collection of Faeces

Freshly dropped pellets were collected at the beginning of each month from the study area. The presence of a shiny mucous coating on fresh pellets distinguishes them from old ones (Dusi, 1952).

Ward (1970) has explained how sample data collected from different faecal groups are more valuable than detailed examination of all material in one dropping. By bulking the faecal material and picking subsamples, a representative sample can be obtained. Dusi (1949) found that in general, the contents of each of the several faecal pellets of rabbits in a dropping pile, were like others in the pile unless the pellets varied greatly in colour, shape and size.

In this study an attempt was made to sample 10 faecal deposits (Stewart and Stewart, 1970, 1971; Scotcher, 1979) each month, taking five pellets from each and bulking these subsamples, the object being to sample 10 individual animals. By sampling a number of faecal piles it was hoped to reduce bias caused by food preferences of individual animals. Faecal material was temporarily stored in plastic bags (for a maximum of 48 hours).

3.2.2 Initial Treatment

The faecal sample was oven dried at 80°C for 48 hours. It was then ground in a Wiley mill fitted with a 1 mm screen and shaken in a 200 mesh sieve to remove dust and very small fragments. This was done in order to standardize the cuticle fragment size (Malechek, 1966) and to reduce the variance (seen as a problem by Stewart, 1967) when assessing cover values for cuticle fragments. Stewart found that estimation of proportions of grasses ingested, by counting all fragments was invalid, because some species broke into smaller fragments and the total number of fragments were therefore more numerous. Analysis by measuring the area of 100 fragments in each of three faecal samples showed considerable improvement in accuracy compared with counts. The variance was high however, and possible causes seemed to be the presence of occasional very large fragments, or differential separation of fragments before or after these were placed on the slide.

3.2.3 Nitric Acid Method of Cuticle Preparation

Cuticles in faecal and vegetation reference samples were cleared using a chemical maceration method. Several Nitric acid/Chromic acid methods were tried and finally a procedure adapted from Stewart's (1967) method was chosen.

A 1 g sample of ground material was taken and 5 ml of macerating fluid* added. After heating in a water bath

*Macerating fluid : 50:50 2 N Nitric acid and Saturated Chromic acid. (Zyznar and Urness, 1969).

at 100°C for 10 minutes, 100 ml of water was added and the solution boiled for up to 15 minutes. Boiling time depended on the time required to just clear the heavily cutinized fragments, for as mentioned (3.1), prolonged boiling may destroy some of the thin cuticles, such as that of clover. Coarse grade filter paper was used when rinsing the residue with water. The residue when thoroughly rinsed, was made up to 50 ml with 70% alcohol and stored in an airtight container until required for analysis.

3.2.4 Reference Cuticle Collection

At the beginning of the study, a collection of possible food species was made. After identification a portion of each sample was stored in a freezer, in case anything should happen to the reference cuticles. The remainder of the sample was halved. One half was dried, ground and a 1 g sample chemically macerated in the same manner as for faecal material: Subsamples of a given species cuticle could be pipetted from this wet reference collection as required. The second half of the sample was cut into small (2 x 2 mm) pieces and placed in the macerating fluid until the cuticle separated from the epidermis. This varied in time (10 minutes to several hours) depending on the species concerned. Cuticle fragments were carefully removed, washed in water and mounted in glycerine on microscope slides. A semipermanent reference collection was made by sealing the coverslips with lacquer.

Photomicrographs were taken of all cuticles. Scale drawings were also made of cuticles from the more common species. These had an advantage over photomicrographs in that various structures e.g. trichomes, found at different focal planes could be depicted on the one illustration.

Glumes, stems and leaf margins were also mounted as semipermanent slides. Gross structures could be seen in these slides without any specific treatments being applied.

3.2.5 Recognition Items

Adams (1957) introduced the idea of "recognition items" as an aid to the identification of plant species in the faeces of the snowshoe hare which he regarded as a representative herbivore. A recognition item was defined as "some small anatomical structure of the forage plant that occurs well distributed over the anatomy of the plant and that resists digestion and is readily recognised in the feces" (Adams, 1957; Adams et al., 1962).

Trichomes from several grass species found in the study area; tall fescue, floating sweet grass, Yorkshire fog and barley grass, were recognisable in the faecal preparations. In addition to trichomes, floating sweet grass yielded a distinctive fibrous substance. Flax contained large amounts of resin which appeared as light amber, irregularly shaped plates amongst the cuticle fragments.

3.2.6 Analysis Procedure

In order to become familiar with the variety of cuticles present in sambar faeces, a large number of slides of prepared faecal material were examined under the compound microscope of x100 magnification. Unknown cuticles were given a number and scale drawings made. Identification was determined later, when greater familiarity with variations of cuticle within species had been attained and as different species were discovered.

When competence in cuticle identification had been achieved, an estimation of the contents in each months pellets was begun.

Prepared faecal material was agitated, a sample pipetted and five drops placed on a microscope slide. A 22 x 40 mm coverslip was then placed on top, allowing an even distribution of material beneath. Five slides were prepared in this manner and 20 fields systematically examined. Stewart (1967) confirmed the validity of recording fragments along systematic traverses of the preparation, rather than at random positions, by comparing the numbers of fragments falling within 50 random quadrats on a slide with a Poisson distribution. A chi-square test indicated that there was no significant difference between the observed and expected frequencies ($P>0.3$). As mentioned (Section 3.2.2) Stewart found that analysis by measuring the area of 100 fragments in faecal samples showed considerable improvement in accuracy, when compared with counts. It was decided to base the approach of this study on his method.

A squared micrometer eyepiece was used to measure the areas of cuticle and non cuticle fractions in the faecal mixture. In order to reduce some of the variance Stewart encountered, two changes were made to his method. One has already been described (Section 3.2.2) i.e. To standardise the size of particles present in the faecal preparations by grinding in a Wiley mill fitted with a 1 mm screen followed by sieving in a 200 mesh sieve. Secondly the areas of all cuticles present in 100 microscope fields were determined, not just the areas of the first 100 cuticle fragments. Although very time consuming (8 - 10 hours per 100 fields) I consider that this would be compensated for by a reduction in the variance, due to the increase in sample size. Areas of cuticle fragments were measured in arbitrary units using the eyepiece grid. The standard error of the mean (Walker and Lev, 1969) was calculated for each species found in the five slides (each slide representing 20 fields) using these units. The percentage area of each species over the total area of material present in the 100 fields examined, was also calculated.

Faecal samples were collected each month over a 15 month period.

3.2.7 Rumen Samples

Although several deer died in the study area during the period spent at Moutoa (Appendix 4), only one animal was found in time to recover the rumen before decomposition rendered it useless for examination. In early May 1980, a mature female was shot by poachers in the reserve and the hind quarters taken. When found, 3 - 4 days later, the rumen was still intact and able to be removed. The rumen contents were divided; one half being frozen and the other preserved by placing in a jar and covering with Formalin Acetic Alcohol (FAA)*. A sample was examined under a dissecting microscope and the species present compared with those present in the faecal material collected that month.

3.3 Results

3.3.1 Rumen Analysis

The single rumen available for analysis failed to reveal any species not present in the faeces collected that month (May). Moreover, several species appearing in faeces in May were not present in the rumen, which in fact validates one of the criticisms of rumen analysis i.e. that it can only be expected to reveal food ingested a few hours prior to collection (Anthony and Smith, 1974; Kessler et al., 1981). Floating sweet grass and flax made up the bulk of rumen material along with some tall fescue. Apparently no other species were present.

3.3.2 Faecal Analysis

When analysing faecal preparations a number of plant components other than cuticles are present in the mixture. Areas of non cuticle components were measured and listed under one of three categories:

(a) 'Resin' - Translucent, amber coloured, platelike fragments. Large amounts were noted in preparations made from flax bases and occassionly were found in preparations of tall fescue, reed canarygrass and floating sweet grass.

(b) 'Unidentified b.' - shiny black, irregularly shaped fragments.
Despite persistent investigation the identity of this material remains unknown. It seems almost certainly to be organic (it is neither natural grit nor a component of the macerating fluid), but is non cellular and can only be assumed to be the product of a chemical reaction, perhaps involving the resin with which it often occurs.

---

* FAA composition (Stewart, 1967): 85 parts 70% alcohol, 10 parts 40% formaldehyde and 5 parts glacial acetic acid.

(c) 'Fibre' - Lignified plant tissue such as xylem or sclerenchyma which resists chemical maceration. Fibre comprised approximately half the area of material in each microscope field.

Thirteen types of plant cuticle were detected in faecal samples collected over the 15 month period. One of these, a monocotyledon, which appeared occasionally was never identified and was listed as 'unidentified a.'

Unit areas (± S.E.) of plant components found each month are listed in Appendix 5. Large standard errors were encountered with some species because their cuticles were absent in a number of fields of view.

A graph of the four most prominent species occurring in faeces (Fig. 7) shows that the relative amounts of those cuticles changes over the study period. There appear to be two opposing cycles. When percentage cuticle areas of flax and tall fescue are at their greatest, reed canarygrass and floating sweet grass are at their minimum and vice versa.

These results indicate that the deer utilise flax and tall fescue over the wetter months (March to October) more than other species, while floating sweet grass and reed canarygrass are consumed in greater quantities during the dry months (November to February). Similar trends are seen in species which occur in smaller quantities than the above four species (Fig. 8). Greatest amounts of chickweed appear in faeces during wet months (March to August). Poa follows this trend, but to a lesser degree in terms of area of cuticle present. Ryegrass is not present in faeces from March to August, but occurs in small amounts from September to February, suggesting that deer tend to utilise it more over these months. It would appear that Yorkshire fog utilisation follows that of ryegrass with peak use over summer. Poplar may also follow this pattern, however the data is not as conclusive as for the above species.

The question of why diet should apparently change in this way will be discussed in detail in the final chapter (8.2). At this stage it can be suggested that the most obvious options are that sambar, like some other deer

Figure 7: Monthly variation in the four major cuticle components of faeces

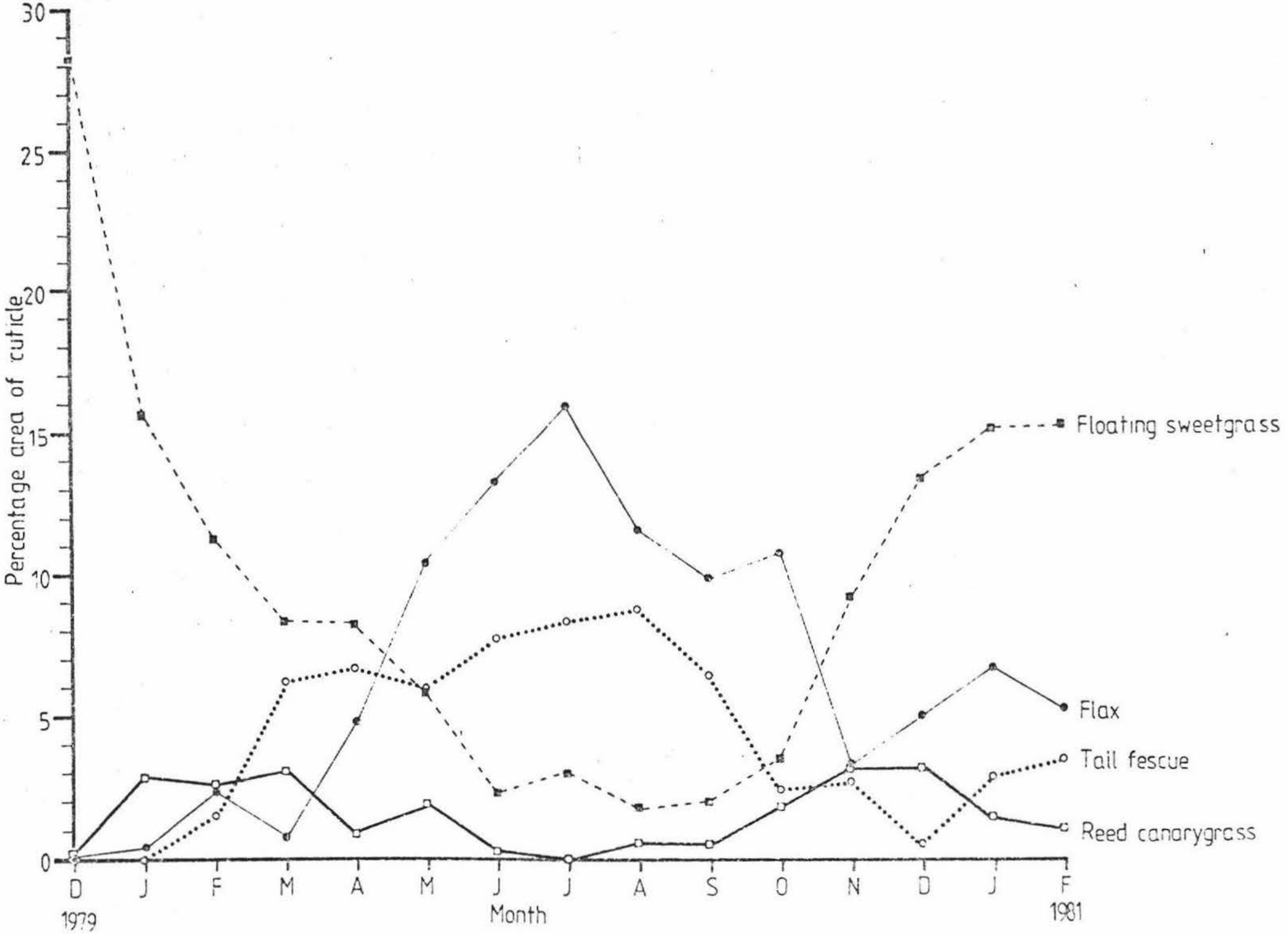


Figure 8 : Monthly variation in five minor cuticle components of faeces

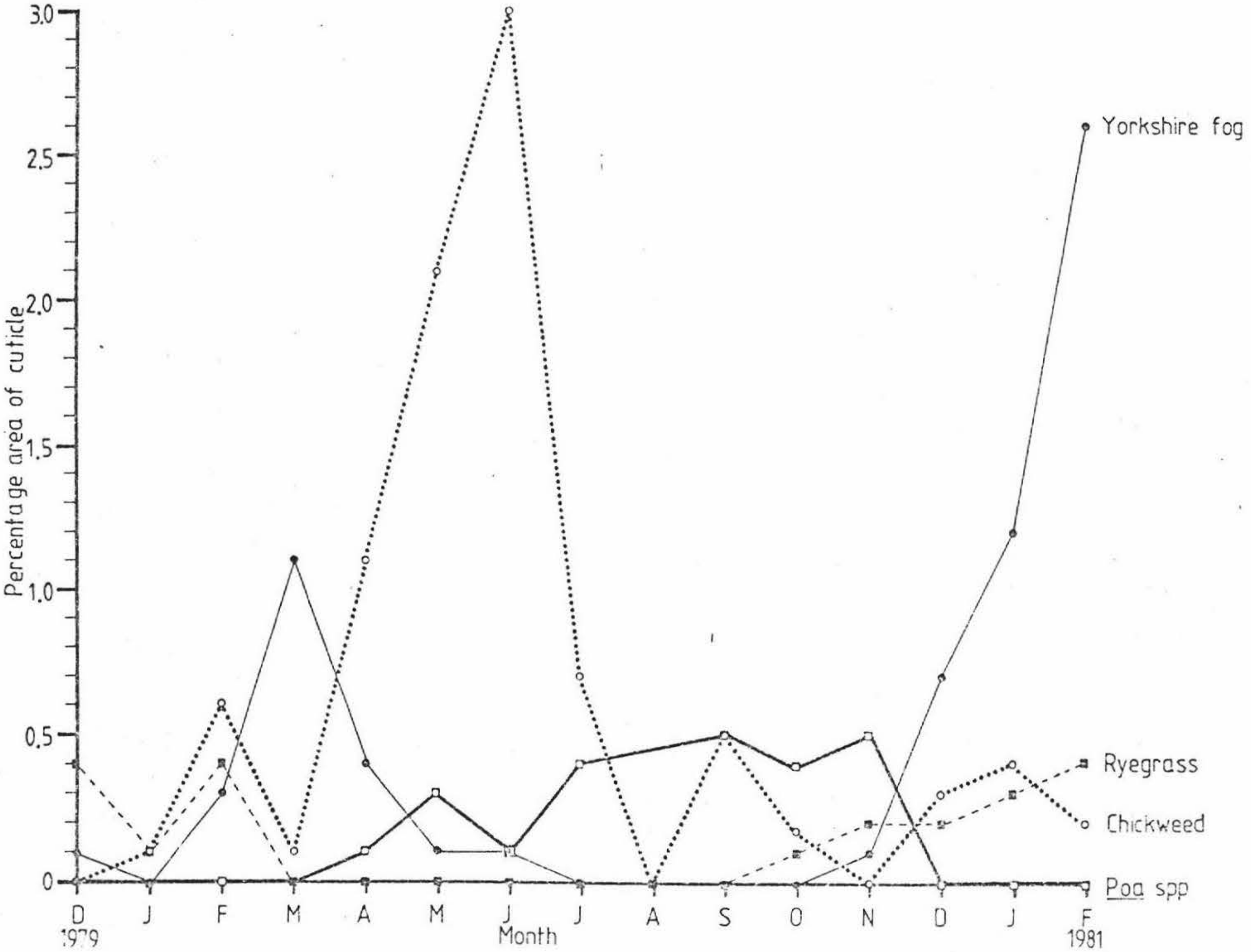
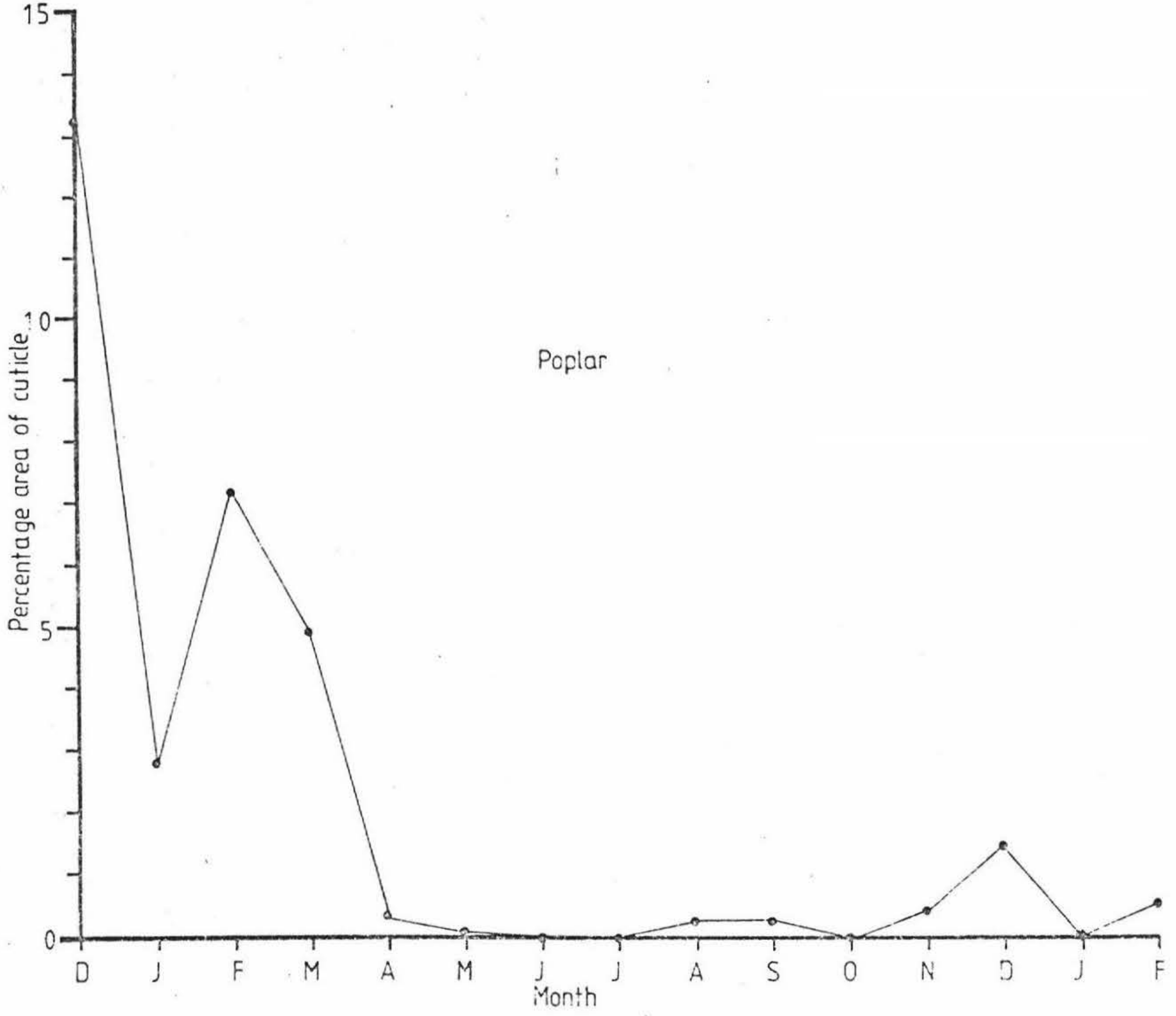


Figure 8: (continued)



species, seek out the most nutritious feed (Swift, 1948), or that they simply make use of those species present in the greatest amounts (Dzieciolowski, 1970).

As a final comment, a faecal sample was obtained and analysed in the manner described above for cattle, which gained access to the reserve in August 1980 via a broken fence. Flax (10.3%), floating sweet grass (7.1%), tall fescue (6.3%), chickweed (2.7%), reed canarygrass (2.4%), ryegrass (0.8%) and unidentified 'a' (0.2%) were present. This indicates that competition between deer and stock for forage may occur in non pasture situations.

CHAPTER 4 : NUTRIENT ANALYSIS

4.1 Introduction

Known forage species were collected for nutrient analysis in April, August and November 1980, and in February 1981.

Although some studies have established that deer select food high in nutritive value (Swift, 1948; Leopold, 1950; Alkon, 1961; Burton and Kale, 1964; Burns, 1978; Drozdz, 1979; Blair and Brunett, 1980), there is at least one report of correlations ranging from zero to "high" (Hurd and Blaser, 1962). A number of authors have suggested that it is availability rather than quality that determines utilization of forage species (Drawe and Thadis, 1968; Segelquist and Pennington, 1968; McCaffery *et al.*, 1974). Results of chemical analyses of "portions of plants normally eaten by deer" led Gastler *et al.* (1951) to the conclusion that differences in chemical composition did not adequately explain the division of species into palatable and non palatable groups. An adequate diet must obviously supply the nutrients required for maintaining metabolism. "Single species never constitute the entire diet of wild deer, and the nutritive value of any diet component depends on its relationship with all other foodstuffs in the diet" (Cowan *et al.*, 1970).

4.2 Forage Quality

4.2.1 Defining Forage Quality

Forage quality has been defined in many ways, but usually in relation to some animal response such as feed intake, weight gain, or production of milk or wool. Dietz (1970) summarized the characteristics of high quality ruminant forage. It will possess:

(a) high palatability to the animal with resultant high feed intake.

(b) optimum levels of various nutrient components in proper ratios during the period of animal use.

(c) high apparent digestibility of the nutrient components with an optimum ratio of nitrogenous to non nitrogenous components.

(d) volatile fatty acids in optimum proportions for efficient energy production.

(e) adequate levels of minerals, vitamins and trace elements.

(f) efficient convertibility into components necessary for the animal body over sustained periods.

4.2.2 Protein

Protein is considered the most important nutrient to the animal (Dietz, 1970). Since crude protein content is significantly correlated to digestible protein content, determination of the crude protein level of a plant can give a reasonably reliable indication of its food value (Sullivan, 1962). Cowan et al. (1970) wrote that a high crude protein content is considered a desirable attribute in a forage, only partly because of the need of protein for growth and other metabolic functions. It is also desirable because high protein forages are usually succulent and palatable, and because their non protein (carbohydrate) constituents are highly digestible. Also, the high content of nitrogen and minerals in such forages, permits the maintenance of a healthy, vigorous population of rumen microbes. Consequently, the animal has the capacity to digest more fibrous foods, which may at times constitute a relatively large proportion of deer diet. Cowan et al. also found that the availability of forage and browse energy and the amounts consumed, were closely related to such factors as stage of maturity and succulence. Such factors were in turn associated with nitrogen (crude protein) content in such a way as to give relatively high positive correlations between nitrogen content and digestibility of energy.

Seven percent crude protein is usually considered a minimum dietary level for deer (Halls, 1970) and 16 - 17% would serve their maximum needs including growing fawns and lactating does (Verme and Ullrey, 1972).

4.2.3 Energy

With the possible exception of protein and phosphorus deficiencies, the most common nutritional deficiency affecting range animals is lack of either available energy, digestible energy, or both (Dietz, 1970). Gross energy is the heat given off by a substance during complete oxidation or burning. A measure of gross energy provides a common basis for expressing nutritive value.

4.2.4 Fibre

Generally a high fibre content in forage indicates low digestibility. Van Soest (1966) found that acid detergent fibre (ligno-cellulose) was inversely related to, and in his opinion, prehaps the best prediction of digestibility.

4.2.5 Moisture Content

Forage succulence is often directly related to palatability and digestibility (Short *et al.*, 1966). A number of deer species can subsist on succulence alone, unless drought or frost reduces succulence and causes them to seek water (Halls, 1970). It has been claimed that sambar can go without water for several days if the diet contains a high proportion of succulent feed such as fruit (Donne, 1924; Cahalane, 1939).

4.3 Sampling Technique

Nutrient concentrations vary within a single plant as well as between plants (Burton *et al.*, 1964; Bailey, 1967; Raymond, 1969; Rogers and Davies, 1973; Mills and Mark, 1977), so care must be taken to obtain a representative sample. Therefore, samples were taken from a number of plants in the study area, taking those portions that would normally be removed by deer. Eight known forage species were sampled viz. chickweed, tall fescue, floating sweet grass, reed canary-grass, flax, Yorkshire fog, ryegrass (H_1), and poplar. Where sambar exhibited distinct preferences for certain parts of the plant as in flax, these portions were collected separately. With grass species, an overall sample of parts available to deer was taken. Vegetation samples were collected quarterly, corresponding to autumn, winter, spring and summer. Ideally, samples should have been taken each month and a seasonal nutrient average calculated, but the time required for analysis of samples collected over 15 months would have prevented other aspects of the study from being carried out.

Where practicable, 0.5kg samples were collected. These were sealed in plastic bags and taken to Massey within 6 hours of collection. Samples were weighed wet, placed in a drying oven at 80°C for 48 hours and reweighed before grinding in a Wiley mill fitted with a 1 mm mesh screen. Ground samples were stored in airtight containers.

4.4 Analytical Methods

Samples were analysed using recommended procedures of the Association of Official Agricultural Chemists (Horwitz *et al.*, 1970). Analyses were repeated until duplicates varied less than one percent.

4.4.1 Crude Protein Determination

This represents both protein and non protein nitrogen and is calculated by multiplying the nitrogen percentage of the feed by a factor, usually 6.25 (Dietz, 1970; Hobbs *et al.*, 1981). The Macro-Kjeldahl Method was used to determine nitrogen content.

4.4.2 Gross Energy Determination

Calorific values were determined using bomb calorimetry and expressed in Joules per gram. This method determines available energy per unit of feed.

4.4.3 Acid Detergent Fibre (A.D.F.) Determination

Acid detergent fibre was determined using the method devised by Van Soest (1963, 1966). This procedure provides a rapid method for ligno-cellulose determination.

4.4.4 Moisture Content Determination

Moisture content was calculated by subtracting the dry weight of the sample from the wet weight and expressing the difference as percentage water.

4.5 Results

The nutritional quality of the grasses, flax base and poplar browse, showed different patterns of change with advancing season. Differences in chemical content between collection dates were analysed using t-tests (Hobbs et al., 1981). Nutritive values (± S.E.) of forages analysed are given in Appendices 6, 7, 8 and 9.

Protein content of the grasses appears to be highest in autumn (April) and winter (August), declining through spring (November) and summer (February). This corresponds to an increase in A.D.F. over summer. Energy and moisture content peak in spring. These trends are reversed over autumn and winter (Figs. 9 - 13). In flax the protein content (% N x 6.25) does not change appreciably throughout the year, whereas its A.D.F. peaks in autumn, is lowest in winter, and increases over spring and summer. Water content also shows little change, but energy content peaks in winter. Poplar is unusual in that A.D.F. apparently peaks in both winter and summer. Also, water content increases over spring/summer, but is lowest in winter. Protein shows a spring peak and is lowest during summer/autumn (Figs. 14 and 15).

These data suggest that the quality of the grasses is highest during autumn and winter, but declines as the season advances. The decline of energy, water and protein content over summer probably corresponds to the browning off of grass species at this time. Spring growth may account for the general increase in energy seen in November samples. Flax would be most nutritious in winter when A.D.F. is lowest and energy highest. It appears that poplar browse is of highest quality in spring and lowest in summer. Although A.D.F. is low in autumn, so are energy and nitrogen values, suggesting a relatively good digestibility but poor nutritive value. Chickweed was not abundant in November or February and sufficient samples were not obtained for full nutrient analysis. However, the analyses that were preformed, indicate that chickweed is a high quality feed, being high in crude protein and low in A.D.F. (Appendices 6 - 9). Poplar bark

Figure 9: Seasonal variation in the content of Acid Detergent Fibre, Energy, Nitrogen, and Water content in floating sweet grass

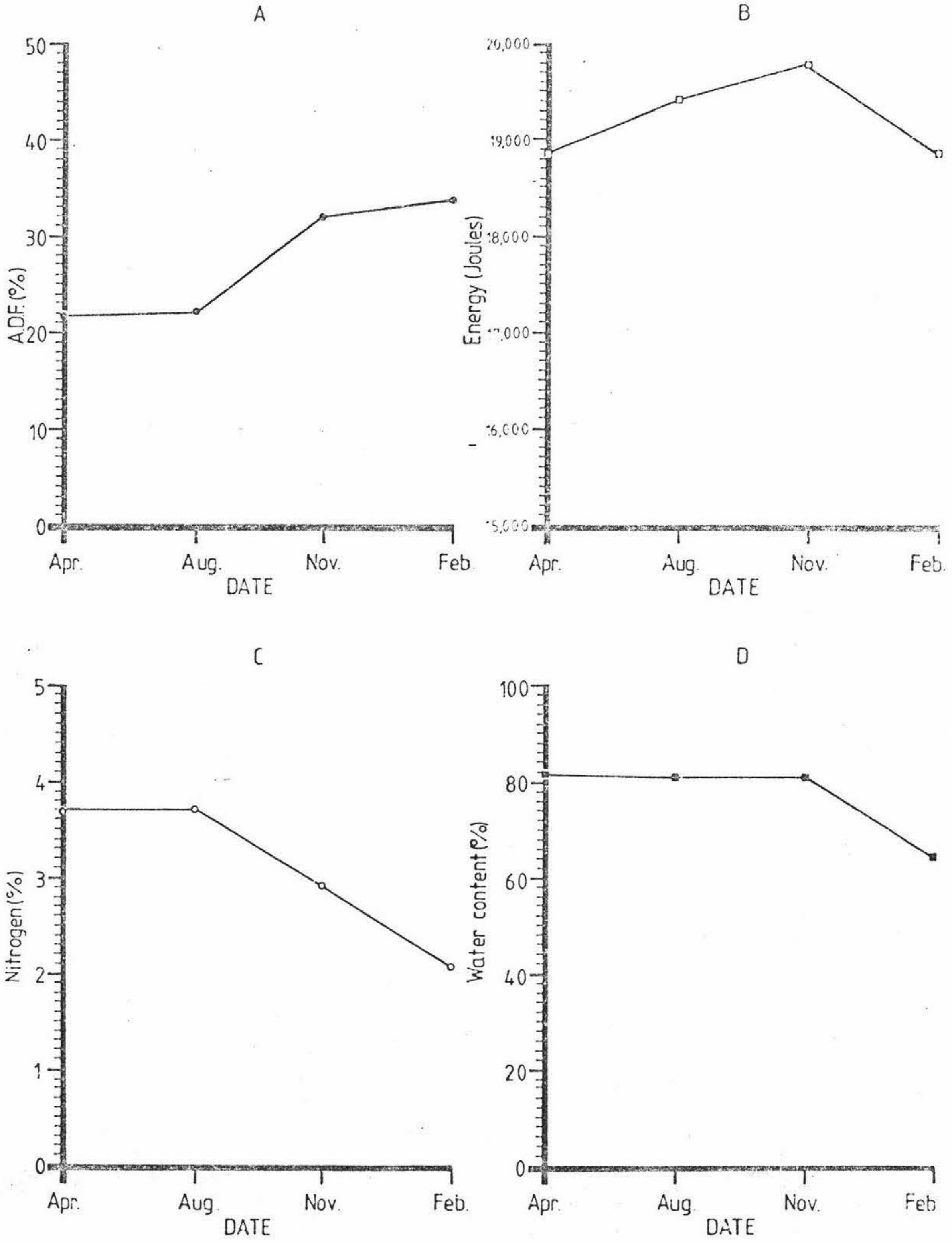


Figure 10: Seasonal variation in the content of Acid Detergent Fibre , Energy ,Nitrogen ,and Water in reed canarygrass

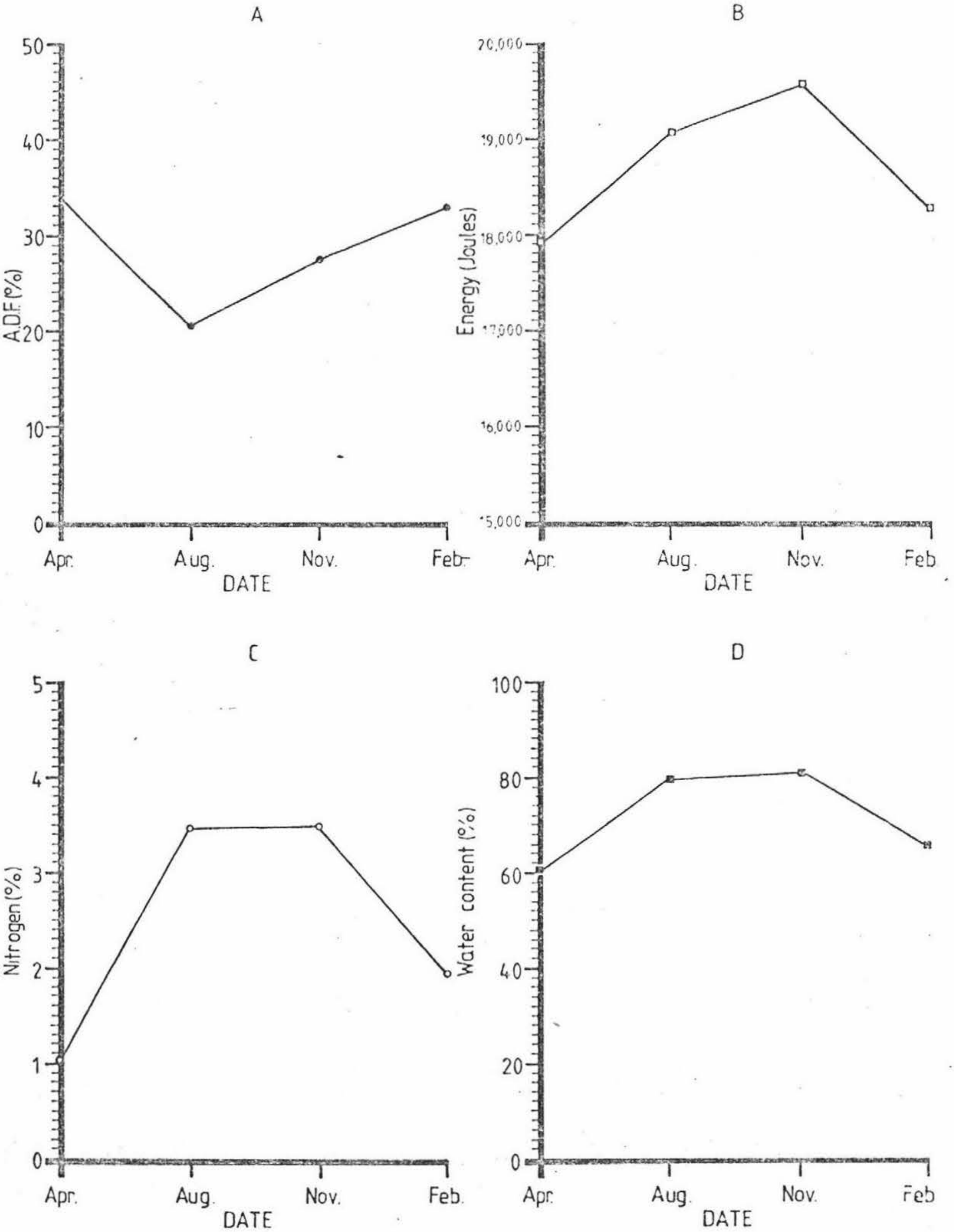


Figure 11: Seasonal variation in the content of Acid Detergent Fibre , Energy ,Nitrogen ,and Water in ryegrass (H1)

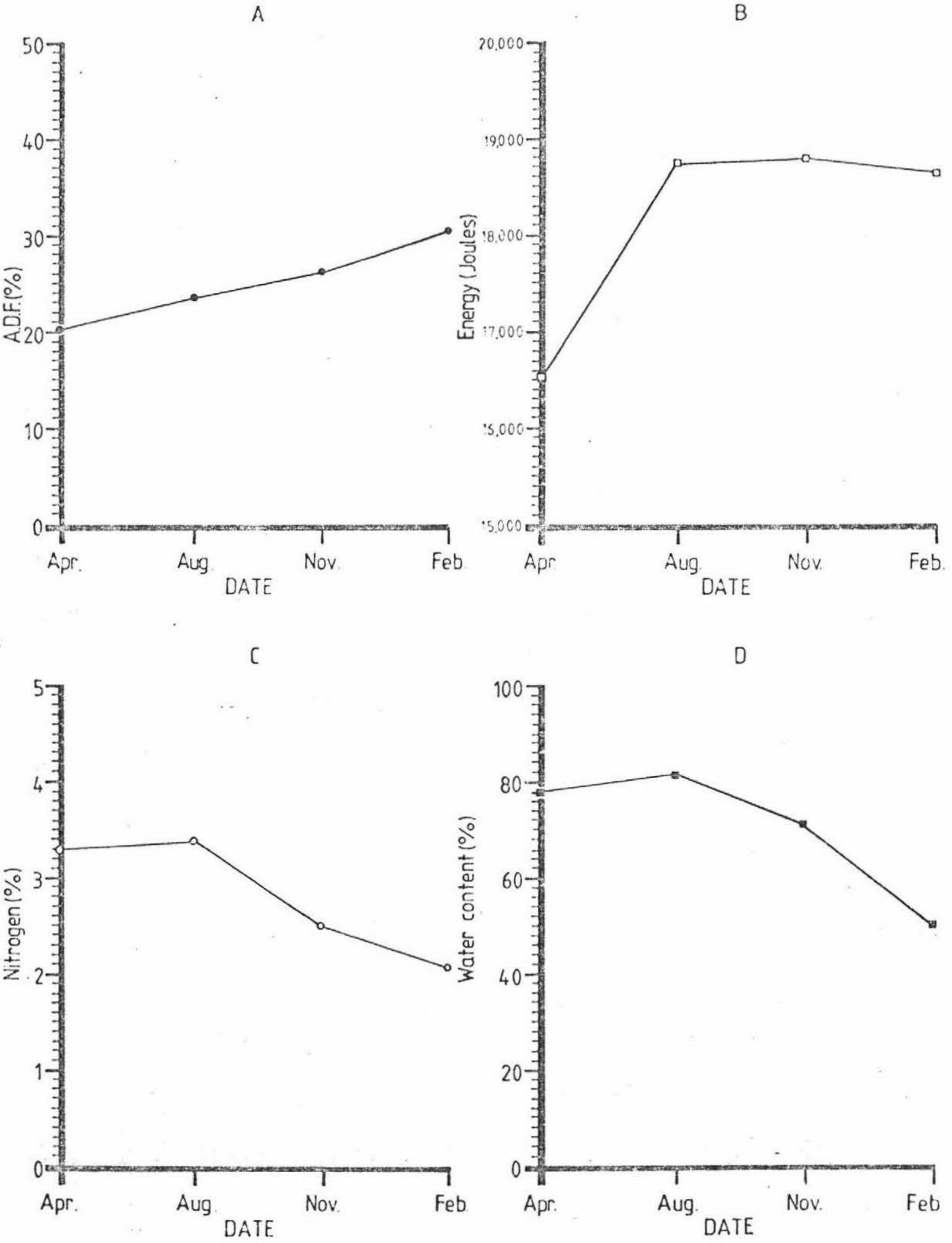


Figure 12: Seasonal variation in the content of Acid Detergent Fibre, Energy, Nitrogen, and Water in tall fescue

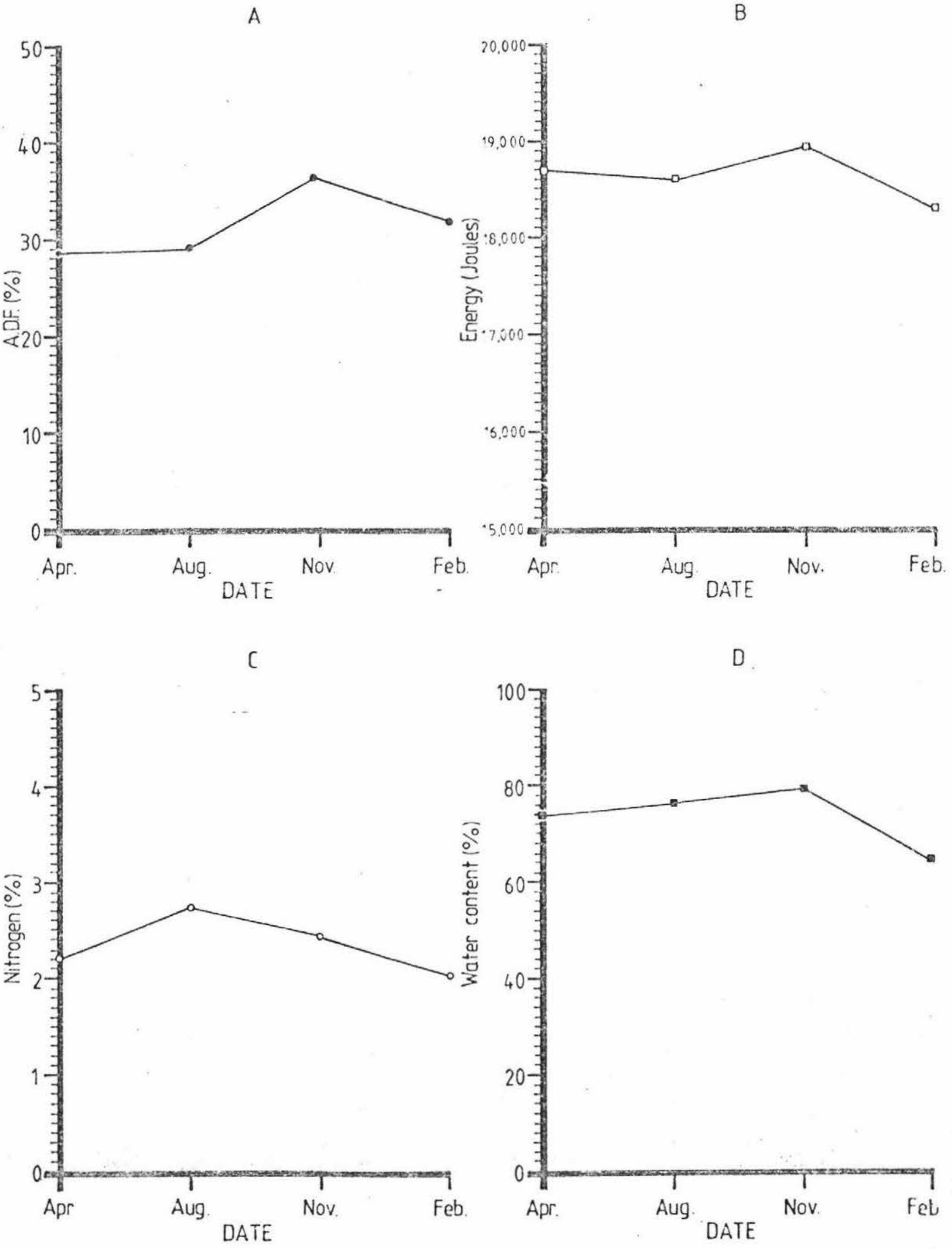


Figure 13: Seasonal variation in the content of Acid Detergent Fibre, Energy, Nitrogen, and Water in Yorkshire fog

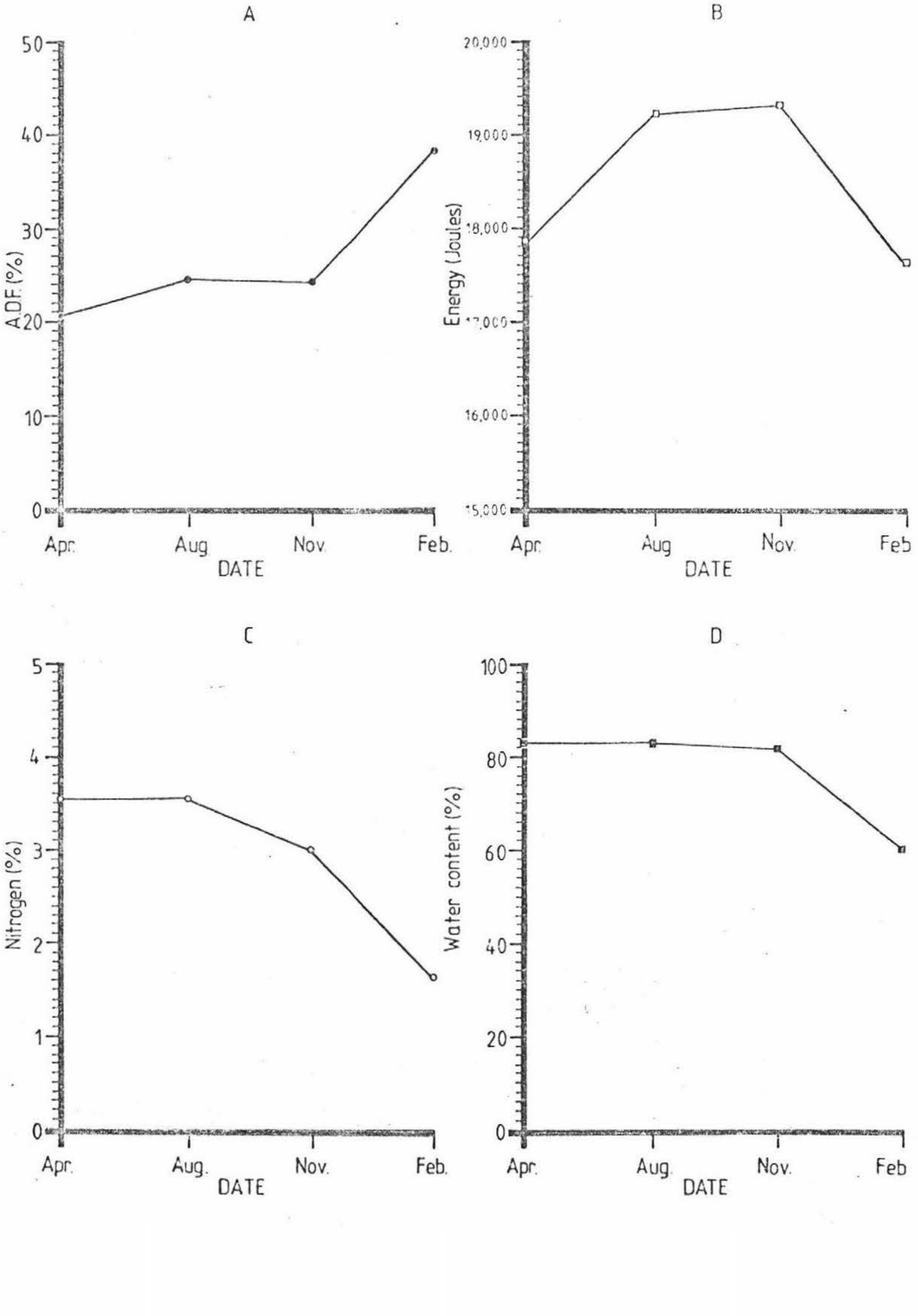


Figure 14: Seasonal variation in the content of Acid Detergent Fibre , Energy , Nitrogen ,and Water in flax

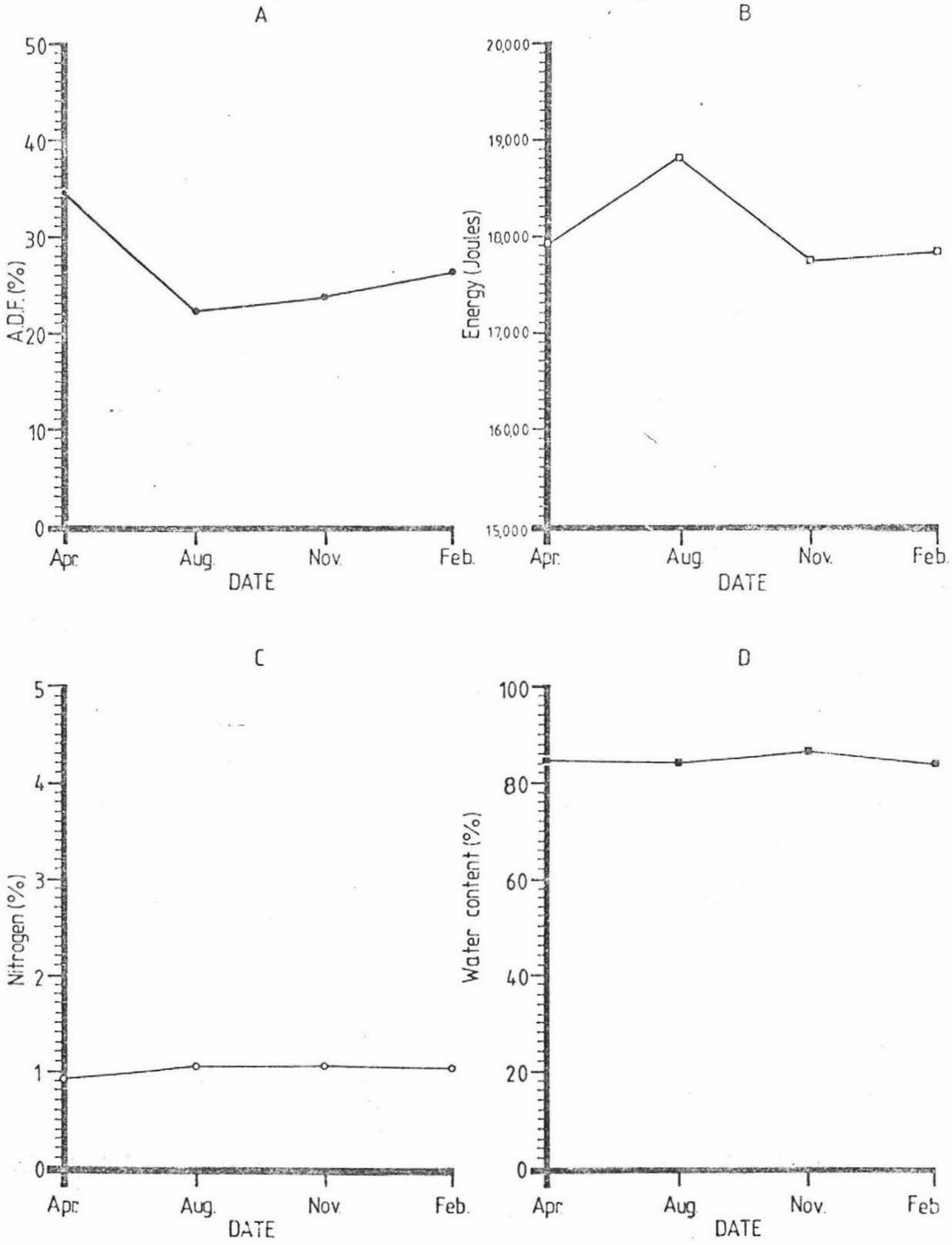
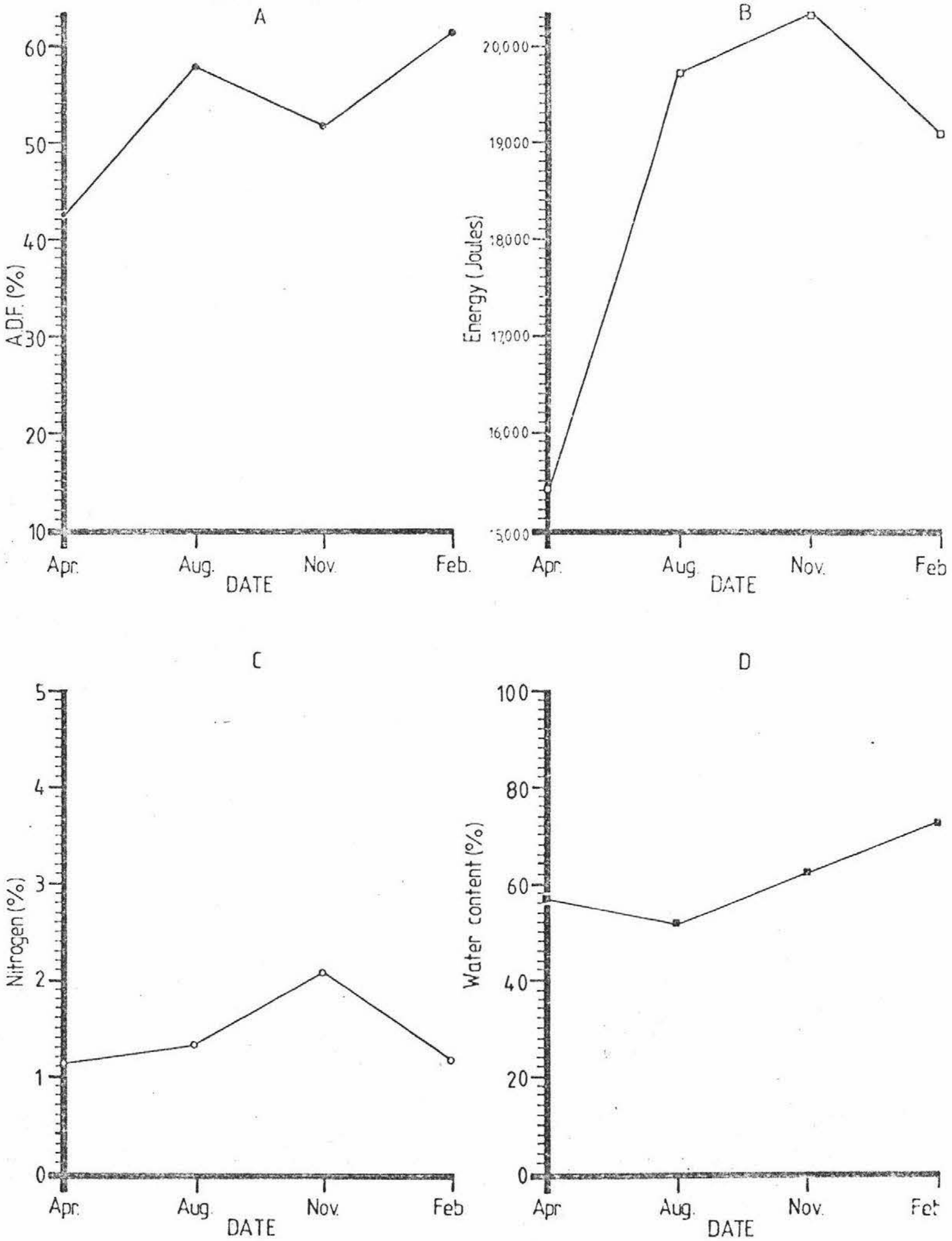


Figure 15: Seasonal variation in the content of Acid Detergent Fibre , Energy ,Nitrogen , and Water in poplar



was sampled in August, November and February and appears to be of lower nutritive value than poplar browse.

These results indicate that the forage available to sambar in the reserve is of sufficient quality to maintain animals throughout the year, despite the decline in quality evident over summer. Discussion of any relationships that there might be between seasonal quality of available forage and utilisation, as suggested by faecal analysis, will be left until the final chapter (8.2).

PART III - GENERAL BIOLOGY

CHAPTER 5 : POPULATION DYNAMICS

5.1 Population Size

One of the most difficult problems in studying these particular deer was devising a means of censusing the animals. It had been agreed at the start of the project that every effort should be made to disturb the animals as little as possible, especially as the manager (A. Hunter) had endeavoured to protect the deer for a number of years by prohibiting shooting on the property. Also, there were several people interested in deer photography who had permission to visit the area, and their interests had to be considered.

Conventional census techniques were not possible. Capture - mark - recapture (Eberhardt, 1969) would have been beyond the resources of the project and besides, stress may have been induced in captured animals. This has been known to cause death in sambar (D. McNeile, pers. comm.; M. Shailer, pers. comm.). Pellet group counts and other transect methods (Neff, 1968; Eberhardt, 1978) were not applicable as much of the area is under water during the winter months. Over the summer period, the dense vegetation would have made finding of sufficient pellet groups excessively time consuming. Also, it would not have been possible to establish transect lines through areas of dense flax. An aerial survey would not have detected animals in areas of heavy cover and if flushed into open areas, advice was that they might have panicked and injured themselves or else left the study area altogether. Serious consideration was given to the use of self attaching collars (Taylor, 1969). Coloured reflective collars would have been useful for both day and night observation. These however, would have spoilt animals for wildlife photography and more importantly, would have made it easier for poachers to locate deer at night.

Leopold _et_ _al_. (1951) found that useful information on local density could be obtained by observing feeding areas. A. Hunter and farm staff reported any deer sightings, the majority of which were in fact in winter. Deer were sometimes seen while mustering stock or encountered on the farm road in the early morning and late afternoon. This information along with that from my own observations, including monthly all night watches, enabled an estimate of animal numbers to be made. A well used deer track existed along the river edge from the study area to Waitarere State Forest and it was evident that the population was subject to change as animals left or moved into the area.

More animals were seen per day in the months March through October than in November, December, January and February (Mann-Whitney : $U = 0$, $P < 0.05$). However, this was likely to have been a consequence rather of the character of the vegetation at this time of year, than the actual number of animals present. As mentioned (2.1.1), vegetation cover is greatest from November through February and this made observations difficult over this period.

An all night watch was conducted on May 17, 1980. The area under observation was that of rough pasture between the Massey caravan and main flax (Fig. 6). Thirty-four sightings were made between 1700 hrs (27.5.80) and 0400 hrs (28.5.80) and 15 different individuals were identified. On 8.11.80, 11 animals were seen in rough pasture at the south-east end of the reserve over a twenty minute period (2020 hrs to 2040 hrs). It is unlikely that all the animals inhabiting the main flax would have ventured from it at the same time or from the same boundary. M. Douglas (pers. comm.) and M. Rudge (pers. comm.) have suggested that a reasonable guess would involve doubling the number seen, and on this presumption the flax reserve held perhaps 30 deer. About five animals were usually present in the stand of flax behind the manager's house (see Section 2.3) and a few in the Maori flax (Fig. 5). The highest total deer population at Moutoa appears then to be in the vicinity of 35 animals.

5.2 Sex and Age Composition

Schaller (1967) found that in a sample of 363 animals "classified" by him in Kanha Park, Central India, hinds outnumbered stags by about 3 : 1. Ratios were in fact 29.7 males : 100 females : 33.7 young. The proportions of the various age and sex classes in the population were 14.9% adult males, 3.5% yearling males, 51.4% adult females, 9.8% yearling females and 20.4% "young". Schaller suggested that selective predation on the males both as fawns and as adults, and perhaps also an unequal sex ratio at birth might account for "disproportion" of the sexes.

For Draisma's (1979) survey of Australian sambar, data was obtained from data cards submitted by hunters in the years 1970 to 1977. The sample comprised 263 animals. Converting these data to percentages gives the following : 38.4% adult males, 20.5% yearling males, 27% adult females, 8.8% yearling females and 5.3% fawns (seven males and seven females). These data yield a sex ratio of 1.6 : 1 stags to hinds. However, this sample is unlikely to have been a random one because as Draisma mentioned, hunters tend to be biased, selecting certain animals, especially large stags in hard antler.

In my study only 135 out of 302 sightings were able to be classified as to age and sex (Appendix 3). The sex ratio favoured hinds (1.3 : 1), with an age composition of 36.3% adult males, 45.9% adult females, 7.4% yearlings (unsexed), and 10.4% fawns. Because of the difficulty in deciding whether immature animals were yearlings or fawns it is more appropriate to combine these two groups i.e. as 17.8% juveniles.

5.3 Breeding Biology

There has been considerable debate among writers on the breeding habits of sambar, both where they are endemic and in countries to which they have been introduced.

5.3.1 India and Sri Lanka

The majority of published accounts on the breeding season of sambar in India and Sri Lanka suggest that it runs from October to December with Forsyth (1889), Blanford (1888-1891), Lydekker (1898), Russell (1900), Comber (1904) and Stockley (1913) limiting it to October and November and Prater (1934) and Brander (1923) to November and December.

Schaller (1967) suggested that the rut was not as discrete as some of these early authors had supposed, but was in fact spread over a period of at least seven months with a peak of activity in November and December. Whitehead (1972) supported this idea, stating that in Central India most of the rut took place during December, although the dates were variable. In the hills of Sri Lanka rutting occurred in October, whereas on the plains it was apparently less fixed.

5.3.2 Australia

Reports suggest that breeding occurs all year round with a peak rutting period from September to November (Harrison, 1979; Bentley, 1978). Draisma (1979) only partly agrees with this, suggesting that continuous mating activity occurs but that there are two peaks, one in late spring and another in late autumn. He bases this on data from two sources :

(a) A sample of 21 pregnant hinds in which the date of conception could be determined from the age of the foetus.

(b) A sample of 60 animals aged up to 30 months.

Draisma states that over that age period sambar can be accurately aged by tooth eruption. Based on work by Asdell (1946) and Bentley (1978), he considers the gestation period to be 8½ months. (Tables III and IV summarize Draisma's data).

5.3.3 New Zealand

Donne (1924) wrote that in New Zealand the rut occurs in March and April and that fawns are dropped in November and December. However, this statement is contestable, it being widely believed that rutting occupies a large part of the year as in Australia (Farmer, 1965; Logan, 1965; M. Shailer, pers. comm.). Riney (1957a) suggested the possibility of two breeding seasons in New Zealand.

Rutting sign such as wallows, antler rubbing and thrashing (Graf, 1956; Harrison, 1979; C. Fergusson, pers.

TABLE III*

Australian breeding data (a). Based on conception dates of 21 pregnant hinds (from Draisma, 1979)

Data	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Conception	5	4	0	1	0	3	0	1	2	1	0	4	21
Birth	0	3	0	1	2	1	0	4	5	4	0	1	

* Note: This table is presented incorrectly in Draisma, 1979 (Dr. M. Draisma, *in lit*.).

TABLE IV*

Australian breeding data (b). Based on ages of 60 sambar not more than 30 months of age (Draisma, 1979)

Data	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Conception	3	1	5	5	9	15	4	3	2	2	4	7	60
Birth	9	15	4	3	2	2	4	7	3	1	5	5	

* Note: This table is presented incorrectly in Draisma, 1979 (Dr M. Draisma, <u>in lit</u>.).

comm.; A. Harnett, pers. comm.; J. Rudd, pers. comm.) was evident in the study area April through July (see next chapter).

In early June two small fawns were seen. Based on the description given to L. and R. Rowe (Rongotea deer farmers who have successfully reared sambar), estimated age was four months. Taking the gestation period to be eight months (Sclater, 1863; Donne, 1924; Finn, 1929; Asdell, 1946), these would have been born in February and conceived in June.

In late August the partially decomposed carcass of a hind, believed to have been seriously wounded by poachers on 23.7.80 was discovered in thick flax*. When examined it was found to have been carrying a foetus about two months old. This suggests conception occurred in May.

These observations along with published data and reliable information from hunting diaries are combined in Table V. Riney (1957a) believed the gestation period to be six months. However, this is not so and his data have been reinterpreted using the more widely accepted eight month figure.

These data, although few, do support the notion of a double peak in rutting activity viz., a main rut from April to August, peaking in June and a second, smaller period in November.

5.4 Antler Growth

5.4.1 Introduction

Antler and pedicle growth is related to testosterone secretion, which in turn is linked with the sexual cycle (Lincoln, 1971; Bubenik _et al_., 1975). Growth of antler is initiated when testosterone levels are at their lowest. Velvet is shed as levels are rising to their peak at the rut and most are cast when levels are falling (Lincoln, 1971). This information on antler condition i.e. whether in velvet or hard antler, can be expected to give an

* The skeleton of this hind was recovered and mounted at Massey (Plate 15).

TABLE V

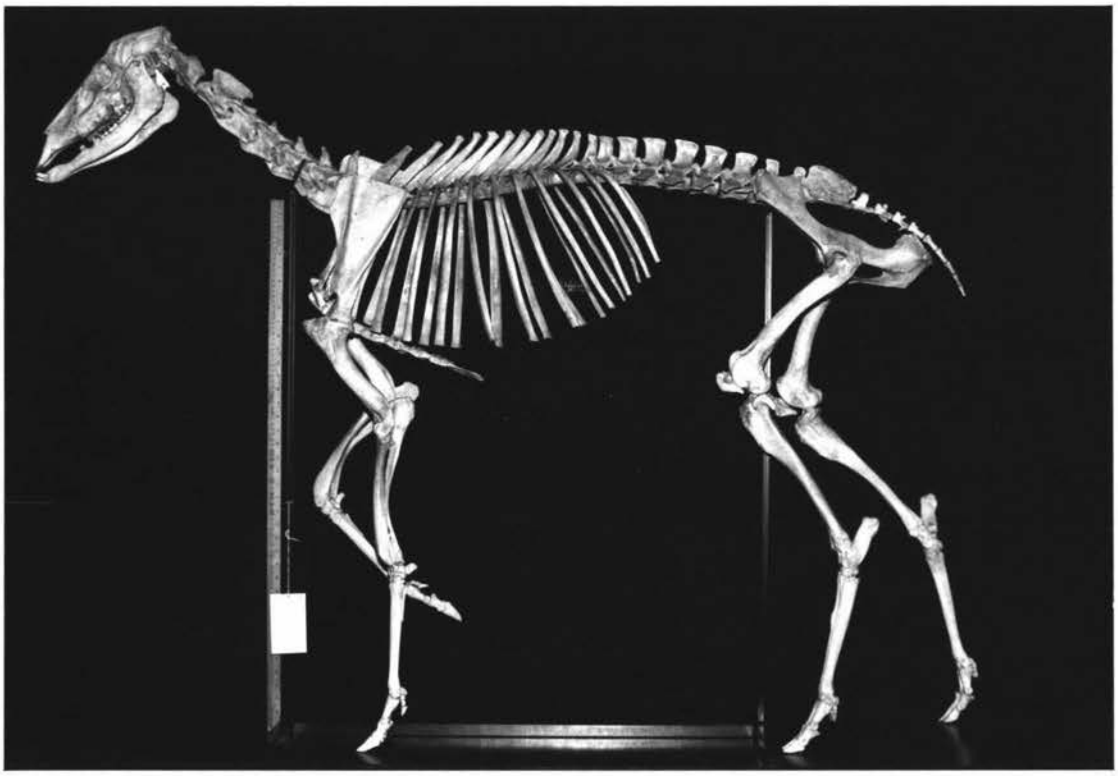
Breeding data of New Zealand sambar

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Farmer (1965)					Rut*	▨	▨	▨	▨	▨	▨	▨	Drop
Farmer (1965)		▨	▨	Drop				Rut*	▨	▨	▨	▨	▨
Riney (1957)		▨	▨	Drop*				Rut	▨	▨	▨	▨	▨
Riney (1957)		▨	▨	▨	Drop*				Rut	▨	▨	▨	▨
Riney (1957)		▨	▨	▨	▨	▨	▨	Drop*				Rut	▨
Riney (1957)		Rut	▨	▨	▨	▨	▨	▨	▨	Drop*			
Fergusson (pers. comm.)					Rut*	▨	▨	▨	▨	▨	▨	▨	Drop
Fergusson (pers. comm.)		Drop				Rut*	▨	▨	▨	▨	▨	▨	▨
Harnett (pers. comm.)		▨	▨	▨	▨	▨	Drop*				Rut	▨	▨
Rowe & Rowe (pers. comm.)		▨	Drop				Rut*	▨	▨	▨	▨	▨	▨
Rowe & Rowe (pers. comm.)		▨	Drop*				Rut	▨	▨	▨	▨	▨	▨
Rowe & Rowe (pers. comm.)		▨	▨	▨	▨	Drop*				Rut	▨	▨	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	Drop				Rut*	▨	▨	▨	▨	▨	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	Drop				Rut*	▨	▨	▨	▨	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	Drop				Rut*	▨	▨	▨	▨	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	▨	Drop				Rut*	▨	▨	▨	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	▨	▨	▨	▨	▨	Drop				Rut*
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	▨	▨	▨	▨	Drop*				Rut	▨
Rudd (<u>in</u> <u>lit</u>.)		▨	▨	▨	▨	▨	▨	Drop*				Rut	▨
Shailer & Shailer (pers. comm)		▨	Drop*				Rut	▨	▨	▨	▨	▨	▨
Shailer & Shailer (pers. comm)		▨	▨	▨	Drop				Rut*	▨	▨	▨	▨
Shailer & Shailer (pers. comm)		▨	▨	▨	Drop*				Rut	▨	▨	▨	▨
Shailer & Shailer (pers. comm)		▨	▨	▨	▨	▨	▨	Drop*				Rut	▨
Kelton (pers. obs.)		Drop				Rut*	▨	▨	▨	▨	▨	▨	▨
Kelton (pers. obs.)		Drop				Rut*	▨	▨	▨	▨	▨	▨	▨
Kelton (pers. obs.)		▨	Drop*				Rut	▨	▨	▨	▨	▨	▨
Kelton (pers. obs.)		▨	Drop*				Rut	▨	▨	▨	▨	▨	▨
Kelton (pers. obs.)		▨	▨	Drop				Rut*	▨	▨	▨	▨	▨
Kelton (pers. obs.)					Rut*	▨	▨	▨	▨	▨	▨	▨	Drop
TOTAL	Drop	3	6	5	4	1	1	4	1	1			3
29	Rut	1			3	3	6	5	4	1	1	4	1

* Indicates actual observation.

Plate 15: Skeleton of adult sambar hind.
(Skeleton prepared by I. McKelvey)

Note the metre rule near the shoulder.



indication of the probable state of sexual activity in the animal (Schaller, 1967). There is however, disagreement as to the antler growth period and time of casting in sambar. Van Bemmel (1949) determined the pattern of sambar antler growth but not the timing : "The first antler consists of a single branch, without ramifications, and is nearly always irregular and asymmetric. The second pair of antlers sometimes consists of single branches too. As a rule four (2 + 2), exceptionally even six (3 + 3) are present. The third pair of antlers normally carries six points (3 + 3)..... At the age of seven years the antlers have attained their full development."

5.4.2 India and Sri Lanka

The majority of authors quoted by Schaller (1967) and Whitehead (1972) have noted that in India, sambar shed their antlers between late March and mid May and are in velvet from May to October or November. It is further suggested that stags sometimes retain the same set of antlers for up to four years and this adds to the confusion surrounding antler shedding. Shedding appears to be irregular in Sri Lanka (Baker, 1890) and the Malayan peninsula (Whitehead, 1972).

5.4.3 Australia

Extensive work on antler growth in Australian sambar has been done by Draisma (1977, 1979) on data collected over a seven year period. "Spikes seem to be carried for up to 19 months and the first full head for 15 to 17 months. (The 27 month old spikers and 42 month old four or six point stags in the survey had very worn antlers). Other sources claim an annual stag cast and this cannot be discounted at this time" (Draisma, 1977). (See Table VI).

Draisma (1977) believes that mature stags do not cast annually but that they grow and cast successive sets of antlers "at varying intervals, increasing in size with each subsequent set until seven to eight years of age, after which further heads decrease in size."

TABLE VI

Early antler growth in sambar stags (Draisma, 1979)

Age range (months)	Details
0 - 7	Knobs
7 - 9	Growing spikes in velvet.
9 - 27	Hard spikes, very worn towards end of this period.
27 - 30	Casting, followed by growth of small 4 or 6 point head.
30 - 48	Hard antlers with small tines
45 - 48	Second cast, new growth commences, third head.

Data from samples of stags collected by Bentley (1978) and Draisma (1979) are combined in Table VII, yielding a sample of 264 animals.

Although hunting bias may have affected this sample, some inferences may be drawn from these data and these will be discussed in chapter 8.3.

5.4.4 New Zealand

Observations of antler growth in New Zealand sambar are few and have not been well documented. Although there is evidence of some stags retaining their antlers for more than a year (Farmer, 1965; Logan, 1965; A. Harnett, pers. comm.) it would appear that the majority of stags cycle annually.

A stag fawn hand reared by L. and M. Shailer (pers. comm.) and another by O. Maher (pers. comm.) both showed annual antler growth. They grew spikes at the end of their first year, cast them a year later and grew a small six point set. Shailers' animal exhibited rutting behaviour in its third year, became dangerously aggressive and was shot. Maher's stag has shed its antlers annually for a number of years.

Riney (1957a) suggested that the main period of antler growth was January through March. He examined 44 adult stags taken in all months of the year and found that the 10 in velvet were collected in January, February and March. From this he concluded that antler shedding conformed to a regular pattern.

Observations made on Bay of Plenty stags by J. Rudd (pers. comm.) appear to support Riney's findings.

When possible, antler condition of stags seen in the study area was noted. Information on stags seen at Moutoa was also supplied by L. Barnard, A. Harnett, A. Hunter and farm staff. A total of 34 observations were made. J. Rudd supplied further data on 42 observations made in the Bay of Plenty. Combined Manawatu and Bay of Plenty data are presented in Table VIII. These data will be discussed fully in the final chapter (8.3) along with those available on Australian animals.

TABLE VII

Monthly variation of antler condition in Australian sambar.

(Combined data from Bentley, 1978; and Draisma, 1979)

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Hard antler	6	1	2	8	19	31	37	42	18	27	10	6	207
In velvet	3	2	9	16	9	8	3	0		2	0	4	57

TABLE VIII

Monthly variation of antler condition in New Zealand sambar

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Hard antler	0	2	0	1	1	6	10	8	8	8	5	1	50
In velvet	2	8	5	2	3	0	0	1	1	2	1	1	26

5.5 Rate of Reproduction

5.5.1 Hind Reproductive Data

Schaller (1967) thought it likely that hinds in India, gave birth to their first fawn when about three years old. However, in a sample of 28 pregnant hinds from Australia, Bentley (1978) found that five would have conceived at 15, 16, 17½, 20 and 23 months of age. On the other hand, he reported an 11 year old hind that was about six months pregnant. Although his oldest hind (13 years) was not pregnant, Draisma (1979) recorded a lactating hind "12 - 13" years of age.

Draisma obtained ovaries and in some cases uteri from eight non gravid hinds taken between the months March and October. Histological examination revealed evidence of cyclic activity in all of these. Bentley (1978) reported a 17 day oestrus cycle for a sambar hind and Draisma (1979) found that the smallest interval between parturition and subsequent conception was "about one month". Thus, it would appear that hinds may conceive annually and not once every three years as stated by Brander (1923).

There are records of sambar having twins (Crandall, 1964; Bentley, 1978) and although none were observed in the study area, two fawns of equal size following one hind were netted on the Manawatu coast on 15.7.81 (L. Rowe, pers. comm.).

5.5.2 Stag Breeding Age

Bentley (1978) recorded a case of a 19 month old stag successfully breeding. Draisma (1979) suggests that the minimum breeding age may be as low as 15 months. He bases this on antler data as well as data obtained from histological examination of testes from 21 animals.

5.6 Mortality

Shooting was the major cause of mortality in the study area. No animals in poor condition were seen and only one, a $3\frac{1}{2}$ year old hind was known to have died of unexplained causes during the study period. However, at least six animals were known to have been taken by poachers over this period. (see Appendix 4). Skulls from three of these were recovered and aged. One was a four year old stag and the other two were hinds, aged eight and nine years. The eight year old was found to be carrying a foetus (Section 5.3.3). The loss of breeding hinds from such a small population can be expected to have a marked effect on population structure.

In captive animals stress appears to be one of the major causes of mortality (A. Hunter, pers. comm.; D. McNeile, pers. comm.; M. Shailer, pers. comm.). Captive animals have also been known to panic at the approach of an unfamiliar person and sustain fatal injuries in their attempts to break through deer fences (A. Hunter, pers. comm.; O. Maher, pers. comm.; D. McNeile, pers. comm.; L. Rowe, pers. comm.; M. Shailer, pers. comm.).

CHAPTER 6 : BEHAVIOUR

6.1 Introduction

In chapter 2 methods of observation as well as some of the difficulties involved with the study of a predominantly nocturnal animal were discussed. Feeding and resting behaviour comprised the majority of observations, but occasionally, other behavioural aspects were noted and these are the basis of this chapter. It is emphasised however, that detail of group social behaviour was not a specific aim in this study.

6.2 Animal Activity

Although bright clear nights were ideal for making observations in that a pair of 7 x 50 mm binoculars were adequate for watching an area without having to use a spotlight, they were found to be nights of little animal activity. The reason for this may be linked to the requirement sambar have for cover (discussed in 8.1). On such nights, any animals that ventured into open areas were well illuminated and therefore more exposed than is the case on moonless or cloudy nights. To a lesser degree, windy conditions seemed also to adversely affect deer activity. In these circumstances, scent would be quickly diffused and lose its directional gradient (Krebs and Davies, 1978). Furthermore, rustling vegetation would make it difficult for animals to detect other sounds in the area. Their intrinsically cautious nature may cause them to restrict their movement at times when perception of stimuli is impaired by the effects of windy conditions. Rain, temperature and humidity appeared to have little effect on animal movements.

6.3 Herd Size and Composition

The largest group seen in the study area numbered eight animals, of which at least three were mature stags. However, the group structure most commonly encountered was an adult hind, a yearling and a fawn. Schaller (1967) regarded them as "family groups" and there is no reason to doubt this interpretation. Occasionally two such groups would be seen together (Plate 16). Mature stags, which apart from the rutting season, evidently lead solitary lives and remain in a particular area for several years (A. Harnett, pers. comm.; A. Hunter, pers. comm.), were rarely seen accompanying family groups. Younger stags, presumably non breeding, were generally in groups of two, three or four. Similar herd structure has been reported in India and Australia where groups typically number fewer than six individuals (Schaller, 1967; Draisma, 1979; Harrison, 1979). In India, Schaller (1967) found the characteristic social unit to be one hind and one fawn or one hind, one yearling and one fawn. He noted that yearling stags usually remained with the hinds and that adult stags, when not with hinds, were either solitary or in groups of two. Schaller suggested that the small family groups probably retained their composition for weeks and even months. It appears likely that groups in the study area remained together for several months, although the verification of this would require techniques beyond the scope of the study.

6.4 Tracking Behaviour

Schaller (1967) noted that, when moving through an area, groups walked in single file with an adult hind in the lead. This behaviour was characteristic of animals in the Moutoa study area. Even when stags were present in a group, a hind generally took the lead.

There are numerous deer tracks and tunnels throughout the study area. Deer used these and overgrown flylines in preference to open flylines. Their tunnels were often found parallel to existing flylines but three or four metres further into the flax.

A. Harnett (pers. comm.) and A. Hunter (pers. comm.) have noted that sambar often form tracks to the lowest part of a fence or to a portion with a broken wire. These tracks are used by a number of different animals, which could mean that they are marked in some way, possibly with secretions from the tarsal glands (Muller-Schwarze, 1971 has found tarsal gland scent to be important in black-

Plate 16: Small herd composed of two family groups
(Photograph by L. Barnard)

Six deer are retreating along a flax boundary. An adult hind is leading while a fawn and yearling almost in line with one another are holding their tails erect. This is a characteristic posture when alarmed. To the right are a yearling stag and immature hind and another adult hind is in the rear, next to the flax on the left. The leading hind and the two immature animals with raised tails probably constitute one of the family units while the remaining three in the rear comprise the second. Note the surface water which is typical of this swamp during winter. Improved pasture lies to the right of the fence.

tailed deer for sex, age and individual recognition at short range).

6.5 Intraspecific and Interspecific Aggression

Intraspecific aggression in sambar has been reported by a number of writers in India, but none was observed during this study. Schaller (1967) saw one hind bite another and Brander (1923) reported seeing hinds fighting "by rearing up and slashing with their hooves." Stags in velvet have been observed fighting in this manner (Singe, 1959) and similarly in hard antler (Thom, 1937). Reports indicate that stags frequently fight during the rut in defence of territories (Brander, 1923; Whitehead, 1972) and sometimes inflict serious wounds with their browtines (Lydekker, 1898; Fletcher, 1911).

Several authors have made mention of "stamping grounds" (Fletcher, 1911; Thom, 1937; Morris, 1938; Schaller, 1967). Thom (1937) described them as "circular bare patches, devoid of all vegetation ..... stamped bare by the hooves of sambar ..... anything from 10 to 40 feet in diameter." Several stamping areas were found in the flax reserve. They varied in size, the largest being about four and a half metres in diameter. Thom (1937) had observed stags fighting on one of these areas, but Schaller (1967) considered stamping grounds to function as "sign posts communicating the stag's presence to other stags and to hinds."

Riney (1957a) indicated that cattle do not tolerate sambar and described an incident where cattle chased a stag from a paddock. Although there appeared to be little deer activity in the poplar nursery when cattle were present, a number of people have observed both in close proximity with no sign of interspecific aggression. For example, A. Harnett (pers. comm.) and W. Wallace (pers. comm.) have observed deer lying in paddocks containing cattle, and on a neighbouring farm a stag was described as being "in with the bulls" (A. Hunter, pers. comm.). Sambar have followed a tractor feeding out hay to cattle (A. Hunter, pers. comm.) and in the flax behind the manager's house, cattle, sheep, horses and deer are all present. Although no interspecific aggression was observed between deer and stock, cattle and sheep were seen to stop feeding and watch a sambar moving across their paddock, and A. Hunter (pers. comm.) has repeatedly noticed that horses become excited when they sense deer.

Schaller (1967) noted that during the rut "stags also direct their aggression at bushes and saplings which they thrash with their antlers until at times only tattered stalks remain." This activity was also found to be associated with rutting stags in the Moutoa study area. Small cabbage trees, flax bushes and fescue clumps were commonly antler thrashed or "belaboured" (Schaller, 1967) and apparently served to mark a stags territory.

6.6 Sexual Behaviour

No sexual behaviour was actually observed, although as mentioned in the previous chapter (Section 5.3.3), rutting sign was seen in the months April through July.

6.6.1 Wallows

Most wallows were circular, shallow muddy pools, between one and two metres in diameter (Plate 17). They were often situated at the bases of 'rubbing trees' (see 6.6.2) in small grassy clearings. Adjacent vegetation was usually flattened and caked with mud as was vegetation either side of tracks radiating from the area. A. Harnett (pers. comm.) found mud rubbed on vegetation to a height of 1.5 m around one wallow.

A number of wallows had a strong smell of urine associated with them, suggesting that their function as a territorial mark was both olfactory and visual in nature.

6.6.2 Rubbing Trees

During the rut, stags frequently rubbed their antlers and also their bodies on trees. Cabbage trees appeared to be favoured for both activities. All cabbage trees examined in the study area showed sign of having at some previous stage, had the outer layers of trunk

Plate 17: Typical sambar wallow

Note small size of wallow, fresh mud splatter, flattened grass around edge, and bark biting damage to willow at rear.
Stags use such wallows during the rut and urinate in and around them. This imparts a characteristic strong odour.

damaged in this way (Plates 18 & 19).

Although it could be that both sexes rub themselves against trees seemingly to scratch, it appears to be more particularly a component of stag rutting behaviour. No hinds were actually observed rubbing trees and on the two occasions when stags were undoubtedly engaged in this activity, it was accompanied by antler rubbing. Both observations were made at times of the year when stags were rutting. On the night of 27.5.80 a stag was watched through binoculars as it rubbed a willow tree. It was difficult to be certain whether or not it was rubbing only antlers, or neck as well. This stag also rubbed its hindquarters on a fallen willow bough in a manner reminiscent of a horse when scratching on a post. On another occasion (30.7.80) a mature stag was seen in the late afternoon, rubbing antlers, neck and facial area on a cabbage tree. The activity lasted seven minutes before the animal stepped back from the tree, pawed the ground and moved from sight into the flax. Although rubbing trees were found throughout the area, they seemed to occur most frequently near wallows.

6.6.3 Roaring

In India rutting stags are known to call (Lydekker, 1898; Cahalane, 1939; Whitehead, 1972). The sound described by Lydekker (1898) as a "loud and somewhat metallic-sounding bellow" is believed to attract hinds to a stags territory as well as to communicate a territory holder's presence to other stags (Whitehead, 1972). Few people in New Zealand have heard sambar stags roar and it is a widely held belief that they have no vocal call during the rut (Logan, 1965). Neither P. Smith (pers. comm.) nor J. Hargraves (pers. comm.) who hunted sambar in the 1920's and 1930's, when the animals were plentiful in the Manawatu, report stags roaring during the rut and A. Hunter (pers. comm.) who has lived at Moutoa for more than 10 years, has never heard stags roaring. However, Farmer (1965) recorded actually seeing a stag roaring at Kaingaroa (Bay of Plenty) in July 1960 and on another occasion in April heard a roar, although the animal was not actually observed.

Plate 18: 'Rubbing tree'

This damage is on a cabbage tree. Note the cabbage tree shoots at the base with fresh shavings on some of the leaves and the chewed tips of other leaves.

Plate 19: Detail of damage caused by antler rubbing.

Note the lighter areas of fresh damage with old damage evident as smoother dark brown to grey areas between.

It could be that the nature of the New Zealand habitat, particularly that found in the Manawatu, obviates the requirement for vocal communication during the rut. The Manawatu habitat is not extensive, animals being limited to pockets of scrub, swamp and exotic forest occurring along a strip of sandhill country (section 1.3). In such localised areas of relatively flat terrain, animals might find each other without the need for vocalisation. Therefore, visual and olfactory cues could be adequate for alerting an animal of the presence of another in the area. In India, where the habitat is hilly forested country (Schaller, 1967), groups may be more diffusely distributed and vocalisation as a means of communication is perhaps more necessary.

6.7 Communication

To a human observer, auditory and visual signals are the most apparent forms of communication, although the importance of olfactory signals among mammals is widely acknowledged e.g. Krebs and Davies (1978).

6.7.1 Auditory

The communicating nature of a rutting stag's call was discussed above (section 6.6.3).

Both hinds and stags have been observed to bark when disturbed. The warning bark of sambar is an unusual "overwhelming sound" (Harrison, 1979), described as "the 'Hee" of a donkey 'Hee Haw'" by Logan (1965) and "not unlike a blast from a railcar horn" by Harnett (1979). Schaller (1967) found that sambar respond to potential danger more readily than other deer species, often reacting to something that other species nearby either "failed to detect or simply ignored".

When alarmed sambar often stamp the ground with a foreleg (Schaller, 1967; Harnett, 1979). No stags were seen doing this, although it was a common warning signal used by hinds, particularly if fawns were present.

Logan (1965) noted that sambar also have a "communicatory nicker". On 11.8.80 at night, an animal seen on the edge of the flax about 20 m from the Massey hide made a short 'cow-like' low before entering the flax cover. A similar sound was later heard coming from the same area.

6.7.2 Visual

Stamping grounds, wallows, belaboured vegetation and antler rubbed trees, all appear to be visual signals defining a stags territory during the rut.

Lydekker (1898) noted that rutting stags often everted their "eye-pits" (presumably preorbital glands) exposing the pink mucous membrane which lines them. M. and L. Shailer (pers. comm.) have also observed this behaviour in sambar harassed by dogs. It has been suggested by Draisma (1979) that this is a threat display.

Postural signals are also important in social interactions (Schaller, 1967). When sambar sense danger, the hair around the neck and down the back becomes erect and the long tail is raised vertically. They may stand motionless and stare at the source of possible danger or else proceed cautiously. This behaviour was frequently seen in hinds and fawns. On 18.6.80, two hinds accompanied by two fawns were observed crossing an open area of rough pasture which I had walked across several hours before. They proceeded slowly, all with their tails held vertically and hair erect.

Schaller (1967) noted that the rump patch is "rust brown" and not as obvious as in other deer species, but the "long tail held vertically is a conspicuous signal". Schaller's comments are quite applicable to the Moutoa deer.

6.7.3 Olfactory

"The preorbital glands, which are everted for aggressive display purposes, are well developed and secrete a yellow waxy substance" (Draisma, 1979). Draisma believes this substance to be "involved with body scent identity". This certainly appears most likely because, in a type of behaviour termed "preaching" by hunters in India (Schaller, 1967), sambar stags stand up on their hindlegs at the bases of trees and wipe their facial regions in the foliage (Fletcher, 1911; Brander, 1923; Schaller, 1967). Brander (1923) believed the secretion to attract hinds. Although preaching was not observed in the Moutoa study area, stags seen antler rubbing also rubbed their facial regions (section 6.6.2) on trunks, possibly scent marking with preorbital gland secretions. Muller-Schwarze (1971) and Volkman _et_ _al_. (1978) have found similar behaviour in black-tailed deer to be related to scent marking. The possibility that sambar tracks are marked with glandular secretions and wallows with urine has already been suggested (sections 6.4 and 6.6.1).

6.8 Territoriality

In India, stags become aggressive during the rut, establishing territories which they defend against other stags (Whitehead, 1972). Schaller (1967) found no evidence of "territorial exclusiveness" but suggested that the accumulation of visual and olfactory signals in a limited area of a stags range, plus its aggressive nature at this time, probably tended to space males out in a forest. His observations caused him to suggest that "hinds move widely, probably entering the ranges of and being joined by a number of different stags, before remaining with one of them for several days and perhaps longer". A similar situation appears to exist in my study area. Stags almost certainly have territories, but unlike in India, fighting was not observed. However, it was difficult to determine the size of territories or the degree of overlap, without having marked animals to observe.

It appears that rutting stags have one or more wallows at the centre of their territories. In one area, three wallows were found, spaced no more than 50 m apart, each one in sight of the next. Because these were in such close proximity, it was likely that they were used by only one stag. A relatively small area (approximately 0.1 ha) around a wallow is intensely marked by a stag with urine, belaboured vegetation and rubbed trees. The greater the distance from the wallow, the less the amount of territorial marking. This observation seems to suggest that a stag's territory consists of a central wallow area, where it spends a considerable amount of time, possibly lying there during the day, surrounded by a 'buffer zone' i.e. an area marked by the stag, but one which may overlap with the range of another. Hinds and young appear to move freely throughout the area.

Sambar have been claimed to be a "very adaptable animal" (Harrison,1979) and it is therefore, perhaps not surprising that their behavioural responses have undergone some degree of modification as they have become established in New Zealand habitat.

CHAPTER 7 : CRANIOMETRY

7.1 Introduction

"The vertebrate skull provides particularly favourable material on which to study the relations of ontogeny to phylogeny" (De Beer, 1937) and Dhaliwal (1962) considered that skull measurements in particular are "important taxonomic characters" in mammals.

Cranial variation within different groups of mammals has been studied by a number of workers e.g. Pearson and Davin (1924) on humans, Deol (1955) on muskrats, Churcher (1960) on the North American red fox, Dhaliwal (1962) on the black rat, Freedman (1963) on baboons, Mystkowska (1966) on red deer, and Yablokov (1974) on mammals in general.

In an early study of deer crania, Phillips (1920) examined 96 skulls of virginia deer. He selected only adult males, taking 10 measurements: "Palatal length, Audito-basal length, Lower tooth row (length), Zygomatic width, Upper tooth row (length), Orbit width, Mastoid width, Nasals (length) and Antler length." Phillips was interested in the variability of these measurements and he hoped they "might form a basis for comparison with other races." Van Bemmel (1949) used cranial measurements as a taxonomic aid in his revision of the rusine group while Mystkowska (1966) anatomically described the red deer skull using 34 cranial characters and looked at variability in specimens from Poland, Western and Eastern Europe.

Caughley (1971) examined skulls from mature female deer taken from an area in Fiordland where wapiti and red deer were sympatric. Using 22 cranial characters, he compared this sample with control samples of red deer and wapiti from other areas, to investigate hybridization between populations in the "zone of overlap".

Batcheler and McLennan (1977) supplimented Caughley's 189 skulls with a further 383 and re-examined the sample using 15 skull measurements. Multivariate analysis was used to determine the degree of hybridization.

In the present study skulls were measured for the following reasons:

(a) There are no published reports on the craniometry of New Zealand sambar.

(b) The use of standard measurements such as those described by Batcheler and McLennan (see section 7.3.1) would enable data to be readily used in future studies.

(c) It is likely that hybridization between sambar and rusa occurs in the Bay of Plenty where the populations are sympatric (M. Daniel, pers. comm.; J. Rudd, pers. comm.) and comparison of skulls from that area with Manawatu samples might determine whether this is so.

At present, the idea of sambar and rusa hybridizing is hypothetical, based on the knowledge that sambar can cross with rusa in captivity (there is such a hybrid, a female, at Rainbow and Fairy Springs, Rotorua) and on the appearance of a number of unusual trophies shot in the Bay of Plenty area. Sambar stags can weigh up to 225 kg, whereas rusa stags weigh up to 135 kg (Morrison and Harris, 1974) and several stags have been taken, which although of sambar size, exhibit antlers characteristic of rusa in shape i.e. "The inner tine of the terminal fork is much longer than the front or outer tine" (Lydekker, 1898). (See Plates 20, 21 & 22).

However, large samples are required for such a comparison and despite enthusiastic cooperation from a number of correspondents, adequate samples unfortunately did not become available.

7.2 Skull Material

A sample of 22 skulls from the Manawatu comprising 11 female and 11 male specimens was obtained. A twenty third skull (male) was badly damaged and discarded. Five specimens were from the study area, five from sambar that had been captured and died in captivity, and the remainder were borrowed from local people who once hunted sambar.

A number of deerstalkers in the Bay of Plenty were visited and asked for skull material to measure. Unfortunately

Plate 20: Head of typical sambar phenotype from Bay of Plenty.

(Shot by P. Carter)

Note large brow tines and even forks at extremity of beams.

Plate 21: Possible sambar/rusa hybrid.

(Shot by G. Winchcombe)

Note unusual depth of terminal forks and length of inner branch suggestive of rusa. The general configuration and robustness are closer to sambar. Compare with Plates 20 and 22.

Plate 22: Typical rusa phenotype.
(Shot by J. Rudd)

Note the tall inner tine and overall smaller size compared with Plates 20 and 21.

only three sambar skulls out of the 10 located were complete and able to be measured. Most hunters had had their good trophies mounted, or had only kept the antlers. For similar reasons only two whole rusa skulls were available.

Antlers on skulls or mounted animals were measured in addition to any cast ones obtained.

7.3 Measurements

7.3.1 Crania

The 15 cranial measurements described by Batcheler and McLennan (1977) combined characters used by previous workers viz. Mystkowska (1966) and Caughley (1971). Several of the characters chosen also correspond to characters measured by Phillips (1920), Van Bemmel (1949) and Daniel (1965). Because the methods of Batcheler and McLennan (1977) were clearly explained and appeared to be standard cranial measurements, they were used in this study (see Table IX).

Linear measurements were made with vernier calipers (0.1 mm) or a tape (1 mm) uniformly to three significant figures. It did not prove possible to make all 15 measurements on every specimen, as some of the skulls were partially damaged.

7.3.2 Antlers

Draisma (1979) found that antler bias followed a "normal biological distribution" and that "averages of right and left antlers tend to be even". For this reason only the left antler was used unless it was damaged or deformed in which case the right one was measured.

Nine out of 12 cast antlers from the Manawatu and all five cast antlers from the Bay of Plenty were from the animals left side.

Nine antler characters were measured:

(a) Number of points.

(b) Length along outer curve (Lydekker, 1898).

(c) Circumference above browtine (Lydekker, 1898).

(d) Width from tip to tip (Lydekker, 1898).

TABLE IX

Cranial measurements (Batcheler and McLennan, 1977)

1. Cranial Cavity - The volume of the cranial cavity was measured to the nearest 5 ml by plugging the foramina with modelling clay and pouring wheat (Batcheler and McLennan used 0.4 cm water rounded gravel or soya bean seeds) through the foramen magnum, shaking down and measuring in a graduated measuring cylinder.
2. Basal length - Ventral ridge of the occipital condyles to the posterior edge of the canine alveolus.
3. Ventral neurocranium - Median ventral lip of the foramen magnum to the posterior medial edge of the palate.
4. Maxillary tooth row length - Anterior rim of P2 alveolus to posterior rim of M3 alveolus.
5. Margo-adentalis - Posterior rim of canine alveolus to anterior rim of P2 alveolus.
6. Lateral viscerocranium - Tip of pre-orbital process to posterior rim of canine alveolus.
7. Lateral neurocranium - Median point of lambdoidal ridge to tip of pre-orbital process.
8. Facial tubers - Width of facial part of skull, across facial tubers.
9. Maxillary tooth row width - Width from left to right buccal alveolus rim at second cusp of M2.
10. Occipital condyle width - Maximum breadth across the condyles.
11. Canine width - Left to right buccal rims of canine alveoli.
12. Nasal cavity circumference - Around the midpoint of the adental region between C and P2.
13. Nasal cavity depth - Mid-dorsal fronto-nasal junction to mid-ventral palato-maxillary junction.
14. Anterior orbital width - Between fronto-lacrymal notches (caliper knife edge held perpendicular to long axis of skull).
15. Posterior orbital width - Maximum breadth across the zygomatic arch.

(e) Widest inside width (Lydekker, 1898).

(f) Weight of antler (cast antlers only).

(g) Pedicle length - shortest distance from burr to fronto-parietal suture.

(h) Pedicle circumference - Around midpoint of pedicle.

(i) Browtine length - Distance from burr to tip.

7.4 Age Determination

7.4.1 Introduction

An accurate age determination technique using samples of dead animals allows information on age/birth schedules and other measures of age specific performance to be readily obtained from field samples, without having to study known-age animals in captivity.

Age determination methods have been studied for a variety of cervids. A number of workers have described ageing techniques using tooth eruption and wear e.g. Banfield (1949), Murie (1951), Hancock and Low (1956), Quimby and Gaab (1957), and Smith (1974) for wapiti; Riney (1957b), Mitchell (1963, 1967), Lowe (1967) for red deer; Van Bemmel (1949), Humphries and Rowler (1976), and Draisma (1979) for sambar.

Tooth eruption is particularly useful for age determination of animals less than 30 months of age (Smith, 1974; Draisma, 1979).

A number of age determination methods which make use of periodic layering in the teeth, have been described for various Cervidae, Bovidae and Antilocapridae (Smith, 1974). Mitchell (1963, 1967) described a technique for ageing red deer by counting annuli in the cementum pad of the lower first molar tooth. This method has also been used by Ranson (1966) for white-tailed deer; Lowe (1967) for red deer; Wolfe (1969) for Moose; Douglas (1970) for red deer and other deer introduced to New Zealand, including sambar; Smith (1974) for wapiti; Batcheler and McLennan (1977) for wapiti and red deer; Humphries and Rowler (1976) and Draisma (1979) for sambar deer.

7.4.2 Method

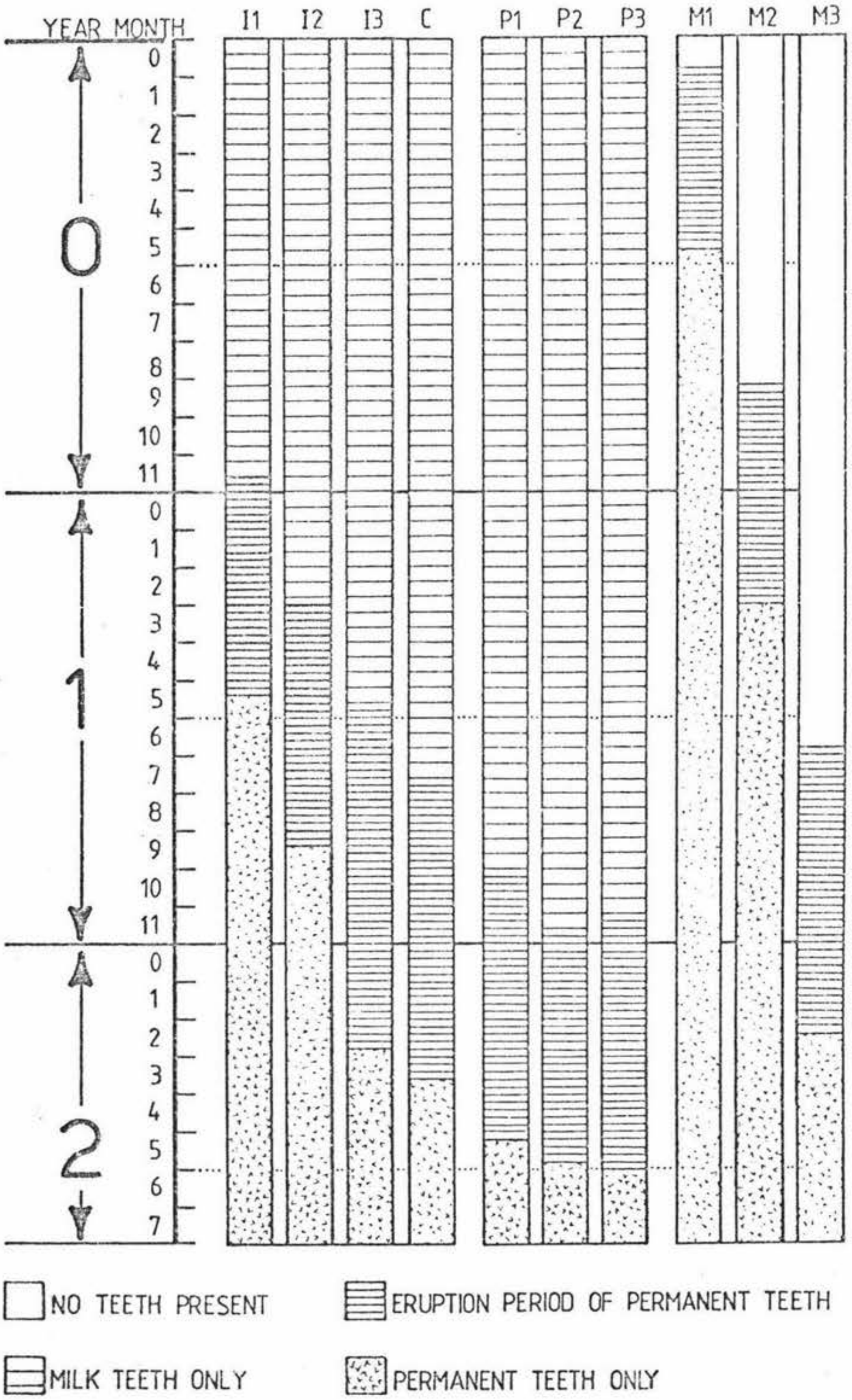
Terminology of teeth follows that described by Riney (1951).

The permanent teeth of cervids continue to erupt throughout life due to the growth of dental cement which occurs as a sheath around each root and as a pad between the roots of the molariform teeth (Mitchell, 1963). The cementum pad is made up of alternate layers of opaque and translucent cementum, the former involving aggregations of cementoblast cells or the air filled spaces once occupied by such cells and the latter containing fewer cells and more fibrous material (Mitchell). "The opaque layers consist of relatively wide summer bands, periods of rapid growth, and the translucent layers consist of narrow winter bands, periods of restricted growth. The two types of layer form an annual deposit" (Humphries and Rowler, 1976).

Mitchell (1963, 1967) found the lower first molar tooth to be the most convenient for collection and examination. The same tooth was used in this study because in sambar, "the calf at birth has, in the lower jaw, one permanent tooth, the first molar which erupts at one month of age and is fully erupted at five months of age. All other lower teeth present at birth are deciduous" (Draisma, 1979). The first molar is therefore as old as the animal itself and is carried throughout life. Humphries and Rowler (1976) found that the time of tooth eruption of permanent teeth in sambar is identical to that in red deer with the exception that the breeding seasons differ (Fig. 16).

After careful removal from the jaw the molar is cut with a diamond saw in the vertical plane, slightly posterior to the midline between the cusps. The cut surface of the front cusp is then ground with 220 grade carborundum paper on a flat surface until the widest area of cementum is located. It is then pre-polished with 600 grade wet and dry paper and polished with a silicon base car wax for viewing under a low power dissecting microscope. Correct orientation of the specimen and of the light source is essential for maximum clarity. A microscope lamp fitted, with a blue filter and directed obliquely across the surface

Figure 16: Chart of tooth eruption in sambar (from Draisma,1979)



was found to give the best results. Most teeth were easily read at this stage (Plate 23) and further etching with formic acid and staining with thionin dye (Pekelharing, 1969) were unnecessary.

Age was calculated by adding one to the number of opaque layers counted. The first opaque layer is deposited in the second summer of life (in red deer, when the animal is between 9 and 17 months of age) and one is added to account for this (Douglas, 1969).

7.5 Results

Raw cranial and antler data are presented in Appendices 10 and 11.

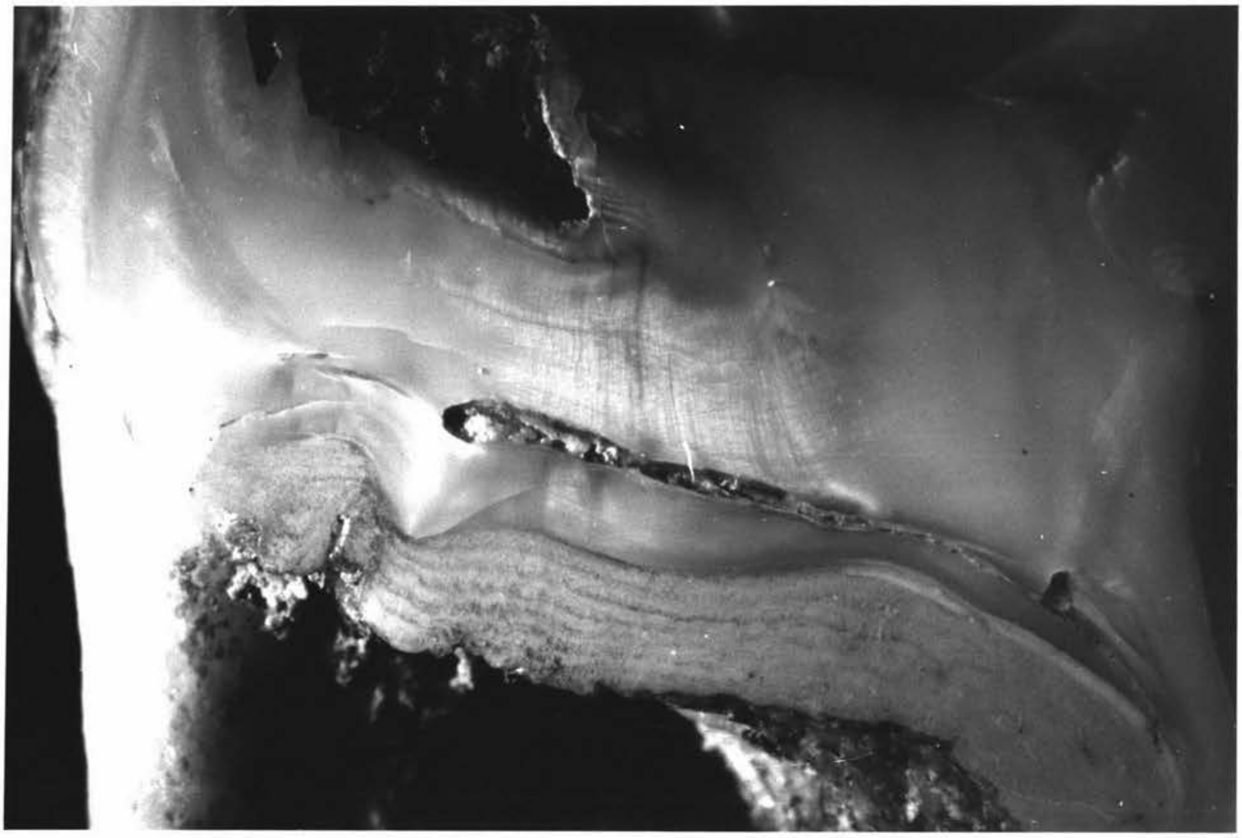
7.5.1 Cranial Data

Because of the small sample size and missing measurements, discriminant multivariate analysis as used by Batcheler and McLennan (1977) was not practicable (L. Batcheler, *in lit.*).

Growth rate and size vary with age in mammals (De Beer, 1937; Van Bemmel, 1949; Mystkowska, 1966; Yablokov, 1974) and specimens must be placed into age classes. Also, unaged specimens have to be neglected and this further reduces the effective sample size. Two age classes were chosen, viz. 'Five years and over' and ' Three to five years' (All but one specimen under five years of age, a yearling stag which was neglected, fell into this category). These particular age categories were chosen because it was considered that young animals would grow more rapidly than mature animals, perhaps even at sexually dimorphic rates (Mystkowska, 1966), and that the cranial measurements would exhibit a greater variance in this age group compared with that for mature animals. In this study animals were classed as mature when five years of age or more. This category was not based on sexual maturity but on factors related to growth. Draisma (1979) in fact, suggests that stags may breed at 15 months of age and hinds at 19 months of age (see Section 5.5) so that animals may reach sexual maturity well before they are fully grown. Van Bemmel (1949), Draisma (1979) and

Plate 23: Cementum layers in sectioned molar tooth

This M_2 molar shows seven annual lamellae in the cementum pad. Its age is therefore nine years. Roots are visible to lower left and mid right while the upper portion of the photograph is occupied by the body of the tooth.



others have claimed that stags are in their prime as trophies at about seven years of age, and Mystkowska (1966) found that in red deer, the most rapid period of growth occurs between the ages of two and three. Therefore, it was assumed, for the purpose of classification according to age, that sambar can be considered to be mature at five years of age.

Using these age categories the effective sample sizes, were as follows:

	5 years +	3 - 5 years
Manawatu Males	6	3
Manawatu Females	8	3
Rotorua Males	3	-

The Rotorua sample and Manawatu '3 - 5 years' sample were too small for any meaningful analysis to be performed, but it was possible to compare individual characters from the Manawatu males with those of Manawatu females (5 years +) in order to detect any morphological differences.

Analysis of variance (ANOVA), F-tests (to statistically test for the equality of the variances) and Mann-Whitney U-tests (Non parametric test for measuring the difference in location of two samples) were performed on the available data (Table X).

Analysis of variance indicated that lateral neurocranium, occipital condyle width, anterior orbital width and posterior orbital width, differed significantly $(P< 0.01)$ between the sexes.

The Mann-Whitney test confirmed this with significant differences $(P< 0.01)$ between the sexes for the same characters and in addition two other characters at $P< 0.05$ viz., nasal cavity circumference and nasal cavity depth. However, these latter characters had U values equal to or very close to the critical value.

TABLE X

Data analysis - Manawatu skulls

Manawatu Females = Sample 1
Age class 5 + yrs Manawatu Males = Sample 2

	ANOVA			Statistics				F-test			MANN-WHITNEY		
	f1	f2	F.S.	$\bar{x}_1$	$\bar{x}_2$	s1	s2	f1	f2	F	n1	n2	U
1. Cranial Cavity	1	12	0.74 n.s	355	367.5	9.3	38.7	5	7	17.3 (P< 0.01)	8	6	34.0 n.s
2. Basal Length	1	12	0.4 n.s	29.3	29.9	0.6	2.9	5	7	23.4 (P< 0.01)	8	6	25.5 n.s
3. Ventral Neurocranium	1	12	0.74 n.s	10.9	11.2	0.4	0.8	5	7	4.0 (P< 0.05)	8	6	31.0 n.s
4. Maxillary tooth row length	1	12	1.52 n.s	10.5	10.8	0.5	0.3	7	5	2.7 n.s	8	6	34.5 n.s
5. Margo-adentalis	1	12	0.13 n.s	6.0	5.9	0.4	0.6	5	7	2.25 n.s	8	6	18.0 n.s
6. Lateral Viscerocranium	1	12	0.12 n.s	15.3	15.2	0.6	0.7	5	7	1.4 n.s	8	6	19.0 n.s
7. Lateral Neurocranium	1	12	15.18 sig. (P< 0.01)	17.6	18.8	0.4	0.8	5	7	4.0 (P< 0.01)	8	6	43.5 (P< 0.01)
8. Facial Tubers	1	12	2.75 n.s	11.3	11.5	0.2	0.3	5	7	2.25 n.s	8	6	35.5 n.s
9. Maxillary tooth row width	1	12	1.15 n.s	10.2	10.4	0.4	0.3	7	5	1.8 n.s	8	6	32.0 n.s
10. Occipital Condyle Width	1	12	25.65 sig. (P< 0.01)	6.9	7.6	0.2	0.3	5	7	2.25 n.s	8	6	47.0 (P< 0.01)
11. Canine width	1	11	2.95 n.s	5.3	5.6	0.3	0.3	6	5	1.0 n.s	7	6	33.0 n.s
12. Nasal Cavity Circumference *	1	10	2.15 n.s	18.3	20.5	0.8	3.7	5	5	21.4 (P< 0.01)	6	6	29.0 (P = 0.05)
13. Nasal Cavity Depth *	1	12	3.6 n.s	8.2	8.8	0.4	0.9	5	7	5.1 (P< 0.05)	8	6	38.5 (P< 0.05)
14. Anterior Orbital Width	1	12	12.25 sig. (P< 0.01)	9.6	10.8	0.3	1	5	7	11.1 (P< 0.01)	8	6	45.0 (P< 0.01)
15. Posterior Orbital Width	1	12	11.51 sig. (P< 0.01)	14.4	15.2	0.2	0.5	5	7	6.25 (P< 0.05)	8	6	44.5 (P< 0.01)

* Very close or equal to critical value of U.

7.5.2 Antler Data

Individual characters were compared using t-tests and Mann-Whitney U-tests. F-tests were performed to test for equality of variances.

Antler spread was calculated according to Draisma (1979):

$$\frac{\text{Length along outer curve} - \text{widest inside width}}{\text{Length along outer curve} + \text{widest inside width}} \times \frac{100}{1}$$

= % Antler spread

Results of analysis are presented in Table XI. Although pedicle length appeared to be significantly different ($P < 0.05$) between the two populations (using a d-test) this difference did not show up with the Mann-Whitney test, indicating that the locations of the sample means were the same and that the large variance of the means ($F = 9$, $P < 0.05$) probably caused the d-test to show significance. The Mann-Whitney test indicated a significant difference ($U = 119$, $P < 0.05$) in antler spread between the Manawatu and Rotorua populations, but this was not supported by t-test ($t = 0.7$, n.s.) and in this case it could be assumed that the variances do not differ significantly ($F = 1.3$, n.s.) This suggests that it would be wiser to treat antler spread as not being significantly different between the two samples, especially as acceptability at $P < 0.05$ is borderline.

Draisma (1979) stated that racial differences can be detected using various antler measurements and this will be discussed along with craniometric data in the next chapter (8.4).

TABLE XI

Data Analysis - New Zealand Antlers.

Manawatu antlers = sample 1
Rotorua antlers = sample 2

	Statistics						F-test			t-test		Mann Whitney
	n1	n2	$\bar{x}1$	$\bar{x}2$	s1	s2	F	f1	f2	t	d.f.	U
1. Antler spread (index)	13	12	11.1	18.0	6.9	7.9	1.3 n.s	11	12	0.70 n.s	21	119 $P < 0.05$
2. Antler length (along outer curve)	19	12	64.6	69.3	14.7	11.5	1.6 n.s	18	11	0.73 n.s	29	118.5 n.s
3. Browtine length	20	12	30.2	30.3	7.5	5.7	1.7 n.s	19	11	0.03 n.s	30	116 n.s
4. Tip to tip	13	12	65.7	53.9	21.9	10.6	4.3 $P < 0.05$	12	11	d=1.73 n.s	17.5	46.5 n.s
5. Widest inside width	14	12	51.1	49.3	13.4	8.6	2.4 n.s	13	11	0.4 n.s	24	60 n.s
6. Pedicle length	8	12	3.5	4.1	0.3	0.9	9 $P < 0.01$	11	7	d=2.1 P 0.05	13.6	26.5 n.s
7. Pedicle circumference	8	12	12.9	14.5	2.5	2.0	1.56 n.s	7	11	1.6 n.s	18	32.5 n.s

PART IV - DISCUSSION AND CONCLUSIONS

CHAPTER 8

In a wide ranging thesis of this type several of the facets are not closely related and these do not necessarily all lend themselves to coordinated discussion at this stage. Accordingly some topics have in effect been discussed in the context of their chapters.

It does remain however to consider particularly sambar requirement for cover, diet selection, breeding and antler cycles, and craniometry before the final conclusions are made.

8.1 Requirement for Cover

In Chapter 2 (section 2.3) it was emphasised that sambar require plenty of cover in their habitat i.e. thick undergrowth, not simply a tree canopy. Early writers had noted that sambar characteristically remained in "dense woodlands" (Donne, 1924; Cahalane, 1939) throughout the day, only venturing into more open areas to feed at night (Forsyth, 1889; Brander, 1923). Lord Powerscourt (1884) considered that this habit caused the death of a herd he tried to establish in an Irish park: "It was a curious thing with the sambar and it was no doubt the cause of their death, that they would never come out of the thickets in the daytime ..... Of Course, by this unnecessary precaution on their part against the meridian rays, they got chilled through and eventually died."

Lawrence and Richard Rowe of Rongotea have successfully kept adult sambar in captivity for a number of years. They realized that unlike red deer which soon adapt to captivity in open pasture, sambar require dense cover, and they have prepared a sambar enclosure (Rowe and Rowe, pers. comm.). An area has been fenced and planted in pampas grass and this offers appropriately dense cover to a height of 3 m. A small stream running through the centre has been dammed to provide a pond. Disturbance to the deer in the enclosure is kept to a minimum and they are rarely seen during the day, preferring to feed around the edges at night.

The Rowe's have also hand reared a sambar fawn and it would appear that if sambar are caught as fawns, they can be brought up in a more open situation. It has been mentioned (Sections 5.1 and 5.6) that captive animals are susceptible to stress related ailments, that they are easily frightened and frequently bring about their own death. These problems seem to be particularly associated with animals caught as adults and then kept under unsuitable conditions. One such case has been reported by D. McNeile (pers. comm.) who lost four out of five deer because of injury and stress. The fifth animal broke through the fence and escaped. These animals had been kept in a paddock containing a stand of Mahoe trees as cover and while this forms a canopy it is open underneath. Such cover is very suitable for red deer (McNeile, pers. comm.) but inadequate for adult sambar.

An area such as the reserve at Moutoa is well suited to sambar as the flax provides not only essential cover and shelter, but also food and water. Sambar exist in a number of habitats in New Zealand, such as coastal dune country, exotic forest and manuka scrub. The over riding factor in all these situations is low understory cover, be it lupin, flax or raupo on the coast, blackberry, grass, or mast in forests, or native broad leafs, fern, raupo and young manuka in the scrub of the Bay of Plenty.

8.2 Discussion of Forage Quality and Diet Selection

Faecal analysis revealed that the diet of animals in the reserve changed seasonally over the 15 month sampling period, in what appeared to be a cyclical manner in response to some seasonal factor(s) i.e. different species predominated the winter and summer diets (Table XII).

Nutrient analysis of forage species showed that the quality of the grasses, flax and poplar browse changed seasonally. There appeared to be a general decline in overall quality of forage species over the summer months, but the nutritional value never fell below the minimum

TABLE XII

Forage species predominating in the summer and winter diet of Moutoa deer

Summer	Winter
Floating sweet grass	Tall fescue
Reed canarygrass	Flax
Yorkshire fog	Chickweed
Ryegrass	Poa
Poplar	

requirement for animal maintenance.

Cuticle and nutrient data were analysed together using:

(a) Two way analysis of variance without replication.

(b) Stepdown multiple regression.

(c) Stepup multiple regression.

Analysis of variance showed that although the mean total amounts of cuticle present in the faecal samples collected in April, August, November and February did not vary significantly, the proportions of the contributing species did (see Table XIII). The source of this variation was due mainly to the species themselves (SS% = 74.15%). Residual error accounted for 23.95% of the variance while the effect of the different collection dates was minimal (SS% = 1.9%).

Apparent relationships between cuticle area, fibre, energy, nitrogen, and water content are shown in Table XIV. As was to be expected (see section 4.2.2), water content was found to be positively correlated with nitrogen content and both were negatively correlated with fibre content. Also, energy was positively correlated with nitrogen, and water content. Fibre showed some degree of negative correlation with cuticle area, indicative of the inverse relationship between fibre and digestibility suggested by Van Soest (1966). However, nitrogen also showed a negative correlation with cuticle, a result that would not be expected if animals were selecting forage on the basis of quality.

Accordingly, a step down multiple regression was run to determine which characters (fibre, energy, nitrogen or water content) had the greatest effect on the variance and what percentage of the variance could in fact, be accounted for by the combined effect of these characters.

Water content was found to have the least effect (T = 0.29) and was dropped. Both fibre and nitrogen had negative regression coefficients (T = -2.13 and -2.25 respectively) while energy was positive (T = 1.75).

TABLE XIII *

Means of cuticle area in faeces collected in April, August, November and February, and of individual species over the four combined collection dates

```
VARIATE : CUTICLE                              TABLE OF MEANS

GRAND MEAN       8.54     TOTAL NUMBER OF OBSERVATIONS  28

DATE             AUTUMN      WINTER       SPRING         SUMMER
                 (April)    (August)    (November)     (February)
                  8.36        7.87         7.97           9.97

SPECIES          FESCUE     FLOATING     REED             FLAX        YORKSHIRE     RYEGRASS     POPLAR
                            SWEET GRASS  CANARYGRASS                     FOG

                  13.13      16.11         6.47           14.03         4.13          2.45        3.47

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE                  DATE               SPECIES
------------------------------------------------------

REP                     7                    4
SED                   2.000                2.645
```

* Table taken from Genstat Printout

TABLE XIV *

Correlation matrix - Degree of correlation between cuticle area, fibre, energy, nitrogen and water content.

CUTICLE	1	1.000				
FIBRE	2	-0.1496	1.000			
ENERGY	3	0.1043	0.1855	1.0000		
NITROGEN	4	-0.1713	-0.5155	0.3188	1.0000	
WATER	5	0.2192	-0.6331	0.0796	0.3050	1.000
		1	2	3	4	5

* Table taken from Genstat Printout.

Only 10.9% of the variance in cuticle area was accounted for by the effects of fibre, energy, and nitrogen.

A step up multiple regression analysis, adding species, indicated that 66.8% of the variance in cuticle area was accounted for by a species effect.

These results suggest therefore, that sambar do not select forage species on the basis of nutritional quality as determined by fibre, energy, nitrogen and water content. Also, the fact that the 'Nutriex' and magnesium saltblocks were hardly used by deer and no seasonal differences in utilization were apparent, suggests that animals obtained sufficient minerals and nutrients from the available forage.

It seems then that palatibility and/or availability of forage species govern diet selection of sambar in the Moutoa area.

8.3 Discussion of Breeding and Antler Cycles

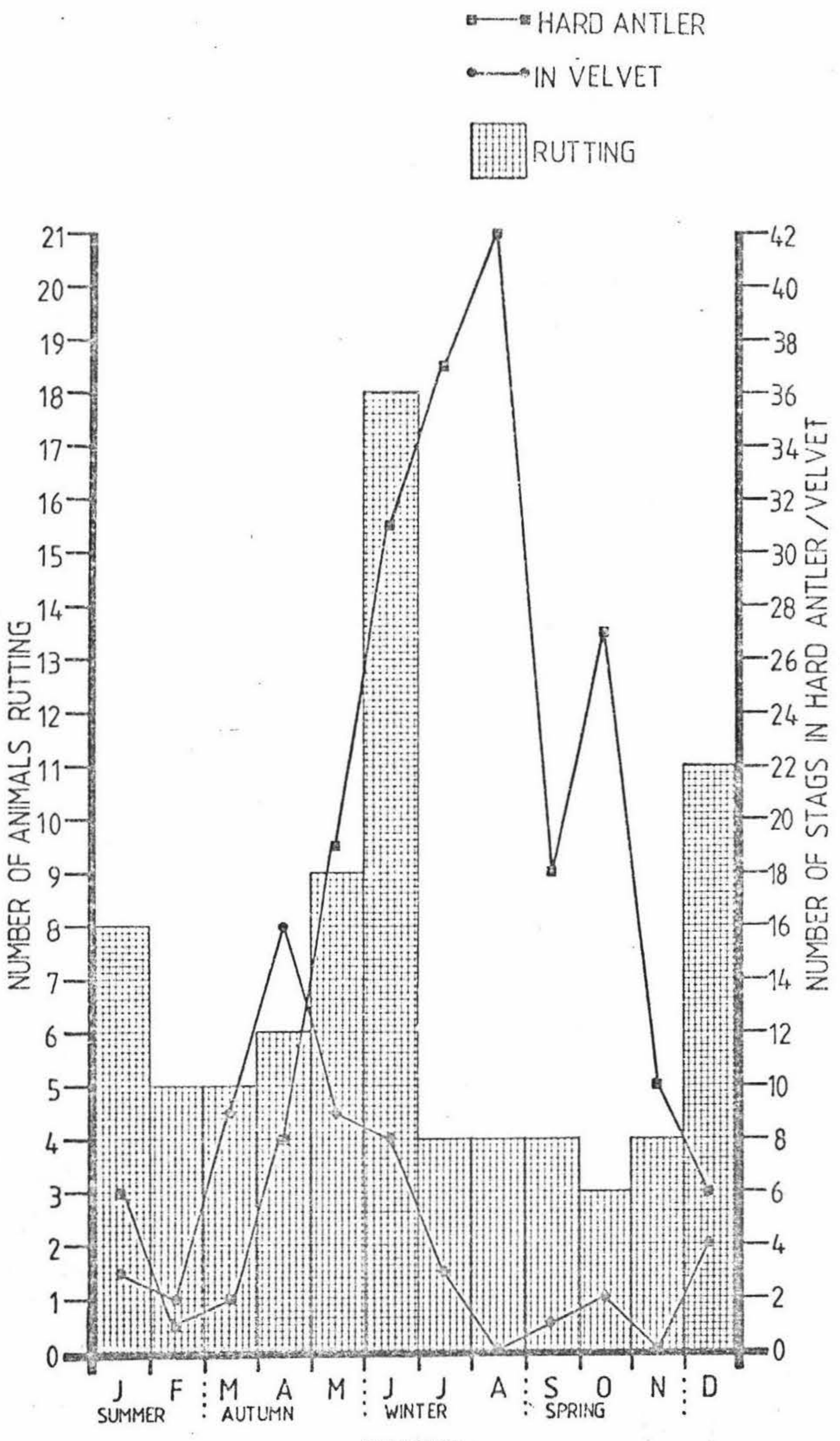
8.3.1 Australian Breeding Data

For breeding data Draisma (1979) had to rely on a sample of shot animals rather than field observations and such a sample must be treated with caution due to hunting bias.

Because of the relationship between antler condition and state of sexual activity (section 5.4.1) one would expect to find rutting stags in hard antler. Draisma found that the majority of stags taken from June to October were in hard antler with a peak number being shot in June, July and August. A similar trend is evident in a sample of 110 stags obtained by Bentley (1978). Combined data from Bentley, and Draisma (1979) were presented in tabular form (Table VII) and are graphed in Fig. 17 which shows antler condition superimposed on rutting data.

A peak of animals in hard antler occur in August with a smaller peak in October. This partly agrees with the breeding data as the peak of hard antlered animals, shot over June, July and August, is in accord with the peak of rutting activity apparent in August, although the smaller

Figure 17: Relationship between antler condition and rutting activity in Australia



peak of hard antlered animals taken in October does not correspond to the second peak of rutting activity seen over December and January.

Stags in velvet were shot in most months although a greater number were taken over March, April, and May, corresponding to a period of lower rutting activity prior to the peak of rutting occurring in June. The number of stags taken in velvet were fewer than the number in hard antler. Behavioural differences between animals in velvet and those in hard antler, or hunting bias towards stags in hard antler may have contributed to this.

Many Australian hunters claim a peak of wallow use and tree rubbing (indication of rutting activity) from May to June (Draisma, 1979) which is in accord with the antler and breeding data.

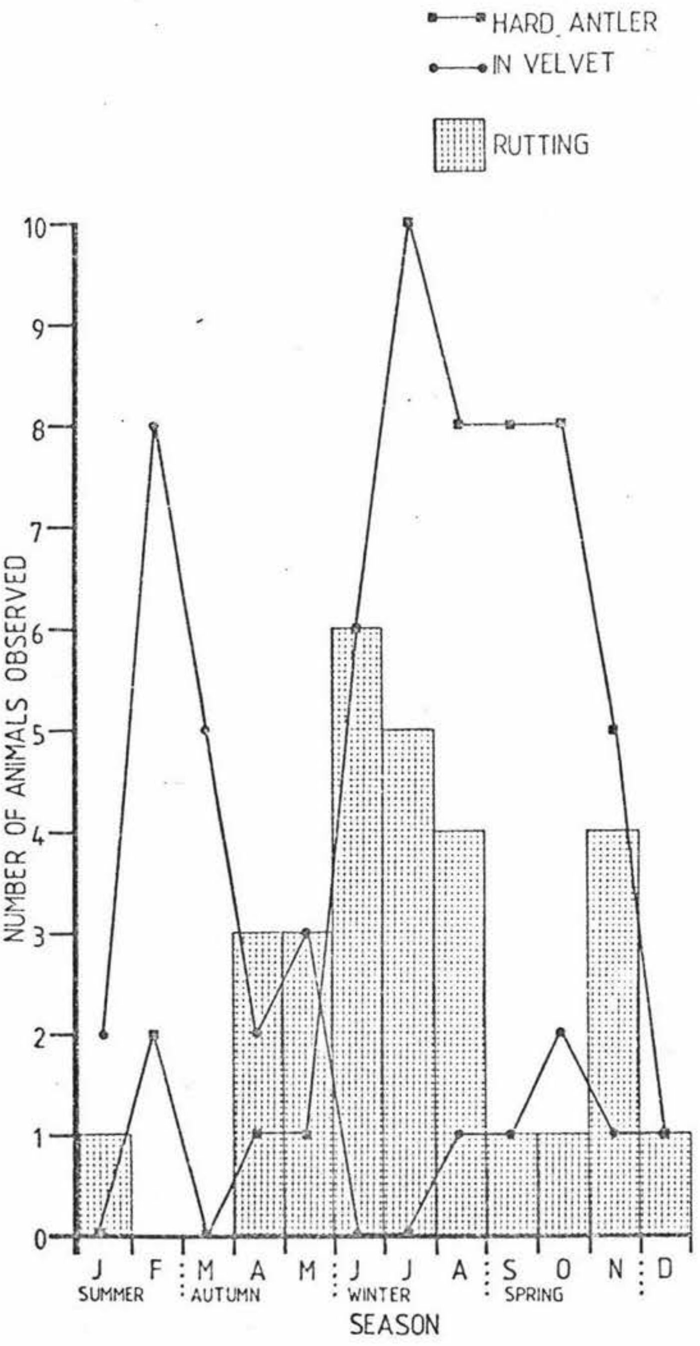
Consideration of the available breeding and antler condition data (Fig. 17) and of the field observations made by hunters does seem to support Draisma's theory of two rutting peaks each year for Australian sambar.

8.3.2 New Zealand Breeding Data

Breeding data on New Zealand animals was presented in Section 5.3.3 (Table V). As in Australia rutting activity appears to occur over a large part of the year with two main periods viz., April through August peaking in June (early winter) and in November (late spring). These figures indicate that the major rutting period is over winter and this is further supported by data on antler condition. Figure 18 presents antler condition superimposed on rutting data.

The greatest number of stags in hard antler were seen over the months June through November with a peak in July. In June and July no stags in velvet were seen and this is in accord with the breeding data which seems to indicate peak rutting activity over these two months. Although the majority of stags seen from August through November were in hard antler, some were seen in velvet and this seems to suggest that over these months not all stags in the population are capable of breeding. This correlates with the smaller peak in rutting activity indicated by the November breeding figures.

Figure 18: Relationship between antler condition and rutting activity in New Zealand



The greatest number of stags in velvet were sighted during the months January through May with peak numbers in February and March. This in fact corresponds to the two months in which no rutting sign was observed. Also, if it is assumed that sambar, like other deer species, are in velvet for four to six months (Whitehead, 1972) then stags seen in velvet in January through May could be expected to be in hard antler sometime between May and November, which would be in accord with the actual data on antler condition.

Although these conclusions are based on a small number of observations, the fact that data was obtained from more than one source, principally field observations, minimises possible bias caused by selective sampling techniques, and of course the evidence aligns with the almost identical breeding cycle in Australian sambar. It is also noteworthy that in Australia, Hog deer, a species possessing many behavioural similarities to sambar (Draisma, 1979) rut at anytime of the year with a large peak of activity from May to June and a smaller peak between October and December (Taylor, 1971).

8.3.3 Antler Cycling Data

Stags in hard antler can be seen together with those in full velvet (Lydekker, 1898; Van Bemmel, 1949; Farmer, 1965; Whitehead, 1972). On this basis Lydekker, Farmer and Whitehead have entertained the supposition that sambar do not shed annually. But this does not necessarily follow if one considers a population that may exhibit continuous mating activity throughout the year with peak activity over winter and late spring to summer.

If antlers were cast once a year and stags were in velvet for four to six months, as suggested by Schaller (1967) and Whitehead (1972), one would expect to see stags in velvet together with those in hard antler, especially around the peak rutting periods (six months apart). If stags rutting in early winter had been in velvet from early December the previous year and those rutting in November in velvet from July, some overlap would occur.

Even though the Australian data on antler condition must be treated with some caution because of sampling bias, and the New Zealand sample is small, the pattern of antler condition is nevertheless suggestive of a 12 month cycle in sambar. This is substantiated by the similarity of the breeding cycles in Australian and New Zealand animals.

Another argument supporting the theory of irregular antler cycling is the fact that stags possessing excessively worn antlers have been taken on a number of occasions (Logan, 1965; Draisma, 1979). But unless these animals can be accurately aged there is no way of determining how long a particular set of antlers has been carried and various environmental or behavioural factors may have contributed to the wear. Draisma was confident of the accuracy of the ageing technique used in his study of early antler development (section 5.4.3) and his results suggest that stags could carry a set of antlers for more than 12 months. A.Harnett (pers. comm.), who has proved a very reliable observer, is also of this opinion so the possibility cannot be discounted. Even so, it is to be remembered that documented accounts of antler cycle in captive stags in a number of zoological gardens, parks and private estates throughout the world (e.g. Woburn Abbey, Lydekker 1898; New York Zoological Garden, Crandall 1964; Calcutta Zoological Garden, Schaller 1967; Pendeside, Australia, Draisma 1979; Melbourne Zoological Garden, Draisma, 1979; Manawatu, New Zealand, Maher, pers. comm.; and Manawatu, New Zealand, Shailer, pers. comm.) all support antler shedding to be an annual occurrence, although not necessarily at the same time of year for individual stags. This widespread regularity occurs in spite of the report by Brander (1944) that captivity may "disarrange" the sexual cycle.

Brander (1923) had earlier exphasised that antlers were shed yearly and Van Bemmel (1949) thought that the retention of antlers for over a year was "not the normal rule."

I consider therefore, that whilst exceptional animals or those in unusual circumstances may carry antlers for more than a year, such an event would be rare.

8.4 Discussion of Craniometry

8.4.1 Cranial Data

Although small sample sizes prevented the taxonomic comparison of Manawatu sambar with Rotorua animals as originally planned, an analysis of adult male and female skulls from the Manawatu population successfully demonstrated the existence of some sexually dimorphic characters. Besides the presence of antlers or pedicles (the most conspicuous secondary sexual characteristics) the most reliable measurements of sexual dimorphism in the crania were found to be the lateral neurocranium, occipital condyle width, anterior orbital width and posterior orbital width (see 7.5.1).

Van Bemmel (1949) wrote that "the sexual characters of the skull are the result of special demands made upon the structure of the skull by the heavy antlers ..... The occipital part of the skull in males is entirely adapted to this purpose." These observations are in accord with the cranial characters that were found to exhibit the greatest degree of dimorphism.

In addition to the occipital condyle width and posterior orbital width (zygomatic breadth), Mystkowska (1966) found that breadth of facial tubers, maximum length of skull, length of mandibula, height of <u>pars</u> <u>rostralis</u>, height of neurocranium, and volume of cranial cavity were sexually dimorphic characters in red deer. He had a sample of 483 skulls and it seems likely therefore, that several other sexually dimorphic characters would be evident in a similarly sized sample of sambar crania.

8.4.2 Antler Data

Draisma (1979) recounted a persistent suspicion "that Victorian sambar stags tend to be overspread i.e. the length of the longest antler is less than the greatest width between the antlers." Antler spread was not recorded in his project but he was able to obtain antler measurements for 90 individuals from the Australian Deerstalkers' Association Trophy Register and for 53 trophy stags from the New Zealand Deerstalkers' Association.

Calculations of antler spread from these samples revealed that the average New Zealand sambar trophy was underspread (length of longest antler is greater than the greatest width between the antlers) by 3.8% whilst the Victorian stags tended to be overspread by 6.6% and this Draisma concluded "showed definite racial differences between the two groups."

In the present study antler spread was calculated for 13 Manawatu and 12 Rotorua stags and in all specimens antlers were found to be underspread ($\bar{x}$ = 14.4%, s = 8.1) thus supporting Draisma's findings.

The possibility of differences in the average antler spread of Rotorua and Manawatu stags was suggested (see section 7.5.2) but discounted because this was only indicated at the 5% probability level by the Mann-Whitney test alone. If however a Type II error (Walker and Lev, 1969) has been committed and the null hypothesis viz., that there is no difference in antler spread between stags from the Rotorua and Manawatu populations, should have in fact been rejected, it could be that sampling bias and not racial difference was the explanation. The Rotorua skulls, were mainly from animals shot as trophies and therefore biased towards larger heads, whereas the Manawatu sample comprised a mixture of average and trophy animals.

None of the other antler characters measured indicated differences in antler form between the two populations.

8.4.3 Antler Deformities

Draisma (1977) found that antler deformities were "not as rare as generally thought." Almost 13% (15 out of 116) of all stags taken showed deformities.

Several antler deformities were noted in this study. A number of skulls from Rotorua and Manawatu had antlers that showed sign of having been damaged while in velvet. Club antlers were seen in one stag at Moutoa and another stag in the area was known to have grown only one antler (A. Hunter, pers. comm.). An unaged Rotorua specimen had a palmated right antler and a normal left antler. These abnormalities appear to have been caused by injury to the pedicle or growing antlers rather than by hormonal or hereditary factors, although one or other of these reasons was most likely the explanation for a 10 point stag taken in the Bay of Plenty. This head, owned by J. Nicholson of Murapara has two "accessorial" (Van Bemmel, 1949) points on each beam. Van Bemmel found that such heads do occur in old animals, but unfortunately no teeth were available to age Nicholson's specimen by.

Apart from these abnormalities, antler form of New Zealand sambar was found to conform to that generally described for the rusine group (Lydekker, 1898; Van Bemmel, 1949; Draisma, 1979).

8.5 Comments on the Future of Sambar in New Zealand

Sambar have been established in the Manawatu since 1875. Although much of their original habitat has been destroyed because coastal swamps have been drained and scrub land brought into production as farmland or forest, small breeding groups still exist in remaining pockets of suitable habitat. Once exotic forest becomes established sambar are able to recolonise the area, which shows their ability to adapt to new situations.

According to Wodzicki (1961) sambar have dispersed little compared with several of the other introduced ungulate species and he suggested that this was "perhaps because of heavy shooting and their habitat requirements". This seems to be a reasonable supposition if one considers the decrease in coastal habitat that has occurred, and the increase in hunting pressure following the establishment of the game meat industry. Also, sambar are sought after as trophy animals and have been subject to this particular pressure for many years. However, not all shooters are "sportsmen" (Murphy, 1978) and shooting by spotlight, often illegally on Crown Land or in State Forest has been a common practise.

Recent years have seen increasing interest in sambar as people have come to realise that overexploitation has severely depleted numbers. In the 1940s there were estimated to be between 400 and 500 sambar in the Manawatu (Wodzicki, 1950) but now they are relatively scarce (M. Shailer, pers. comm.; A. Harnett, pers. comm.). A 1979 census conducted by local branches of the New Zealand Deerstalkers' Association estimated the coastal population to be as low as 60 animals (A. Harnett, pers. comm.).

Survival in a number of areas has been due to active protection by property owners or managers such as the Hunters of Moutoa, who have for a number of years endeavoured to preserve some areas of suitable sambar habitat.

In July 1980 a ban on shooting sambar in local State Forests was imposed by the Minister of Lands and since that time sambar have been accorded full protection for a limited period (5 years) in the Manawatu. Without the combined efforts of various branches of The New Zealand Deerstalkers' Association it seems unlikely that the situation regarding sambar in the Manawatu would have otherwise received ministerial attention.

The sambar population at Moutoa is almost certainly a viable one, as is indicated by age structure, sex ratio and the occurrence of rutting activity. However, the population is subject to fluctuation as animals enter or leave the area. If the reserve were to be left as it is now, it seems likely that the population would survive. But the study area is only a remnant of the once large Moutoa flax estate, and with the draining of surrounding land for dairy production, the future of the reserve and animals within it is uncertain.

There is a paucity of published information on sambar, particularly in New Zealand, and for this reason the aim of the project was to present a general account of their biology. However, some aspects studied inevitably apply rather particularly to the Moutoa flax swamp e.g. diet analysis and perhaps population structure. Nevertheless, the techniques described are intended to be applicable to sambar study in a number of different habitat types.

Although I was frequently only a few metres from animals in the study area, they never came to accept my presence as did the red deer studied by Darling (1937). Therefore observation had to be made from places of concealment such as hides or suitable vegetation.

In this study binoculars and a spotlight were used for night observation but for future studies the use of light intensifying equipment would be a substantial improvement.

The faecal pellet method of diet analysis is particularly suited to sambar study. No animals need to be sampled; it is not necessary for animals to even be observed, although subjective observation is a useful addition; pellet collection can be made during the day, when animals are least active and therefore disturbance is minimal. Furthermore the technique may be used in areas where other herbivores are also present, including other deer species. J. Knowlton (pers. comm.) has found that red deer pellets and sambar pellets can be readily distinguished by their shape. Faecal analysis would therefore be a valuable technique for future dietary research in differing habitats.

Whether or not sambar and rusa do actually hybridise in the wild was not determined. It seems likely that some hybridisation occurs where the two species are sympatric, but unless sufficient skulls become available for a craniometric study or some other comparative method such as tissue typing is used, it is likely to remain conjecture.

Under the 1977 Wild Animal Control Act the Forest Service has the power to gazette areas to be set aside solely for recreational hunting purposes. Following submissions from hunting clubs it is Forest Service policy to investigate the potential of such areas and "set things in motion if suggested areas meet the established criteria" (H. Vipond, in lit.).

Since January 1979 when the Forest Service received a submission from the Rotorua and Eastern Bay of Plenty branches of the New Zealand Deerstalkers' Association proposing the designation of certain areas in the Bay of Plenty as sambar deer recreational hunting areas, there has been increasing interest in the idea of sambar management. A management policy would prevent future overexploitation of sambar as has occurred in the past.

However, before a management policy can be formulated for a particular area, a research programme must be undertaken to determine the viability of the proposal. For sambar this would mean an investigation of a similar nature to this project and the following questions would need to be answered:

(a) How many animals inhabit the proposed recreational hunting area? Would the population be able to sustain continuous hunting pressure?

(b) What is the breeding status of the population? Would replacement match loss due to hunting?

(c) What forage species are eaten? Is there sufficient forage to maintain the population at the desired stocking level?

(d) How large are individual home ranges and territories? Is the proposed area large enough?

(e) Are the animals likely to become a problem and adversely affect the area?

Because of the relatively short research period (15 months), limited equipment and only a small herd among which disturbance had to be kept to an absolute minimum, the study had limitations. It was not for example possible to mark animals, night viewing equipment was not available and on average one animal was seen (often obscured or at considerable distance), for every 4 hours in the field. But it is hoped that this study will form the basis of future research into sambar deer in New Zealand.

8.6 Conclusions

The diet of sambar in the Moutoa study area varied seasonally, but this did not appear to be related to seasonal changes in the nutritional quality of forage. It seems therefore, that palatibility and/or availability of plant species determines the diet of animals in this area. Rank grasses and flax present in the reserve comprised the major dietary components.

The fact that the seven wire fence surrounding the flax reserve was no barrier to sambar, and yet improved pasture species occurred infrequently in faecal samples, indicates that competition between deer and stock for good pasture is minimal. However stock allowed access to the reserve do take deer forage.

The Moutoa population is a breeding one and if left undisturbed should be capable of sustaining itself. Breeding appears to occur throughout the year with two peaks in rutting activity over winter and late spring/early summer. This is in accord with the breeding biology of Australian sambar.

Hinds usually give birth to one fawn each year although twins have been recorded.

Stags seem to have a 12 month antler cycle as do other Cervidae, but the timing depends on the individual.

Rutting stags mark a territory around a central wallow area and these territories are avoided by other adult stags. Aggressive behaviour is rare, possibly due to visual and olfactory cues demarcating the territory.

Although both sexes use vocalisation as a means of communicating danger, it is rare for rutting stags to roar in New Zealand.

Herd structure appears to be fairly loose, being composed of small family groups, usually of a hind, yearling and fawn. Young stags tend to be seen in small groups of up to four animals, while mature stags are generally solitary. It would seem that during the rut hinds are attracted to a particular territory and are not actively herded as in red deer.

A study of their craniometry indicated several sexually dimorphic characters besides the presence of pedicles and antlers. New Zealand stags were found to have underspread antlers and are therefore likely to be racially different to Australian animals which tend to be overspread.

The phenotypes of a number of animals from the Bay of Plenty suggested possible sambar/rusa hybridisation, but this was not able to be verified using craniometric techniques.

Sambar are predominantly nocturnal. They require heavy understory cover and tend to avoid open areas. Their cautious nature and ability to readily adapt to changes in their environment have been major factors determining their survival for so many years despite persistent destruction of habitat, and severe hunting pressure.

APPENDIX 1

Common name	Scientific name
Annual mouse ear chickweed*	Cerastium glomeratum Thuill
Barley grass*#	Hordeum murinum L.
Beet	Beta spp.
Bellis daisy *#	Bellis perennis L.
Bitter sweet*	Solanum dulcamara L.
Black berry*#	Rubus fruticosus agg.
Bracken fern (member of) *#	Hypolepis tenuifolia (Forst.f) Bernh.
Broad leaved dock*#	Rumex obtusifolius L.
Broad leaved plantain*#	Plantago major L.
Brown top *#	Agrostis tenuis Sibth.
Cabbage tree *#	Cordyline australis (Forst.f.) Endl
Californian thistle *	Cirsium arvense (L) Scop.
Carex *#	Carex spp.
Catsear*	Leontodon taraxacoides (Vill.) Mérat
Chickweed *#	Stellaria media (L) Vill.
Clustered dock*	Rumex conglomeratus Murr.
Creeping bent *	Agrostis stolonifera L
Creeping buttercup *#	Ranunculus repens L.
Crested dogstail*#	Cynosurus cristatus L.
Dandelion *#	Taraxacum officinale Weber ex Wiggers
Eleocharis acuta*	Eleocharis acuta R.Br.
Field bindweed *#	Convolvulus arvensis L.
Field madder*	Sherardia arvensis L.
Flax *#	Phormium tenax J.R. et G. Forst.
Floating sweet grass *#	Glyceria declinata Bréb, G. fluitans (L) R. Br.
Goats rue *#	Galega officianalus L.
Hawkbit *	Leontodon taraxacoides (Vill.) Mérat
Hemlock *#	Conium maculatum L.
Italian ryegrass *#	Lolium multiflorum Lam.
Lotus major *#	Lotus pedunculatus Car.

Lupin (see Tree lupin)	
Mahoe	*Melicytus ramiflorus* J.R. *et* G. Forst.
Maize #	*Zea mays*
Manuka	*Leptospermum scoparium* J.R. *et* G. Forst.
Narrow leaved plantain *#	*Plantago lanceolata* L.
Pampas grass	*Cortaderia selloana* (Schult.) Asch *et* Graeb
Penny royal *	*Mentha pulegium* L.
Perrenial ryegrass *#	*Lolium perenne* L.
Poa annua *#	*Poa annua* L.
Poa pratensis *#	*Poa pratensis* L.
Poa trivialis *#	*Poa trivialis* L.
Polygoneum decipiens *	*Polygoneum decipiens* R. Br.
Poplar *#	*Populus* spp.
Potamogeton crispus *	*Potamogeton crispus* L.
Praire grass *#	*Bromus catharticus* Vahl (*B. unioloides auct*).
Prickly sow thistle *	*Sonchus asper*. L. Hill.
Radiata pine	*Pinus radiata* D. Don.
Ragwort *	*Senecio jacobaea* L.
Raupo *#	*Typha orientalis*.
Reed canarygrass *#	*Phalaris arundinacea* L.
Ripgut brome *#	*Bromus diandrus* Roth.
Ruppia polycarpa *	*Ruppia polycarpa* R. Mason.
Rush *#	*Juncus* spp.
Ryegrass (see Italian and Perennial ryegrass: H1 denotes hybrid of these two species)	
Sand spurrey *	*Spergularia rubra* (L)
Scirpus lacustris *	*Scirpus lacustris* L.
Scotch thistle *	*Cirisium vulgare* (Savi.) Ten.
Slender winged thistle *	*Carduus pycnocephalus* L.
Sow thistle *	*Sonchus oleraceus* (L).
Stinking mayweed *#	*Anthemis cotula* L.
Suckling clover *#	*Trifolium dubium* Sibth.
Swede	*Brassica rutabaga*
Sweet vernal *#	*Anthoxanthum odoratum* L.
Tall fescue *#	*Festuca arundinacea* Schreb.
Timothy *#	*Poa pratense* L.
Tree lupin *#	*Lupinus arboreus* Sims.

Appendix 1 continued

Turnip	*Brassica rapa*
Veronica serpyllifolia *	*Veronica serpyllifolia* L.
Water celery *	*Apium nodiflorum* (L.) Lag.
Water pepper *	*Polygonum hydropiper* L.
Water plantain *	*Alisma plantago - aquatica* L.
White clover *#	*Trifolium repens* L.
Willow *	*Salix* spp.
Willow weed *#	*Polygonum persicaria* L.
Winged thistle *	*Carduus tenuiflorus* Curt.
Wireweed *	*Polygonum aviculare* agg.
Yarrow *	*Achillea millefolium* L.
Yorkshire fog *#	*Holcus lanatus* L.

* Species found at Moutoa

\# Cuticle reference

APPENDIX 2

Monthly temperature and humidity recordings

	Mean maximum temperature	Mean minimum temperature	Mean maximum humidity	Mean minimum humidity
Feb	20.0	8.8	77.5	48.0
Mar	20.2	10.5	76.2	51.8
Apr	19.6	9.6	77.2	52.9
May	18.7	8.4	77.9	53.1
Jun	17.7	7.2	78.3	53.7
Jul	16.8	6.4	78.4	54.0
Aug	16.5	6.1	78.4	53.6
Sep	16.4	6.5	78.5	54.1
Oct	16.6	6.8	78.5	53.2
Nov	16.8	7.2	78.6	53.7
Dec	17.3	7.6	78.6	53.7
Jan	18.1	8.0	78.6	52.2
Feb	18.6	8.5	78.1	50.2

APPENDIX 3

Record of deer sightings and weather conditions at Moutoa.
(Cloudy = Cloud cover > 50%; Fine = cloud cover < 50%; Overcast = cloud cover > 50% plus periodic showers; Rain = continuous precipitation; Windy = blustery conditions)

Date	Stags	Hinds	Juveniles	Unidentified	Weather
3/1/80	0	1	0	1	Overcast
11/2/80	0	1	1	0	Cloudy/windy
12/2/80	1	2	0	0	Fine/windy
4/3/80	0	4	1	2	Cloudy
10/3/80	2	2	0	1	Fine/windy
11/380	2	3	0	1	Overcast
12/3/80	1	3	1	0	Rain
17/3/80	2	0	0	0	Overcast/windy
28/3/80	1	0	0	0	Rain
10/4/80	1	1	0	0	Rain/windy
23/4/80	0	1	1	4	Fine
29/4/80	0	0	0	1	Overcast/windy
30/4/80	2	2	0	3	Overcast
1/5/80	1	2	0	2	Fine
3/5/80	0	0	0	2	Overcast
4/5/80	0	0	0	4	Cloudy
8/5/80	0	3	0	0	Fine
19/5/80	0	0	1	2	Fine/windy
20/5/80	0	3	2	4	Cloudy
26/5/80	0	1	0	5	Cloudy
27/5/80	2	0	2	11	Cloudy
5/6/80	0	0	0	1	Overcast/windy
6/6/80	0	1	0	2	Cloudy
11/6/80	0	1	0	0	Cloudy
12/6/80	1	0	0	3	Cloudy
18/6/80	0	0	2	3	Fine
19/6/80	0	0	0	2	Fine
24/6/80	1	1	0	2	Overcast/windy
25/6/80	0	0	0	3	Overcast
1/7/80	1	0	1	3	Fine
2/7/80	0	0	0	2	Overcast
15/7/80	0	1	0	5	Fine/windy
16/7/80	0	1	0	2	Fine
21/7/80	0	0	0	2	Overcast
27/7/80	0	0	0	2	Cloudy
28/7/80	0	0	0	2	Cloudy
29/7/80	0	0	0	1	Fine
30/7/80	1	0	0	3	Cloudy
4/8/80	1	0	0	1	Fine
5/8/80	0	0	0	1	Overcast/windy
6/8/80	0	0	0	2	Cloudy/windy
11/8/80	0	0	0	3	Overcast/windy
12/8/80	0	0	0	2	Overcast/windy
13/8/80	0	0	0	2	Overcast/windy
18/8/80	0	0	0	3	Cloudy/windy
21/8/80	2	0	0	6	Rain
25/8/80	0	0	0	4	Overcast/windy

Appendix 3 continued

	Stag	Hind	Juvenile	Unidentified	Weather
1/ 9/80	0	0	0	5	Rain/windy
2/ 9 80	0	0	0	3	Overcast/windy
3/ 9/80	1	1	0	2	Cloudy
8/ 9/80	3	1	2	0	Overcast/windy
9/ 9/80	0	0	0	8	Overcast/windy
10/ 9/80	1	0	0	2	Overcast/windy
17/ 9/80	0	0	0	1	Overcast/windy
23/ 9/80	0	1	0	1	Overcast/windy
30/ 9/80	0	0	0	1	Overcast
1/10/80	0	0	1	2	Overcast
7/10/80	0	1	0	4	Fine
8/10/80	3	1	2	5	Fine
11/10/80	1	1	1	4	Cloudy
14/10/80	2	1	0	1	Fine
15/10/80	3	5	2	4	Overcast
16/10/80	1	2	1	1	Rain
21/10/80	1	2	0	0	Fine
22/10/80	1	2	0	5	Overcast
29/10/80	0	0	0	1	Overcast/windy
30/10/80	0	1	0	1	Overcast
4/11/80	1	0	0	1	Cloudy
5/11/80	1	1	0	0	Overcast
11/11/80	0	2	0	0	Rain
12/11/80	0	0	0	1	Cloudy
19/11/80	0	1	1	1	Overcast
20/11/80	1	0	0	0	Overcast
26/11/80	1	0	0	1	Overcast
2/12/80	1	0	0	0	Cloudy
10/12/80	0	2	0	1	Cloudy
21/12/80	1	0	0	0	Cloudy
4/ 1/81	1	1	1	0	Fine/windy
19/ 1/81	1	1	0	3	Cloudy
20/ 1/81	1	0	0	1	Cloudy
26/ 1/81	1	0	0	0	Fine
23/ 7/81	0	1	0	1	Cloudy
18/ 8/81	0	0	1	1	Fine/windy
Totals	49	62	24	167	

APPENDIX 4

Animals that died at Moutoa during study period

Date	Sex	Age	Cause
February 1980	Hind	3½ years	Unexplained (skull recovered)
18/3/80	Unknown	Unknown	Shot by poachers
circa 7/5/80	Hind	9 years	Shot by poachers (skull and rumen contents recovered)
16/6/80	Hind	Unknown	Shot by poachers *
16/6/80	Hind	Unknown	Shot by poachers *
22/7/80	Stag	Mature	Shot by poachers
22/7/80	Hind	Mature	Shot by poachers
22/7/80	Hind	8½ years	Shot by poachers (entire skeleton recovered: Plate 15)
July 1981	Stag	4 years	Shot by poachers (skull recovered)

* Unconfirmed

APPENDIX 5

Unit areas of forage components occurring in faeces collected each month

(For plant species:area = cuticle area)

Date	Dec 7/12/79	Jan 3/1/80	Feb 12/2/80	Mar 5/3/80	Apr 17/4/80	May 1/5/80	Jun 6/6/80	Jul 2/7/80	Aug 6/8/80	Sep 3/9/80	Oct 1/10/80	Nov 6/11	Dec 3 12 80	Jan 5/1/81	Feb 2/2/81
Barley grass*	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	0.02±0.02*	0.11±0.09*	N.D.	N.D.	N.D.	N.D.	N.D.
Cabbage tree	N.D.	N.D.	N.D.	N.D.	N.D.	0.09±0.09*	0.51±0.22	0.98±0.59*	0.71±0.15	0.85±0.23	0.37±0.15	0.30±0.12	N.D.	0.35±0.22*	0.05±0.05*
Chickweed	N.D.	0.03±0.03*	0.21±0.03	0.02±0.02*	0.42±0.17	0.73±0.24	1.1 ±0.3	0.29±0.10	N.D.	0.17±0.07	0.09±0.06*	N.D.	0.12±0.06*	0.15±0.07	0.10±0.10*
Fibre	19.4±0.4	17.1±2.7	18.7±1.8	21.1±2.5	22.5±0.9	19.9±1.7	16.7±1.4	19.2±1.8	18.7±1.6	18.1±0.8	15.2±1.3	21.7±1.0	16.2±1.5	19.9±0.4	25.4±0.9
Flax	N.D.	0.11±0.06*	0.80±0.22	0.23±0.15*	1.8 ± 0.4	3.6 ± 0.9	4.8 ± 0.4	6.6 ± 0.2	4.1 ±0.5	3.4 ± 0.6	3.9 ± 0.3	1.3 ±0.2	1.9 ± 0.4	2.4 ± 0.4	2.2 ± 0.3
Floating sweetgrass	10.3±0.8	5.1 ± 0.5	3.7 ± 0.4	2.9 ± 0.3	3.0 ±0.2	2.0 ± 0.5	0.84±0.21	1.2 ±0.3	0.59±0.14	0.74±0.29	1.3 ±0.4	3.5 ±0.3	5.1 ±0.4	5.4 ±0.3	6.3 ± 0.5
Poa sp	N.D.	N.D.	N.D.	N.D.	0.05±0.05*	0.12±0.12*	0.03±0.03*	0.15±0.10*	N.D.	0.18±0.08	0.11±0.08*	0.21±0.13*	N.D.	N.D.	N.D.
Poplar	4.9 ± 0.8	0.92±0.33	2.4 ± 0.5	1.8 ± 0.3	0.14±0.11*	0.02±0.02*	N.D.	N.D.	0.08±0.05*	0.06±0.06*	N.D.	0.16±0.10*	0.53±0.06	N.D.	0.20±0.07
Reed canary grass	0.04±0.04*	0.93±0.24	0.86±0.28	1.1 ±0.3	0.28±0.13	0.60±0.12	0.11±0.08*	N.D.	0.21±0.14*	0.21±0.07	0.66±0.31	1.2 ± 0.4	1.2 ±0.2	0.52±0.19	0.44±0.03
Resin	0.49±0.17	4.9 ± 0.4	4.1 ±0.2	3.9 ± 0.5	2.6 ± 0.5	1.3 ± 0.3	4.7 ± 0.5	3.3 ± 0.2	1.5 ± 0.08	6.6 ± 0.6	6.2 ± 0.5	4.6 ± 0.6	4.9 ± 0.2	2.2 ± 0.2	2.6 ± 0.3
Ryegrass	0.15±0.15*	0.04±0.04*	0.13±0.12*	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	0.02±0.02*	0.07±0.07*	0.08±0.06*	0.12±0.09*	0.18±0.08
Tall fescue	0.09±0.09*	N.D.	0.49±0.02	2.2 ±0.2	2.5 ± 0.3	2.1 ± 0.3	2.7 ± 0.4	3.4 ±0.7	3.1 ± 0.3	2.4 ± 0.6	0.88±0.44*	1.0 ±0.3	0.23±0.07	1.1 ± 0.3	1.5 ± 0.2
Unidentified	0.17±0.07	0.55±0.13*	0.36±0.09	0.25±0.13	0.36±0.09	0.28±0.05	0.13±0.08*	N.D.	0.08±0.05*	0.17±0.04	0.18±0.05	0.20±0.09	0.07±0.05*	0.09±0.05*	0.13±0.09*
Unidentified (a)	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	0.28±0.12	0.09±0.06*	0.08±0.06*	0.02±0.02*	0.10±0.10*	N.D.	0.02±0.02*	N.D.
Unidentified (b)	N.D.	2.7 ± 0.8	1.5 ±0.3	1.5 ±0.3	2.7 ± 0.7	4.2 ±0.9	4.0 ± 0.8	6.4 ±0.9	6.3 ± 0.8	4.3 ± 0.4	7.4 ± 1.3	4.3 ±1.1	7.5 ±1.4	3.5 ± 0.6	1.6 ± 0.3
Yorkshire fog	N.D.	N.D.	0.11±0.07*	0.40±0.07	0.16±0.10*	0.05±0.05*	0.02±0.02*	N.D.	N.D.	N.D.	N.D.	0.04±0.04*	0.27±0.09	0.44±0.27*	1.1 ± 0.4

N.D. = Not detected in sample

* $S.E. \geq \frac{\overline{x}}{2}$

APPENDIX 6

Crude Protein content (%) of forage species : Nitrogen values S.E. in brackets

	17/4/80	6/8/80	6/11/80	4/2/81
Chickweed	19.4 (3.11±0.01)	25.3 (4.05±0.08)	19.6 (3.13±0.01)	- -
Flax base	5.8 (0.92±0.05)*	6.4 (1.03±0.00)*	6.7 (1.07±0.00)*	6.5 (1.04±0.01)*
Floating sweet grass	23.1 (3.69±0.00)*	23.2 (3.71±0.01)	17.9 2.86±0.01)	13.1 (2.09±0.00)
Poplar bark	- -	4.1 (0.66±0.07)	9.6 (1.53±0.00)	3.7 (0.59±0.00)
Poplar twigs	7.3 (1.17±0.00)*	8.3 (1.33±0.00)	13.1 (2.09±0.01)	7.4 (1.19±0.03)*
Reed canarygrass	6.6 (1.06±0.00)	21.8 (3.49±0.00)*	22.3 (3.57±0.00)	12.1 1.94±0.01)
Ryegrass	20.6 (3.30±0.03)*	21.2 (3.39±0.02)	15.3 (2.45±0.01)	13.1 (2.09±0.01)
Tall fescue	13.9 (2.22±0.02)	17.1 (2.73±0.01)	15.2 (2.43±0.00)	12.6 (2.02±0.01)
Yorkshire fog	22.3 (3.56±0.00)*	22.4 (3.59±0.00)	18.7 (2.99±0.01)	10.1 (1.62±0.01)

* No significant difference at 0.05 probability level between this value and the following value.

APPENDIX 7

Energy content (Joules) of forage species

	17/4/80	6/8/80	6/11/80	4/2/81
Chickweed	15892±241	17541±314	–	–
Flax base	17982±196 *	18812±157	17769±7*	17832±33*
Floating sweet grass	18819±81 *	19437±200 *	19756±177	18945±40*
Poplar bark	–	18502±11*	18536±135*	18929±35
Poplar twigs	15835±935	19727±87	20303±95	19117±73
Reed canarygrass	17932±161	19060±298*	19588±109	18280±15*
Ryegrass	16581±88	18758±35*	18776±16*	18653±152
Tall fescue	18719±2 *	18646±48 *	18958±124	18442±20
Yorkshire fog	17855±158	19210±95*	19284±37	17638±2 *

* No significant different at 0.05 probability level between this value and the following value

APPENDIX 8

Acid Detergent Fibre content (%) of forage species.

	17/4/80	6/8/80	6/11/80	4/2/81
Chickweed	21.9±0.6 *	20.7±0.6	-	-
Flax base	34.7±1.3	21.9±1.4 *	23.9±0.9 *	26.2±0.6
Floating sweet grass	21.8±0.1 *	22.1±0.2	32.1±0.5 *	33.8±0.1
Poplar bark	-	47.5±0.7	55.2±1.1 *	49.3±1.3
Poplar twigs	42.4±0.5	57.9±0.5	52.2±0.2	61.1±0.6
Reed canarygrass	33.3±0.6	20.7±0.1	27.3±0.2	32.8±0.3 *
Ryegrass	20.1±0.3	23.8±0.4	26.3±0.1	30.9±0.2
Tall fescue	28.9±1.2 *	29.0±0.1	36.6±1.4 *	35.4±0.1
Yorkshire fog	20.6±0.1	24.7±0.9 *	24.2±0.6	38.2±0.2

* No significant difference at 0.05 probability level between this value and the following value

APPENDIX 9

Water content (%) of forage species

	17/4/80	6/8/80	6/11/80	4/2/81
Chickweed	92.9	92.6	90.9	-
Flax base	85.5	84.9	86.5	84.9
Floating sweet grass	81.8	81.1	81.1	65.1
Poplar bark	-	58.9	57.6	50.3
Poplar twigs	57.6	53.1	62.2	72.9
Reed canarygrass	61.1	79.2	80.5	66.3
Ryegrass	78.1	81.1	77.9	50.1
Tall fescue	74.5	76.7	79.1	65.5
Yorkshire fog	83.9	83.9	82.9	60.0

Appendix 10: New Zealand antler data (raw)

Manawatu sambar

NUMBER OF ANTLER....	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
SKULL NO	13	14	15	16	17	**	**	**	**	**	**	**	**	**	**	**	**	19	20	22
AGE OF STAG	4.5	4.0	7.0	6.5	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.5	8.0	4.0
LOCATION	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
NUMBER OF POINTS	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
OUTER CURVE LENGTH	45.0	36.0	58.5	69.5	55.0	55.0	71.0	63.5	71.0	58.5	78.0	91.0	83.0	76.0	71.0	71.0	68.5	0.0	70.0	35.0
CIRCUM. OF BEAM	9.5	9.0	15.5	14.0	12.0	12.5	13.5	12.5	15.0	12.5	15.0	15.0	14.0	13.5	15.0	12.5	13.5	12.0	12.0	7.0
TIP TO TIP WIDTH	57.0	28.5	63.5	77.0	56.0	0.0	0.0	0.0	0.0	0.0	71.0	101.5	103.0	0.0	54.5	78.0	65.0	0.0	66.5	33.0
WIDEST INSIDE WIDTH	43.5	26.0	43.0	54.0	50.5	0.0	0.0	0.0	0.0	0.0	60.0	61.0	72.5	0.0	41.5	59.0	54.5	49.0	68.0	28.0
WEIGHT OF ANTLER	0.0	0.0	0.0	0.0	0.0	1.1	1.4	1.1	1.8	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PEDICLE LENGTH	3.5	3.5	4.0	3.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	3.5	3.5
PEDICLE CIRCUM	10.5	10.0	15.0	17.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.0	13.5	10.5
BROWTINE LENGTH	23.0	13.5	40.0	33.0	27.0	30.5	29.0	28.5	33.0	30.5	24.0	44.0	36.0	35.5	32.0	35.0	32.5	34.5	28.5	14.0
LEFT OR RIGHT ANTLER	L	L	L	L	L	R	L	R	L	R	L	L	L	L	L	L	L	R	R	R

Rotorua sambar

NUMBER OF ANTLER....	1	2	3	4	5	6	7	8	9	10	11	12
SKULL NO	1	2	3	4	5	6	7	**	**	**	**	**
AGE OF STAG	10.5	0.0	0.0	8.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0
LOCATION	R	R	R	R	R	R	R	R	R	R	R	R
NUMBER OF POINTS	3	3	3	3	3	3	3	3	3	3	3	3
OUTER CURVE LENGTH	77.0	94.5	63.5	59.5	68.0	77.0	63.5	55.5	55.0	80.5	70.0	67.0
CIRCUM. OF BEAM	14.0	15.5	12.0	12.0	14.0	13.0	13.5	10.5	10.5	15.0	12.5	13.5
TIP TO TIP WIDTH	49.5	58.5	54.0	53.0	44.5	29.5	45.0	59.5	60.0	70.5	61.0	57.0
WIDEST INSIDE WIDTH	57.0	55.5	44.5	43.0	45.5	37.0	37.0	46.5	47.0	60.5	55.0	47.0
WEIGHT OF ANTLER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PEDICLE LENGTH	5.5	6.0	4.0	3.5	3.5	2.5	4.5	4.0	4.0	4.0	3.5	4.0
PEDICLE CIRCUM	16.5	14.0	12.5	12.5	14.5	18.5	16.5	12.5	12.0	15.5	13.5	15.0
BROWTINE LENGTH	34.5	36.0	23.0	25.5	32.5	36.0	32.0	23.0	23.0	39.0	31.0	20.0
LEFT OR RIGHT ANTLER	L	L	L	L	L	L	L	L	L	L	L	L

Rusa

NUMBER OF ANTLER....	1	2	3	4
SKULL NO	1	2	3	4
AGE OF STAG	0.0	6.5	10.0	0.0
LOCATION	R	R	R	R
NUMBER OF POINTS	3	3	3	3
OUTER CURVE LENGTH	67.0	46.5	61.0	30.0
CIRCUM. OF BEAM	10.0	9.0	11.0	7.0
TIP TO TIP WIDTH	42.0	31.0	40.5	24.0
WIDEST INSIDE WIDTH	39.5	28.5	37.0	22.5
WEIGHT OF ANTLER	0.0	0.0	0.0	0.0
PEDICLE LENGTH	4.5	2.5	4.5	2.2
PEDICLE CIRCUM	10.5	8.0	12.5	7.5
BROWTINE LENGTH	12.5	14.0	20.0	12.0
LEFT OR RIGHT ANTLER	L	L	L	L

Appendix 11: New Zealand cranial data (raw)

Manawatu sambar

Number of skull	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
SEX	F	F	F	F	F	F	F	F	F	M	M	M	M	M	M	M	M	M	M	M	F	M	F
AGE OF ANIMAL	6.5	3.5	9.0	3.0	13.0	8.5	6.0	8.0	8.0	3.5	5.0	****	4.5	4.0	7.0	11.0	5.5	1.0	6.5	8.0	4.5	4.0	14.0
CRANIAL CAVITY	350	330	360	320	350	350	370	360	340	300	310	345	360	350	360	420	360	300	380	365	335	***	360
BASAL LENGTH	29.6	28.4	30.2	25.3	29.1	28.9	28.3	29.2	29.8	25.4	27.8	****	29.2	27.2	29.7	35.5	27.6	23.0	29.6	29.7	28.7	****	29.5
VENTRAL NEUROCRANIUM	11.2	10.9	11.4	9.7	10.6	11.6	10.5	10.6	10.9	9.8	10.1	****	****	11.0	12.3	10.9	10.9	9.0	11.6	11.6	10.4	****	10.9
MAX TOOTH ROW LENGTH	11.2	10.9	10.5	8.9	9.9	10.9	10.0	9.8	10.0	10.1	19.0	****	11.4	10.5	10.3	11.0	10.9	8.6	10.9	19.9	10.9	11.4	10.2
MARGO ADENTALIS	5.8	5.4	5.9	4.6	6.6	5.7	5.6	6.0	6.5	5.1	5.5	***	5.8	5.1	5.9	7.0	6.2	4.7	5.3	5.6	5.6	5.1	6.0
LATERAL VISCEROCRANIUM	15.5	14.5	16.6	12.8	15.4	15.1	14.4	14.9	15.5	13.3	15.0	****	15.4	13.5	14.7	16.4	15.7	11.5	14.6	14.0	14.7	14.5	15.2
LATERAL NEUROCRANIUM	17.7	17.1	17.8	16.1	17.4	17.2	17.1	17.9	17.3	16.0	17.6	****	18.1	17.6	18.9	19.6	18.9	15.7	19.4	18.2	16.5	19.2	18.2
FACIAL TUBERS	11.5	10.9	11.1	9.2	11.4	11.3	10.9	11.2	11.2	9.8	11.2	****	11.1	10.4	11.7	11.8	11.1	8.8	11.6	11.6	11.2	10.9	11.6
MAX TOOTH ROW WIDTH	10.3	9.9	10.8	8.9	10.2	10.6	9.8	9.8	9.7	9.3	9.9	****	10.2	10.0	10.8	10.5	10.2	8.8	10.5	10.7	10.3	10.2	10.5
OCCIPITAL CONDYLE WIDTH	6.8	6.4	6.7	6.8	7.0	6.7	6.7	7.1	7.1	6.9	7.3	7.4	7.5	7.1	7.1	7.7	7.5	***	7.9	7.8	6.9	***	7.0
CANINE WIDTH	5.5	5.0	5.4	4.5	4.9	5.2	4.9	***	5.6	4.5	5.3	***	5.8	***	5.7	5.0	5.6	4.8	5.9	5.8	5.5	5.8	5.3
NASAL CAVITY CIRCUM	18.6	18.1	19.4	****	****	17.4	17.6	****	17.6	17.2	19.1	****	18.3	****	19.1	20.0	19.8	****	18.7	18.5	17.1	17.8	19.0
NASAL CAVITY DEPTH	6.1	7.8	8.9	7.3	8.3	8.1	7.7	8.3	7.9	7.6	7.3	***	***	7.9	8.4	9.8	9.2	7.0	9.3	9.9	7.7	8.9	8.1
ANTERIOR ORBITAL WIDTH	9.3	8.9	9.3	8.1	9.9	9.5	9.3	9.9	9.4	8.3	9.6	9.9	10.8	9.6	10.5	12.5	10.8	7.5	10.9	10.4	9.2	9.9	9.8
POSTERIOR ORBITAL WIDTH	14.3	13.9	14.6	15.1	14.1	14.5	14.2	14.4	14.7	13.0	14.5	14.6	15.2	14.7	15.5	16.0	14.8	14.2	15.2	14.9	14.1	14.9	14.7

Rotorua sambar

Number of skull	1	2	3	4	5	6	7
SEX	M	M	M	M	M	M	M
AGE OF ANIMAL	10.5	****	****	8.0	****	7.5	****
CRANIAL CAVITY	350	***	***	***	***	320	***
BASAL LENGTH	30.9	****	****	25.0	****	33.0	****
VENTRAL NEUROCRANIUM	11.6	****	****	12.0	****	11.5	****
MAX TOOTH ROW LENGTH	10.6	****	****	9.9	****	10.2	****
MARGO ADENTALIS	6.2	***	***	5.7	***	5.6	***
LATERAL VISCEROCRANIUM	15.9	****	****	13.9	15.1	14.3	****
LATERAL NEUROCRANIUM	19.0	10.2	15.7	17.5	17.3	19.6	****
FACIAL TUBERS	10.3	****	****	10.6	11.4	12.6	****
MAX TOOTH ROW WIDTH	10.4	****	****	10.6	****	11.0	****
OCCIPITAL CONDYLE WIDTH	6.7	***	***	***	***	7.2	7.3
CANINE WIDTH	5.7	***	***	5.5	5.3	5.6	***
NASAL CAVITY CIRCUM	21.6	****	****	17.5	13.5	23.0	****
NASAL CAVITY DEPTH	9.8	***	***	7.6	***	8.9	***
ANTERIOR ORBITAL WIDTH	11.5	11.1	10.6	10.1	11.0	11.5	****
POSTERIOR ORBITAL WIDTH	15.8	****	****	14.7	****	15.5	****

Rusa

Number of skull	1	2	3	4
SEX	M	M	M	M
AGE OF ANIMAL	****	6.5	10.0	****
CRANIAL CAVITY	***	***	***	***
BASAL LENGTH	20.9	****	****	****
VENTRAL NEUROCRANIUM	****	****	****	****
MAX TOOTH ROW LENGTH	8.1	8.2	7.3	****
MARGO ADENTALIS	4.8	4.6	4.2	***
LATERAL VISCEROCRANIUM	11.8	11.9	11.2	****
LATERAL NEUROCRANIUM	15.3	13.1	15.6	12.9
FACIAL TUBERS	10.2	9.7	9.6	****
MAX TOOTH ROW WIDTH	8.7	8.9	8.6	****
OCCIPITAL CONDYLE WIDTH	***	***	***	***
CANINE WIDTH	4.7	4.9	4.6	***
NASAL CAVITY CIRCUM	16.8	16.0	15.5	****
NASAL CAVITY DEPTH	6.9	6.7	6.5	***
ANTERIOR ORBITAL WIDTH	9.9	9.7	9.8	7.9
POSTERIOR ORBITAL WIDTH	12.9	****	12.4	****

REFERENCES

ADAMS, L. (1957) A way to analyse herbivore food habits by fecal examination. Transactions of North American Wildlife Conference 22: 152-159

ADAMS, L., O'REGAN, W.G., and DUNAWAY, D.J. (1962) Analysis of forage consumption by fecal examination. Journal of Wildlife Management 26: (1): 108-111

ALKON, P. (1961) Nutritional and acceptability values of hardwood slash as winter deer browse. Journal of Wildlife Management 25 (1): 77-81

ANTHONY, R.G. and SMITH, N.S. (1974) Comparison of rumen and fecal analysis to describe deer diets. Journal of Wildlife Management 38 (3): 535-540

ASDELL, S.A. (1946) Patterns of Mammalian Reproduction. Comstock Publishing Co. Inc. U.S.A.

BAILEY, J. (1967) Sampling deer browse for crude protein. Journal of Wildlife Management 31 (3): 437-442

BAKER, S. (1890) Wild beasts and their ways. London.

BANFIELD, A.W.F. (1949) An irruption of elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management. 13 (1): 127-134

BATCHELER, C.L. and McLENNAN, M.J. (1977) Craniometric study of allometry, adaptation and hybridism of red deer (Cervus elaphus scoticus, L.) and wapiti (C.e. nelsoni, Bailey) in Fiordland, New Zealand. Proceedings of the New Zealand Ecological Society 24: 57-75

BAUMGARTNER, L.L. and MARTIN, A.C. (1939) Plant histology as an aid in squirrel food-habits studies. Journal of Wildlife Management 3: 266-268

BENTLEY, A. (1978) An introduction to the deer of Australia - with special reference to Victoria. Koetong Edition. Koetong Trust Service Fund. Forests Commission of Victoria, Melbourne.

BLAIR, R.M. and BRUNETT, L.E. (1980) Seasonal browse selection by deer in a southern pine-hardwood habitat. Journal of Wildlife Management 44: 79-88

BLANFORD, W. (1888-91) The fauna of British India: Mammalia. London.

BRANDER, A. (1923) Wild animals in Central India. London.

BRANDER, A. (1944) Breeding season of the Indian sambar. Journal of Bombay Natural History Society 44 (4): p. 587

BUBENIK, G.A., BUBENIK, A.B., BROWN, G.M. and WILSON, D.A. (1975) The role of sex hormones in the growth of bone tissue: 1 Endocrine and metabolic effects of antiandrogen therapy. Journal of Experimental Zoology 194: 349-358

BURNS, J.C. (1978) Antiquality factors as related to forage quality. Journal of Dairy Science 61: 1809-1820

BURTON, G.W., KNOX, F.E. and BEARDSLEY, D.W. (1964) Effect of age on the chemical composition, palatability and digestability of grass leaves. Agronomy Journal 56: 160-161

CAHALANE, V.H. (1939) Deer of the World. The National Geographic Magazine LXXVI (4): 463-510

CAUGHLEY, G. (1971) An investigation of hybridization between free-ranging wapiti and red deer in New Zealand. New Zealand Journal of Science 14: 993-1008

CHAPLIN, R.E. (1977) Deer. Blandford Mammal Series. Blandford Press Ltd.

CHURCHER, C.S. (1960) Cranial variation in the North American red fox. Journal of Mammalogy 41: 349-360

COMBER, E. (1904) Breeding seasons of big game. Journal of Bombay Natural History Society 16 (1): 176-179

COWAN, R.L., JORDAN, J.S., GRIMES, J.L., GILL, J.D. (1970) Comparative nutritive values of forage species. In Range and Wildlife Habitat Evaluation - A Research Symposium. U.S. Department of Agriculture Miscellaneous Publication No. 1147.

CRANDALL, L. (1964) The management of wild animals in captivity. Chicago.

CROCKER, B.H. (1959) A method of estimating the botanical composition of the diet of sheep. New Zealand Journal of Agricultural Research 2: 72-85

DANIEL, M. (1965) Sambar deer. Unpublished paper.

DARLING, F.F. (1937) A Herd of Red Deer. London, Oxford University Press.

DEARDEN, B.L., PEGAU, R.E. and HANSEN, R.M. (1975) Precision of microhistological estimates of ruminant food habits. Journal of Wildlife Management 39: 402-407.

DE BEER (1937) The Development of the Vertebrate Skull. Oxford University Press.

DEOL, M.S. (1955) Genetical studies on the skeleton of the mouse: XIV Minor variation of the skull. Journal of Genetics 53: 498-514

DHALIWAL, S.S. (1962) Studies on body measurements and skeletal variations of two taxa of Rattus rattus in Malaya. Journal of Mammalogy 43: 249-261.

DIETZ, D.R. (1970) Animal production and forage quality. In Range and Wildlife Habitat Evaluation - A Research Symposium. U.S. Department of Agriculture Miscellaneous Publication No 1147.

DONNE, T.E. (1924) The Game Animals of New Zealand. John Murray, London.

DOUGLAS, M.J.W. (1969) Ageing of deer by dental cement layers. In Journal of Mammalogy 50 (3): p678

DOUGLAS, M.J.W. (1970) Dental cement layers as criteria of age for deer in New Zealand with emphasis on red deer, Cervus elaphus. New Zealand Journal of Science 13: 352-358

DRAISMA, M. (1977) Data analysis - Sambar deer: sambar antler data 1970-76. Australian Deer 2 (6): 15-22

DRAISMA, M. (1979) Some Aspects of the Biology of Wild Sambar in Victoria, Australia. Unpublished paper presented at New Zealand Deerstalkers' Association International Wildlife Forum.

DRAWE, D.L. and THADIS, W.B. (1968) Forage ratings for deer and cattle on the Welder Wildlife Refuge. Journal of Range Management 21 (4): 225-228

DROZDZ, A. (1979) Seasonal intake and digestibility of natural foods by roe deer. Acta Theriologica 24: p.137.

DUNHAM, K.M. (1980) The diet of Impala in the Sengwa Wildlife Research Area, Rhodesia. Journal of Zoology 192 (1): 41-57

DUNNET, G.M., HARVIE, A.E. and SMITH, T.J. (1973) Estimating the proportions of various leaves in the diet of the opossum Trichosurus vulpecula Kerr, by faecal analysis. Journal of Applied Ecology 10: 737-745

DUSI, J.L. (1949) Methods for the determination of food habits by plant microtechniques and histology and their application to cottontail rabbits. Journal of Wildlife Management 13: 295-298

DUSI, J.L. (1952) Food habits of several populations of cottontail rabbits in Ohio. Journal of Wildlife Management 16: 180-186

DZIECIOLOWSKI, R. (1970) Foods of the red deer as determined by rumen content analysis. Acta Theriologica 15 (6): 89-110

EBERHARDT, L.L. (1969) Population estimates from recapture frequencies. Journal of Wildlife Management 33 (1): 28-29

EBERHARDT, L.L. (1978) Transect methods for population studies. Journal of Wildlife Management 42 (1): 1-31

ENVIRONMENTAL IMPACT REPORT (1976) Land Development, Moutoa Farm Settlement. Department of Lands and Survey.

ESLER, A.E. (1978) Botany of the Manawatu District of New Zealand. New Zealand Department of Scientific and Industrial Research Information Series No 127.

EVANS, W.E. (1976) North Island Hunter. Swiftcopy Centre Ltd. Palmerston North, New Zealand.

FARMER, A.P. (1965) The Sambar Deer (Cervus unicolor). Unpublished Forest Service Report.

FINN, F. (1929) Sterndale's Mammalia of India. Calcutta.

FITZGERALD, A.E. and WADDINGTON, D.C. (1979) Comparison of two methods of faecal analysis of herbivore diet. Journal of Wildlife Management 43 (2): 468-473

FITZGERALD, A.E. and WARDLE, P. (1979) Food of the opossum Trichosurus vulpecula (Kerr) in the Waiho Valley, South Westland. New Zealand Journal of Zoology 6 (2): 339-345.

FLETCHER, F. (1911) Sport on the Nilgiris and in Wynaad. London.

FORSYTH, W. (1889) The Highlands of Central India. London.

FREEDMANN, L. (1963) A biometric study of Papio cynocephalus skulls from Northern Rhodesia and Nyasaland. Journal of Mammalogy 44: 24-43

GASTLER, G.F., MOXON, A.L., McKEAN, W.T. (1951) Composition of some plants eaten by deer in the Black Hills of South Dakota. Journal of Wildlife Management 15: 352-357

GRAF, W. (1956) Territorialism in deer. Journal of Mammalogy 37 (2): 165-170

HALLS, L.K. (1970) Nutrient requirements of livestock and game. Range and Wildlife Habitat Evaluation - A Research Symposium. U.S. Department of Agriculture Miscellaneous Publication No 1147.

HANCOCK, N.V. and LOW, J.B. (1956) Ageing of Rocky Mountain elk Cervus canadensis nelsoni by dentition. Utah State Department of Fish and Game.

HANSSON, L. (1970) Methods of morphological diet micro-analysis in rodents. Oikos 21: 255-266

HARNETT, A. (1979) Manawatu sambar deer. Unpublished article.

HARRIS, L.H. (1966) Hunting Sambar Deer. New Zealand Forest Service, Wellington.

HARRISON, M. (1979) Sambar. Chapter in Deer in Australia. Published by Deer Advisory Council of Victoria c/o Fisheries and Wildlife Division Ministry for Conservation, Melbourne.

HEGG, O. (1961) Analysen von Grosswildkot aus dem schweizerischen National park zur ermittlung der nahrungszusammensetzung. [Analyses of big-game droppings to determine their dietary composition in the Swiss National Park.] Revue Suisse de Zoologie 68 (12): 156-165

HERCUS, B.J. (1960) Plant cuticle as an aid to determining the diet of grazing animals. Proceedings of the 8th International Grasslands Congress: 443-447

HOBBS, N.T., BAKER, D.L., ELLIS, J.E. and SWIFT, D.M. (1981) Composition and quality of elk winter diets in Colorado. Journal of Wildlife Management 45 (1): 156-171

HORWITZ, W., CHICHILO, P., REYNOLDS, H. (Editors). (1970) Official methods of analysis of the Association of Official Analytical Chemists. 11th ed. Association of Official Analytical Chemists, Washington.

HUMPHRIES, I. and ROWLER, D. (1976) Data analysis - Sambar deer: Ageing of sambar deer. Australian Deer 1 (4): 3-7

HUNT, H.M. (1979) Summer, autumn and winter diets of elk in Saskatchewan. Canadian Field-Naturalist 93 (3): 282-287

HURD, R.M. and BLASER, R.E. (1962) Palatability of herbage. In Pastures and Range Research Techniques pp65-69. Comstock Publishing Co. Inc. U.S.A.

JACKSON, J. (1980) The annual diet of the roe deer in the New Forest, Hampshire, as determined by rumen content analysis. Journal of Zoology 192 (1): 71-83

KESSLER, W.B., KASWORM, W.F. and BODIE, W.L. (1981) Three methods compared for analysis of pronghorn diets. Journal of Wildlife Management 45 (3): 612-619

KORSCHGEN, L.J. (1962) Foods of Missouri deer with some management implications. Journal of Wildlife Management 26: 164-172

KREBS, J.R. and DAVIES, N.B. (1978) Behavioural Ecology. An evolutionary approach. Blackwell Scientific Publications.

LEOPOLD, A.S. (1950) Deer in relation to plant successions. Journal of Foresty 48 (10): 675-678

LEOPOLD, A.S., RINEY, T., McCAIN, R., and TEVIS, L. Jr. (1951) The Jawbone Deer Herd. State of California Department of Natural Resources Division of Fish and Game. Game Bulletin No 4.

LINCOLN, G.A. (1971) The seasonal reproductive changes in the red deer stag. Journal of Zoology 163: 105-123

LOGAN, I.R. (1965) The Sambur Deer (Cervus unicolor). Unpublished Forest Service Report.

LOOMIS, F.B. (1928)
(Quoted by Van Bemmel, 1949) On the taxonomy of rusine deer. American Journal of Science 16 (5): 534-535

LOWE, V.P. (1967) Teeth as indicators of age with special reference to red deer (Cervus elaphus L) on Rhum. Journal of Animal Ecology 38 (2): 425-457

LYDEKKER, R. (1898) The Deer of All Lands - A History of the Family Cervidae Living and Extinct. Rowland Ward Ltd. London.

MALECHEK, J.C. (1966) Cattle diets on native and seeded ranges in the ponderosa pine zone of Colorado. U.S. Forest Service, U.S. Department of Agriculture, Res. Note RM-77.

McCAFFERY, K.R., TRANETZKI, J. and PIECHURA, J. (1974) Summer foods of deer in Northern Wisconsin. Journal of Wildlife Management 38 (2): 215-219

MEDIN, D.E. (1970) Stomach content analysis: collections from wild herbivores and birds. In Range and Wildlife Habitat Evaluation - A Research Symposium. U.S. Department of Agriculture Miscellaneous Publication No. 1147.

MILLS, J.A. and MARK, A.F. (1977) Food preference of Takahe in Fiordland National Park, New Zealand and the effect of competition from introduced red deer. Journal of Animal Ecology 46: 939-958

MITCHELL, B (1963) Determination of age in Scottish red deer from growth layers in dental cement. Nature 198: 350-351

MITCHELL, B (1967) Ageing of red deer from dental cement. Journal of Animal Ecology 36: 279-293

MORRIS, R. (1938) 'Stamping grounds' and 'sore neck' in sambar. Journal of Bombay Natural History Society 40 (3): 560-561

MORRISON, P and HARRIS, L.H. (1974) Forest Wildlife. Published by Wildlife Service, Department of Internal Affairs and New Zealand Forest Service, Wellington, New Zealand.

MULLER-SCHWARZE, D. (1971) Pheremones in blacktailed deer. Animal Behaviour 19: 141-152

MURIE, O.J. (1951) The elk of North America. Stackpole Co., Harrisburg Pa.

MURPHY, J.M. (1978) New Zealand Exhibition of Hunting. New Zealand Wildlife 7: 5-24

MYSTKOWSKA, T. (1966) Morphological variability of the skull and body weight of the red deer. Acta Theriologica 11: 129-194

NEFF, D.J. (1968) The pellet-group count technique for big game trend, census and distribution: a review. Journal of Wildlife Management 32: 597-614

NORRIS, J.J. (1943) Botanical analyses of stomach contents as a method of determining forage consumption of range sheep. Ecology 24: 244-251

PEARSON, K and DAVIN, A.G. (1924) 'On the Biometric Constants of the Human Skull.' Biometrika 16: 328-363

PEKELHARING, C.J. (1969) Cementum deposition as an age indicator in the Brush-tailed Possum. Paper available from Forest Research Institute P O Box 106, Rangiora, New Zealand.

PHILLIPS, J.C. (1920) Skull measurements in the Northern Virginia deer. Journal of Mammalogy 1: 130-133

POWERSCOURT, LORD (1884)
(Quoted by Lydekker, 1898) On the acclimatization of sambar deer at Powerscourt. Proceedings of the Zoological Society (London) 1884).

PRATER, S. (1934) The Wild Animals of the Indian Empire. Madras.

PUGLISI, M.J., LISCINSKY, S.A. and HARLOW, R.F. (1978) An improved methodology of rumen content analysis for white tailed deer. Journal of Wildlife Management 42 (2): 397-403.

QUIMBY, D.C. and GAAB, J.E. (1957) Mandibular dentition as an age indicator in Rocky Mountain elk. Journal of Wildlife Management 21 (4): 435-451

RANSOM, A.B. (1966) Determining age of white tailed deer from layers in cementum of molars. Journal of Wildlife Management 30 (1): 197-199

RAYMOND, W.F. (1969) The nutritive values of forage crops. Advances in Agronomy 21: 1-100.

REYNOLDS, H.W., HANSEN, R.M. and PEDEN, D.G. (1978) Diets of the Slave River lowland bison herd, Northwest Territories, Canada. Journal of Wildlife Management 42: 581-590

RINEY, T. (1951) Standard terminology for deer teeth. Journal of Wildlife Management 15 (1): 99-101

RINEY, T. (1955) Identification of big game animals in New Zealand. Dominion Museum Handbook No. 4.

RINEY, T. (1957a) Sambar (Cervus unicolor) in sand hill country. Journal of the New Zealand Ecological Society 5: 26-27

RINEY, T. (1957b) Milk tooth replacement in red deer. Unpublished Forest Service Report.

ROBEL, R.J. and WATT, P.G. (1970) Comparison of volumetric and point-analysis procedures to describe deer food habits. Journal of Wildlife Management 34 (1): 210-213

ROGERS, J.A. and DAVIES, G.E. (1973) The growth and chemical composition of four grass species in relation to soil moisture and aeration factors. Journal of Ecology 61: 455-472

ROGERSON, S.J., STEVENS, E.J., and HUGHES, J.G. (1976). An improved technique for identification of plant cuticle in animal faeces. New Zealand Journal of Botany 14: 117-119

RUSSELL, C. (1900) Bullet and shot in Indian forest, plain and hill. London.

SCHALLER, G.B. (1967) The Deer and the Tiger; a study of wildlife in India. University of Chicago Press, Chicago.

SCLATER, P. (1863) Record of the period of gestation of certain ruminants which bred in the society's gardens. Proceedings of the Zoological Society (London) 1863: 230-231

SCOTCHER, J.S.B. (1979) A review of faecal analysis techniques for determining the diet of wild grazing herbivores. Proceedings of the Grassland Society of South Africa 14: 131-136

SCOTT, T.G. (1941) Methods of computation in fecal analysis with reference to red fox. Iowa State College Journal of Science 15: 279-285

SEGELQUIST, C.A. and PENNINGTON, R.C. (1968) Deer browse in the Ouachita forest in Oklahoma. Journal of Wildlife Management 32 (3): 623-626

SHORT, H.L., DIETZ, D.R., and REMMENGA, E.E. (1966). Selected nutrients in mule deer browse plants. Ecology 47 (2): 222-229

SINGE, P. (1959) The Old Dholpur Sanctuary. The Cheetal 1 (2): 3-6.

SKIPWORTH, J.P. (1972) Faecal-analysis: Methods and potential. Unpublished paper presented to New Zealand Ecological Society.

SLATER, J. and JONES, R.J. (1971) Estimation of the diets selected by grazing animals from microscopic analysis of the faeces - a warning. The Journal of the Australian Institute of Agricultural Science 1971: 238-239.

SMITH, H. (1827) In Griffith's Animal Kingdom, Volume V.

SMITH, M.C.T. (1974) Biology and Management of the wapiti (Cervus elaphus nelsoni) of Fiordland New Zealand. Published by New Zealand Deerstalkers Association.

SMITH, A.D. and SHANDRUK, L.J. (1979) Comparison of fecal, rumen and utilization methods for ascertaining pronghorn diets. Journal of Range Management 32 (4): 275-279

STAINES, B.W. (1976) Experiments with rumen-canulated red deer to evaluate rumen analysis. Journal of Wildlife Management 40: 371-373

STEWART, D. (1967) Analysis of plant epidermis in faeces in a technique unique for studying the food preferences of grazing herbivores. Journal of Applied Ecology 4: 83-111

STEWART, D. and STEWART, J. (1970) Food preference data by faecal analysis for African plains ungulates. Journal of Mammalogy 51: No 4, supplement: 10-400

STOCKLEY, V. (1913) Big game shooting in India, Burma and Somaliland. London.

STORR, G.M. (1961) Microscopic analysis of faeces, a technique for ascertaining the diet of herbivorous mammals. Australian Journal of Biological Science 14: 157-164

SULLIVAN, J. (1962) Evaluation of forage crops by chemical analysis: A critique. Agronomy Journal 54 (6): 511-515

SWIFT, R.W. (1948) Deer select most nutritious forages. Journal of Wildlife Management 12: 109-110

TAYLOR, P.G. (1971) Aspects of the biology of the Hog Deer (Axis porcinus Zimmerman). PhD. Thesis, Department of Zoology, Monash University Australia.

TAYLOR, R.H. (1969) Self-attaching collars for marking red deer in New Zealand. Deer 1 (10): 404-407

THOM, W. (1937) The Malayan or Burmese sambar (Rusa unicolor equinus) Journal of Bombay Natural History Society 39 (2): 309-319

THOMSON, G.M. (1922) The Naturalization of Animals and Plants in New Zealand. Cambridge University Press. England.

TILTON, M.E. and WILLARD, E.E. (1981) Winter food habits of mountain sheep in Montana. Journal of Wildlife Management 45 (2): 548-553

TODD, J.W. and HANSEN, R.M. (1973) Plant fragments in the feces of big horns as indicators of food habits. Journal of Wildlife Management 37 (3): 363-366.

VAN BEMMEL, A.C.V. (1949) Revision of the Rusine Deer in the Indo-Australian Archipelago. Buitenzorg, Treubia 20 (2): 191-262

VAN SOEST, P.J. (1963) I: Use of detergents in the analysis of fibrous feeds. II: A rapid method for the determination of fiber and lignin. Journal of the Association of Official Analytical Chemists 46: 829-835

VAN SOEST, P.J. (1966) Non-nutritive residues: A system of analysis for replacement of crude fiber. Journal of the Association of Official Analytical Chemists 49 (3): 546-551

VAVRA, M., RICE, R.W. and HANSEN, R.M. (1978) A comparison of esophageal fistula and fecal material to determine steer diets. Journal of Range Management 31: 11-13

VERME, L.J. and ULLREY, D.E. (1972) Feeding and nutrition of deer. In The Digestive Physiology and Nutrition of Ruminants. Practical Nutrition 3: 275-291. Published by D.C. Church, Corvallis, Oregon.

VOTH, E.H. and BLACK, H.C. (1973) A histologic technique for determining feeding habits of small herbivores. Journal of Wildlife Management 37: 223-231

VOLKMANN, N.J., ZEMANEK, K.F., and MULLER-SCHWARZE, D. (1978) Antorbital and forehead secretions of black-tailed deer (*Odocoileus hemionus columbianus*): Their role in age class recognition. *Animal Behaviour* *26*: 1098- 1106

WALKER, H.M. and LEV, J. (1969) *Elementary Statistical Methods.* 3rd Edition. Holt, Rinehart and Winston, Inc. U.S.A.

WARD, A.L. (1970) Stomach content and fecal analysis: Methods of forage identification. In Range and Wildlife Habitat Evaluation - A Research Symposium. U.S. Department of Agriculture Miscellaneous Publication No. 1147.

WHITEHEAD, G.K. (1972) Deer of the World. Published by Constable and Company Ltd.

WILLIAMS, O.B. (1969) An improved technique for the identification of plant fragments in herbivore feces. *Journal of Range Management* *22*: 51-52

WODZICKI, K.A. (1950) Introduced Mammals of New Zealand. New Zealand Department of Scientific and Industrial Research. Bulletin No. 98.

WODZICKI, K.A. (1961) Ecology and management of introduced ungulates in New Zealand. *Extrait de La Terre et la Vie* *1*: 130-157

WOLFE, M.L. (1969) Age determination in moose from cemental layers of molar teeth. *Journal of Wildlife Management* *33* (2): 428-431

YABLOKOV, A.V. (1974) Variability of Mammals (Izmenchivost' Mlekopitayushchikh) Translated version published by Amerind Publishing Co. Ltd. New Delhi: For Smithsonian Institution and National Science Foundation.

ZYZNAR, E. and URNESS, P.J. (1969) Qualitative identification of forage remnants in deer feces. *Journal of Wildlife Management* *33* (3): 506-510