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THE USE OF ANATOMICAL FEATURES OF THE STOMACH TO  
INVESTIGATE THE NUTRITIONAL STATUS OF DEER POPULATIONS

A thesis presented in partial fulfilment of the requirements

for the degree

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Roger Graham Lentle

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## ABSTRACT

A feasibility study is undertaken for the development of indices recording interaction of individual ruminant herbivores with their nutritional environment with a view to their use as an individual based game management method. A current need for individual based methods having short response times is highlighted by a review contrasting population based and individual based methods of game management. Features desirable in a short time based individual method are discussed. Techniques which quantify the response of inbuilt mechanisms of nutritional thrift that operate in ruminants in response to declining quality of diet, (which I term "intrinsic nutritional optimisation") are reviewed from a viewpoint of their potential as tools for game management.

Methods which record change in response to diet of rumen volume, papillary and omasal anatomical characteristics, are examined. Techniques that utilise simple anatomical parameters i.e. papillary length, papillary width, papillary site, omasal weight, omasal volume, omasal laminar area and omasal laminar number are favoured.

A study of the extent of rumen wall shrinkage during preservation in formalin at various sites in wild red deer (Cervus elaphus), was undertaken. This demonstrated a degree of unpredictable variability sufficient to cast doubt on the accuracy of papillary density measurements such as are incorporated into FISA values.

In these studies the effect of differing diet was evaluated using wild red deer as representative of an 'intermediate feeder' browsing and grazing habit, farmed red deer as representative of an obligate 'bulk feeder' grazing habit and wild fallow deer (Cervus dama) as representative of voluntary "bulk feeder grazing habit.

A multivariate analysis of rumen papillary size at six objectively defined

sample sites in wild and farmed red deer and in wild fallow deer was undertaken. Three significant axes were generated, overall papillary size, overall papillary shape and site specific papillation. These responded differently to changes in age, sex, diet and species. The results supported previous descriptive work demonstrating that papillation at certain sites varied with diet and that overall papillary size increased with age. However the rate of increase of papillary size was shown to vary according to the sex in concordance with known differences in bionomic strategy. Overall papillary shape was influenced solely by species.

A multivariate analysis of omasal anatomical characteristics including laminar number and area, from wild and farmed red deer and from wild fallow deer was undertaken. Two axes were generated, overall size and overall leafiness. The latter axis showed significantly more variance in "intermediate feeder" wild red deer than in farmed red deer or in "roughage feeder" wild fallow deer.

Rumen content analysis was carried out concurrent with other studies. As with the papillary analysis, there was no significant seasonal variation in wild deer samples, further supporting a hypothesis of little seasonal variation of dietary quality at population densities well below carrying capacity.

A jaw length condition index was derived using Weibull curves derived from population samples obtained two years prior to the current study. Whilst these curves were shown to give a good description of the jaw length condition index distribution of the current population, there was no significant correlation of the index values with results from the papillary or omasal study. Possible explanations for this were considered. Firstly that the methods recorded different aspects of nutrition. Secondly that the jaw length index exhibited a cumulative damping of sensitivity as a consequence of progressive accumulation of non demarcated annual growth increments, a problem that did not occur in indices such as the site specific papillation factor, where there was no age related

increase.

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# THE USE OF ANATOMICAL FEATURES OF THE STOMACH TO INVESTIGATE THE NUTRITIONAL STATUS OF DEER POPULATIONS

M.Sc. Thesis R.G.Lentle

## CHAPTER 1

### INTRODUCTION

The purpose of this thesis was to undertake a feasibility study of the use of rumen anatomical features as an aid to deer management. Such methods may offer distinctive advantages. These are best seen in the light of a review of existing management techniques.

#### 1.1 GAME ANIMAL MANAGEMENT

##### 1.1.1 DEFINITION

Game animal management defined by Robinson and Bolen (1989) as "The husbandry and regulation of populations hunted for sport" is now more properly included in the broader realm of wildlife management. Wildlife management includes the autecological (sensu Krebs 1985) attributes of the game animal species in question and the synecological considerations of associated ecosystem and community welfare.

##### 1.1.2 AIMS

Hickey (1974) expressed the fear that game animal management, in conquering



nature, contradicted the ethic of resource conservation. However there is general acceptance of the desirability of management for preservation when a native game animal or other species is seen to be in decline (Robinson and Bolen, 1989).

In respect of the husbandry of game animals for sport or commercial gain, aims are less clearcut, varying with management situation. They may include:-

1) Avoidance of extinction of the game animal being managed.

McCulloch (1984) named this as a primary aim in the context of preserving native deer species. In New Zealand where introduced game animal species are seen as pests, extinction is seen by some as a primary goal (Parkes, 1988).

2) The establishment of a sustainable harvest of the animals being managed.

This emphasises the goal of long term population stability. Management strategy can vary according to the sustainable harvest goal. Where management is for maximum quality trophy yield, methods promote optimum nutrition with protection of younger bucks (McCulloch, 1984). Where there is management for maximum hunter kills, methods maximise the population's " optimum sustainable yield" of individuals from a stable residual population (McCulloch, 1984).

3) Prevention of deleterious effects of the game animal population on associated ecosystem values. Apart from being undesirable from a conservation viewpoint, damage to associated ecosystems can indicate potential for instability in a managed game animal population. In New Zealand where introduced game animal species are seen as pests by managers, prevention of damage to ecosystems by game animals is seen as a primary goal.

## 1.2. ESTABLISHED METHODS

Leopold (1933) developed decision making strategies for game management based on game animal population responses. Since then two basic techniques have evolved as

aids in formulating animal management decisions.

### 1.2.1 POPULATION BASED METHODS.

Population based methods measure interactions between animal populations and their environment. The demographic characteristics of the population under study are determined either directly or indirectly. Analysis of a temporal sequence allows an evaluation of the effect of management on population and environment.

Studies on hunted populations frequently utilise the harvest as a sample (McCulloch, 1979). This allows estimation of age, sex and fecundity. Other methods infer animal densities and populations from helicopter surveys (Teer et al., 1985), spotlight counts (Wood et al., 1985) and transect line encounters (Gates et al., 1985). Animal densities may be assessed indirectly from their effect on vegetation (Wardle, 1984) and from faecal pellet counts (Neff, 1968; Baddeley, 1985) or track counts (Tyson, 1985). The latter techniques do not always allow determination of demographic divisions of the population under study.

Population based methods have been employed in the management of New Zealand forests in particular those utilising vegetation condition assessment and assessment of animal density by faecal pellet count (Tustin, 1972(b); Wardle et al., 1973; Batchelor and Craig, 1985; Challies, 1973). Vegetation condition assessments involve extensive, time consuming, surveys which do not permit evaluation of changes occurring over a short time scale. There is a trend of decreasing reliance on such studies (Tustin, 1972(a); Wardle et al., 1973; Batchelor and Craig, 1985) in New Zealand with a concomitant increase in individual based studies (Nugent, 1983; 1990; Nugent and Challies, 1988; Frazer, 1993). Nevertheless animal density estimates by pellet count continue in use (Baddeley, 1985; Frazer and Lethwick, 1990). Thus both population

based and individual based methods continue to have a place in modern wildlife management strategies and are often used concurrently.

### 1.2.2 INDIVIDUAL BASED METHODS.

These methods concentrate on the responses of individuals within the animal population being managed (Challies, 1978). Typically there is measurement of some anatomical parameter influenced by the interaction of that individual with its environment. The anatomical parameters used vary widely (Challies, 1978) but commonly are associated with the concept of nutritional wellbeing (section 1.2.2.2 ).

Individual based methods generate statements on the well being of the population that are independent of population density measurements, yet they have a bearing on a populations potential for increase or decrease (Challies 1978). Riney (1955) noted a decline in the winter fat reserves of an irruptive population of red deer (*Cervus elaphus*) which he related to the population based parameters of winter death and fecundity. Winter fat reserve decline was a statement of population status that could be obtained independently of knowledge of population density and trends. In this respect individual methods can circumvent the costs of population estimations.

It is also noteworthy that individual and population based methods when used together, can often bring reciprocal illumination. McCulloch (1984) noted that whilst the population densities of two herds may be identical, their nutritional status may be very different. Such is the case where populations in the climbing and in the declining phases of a population irruption have identical population densities. In management situations where only infrequent population assessments are practicable, individual based methods used concurrently can allow population statistics to be placed in appropriate context.

### 1.2.2.1 ANATOMICAL PARAMETERS: PRACTICAL CONSIDERATIONS

Challies (1973) lists a number of qualities that are desirable in any anatomical parameter that is to be used as the basis for an individual based method of assessment.

It should be:-

- 1) readily accessible and easily measured or collected for measurement under field conditions.
- 2) able to be measured to a level of accuracy sufficient to adequately describe its variability.
- 3) obtainable from all, or at least a high proportion of the animals in a mixed age/sex sample.
- 4) sensitive to small differences or changes in nutritional well-being.

( Point 1 includes considerations of carcass spoilage. Where carcasses have commercial value, measurement must not cause loss of commercial or sporting value of the carcass .)

To these should be added :-

- 5) should be responsive over the whole range of nutritional conditions that it is required to evaluate.
- 6) should have a response time such that seasonal variation can be recorded.

The latter quality is necessary in order to evaluate the effects of seasonal variations in food supply. Such variations may increase as animal densities near carrying capacity i.e. become more liable to cause shortages during seasons of poorer food availability.

### 1.2.2.2. INDICES OF WELLBEING

#### 1.2.2.2.1. Development and use

The nutritional wellbeing of an animal may be viewed as an outcome of dietary adequacy or "adequacy of nutritional range" (Klein, 1970; Lowe, 1971). Assessment of nutritional wellbeing provides information on the interaction of a population with its

nutritional environment although there is temporal displacement between cause and effect.

In the development of any new index of wellbeing the connection between dietary adequacy and variation of the contemplated anatomical parameter must first be established. Feeding trials of penned deer undertaken in North America have demonstrated close relationships between dietary adequacy and a variety of anatomical parameters (French et. al., 1956; Robinette et. al., 1973; Verme, 1963) including body weight and antler size. Numerous studies of wild deer have described geographic differences in anatomical parameters of wellbeing subsequently relating them to differences in dietary environment (Gill, 1956; Hesselton and Saur, 1973; Klein, 1964; Ritchie, 1970). In New Zealand, significant differences in age specific carcass weight, skeletal size and fatness shown to exist between different populations have been related to dietary adequacy (Caughley, 1971; Challies, 1970; 1973; 1974; Riney, 1955; 1956).

Formal mathematical methods for producing indices of nutritional wellbeing based on body weight (Hesselton and Saur, 1973; Severinghaus, 1955; Challies, 1978; McCance and Widdowson, 1951; Bailey, 1968; Bamford, 1970), skeletal size including jaw length (Challies, 1974; 1978; Pekelharing, 1973; Caughley, 1967) fatness including perinephric fat (Anderson et. al., 1972; Caughley, 1970b; Dauphine, 1971; Mitchell et al., 1976; Challies, 1978) and proportion of animals showing signs of recent pregnancy or ovulation at post mortem (Challies, 1978) have been developed and employed in game management (Challies, 1978; Kelton, 1983). Typically these methods allow collection of data from animals of all demographic groups rather than from limited subsets of the population.

#### 1.2.2.2.2. Shortcomings

##### 1.2.2.2.2.1 Response time

Most established methods have response times that do not meet requirement (6) in (1.2.2.1) above. Problems arise because of the time lag between ingestion of foodstuffs and the subsequent change in the physical parameter. If the time lag is long, the effects of a number of separate short term nutritional events can become superimposed. In the case of post mortem evaluation of animal fertility as an index of condition (Hesselton and Sauer, 1973; Klein, 1970; Robinette et al., 1973; Thorne et al., 1976; Chaplin, 1977), the time base extends from the period of nutrition prior to the time of mating, through nutrition during gestation, to include nutrition immediately prior to the time of parturition. Nutritional conditions present at specific phases of the reproductive process can separately influence: the likelihood of conception (Morton and Cheatum, 1946; Cheatum and Severinghaus, 1950), the likelihood of twin pregnancy (Cowan, 1950), the likelihood of spontaneous abortion or absorption (Bubenik, 1982) and the likelihood of fawn survival at parturition (Verme 1962). An estimate of fertility based on post mortem evidence of recent parturition or suckling will, because of incorporated time lags, combine the reproductive consequences of a number of separate nutritional events.

A particular requirement is a response time sufficiently short to respond to seasonal changes in dietary availability. There is however a notable lack of such indices.

Although kidney fat indexes have been described as "lagging only slightly behind calorific intake" (Caughley, 1967) more recent work with red deer has demonstrated no obvious seasonal variations of this index (Challies 1978). The deficiency may arise in part from failure of indices to promptly respond to dietary change because of the buffering effect which I propose to call 'intrinsic nutritional optimisation' (see section 1.4.1). This mechanism gives scope for a considerable shift in type and quality of forage consumed before there are any nutritional shortcomings and consequent loss of

wellbeing (Ammann et al., 1973) . Intrinsic nutritional optimisation operates in the model described by Montgomery and Baumgardt (1965) where a decline in nutritional quality of available diet can to some extent be compensated for by increase of voluntary intake with concomitant increase in rumen retention time. The net effect of the mechanism is the processing of a greater volume of foodstuff in order to obtain the same amount of nutrient. With continuing decline in dietary quality the process of intrinsic nutritional optimisation will continue until a point is reached where rumen retention time becomes so prolonged that it prohibits the dietary throughput necessary to maintain optimal nutrition. It is only at this latter point that current indices based on nutritional wellbeing will begin to respond to change. Conversely indices based on intrinsic nutritional optimisation may respond to any change in the nutritional quality of the available diet.

#### 1.2.2.2.2 Responsiveness over the range of nutritional conditions under evaluation.

Many indexes that are currently in use do not meet requirement 5 in 1.2.2.2 above, their anatomical parameters being responsive to a limited range of nutrient conditions. Physiological mechanisms regulating responses in anatomical parameters often have inbuilt priorities of growth and resorption such that readily measurable response in a particular site only occurs over a limited range of nutritional conditions (Challies, 1978). The problem can sometimes be circumvented by evaluation of similar anatomical parameters at a variety of body sites but this increases the complexity and expense of the study. The following examples illustrate this problem..

#### Measurement of fat stores.

A number of fat deposition sites have been utilised as bases for anatomical indices of condition, namely subcutaneous fat (Riney, 1955; Mitchell et al., 1976), long bone marrow (Neiland, 1970; Verme and Holland, 1973) and abdominal fat, most notably in

the perinephric area, (Riney, 1955; Monson et al., 1974; Mitchell et al., 1976).

It is now generally accepted that there is a physiological order of primacy of fat deposition and presumably mobilisation (Bubenik, 1982) with fat being deposited first in the long bones (Ransom, 1965) subsequently in the abdomen and lastly subcutaneously (Challies, 1978). As a consequence of this it is considered (Challies, 1978) that marrow fat is likely to be a useful indicator of condition "only at the lower end of fatness range", abdominal fat "in the middle and upper levels" and subcutaneous fat "only at the upper end of the range".

The technique known as "condition scoring" used in livestock production (Gerloff, 1987; Northcutt et al., 1992; Rae, 1993) permitting evaluation of body condition in vivo, uses subcutaneous fat as an anatomical parameter. The technique is currently being evaluated for use in farmed red deer (Personal communication L. Audige. Faculty of Veterinary Science, Massey University) moreover it is stated that the loss of condition score in adversity is rapid (K. Stafford. Dept. Veterinary Clinical Science, Massey University. personal communication). However in the light of what has been stated by Challies (1978), use of the method may be of limited to wildlife management situations where there is near optimal nutrition and high body fat content in the animals under study, such that subcutaneous fat levels give a reliable measure of condition.

Body weight compensated measurements of perinephric fat show "telescoping" i.e. lesser degree of response per unit increase in nutritional adequacy, during the phase of marrow fat change (Challies, 1978) that occurs in range areas of poorest nutrition and lowest body fat content. Such telescoping curtails ease of measurement and usefulness of kidney fat indexes in areas where there is poorest nutrition.

Thus wildlife managers working in a geographic and temporal mosaic of differing nutritional conditions need to evaluate all three fat deposition sites to obtain meaningful results.



### Measurements of bone growth.

Peripheral skeletal components have been shown to have a higher priority of growth, that is, to grow more nearly optimally than their proximal counterparts, in conditions of poor nutrition (McMeekan et al., 1943). Thus the relationship between different bone based indices of nutritional wellbeing that use different skeletal measurement sites such as jaw length, body length, foot length and tooth row length is complex. Studies on bone length at these sites under differing conditions of nutrition have been carried out with red deer in New Zealand (Challies, 1978), and tentatively confirm site specific variation of priority of growth. However Challies (1978) warned that his results may not be applicable to populations in different locations.

#### 1.2.2.2.3. Non-equivalence of various nutritional indices of wellbeing.

Nutritional status is multifaceted and a loss of nutritional wellbeing as defined by Klein (1970) can be the consequence of one of a number of specific nutritional deficiencies. Lack of energy intake as dietary carbohydrate or fat will lead to loss of wellbeing through starvation (Kay and Staines, 1981; Ullrey et al., 1970), protein or non-protein nitrogen deficiency through nutritional marasmus (Thorne et al., 1976; Ullrey et al., 1967) and mineral deficiencies via a variety of syndromes (French et al., 1956; Verme and Ullrey 1984).

As a consequence of this, few of the various methods for evaluating nutritional status in current usage by wildlife managers (Challies, 1978) are directly comparable, each evaluating a differing composite of energy, protein and or mineral adequacy. Thus kidney fat indices (Riney, 1955) accentuate adequacy of energy intake, skeletal parameters such as body length (Caughley, 1971; Challies, 1978) long bone length (Klien, 1964) and jaw length (Challies, 1978) yield data based on a composite primarily of protein and mineral intake, whilst whole body weights (Challies, 1978) produce data based on a mixture of all nutrient elements. Therefore when estimating

trends in nutritional wellbeing it is wise to use a number of parameters to overcome this difficulty. A result set in the context of a single index of nutritional wellbeing can seem easy to interpret but data from other nutritional indices can render the interpretation more complex. Thus Challies (1978) in an extensive study of indices measuring different aspects of condition of red deer (*Cervus elaphus*) was able to show concordance of indices of nutritional wellbeing based on measurements of body length and jaw length. There was a significant increase of both parameters with decreasing animal densities and presumed better nutrition. Such clear cut interpretation was however confounded by the outcome of concurrent studies of modified Riney fat indices which showed a decrease in kidney fat indices with decreasing animal density.

Part of the reason for non-equivalence of various nutritional indices may be a consequence of the fact that specific nutritional requirements change with the age and sex of the animal. Thus energy intake (Fennessy, 1982; Silver, 1968; Moen, 1968; Moen, 1973), protein and non-protein nitrogen requirement (Ullrey et al., 1967) and mineral requirements (Ullrey et al., 1973; Ullrey et al., 1975), all can vary with demography. If a given age group has a higher dietary protein requirement than another then that group will be more susceptible to dietary protein deficiency and any index of nutritional wellbeing that is based primarily upon protein metabolism will exhibit greater sensitivity when applied to that age group. Under such conditions indices of wellbeing will be sensitive to demographic composition of population a problem that must be allowed for in any assessment of a new index.

### 1.2.2.3 DIETARY ANALYSES

These methods identify and quantify ingested flora from individual animals and by temporal comparisons attempt to detect trends in patterns of consumption.

#### 1.2.2.3.1 Methods

Currently two techniques are in use (Nugent, 1983), rumen content analysis which demands sacrifice of the study animal and faecal cuticle analysis which does not.

In rumen content analysis whole rumen content is seldom analysed, a sample being taken after mixing to dissipate layering (Wilson et al, 1977). Analysis is carried out either by physical sorting of identifiable fragments with measurement of relative proportions of the sorted samples by volume or dry weight (termed the macroscopic technique, Nugent, 1983), or by a systematic subsampling technique known as point sampling (Chamrad and Box, 1964) which samples the relative surface area of each food species in the rumen (termed the microscopic technique; Nugent, 1983).

In cuticle analysis the method of Sparkes and Malecheck (1968) is usually followed (Nugent, 1983). The dried ground faecal or rumen sample is subject to microscopic comparison with reference slides of cuticles of plant species available to the animal.. Of the two methods, rumen content analyses by macroscopic technique are considered to have the best potential for accurate quantification of deer diet (Kessler et al., 1981; Nugent, 1983). This is on the basis that biases due to differential digestion are minimised in larger particles, dry weight composition estimates are more accurate when directly measured rather than calculated from surface area, and finally because plant species are likely to be more accurately identified using macroscopic features.

#### 1.2.2.3.2. The continuing need for dietary analysis.

A variety of ruminant species have been shown to exhibit short term seasonal shifts of

diet as a consequence of a number of factors e.g. plant phenology and toxin content (Bryant and Kuropat, 1980). In areas where ruminant population densities reach high levels with respect to carrying capacity, food shortages can exhibit strong seasonal variation causing "winter death" (Ellig, 1975; Verme and Ozoga, 1971) In this situation short term overgrazing with permanent damage to other ecological values can occur. Indexes of nutritional wellbeing with short response times are needed to detect when this situation is likely to occur.

In New Zealand, species of native flora have come under threat from populations of introduced herbivores (Brockie, 1992). These animals did not coevolve with the ecosystems they now inhabit and because of this are more prone to rapid increases in population numbers (Caughley, 1970a) which can bring indigenous flora under threat in comparatively short time intervals. In such conditions season by season assessment becomes even more important.

Currently the lack of individual based methods with short response times (section 1.2.2.2.2.(1)) precludes their effective use in monitoring seasonal changes and situations where rapid population increases can occur. Range managers who wish to assess herd status are only able to use the less satisfactory, longer time based, methods of assessment of nutritional well being and to supplement the information gained from these with dietary studies.

#### 1.2.2.3.3 Shortcomings of dietary methods

Methods which measure diet directly, when correctly interpreted, have the potential to avoid the physiological complexities entailed in assessing nutritional wellbeing and provide a range manager with more direct information on nutritional status of the herd. However in order for dietary methods to be useful a thorough knowledge of the nutritional significance of food plant species along with other factors involved in the process of dietary choice is required. Successful interpretation demands baseline data

that include :-

1) The nutritional content of, and seasonal variation of nutritional qualities in, individual food plant species (Nelson and Leege, 1982).

If herbivores exhibit "nutritional wisdom" i.e. possess the innate ability to sense through taste and smell, specific nutrients and toxins in plants (Provenza and Balph, 1990) there may be change in dietary content according to plant nutritional content and with plant phenology (Arnold and Dudzinski, 1978). Only when the nutritional status of a food plant and its phenology is known can shifts in food plant species be appropriately interpreted. Whilst nutritional wisdom is recorded in the case of dietary sodium content (Denton and Sabine, 1961) little is known as to whether this occurs in respect of parameters of chemical composition such as protein, soluble carbohydrate, sugar or organic acid content (Arnold and Hill, 1972) and digestibility of cellulose (Van Soest, 1964; Nelson and Leege, 1982). Until this is more completely understood interpretations of species choice based on nutritional content must be tentative.

2) The incidence of food plants in the area under study .

Variation of plant frequency of occurrence influences diet (Nugent, 1983; Nugent and Challies, 1988). Dietary switching (Crawley, 1983) from less to more common plants may arise solely as a consequence of increased frequency of encounter and be unrelated to differences in nutritional content (Smith and Follmer, 1972).

3) Incidence of, and seasonal variation in, toxin content of food plants (Rhoades, 1979).

As with all plant defences toxins may cause changes in diet that are unrelated to plant nutritional content (Bryant and Kuropat, 1980). Only when the occurrence and phenology of plant toxins is known can shifts in dietary species be appropriately interpreted. Adequate knowledge of the spatial distribution of toxins though the plant

can be important as some herbivores have developed browsing stratagems that avoid plant parts with high toxin content (Bryant and Kuropat, 1980).

#### 4) Endogenous factors in the herbivore.

It is important to note that food preferences of herbivores may be to some extent unrelated to plant chemical content or physical characteristics and influenced instead by endogenous factors such as previous behavioural conditioning (Matthews and Kilgour 1980; Keogh and Lynch, 1982) and innate mechanisms that influence overall nutritional strategy (Pierce and Ollason, 1987) for example with regard to sex and season (Clutton-Brock, 1982; Suttie, 1981; Fennessy, ). Such mechanisms can operate in the face of adequate food availability (McEwan and Whitehead, 1970; Bandy et al., 1970; Loudon et al., 1989). Thus on site studies of herbivore behaviour and physiology are needed before the process of food plant species selection in a given area can be completely understood e.g. Hunt and Hay, 1990).

#### 5) Interpretation of dietary analyses.

The fundamental unit of dietary analysis is actual diet ingested and there are doubts as to whether current techniques of dietary analysis give an accurate portrayal of this. In rumen analysis errors may arise from different rates of passage of differing plant materials through the rumen (Anderson et al., 1965; Norris, 1943; Smith, 1952; Bergeraud and Russell, 1964). Information is needed on the qualities of dietary particulate matter that effect its rate of passage through the rumen and on the particulate yield from given plant species. Kessler et al. (1981) compared results from macroanalysis of rumen content with those from microanalyses of rumen content and faeces in assessing diet of pronghorn (*Antilocapra americana*). There were, in some cases, significant differences in the species content lists produced by the three methods. Anthony and Smith (1974) compared macroscopic with microscopic analyses of rumen

contents. Composition estimates were similar but grasses were "overestimated" by the microscopic technique, and herbs flowers and fruit "overestimated" by the macroscopic method. These workers felt the differences arose from a combination of bias in the techniques and differential digestion. Of the three methods Nugent (1983) favoured macroscopic rumen content methods based on sieved fractions as plant identification by large fragments would be less likely to be subject to error and larger particles less likely to be differentially effected by digestion. However his comparison did not address the problems in assessing mixed diets of short sward and browse nor did it address the problem of differential passage rate of particulate matter.

Information of the type needed in order to meaningfully translate rumen content and faecal content analyses into ingested diet, and thus into information on nutrient status, is not currently available. Dietary studies are useful to the wildlife manager only for identification and limited quantification of herbivory pressure on individual plant species, accurate quantification being limited by the same shortcomings described above.

### 1.3 ALTERNATIVE INDIVIDUAL BASED METHODS FOR GAME ANIMAL MANAGEMENT

#### 1.3.1. THE NEED FOR ADDITIONAL METHODS BASED ON THE CONCEPT OF INTRINSIC NUTRITIONAL OPTIMISATION.

Discussion thus far has shown that individual and population based methods in current use possess a number of drawbacks and highlight a particular need for methods having a short based response time.

One potential basis for such a method is the mechanism whereby intrinsic nutritional optimisation arises. Changes brought about by the quality of the ingested herbage in

ruminants, cause adjustment to rumen retention times, onflow rates and absorption rates such that there is an optimal yield of assimilable nutrients from the elected intake (Montgomery and Baumgardt, 1965). In monitoring changes in a mechanism that responds to dietary variation according to inbuilt strategy, the observer is recording data that are at the same time describing trends in browse quality. These are of potential value to the wildlife manager.

### 1.3.2. THEORETICAL CONSIDERATIONS

Before exploring any specific method that is dependant on measurement of an anatomical parameter the general bases of anatomical variation should be considered. In this manner it is possible to pinpoint salient features that need to be evaluated in the new method.

#### 1.3.2.1. Growth and resorption.

Many physical parameters chosen to monitor nutritional wellbeing are assumed to always exhibit positive growth, for example bone. However more dynamic biological parameters that may be used as indexes of nutritional wellbeing are likely to undergo significant episodic negative growth phases (i.e. resorption), for example fat deposits. In this case if the index is to be viable it is essential that unit rates of resorption per unit change in nutrition, match those of growth. This equivalence seems to be tacitly assumed in the literature pertaining to fatness measurements (Challies, 1978). However in the case of methods where response times are shorter, it becomes important to determine relative rates of resorption and growth.

#### 1.3.2.2. Progressive increase through the life of the animal.

Continuous and progressive growth will only occur when growth processes



consistently outweigh resorptive ones. Where this is not so and there is growth and/or resorption continuing through the life of the animal the parameter will vary in a manner that is not a function of the age of the animal. These latter conditions may be thought to offer greater prospects of a record of current environmental conditions uncontaminated by a record of what had gone before. However recent work (Albon et al., 1992) demonstrated long term cohort differences in reproductive capacity brought about by nutrient conditions at the time of that cohorts intra uterine life. Because of such cohort effects it may be more desirable to use positively accumulative parameters as, when appropriately interpreted, these can offer a long term record of cohort nutrient history in successive seasons.

#### 1.3.2.3. Demarcation of annual growth

It is important to note whether positively accumulative characters have some property enabling identification of annual growth increments. Those that do will have an additional advantage in that conditions prevalent in an individual year can be more easily identified. Thus in cementum analysis of teeth (Frazer and Sweetapple, 1993) the presence of a line separating progressive annual increments enables identification of a specific years growth. Of course, where it is not possible to distinguish annual growth, overall estimates of nutrition through the lifespan of the animal can be obtained by measuring the total cumulative value of the parameter of nutritional wellbeing. By collating these measurements from different aged animals shot at the same time (Challies, 1978) some idea of year by year increases can be obtained. However in this case because only "total cumulative" values may be recorded, there will occur a cumulative damping of year by year variations of the index. In this respect it is desirable to choose an anatomical parameter which exhibits overall progressive growth preferably with identifiable annual increments. Failing this it is important to use concurrently some other index of animal age.

#### 1.3.2.4. Variation of growth rate due to physiological effects.

These have already been discussed in the context of range of responsiveness in a previous section (1.2.2.2.2.) but a particular aspect of growth rate variation is relevant here. Anatomical indices which are highly responsive to nutritional conditions in the mature animal may be less responsive in juveniles and grow in a manner that is less dependant on current nutritional environment. During fawn growth, maternal fat stores can be used to offset nutritional shortages resulting in continued growth of the fawn at the expense of maternal condition (Bahnak et al., 1979).

In this respect it is important in the evaluation of any method to monitor not only the change in the parameters in response to changes in nutrient level but also to describe age related growth rates where such exist. Trends in the latter will give an indication of the existence of age specific variation of growth rate.

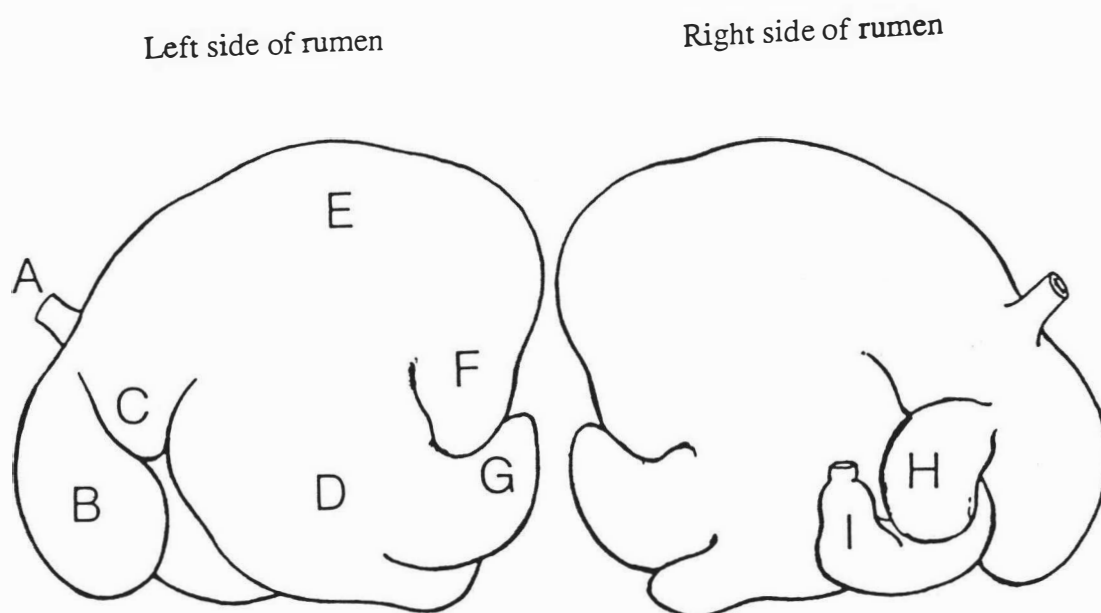
### 1.3.3. THE POTENTIAL OF STOMACH ANATOMICAL PARAMETERS FOR USE IN INDIVIDUAL BASED METHODS.

#### 1.3.3.1. INTRODUCTION

The relative indigestibility of plant celluloses (Van Soest, 1982) along with scarcity of cellulases (Cheng et al, 1991) has resulted in the development of a plethora of herbivores with specialised gastrointestinal anatomy (Van Soest, 1982; Langer and Snipes, 1991). Although biogeographical factors can have an influence on the gastrointestinal site at which specialisation occurs (Langer and Snipes, 1991), the themes of such specialisation can be viewed as, providing adequate housing and nutrition of symbiont cellulase producers, creating of sufficient delay in food transit time for the slow acting cellulases to achieve significant digestion, and finally resorption of the products of this bacterial activity. In the case of ruminants there is

Fig. 1. Rumen anatomy of deer.

- A Oesophagus
- B Reticulum
- C Atrium ruminis
- D Ventral sac
- E Dorsal sac
- F Caudodorsal blind sac
- G Caudoventral blind sac
- H Omasum
- I Abomasum



concentration of these anatomic specialisations in the stomach (fig 1).

The ruminant stomach comprises four compartments:-

#### 1) The Rumen.

A large sacculated structure that is offset from a variable groove (the oesophageal groove) through which certain foodstuffs are able to bypass entry into the rumen (Getty, 1975). The rumen is divided by a series of pillars into freely communicating but discrete sacs (see fig 1). A transversely situated cranial pillar separates the ventral most proximal sac, the atrium ruminis, from the next most caudal and ventral compartment, the ventral sac. Another transverse pillar, the caudal pillar, separates the caudal limit of the ventral sac and its caudal extensions, the caudoventral blind sacs, from the upper part of the rumen, the dorsal sac, and its most caudal extension the caudodorsal blind sac. In some species of ruminant the whole of the rumen excepting the pillars is lined by flattened finger-like extensions of varying shape (see fig 2), the ruminal papillae. These extensions are thought to absorb nutrients (Van Soest, 1982). Papillae vary in size between different species of ruminant as a consequence of the evolution of differing dietary habits (Hofmann, 1985; 1989).

#### 2) The Reticulum.

A similarly offset, thin walled, highly contractile structure connected caudally with the atrium ruminis. The rumen and reticulum are only partially separated and are usually considered as a single organ, within the confines of which, the major part of the fermentation and absorption of fermentation products from ingested fodder are considered to occur (Van Soest, 1982).

#### 3) The Omasum.

A small, bean shaped, structure connected with the reticulum and the oesophageal groove. The omasum contains a number of leaves which may serve to absorb water and nutrients but may be more important as a filter (Van Soest, 1982).

#### 4) The Abomasum.

The acid secreting distal portion of the ruminant stomach which is connected with the omasum proximally and, via the pylorus, with the duodenum distally. The abomasum is thought to have a similar function to the true stomach of non-ruminants (Van Soest, 1982).

### 1.3.3.2. SPECIFIC MECHANISMS OF INTRINSIC NUTRITIONAL OPTIMISATION IN THE RUMEN AND THEIR POTENTIAL FOR USE IN INDIVIDUAL BASED METHODS.

Changes in dietary quality in ruminants bring into play mechanisms of intrinsic nutritional optimisation, which each effect changes in rumen onflow rate (Francoise Domingue et al., 1991). Measurement of rumen onflow rate (Francoise Domingue et al., 1991), an integrated outcome of all modes of intrinsic nutritional optimisation, therefore has potential for use as an individual based method. However, current techniques are not applicable to wildlife management as they require ongoing laboratory study of live animals (Francoise-Domingue et al., 1991). Failing monitoring of overall outcomes, a study of the practicability of techniques employed in measurement of individual mechanisms contributing to nutritional optimisation may be useful. Currently three ruminal consequences of changes in dietary quality are known and each could be viewed as a specific mechanism of nutritional optimisation.

Considering each in turn:-

#### 1.3.3.2.1. Change in rate of mechanical and microbial particle breakdown processes.

With the death of the animal, mechanical food breakdown (Reid et al., 1979; Ulyatt et al., 1985) ceases and the rate of microbial breakdown (Cheng et al., 1991) changes, thus assessments are limited to inferential analyses. Currently there are three possibilities.

a) assessment of rumen fermentation rates of rumen contents (Maloiy et al., 1982; Hoppe et al., 1977).

- b) assessment of particle size distributions in rumen contents (Spalinger et al., 1993)
- c) assessment of rumen microbial populations as total counts (Hobson, 1976; Hobson et al., 1976; Dehority, 1975)) and in relation to their relative generation times and rumen turnover times (Prins and Geelan, 1971; Giesecke and Van Gylswyk, 1975)

All are complex experimental procedures. Bearing in mind the practical guidelines listed by Challies (1978) (see Sect 1.2.2.1.) utilisation of this mode of intrinsic nutritional optimisation as a potential individual based method presents considerable practical difficulties.

#### 1.3.3.2.2. Change in rumen volume and papillary density.

Rumen volume changes may be used within species as a nutritional strategy (Kay and Goodall, 1976). Such changes may increase retention time, thus digestibility (Milne et al., 1978; Kay and Goodall, 1976; Person et al., 1975), in the face of changes of dietary nutrient level and intake (Milne et al., 1978; Person et al., 1975). Evidence suggests that such changes take place comparatively slowly. In the short term, sudden increases in volume of food consumed as a consequence of declining quality results in reduction of food retention time and consequent reduction of digestibility (Kay et al., 1976). Over a period of months, ruminants show an ability to adapt to dietary need by changing the relative size of forestomach compartments. In a study in which red deer were slaughtered when eating grass and hay at different seasons (Milne, 1980), rumen volumes measured at post mortem were shown to vary by as much as 28%.

Tamate et al. (1962), by studying the effect of inclusion of plastic sponges that were small enough to be ruminated in the calf rumen, concluded that these produced an expansion of rumen volume and an increase in rumen muscular development. This effect was independent of papillary development. These findings concurred with the studies of Sander et al. (1959) who stated that "muscular development of the rumen is not parri passu with papillary growth". A further possible separate mechanism in the

control of rumen volume settings is thought to be related to photoperiod, whereby rumen volumes increase with voluntary food intake in spring and likewise decrease in winter (Sibbald and Milne, 1993). It is notable in this case that volume increased with no change in wall mass. The physiological independence of rumen papillary size change and rumen volume change is further underscored by the studies of Langer (1988) who reviewed the literature on changes of papillary parameters in various ruminants with increasing age. There was a general trend of decreasing papillary density with age whereas papillary lengths increased with age.

Hofmann (1973) described changes in the relative volume of rumen compartments arising out of removal from the abdomen and went to considerable lengths to study relative volumes only in postmortem specimens preserved in the standing position. Bearing this in mind, techniques such as are described by Sibbald and Milne (1993) must be seen as giving reliable results only under standardised experimental conditions. The possibility of using rumen organ weight as an indirect measure of rumen volume does not seem viable as rumen volume has been shown to change seasonally without concomitant change in organ weight (Sibbald and Milne, 1993). Theoretically, rumen volume changes may be inferred from changes in papillary density in specimen portions of rumen wall. However note should be made of practical difficulties in the procedure of estimating papillary density post-mortem. It is likely there will be some degree of post mortem change in wall length and thickness, arising as a consequence of differing thicknesses of circular, longitudinal and oblique muscle layers and their differing orientations, each according to embryonic anlage of the site being sampled. It is thus possible that the degree of post mortem changes may vary with the site sampled. Langer (1974) makes allusion to this possibility in his paper on roe (*Capreolus capreolus*) and fallow (*Cervus dama*) deer stating "Values of papillar density cannot be compared and are not discussed since the pieces of ruminoreticular wall had been fixed under different contractions". Hofmann (1973) records the variation of rumen volume from its

in vivo state when not preserved in situ i.e on removal from the abdominal cavity. Fixation of wall specimens in preserving media may further complicate this problem (see chapter 2). A review of variation of papillary density estimates that are recorded in the literature gives some indication of the difficulties in standardising papillary density estimates. Langer (1988), in a compilation of reported papillary densities in deer found wide variation. e.g. Red Deer, 116 papillae per sq. cm. (Langer, 1988) 48 papillae per sq. cm. (Hofmann, 1976). Fallow Deer, 129 papillae per sq. cm. (Langer, 1988) 52 papillae per sq. cm. (Geiger et al., 1977).

Measurements such as "surface enlargement factor"(S.E.F.) described by Langer (1988) incorporate a papillary density measurement, a function of rumen volume, subject to the same limitations described above. Moreover, if rumen volume change is primarily in response to dietary roughage (Tamate et al., 1962; Francoise Domingue, 1991) whilst papillary surface area responses are primarily to soluble nutrients (Tamate et al., 1962), S.E.F. calculations comprise an admixture of measurements which respond to different nutritional factors. Reports of variation of S.E.F. with dietary "quality" may underestimate the rumen dietary nutrient response, as nutrient induced rumen papillary measurement changes may have been overshadowed by a rumen volume effect due to changes in roughage content of the diet. This possibility is exemplified by the work of Langer (1974) comparing the papillary lengths and S.E.F. values of roe deer (*Capreolus capreolus*) and fallow deer (*Cervus dama*) shot in "Geest" and "Jungmorane" areas these regions each having differing nutrient characteristics. Whilst no significant differences between S.E.F.s could be found between animals shot in the two areas there was a clear distinction in mean papillary lengths of the same groups.

#### 1.3.3.2.3. Change in absorptive surface area

The surface area of a number of internal structures within the ruminant stomach have



been shown to change with diet (Tamate et al., 1962; Ortega-Reyes et al., 1992; Clark, 1982), such anatomical changes may be viewed as a mode of intrinsic nutritional optimisation. Evidence comes from two types of study :-

- 1) The more physiological database categorising variations of anatomical parameters with changes in the rumen concentrations of various nutrient and other dietary materials.
- 2) The more ecological database categorising the variation of anatomical parameters in different species of herbivore and correlation of these differences with differences in dietary habit termed by Hofmann (1973) as "dietary type".

Evidence from both sources will be cited in the following outline.

In respect of the practical considerations outlined by Challies (1978)(section 1.2.2.1.), these structures are easily accessible, measurements relatively simple and the sampling easily carried out by unqualified personnel.

#### 1.3.3.2.3.1. Overall papillary anatomy:

Sander et al., (1959) and Tamate et al., (1962) reported increases in mean length and width of rumen papillae in calves in response to diet supplemented with grain and to intraruminally administered V.F.A. (volatile fatty acid) solutions. Similarly Clark (1982) reported that the length of ruminal papillae in weaned lambs varied as a function of V.F.A. energy intake. In the induction of papillary growth, individual V.F.A.s have been reported as having differing potencies with butyrate being more potent than propionate which is in turn more potent than acetate (Tamate, 1962; Sander et al., 1959). In concordance with this, increases in intraruminal acetic acid concentration are inversely correlated with papillary development (Omar et al., 1964). The microbial fermentation yields of butyrate and propionate increase with increasing nutrient quality of herbage (Carrol and Hungate, 1954; Allo et al. 1973). Capote and Hentges (1967) reviewed the effects of diet on domestic ruminant forestomachs and stressed that

animals receiving a low protein diet had long but thin papillae.

Ortega-Reyes et al.(1992) studying ruminal papillary development in lambs (*Ovis ovis*) showed reversal of dietarily induced papillary lengthening within three weeks of the animals being changed to a different diet. Likewise Langer (1974) showed involution of papillae of roe deer (*Capreolus capreolus*) during winter. Hofmann (1973) demonstrated seasonal changes in the size of papillae in a number of african bovid species including impala (*Aepyceros melampus*). He also reported (Hoffman, 1973) differences in the mean papillary sizes of impala (*Aepyceros melampus*) between individuals taken from locations with differing feed characteristics. Langer (1988) reviewed the literature for evidence of age related growth of papillae and citing bovine and ovine examples, he demonstrated an almost linear variation of age with papillary length.

In addition to the macroscopic changes noted hitherto it has been demonstrated that histological changes can also be related to diet. Hofmann (1973) reviewed the histological evidence demonstrating changes in the papillary epithelial thickness and surface character and changes in the site and calibre of papillary blood vessels induced by seasonal changes in the nutrient and abrasive quality of diet. He noted the development of layers of densely packed "barrier scales" with narrow intercellular spaces in "dry roughage grazers" particularly in areas that were "mechanically stressed" such as the free edges of pillars. He also noted transformation of this layer, with the formation of balloon cells and increasing subepithelial vascularisation induced by changes to a diet of lush grass in the rainy season. Nockels et al., (1966) studied dietarily induced papillary changes in adult castrated sheep and demonstrated macro and microscopic changes when animals were transferred from a medium to a low energy ration and with transfer from a medium to a high energy pelletised feed. Histological changes were evident at between 8 and 32 days in the former case and 24 to 35 days in the latter.

In summary, there is evidence for reversible rumen papillary changes at micro and macroscopic level in response to changes in intraruminal availability of protein and various V.F.As, over a time base of 2-3 weeks arising from changes in dietary quality as well as from the mechanical factors of the ingested feed. There is also evidence of overall positive growth through the life of the animal. There is no evidence of microscopic or macroscopic features that would enable the identification of individual seasonal or annual increments of growth on a year by year basis. There is no evidence demonstrating the relative rates of growth and resorption of papillae to be equal. Likewise there is no evidence that demonstrates that papillary width and breadth parameters are equally responsive to a given change in dietary quality.

#### 1.3.3.2.3.2. Site specific changes in papillary anatomy.

Hoffman defined "concentrate feeder" ruminant herbivores as animals specialised to deal with low volume high nutrient dietary items that are significantly amylolytically fermented. In contrast "roughage" feeders" were defined by him as specialised to deal with a high volume, lower nutrient diet which is processed mainly by cellulolytic fermentation. Ruminant species showing dietary specialisation intermediate between these two classifications were defined as "intermediate feeders". Hofmann (1973; 1989) reported variation of papillary length at specific rumen sites in different types of feeders. Typically "concentrate feeders" showed more uniform distribution of papilla length throughout the rumen, whereas "roughage feeders" showed variation of papilla dimensions with the shortest and narrowest papillae being found on the dorsal sac and the most luxuriant growth in the atrium ruminis and blind sacs. In a study of "intermediate feeder" impala herds grazing under conditions of differing food availability, Hoffman (1973) reported variations not only in overall papillary length but also in papillary length at particular ruminal sites according to the type of bush which the impala herd inhabited. Impala grazing in lush conditions had well developed

papillae on the dorsal sac whereas those grazing in drier conditions had poor papillary development at the same site.

Two possible mechanisms could account for such differences:-

a) Differing abrasive quality of the diets

In roughage feeders there is greater "stratification of rumen contents" i.e. the build up of a transverse layer of compacted vegetation within the cavity of the rumen (Capote and Henges, 1967). The poor papillation in the dorsal sac of this group could be due to abrasion by the floating mat of coarse vegetation. In concentrate selector types the more generalised distribution of a less abrasive "mud" layer described by Capote and Henges (1967) would exert less mechanical abrasive effect on the dorsal rumen and other upper walls. i.e. a more uniform effect resulting in less regional differences.

b) Differing nutrient environments within the rumen

The mechanism of flow of digesta within the rumen of cattle and sheep postulated by Reid, (1962; 1984), Waghorn and Reid, (1977) and Wyburn (Wyburn, 1979) is to a large extent dependant upon the formation of a floating mat of digesta. First there is passage of floating incoming ingesta dorsally into the dorsal sac where it becomes incorporated into the mat, from which it progresses ventrally as the bacterial and fungal digestion proceeds. Denser more nutrient rich ingesta, on the other hand, if it does not bypass circulation in the distal rumen completely, is liable to move more directly into a flow system occupying the ventral sac.

The mat, whilst forming part of the above described circulation, also obturates compartments of the rumen, in particular separating the proximal cup and spill mechanism of the reticulum and atrium ruminis from the more distal ruminal sacculations and the dorsal from the ventral sac. Where dietary conditions promote mat formation there will be a concurrent separation of nutrient environments within the rumen, notably a separation of more proximal amylolytic (starch digesting) from more distal cellulolytic (cellulose digesting) sites along with a separation of dorsal, less

nutrient rich, from ventral, more nutrient rich, sites. When a concentrate diet, rich in high density particulate matter and poor in raft forming material is ingested, the pattern of circulation will be modified, there being no obturation by a raft and thus freer flow of nutrients between the sacculations both craniocaudally and dorsoventrally. Changing dietary intake is therefore likely to change flow dynamics of digesta and effect the nutrient milieu interieur. Langer (1974) makes allusion to the importance of this effect in correlating papillary length values at different sampling sites in roe and fallow deer.

Thus studies comparing dimensions of papillae in dorsal and ventral ruminal sites have the potential to yield data pertaining to raft forming potential of diet i. e. concentrate versus abrasive/roughage components. Such an assessment of the roughage component of the diet, if practicable, could obviate the need for the more complex techniques, discussed hitherto, which assess the roughage component via its effect on rumen volume. In conditions where there is good raft formation with effective obturation of the various rumen compartments, comparison of cranial versus caudal papillary dimensions may allow assessment of amylolytic (starch digesting) versus cellulolytic (cellulose digesting) VFA production components.

Currently, as no formal studies are available which compare papillary growth response times at different sites in the rumen, one is driven to assume that these are of the same order as those reported by Ortega-Reyes et al. (1992) and Nockels et al. (1966), that is, between one and five weeks for all sites. However if there were site specific variations these would mitigate against direct comparisons of the type discussed above. i.e. regional inequality of papillary growth in response to unit dietary change would necessitate consideration of specific loading factors when undertaking site comparisons.

#### 1.3.3.2.3.3. Change in reticular anatomy.

Hoffman (1973; 1989) described variation in the anatomy of reticulum wall construction with dietary feeding type. In concentrate feeders, in accordance with a presumed greater importance of cup and spill type particulate separation mechanisms, there is greater reticular volume relative to rumen volume. The reticular wall in concentrate feeders was thin with cellulae reticulæ arranged in simple honeycomb pattern and having low and spiky crests. Conversely, the reticulum of roughage feeders was comparatively small relative to volume of rumen. In this case the reticular wall was thicker and the cellulae more complexly arranged sometimes consisting of primary high walled cellulae containing within them secondary patterns of lower walled cellulae. The walls of all cellulae in roughage feeders were said to have little papillary spicule development.

The literature is sparse with respect to plasticity between the two types of reticular structure induced by dietary changes. Hoffman (1973) described differences in the reticular structure between forest and grassland impala but this does not prove plasticity in the individual animal. The reticular cellulae of forest impala were shallow and simple having no internal secondary cristae, the crests, though shallow, had prominent development of long conical spikes with similar spikes being found in the floor of the cellulae. Grassland impala on the other hand were said to have deeper cellulae whose larger cristae bore less prominent spikes, in this case cellulae were often subdivided into secondary patterns by secondary cristae.

No comparison of reticular volumes in the two types is given. Part of the reason for this may be variability of post mortem changes in this organ. Unaccounted variation in the post mortem reticular volumes of farm stock has been reported (C.S.Reid. Dept of Veterinary Science, Massey University personal communication). Post mortem fixation with formal saline does not modify these differences.

#### 1.3.3.2.3.4. Changes in Omasal anatomy.

Hoffman (1973; 1989) describes the typical omasum of concentrate selectors as low in volume per unit rumen volume. Internally its structure comprises relatively few omasal leaflets each being thick walled and bearing well developed papillae in contrast to those of the roughage selecting counterparts. Conversely, omasums of roughage feeders are of comparatively large volume and bear greater numbers of thinner laminae with these laminae having less well developed papillae.

Hoffmans (1973; 1989) studies are interspecies comparisons but Lauwers (1973) describes a greater laminal surface area in dairy cattle compared to that of beef cattle. This difference is presumed to be a consequence of the higher fibre ration fed to dairy cattle although genetic differences between the breeds may play some part. Lauwers (1973) study is of the outcome of a long term exposure to the two dietary experiences and no comment is made as to the response time of dietarily induced divergences in omasal structure.

On the basis of Lauwers (1973) evidence reporting a progressive increase in the total surface of bovine omasal laminae up to the about the tenth year of life, it is less likely that significant phases of laminal involution are able to be induced by change in dietary character. However there were wide variations of laminar number and area in individual animals and this could have obscured small involutional trends.

The same worker studied the laminal papillary area in beef and dairy cattle and was able to report no significant difference (Lauwers, 1973). This is in contrast to that which would be expected from Hoffmans (1973; 1989) work.

I was unable to find any work demonstrating zonal macroscopic or microscopic changes demarcating annual growth increments in omasal laminae.

#### 1.3.3.4. THE USE OF INDIVIDUAL BASED METHODS FOUNDED ON STOMACH ANATOMY PARAMETERS: CONSIDERATIONS PARTICULAR TO NEW ZEALAND

Past workers (Cockayne, 1928; Batchelor, 1989) have on occasion assumed New Zealand vegetation has not been subject to any significant pressure of herbivory. However, toxins have subsequently been identified in a number New Zealand native plants (Batchelor, 1989) and it is accepted they could coevolve with native or introduced herbivores (Batchelor, 1989). On an ecological timescale introduced ruminant herbivores have had little time for complex coevolution with New Zealand plants. Thus in situations where methods founded on stomach anatomy parameters are used to study nutritional responses in wild deer in New Zealand, results are less likely to be confounded by the effects of specifically targeted plant toxins. Moreover, it is possible that a subsequent comparative study of a similar nature undertaken in an area of ancient endemism of these same ruminant herbivore species could yield information on the relative contribution of coevolved agents compared to that of broad spectrum toxins.

#### 1.3.3.5. SUMMARY OF SALIENT POINTS FOR AN INVESTIGATION OF PROSPECTIVE INDIVIDUAL BASED METHODS BASED ON MECHANISMS OF INTRINSIC NUTRITIONAL OPTIMISATION

There is currently no practical (*sensu* Challies, 1978) rapidly responding individual based, method utilising rates of mechanical or microbial food breakdown nor an individual based method utilising rumen volume changes. There is however a sufficient body of experimental evidence available to suggest that simple anatomical studies of stomachs obtained from free ranging animals may provide an insight into the operation of intrinsic nutritional optimisation mechanisms and form the basis for a rapidly responding individual based method.



Theoretical considerations given hitherto show that in exploratory studies of the variation of any anatomical parameter with differing nutritional conditions, there should be a concurrent assessment, under differing nutritional conditions, of age specific growth rates and comparative rates of growth and involution. Moreover, there should be provision in the experimental design to identify parameter changes that are brought about by changes unrelated to nutrition, for example physiological events, such as those which occur with season.

Prior to the undertaking of studies on stomach anatomical parameters, in view of a deficiency of data in the literature, there is a need for study of the extent and consistency of post mortem rumen papillary shrinkage following formalinisation. Likewise there is a need for study of post mortem rumen wall shrinkages before there can be meaningful interpretation of papillary results in terms of FISA values.

In respect of stomach anatomical parameters, literature review indicates a particular potential for rumen papillary and omasal lamina measurements. For these particular cases there is a need for assessment of changes in the following anatomical parameters relative to the variables described above:- rumen papillary width, length and site, omasal leaflet order and number and area along with variance of omasal leaflet area order and number.

## CHAPTER 2

RH Red deer rumen shrinkage in formal saline. Lentle et al.

## THE EFFECT OF FORMALIN INDUCED SHRINKAGE ON MEASURES OF RUMEN SURFACE AREA IN RED DEER.

ROGER G. LENTLE. Department of Ecology, Massey University, New Zealand

KEVIN J. STAFFORD. Department of Veterinary Clinical Sciences, Massey University, New Zealand

IAN M. HENDERSON. Department of Ecology, Massey University, New Zealand

Abstract: We studied changes in surface area of different sections of red deer (*Cervus elaphus*) rumen wall after immersion in 10% formal saline solution at room temperature for two, seven and fourteen days. There was a high degree of unpredictable variability (0%-39.5%) in wall area reduction. Ignoring changes of this magnitude when calculating the factor of increase in surface area (FISA), a composite of papillary surface area and density values can result in errors of up to 39.5%. We question the validity of FISA calculations when formalinised specimens are used in studies of rumen response to diet. Rumen papillary dimensions were not significantly changed by formalin.

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Keywords: *Cervus elaphus*. Contraction. Papillary density. Formalinisation. Red deer. Rumen wall.

## INTRODUCTION

The extent to which the internal surface area of the rumen is increased by papillation varies between different species and within species between groups of animals living under different dietary conditions (Hoffman 1973). In quantifying

this epithelial enlargement a numerical value, the factor of increase in surface area (FISA or OVF) was developed by Langer (1974, 1988).

$$FISA = \frac{2LWN + BS}{BS}$$

where:- L = Length of Papilla

W = Width of Papilla

N = number of papilla per basal surface area

BS = Basal surface area. (Langer, 1988).

Using FISA Langer (1974) compared roe (*Capreolus capreolus*) and fallow deer (*Cervus dama*) from different areas, in order to determine "seasonal and biotic influences" on nutritional strategy. To prevent post mortem shrinkage, Langer (1974) fixed rumen wall specimens onto a plastic foam base with needles shortly after excision. However, Langer (1988) commented that not all workers adhered to this procedure.

FISA data can only be meaningful if they relate to in vivo conditions of rumen volume and papillary dimension. For this to be the case any change induced by death or preservation in formalin solutions must be constant within species, between species and between different rumen compartments. In this respect it should be noted that Hoffman (1973) recorded changes in the anatomy of rumens after their removal from the abdomen. Changes in the overall shape that arise when the rumen is removed from its in situ constraints could influence FISA estimations even in Langers (1974) more careful procedure.

This study monitored the effects of 10% formalin solution on papillary anatomy and density and subsequent effect on FISA estimations.

## METHOD

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This study monitored the effects of 10% formalin solution on papillary anatomy and density and subsequent effect on FISA estimations.

## METHOD

### Specimens

Four red deer were obtained from the Western slopes of the Ruahine ranges, North Island, New Zealand in the summer and autumn of 1993. Following shooting, the intact stomach was removed via a ventral incision in the abdomen. The contents of the rumen were carefully removed via an incision in the left wall of the dorsal sac. The stomach was kept cool pending return to the laboratory when it was frozen at  $-10^{\circ}\text{C}$  until required for analysis.

## Procedure

After complete thawing a circumferential cut was made in the wall of the dorsal sac at a level dorsal to the cranial and caudal pillars, thus detaching the bulk of the dorsal sac wall and roof and giving easy access to the sampling site centres. Samples were taken from seven sites in the rumen wall (fig 2).

1) Atrium ruminis (AR). The sample site was centred at the lowest point of fusion of the posterior wall of the atrium ruminis with the anterior wall of the ventral sac, at a position immediately below the midpoint of the cranial pillar.

2) Ventral sac (VS). The sample site was centred on the point at which the anterior wall of the ventral sac fuses with the posterior wall of the atrium ruminis in a position immediately below the mid point of the cranial pillar.

3) Dorsal sac (DS). The sample site was centred at the point of least papillation on the roof of dorsal sac.

4) Left ventral sac (LVS). The sample site was centred at a point on the same level as in the atrium ruminis and the anterior ventral sac but below the mid point of the left longitudinal pillar.

5) Right ventral sac (RVS). The sample site was centred at a point on the same level as in the atrium ruminis and the anterior ventral sac but below the mid point of the right longitudinal pillar.

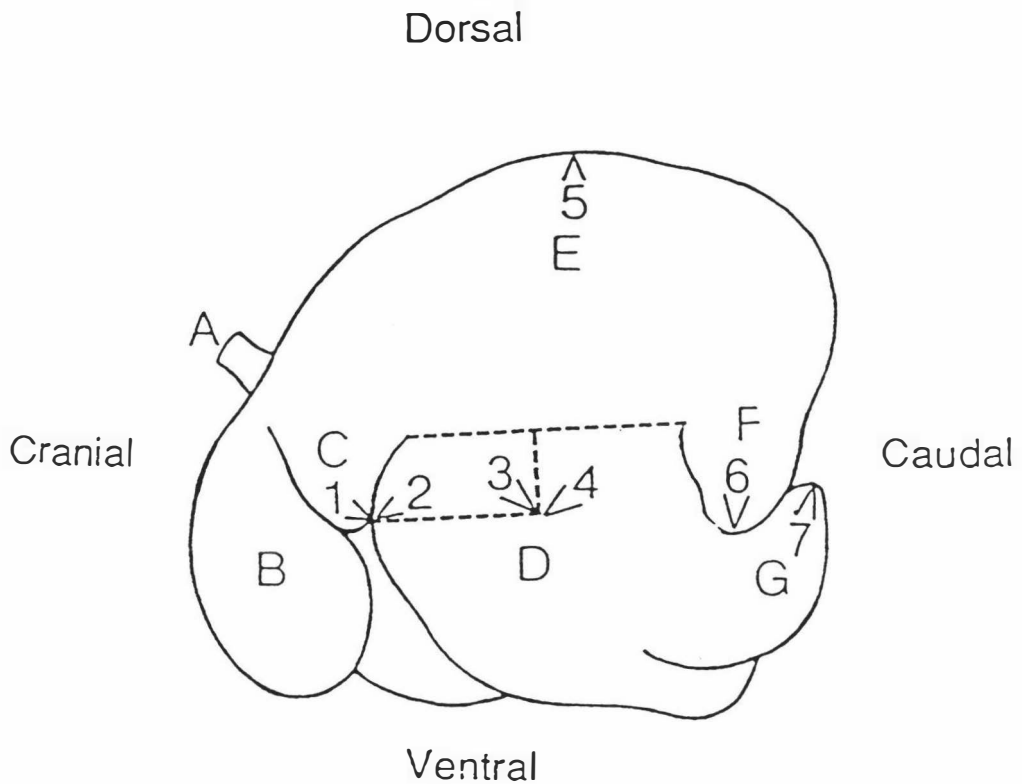


Fig. 2. Rumen anatomy of deer showing standardised sample sites

- A Oesophagus
- B Reticulum
- C Atrium ruminis
- D Ventral sac
- E Dorsal sac
- F Caudodorsal blind sac
- G Caudodorsal blind sac

< Centrepont of sampling site

- 1 Site of atrium ruminis sample
- 2 Site of anterior ventral sac sample
- 3 Site of right wall of ventral sac sample (en face)
- 4 Site of left wall of ventral sac sample (en face)
- 5 Approximate site of dorsal sac sample (varies with specimen)
- 6 Site of caudodorsal blind sac sample
- 7 Site of caudoventral blind sac sample

6) Caudodorsal blind sac (CDBS). The site was centred at the most caudal point of caudodorsal blind sac.

7) Caudovertral blind sac (CVBS). The site was centred at the most caudal point of caudovertral blind sac.

A rectangular sample of approximately seven by nine centimetres size was cut out of the rumen wall around the sampling site centres in the atrium ruminis, the ventral sac and the dorsal sac. The most caudal portion of each blind sac was removed by a cut applied transversely across the junction with the main sac.

Rectangular samples were cut so that their sides were parallel or at right angles to the longitudinal pillars of the rumen. The relevant samples and sides were marked with pins for identification.

The specimens were laid out on the bottom of a large flat container and the lengths of the four sides recorded. An average of the two lengths and the two breadths was taken. The area calculation was obtained by multiplication of these two averages.

In the case of the blind sacs, the samples consisted of a pouched sac. In order for the sample to lie flat for area measurement, a radial cut was made from the base of the pouch to the apex. The area calculations were based on an average radial measurement and did not allow for the missing segment due to the radial cut.

The maximal widths and lengths of fifty papillae were measured. No more than five papillae from one edge of each specimen were measured.

The specimens were then completely immersed to a depth of two centimetres in 10% formal saline at room temperature. The specimens were not fixed to the base of the container and were left undisturbed for either 2 or 7 days. The samples that were left for an initial period of 7 days were subsequently left for a further 7 days under the

same conditions and their length and breadth were subsequently remeasured.

2:3 RESULTS

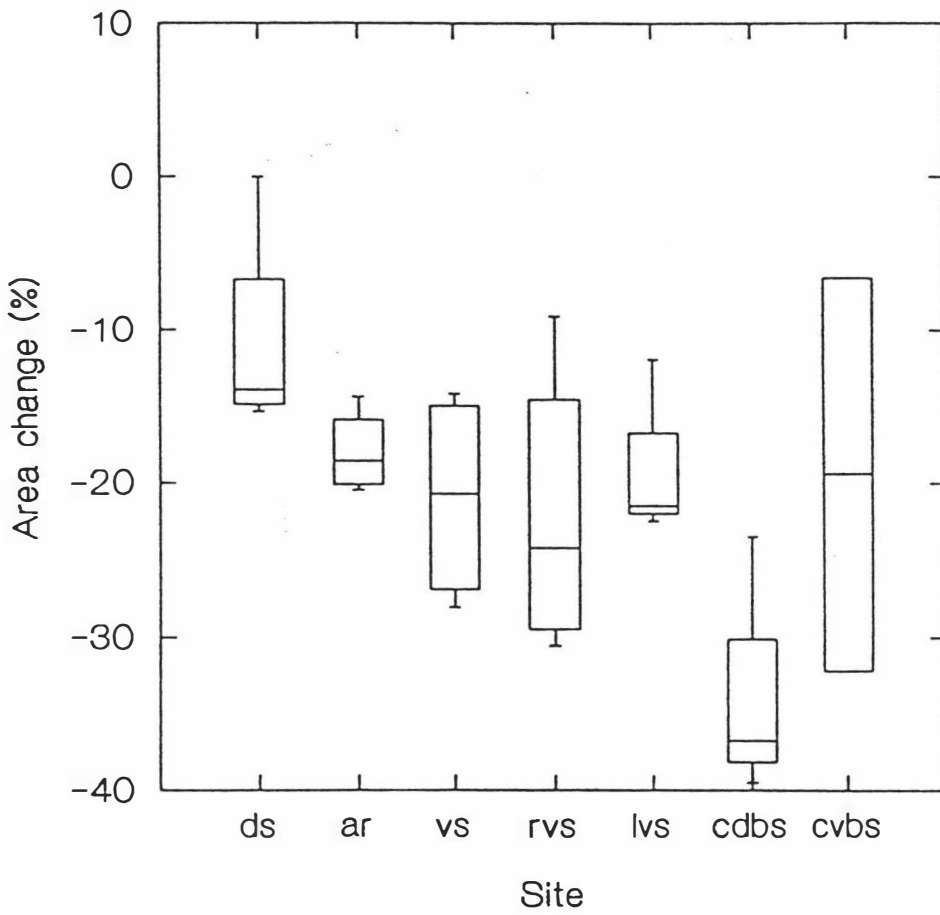
a) Rumen wall shrinkages

TABLE I Linear and area shrinkages of formalinised deer rumens  
sampling sites and measurement interval

Sample measurement interval	Site	%Change		
		Length	Breadth	Area
4yr old Summer stag One week	AR	14.00	6.67	19.73
	DS	9.33	4.44	13.36
	VS	23.20	6.25	28.01
	RVS	25.00	4.44	28.33
	LVS	9.23	14.54	22.43
	CDBS	22.22	-	39.51
	CVBS	17.65	-	32.18
2yr old Autumn stag One week	AR	11.29	3.45	14.35
	DS	6.67	8.33	14.44
	VS	0.00	15.71	15.71
	RVS	9.09	0.00	9.09
	LVS	4.76	17.50	21.43
	CDBS	12.50	-	23.44
4yr old Autumn stag One week	AR	12.50	9.09	20.45
	DS	5.88	10.00	15.29
	VS	0.00	14.14	14.14
	RVS	11.11	10.00	20.00
	LVS	5.88	6.41	11.92
	CDBS	20.45	-	36.72
	CVBS	3.33	-	6.56
3yr old Autumn stag 48 hours	AR	9.09	9.09	17.35
	DS	0.00	0.00	0.00
	VS	7.14	20.00	25.71
	RVS	16.67	16.67	30.56



Fig. 3. Box plot of % area shrinkages with formalinisation, at specific sites in red deer rumen wall sections.



Most specimens from the different sites in the rumen shrank, (table I and fig 3 ) with a wide variation in change of area (0%-25%)(table I). Changes in length and breadth were not consistently equal (table I). The shrinkage rate was not consistent for individual sites even with the small age and seasonal spread of our samples. It is notable that in the case of the two four year old winter stags there were widely differing shrinkage rates for the same site.

The samples that were remeasured after a second week in formal saline showed no further shrinkage within the limits of our measurement ( $\pm 0.025$  cm). However in the case of the three year old stag there was notable shrinkage after 48 hours at some sites showing that significant changes can take place after relatively short periods of formalinisation.

#### b) Papillary shrinkages

Fifty length and fifty breadth measurements from various sites and samples were recorded before and after one weeks formalinisation. No differences in length or breadth were recorded within the limits of our measurement technique ( $\pm 0.025$  cm)

### DISCUSSION AND CONCLUSIONS

The results showed wide variations in shrinkage rates of formalinised rumen wall samples. However there was no detectable change of papillary dimensions under the same conditions. Thus whilst estimates of papillary surface area will be unaffected by formalinisation, calculations that involve estimates of papillary density or other functions of volume will show considerable variation. A notable case is the calculation of the "factor of increase in surface area" (FISA).

Assuming FISA as stated previously and  $N = d \times BS$  where  $d$  is the density and let  $P = 2LW$  (an approximation to the surface area of a papilla)

$$FISA = \frac{PN + BS}{BS} = \frac{PdBS + BS}{BS} = Pd + 1$$

Now let there be a proportional shrinkage of  $H$  ( $0 < H < 1$ ) i.e. a sample originally 1

cm<sup>2</sup> becomes  $1 \times (1-H)$  cm.<sup>2</sup>

The papillary density observed will now be =  $\frac{d}{(1-H)}$

If we assume that shrinkage does not affect papillary dimensions

$$ApparentFISA = \frac{Pd}{1-H} + 1 \text{ but } TrueFISA = Pd + 1$$

$$\text{Therefore Proportional change in } FISA = \frac{TrueFISA - ApparentFISA}{TrueFISA}$$

$$\text{Substituting and simplifying, change in } FISA = \frac{Pd(H / H - 1)}{Pd + 1} \dots\dots\dots(1)$$

Now if  $Pd$  is very large compared to 1

$$\text{Change in } \approx \frac{H}{H - 1} \dots\dots\dots(2)$$

Assuming parameters for red deer quoted by Langer (1988)

$L = 1.0$  cm.  $W = 0.3$  cm.  $d = 50-100$

$Pd = 30$  to  $60$  i.e.  $Pd$  is large compared to 1.0

So FISA can be approximated by (2) above. If shrinkage rates are small (0-25%)

then  $H/(H-1) \approx H$  and the increase in FISA is approximately equal to the % shrinkage (fig 4).

Fig. 4. Calculated effect of uniform rumen wall shrinkage rates on FISA for a variety of papillary densities. Number of papillae per square cm. inset at right border. Dotted line is the approximation assuming  $Pd$  is large and shrinkage rates are small.

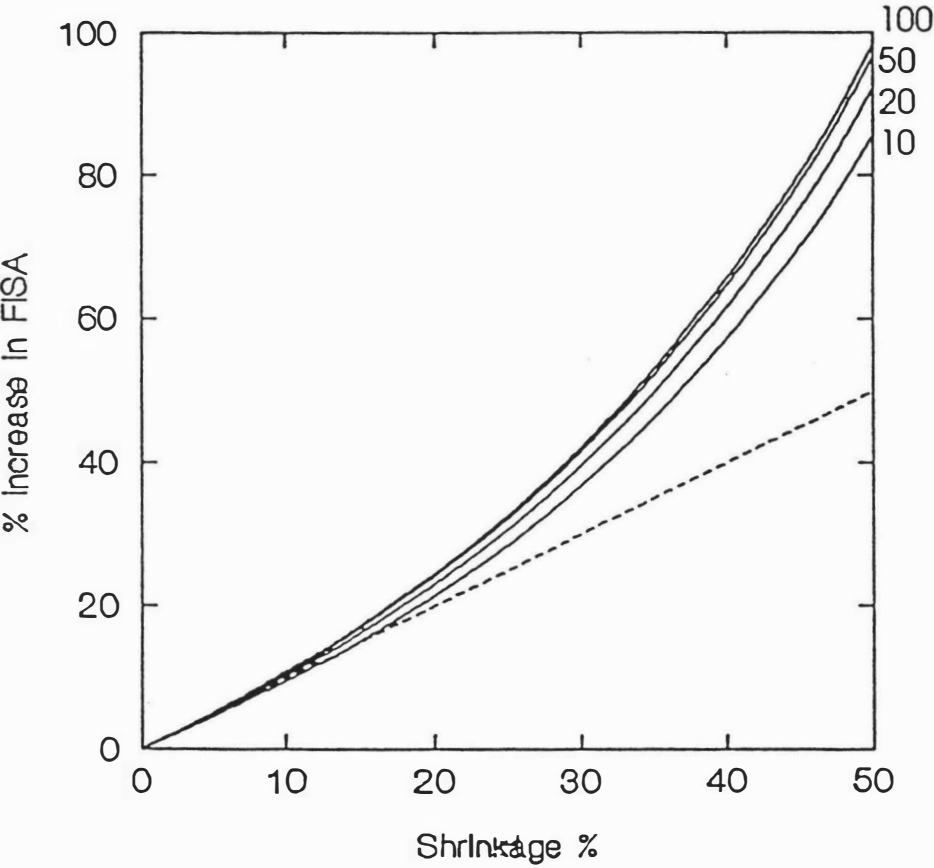
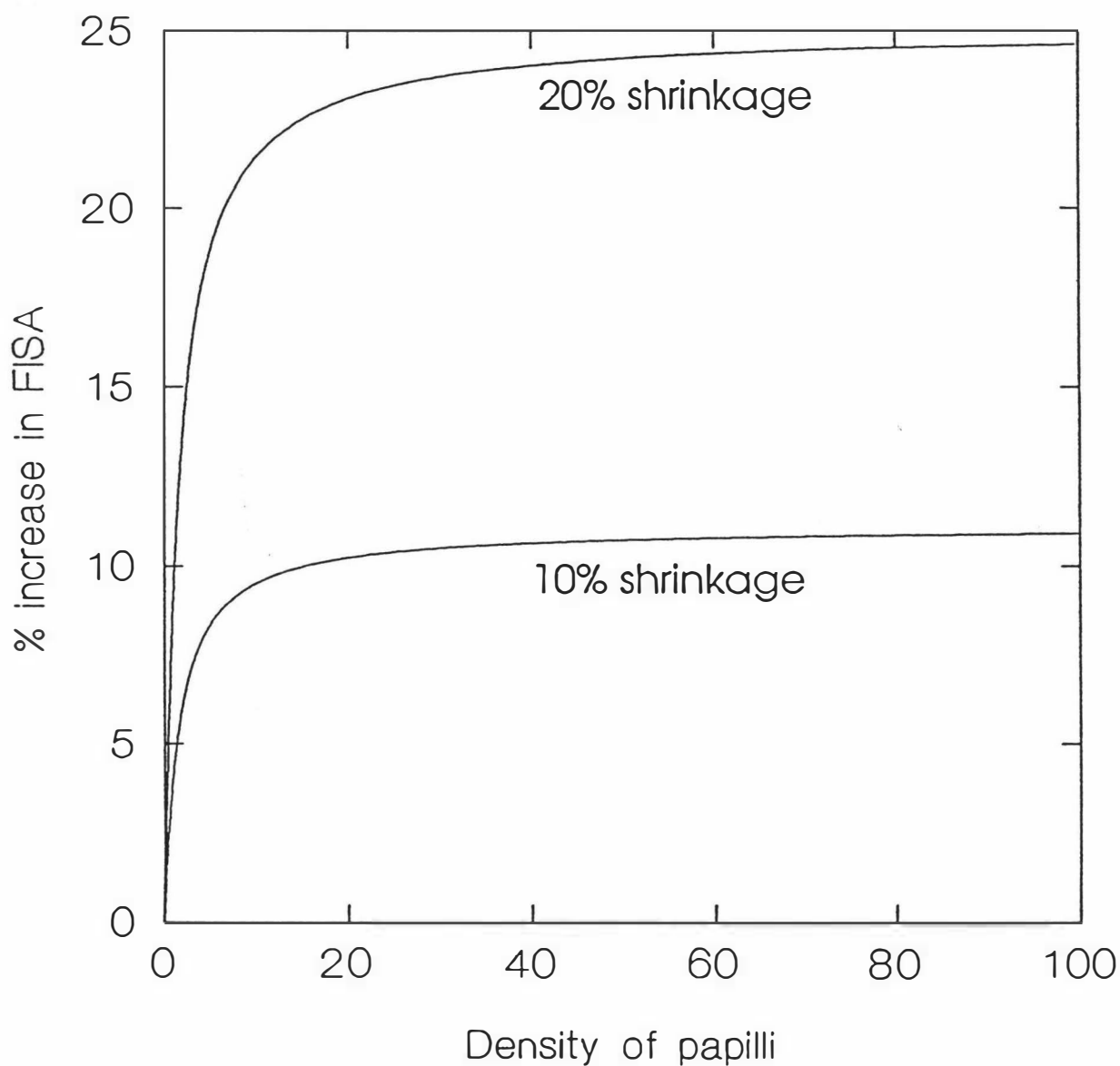


Fig. 5. Calculated effect of papillary density (number of papilli per square cm ) on FISA assuming uniform rumen wall area shrinkages of 10% and 20 %.



The change in FISA is also affected by papillary size and density but only if values are small (fig 5). For densities greater than 20, FISA is almost constant for a given  $H$  although for higher shrinkage rates this threshold is marginally greater. The same effect would be seen if papillae are small since the critical factor is  $Pd$ . If papillary size is less than half the value used here for illustration and density remains at between 50 and 100 then the approximation in (2) will be inadequate.

Thus in the context of this analysis a constant shrinkage rate results in an approximate increase in FISA of  $H$  or greater.

As a consequence of the low sample numbers the results from this study should be viewed with caution. We acknowledge that our method does not incorporate the techniques that are used by all workers in the field (Langer 1974). Formalinisation of small separate pieces of rumen wall was chosen as this allowed accurate measurements prior to and after formalinisation. Whilst this follows the most convenient sampling technique used in the field whereby only small pieces of the rumen are kept for analysis, we recognise that other workers may formalinise the whole rumen and create different contraction conditions which were not described by our data.

10% formal saline solution was used in this study but different strengths have been used by different workers, 10% ( Tamate et al. 1962), 6% ( Hoffman, 1976) and 4% (Langer, 1974). Further work is needed to assess whether or not different concentrations produce different degrees of rumen contraction.

We hold our area calculation to be a reasonable measure for a variety of quadrilateral shapes but extreme distortion as sometimes occurs could invalidate this assumption.

A variety of mechanisms may be operating to produce the results we obtained. At given sites rumen muscle thickness and type varies ontogenically (Langer 1988) and with age (Dresher-Kaden 1981). Rumen muscle tensions may be a function of rumen volume which is known to change with season (Milne, 1980; Francoise-Domingue,

1991; Sibbald and Milne, 1993) and age (Bubenik 1982). Future studies based on larger sample numbers may allow prediction of shrinkage rates and enable appropriate allowances to be made in FISA calculations but in view of the presumed variety of contributing factors this is unlikely.

Meanwhile because of the wide and unpredictable variation in rumen wall shrinkage demonstrated in this study, it is preferable to use papillary analysis as this is not affected by formalin shrinkage and other post mortem volume changes. There is support in the literature for the validity of this approach as Langer (1974) noted that in roe deer (*Capreolus capreolus*) shot on "geest" and "altmoraine" regions of Germany, areas of considerable difference in soil fertility, there was a notable difference of papillary length whereas no significant FISA differences were found.

A separate study of rumen papillary dimension and volume is also consistent with the current concept of considerable independence of rumen volume and papillary development. The work of Tamate et al. (1962) highlights local chemically signalled responses of rumen papillae whereas the work of Ulyatt et al. (1984), Reid (1984), Kennedy and Murphy (1988), Francoise-Domingue (1991), and Spalinger et al. (1993), all emphasises the variability of rumen volume and onflow rates which are thought to be mediated primarily by complex nerve pathways that link rumen, reticulum, omasum, abomasum, intestine, spinal cord and brain.

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## CHAPTER 3

RH Multivariate analysis of rumen papillae. Lentle et al.

# A MULTIVARIATE ANALYSIS OF RUMEN PAPILLARY SIZE IN RED DEER.

ROGER G. LENTLE. Department of Ecology. Massey University. Palmerston North. New Zealand.

IAN M. HENDERSON. Department of Ecology. Massey University. Palmerston North New Zealand

KEVIN J. STAFFORD. Department of Veterinary Clinical Sciences. Massey University. Palmerston North. New Zealand.

Abstract: We measured length and width of ruminal papillae from six anatomically defined sites in rumens of farmed and wild red (*Cervus elaphus*) and wild fallow (*Cervus dama*) deer. A multivariate (principle components) analysis was used to explore papillary response to diet. Three axes of variation were discovered, overall papillary size, papillary shape and site specific papillation (variation according to anatomical site within the rumen). These axes responded differently to changes in age, sex, diet and species. Overall papillary size increased with age in wild but not in farmed stock, was significantly affected by sex, but showed no interspecies difference. Papillary shape was not influenced by age, sex or diet but was influenced by species. Site specific development was influenced by age or sex but not by diet and species. These results validate previous descriptive work and offer a technique for quantitative study of the interaction between wild ruminants and their dietary environment.

Key words: Anatomy, Cervus dama, Cervus elaphus, Farm deer, Multivariate analysis, New Zealand, Rumen papillae, Wild deer.

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## INTRODUCTION

The anatomy of the digestive systems of ruminants is a consequence of ecophysiological adaptation and diversification (Hoffman, 1989). The array of inter- and intraspecific anatomical variants is attributed to an interaction of environmental forces with a complex "morphophysiological master plan" (Hoffman, 1989). Using evidence from 65 ruminant species, anatomical variation in the structure of the rumen, was correlated with broad dietary preferences according to three "ruminant feeding types" (Hoffman and Stewart, 1972). These were, "concentrate selectors", equipped to cope with a selected diet of dicotyledonous foliage and fruit low in fibre and high in cellular fluid content, "grass/roughage eaters" equipped to deal with a more bulky and fibrous diet of predominantly monocotyledonous foliage and a more versatile "intermediate type" able to utilise both monocotyledonous and dicotyledonous food sources. Broadly speaking Hoffman and Stewarts (1972) ruminant feeding types correspond to Langers (1988) herbivory ratings (HR), where concentrate selectors were rated HR2-HR3, intermediate feeders HR3-HR4 and grass/roughage feeders HR5-HR6.

Rumen papillae maintain an ability to change morphologically with changing dietary conditions through life (Hoffman, 1973,1989). Volatile fatty acids in particular, have been shown to stimulate rumen papillary development in young calves (Tamate et al., 1962). Previous anatomical studies of rumen papillation in various species ( Hoffman, 1973; 1976; 1985; 1989; Konig et al., 1976; Langer, 1974; Stafford and Stafford, 1990, 1991) did not attempt to quantify variation of

rumen papillae in relation to animal age, sex and diet. Some monitoring of change in papillary dimensions in relation to these variables is required if we are to understand their contribution to the interaction of the animal with its environment.

Assessment of papillary morphology could be of value in the context of game management. If rumen papillary morphology is pliant (Hoffman; 1973,1989) it will respond within a short time to changes in diet ( Tamate et al., 1962; Clark, 1982; Nockels et al., 1966) and maintain function as near to optimal as other constraints allow. Thus differences in papillary morphology that correlate with dietary quality and quantity may be used to quantify nutritional constraints. If an increase in dietary fibre or plant toxin intake correlates with decreasing dietary quality due to overpopulation and these changes correlate with changes in papillary morphology, then the latter could be used to assess overstocking. This may be possible only if the contribution of demographic variables, such as age and sex, to papillary morphology are known and allowed for.

Conversely if diet is maintained at an optimal level then papillary morphological differences could allow a quantitative assessment of the role of demographic factors such as age and sex in overall bionomic or lifetime reproductive strategy (Clutton-Brock et al., 1982).

This study attempts to quantify the extent of rumen papillary change in response to dietary and demographic variables in both farmed red deer and wild red and fallow deer.

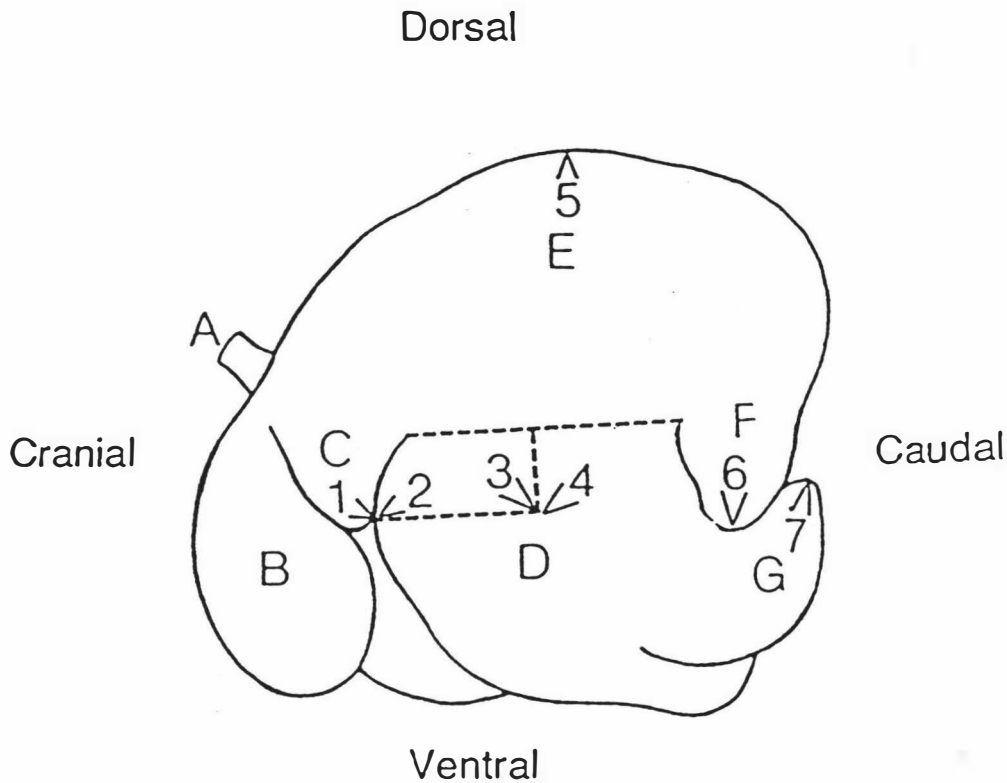


Fig. 6. Rumen anatomy of deer showing standardised sample sites

- A Oesophagus
- B Reticulum
- C Atrium ruminis
- D Ventral sac
- E Dorsal sac
- F Caudodorsal blind sac
- G Caudodorsal blind sac

< Centrepont of sampling site

- 1 Site of atrium ruminis sample
- 2 Site of anterior ventral sac sample
- 3 Site of right wall of ventral sac sample (en face)
- 4 Site of left wall of ventral sac sample (en face)
- 5 Approximate site of dorsal sac sample (varies with specimen)
- 6 Site of caudodorsal blind sac sample
- 7 Site of caudoventral blind sac sample

## MATERIALS AND METHODS

### Sampling sites and species

Stomachs were obtained from wild red deer shot on the western ranges of Ruahine State Forest Park, North Island, New Zealand. This park comprises 93,564 hectares of continuous native New Zealand vegetation comprising alpine tussock uplands that are largely snow covered in winter below which are montane scrub and extensive Podocarp-Hardwood and Podocarp Hardwood Beech (*Nothofagus* spp.) forests with some interspersed kanuka (*Leptospermum ericodes*) and manuka (*Leptospermum scoparium*) scrubland (Newsome, 1987). Red deer have inhabited the area since 1862 (Wodzicki, 1950) and have free access throughout but avoid open areas during daylight hours as a consequence of hunting pressure.

Since 1973, deer numbers have been maintained below carrying capacity and evidence from jaw length-age relationships shows a trend of increasing nutritional status (Kelton, 1983; Landcare, 1992). It is thus probable that there is good year round food availability.

Rumen samples were obtained by ground shooting and by helicopter hunting during morning daylight hours. Rumens were removed via a ventral abdominal incision and emptied via an incision in the dorsal sac. One hundred millilitres of 10% formal saline was poured into each rumen via the incision. The specimens were kept cool until returned to the laboratory whereupon they were frozen at -4°C until required for analysis. The lower jaw was removed from each deer for use in determining its age. The animals sex and date of death were also recorded.

Rumens from farmed red deer of known age and sex were obtained at the Venison New Zealand limited (Feilding) deer abattoir. Rumens from wild fallow deer were obtained from animals shot in the Ahu ahu stream region of the Whanganui river catchment area, North Island, New Zealand. The vegetation is extensive manuka

farm pasture areas (Newsome, 1987), the latter providing the principle food supply (Harris, 1973). The area has been subject to steady hunting pressure for the last ten years with animal numbers declining steadily for that period (personal communication land owner) thus animal densities were likely to be below carrying capacity.

Papillary measurement technique.

Sampling sites (fig 6);

As an important aim of this study is to quantify the intraruminal variability of papillary dimensions, it is important to define the sampling sites accurately with reference to definite anatomical landmarks. Square samples (50 x 50 mm) with their central point located at one of the "centrepoinets" described below were taken from each rumen wall after thawing.

- a) Atrium ruminis; The centrepoinet was located at the lowest point of fusion of the posterior wall of the atrium ruminis with the anterior wall of the ventral sac, at a position immediately below the midpoint of the cranial pillar.
- b) Anterior wall of the ventral sac; The centrepoinet was located at the lowest point of fusion of the anterior wall of the ventral sac with the posterior wall of the atrium ruminis at a position immediately below the midpoint of the cranial pillar. This sample site was in a position corresponding that of the atrium ruminis sample site but on the caudal side of the cranial pillar.
- c) Right wall of the ventral sac; The centrepoinet was located at the point of intersection of a line projected caudally parallel to the main axis of the right longitudinal pillar along the right wall of the ventral sac from the centrepoinet of the anterior wall site with a line projected ventrally at right angles to the right longitudinal pillar from its midpoint. The midpoint of the right longitudinal pillar was taken as half the distance along a line running from the point at which the anterior pillar and the right longitudinal pillar fuse, to the point at which the left

superior coronary pillar and the right longitudinal pillar fuse.

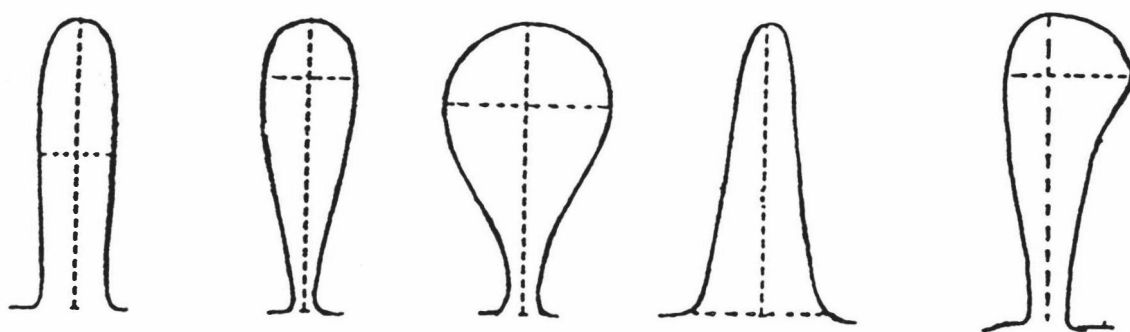
- d) Left wall of the ventral sac; The centrepoint was located at the point of intersection of a horizontal line projected caudally from the centrepoint of the anterior wall sampling site parallel to the main axis of the left longitudinal pillar with that of a line projected ventrally at right angles to the mid point of the left longitudinal pillar. The mid point of the left longitudinal pillar being half the distance from the point of fusion of the anterior pillar with the left longitudinal pillar to that of the point of fusion of the left superior coronary pillar with the caudal pillar. This caudal point was determined from the base of the caudal pillar rather than the left longitudinal pillar as the caudal projection of the latter was indistinct.
- e) Dorsal sac; The centrepoint was located at a site considered to be the highest point of the dorsal sac. However because there are no suitable fixed anatomical landmarks in this area, the site selected was that with the least papillary development. This area varied in position on the superior midline of the dorsal sac as a consequence of variations in overall rumen volume.
- f) Caudodorsal blind sac. The caudal tip of the structure.
- g) Caudoventral blind sac. The caudal tip of the structure. In mature red deer two caudoventral blind sacs were present, in which case the caudal tip of the more dorsal sac was sampled.

#### Measurement Procedure.

Specimens were washed in 10% formal saline to remove any particulate matter, then blotted with absorbent tissue to remove excess fluid before being placed under a binocular microscope for measurement. In the case of the caudodorsal and caudoventral blind sac samples, a radially oriented cut was made from the periphery to the centre of the specimen to allow the sample to lie flat. Individual papillae were



Fig. 7. Length and breadth measurement sites for various papillary shapes.



grasped using a pair of fine forceps and applied to a plastic scale held with its zero point at the papillary base and the papillary length was measured. The same scale was used to measure the maximum width of the papillae. Measurements were read directly from the scale via the microscope with an accuracy of  $\pm 0.05$  mm (fig 7).

In the case of asymmetrical or curved papillae the measurement was the maximal straight line distance from base to tip (fig 7).

Only papillae which were visible on the surface of the specimen were measured. Small papillae which were concealed from view beneath the tips of adjacent larger papillae were not measured thus avoiding partially avulsed or atypically short papillae. The true length of individual papillae only became evident when they were grasped and held against the scale for measurement, which prevented bias towards the selection of the largest papillae. The length and width of ten papillae were recorded from each sample.

#### Dental Aging

Wild deer were aged using tooth eruption sequence and, for older animals, molar tooth cementum analysis (Frazer and Sweetapple, 1993). Ages were computed from a mean assumed birth date of 9 December (Caughley 1971) in the case of red deer and 20 December in the case of fallow deer (G. Nugent personal communication in Frazer and Sweetapple 1993).

#### Statistics and calculations

Previous workers have utilised a number of different numerical characteristics such as the largest dimension, the modal dimension, or the average dimension when comparing rumen papillation. In this study the average for each site was calculated. The largest value from each sample was not chosen for analysis as a much greater sampling effort would have been required in order to obtain a reliable estimate of the largest value. i.e. In the case of our papillary sampling it was likely that an estimate based on ten values was inadequate. Modal values from each dataset were not

utilised as it was considered that the mean is a better measure of the central tendency of the data in that the central limit theorem states that the means will always approach a normal distribution which is useful for further statistical analysis (Mendenhall and Ott, 1980).

Mean values for 266 sites from 38 rumens from 22 wild red 10 farmed red and 6 wild fallow deer of known age and sex were subjected to principle components analysis using SYSTAT (Wilkinson, 1990). Principal components analysis is a method of mathematically ordering a swarm of data points in mutually perpendicular axes and estimating elements of overall structure arising out of data redundancy (Pielou, 1984). As such it has been useful in the investigation of biological variation along gradients (Guich 1982) and could be useful in describing trends of papillary growth in relation to nutrient and other gradients within the rumen.

## RESULTS AND ANALYSIS

Component loadings of the first three principal components with eigenvalues and percent total variance explained are shown in table II.

TABLE I : PAPILLARY PRINCIPAL COMPONENTS ANALYSIS ;  
Papillary length and breadth data from farmed and wild red and wild fallow deer.

Rumen Site	Papillary Dimension	Component loadings		
		PC1	PC2	PC3
AR	Length	0.733	-0.012	-0.332
RVS	Length	0.752	-0.493	0.221
VS	Length	0.750	-0.300	-0.184
LVS	Length	0.760	-0.171	0.309
DS	Length	0.578	-0.333	0.491
CDBS	Length	0.758	-0.307	-0.308
CVBS	Length	0.752	-0.369	-0.449
AR	Width	0.578	0.585	-0.230
RVS	Width	0.746	0.322	0.236
VS	Width	0.716	0.132	0.215
LVS	Width	0.778	0.288	0.316
DS	Width	0.622	0.258	0.100
CDBS	Width	0.800	0.196	-0.127
CVBS	Width	0.740	0.303	-0.183
EIGENVALUES		7.302	1.447	1.141
%TOTAL VARIANCE		52.157	10.336	8.151

Plots of PC1 on PC2 and PC1 on PC3 are shown in fig 8 and 9 (Discussion see below)

An analysis of variance of age, sex and species was carried out against PC1, PC2 and PC3 scores. The results are tabulated and probabilities listed where significant in table III .

Table III: Analysis of Variance of age, sex, diet (farmed or wild) and species (red or fallow) with PC score (Probabilities listed where significant.)

PC vector	Age	Sex	Diet	Species
1. Overall size	0.000	0.002	0.014	NS
2. Overall shape	NS	NS	NS	0.019
3. Site	NS	NS	0.004	0.029

Note: Correlation with age and sex on PC1 was not significant when farmed deer only were considered.

Interpretation of the PC axes.

On PC1 a distribution of component loadings that are of more or less equal value and the same sign indicated an index of overall papillary size . On PC2 a series of uniformly negative component loadings of length variables and positive loadings of width variables indicate an axis representing shape as expressed by length/width comparison. Both PC1 and PC2 reflect patterns consistent over all sites in the rumen.

PC3 reflects a comparison of the state of development of papillae in different regions of the rumen. The axis contrasts rumens having greater development of blind sac and atrium ruminis papillae against those rumens having greater dorsal sac papillary development. The pattern of loadings on PC 3 also suggest a smaller horizontal trend across the floor of the ventral sac grading from most negative in the

blind sacs and less negative on the anterior wall of the ventral sac (fig 11).

#### Effects of age and sex

Analysis of covariance of PC axis 1 (overall papillary size) against age and sex (Table III) shows significant effects of age ( $F = 25.850$ ,  $p = 0.001$ ) and sex ( $F = 11.363$ ,  $p = 0.002$ ). The y intercept of the male age regression line (15 male samples) was significantly higher than that of females ( $p=0.002$ ) (19 female samples), and there was a barely significant difference in the slope of the age regression lines in the two sexes ( $p=0.069$ ) the female line being steeper (fig 10). Thus PC1 values tended to be higher in younger males than younger females but values became more similar in the two sexes in older age groups. The four animals over the age of 70 months were excluded from this analysis on the basis that plots of PC1 (overall papillary size) or PC2 (shape as a length/width comparison) against age showed a linear increase with age in the early years and a plateau being reached at age 70 months.

When wild red deer only were subject to analysis the results remained significant (age,  $F$  ratio = 33.291,  $p = 0.000$ ) (sex,  $F$  ratio = 7.535,  $p = 0.013$ ). However with farmed red deer alone, analysis failed to demonstrate any significant effect of either age or sex on PC1. Regressions of PC2 and PC3 against age or sex showed no significant effects.

Fig. 8. Plot of papillary principal component analysis PC vector 1 (Overall papillary size) values against PC vector 2 (shape as a length width comparison) values. Small squares, wild red deer. Circles, wild fallow deer. Triangles, farmed red deer.

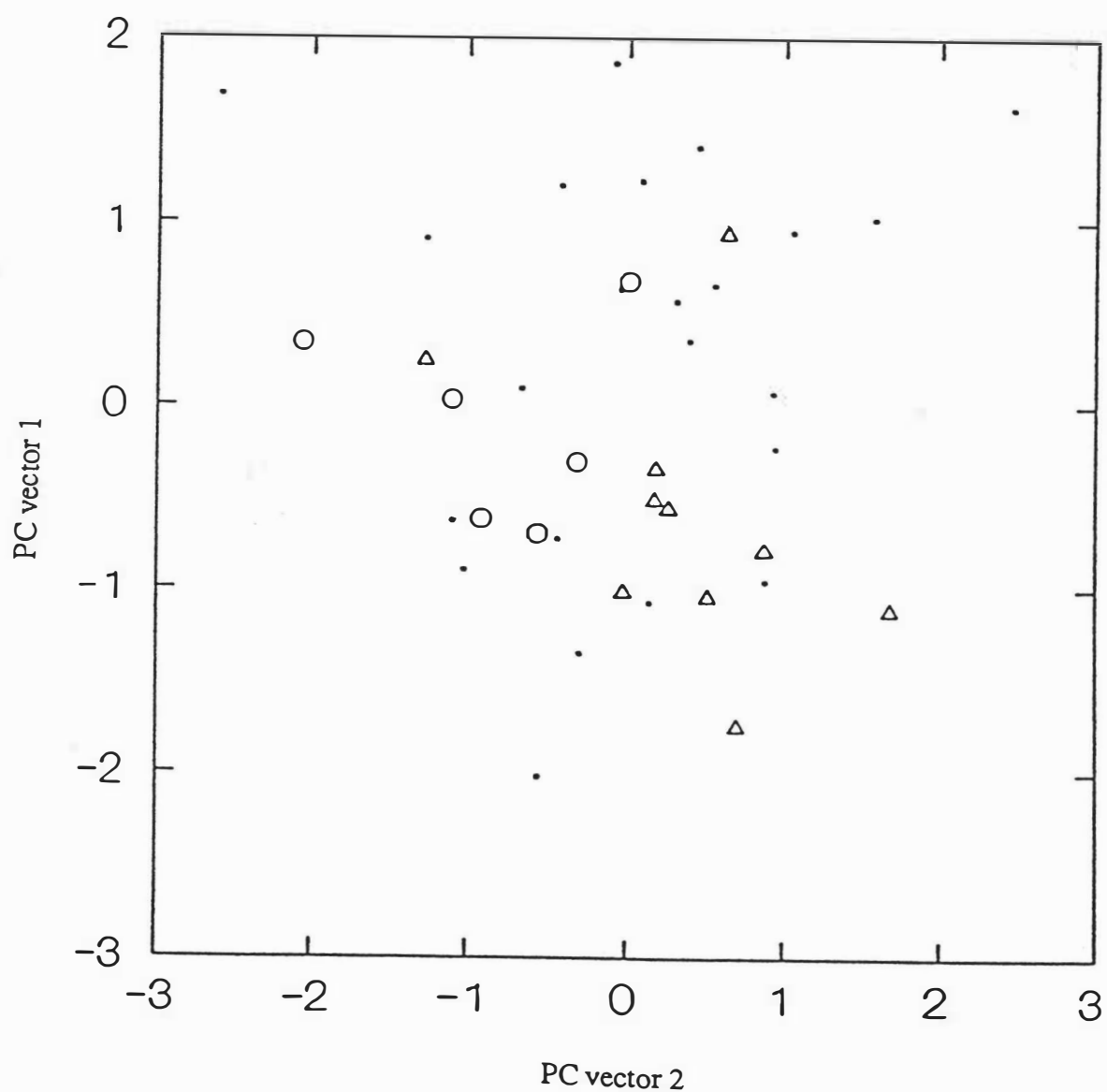


Fig. 9. Plot of papillary principal component analysis PC vector 1 (Overall papillary size) values against PC vector 3 (Site specific factor) values. Small squares, wild red deer. Circles, wild fallow deer. Triangles, farmed red deer.

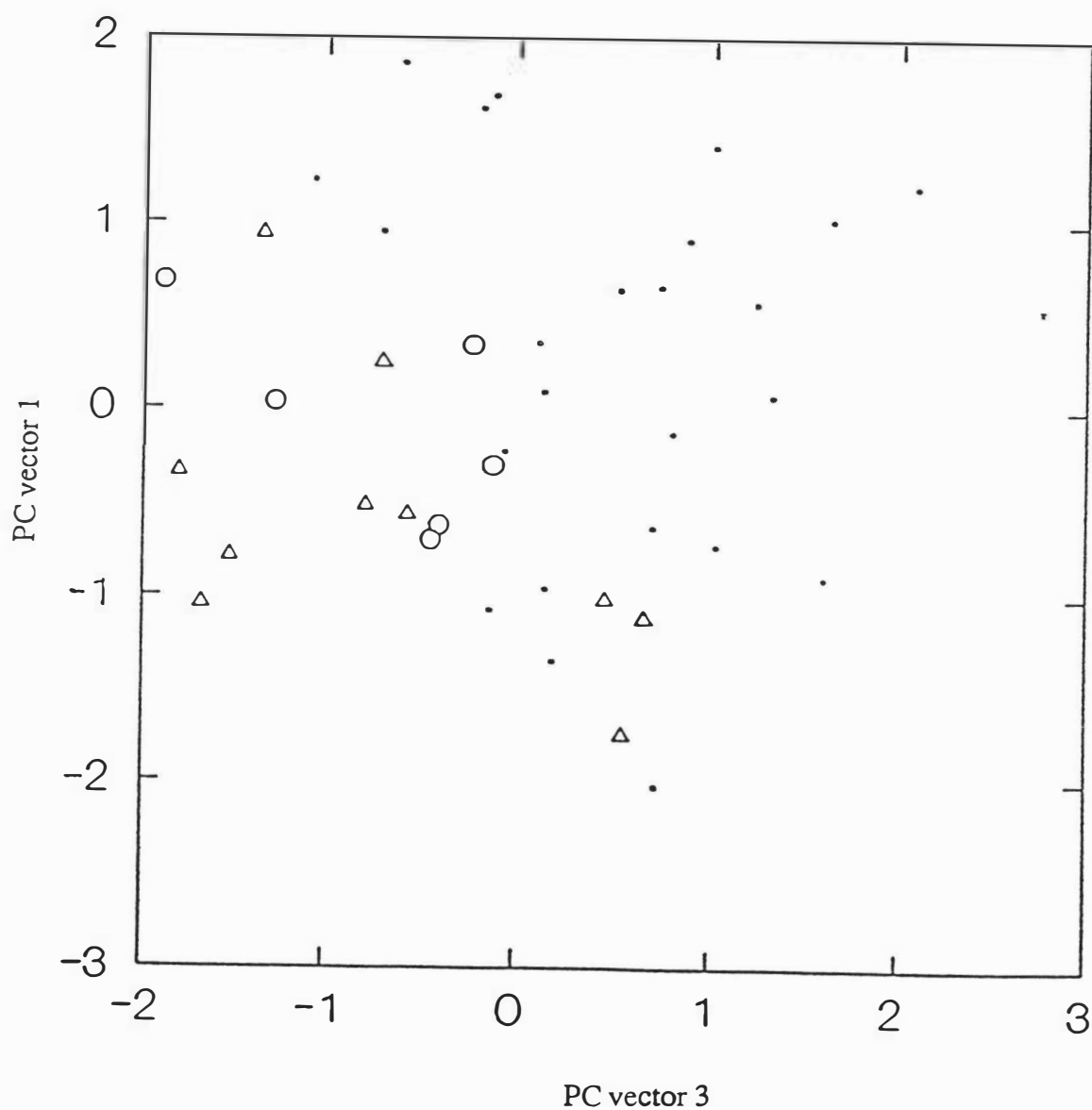




Fig. 10. Plot of papillary principal component analysis PC 1 values for all categories of deer (wild fallow, farmed red and wild red deer) against age. Males (solid circles), females (solid triangles). Separate linear regressions shown for males (solid line) and females (dotted line).

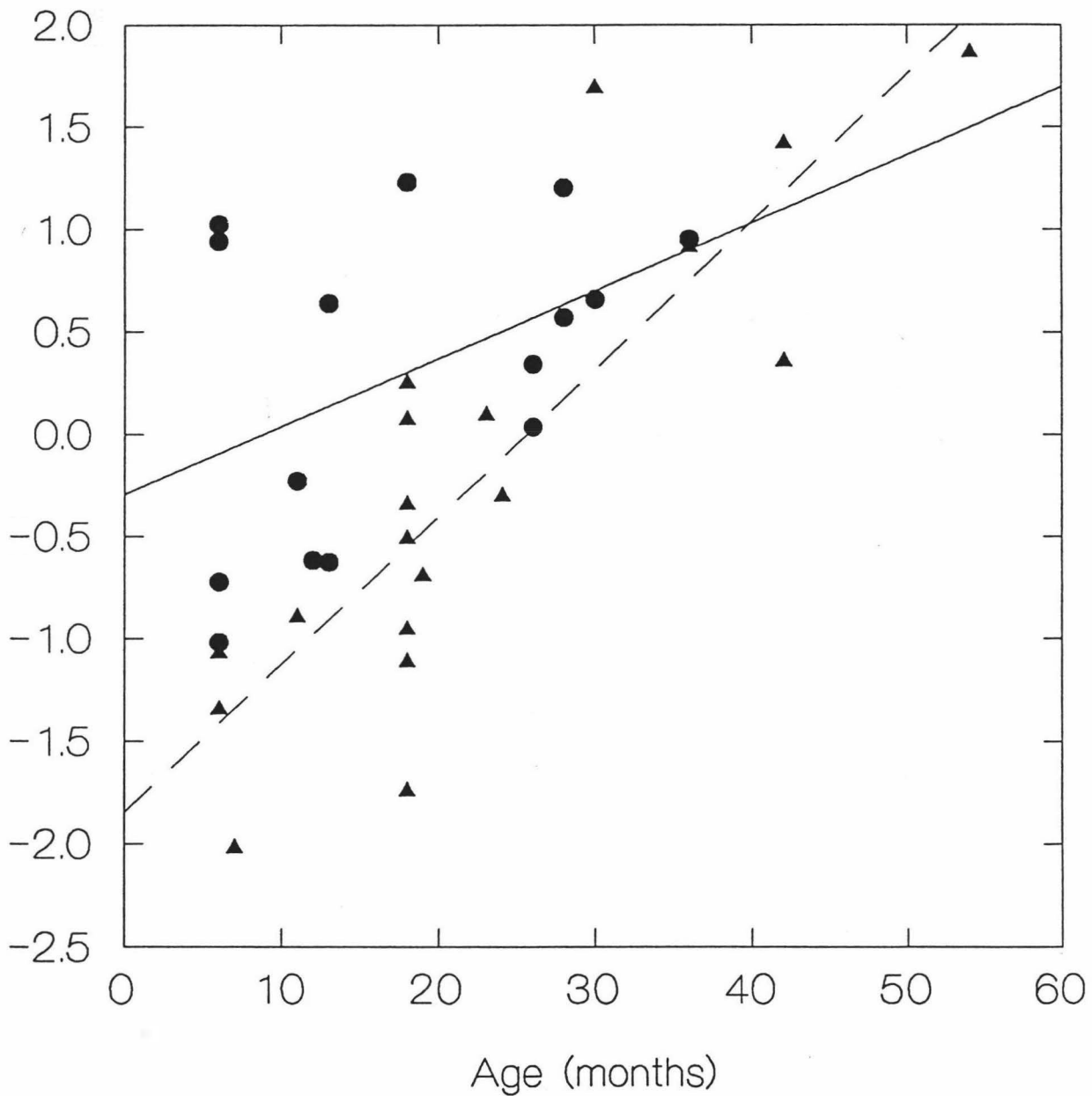
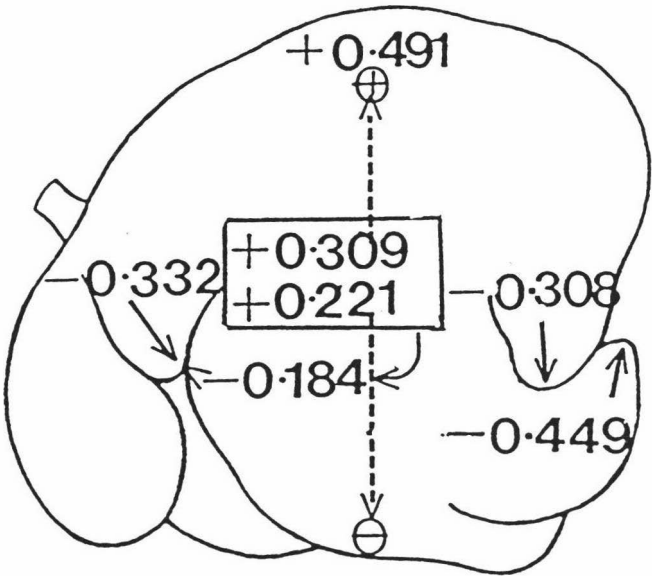


Fig. 11. Ordination of papillary principal component PC axis 3 (site specific) papillary length loading factors. Factors are shown superimposed on the sampling site (Dotted line shows general orientation of +ve to -ve values).



### Effects of species and habitat

The results of independent sample t tests on PC factors one to three are summarised in Table III. There was no significant difference in PC1 (overall papillary size) scores between Red and Fallow deer ( $T=0.368$   $p=0.718$ ). There were however significant differences between species in PC2 (shape as width/length ratio) scores ( $T=2.862$   $p=0.019$ ) and PC3 scores ( $T=2.584$   $p=0.029$ )

In the case of habitat (farmed or wild) there was no significant difference with PC2 scores ( $T=0.976$ ,  $p=0.339$ ) but a significant difference in PC1 ( $T=2.651$ ,  $p=0.014$ ) and PC3 ( $T=3.378$ ,  $p=0.004$ ) scores.

### Effects of season

Coding for season on PC axis plots showed no clear separation on any axis i.e. there is no relationship of season with any of the PC axes.

## DISCUSSION

Principal components analysis is a statistical method of data analysis that enables the identification of trends in multivariate data sets. A further advantage arises out of the use of this approach as it makes no reference to pre established axes of variation (Pielou, 1984). The significance and relative contributions to total variance of the principal component axes are therefore of particular interest as they are the outcome of an unbiased pattern search. Any concordance of these axes with conclusions derived from more descriptive previous work that indicates change of rumen papillary parameters along predetermined axes of variation (such as for example herbivory rating) must therefore have a powerful validating effect. Moreover relative contributions to total variance offer an independent assessment of the relative order of these effects.

The first principal component axis (PC1 overall papillary size) accounted for 52% of the total variance and was demonstrated by the statistical analysis to be strongly age, sex and habitat dependant. Increase in papillary length with age has been

previously described in cattle (Tamate et al., 1962; Arias et al., 1980) sheep (Omar et al., 1964) and roe deer (Langer, 1974).

The dimorphism of the fitted regression lines for male and female red deer (fig 10) could be viewed as concordant with studies by Clutton Brock et al. (1982) on lifetime reproductive strategies in red deer in Scotland. In a synopsis of "ultimate factors affecting reproductive success" these workers state "Success of stags is related to body size, early growth and maternal investment during the first year of life. Success of hinds is not closely related to size or (by implication) to investment before weaning, but strongly affected by resource access during adulthood and the size of the matrilineal group to which they belong". The higher Y intercept point and lesser slope of the overall papillary size versus age regression line in males may reflect differences in bionomic strategy i.e. early overall papillary size development may be more vigorous in male than in female deer.

The failure of PC axis 1 to separate red and fallow deer papillary characteristics on the basis of size may seem surprising. However considerable variation of mean papillary lengths of fallow deer has been reported, ranging from 4.29mm (Langer, 1974) to 9.77mm (Geiger et al., 1977). Hoffman (1976) reported a mean papillary length of 10.27 mm. for red deer. Thus the reported values for the two species are similar.

Previous work has demonstrated an inverse relationship between the average body size of species and rumen fermentation rate (Prins et al., 1971; Maloiy et al., 1982). Fermentation rate is, because of its stoichiometric relationship to substrate, an indirect measure of VFA production (Hoppe et al., 1977). Fermentation rate is also related to dietary composition (Hungate, 1965; Hoppe et al., 1977). If the relationship between dietary type and fermentation rate proposed by Hoffman (1989) is correct, grass and bulk feeders will have lower fermentation and VFA production rates than intermediate and concentrate selectors. Species body size related

differences may offset species feeding type differences yielding similar overall fermentation and VFA production rates. If these then promote similar absorptive capacities, this may in turn cause similar overall papillary size development in small bodied grasseaters (fallow deer) and larger bodied intermediate feeders (red deer).

PC 1 also separated farmed from wild red deer i.e. farmed deer have significantly smaller overall papillary size. In this case there were no species differences and it is possible that any change in fermentation rate would have been primarily a consequence of diet change similar to that reported by Hoppe (1977). If indeed overall papillary size is related to fermentation rate then this result may be seen to fit in with the work of Hungate (1965) demonstrating lower fermentation rates in grass eaters. It is interesting to note that in farmed deer where all the animals are fed the same diet, age and sex differences become non-significant.

The season of sampling showed no significant relationship with any PC axis. This result may be considered surprising in the light of reported morphological papillary response times to change of diet of 3 weeks (Ortega-Reyes et al., 1992) and previous reports of seasonal variation of papillary size in roe deer (Langer 1974) and wild african bovids (Hoffman, 1973). However this could be because quality of browse does not vary seasonally at animal densities below carrying capacity i.e. at low population densities sufficient high quality feed will be available year round. In the Ruahine herd, animal density is well below carrying capacity (Kelton 1983, Landcare 1992). Moreover a concurrent analysis of rumen vegetation contents (Lentle, 1994) showed no significant change with season but a significant difference between wild and farmed red deer.

There is significant separation of red and fallow deer on PC2 axis (papillary shape as length/width), fallow deer tending to more negative values i.e having thin and long papillae. PC2 however fails to separate wild from farmed red deer. This implies that the dietary variable applied to deer of same species does not influence overall

papillary shape. Papillary shape may be thus more an outcome of inherent properties of the rumen e.g. flow characteristics, that are brought about by species differences. The failure of PC2 to correlate significantly with age indicates that body size effects are less likely to effect shape.

It is the opinion of a number of workers that in roughage selectors differentiation between papillae in different ruminal regions is correlated with the stratification of rumen contents (Langer, 1988; Schoenemann and Kilian, 1960; Capote and Hentges, 1967; Hofmann, 1973). The site specific variation may be caused not only by the formation of an abrasive less easily digestible mat but also by the shedding of particulate matter which accumulates in lower sites (Capote and Hentges, 1967). Conversely in intermediate and concentrate selectors, less complete mat formation will produce less abrasion to the dorsal sac wall along with a more uniform dispersal of nutrients.

In this analysis PC3 was interpreted as a site specific papillation factor that contrasted dorsal versus ventral papillary development. Here a primary vertical site separation axis and a smaller secondary horizontal axis (see fig 11) relate the site specific (PC3) component loadings. Farmed deer have lower scores on PC3 as do fallow deer. Indeed the scatter of farmed red and fallow data overlap considerably (Fig 9). PC3 could be viewed as separating the three groups of animals on the basis of the ruminal dispersal of nutrients discussed above. In this case farmed red deer constrained to eat grasses mimic what is the free choice of wild fallow and may ingest a more " mat-forming" diet than their wild counterparts.

The multivariate approach offers exiting possibilities for the analysis of papillary change in response to many variables. It offers possibilities for the close study of the direct interaction of wild ruminants with their dietary environment whereby effects of dietary nutrient content and mat forming propensity may be assayed. Such studies may be useful in herd management and are not dependent upon detailed knowledge

of population numbers and densities. A notable finding of this study is the difference in rumen papillary development between wild and farmed red deer. The technique may be useful in assessment of the optimal nutritional parameters that are required for farmed deer and the relationship of these to optimal productivity.

This study did not consider papillary density measurements as have a number of papers (Hoffman, 1976; Langer, 1974; Konig et al., 1976) which incorporate papillary length and breadth measurements along with density figures into a composite such as "Factor of increase in surface area" (F.I.S.A.). Density of papillation is influenced by changes in rumen volume on formalinisation after death which are unrelated to factors influencing papillary change (Lentle et al. unpublished).

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## CHAPTER 4

RH Omasal mutivariate analysis of red and fallow deer. Lentle et al

OMASAL ANATOMY IN NEW ZEALAND RED AND FALLOW DEER: AN  
EXPLORATORY MULTIVARIATE ANALYSIS.

ROGER G. LENTLE, Department of Ecology, Massey University, New Zealand

KEVIN J. STAFFORD, Department of Veterinary Clinical Sciences, Massey  
University, New Zealand

IAN M. HENDERSON, Department of Ecology, Massey University, New Zealand.

Abstract: Omasal weight and volume plus omasal laminar number, weight and area in wild fallow (*Cervus dama*) and wild plus farmed red (*Cervus elaphus*) deer were analysed by principal components. Two components interpreted as overall omasal size and laminar "leafiness" were extracted. The latter axis showed significantly greater variance in wild red deer than in farmed red or wild fallow deer. Intermediate feeders may exhibit greater plasticity of omasal form. A relationship is derived by which laminar area can be derived from laminar width and number.

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Keywords: Cervus dama. Cervus elaphus. Fallow deer. Farm. Feeding type.

Multivariate analysis. New Zealand. Omasum. Omasal lamina. Red deer. Wild.

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## INTRODUCTION

In this paper we report the results of a principal components analysis of variations of omasal macroscopic anatomy in red deer (*Cervus elaphus*) and fallow deer (*Cervus dama*) with differences in diet and demography. Such an analysis may yield a greater understanding of the relationship of form to function in this structure.

The omasum, third compartment of the ruminant stomach, contains a series of closely arrayed laminae which sometimes bear claw shaped papillae (Hoffman, 1973) (figure 12). The laminae are not equal in size and Langer (1988) refers to three orders based on size. Whilst omasal anatomy has been well described, the relationship of structure to function is more tenuous. There is some controversy concerning the principal role of the omasum and its laminae which "may serve to absorb some water and nutrient but probably are more important as a filter" (Van Soest, 1982). Langer (1988) comments with respect to omasal function "absorption of water and electrolytes have clearly been demonstrated" but the question remains as to whether this absorption is incidental to its action as a "flood gate" (Bost, 1970). There is therefore a need for studies relating structure to function and a number have been undertaken. Langer (1988) reported that analysis of combined data (Langer, 1973; Hoffman, 1969; 1973) showed a significant correlation between number of laminae and "herbivory rating" (HR). HR is a numerical value assigned to dietary habit ranging from "1" (omnivores) to "6" (specialised grazers) (Langer, 1988). Lauwers (1973) found a significantly higher total omasal surface area in dairy cattle maintained on a high fibre diet than in beef cattle fed a low fibre diet. In a comparative study of African ruminants Hoffman (1973) reported fewer thicker laminae with larger claw shaped papillae in species classified by him as "concentrate selectors" (equivalent to HR 2-3) having a low fibre diet than in "bulk or roughage eaters" (equivalent to HR 5-6). It has been suggested that these variations of structure are a consequence of different onflow requirements in concentrate

Fig. 12. Omasal and Omasal laminar anatomy showing measurement detail.

(a) Whole rumen showing omasum (shaded)

(b) Surface anatomy of omasum

(c) planar section

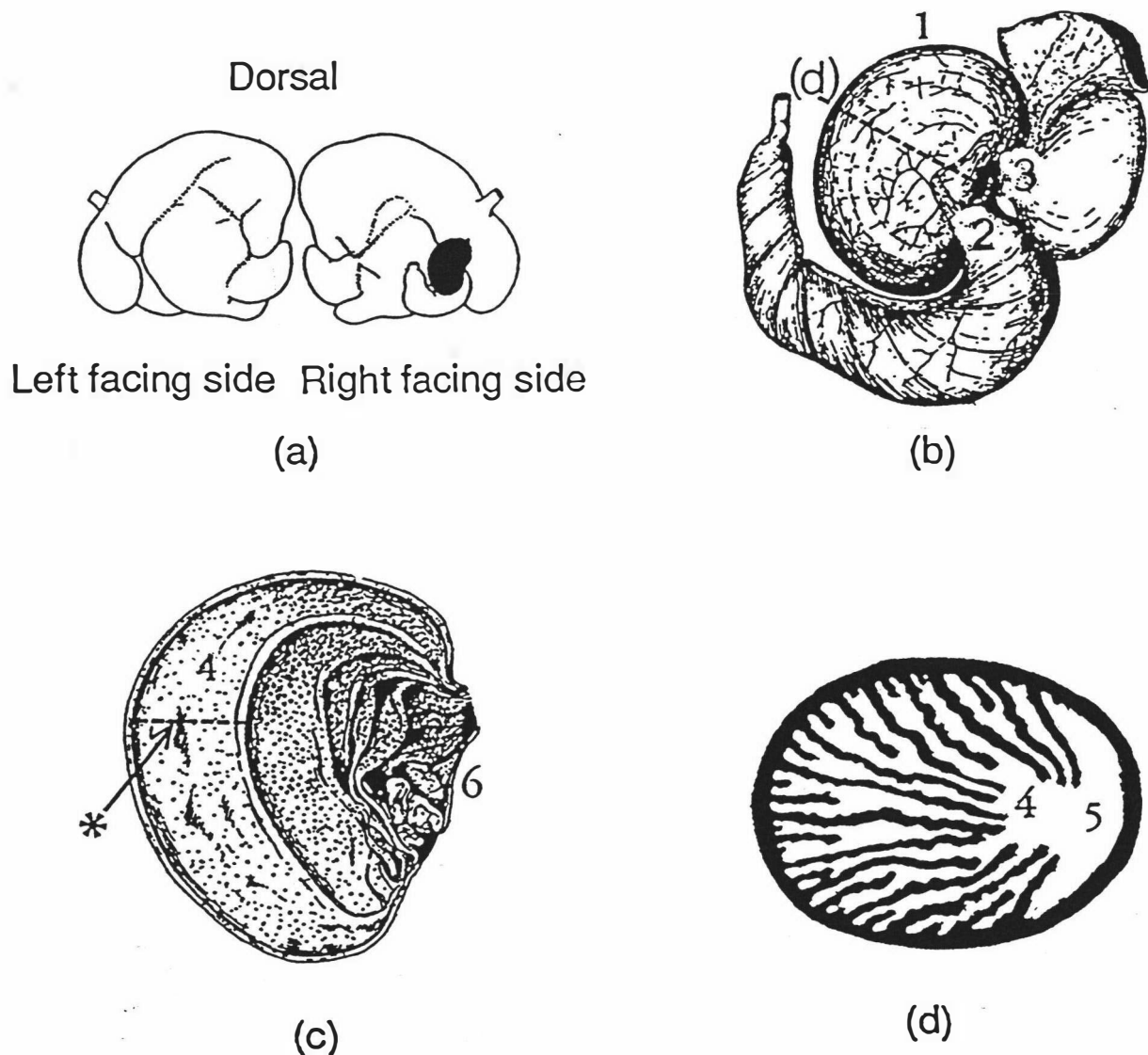
(d) transverse section

Dotted line in (b) shows plane of transverse section i.e. plane of (d)

Dotted line in (c) shows laminar height measurement (\*)

1. Greater curvature of Omasum; 2. Omaso-abomasal orifice; 3. Reticulo-omasal orifice;

4. lamina of first order; 5. Lumen of Omasum; 6. Lesser curvature of Omasum.



selecting ruminants as opposed to bulk or roughage feeding species (Langer 1988).

Demographic variation of omasal structure has also been identified. A progressive increase in the omasal surface area of domestic cattle up to the age of ten years has been reported (Lauwers, 1973). This increase was not due to an increase in the number of laminae which only increased up to an age of 20 weeks (Langer, 1988). Laminar number showed a considerable variation in mature cattle (90-150 in animals over the age of 40 months) with values averaging around 120 laminae. The age related increase in laminar area may reflect an increase in the size of the animal or constitute a continued growth response to dietary stimulation. A significant proportion of laminar growth in sheep takes place during embryological development with no direct dietary influence (Lubis and O'Shea, 1978). In lamb embryos, laminae of the first order were seen at 35 days, second order laminae at 39 days and third order laminae were found in 90 day old fetuses (Langer, 1988).

As it is probable that both age and dietary mechanisms influence omasal growth, it is important to simultaneously assess the relative contributions of these factors. The method of principle components analysis enables the identification of trends in multivariate data sets at the same time making no reference to pre-established axes of variation (Pielou, 1984). Its use in this study allows some assessment of the relative contributions of demographic and dietary effects, at the same time providing data with respect to omasal dietary function by an unbiased pattern search

The counting and classification of laminae into orders is a simple procedure but the measuring of laminar area is time consuming. This study also undertakes an analysis of the mathematical relationship between these values.

## MATERIALS

Omasums were obtained from three sources:-

- 1) Wild red deer from the western Ruahine ranges of central North Island, New Zealand.
- 2) Wild fallow deer (*Cervus dama*) from the Ahu ahū catchment of the Whanganui river in southern North Island, New Zealand.
- 3) Farmed red deer obtained at the Venison New Zealand deer slaughter facility at Feilding, North Island, New Zealand.

## METHOD

Omasums were removed immediately post mortem and then placed in a plastic bag containing 50 ml of 10% formal saline. These specimens were frozen at -10°C on return to the laboratory. The specimens were thawed prior to measurement of the following :-

- 1) Weight of digesta filled omasum (to  $\pm 0.1$  g). Weighed after 12 hours thawing at room temperature. No attempt was made to remove the omasal contents but prior to weighing the specimens were placed on absorbent paper for 30 minutes and excess fluid allowed to drain off.
- 2) Volume of Omasum (to  $\pm 10.0$  ml). Measured by displacement in a 1000 ml measuring cylinder.
- 3) Laminar measurements. Omasums were placed on a table on their visceral surface and a longitudinal cut was made through the wall parallel to the long axis along the greater curvature. The omasum was bisected along its long axis and the laminae of each half were preserved intact. Using a binocular loupe and probe, each lamina was carefully dissected free from the outer wall by a single cut applied to its base. Following removal of all the laminae the two halves of the omasal wall were bulked, blotted dry and weighed.

The individual laminae were washed clean of digesta, blotted dry and the following

laminar measurements were made:-

a) The height ( $\pm 0.1\text{cm}$ ) measured at right angles to the longitudinal axis of the organ (fig 12 c). Laminae were subsequently classified into orders on the basis of height measurement according to the following schedule (after Langer, 1988). 1st order laminae height was greater than 4 cms; 2nd order laminae 3 to 4 cms; 3rd order laminae 2 to 3 cms; 4th order laminae 1 to 2 cms; 5th order laminae 0.5 to 1 cms; and 6th order laminae less than 0.5cms.

Lamina of the same order were collected and the following measurements taken.

b) Total number of lamina in each order.

c) Weight of each order ( $\pm 0.01\text{g}$ ).

d) Total area of each order ( $\pm 1\text{mm}^2$ ). This measurement was obtained by overlaying the laminae of each group onto water resistant graph paper.

e) The number of laminae in each order were summed for each omasum to obtain the total number of laminae.

f) The weight of laminae in each group were added for each omasum to obtain the total laminar weight.

g) The total area of each order was added for each omasum to obtain the total laminar area.

#### Statistical analysis

Principal components (PC) analysis (Wilkinson 1990) was used to explore the interrelationship of six variables (omasal weight, omasal volume, omasal wall weight, total laminar number, total laminar area and total laminar weight) and their relationship with species, sex, age and diet.

Omasal PC axis factors were compared with rumen papillary PC axis factors obtained from a concurrent study using the same animals (Lentle, 1994; Lentle et al., 1994) by Pearson correlations.

A regression analysis using a laminar "width/number value" against laminar area was



carried out for best fit with linear, power and polynomial functions. The laminar "width / number value" "x" was calculated as follows; Average height values were calculated by averaging the limiting measurement values for each order of lamina. Thus average height values used in this study were 6th order, 0.25 cm.; 5th order 0.75 cm.; 4th order 1.5 cm.; 3rd order, 2.5 cm.; 2nd order, 3.5 cm.; 1st order 4.5 cm. (the latter as greatest height value average in this study was 5cm.). The product of the number of laminae in each order with corresponding average height value was obtained for each order of laminae in each omasum. The products for constituent orders of lamina were then summed for each omasum in order to obtain "x".

RESULTS

TABLE IV: Omasal Principal Components Analysis: Component loadings

	PC1	PC2
Weight	0.883	0.357
Volume	0.908	0.361
Wall Weight	0.821	0.268
Laminar number	0.734	-0.576
Laminar area	0.908	-0.211
Laminar weight	0.840	-0.296
Eigenvalue	4.347	0.794
%Total variance	72.5	13.4

### PC component axes

Table IV shows the principal component loadings for the first two axes along with their eigenvalues and percent total variance explained. Omasal PC1 component loadings are all roughly equal suggesting that on this axis data separation is principally by overall size.

Omasal PC2 component loadings are negative for all laminar variables but positive for overall omasal physical characteristics. This suggests that this axis is separating data on the basis of their "leafiness" i.e how relatively packed with laminae omasums are.

Graphs of omasal PC axis 1 on 2 are shown in figures 13, 14 and 15 with points coded points by species, sex and age.

### Relationship of omasal PC axes to other factors:-

#### Age

Graphs of omasal PC axes with coded age of individuals show no correlation with age (figure 13)

#### Species

There was good separation of fallow and red deer species on the basis of factor 1 but not on factor 2 (figure 14).

#### Sex

There was no significant separation of sexes by omasal PC axes 1 or 2 (Figure 15) although sample sizes are very small for males.

#### Diet

Wild deer always had a choice between browsing or grazing. Farmed deer on the other hand, had no opportunity to browse and had a more limited choice of species available for grazing. On omasal PC axis 1 and 2 there is no significant separation of farmed and wild specimens. There is however a broader spread of values on factor 2

Fig. 13. Plot of omasal principle component analysis factor 1 (overall size factor) values against factor 2 (Leafiness factor) values. Wild deer circles. Farmed deer triangles. Size of symbol proportional to age. Fallow deer shaded symbol.

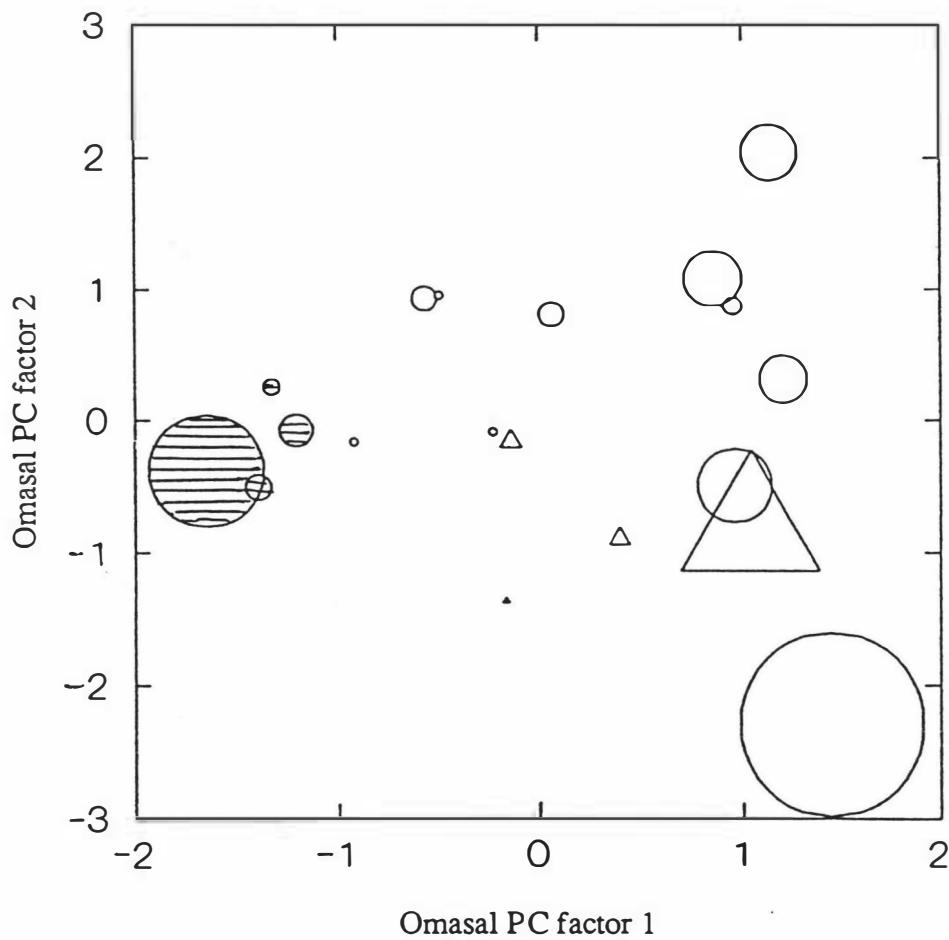


Fig. 14. Plot of omasal principal component analysis factor 1 (overall size factor) values against factor 2 (leafiness factor) values showing species. Fallow deer circles. Red deer dots.

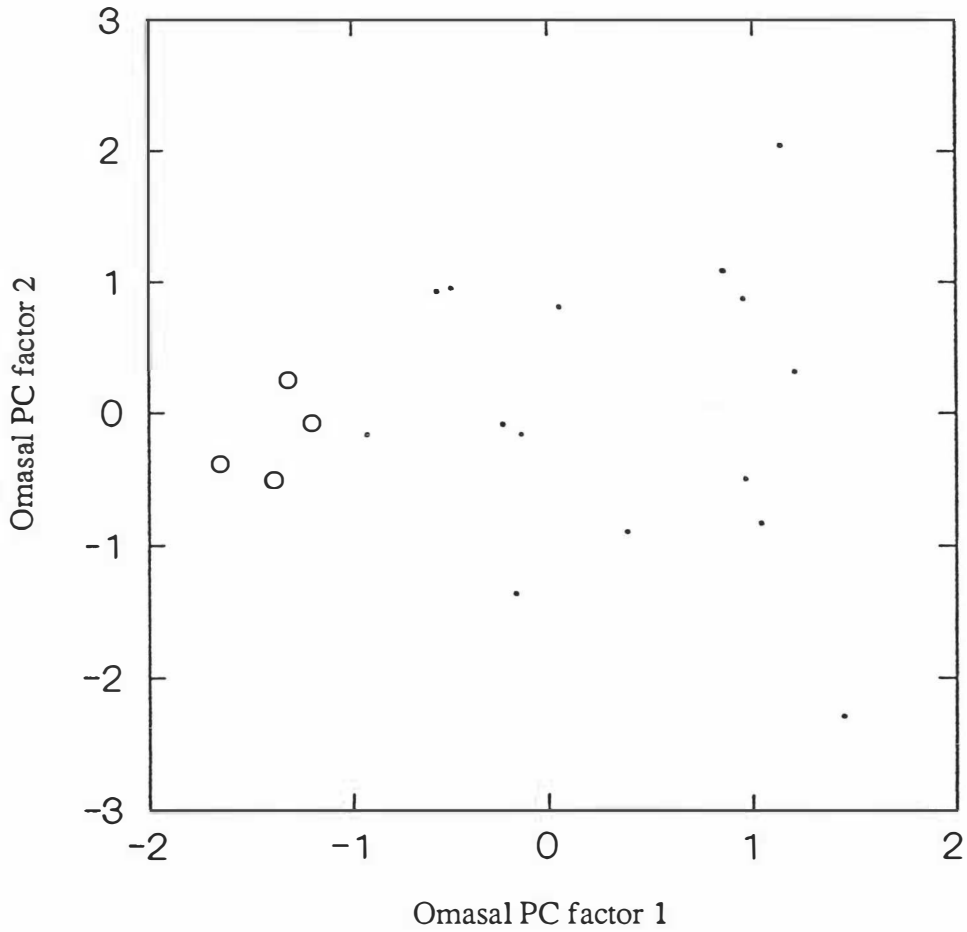
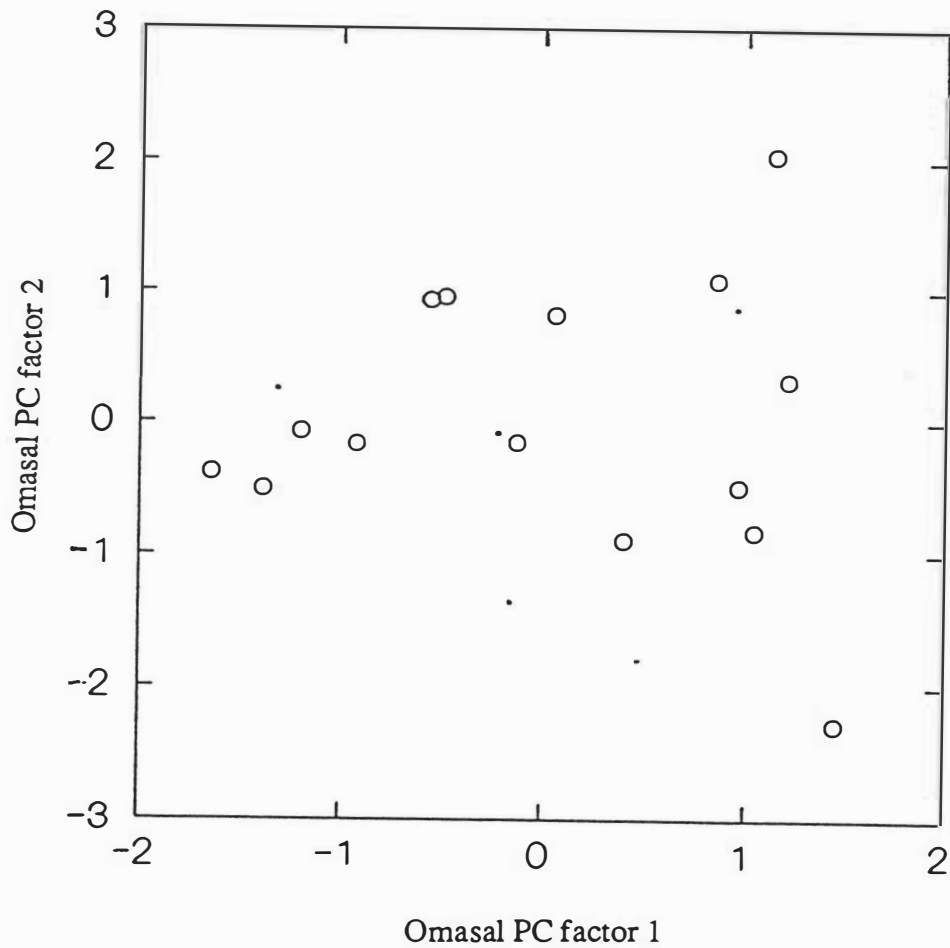


Fig. 15. Plot of omasal principal component analysis factor 1 (overall size factor) values against factor 2 (leafiness factor) values showing sex. Males shown as dots females as circles.



axis for wild red deer than for the grazing group (farmed red deer and fallow) (figure 13).The variance of omasal PC2 in the grazing group is significantly less than in the wild red group ( $F=4.73, p < 0.05, 1$  tailed) although the means of the two groups are not significantly different (table V).

TABLE V.Comparison of variances of omasal PC components

	Wild red deer		Grasseaters	
Sample size	11		8	
	PC1	PC2	PC1	PC2
Minimum	-0.923	2.307	-1.646	-1.363
Maximum	1.448	2.037	1.041	0.251
Mean	0.403	0.360	-0.554	-0.495
Variance	0.708	1.273	0.955	0.269
Standard deviation	0.841	1.128	0.977	0.519
C.V.	2.090	3.131	-1.766	-1.047

Comparison with rumen papillary characteristics

The only significant correlation was rumen factor 1 (an axis of separation based on overall papillary size)(Lentle et al., 1994) against omasal PC1 (overall omasal size) when red deer only were considered ( $r=0.568$   $p=0.027$ ). In the case of the combined fallow and farmed red "grazing group" the only significant correlation was that of rumen PC 2 (an index of overall rumen papillary shape )(Lentle et al., 1994) with

omasal PC 1 (Pearson  $r=0.834$   $p=0.010$ ).

Mathematical relationship of laminar number to laminar area

Formulae that give some degree of fit for regression of laminar width and number value on laminar area are given below along with  $r^2$  values (table VI). Linear regression gives as good a fit as non linear models using power function or polynomial expressions (figure 16) and provides a simple means of estimating laminar area from summed multiples of averaged laminar width and number of laminae.

TABLE VI :REGRESSION FORMULAE FITTING OMASAL LAMINAR AREA AND  
OMASAL LAMINAR WIDTH NUMBER

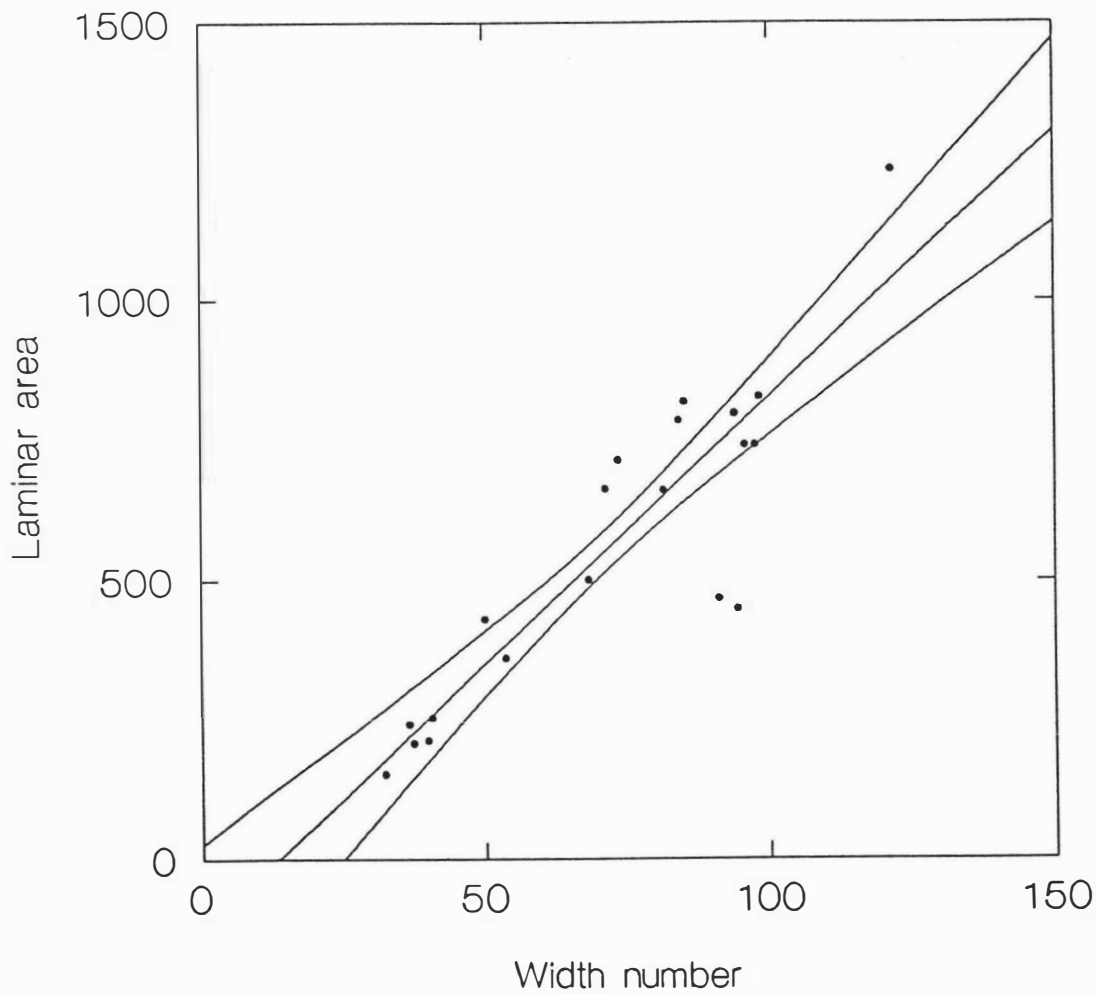
Y= true area,  $X=\sum \text{width} \times \text{number of leaflets}$

Type	Formula	$r^2$ value
Polynomial	$y = 5.510x + 0.028x^2$	0.962
Power function	$y = 2.407x^{1.27}$	0.962
Linear	$y = 7.996x$	0.957

DISCUSSION.

Farmed red deer, as well as wild red and fallow deer were used in this study. In New Zealand red deer have only recently been kept as farmed animals and the findings from this species are less likely than those from other domestic stock to have been influenced by artificial selection. They therefore more closely reflect responses that were evolved in the wild.

Fig. 16. Regression analysis of omasal laminar "width number" (see text) against measured omasal laminar total area ( in  $\text{mm}^2$  ) using combined data from farmed and wild red, plus wild fallow deer. Curved lines show 95% confidence interval.





The principal components analysis in this study shows two axes interpretable as aspects of variation in omasal gross anatomy, omasal size (omasal PC1) and relative "leafiness" (omasal PC2).

The "leafiness" factor should not be interpreted as directly equivalent to laminar surface area. Omasal PC2 axis is in effect recording surface area changes over and above those concurrent with size change.

Omasal PC1 (overall omasal size) separates fallow deer from red deer which is not surprising given the differences in mean body weights of the two species in New Zealand (mean female carcass weights: red= 45.2 Kg. fallow= 21.7 Kg. King, 1990). Omasal PC2 (leafiness) on the other hand fails to separate either wild red or farmed red deer from fallow thus leafiness does not seem significantly different in the two species.

Although leafiness as represented by omasal PC2 is not directly equivalent to number of laminae, this factor has an influence on omasal PC2. Thus this may seem a surprising result, as, according to Hoffman (1969;1973) and Langer (1973) smaller animals have fewer laminae. However this conclusion is derived from data that include only two cervid examples. Langer (1973) reports a value of 40 for fallow whilst Geiger et al.(1977) report 20 for the same species. Our results fall within this range (28-34). Langer (1973) gives a value for red deer of 52, a figure close to our average. However our results show wide variation in red deer (23-67) overlapping considerably the range detailed in the literature for fallow. There is wide variation of laminar number in both species perhaps suggesting that leafiness variations may be sufficient to obscure species differences. The wide variation in number of laminae recorded in this study parallels that described in cattle (Lauwers, 1973), in domestic sheep (Geiger et al., 1977; Nickel et al., 1967; 1973) and in various african bovid and antelope species (Hoffman, 1973).

Whilst PC2 axis fails to separate the two species there are clear differences in the

scatter of results. The significant difference of variances of PC2 results for the grazing group (farmed red deer and wild fallow deer) versus wild red deer shows that leafiness varies more in red deer when they are allowed free choice between browsing and grazing and less in deer that are grazing. These results suggest that Hoffmans (1989) classification of feeding types with regard to omasal structure, pertains more to the outcome of dietary effect on the development of omasal size and laminar structure than to species effect. Thus red deer constrained to a diet that is similar to that of fallow deer may not be required to generate changes of leafiness according to dietary environment as are their wild counterparts who live in a variety of different dietary situations.

It may be that intermediate feeders such as red deer have greater omasal plasticity in response to dietary changes. However to validate this point more thorough feeding and anatomical studies are required.

Correlations between rumen and omasal principle components do not give further insight into the manner of variation of omasal structure with diet. This may a consequence of small sample sizes. The only correlation of any notable significance was, that the comparison of overall rumen papillary size, a function of age, with overall omasal size in red deer showed significant correlation suggesting in effect that as the rumen grows so does the omasum.

The failure of either omasal PC1 or omasal PC2 axes to correlate with age may again be a consequence of the wide variation between individuals. Better correlation may be expected in the grazing group where variance is less but in our study this group consists of small numbers of two species bulked together and this may obscure correlation. It seems that in deer of the age group and species studied, variation of laminar area in response to diet far outweighs variations that are due to age.

Relationship between laminar number and laminar area.

In the literature concerning omasal function, both laminar number and/or laminar area are used to describe responses to changes such as diet and age (Langer 1988). It would be preferable for reasons already stated to estimate laminar area from the laminar number and order.

However the relationship between the parameters is not a simple one. Firstly there are shape changes with increase in laminar size, changing from thin crescent to almost ellipsoid. Secondly with increasing age of the animal there are changes in interrelationships between linear dimensions and surface area. As noted previously, there is a relatively short early phase of increase in laminar number but a much more prolonged phase of extension of laminar area. Thus a single regression analysis must be a generalisation and applied with caution.

Our analysis assumes a common baseline length for all laminae and gives an acceptable fit with a linear model (see fig 16). Thus using the summed products of averaged laminar width and laminar number seems a useful approach for laminar area estimations in deer aged 6 to 54 months.

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## CHAPTER 5

### ANALYSIS OF RUMEN CONTENTS.

#### 5:1 INTRODUCTION

The analysis of rumen contents in killed deer has been used in New Zealand as an aid to deer management decision making based primarily on deer density and vegetation condition estimates (Nugent, 1983). Theoretically it should be possible to use rumen analysis results in conjunction with forage availability studies to determine the status of particular conservation areas independent of population estimates. However there are practical limitations to this approach. Individual variation in dietary intake necessitates analysis of large numbers of rumens (50 per season or 200 per year) are required even for the study of dietary preference (Anthony and Smith, 1974).

The formation of rafts of vegetation in the rumen influences the distribution of physically distinctive fragments of individual plant species and they are not randomly distributed. Thus specialised sampling procedures are needed (Nugent, 1983; Chamrad and Box, 1964). Apart from practical limitations there are other difficulties as discussed in chapter one. In particular, percentage composition of identified flora may not reflect the percentage composition of dietary intake due to differences in rate of breakdown and rumen onflow of individual plant species (Anderson et al., 1965; Bergerud and Russell., 1964; Brown, 1961; Courtright, 1959; Smith, 1952; Norris, 1943.). Further, the numerous factors pertaining to plant availability and food preference of the animal make interpretation of results tenuous. Bearing these limitations in mind along with the relatively low number of samples in our analysis it may be considered unlikely that detailed rumen content floristic

analysis will have anything to contribute to the rumen papillary analytic technique described. However general trends in rumen content could, if correlated with rumen papillary data, validate that papillary parameters are covarying with diet rather than other factors arising more out of the "milieu interieur" of the animal.

Thus a simplified analysis of rumen vegetation content was undertaken whereby vegetation fragments were classified as "twig" "leaf" or "blade" (see method).

Previous work using such a classification on ingested diet (Baccus et al., 1985) has demonstrated that there are shifts in the relative proportions of these classes with herbivore species and with variations of graze and browse availability.

## 5:2 MATERIALS AND METHOD

In conjunction with the collection of rumen samples described in Chapter 3, grab samples of rumen contents were taken following a mixing procedure described by Nugent (1983). 50 ml of 10% formalin was added to the sample in the field prior to freezing on return to the laboratory.

Following thawing, a 50 gram rumen content sample was washed repeatedly in a 4.00 mm sieve. Retained vegetation fragments were suspended in water and examined with a binocular microscope. Fragments were classified according to the schedule below and sorted into separate containers.

Sample categories:-

- a) Blade. Any specimen that was flattened in cross section with parallel edges and exhibited parallel venation. Not included in this category were specimens having breadth greater than 1cm and thickness greater than 1mm (this principally excludes flax from this category and as detailed below adds it to leaf category).
- b) Leaf. Any specimen having flattened profile in cross section, having rounded or other identifiable leaf edge profile and with venation other than parallel. In addition

flax leaves were placed in this category.

c)Stem. Any fragment of vegetation having a rounded i.e. cylindrical profile and not being attached to an identifiable blade or leaf fragment of the two categories listed above. This effectively ruled out any evident leaf petioles and grass stalks. Also categorised in this group were bark fragments and lignified seed material.

The samples were air dried at 25°C for one week and then weighed. Individual sample category weights were added and relative percentages calculated. Percentage contributions were analysed for correlations with species, sex, age, season and dietary variables using SYSTAT (Wilkinson, 1990).

### 5:3 RESULTS

TABLE VII: Analysis of Variance of rumen vegetation content analysis with diet (farmed or wild) and species (red or fallow). (F values {F} and probabilities {p} for one way ANOVA based on dry weight of sorted vegetation categories.)

		Leaf	Stem	Blade
Farmed	F	17.902	4.830	6.092
	p	0.000	0.0360	0.020
Species	F	7.0	0.505	4.315
	p	0.009	0.483	0.047
Season	F	1.788	1.762	2.455
	p	0.172	0.177	0.083

There was no significant variation of sex or age with rumen leaf stem or blade content

Table VII shows the results of the analysis (One way ANOVA) for variance of rumen content with species, wild, farm, or season.

These show:-

- 1) Significant correlation between wild versus farm diet in proportions of leaf ( $F = 17.902$ ,  $p = 0.000$ ) blade ( $F = 6.092$ ,  $p = 0.020$ ) and stem ( $F = 4.830$ ,  $p = 0.0360$ )
- 2) Significant correlation between species difference and proportion of leaf ( $F = 7.93$ ,  $p = 0.009$ ) and blade ( $F = 4.315$ ,  $p = 0.047$ ) but not stem ( $F = 0.505$ ,  $p = 0.483$ ).
- 3) No significant correlation between seasonal difference and proportion of blade ( $F = 2.455$ ,  $p = 0.083$ ) and no correlation with leaf or stem proportions.

#### 5:4 DISCUSSION

Wild red and fallow deer selected diet according to that expected from Hoffmans (1989) classification as intermediate feeders and roughage feeders respectively. There was an obvious difference in rumen contents between wild and farmed deer. This was important with respect to interpretation of the wild/farmed variables effect on papillary morphology hitherto described.

These results go some way to explain the failure of the papillary morphology analysis to separate rumens on a seasonal basis. In this case the similarity of diet in all seasons is associated with similar papillary morphology. Such a finding could also lend support to the concept that at deer densities well below carrying capacity there is relative abundance of forage all year, which results in more uniform diet bringing about increased stock recruitment as described by McCulloch (1984). This fits in with the frequently recorded observation that at densities of animals that approach carrying capacity there is a particular increase of winter death (Ellig, 1975; Houston, 1971) indicating in turn that there may be greater fluctuation of seasonal



diet at higher animal densities.

Little information was produced by this analysis indicating its limited usefulness with small sample numbers. However it is noted that this outcome may in part be a consequence of the simplified classification of vegetation fragments adopted obscuring seasonal effects i.e. seasonal effects may have been revealed by a more detailed method of floristic analysis.

## CHAPTER 6

### RELATIONSHIPS BETWEEN RUMEN ANATOMY AND JAW LENGTH INDICES.

#### INTRODUCTION

An extensive evaluation of red deer carcass measurements known to be sensitive to nutritional change was carried out on south westland deer by Challies (1978). Jaw length was included in the range of physical parameters that were used. A method was developed that enabled an assessment of nutritional wellbeing of groups of animals regardless of age and sex using "normal growth curves". A mathematical technique based on these curves was developed WHICH allowed transformation of jaw lengths of animals to percentages of an age and sex specific minimum to maximum range. Data was then grouped by year of birth cohort and presented as a time trend series. Comparisons were derived for areas in different stages of irruptive fluctuation of population. Trends were compared and found to be "entirely in accord with what have been expected considering the establishment pattern and hunting history".

In the light of these results, the method has been used to monitor nutritional trends and infer population levels in other New Zealand deer populations including that in the Ruahine area (Kelton,1983). It was thus relevant to examine whether jaw length data from wild red deer gave an indication of nutritional status and history concordant with PC axes of rumen papillation.

## METHOD

" Weibull curves" have been generated from jaw length data from Keltons (1983) study and Landcare Research's analysis of 1990-1992 Ruahine helicopter cull specimens. As the latter described the population then resident in the area from which my wild red deer samples were obtained, it was possible to employ them and obtain predicted jaw length figures for animals of known age. The curves described the nutritional status of a deer population that was present in the sampling area two years prior to this work, however it is unlikely that there was significant departure from nutritional conditions such as existed then, as there have been no significant changes in hunting pressure (Personal communication D.O.C. Regional Officer, Napier).

Jaws were air dried and their lengths determined according to the method described by Frazer and Sweetapple (1993). Both hinge (distance from the anterior tip of the alveolus of 1st incisor to the posteriormost limit of the condyle of the jaw) and heel (distance from the anterior tip of the alveolus of the 1st incisor to the posteriormost limit of the ramus of the jaw) measurements were taken. A jaw length condition index was derived. This was the ratio of actual jaw length to that predicted from Weibull curves.

Assuming that a sample drawn from a population identical to that from which the 3 year old Weibull curve was calculated would have an average jaw length condition index of 1.0, the extent to which the average value of jaw length indices obtained in this work deviated from this figure could give some indication of the extent of change in population status. A simple average of the jaw length condition indices was calculated so that this assessment could be made.

The jaw length condition index was checked for correlation with PC axes one to three derived from the papillary study (Ch2) and for correlation with PC axes one

and two obtained from the omasal study (Ch3).

RESULTS

The mean jaw length condition index was 0.98 i.e. close to 1.0 showing that the Weibull curves gave a good description of the current population.

No significant correlation of the jaw length condition index was obtained with any of the PC axes obtained from the rumen papillary study ( the best correlation was with PC2  $r = - 0.034$ ,  $p = 0.142$ ) nor from the omasal study.

TABLE VIII

Pearson correlation matrix probabilities of jaw length indices with papillary and omasal PC axis values

	PC1	PC2	PC3	OmPC1	OmPC2
Heel	0.919	0.869	0.928	0.602	0.526
Hinge	0.769	0.457	0.996	0.848	0.614

DISCUSSION

The results indicate that there is no significant correlation of the lifetime nutritional history estimated from jaw length with rumen papillary parameters.

Papillary parameters are known to respond to changes in quality of nutrition on a time base of 8-35 days (Nockels et al., 1966) and from the work described in Chapter 2, overall papillary size is, like jaw length, cumulative with age.

The lack of correlation may be due to a number of factors. Firstly as discussed in chapter one, nutritional indexes that are based on different aspects of nutrition may not necessarily concur. This has been reported by Challies (1978) who demonstrated a lack of correlation between changes in modified Riney fat indices (an index of carbohydrate nutrition) and jaw length indexes in red deer in South Westland. In the present study the nutritional history described by jaw length growth results from mineral and protein accumulation and may respond differently than papillary indices which are consequent on protein accumulation under ambient rumen conditions resulting from diet.

Secondly as discussed in chapter one, in nutritional indices such as jaw length, where there is accretion of numbers of small annual increments without year by year demarcation, these will have the affect of a cumulative damping of sensitivity with respect to the current seasons increment. Comparison with an index that has faster response time and no accretion with age (as in the case of PC axes 2 and 3) may be confounded by the cumulative "noise".

Finally it should be noted that previous work in this field (Challies 1978) has been based on much higher animal numbers than were used in this study and high individual variation within age and sex cohorts could invalidate use with smaller sample sizes.

In conclusion, bearing in mind the limitations of small sample size the study shows no correlation between an index with short response time and that of a longer one, a result similar to that obtained by Challies (1978) hitherto discussed which compared jaw length index changes to those of the shorter time base Riney fat index of well being. More work is needed to understand the reasons for these failures of

correlation.

## CHAPTER 7

### CONCLUSIONS AND FUTURE DIRECTIONS

To date, the management of introduced game animal herbivores in New Zealand native forests has been by a concerted approach employing both population based and individual based methods. The use of individual based methods in which "nutritionally sensitive physical parameters" are used to evaluate the interaction of an animal with its nutritional environment has been justified in an extensive literature review by Challies (1978). Since 1978 the use of jaw length and kidney fat indices along with more basic carcass measurements of nutritional adequacy or wellbeing have become commonplace. There remain however a number of shortcomings, the most notable being a need for measurements of nutritionally sensitive parameters having a short enough response time to show variation with seasonally induced nutritional change. Game animal management, albeit for botanical values, is often pivotal during periods of short term seasonally induced food shortage. A parameter that allows prompt identification of a period of nutritional stress will not only indicate a period of greater threat to conservation values but may at the same time indicate a period of maximal susceptibility to foliage poison baiting in the game animal concerned. Jaw length changes, whilst able to evaluate broad trends in the nutritional status of populations over periods measured in years, do not show significant variation with seasonally induced nutritional change. Kidney fat indexes show seasonal variation in some limited age/sex groupings but this sensitivity is not widespread enough in the population to be of practical use (Challies, 1978). Dietary analysis may have potential to indicate short term nutritional stress but the nutritional significance of the numerous food plants is largely unknown and may vary with district.

Changes in the quality of ingested food have been shown to have a relatively rapid effect on the internal mechanisms of dietary thrift that operate in ruminants. Because of this prompt response it was likely that a study of these mechanisms, which I term strategies of "intrinsic nutritional optimisation" (INO), would be more likely to yield nutritionally sensitive physical parameters with a short response time. The concept of utilising physical outcomes based on strategies of INO in order to provide information on environmental nutritional stress is a novel one which may have broader applications than are addressed in this thesis.

The papillary analysis shows that papillary overall size and site specific papillation are both effected by diet . However the dietary differences between farmed and wild red deer and wild fallow deer, include a number of variables such as abrasive ability, nutrient content and roughage content. The effects of these components need more investigation. The work failed to show seasonal changes in wild red deer which may be because herd numbers were well below carrying capacity and under these conditions there may be minimal changes in winter food quality. More work is needed to determine sensitivity of the method to short-term nutritional change.

The omasal analysis demonstrated a change in the degree of scatter of a parameter based on omasal leafiness with differing lifetime diet. Obligate ( farmed red deer) and voluntary (wild fallow deer) grass eaters both exhibited lesser variance of this parameter. This finding also points toward the plasticity of omasal structure in response to diet but again further work is needed to determine sensitivity to short term dietary changes.

One finding incidental to the main thrust of this work may have applicability in game animal biology. The identification of a sexual dimorphism of age-related changes in overall papillary size in deer may offer some insight into differences in the bionomic strategies of the two sexes in red deer identified by Clutton-Brock (1982).



A number of important practical points arise from this work. Much of the previous work on papillary anatomical features is not directly comparable due to inconsistencies of sampling site. Workers should carefully define sampling sites and, in situations where retrieval of whole rumens is not possible, train field workers to accurately determine sample sites. It is notable that sampling of blind sacs is simpler than other parts of the rumen as it does not entail evacuation of the rumen contents and requires no measurement procedure. Sampling the atrium ruminis is almost as easy as it is distinguished by the distinctive pattern of the adjacent reticular mucosa and relative ease of evacuation. However some skill is required in order to correctly determine the mid point of the cranial pillar and the ventral projection of this to the point of fusion of the atrium ruminis and ventral sac. In the case of the atrium ruminis, this fusion point needs careful delineation as there are considerable gradients of papillary size in this small compartment. Similar problems exist with the anterior ventral sac site. The right and left ventral sac sites require most skill in that accurate determination of two anatomical landmarks, the midpoint of the anterior and of the longitudinal pillars, is required along with an accurate determination of points of intersection derived from them. Where it is desired to reduce the number of sample sites the ventral sacs should be the first to be deleted. The dorsal sac site is ostensibly an easy site to sample because its characteristically poor papillation leads to ease of identification, but as there are no anatomical landmarks, care is needed to correctly sample the site of least papillation.

It may be desirable to reduce the number of sampling sites for reasons of economy and convenience. Workers whose primary interest is in the assessment of variations of overall papillary size (PC1) could sample a single site. A single sample site is all that is required to assess papillary change with age and sex (only PC1 showed variance with demographic factors in our study). However for assessing dietary and species effects, papillary shape and specificity of site are both affected and more

than one rumen site should be evaluated. Whilst an atrium ruminis or an anterior ventral sac site will adequately assess shape variation of papillae, assessment of site specificity requires the evaluation of at least two sites. The magnitude of the difference in length component loadings indicates that the most appropriate sites would be the dorsal sac and caudoventral blind sac. Slightly less information is obtained by using a combination of atrium ruminis and dorsal sac sites.

In the light of the studies on post mortem rumen wall contraction, workers assessing papillary densities should perform such assessments on fresh, carefully site delineated, rumen wall samples and avoid formalinisation. Bearing in mind the potential for unpredictable changes in rumen volume, papillary results should always be evaluated separately as well as when incorporated into FISA.

Omasal studies may conveniently provide useful information on variations in the quality of diet. Sampling by inexperienced workers is relatively easy because the small readily identifiable structure is sampled in toto. However, where refrigeration is not readily available a longitudinal cut should be applied along the long axis of the organ to allow more complete penetration of formalin. There is need for standardisation of formalin strength until effects of varying concentrations have been more carefully assessed. I suggest using 10% as it is used most commonly and is in line with that used in other disciplines e.g. medical histology.

Finally, comment should be made on the range of nutritionally sensitive physical parameters that are best employed in field studies where a predominantly preselective approach has yielded a variety of indices whose interrelationships are unclear. Thus Challies (1978) concluded a comparative evaluation of parameters related to nutritional wellbeing in which the results of jaw length index evaluations were stated to be "exactly in accord with what would have been expected" whilst those of kidney fat index evaluation were stated to be "most unexpected", stating the need for a study of their precise interrelationship. In view of the complexity of the

various mechanisms that underlie the differences in the various indices (as are discussed in Chapter 1 of this thesis ) such a study would be a considerable undertaking. In the meanwhile in order to avoid the clear danger of preemptive choice of individual based method, there is a need for workers to assess as wide a range of nutritionally sensitive parameters as possible, allowing their subsequent analysis by principal components to serve as an unbiased assessment of appropriateness. Therefore, I recommend that my methods based on INO strategies are used concurrently with existing methods, rather than in place of them.

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## APPENDIX 1 : DATA KEY

Raw data on diskette in back cover.

MS-DOS formatted disk contains one file of plain ASCII text, blank delimited variables.

COLUMN VARIABLES

DEER\$	Identification code of animal.
SEASON	Season when shot. 1 Spring. 2 summer. 3 autumn. 4 winter.
AGE	Age in months obtained from jaw analysis.
SEX	1 Male. 2 Female.
SPECIES	1 Red Deer. 2 Fallow deer.
FARMED	0 Wild deer. 1. Farmed deer.
HEEL	Jaw measurement in mms from heel to 1st incisor.
HINGE	Jaw measurement in mms from hinge to 1st incisor.
LEAF	Air dried weight of rumen content vegetation of leaf category (see page 94) in grms.
BLADE	Air dried weight of rumen content vegetation of blade category (see page 95) in grms.
STEM	Air dried weight of rumen content vegetation of stem category (see page 94) in grms.

## PAPILLARY MEASUREMENT AVERAGES

These figures are the averages obtained from ten measurements at each site. All are in millimetres.

ARL	Atrium ruminis papillary length average.
RVSL	Right wall of ventral sac length average.
VSL	Anterior wall of ventral sac length average.
LVSL	Left wall of ventral sac length average.
DSL	Dorsal sac length average.
CDBSL	Caudodorsal blind sac length average.

CVBSL	Caudoventral blind sac length average.
ARW	Atrium ruminis width average.
RVS	Right wall of ventral sac width average.
VSW	Anterior wall of ventral sac width average.
LVS	Left wall of ventral sac width average.
DSW	Dorsal sac width average.
CDBS	Caudodorsal blind sac width average.
CVBS	Caudoventral blind sac width average.
WEIHINGE	Predicted length in mms of jaw measured from hinge to 1st incisor, based on 1992 Ruahine Weibull curves supplied by Department of Conservation.
WEIHEEL.	Predicted length in mms. of jaw measured from heel to 1st incisor, based on 1992 Ruahine Weibull curves supplied by department of Conservation.
OMWT	Weight of digesta filled omasum in grams.
OMVOL	Omasal displacement volume in mls.
OMWALWT	Weight of cleaned and blotted dry outer wall of omasum following removal of laminae.
LAMNO	Laminar width number calculated according to text (page 81).
LAMAR	Total laminar area of omasum in square mms.
LAMWT	Weight of pooled omasal lamina in grams.