“GRAZING SPEED :
THE TEST OF A MODEL”

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Declaration.

The work presented in this thesis is the result of my own investigations and has not been submitted for any other degree to the best of my knowledge.

JMaine

John Maina Githaiga

Date 8/1/91

This thesis has been submitted for examination with my approval as University Supervisor.

WaruiKaranja

DR. Warui K. Karanja.

Date 8/1/91

Dedicated to my parents Maina and Wambui
...who thought I can do better than look
after cattle...

and to all those who cherish the
beauty of the African bush..

ABSTRACT

This thesis describes a test of the optimal grazing speed model which postulates that the "grazing speed" of a grazer on a relatively uniform pasture is a function of animal forage requirements dictated by body size, pasture herbage yield and quality and the group size a grazer finds itself in. According to this model, the rate of progression over the pasture directly influences the quantity and quality of forage harvested. This model was tested at the Game Ranching Ltd. ranch in Athi River using cattle and sheep as test animals.

From fistulated cattle and sheep, forage harvested from specifically designated pastures, at different grazing speeds and group sizes was collected. This extruded forage was used to determine the quantity of forage intake and its crude protein content for 10 minutes grazing sessions. Under free ranging conditions, grazing speed was lowest on the low quality low biomass pastures for cattle but similar on the other pasture categories. For sheep grazing speed was highest on the high quality and high biomass pasture and lowest on the low biomass pasture. Forage intake was a function of pasture herbage yield for cattle with the highest amounts harvested on the high biomass pastures. Pasture yield, however had no influence on forage intake for sheep and equivalent amounts were harvested on both low and high biomass pasture categories.

Pasture heterogeneity with respect to sward structure affected the quality of forage harvested with intake quality differing from that of the herbage significantly only on the heterogeneous high biomass pastures. Sheep on both pasture categories where experiments were carried out had forage intakes with a crude protein content twice that of the pastures.

When grazing speeds were raised above free ranging levels, asymptotic declines in forage intake were found for cattle on all pasture categories except on the high quality high biomass pastures. A similar trend was found for sheep on the high quality low biomass pastures. On the low quality pastures the crude protein content of forage declined as grazing speed increased but remained constant for cattle and sheep on the high quality pastures.

Group size had no effect on forage intake or its crude protein content. The deployment patterns of individuals on the pastures, however, strongly influenced the effects of group size with faster progression rates when clumped than when deployed as a grazing front. Reduction in the spacing between individuals resulted in the grazers moving faster over the pastures.

The results of these experiments are discussed in

light of the hypotheses derived from the optimal grazing speed model and grazing behaviour of the experimental animals.

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CHAPTER ONE

GRAZING RUMINANT NUTRITION AND THE OPTIMAL GRAZING SPEED MODEL

1.1 : Introduction.

Foraging is an important component of fitness and many aspects of behaviour and morphology are shaped by the need to gather food. Foraging efficiency in part determines the inclusive fitness of an individual, and though food acquisition is central to activities, it competes for time with other activities such as mating, territory defence and predator vigilance (Krebs 1978). As natural selection favours individuals with the highest inclusive fitness, animals are under pressure to forage efficiently.

This notion of foraging efficiency has led to the formulation of mathematical models investigating how animals optimize energy returns when foraging. This area is one of the most rapidly expanding in ecology with several models formulated and successfully applied to carnivores, nectarivores, and frugivores (Pyke _et al_ 1977). The models have been assumed general and applicable to herbivores though this has, however, been problematic (Senft _et al_ 1987, Belovsky 1978 , Southwood, cited in Owen-Smith and Novelle 1982). The problems arise from the nature of herbivore diet and constraints it imposes on the digestive process which include those of animal physiology (dictating diet selection), foraging time limitations, and nutritional constraints from the food (Belovsky and Jordan 1978, Demment _et al_ 1986, Van Soest 1982)

A few models taking these constraints into account have been designed for herbivores but they only consider diets in habitats already chosen and for individual animals (Belovsky 1978, Owen-Smith 1979, Westboy 1974). Constraints imposed by group membership on food acquisition are not considered inspite of their potential effects on individual's feeding strategies (Jarman 1974). In this thesis the foraging of animals on different pasture types and group configurations was examined for two different body sized grazers, cattle and sheep to test a grazing speed model (Section 1.4.1).

1.2 : Optimal foraging theory and grazing ruminants nutrition.

Optimal foraging models have been applied with success to carnivores, nectarivores and frugivores (Elner and Hughes 1978, Krebs 1978, Waddington 1980). These animals depend on highly digestible foods, often distributed in patches differing in quality and quantity, a situation in which patch yield, distribution and exploitation can be easily modelled or simulated (Charnov 1976, Mcnair 1979, Valone 1989, Belovsky 1984). The nature of a ruminant herbivore's diet and the specialized digestive process it requires discourage the application and formulation of optimal foraging models to ruminants. Body size dependent relationships between diet selection, gut capacity and social organization would have to be taken into account as their interactions will to a large extent influence foraging models developed for herbivores.

1.3 : Ruminant nutrition.

Ruminants, and especially grazers, find themselves in a paradoxical nutritional situation, encountering an apparent surplus of low quality food dispersed over the landscape (Senft _et_ _al_ 1987). This low quality food necessitates bulky intakes to meet nutritional needs, such that digestive processes and grazing time become limiting (Kay 1983).

Plants vary in nutrient content between species and parts, with older plant parts and structural tissues having a large proportion of fibrous materials and cell wall contents of low nutritive value to herbivores (Westboy 1978, McNaughton 1976, Van Soest 1967, 1982).

Faced with a diet of low quality difficult to digest, ruminant herbivores have evolved a specialized digestive system to deal with this food supply. This digestive system incorporates fermentation chambers accommodating symbiotic micro-organisms which, together with rumination, makes possible quick intake of herbage which can then be fermented, ruminated and digested in an energy saving and safe resting position (Hoffman 1972).

Foliage digestion is to a large extent influenced by its fibrous material content as it is difficult to digest and encapsulates the easily processed cell contents. The fibrous material forms the structural system in plants and is composed of interconnected cellulose fibrils which have to be broken down into their glucose building units to be of any nutritive value to herbivores. Ruminant herbivores lack the enzymes for this process and rely on the unicellular symbionts in their rumens and the rate at which these micro-organisms break down the plant material is strongly influenced by particle size. In cattle variations in voluntary intake is controlled by rumen content turnover rate and decline with rumen fill (Thornton and Minson 1972). Food passage into the omassum is dependent on particle size and has to reach a certain level of reduction before passing through, achieved through rumination and fermentation (Kay 1983). The protein content of forage affects the performance of the rumen micro-organisms in carbohydrate fermentation and at low protein levels the process is severely affected and rumen turnover rate depressed (Baile and Forbes 1974). As rumen capacity is fixed, with low processing rates rumen fill reduces voluntary intake and therefore the nutritional returns to the animal (Van Soest 1982).

As diet quality declines, with a higher incidence of fibrous materials, more time at the expense of feeding must be set aside for rumination which is thus a critical component of foraging. Thus what a grazer does when not foraging is as important as it does in its overall feeding strategy (Demment et al 1986). The fibrous material content of a diet ultimately controls ingestion and assimilation of other nutrients (Van Soest 1967). The constraints imposed by the digestive physiology dictate that ruminants select an easily digestible diet of high quality. This selectivity with a preference for green grass parts, has been documented in several studies in domestic and wild grazing herbivores (Sinclair 1972, Stobbs 1975, Duncan 1975, Talbot and Talbot 1962, Jarman 1974, Black and Keeney 1984, Gakahu 1982). Ruminant species have been found to display different selectivity regimes closely associated with body size, with profound effects on the ecology and behaviour of the species.

The degree of selectivity determines the dispersion and availability of food items for a herbivore. A highly selective herbivores have a diet composed of buds and flowers, which are highly digestible but making up only a tiny fraction of the total plant biomass. This type of food is highly dispersed , relatively rare and only small amounts can be harvested (Geist 1974). By lowering its acceptance threshold, a larger proportion of the plant community becomes available as food to a grazer, bites are almost continuous and search time is reduced (Jarman 1974). The patterning of the nutrient content and its distribution in the vegetation is therefore critical in the feeding strategy of a ruminant grazer depending on its selectivity regime.

1.4 : Body size, gut capacity and feeding strategy.

Diet selectivity in ruminant herbivores is determined by an animal's physiology and is related to its surface area: volume ratio (S:V). Large bodied herbivores have greater absolute energy needs than smaller bodied herbivores though the latter have higher metabolic rates per unit body weight. The large herbivores require bulky intakes to sustain the biomass whereas the small bodied herbivores need easily digestible high energy yielding diets to maintain their metabolic rates. The relationship between body weight and metabolic rates is a 0.75 power of weight (Demment and Van Soest 1983, Moir 1973) but body weight and gut capacity have an isometric relationship (Demment and Van Soest 1986).

As gut capacity determines the ability to process food into nutrients, large bodied herbivores with large guts and higher retention times can process low quality food into nutrients more efficiently than smaller bodied herbivores. They can therefore tolerate and subsist on low quality diets. Smaller bodied herbivores, with small guts and high metabolic rates, need high quality easily digestible diets. The implication of these relationships is that smaller bodied herbivores must be more selective foragers than their large bodied counterparts. This physiologically driven selectivity has far reaching effects on the ecology and behaviour of herbivores (Jarman 1974).

1.5 : Feeding style and herd dynamics.

The feeding style adopted by a grazer plays a central role in its social organization (Jarman 1974, Geist 1974). For highly selective herbivores, discrete plant parts constitute a food item. Large groups are not possible as individuals feeding in the same area at the same time will compete for these items. To avoid this competition small herbivores usually forage in small groups. Large bodied grazers would not incur great feeding cost as successive bites on a food item only relatively lowers its quality, intraspecfic competition is less severe and large groups are possible. As group size increases, small bodied herbivores food resources would be depleted while for large bodied herbivores, resource quality and quantity would only be relatively depressed (Jarman 1974).

The effects of group size and dispersion patterns of individuals within the group have not been quantified in herbivores. As in other foraging categories the cost of being in a feeding group would be expected to increase with group size as the competition for resources intensifies. These costs may increase at a greater rate than benefits as group size increases beyond a certain point (Metcalfe 1989). Studies on non-human primates indicate that group size have an effect on foraging behaviour and large troops forage longer and have correspondingly larger home ranges (Stacey 1986, Takasaki

1981).

1.6 : Large herbivore foraging models.

Despite the potentially complex interaction of variables, a few optimal foraging models have been formulated for large bodied ruminant herbivores (Belovsky 1978, Owen-Smith and Novelle 1982, Westboy 1974). Belovsky's model for the moose considered four constraining variables on the moose diet viz sodium, heat load, rumen fill and energy requirements. The actual diet of the moose closely approximated that predicted by the model. In formulating the foraging model for the kudu, Owen-Smith and Novelle (1982) adopted a utility approach with variables such as animal height, walking rates, search time and other activities apart from foraging being considered. The model output closely reflected the diet observed although there were some discrepancies. This was probably due to factors such as lack of precise information of environment by the kudu or the model's emphasis on variables not of importance to the animal. Westboy's model is more applicable to omnivores than ruminant herbivores as heavy emphasis is placed on specific nutrients whose synthesis by the rumen biota frees them from this need.

1.7 : Optimal grazing speed model.

The above models do not address herd dynamics which, an especially important aspect of herbivore social organization with far reaching implications on individual fitness. A theoretical model proposed by Western (unpublished), states that the rate of passage of a grazing ruminant over a relatively uniform pasture directly affects its digestible energy intake.

Assuming other variables affecting intake remain constant, then the progression rate determines the potential food items a grazer comes into contact with. For a given pasture, therefore, a grazer will show a grazing speed at which an optimal intake with respect to quality and quantity will be achieved. In order to meet its metabolic needs a grazer will have optimal grazing speeds over pastures, varying with pasture quality and quantity. As metabolic energy needs are determined by body size, different body sized grazers will show different grazing speeds, over similar pastures, reflecting forage requirements.

For a single grazer if the average digestible energy content of the pasture is known, the area needed for the grazer to meet its energy needs can be known. Two grazers, grazing side by side will cover twice the area if the spacing between them is constant, three animals thrice the area and so on. From this it can be hypothesized that the area covered by an individual is dependent on group size where animals are under constraints to remain close together. If spacing between animals is reduced then animals will have to move faster over the pasture in order to cover the area needed for the day's intake. Yet, the speed of movement over the pastures will directly affect digestible energy intake, though potential food items a grazer comes into contact with increase in direct proportion to the speed of movement. Forage selection and intake would vary as a function of grazing speed, with diet selectivity declining with grazing speed. Quantity would be expected to rise initially and then fall off as speed increases. The trade-off between these components of forage intake is the basis of the model, graphically presented in Figure 1. The model probably involves interactions of variables shown in Figure 2.

1.8 : Hypotheses.

In the wild situation, these variables may acting in concert produce the foraging and socio-dispersions observed. In a controlled system the contribution of each variable can be examined and the point at which it imposes a cost to an individual, through diminishing returns determined. The interaction of these variables in the model was examined by testing the following hypotheses :

(a) That a grazer will show different grazing speeds on different pastures and deviations from this will adversely affect both quantity and quality of forage intake.

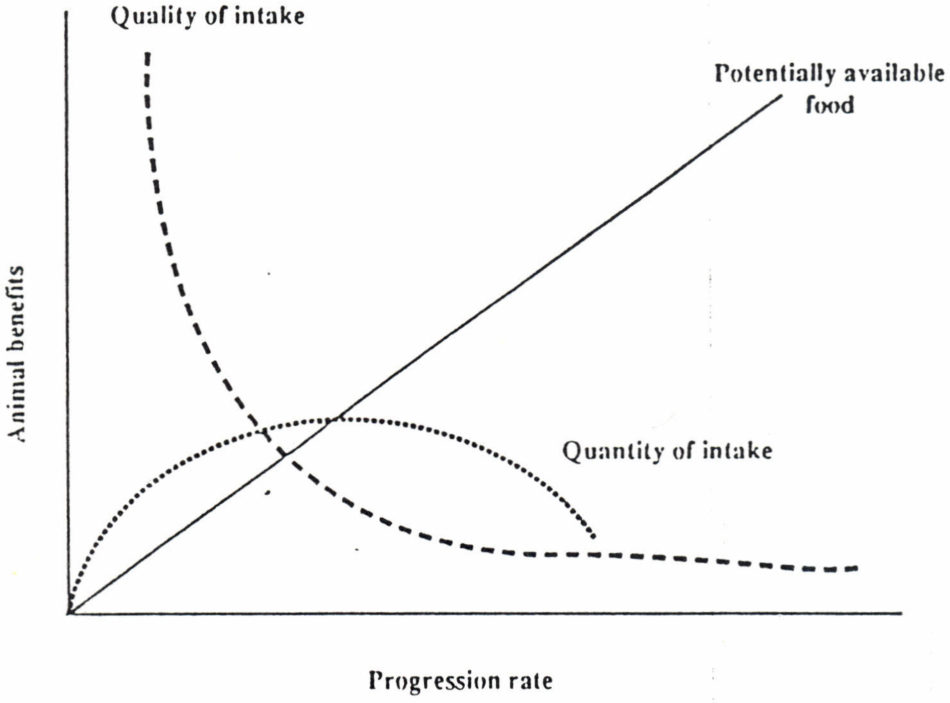


Fig 1. Graphical presentation of the optimal grazing speed model.

(Western, unpublished)

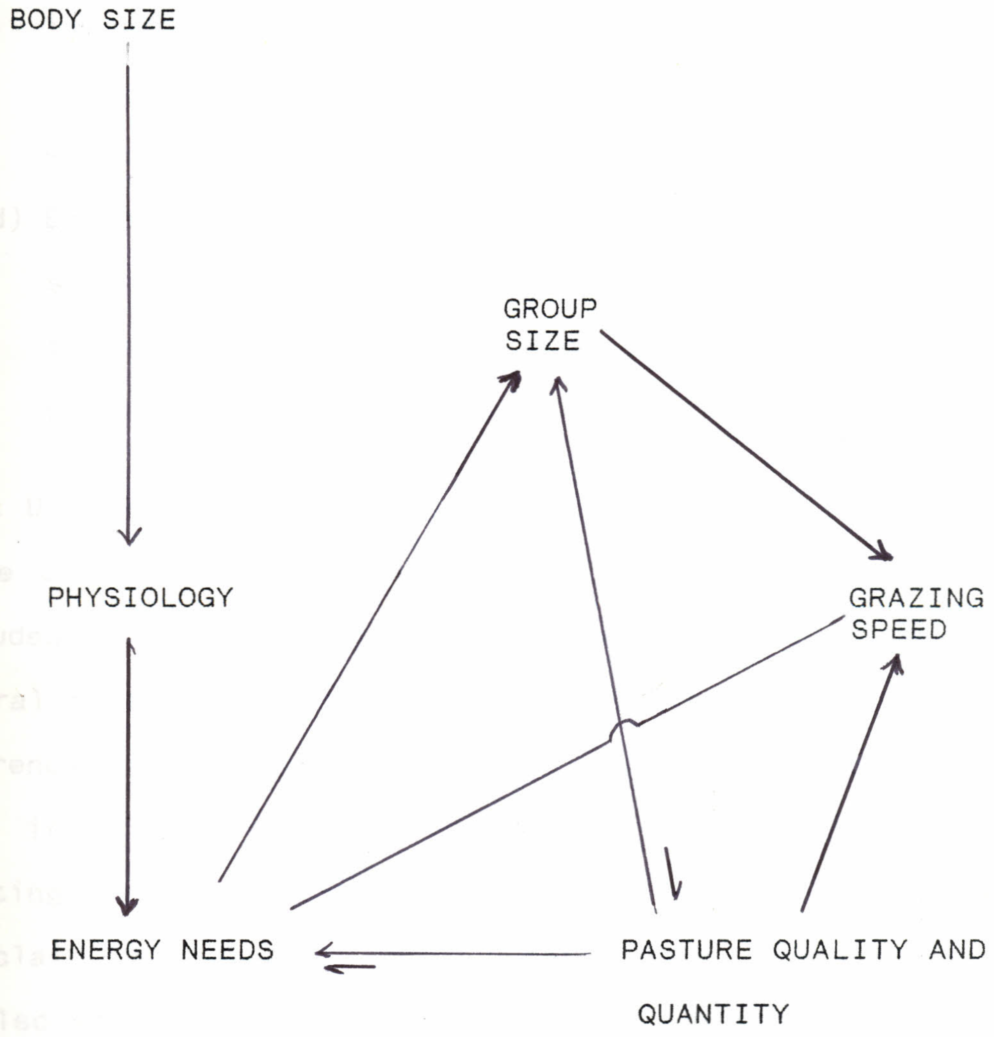


Figure 2. The hypothesized interaction of variables involved in the Model.

(b) Increased group size would proportionately constrain an individual's intake.

(c) To maintain the nutritional requirements individuals would be expected to adopt strategies offsetting negative foraging impacts of group size.

(d) Effects of grazing speed deviations and group size will differ in the intensity of their impacts depending on the body size of the grazer under consideration.

1.9 : Use of crude protein as "currency".

The crude protein content of herbage and forage extruded were analysed as a measure of its quality and several factors contributed to its choice as the quality "currency" in this study. Tropical pastures are generally low in crude protein which is considered a limiting nutrient for both wild and domestic grazers (Sinclair 1972, Fryxell 1985, Duncan 1975). Crude protein is also strongly correlated with the concentration of other nutrients being high in tissues such as leaves, growing parts, and storage organs of plants (Van Soest 1967, Dietz 1970). The crude protein content also has an inverse relationship with crude fibre and as such positively related to digestibility. Its determination is more direct and less complicated compared to other nutrients (Short 1970, Van Soest 1967).

Working on East African grasses, Glover *et al* (1962) developed equations from which the energy content of forage can be predicted from its crude protein content for forage with between 3 and 30 % crude protein per gram. These equations were adopted in this study:

$$DCP = CP\ (\ 70 \log CP - 15\ )$$

$$\log NR = 2.63 - 1.65 \log CP$$

$$GDE = DCP\ (\ NR + 1)$$

Where DCP - Digestible crude protein
CP - Crude protein content of forage
NR - Nutritive ratio
GDE - Gross digestible energy

CHAPTER 2

STUDY AREA AND GENERAL METHODS

2.1 : Study area.

The study was carried out at the Game Ranching Ltd. ranch located 40km South-East of Nairobi on the Athi Kapiti plains. The ranch occupies 8094 ha with elevation varying between 1600 and 1700 M; Latitude $01^{\circ}\ 30'$ S and longitude $37^{\circ}\ 02'$ East (Stelfox 1985).

According to the classification of East African rangelands, (Pratt and Gwyne 1977), the ranch falls within ecoclimatic zone IV (semi-arid zone). Rainfall is strongly influenced by the Intertropical Convergence Zone (I.T.C.Z.) and shows a bimodal distribution pattern. The long rains fall from March through May and are followed by a cloudy cool dry season from June to September with the short rains commencing in October and ending in December. A dry season from December to mid-March follows. There is a considerable seasonal and year to year variation in the amount of rainfall received. Table 1 shows the rainfall amount received for a period of seven years from 1981 and Figure 3 shows the amount received during the study period.

The soils of the ranch and the Athi Kapiti plains consist of volcanic deposits and basalt rocks formed during Tertiary period (Stelfox 1985). The ranch topography is gently undulating with occasional riverine depressions. These undulations have an associated soil catena with sandy well drained soils on the ridge tops

Table 1. Rainfall (mm) received at Game Ranching for a period of seven years from 1981 to 1987.

	1981	1982	1983	1984	1985	1986	1987
JANUARY	0	0	5	10	9	35	56
FEBRUARY	0	0	72	0	314	0	10
MARCH	111	55	30	18	25	24	38
APRIL	128	32	81	73	184	224	35
MAY	99	55	14	0	27	0	31
JUNE	12	11	20	0	0	0	93
JULY	1	6	2	0	0	0	0
AUGUST	0	6	0	0	0	0	0
SEPTEMBER	18	20	18	21	0	0	46
OCTOBER	21	64	15	17	19	0	0
NOVEMBER	28	112	39	37	75	145	88
DECEMBER	24	112	139	37	75	60	7

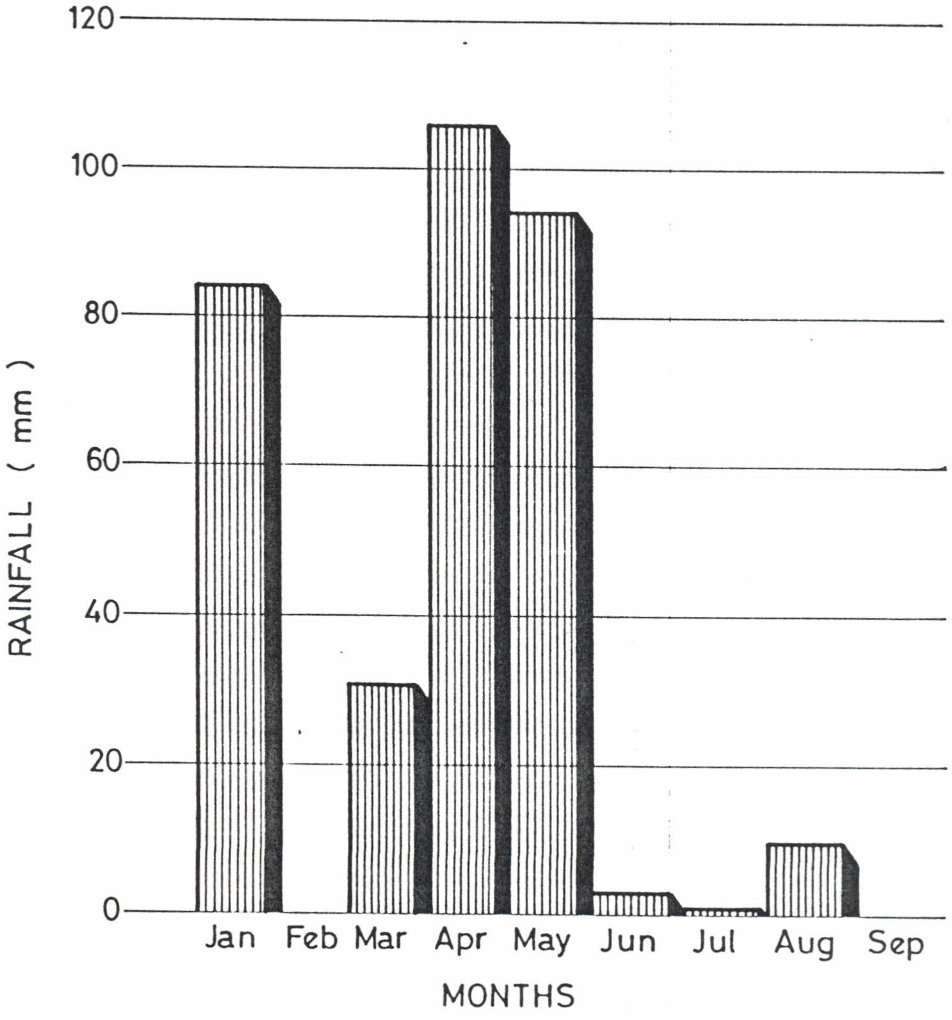


Figure 3. Amount of rainfall (mm) received during the study period (NB. No rain fell in october).

and poorly drained soils in the depressions (Reed 1983, Stelfox 1985). Black cotton soils are the dominant soil types on the ranch. They have a high cation exchange capacity, high base saturation poor drainage, black colour, characteristically swell when wet and become hard and crack when dry. The ranch soils are generally deficient in nitrogen.

Figure 4 shows the distribution of vegetation types on the ranch. Topography and its consequent soil catena strongly influences vegetation distribution and land use on the ranch (Reed 1983, Sinnary 1988). From the hilltop at the compound moving North towards Mombasa road , the vegetation types encountered are; Grasslands dominated by _Themeda triandra_, _Pennisetum mezianum_, _Digitaria milanjiana_, and _Ischaeum afrum_; _Balanites glabra_ or _Acacia seyal_ wooded grasslands and _Acacia drepanolobium_ dwarf wooded grasslands.

The woodlands and wooded-bushed grasslands are restricted to the riverine depression along the Northern border of the ranch through which a seasonal river runs in the wet season. _Acacia xanthophloea_, _A. seyal_ and _A. drepanolobium_ dominate this vegetation type. Roads, cattle bomas and houses are mostly located on the ridge tops with well drained firm soils.

The ranch is a mixed domestic and game animals enterprise. Game animals include Masai giraffe (_Giraffa camelopardalis_), impala (_Aepyceros melampus_), wildebeest

(*Connochaetes taurinus*), fringed-eared oryx (*Oryx oryx*), kongoni (*Alcephalus buselaphus*) Thompson's gazelles (*Gazelle thompsonii*), Grant's (*G. gazelle*) and zebra (*Equus burchelli*) as the main large mammalian herbivores. The spotted hyaena (*Crocuta crocuta* and black-backed jackal (*Canis mesomela*) are the resident predators. Lions (*Panthera leo*) occasionally pass into the ranch from the surrounding area.

2.2 : Pastures.

The pastures chosen for the experiments were from the treeless grasslands, *Balanites Acacia* ecotone and the riverine mixed shrubland area. Open relatively uniform pastures with good visibility were available in these areas. The biomass of the pastures and quality of herbage varied with rainfall and these variations were utilized in assigning the pastures to the different categories (Table 2). High quality pastures were only available during the wet season and low quality pastures in the dry season. To avoid overgrazing on the pastures types, different plots with similar attributes were used. Grazing was suspended on the identified areas and those frequented by wild animals avoided.

2.2.1 : Methods.

Pastures were visually surveyed and relatively uniform ones identified. Vegetation structure, growth stage, species composition where possible, and ground cover were taken into account. Areas with a continuous

Table 2. Pasture categories and their constituent experimental plots and dates of use.

HL - High quality Low biomass,

HH - High quality High biomass,

LH - Low quality High biomass,

LL - Low quality Low biomass,

CATEGORY	HL	HH	LH	LL
	Kaburi Ndege Maziwa	Otieno Raphael Gate Jioni	Gate M Gate Boma	Kaburi Ndege Twiga Maziwa Lister
	3/1 - 10/2/89 20/3 - 6/6/89	10/4 - 10/6/89	27/6 - 30/10/89	20/6 - 30/10/89
WET SEASON			DRY SEASON	

HIGH BIOMASS PASTURES - LH HH

HIGH QUALITY PASTURES - HL HH

LOW BIOMASS PASTURES - LL HL

LOW QUALITY PASTURES - LL LH

* These abbreviations and terms are used throughout the text.

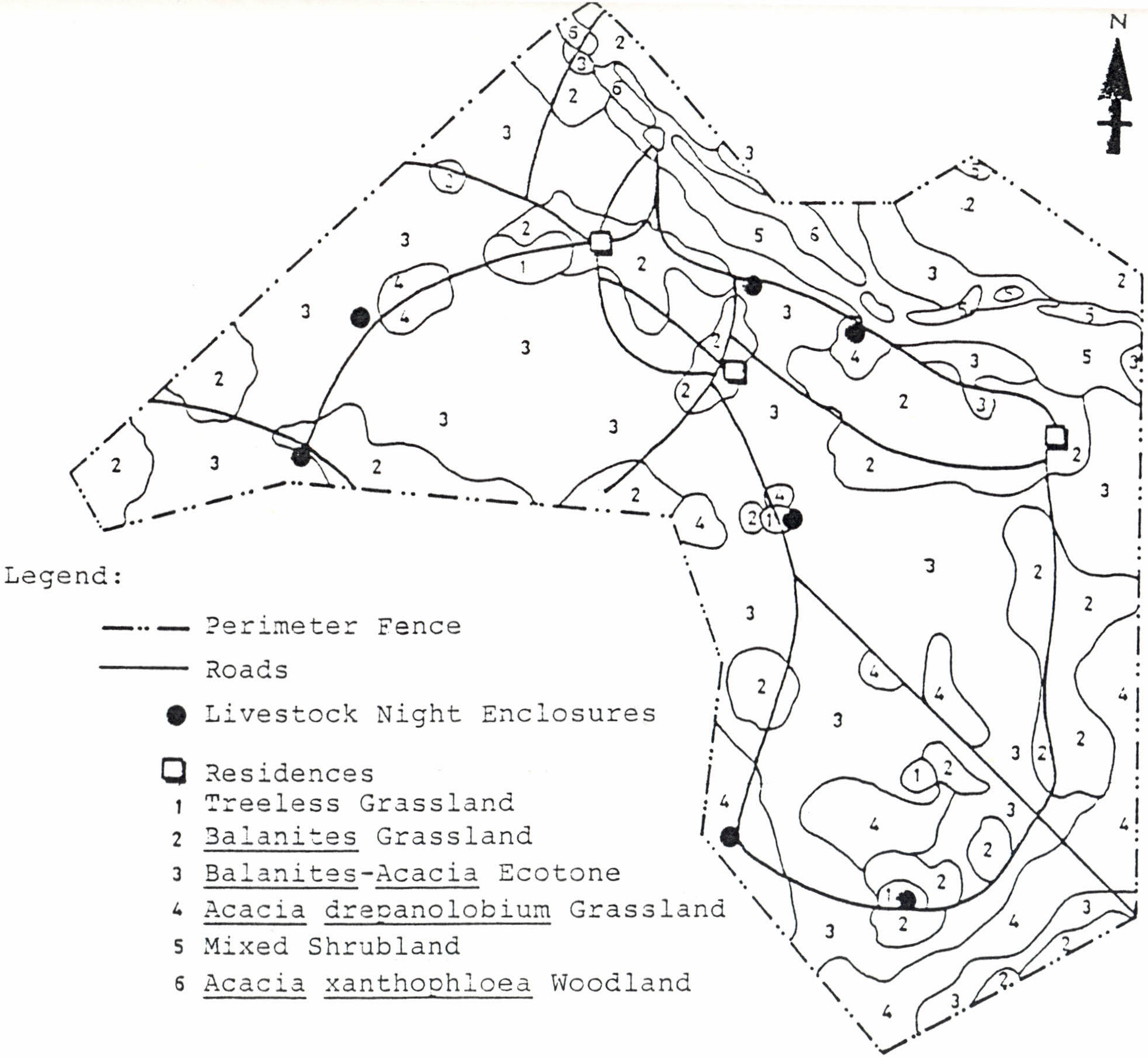


Fig. 4: Distribution of vegetation types at Game Ranching Ltd.

grass cover of more than 90% were used.

Where species composition determination was possible, pastures dominated by Themeda triandra (relative frequency 60%) were selected as it is an important forage species in East African grasslands and highly preferred by grazers (Reed 1983, Hatch et al 1984, McNaughton 1976). A similar pattern of utilization was observed on the ranch with areas dominated by T. triandra being heavily grazed and clumps of Pennisetum mezianum left unutilized.

2.2.2 : Sampling points.

A base line was established along the long edge of the identified pastures and markers established at 20m intervals. Point frame readings on herbage composition were taken at 10m intervals perpendicular to this line. A coin toss was used to decide the location of two other sampling points 5 and 10m on either side of the 10m interval sampling points.

The vegetation in the pastures was quantified using the point frequency frame and $0.25m^2$ quadrats. The frame has been found a useful tool in the study of herbaceous and dwarf vegetation 20-50 cm high (Mueller-Dumbois 1974) and pastures used in the study did not exceed 50 cm in height. The frame is also useful in species composition and plant part proportion studies (Hoffman et al 1978, Gakahu 1982). In this study the frame was used in determining pasture composition by plant parts for quality estimation. When a pin is inserted into the herbage it comes into contact with plant parts, and if the canopy consists of only green or dry leaves then all hits will be for these plant parts. This then means that the frequency of a pin coming into contact with a plant part is proportional to its abundance in the vegetation. 10 pins spaced 10cm apart on the frame were lowered to the ground and interceptions of the pins by the vegetation recorded as hits of plant parts viz; leaf; stems and sheath; inflorescence. This were then categorized as green or brown (dry) and the percent contribution of the parts to the total hits computed.

Using the 0.25 m^2 quadrat vegetation at some points where point frame frequency readings were taken was harvested. The harvested vegetation was used to determine the biomass and crude protein content of the pastures. The pastures used in the experiments were sampled once every week to monitor changes in composition by plant parts. When the frame readings differed significantly from those in the original samples, experiments were discontinued in the plot concerned.

2.2.3 : Pasture categories.

Analysis of variance revealed no significant differences between plots in each pasture category with respect to biomass and composition by plant parts and as such they were pooled as shown in Table 3. Analysis of

Table 3. Biomass (g/$^{m-2}$), % Total green components and Crude protein content (mg/g) of herbage in pastures used in the study.

PASTURE		BIOMASS (gm^2)	%TOTAL GREEN COMPONENTS	CRUDE PROTEIN (mg/g)
HH	x	258.24	73.53	58.3
	n	54	91	26
	s.e	90.98	7.58	15.7
HL	x	138.59	70.38	72.5
	n	63	98	20
	s.e	49.35	11.26	13.0
LH	x	179.53	49.69	31.97
	n	57	88	27
	s.e	45.46	13.54	6.8
LL	x	115.87	40.25	47.3
	n	76	83	24
	s.e	32.84	13.24	7.6

variance was performed for all the pastures with respect to per cent total green hits and biomass (g/m^2) to determine whether the identified pasture categories overlapped. The pastures were found significantly different confirming the initial categories identified (%total green, F= 31.45, d.f = 15,410 , $p < 0.05$; biomass F = 22.40 , d.f= 15, 368 , $p < 0.05$ (Zar 1984)).

Crude protein content for 103 samples of harvested vegetation were regressed against total percent green components. A significant relationship was obtained between these variables given by the equation given below :

$$y = 2.205 + 0.05x, \quad r^2 = 0.393, \quad p < 0.05$$

This relationship is graphically presented in Figure 5 and was used to estimate the quality of pastures from % total green components obtained from the pin-frame readings.

2.3 : Experimental animals.

Testing the model required the control of grazing speed, group size, spacing and pasture condition but these variables could not be controlled for free ranging wild herbivores. Taming could provide a way around this problem, though the large numbers required, time and handling made this option impossible.

Sheep and cattle span a large proportion of body sizes found among wild grazers to which they are physiologically and metabolically identical in all

$y = 2.205 + 0.05x,\ r^2 = 0.393,\quad p < 0.05$

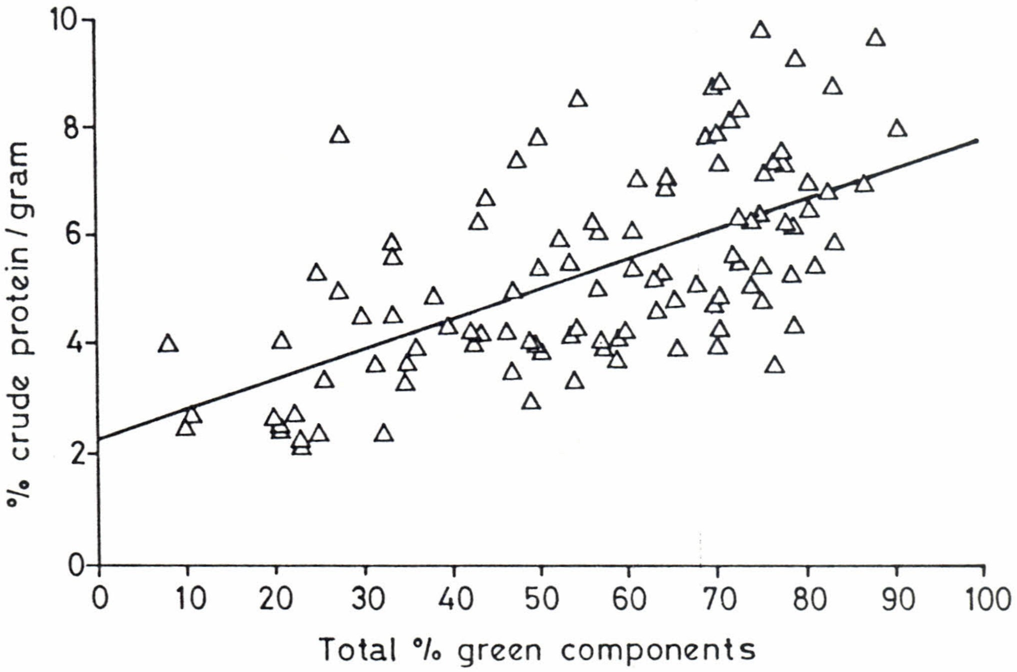


Figure 5.

The relationship between percent crude protein content (%/g) and the total per cent green parts hits of the pasture vegetation obtained using the pin frame. This relationship was used to estimate the quality of pastures during routine sampling.

important respects (Demment and Van Soest 1983). They can be fistulated and herded in any configuration on pre-selected pastures as they are used to being handled without disrupting foraging behaviour. They were therefore suitable subjects for testing the model and to tease apart the factors acting in concert to produce the observed grazing patterns.

A herd of 220 cattle composed of heifers and steers and a flock of 300 sheep were used in testing the model. Fistulated cattle and sheep were grazed along with the groups to provide an estimate of the quantity and quality of forage intake. The selected experimental groups were free ranging and not provided with supplementary feed. Pregnant and lactating animals were avoided for experimentation due to their different behaviour and nutritional requirements (Owen-Smith 1982).

2.3.1 : Fistulation as a method of herbivore diet study.

Oesophageal fistulation is one of the major methods used in the study of large mammalian herbivore diets. The method has been successfully used in the study of domestic livestock and wild herbivores foraging behaviour (Stobbs 1973a, 1973b, Keeney and Black 1984, McManus 1961, 1962, 1981, McManus <u>et al</u> 1962, Duncan 1975, Kautz and Van Dyne 1978). Oesophageally fistulated cattle and sheep fitted with a Van Dynne and Torrel (1964) closing device (Figure 6) were used in this study to obtain forage samples from which the quality and

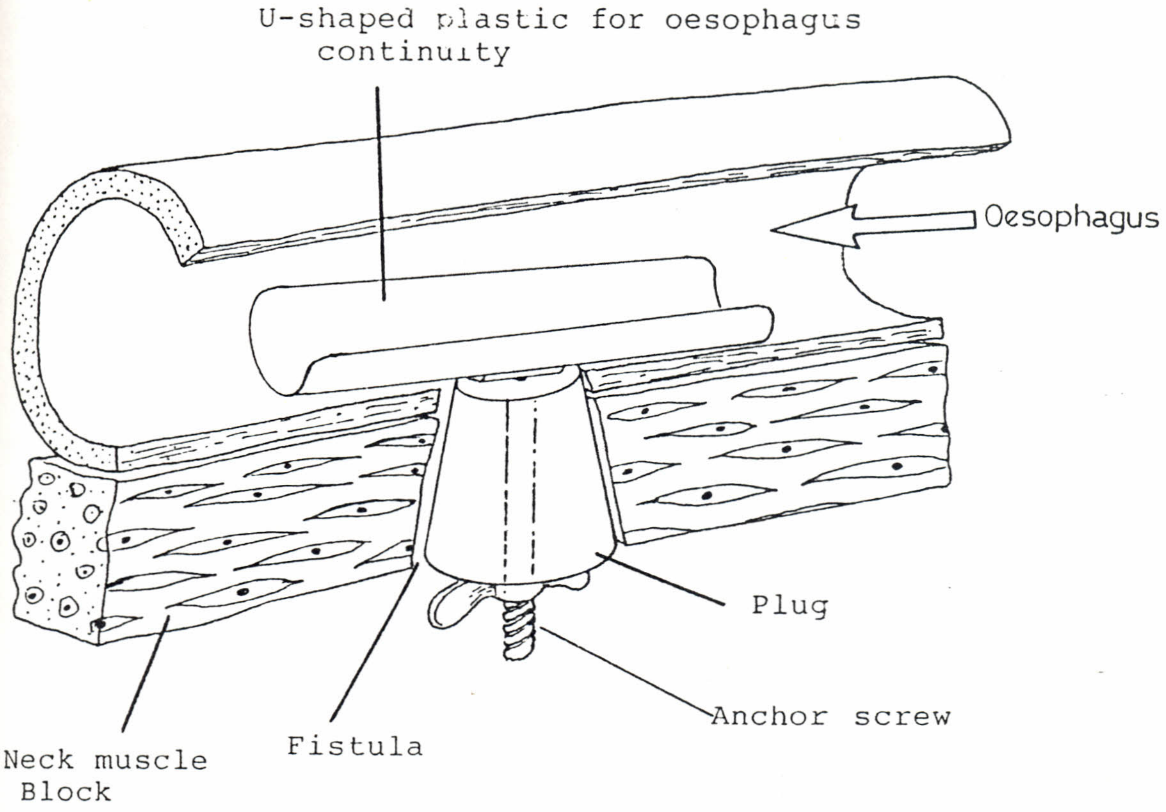


Figure 6. Van Dynne and Torrel (1964) type of fistula closing device fitted used on the fistulated device. This type was chosen as it is easily adjusted.

quantity of diet could be determined.

Problems in the use of this method may arise from fistula closure or the healing process. Lack of effective closure results in excessive saliva loss, leading to dehydration and salt loss raising the rumen pH and interfering with the fermentation process (McManus 1959). Lesions or inflammations at the fistula may compel the animal to select a soft diet, biasing results of grazing experiments (Duncan 1975).

With well recovered animals the method is excellent and overcomes some major limitations of other methods used in large herbivore diet analyses (Martins 1970). Predictive equations and calibration curves have to be developed before any quantitative analysis on diet can be attempted using these other methods. Rumen and faecal analyses are biased by the selective retention of ingesta components in the rumen and the differential digestibility of plant parts (Rice 1970, Robards 1981, Ward 1970). Predictive equations are needed, taking these effects into consideration before quantitative analysis is attempted. With oesophageal fistulation, forage is collected at the point of intake (Rice 1970, Corbett 1981) and compared to the direct observation the animal is the collecting agent and observer errors are eliminated (Bjugstad _et al_, 1970). Studies have found no changes in the chemical and physical properties of diets recovered from fistulated animals when compared to the feed offered (McManus 1961). As Talbot and Talbot (1962) notes "oesophageal fistulation is probably the most efficient method of assessing the diet of large herbivores".

2.3.2 : Fistulated animals used.

Three fistulated heifers of Simmental-Boran crosses and a Boran steer were used in the study on foraging in cattle. Neutered fistulated rams of Dorcester horn and Red masai breeds were used in sheep foraging studies. Previous studies did not show any differences in these grazers along breed lines (Van Dynne, 1968). The fistulated sheep usually lost condition in the dry season as the type fistula plug used induced stress as grass became drier and difficult to swallow.

An ungulate behaviour sampling programme was used to compare fistulated and non-fistulated animals for bites per minute and foraging time for ten minute intervals. No statistically significant differences were found for these two foraging aspects between fistulated and non fistulated animals (Table 4).

The fistulated animals were compared to each other for forage extrusion and crude protein content (Tables 5 and 6). The steer used in the experiments differed significantly from the heifers in forage extrusion due to fistula size. In sheep no such differences were detected. The crude protein content of forage revealed no significant differences for cattle on low quality high biomass pastures where animal differences in selectivity would have been expected (Table 7 a). Sheep similarly on the HH pastures did not show any differences with respect to the quality of forage extruded (Table7 b).

Table 4. Comparison between fistulated and non fistulated animals with respect to bites per minute and and time spent foraging in 10 minute foraging intervals.

SHEEP	Fistulated	Non - fistulated	t
Bites/min	x = 35.6	35.5	
	n = 18	16	
	s.e.= 0.72	0.72	0.014 n.s.
Time foraging	x = 8.4	8.63	
	n = 17	20	
	s.e.= 0.1	0.19	0.722 n.s.
CATTLE			
Bites/min	x = 33	36.2	
	n = 18	15	
	s.e.= 1.11	1.36	1.844 n.s.
Foraging Time (minutes)	x = 8.0	8.07	
	n = 21	20	
	s.e.= 0.23	0.22	0.216 n.s.

n.s. - not significant

where x = mean

n = sample size

s.e. = standard error

Table 5. Forage extrusion (grams/10 minutes) by the fistulated cattle (where F = fistulated animal code, x = mean of forage amount extruded, n = sample size and s.e. = standard error of estimate).

F		Quantity Extruded (g/10 min.)	Sample size (n)		s.e.
SO1	41	110.85	8.91	*	
SO2	6	32.83	6.73	!	
SO3	8	50.35	13.84	!	
HO5	30	138.41	12.64		
H11	44	164.23	12.99		
H27	45	156.67	11.70		

F (5 ,168) = 7.856, $p < 0.05$

* Forage recovered was corrected with a factor of 28.16 % to attain similar levels with H05, H11, H27.

! Withdrawn from the experiments.

Tukey Test

SO1 vs HO5 q = 2.64 n.s. H11 vs HO5 q = 11.2 n.s.

SO1 vs H11 q = 4.23 * H11 vs H27 q = 1.42 n.s.

Ho1 vs H27 q = 4.52 * HO5 vs H27 q = 1.65 n.s.

* significant differences before the correction factor was applied ($p < 0.05$).

n.s. = not significant.

Table 6. Forage extrusion by the fistulated sheep used in the study. F- Fistulated animal code, n - sample size, s.e. - standard error of estimate.

F	n	x	s.e.
02	8	15.83	0.81
03	8	15.60	0.94
05	13	15.00	1.01
06	10	15.54	0.69
07	10	15.24	1.00

Analysis of variance (one way)

$F_{(5, 48)} = 0.098$, $p > 0.05$.

Table 7. Comparison Crude protein content (mg/g) of forage extruded by fistulated (a) cattle and (b) sheep used in the grazing experiments.

(a) Cattle

Fistulated animal code	Sample size	Mean forage CP content	s.e.
SO1	7	91.00	8.20
HO5	6	66.41	3.00
H11	9	84.96	8.10
H27	10	76.29	1.20

(b) Sheep

O2	10	128.43	1.01
O3	8	158.80	13.40
O5	10	164.03	12.90
O6	8	150.70	7.20
O7	9	138.30	4.30

(a) Cattle, Analysis of variance $F_{(3, 28)} = 1.328$, $p > 0.05$.

(b) Sheep, Analysis of variance $F_{(4,40)} = 2.28$, $p > 0.05$.

CHAPTER 3

TEST OF THE GRAZING SPEED MODEL

3.1 : Introduction.

Most animals have to move within their habitats in search of food whose probability of encounter is dependent on search rate and distribution of the food cues (Krebs and Mcleery 1984). Speed at which animals move in search of their food has been assumed constant in the majority of optimal foraging models and studies (Pyke *et al* 1977). The problem of optimal speed of movement in relation to energy intake has, however, not been well investigated. Investigating the effect of speed of movement on the caloric intake of planktivorous fish, Ware (cited in Pyke *et al* 1977) found that though the energetic cost of movement increased with speed, net caloric returns reached a maximum at speeds dependent on food density. Yellow baboons (*Papio cynocephalus*) foraging efficiency in open grasslands was found to be strongly influenced by movement rates and declined at high speeds (Altmann 1974). In pipistrelle bats (*Pipistrellus subflavus*) buzzing rate was strongly correlated with prey insect density, declining and ceasing completely as density dropped (Racey and Swift cited in Kacelnik and Bernstein 1988). Apparently the speed of travel through a habitat has to ensure favourable energy returns while keeping the energetic cost of movement at a minimum, and is strongly influenced

by the abundance and distribution of the food.
and quality in space and time in their habitats (Jarman 1974, Stobbs 1973 a, Senft et al 1987). In spite of the apparent continuous cover formed by grass, items of high quality sought for are spaced far apart with low quality items in between (Geist 1974, Jarman 1974). Depending on a grazer's preferences speeds of travel would be expected to be strongly linked to the density of the forage sought. On contrasting swards a grazer should move at grazing speeds that ensure an optimal energy intake but the effect of body size dependent selectivity regimes on the optimal grazing speed is not clear. The large bodied animals may cover large areas to meet their greater energy needs or as they can subsist on a lower quality diet movement rate over the pastures may be slow.

Using cattle and sheep the above issues were investigated by testing the following hypotheses derived from the optimal grazing speed model (1.3.4):

(a) Contrasting sward will impose different grazing speeds on grazers, and on similar sward types grazing speed adopted will depend on the metabolic requirements of a grazer.

(b) The two aspects of grazing i.e. herbage intake and quality will be differentially affected by speeds different from the optimal.

Most grazers spend part or most of their lives in groups as this increases their inclusive fitness (Bertram

1978). More recent models of group living view membership as a function of benefits and costs influencing an individual's decision for continued membership. One of the immediate costs of group membership involves access to food and this increases as competition for resources intensifies with increased group size. This cost increases at a greater rate than benefits at group size beyond a certain limit (Metcalfe 1989). The density of food available to an individual is lowered by too many feeders at the same site at the same time as studies on birds and non human primates have shown (Metcalfe 1989, Stacey 1986). For herbivores feeding in a herd, group configuration may be more important than absolute group size as less food may be available to those at the rear (Jarman 1974). Group size, an individual's position in the group and the spatial deployment of resources would be expected to strongly influence an individuals foraging performance and rate of movement over pastures. Where animals are under pressure to remain close together (Estes 1976) the grazing speed model postulates that grazing speed would increase proportionately with group size.

3.2 : Materials and methods.

In testing the optimal grazing speed model, observations were made with the animals either free ranging or experimentally manipulated over the pastures. Under the free ranging situation the animals were allowed to settle on the pastures without interference from the observers. Under the experimental manipulations, the animals were actively herded according to investigations being carried out.

3.2.1 : Free ranging.

3.2.2 : Grazing speed.

Groups of 40-60 animals were grazed on pastures with contrasting attributes (Section 2.2). This group size range was stable with no tendency to rejoin bigger groups or split into smaller units.

Animals were taken to the selected pastures and grazed for one hour to reduce the effects of rumen fill on foraging before experiments commenced. To determine grazing speed, distance covered by animals in 10 minute intervals was measured by placing plastic markers at points passed through by the animals. Four focal animals, selected on the basis of their position in the group, with one from the group centre, flank, front and rear were used in each session and their grazing speeds averaged. Animal visibility was a major problem and the use of individuals with conspicuous traits, such as uniquely shaped horns or body spots provided a way around this problem. Fistulated animals when used for forage intake determination were taken as focal animals.

3.2.3 : Dispersion patterns.

The grazers in the above group size were observed with respect to their settlement patterns over the pastures, progression rates and nearest neighbour distances were recorded. Nearest neighbour distances (N.N.D.) were taken as the distance between an animal and its closest neighbour. Where groups exceeded 30 animals, distances were taken for at least 15 animals and recordings made at 3 minute intervals. The observers were not more than 15m away from the group during these estimates. Sample estimates using shrubs were always taken before the actual measurements for the animals were made.

3.2.4 : Experimental manipulations.

3.2.5 : Manipulations of grazing speeds.

Animals were moved at progressively higher speeds over the pastures. Grazing speeds were increased until grazing ceased and animals just walked through the pastures. Depending on the time of day animals could stop feeding at relatively low grazing speeds. In late morning, the animals tended to move towards watering points and night enclosures in the evening.

3.2.6 : Group size.

Animals were put on the selected pastures in different group sizes. The group size ranges were progressively increased from 15 - 25, 40 - 60, 80 - 120 and 150 - 250 animals. Progression rates and nearest neighbour distances (N.N.D.) were estimated for the different group sizes. The effect of the settlement pattern on these parameters was also observed.

3.2.7 : Constraintment of spacing.

Spacing between animals was systematically reduced by observers approaching a group from the periphery. The animals when approached closely tended to bunch closer to each other and this was related to the distance of the observers from the group. The resultant nearest neighbour distances and progression rates were determined.

3.2.8 : Feed recovery.

In grazing experiments where the fistulated animals were used to estimate forage intake, they were allowed to graze for one hour to reduce the effect of rumen fill prior to sampling. Fistulated cattle were taken to crushes erected near the pastures and the fistula plugs removed. They were then fitted with non leaking forage sample collection bags and returned to pastures where they were grazed with the rest of the herd according to the chosen experimental regime. The fistulated animals were prevented from feeding before rejoining the groups and after the expiry of the grazing session.

This was achieved by observers staying close to the animals. Sample removal and plug refitting for cattle was carried out in the crushes but for sheep plug removal, sample recovery and processing was carried out in the pastures. The forage extruded by fistulated animals was used to determine quantity and quality of forage harvested. Two animals were used per session and two sample sets recovered from each.

3.2.9 : Sample processing.

Samples collected were put in polythene bags to avoid leakage of the finely masticated parts along with saliva. They were sun dried for 2-3 days under black polythene to drive off excessive moisture. Samples were then oven dried at 80°C for 72 hours to constant weight, weighed and ground for crude protein content analysis.

3.3 : Results.

3.3.1 : Free ranging.

3.3.2 : Grazing speed.

Grazing speeds for cattle and sheep are shown in Table 8 along with forage intake for free ranging animals. The grazing speeds of cattle on LH, HL and HH did not differ significantly (Tukey, $q = 0.388$, d.f. = 74, 4, $p > 0.05$). Grazing speed was lowest on LL pastures for cattle differing significantly from that on HH, LH and HL pastures (Tukey test after Anova, $q = 7.27$, $p < 0.05$).

Grazing speed for sheep differed significantly on all pasture categories (Anova $F = 11.78$ d.f.= 2, 86, $p < 0.05$). The highest grazing speeds were on the HH pastures, intermediate on HL and lowest on LL pastures.

When grazing speed was expressed as a proportion of body length, significant differences in the grazing speeds of cattle and sheep was detected with sheep moving faster than cattle over similar pastures (Table 9).

Table 8. Grazing speeds, herbage intake and energy returns for cattle and sheep grazing on different pasture types.

CATTLE	Pasture Type		Grazing speed (m/min)	Forage (g/10min)	Energy (cal)
	HH	x	5.828	249.30	559.30
		n	27	18	18
		s.e	0.29	10.84	26.14
	LH	x	5.88	228.28	454.84
		n	36	25	25
		s.e	0.28	9.80	2.29
	HL	x	6.07	165.17	352.56
		n	27	20	20
		s.e	0.12	9.52	21.92
	LL	x	3.85	144.85	257.58
		n	32	22	22
		s.e	0.27	11.06	20.84
SHEEP	HH	x	5.99	22.78	57.24
		n	17	17	36
		s.e	0.62	1.44	3.52
	HL	x	4.53	21.87	51.97
		n	38	36	36
		s.e	0.25	1.21	3.02
	LL	x	3.45	-	-
		n	34	-	-
		s.e	0.24	-	-

Table 9 A comparison of grazing speeds of cattle and sheep expressed as ratios of body length.

PASTURE	SHEEP	CATTLE	t-value	df
HH	5.24	2.96	8.220 *	35
LH	---	2.89	-----	---
HL	4.34	3.21	2.688 *	50
LL	3.35	1.958	5.21 *	64

* - significant, $p < 0.05$

Grazing speed observations on LH were not carried out for sheep.

3.3.3 : Herbage intake and energy returns.

Cattle forage intake on LL and HL pastures was low and comparable (t, test two-tailed, $t = 0.34$ d.f. $= 41$ $p > 0.05$ (Table 8)). Forage intakes were highest on LH and HH (high biomass pastures) with no statistical difference detected on these pastures (t, test two tailed $t= 0.34$ d.f. $= 34$, $p > 0.05$). Sheep forage intake on HL and HH were not significantly different (t test, two-tailed $t = 0.45$, d.f. $= 53$, $p > 0.05$).

Energy values were calculated using equations in section 1.5 to determine the gross digestible energy (G.D.E) content of forage. The values obtained were then multiplied with 3.765 calories and the weight of forage extruded. When converted into energy values, pastures where forage intakes were similar showed significant differences with respect to energy returns. Gross digestible energy (GDE) values (cal) of intake were highest for cattle on HH pastures and differed significantly from those on LH pastures (t test one tailed, $t = 30.135$, d.f. $= 40$, $p < 0.05$). Cattle on HL pastures had higher energy intake than on LL pastures (t test, one tailed $t = 3.045$ d.f. $= 41$, $P < 0.05$). Energy intakes in descending order were as follows HH > LH > HL > LL for cattle. Energy returns were similar for sheep on both pasture types (HH and HL) (t test two tailed $t = 1.046$ d.f.$= 51$, $p > 0.05$) where grazing experiments were carried out.

3.3.4 : Quality of forage extruded.

In assessing selectivity, crude protein content of the herbage on offer was compared with that of the extruded forage (Table 10). Cattle were found to be significantly selective on LH and HH (high biomass) pastures. The quality of forage intake on the low biomass pastures LL and HL pastures closely matched that of the herbage on offer.

On both HL and HH pastures sheep selected a diet with a crude protein content above that of the herbage on offer. On LL pastures sheep were observed to selectively feed on the green leaves and emergent young stems with 60 % of the bites observed on these plant parts.

3.3.5 : Dispersion patterns and progression rates.

Two predominant dispersion patterns on the pastures were observed with the animals either dispersed as a grazing front or clumped.

(a) Grazing front: In this pattern the animals were spread out in the pastures in rows. Three rows were commonly observed with individuals rarely in line.

(b) Clumped : The animals were mostly clustered together in distinct with no discerned alignment pattern.

When clumped cattle had a grazing speed of 8.0 m/min (n = 63, s.e = 0.39) which was significantly greater than when a grazing front was adopted of 4.74 m/min (n = 63, s.e.= 0.23) (t - test, one tailed, t = 7.928, d.f. = 124,

TABLE 10 A comparison of crude protein (CP mg/g) content of forage harvested by the fistulated animals and clippings from the pastures.

	PASTURE		PASTURE CP(mg/g)	INTAKE CP(mg/g)	CP DIFFERENCE	t
CATTLE	HH	x	59.7	88.7	29.0	5.488 *
		n	30	25		
		s.e	2.8	0.7		
	HL	x	70.27	74.08	3.81	0.972 ns
		n	23	31		
		s.e	2.5	1.8		
	LH	x	32.98	51.1	18.12	5.575 *
		n	31	59		
		s.e	1.8	1.7		
	LL	x	41.97	43.38	1.86	0.586 ns
		n	27	41		
		s.e	0.22	0.26		
SHEEP	HL	x	70.27	153.1	82.82	13.72 *
		n	23	65		
		s.e	0.25	0.57		
	HH	x	57.91	159.71	102.2	22.00*
		n	24	24		
		s.e	0.31	0.23		

* - Significant ($p < 0.05$)

ns. - not significant

$p < 0.05$). A similar trend was found for sheep which similarly moved faster when clumped 7.52 m/min ($n = 42$, s.e. = 0.44) than when spread as a grazing front 4.07 m/min ($n = 42$, s.e.= 0.59), (t - test one tailed, $t = 6.229$, d.f. = 82, $p < 0.05$).

3.3.6 : Experimental manipulation.

3.3.7 : Grazing speed manipulations

Scatter plots were made with forage intake as the dependent variable and increased grazing speed as the independent variable (Figures 7, 9, 11, 13, 15, Appendices 1 to 5). A non linear decline in forage intake was found for cattle on LL, HL and LH pastures and sheep on HL pastures. A curve with a 1/X function best described the observed declines (Cattle LL $F = 158.48$, d.f. = 1, 57; HL $F = 175.09$, d.f. = 1, 31 ;LH $F = 688.8$, d.f. = 1, 69 ; sheep HL $F = 216.016$, d.f. = 1, 67 ; $p < 0.05$ (Statigraphics 1986)). Cattle forage intake on the HH pastures remained constant with grazing speed though there was a slight drop before feeding cessation (Fig 13). Energy intake on the pastures showed the same patterns (Figs 8, 10, 12, 14, 16). HH pastures were wet and muddy forcing cattle and sheep to give up feeding at fairly low grazing speeds and grazing speed manipulations above these levels were not possible (cattle 13 m/min ; sheep 9 m/min).

Log transformation of the data resulted in the smoothing of the curves onto which simple linear regression

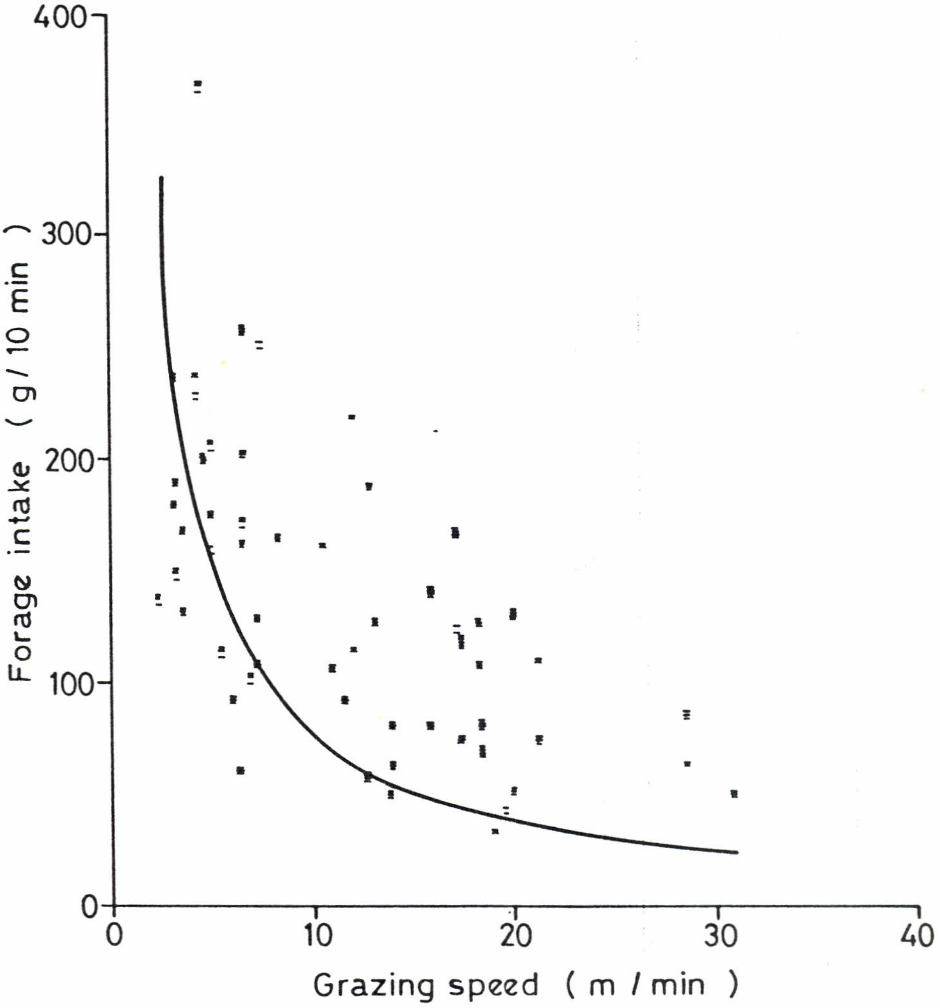


Fig. 7 Weight of Forage (g/10 minute), Extruded with Grazing Speed by Cattle Grazing on Low Quality Low Biomass (LL) Pastures

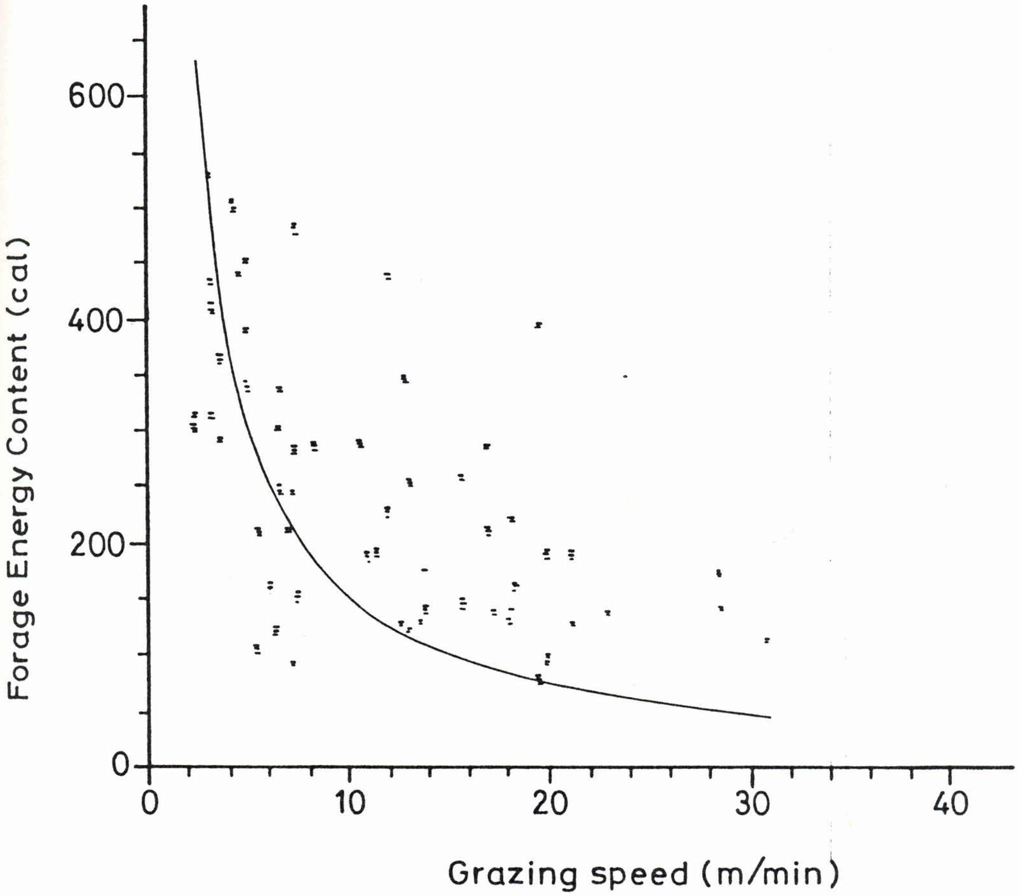


Fig. 8 Energy Content (calories) of Extruded Forage by Cattle on (LL) Pastures with Increased Grazing Speed

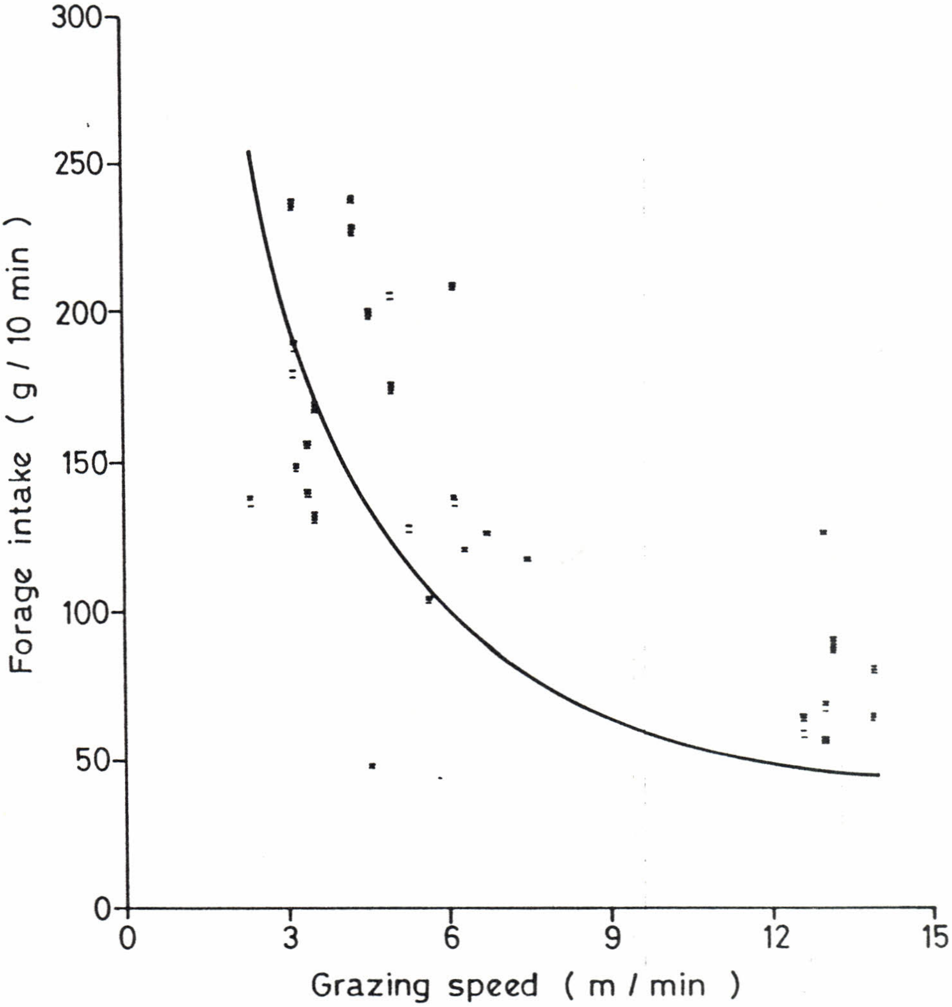


Fig. 9 Weight of Forage (g/10 minute) Extruded with Increased Grazing Speed by Cattle on High Quality Low Biomass Pasture (HL)

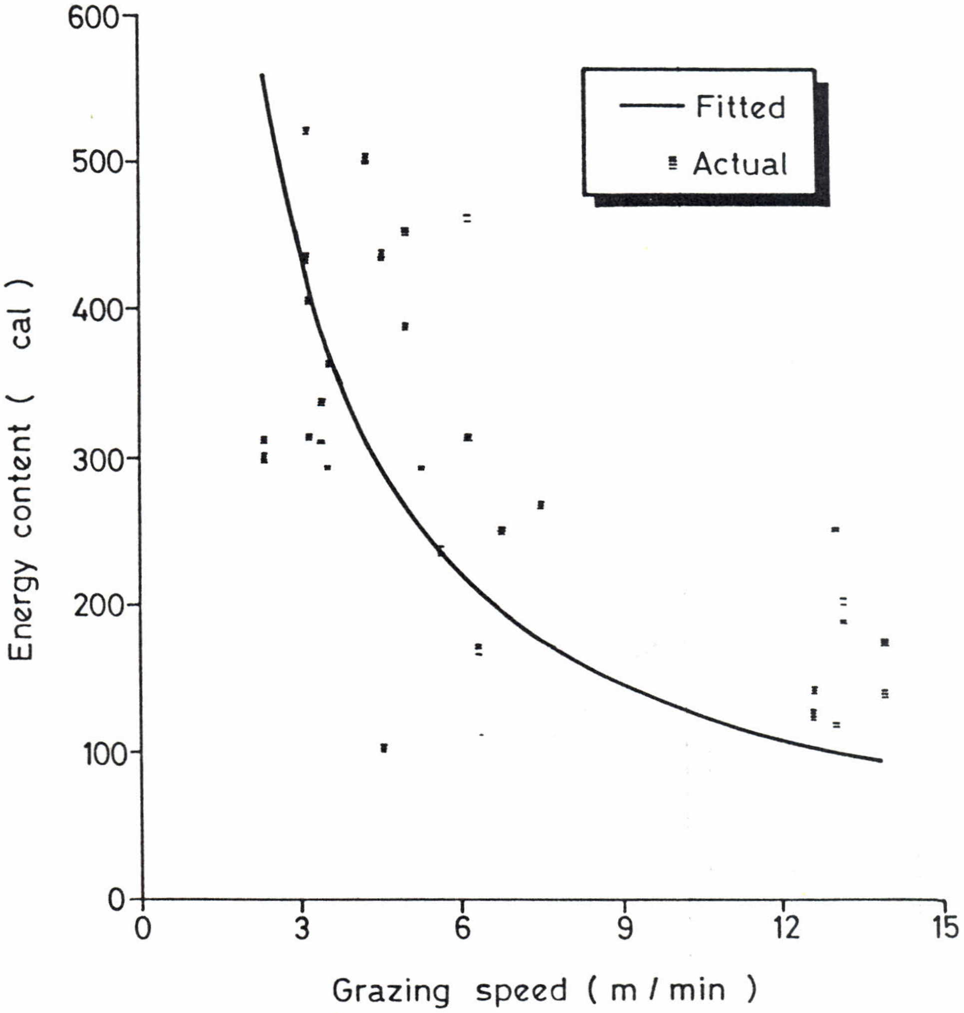


Fig. 10 Energy Content (calories) of Forage Extruded by Cattle on High Quality Low Biomass (HL) Pastures with Increased Grazing Speed

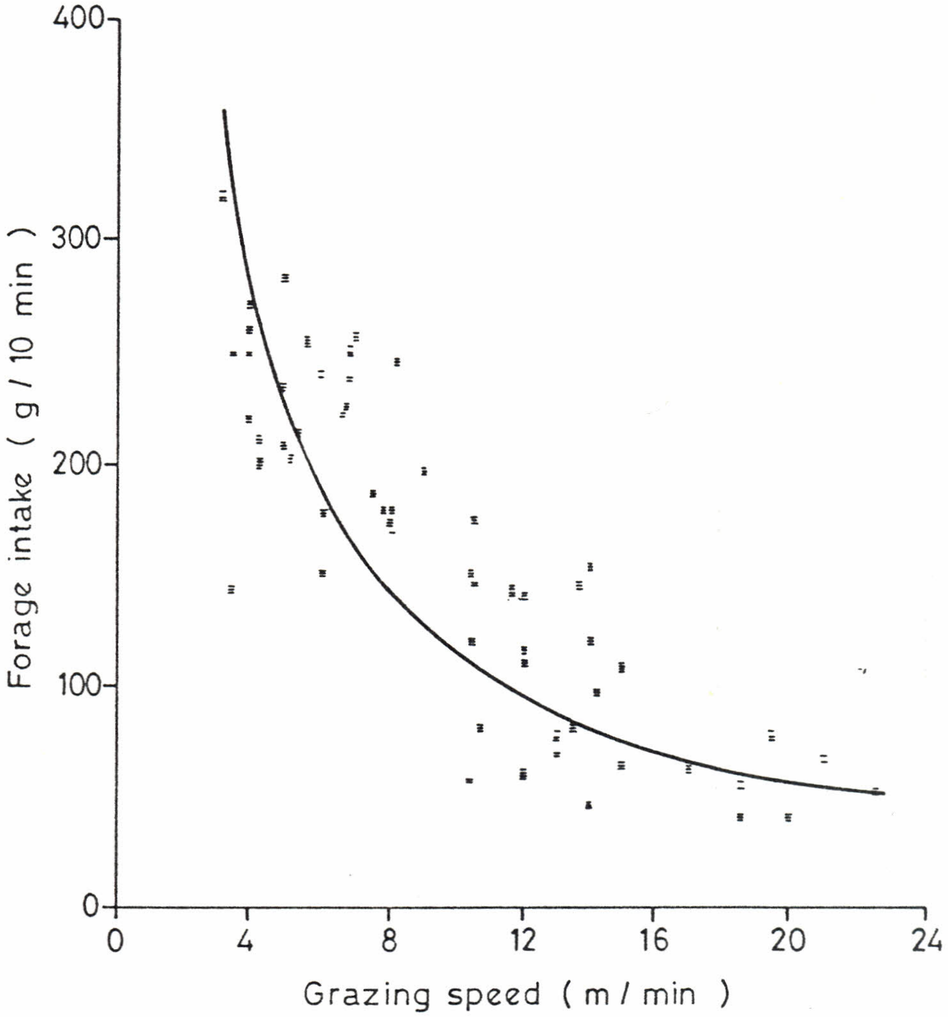


Fig. 11 Weight of Forage (g/10 minute) Extruded by Cattle Grazing on Low Quality High Biomass Pastures (LH) as Grazing Speed was Raised

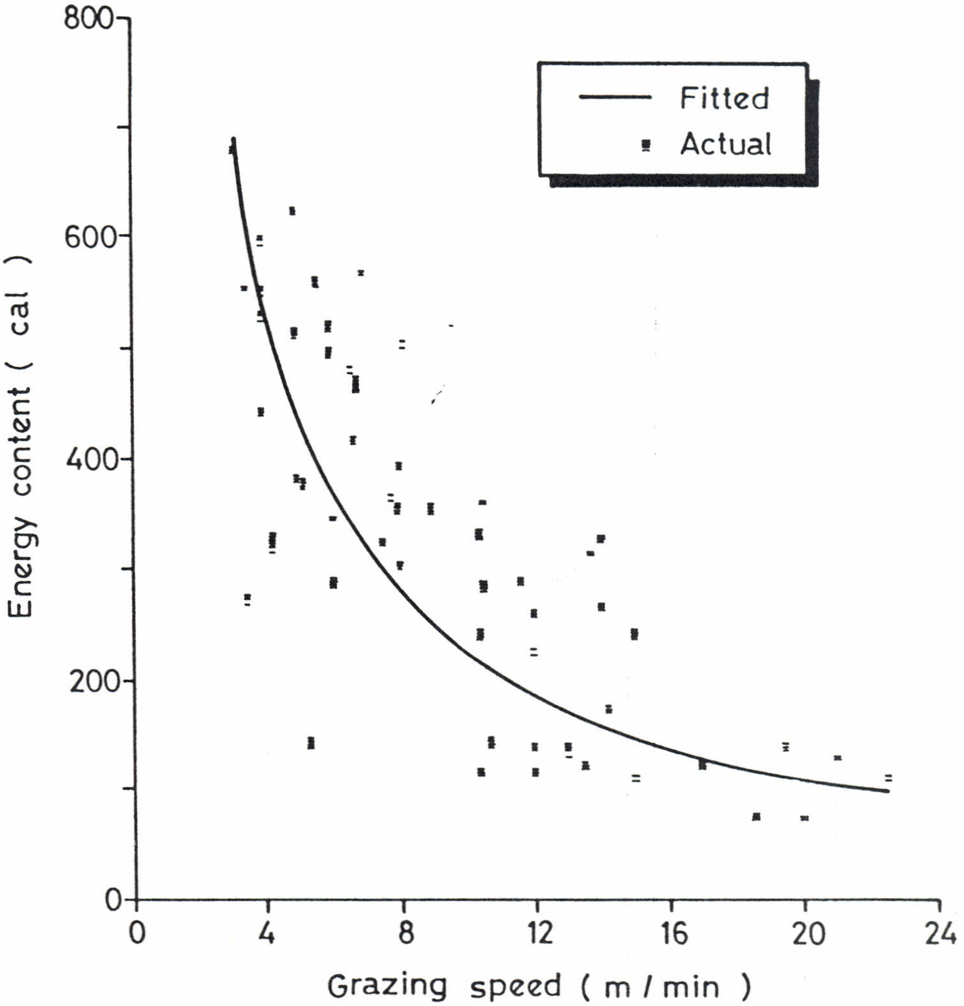


Fig. 12 Energy Content (calories) of Forage Extruded by Cattle on LH Pastures as Grazing Speed was Increased

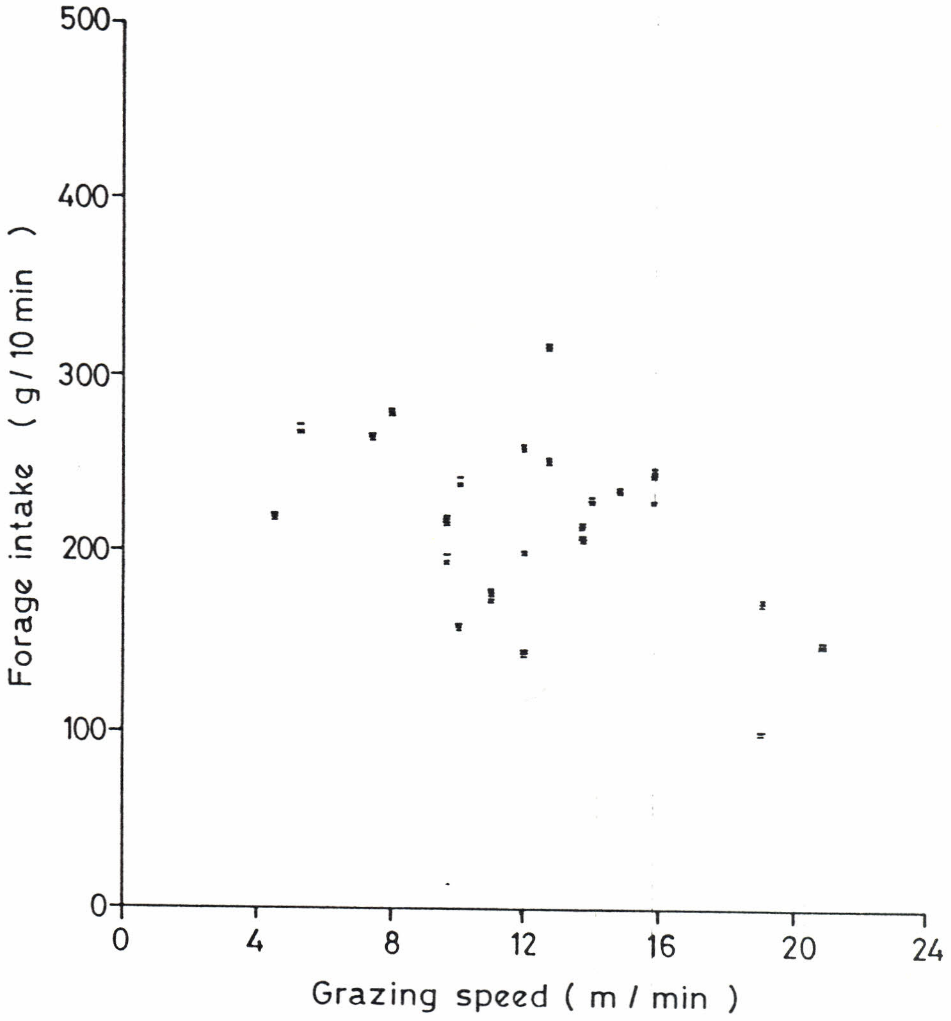


Fig. 13 Weight of Forage (g/10 minute) Extruded by Cattle with Grazing Speed on High Quality Biomass Pastures (HH).

<u>NOTE</u>: There was no Correlation Between Grazing Speed and Forage Intake as Compared to Other Pasture Catagories

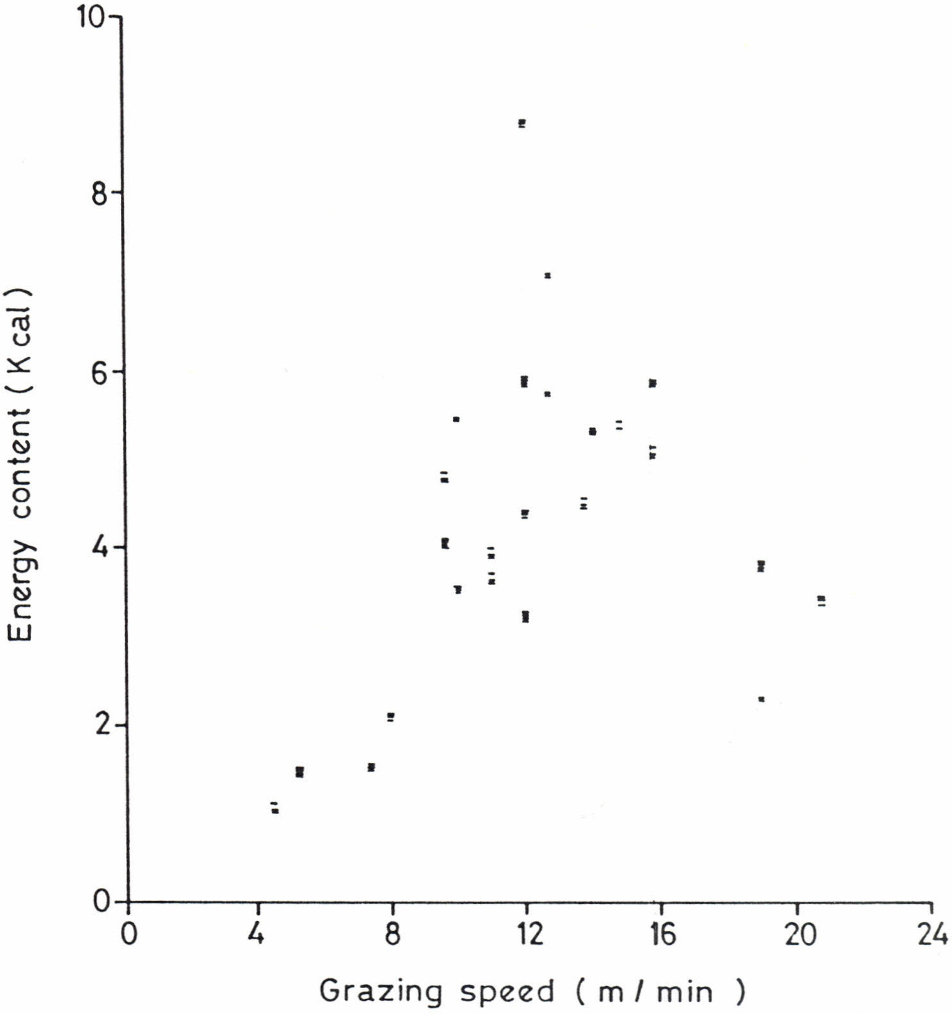


Fig. 14 Energy Content (calories) of Forage Extruded by Cattle on HH Pastures with Increased Grazing Speed

<u>NOTE</u>: There was no Correlation Between Energy Content of Forage and Grazing Speed

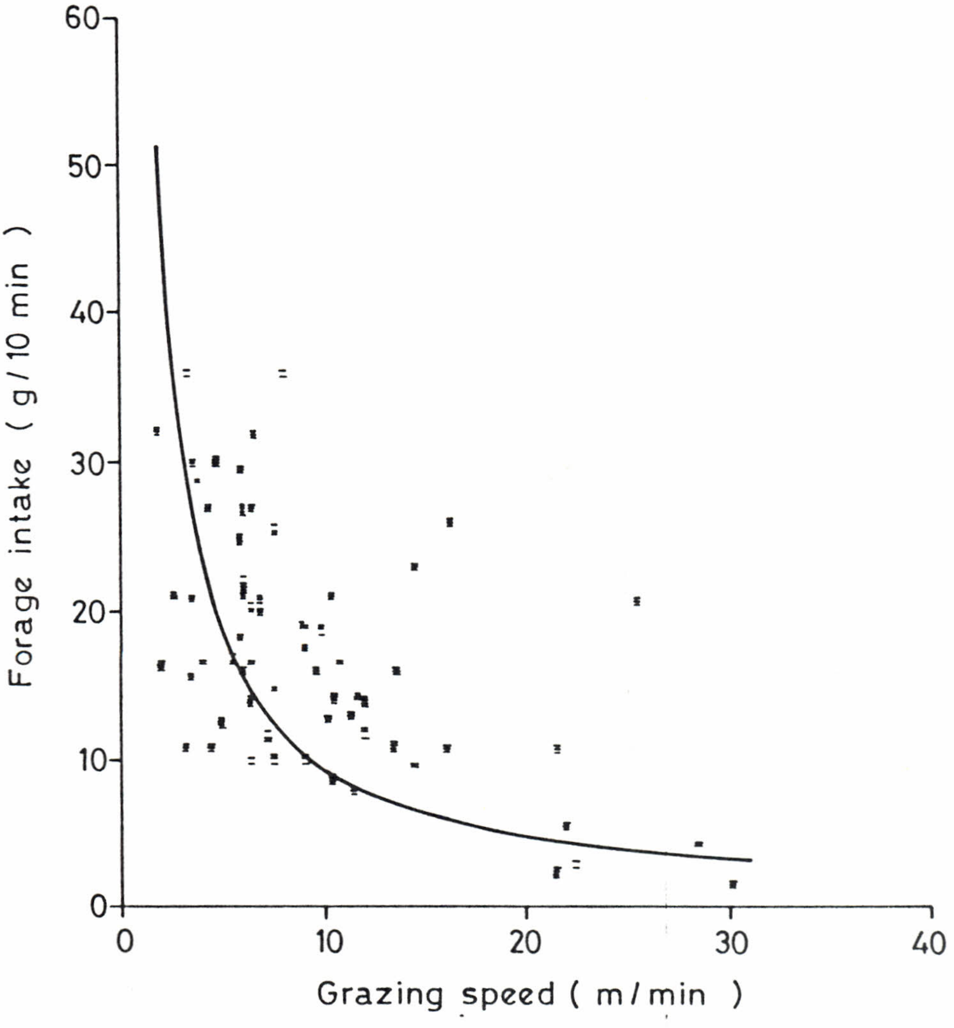


Fig. 15 Weight of Forage (g/10 minute) Extruded by Sheep as Grazing Speed was Raised on High Quality Low Biomass (HL) Pastures

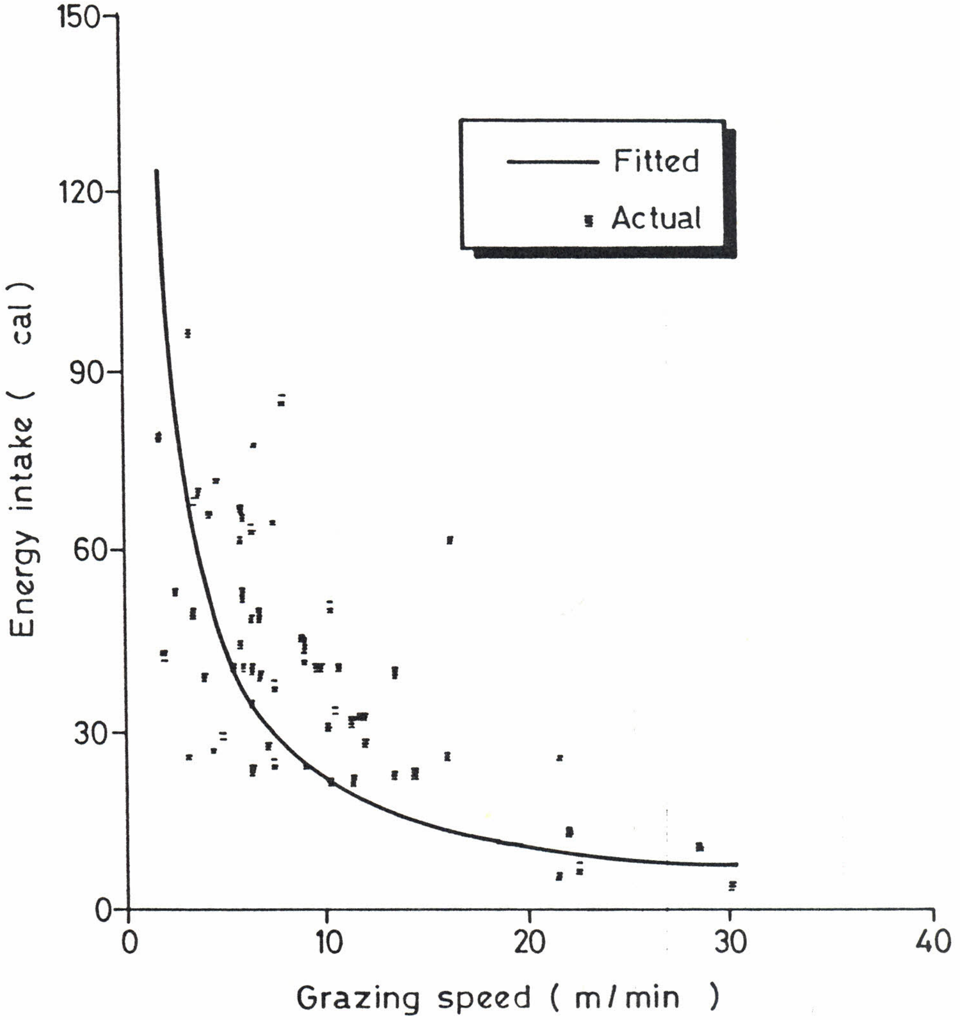


Fig. 16 Energy Content (calories) of Forage Extruded by Sheep Grazing on High Quality Low Biomass (HL) Pastures with Increased Grazing Speeds

equations were fitted.

Cattle HH $Y = 2.513 - 0.17X$ n.s. LH $Y = 3.05 - 0.97X$ *

HL $Y = 2.491 - 1.52X$ * LL $Y = 2.26 - 0.48$ *

Regression Anova, $F_{(2,127)} = 7.454$

Sheep HL $Y = 1.496 - 0.32X$ *

* = Significant ($p < 0.05$)

n.s.= not significant

The greatest decline in intake for cattle was on the LH pastures (Tukey test after anova $q = 21.563$, d.f. = 67, 3, $p < 0.05$). On HL and LL pastures the rate of decline in herbage intake were similar ($q = 1.593$, d.f. = 66,2, $p > 0.05$). Slopes of herbage intake for both cattle and sheep on HL pastures were not statistically different (t test for slopes $t = 1.986$, d.f. = 94, $p > 0.05$).

A regression of cattle and sheep bites per minute against grazing speed was significant ;

$y = 43.85 - 0.77x$, $r^2 = 0.244$ *

$y = 38.925 - 0.88x$, $r^2 = 0.27$ *

* significant, ($p < 0.05$)

Crude protein content (Appendix 1 - 5) of the ingested herbage were regressed against grazing speed . Cattle on LL and LH pastures showed a decline in crude protein of intake with progression. No declines were detected for cattle on HH and HL pastures and sheep on HL pastures;

SHEEP HL $y = 162.4 - 0.101x$, $r^2 = 0.047$ n.s

CATTLE HL $y = 83.3 - 0.119x$, $r^2 = 0.057$ n.s.

HH $y = 93.9 - 0.04x$, $r^2 = 0.006$ n.s.

LH $y = 63.3 - 0.116x$, $r^2 = 0.151$ *

LL $y = 57.59 - 0.08x$, $r^2 = 0.138$ *

* = significant ($p < 0.05$)

n.s.= not significant

3.3.8 : Group size.

The effect of group size on nearest neighbour distances and progression rates depended on the dispersion patterns adopted by the grazers on the pastures. Table 11 and 12 show the effect of group size on cattle and sheep under the grazing front dispersion pattern on grazing speed and nearest neighbour distances which remained constant.

When clustered cattle responded to changes in group size along pasture biomass (Appendix 6 -10). On the high biomass pastures N.N.D. increased with group size though this was not significant on the LH pastures :

HH $y = 1.37 + 0.0024x$, $r^2 = 0.114$, $p < 0.05$

LH $y = 1.11 + 0.0025x$, $r^2 = 0.028$, $p > 0.05$

On the low biomass pastures (LL and HL) group size tended to be associated with a decline in N.N.D. though this again was not significant on the Low quality pasture:

HL $y = 2.60 - 0.037x$, $r^2 = 0.103$, $p < 0.05$

LH $y = 1.46 - 0.005x$, $r^2 = 0.001$, $p > 0.05$

Table 11. Group size and its effects on nearest neighbour distances (m) for cattle and sheep when spread out as grazing fronts on the pastures.

CATTLE		GROUP SIZE					
PASTURE		5	10	20	50	100	200
HL	x	1.87	1.90	1.38	1.23	1.34	1.43
	s.e	0.20	0.70	0.10	0.02	0.11	0.16
	n	8	10	12	9	15	16
HL	x	1.46	1.47	1.65	1.48	1.37	1.31
	s.e	0.08	0.12	0.23	0.15	0.19	0.12
	n	6	13	8	11	12	7
LL	x	1.51	1.86	1.40	1.28	1.91	1.39
	s.e	0.27	0.38	0.08	0.05	0.20	0.16
	n	5	18	19	21	12	8
HH	x	1.26	1.18	1.25	1.09	2.02	1.58
	s.e	0.04	0.07	0.07	0.05	0.19	0.14
	n	5	6	12	7	8	8
IEEP							
LL	x	1.37	1.19	1.12	0.96	0.61	1.31
	s.e	0.31	0.09	0.12	0.10	0.05	0.15
	n	6	14	12	10	8	6
HL	x	1.03	0.90	0.95	0.78	0.82	0.83
	s.e	0.01	0.01	0.06	0.03	0.04	0.05
	n	5	10	20	11	6	6

able 12. Effects of increased group size on grazing speed of cattle (a) and sheep (b) for the front grazing pattern.

(a) CATTLE

		PASTURE			
		LH	HH	HL	LL
GROUP SIZE					
5	x	5.6	5.9	3.02	4.4
	s.e	0.3	0.65	0.38	0.42
	n	22	12	14	12
20	x	4.9	5.8	5.2	5.6
	s.e	0.29	0.68	0.50	0.59
	n	16	10	7	13
50	x	5.5	5.8	6.1	5.9
	s.e	0.42	0.68	0.50	0.36
	n	19	10	7	16
100	x	5.1	7.0	6.1	5.2
	s.e	0.33	0.70	0.46	0.68
	n	14	9	8	10
200	x	5.5	6.8	5.7	6.3
	s.e	0.49	0.74	0.68	0.75
	n	15	11	10	9

(a) SHEEP

				HL	LL
5	x	-	-	3.0	3.3
	s.e	-	-	0.31	0.45
	n	-	-	14	10
20	x	-	-	4.8	4.3
	s.e	-	-	0.58	0.70
	n	-	-	15	8
50	x	-	-	4.4	4.4
	s.e	-	-	0.41	0.39
	n	-	-	19	13
100	x	-	-	5.6	4.8
	s.e	-	-	0.74	0.65
	n	-	-	13	7
200	x	-	-	5.9	4.6
	s.e	-	-	0.77	0.73
	n	-	-	10	11

On the low biomass pastures, nearest neighbour distances declined as group size was increased for sheep:

HL $y = 1.04 - 0.002x$, $r^2 = 0.081$, $p < 0.05$

LH $y = 1.80 - 0.009x$, $r^2 = 0.263$, $p < 0.05$

Figure 17 shows the effects of increased group size on N.N.D. for sheep on HL pastures. Regression analysis was carried out to determine whether group size had any effects on grazing speed over the pastures. Only on the high biomass pastures were significant regressions obtained for cattle (Appendix 6 - 10):

HH $y = 8.33 + 0.029x$, $r^2 = 0.029$ *

LH $y = 8.06 + 0.031x$, $r^2 = 0.087$ *

LL $y = 9.55 + 0.094x$, $r^2 = 0.013$ n.s.

HL $y = 6.16 + 0.02x$, $r^2 = 0.035$ n.s.

* = significant , $p < 0.05$

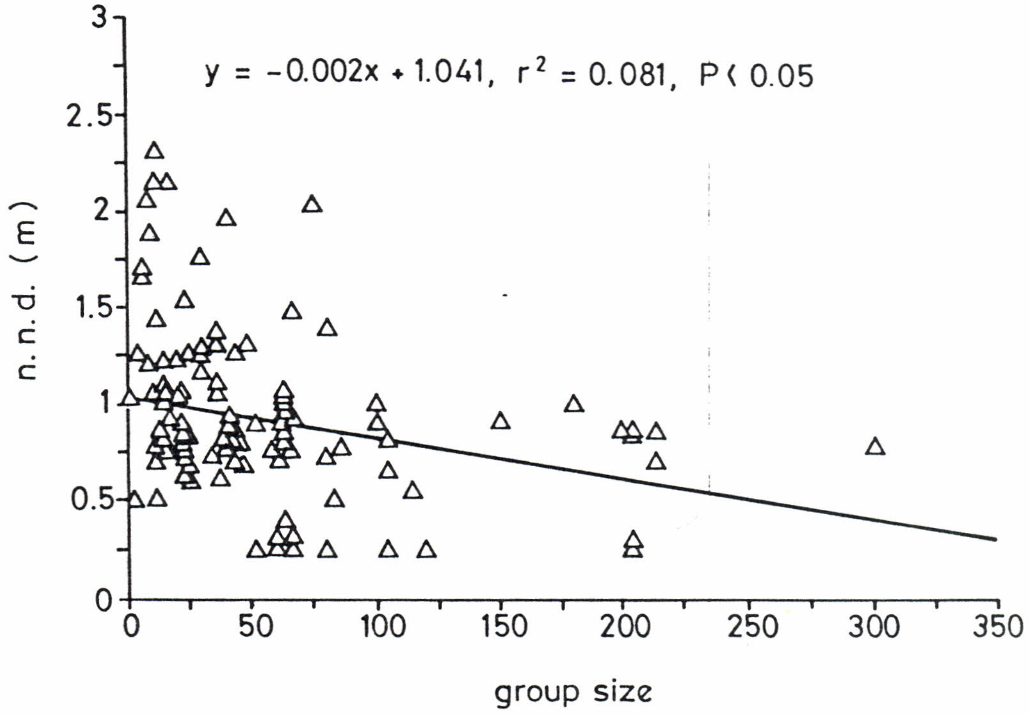
n.s.= not significant

On the high biomass pastures group size manipulations were carried out for sheep, but significant increases in grazing speed were only found on the low biomass pastures:

HL $y = 5.56 + 0.02x$, $r^2 = 0.095$, $p < 0.05$

LL $y = 2.61 + 0.08x$, $r^2 = 0.71$, $p < 0.05$

Group size did not have any significant effects on forage intake.



igure 17. Relationship between nearest neighbour distances (N.N.D.) and group size for sheep when showing the clumped dispersion pattern.

3.3.9 : Spacing constraintment and grazing speed.

When N.N.D. reduction was regressed against resultant grazing speeds, a negative relationship was found showing that spacing reduction resulted in higher grazing speeds for cattle on all pasture categories and sheep on HL pastures (Appendix 6 -10) :

Cattle LL $y = 12.06 - 1.18x$, $r^2 = 0.06$ *

HL $y = 8.27 - 0.82x$, $r^2 = 0.13$ *

HH $y = 14.63 - 3.54x$, $r^2 = 0.11$ *

LH $y = 11.43 - 1.63x$, $r^2 = 0.61$ *

Sheep HL $y = 16.46 - 8.87x$, $r^2 = 0.28$ *

* significant, $p < 0.05$

3.3.10 : Spacing constraintment and forage intake.

On HH and LL pastures cattle forage intake increased with N.N.D. On LH and HH pastures no significant changes in forage intake with spacing were found :

LL $y = 90 + 27.39x$, $r^2 = 0.10$, $p < 0.05$

HL $y = 176.12 + 43.11$, $r^2 = 0.05$, $p < 0.05$

A similar relationship was found for sheep on the HL pastures :

$y = 12.47 + 6.09x$, $r^2 = 0.09$, $p < 0.05$

Cattle on the LL pastures showed an increase in the crude protein content of forage intake as N.N.D. increased. No such changes were found for cattle on the other pasture categories and sheep on HL pastures.

LL $y = 3.99 - 0.97x$, $r^2 = 0.34$, $p < 0.05$

3.3.11 : Group flux.

When clumped cattle and sheep did not move at uniform rates over the pastures and movement alternated between bouts of fast movement with little feeding and slow rates with feeding periods. This movement pattern resulted in "anomalous" forage intakes (Appendix 10).

3.4 : Discussion.

The observed grazing speeds, quantity of forage intake and crude protein content on the different pasture types are best understood in relation to the grazing mechanisms adopted by these grazers, and their interactions with sward structure. Cattle use their tongues to gather herbage into their mouths before biting and tearing it off, unless the vegetation is too short. Sheep bite off individual plant parts or break them off as they are held between the teeth and dental pad (Demment et al 1986). In both grazers muzzles are moved horizontally and vegetation is selected vertically (Chacon et al 1978, Stobbs 1975, Freer 1981). On a daily basis, forage intake is a function of bite size, bite rate and grazing time available. When instantaneous intake rate is under consideration as in these experiments, bite size and bite rate are important as they determine harvest per unit time (Demment et al 1986, Chacon and Stobbs et al 1976, Stobbs 1973 a, 1973 b, 1975, Young and Corbett 1972). Bite size is largely determined by the sweep of the tongue, bulk density and tensile strength of the sward in cattle. The distribution of feeding stations is determined by sward structure and animal preferences and this in turn determines bite rate (Demment et al 1986). Selectivity is dependent on sward heterogeneity and requires complex movement to separate the high from the low quality plant materials (Freer 1981, Demment et al 1986).

On the low biomass pastures (LL and HL), the short herbage was difficult to prehend for cattle and hence the low forage intakes observed on these pastures. On the LL pastures, the swards had greater tensile strength and more energy was required for harvesting thereby depressing forage intake. Processing times for a bolus on LL pastures were long and grazing speeds were thus lower. On both low biomass pastures swards were relatively homogeneous, selectivity minimal and bites reflected the quality of herbage on offer. The higher grazing speed on the high quality (HL) pasture were due to ease of harvest and the higher quality of swards resulted in greater energy returns. Similar results have been obtained by other workers. When investigating the effect of progressive defoliation of tropical swards by cattle, Chacon and Stobbs (1976), found diminishing forage intake with defoliation and lack of selectivity with increased sward homogeneity.

On high biomass pastures there was an array of plant parts for cattle to choose from. The herbage was high yielding, easily prehended and harvested and forage intake and energy content were highest on these pastures. On the lower quality (LH) pastures leaves with low tensile strength were abundant and processing times were short. Cattle thus achieved grazing speeds comparable to those on the high quality pastures. In spite of their abundance, leaves and palatable clumps were relatively dispersed necessitating faster over the pastures. The preference for leaves with a relatively higher quality compared to stems explained their high incidence in extruded forage samples on the LH pastures. On HH pastures leaves and young shoots were readily available making forage intakes and energy returns highest on this pasture category.

Sheep had their lowest grazing speeds on the low quality low biomass (LL) pastures, which were mainly composed of tiller stumps and carry-over dead biomass. As they have narrow muzzles and select further down in the herbage to separate individual plant parts, sheep spent more time separating and teasing out individual plant parts. Handling times were long and movement over the pasture slow. The higher tensile strength contributed to the low grazing speeds as sheep avoided injury to their dental pads by selecting soft plant parts (Robards _et al_ 1967).

On the high quality pastures (HL and HH) sheep had identical forage intakes and quality levels inspite of different grazing speeds. Grazing speeds were higher on the high quality high biomass (HH) pastures due to the greater dispersion of preferred items. On this pasture high quality leaves were interspersed with low quality mature parts and carry-over dead biomass compelling sheep to move faster. When grazing experiments were carried out at locations where the two pastures types (HL and HH) were adjacent, sheep always turned back into the low biomass pastures, avoiding the high biomass pastures though equivalent forage intakes could be attained on both.

The proportionately higher grazing speeds of sheep than cattle over similar pastures reflected the difference in foraging and distribution of forage for these two different body sized grazers. Sheep had to necessarily move faster as there were relatively longer distances to cover between food items and larger areas covered in search of high quality forage. Cattle have lower quality acceptance thresholds and need bulky intakes, a more continuous food supply was thus available to them and progression over the pastures was relatively slow compared to sheep.

This difference in progression rates demonstrated that highly selective grazers have to move faster over similar pastures than less selective ones. As selectivity is determined by body size relationships, small bodied herbivores with high metabolism rates have to spend more energy in search of high quality forage which can offset this cost. On a body size ratio, small bodied herbivores therefore need proportionately larger foraging areas than their large bodied counterparts. In absolute terms, however, the large herbivores may cover large areas for their bulky intakes.

Grazing speeds optimal for different pastures are adopted by grazers as demonstrated by the effects of grazing speed manipulations (Figs 7 to 16). When increased beyond free ranging levels, there were declines in forage intake and energy returns on the pastures, showing that grazing speed is an important component of a grazer's ability to harvest pastures. Ease of harvest is a major limiting factor in this respect as indicated by similarities in harvest decline rates on the low biomass pastures. The sharpest decline occurred on the LH pastures and from this it can be deduced that the dispersal of forage items is critical in a grazer's choice of its grazing speed on a given pasture. The declines in crude protein content of forage for cattle on low quality pastures at high grazing speeds indicate optimization of the quality and quantity to be an important determinant of grazing speed. Grazing speed is therefore an important component of a grazers foraging strategy, varying as a function of pasture yield, quality and animal selectivity. On pastures, such as those of low quality, factors imposing grazing speeds above the optimal have direct costs on foraging efficiency.

The results concur with Kacelnik and Bernstein's (1988) contention that foraging is a trade off between speeds of movement and foraging efficiency. The faster a forager moves through a patch, the less efficient it is in foraging.

The decline in the quality of forage may have been due to the disruption of the momentary maximization process used by grazers when foraging (Senft et al 1987). This involves a feedback system where several factors are integrated in the choice of food items (Freer 1981). This process was disrupted at high grazing speeds, lowering the amount and quality of herbage harvested.

The optimal grazing speed model holds with respect to the effects of pasture quality and quantity on the rate of movement over pastures. Deviations from the optimal grazing speeds were clearly associated with changes in the quality and quantity of forage harvested. The animals, not having accurate and complete information on the next food items to be encountered, moved at rates at which the most "optimal" decisions were made as they progressed over the pastures.

Herd geometry had significant effects on the grazing speed of cattle and sheep and influenced the effects of group size and nearest neighbour distances. The grazers moved faster over the pastures when clustered than when spread out as a grazing front. Conspecifics feeding at the same time in an area lowers the density of available food and group membership therefore implies potential food competition (Post 1984). The nature of the food, however, influences the extent and nature of this competition (Pulliam and Caraco 1984). In carnivores and nonhuman primates this competition may involve dominance hierarchies with direct interference and displacement from feeding sites (Pulliam and Caraco 1984, Post et al 1980, Shopland 1987, Belzung and Anderson 1986, Muruthi 1989). Strong and dominant individuals rob or displace subordinates from coveted feeding sites. For grazers food resources are more abundant though scattered, and energetically expensive fighting for (Pulliam and Caraco 1984).

Inspite of this ubiquitous food source there is still scope for indirect competition and interference. Grazers passing over an area exploited by others will encounter an altered herbage with preferred items removed and the rest reduced in amount. The position occupied in a group is clearly important in the foraging performance of a group member. By adopting a grazing front individuals avoided areas already exploited by others in the herd. Almost similar feeding opportunities were available and possible negative effects of group membership nullified. When clustered animals at the group rear were exposed to a changed food source and by moving faster got into more favourable positions in the group or possibly came into contact with more food. These two responses could account for the observed high progression rates for cattle and sheep over the pastures when clumped. Group geometry rather than absolute group size is therefore important in determining the feeding costs associated with group membership in grazers. This effect would be pronounced where grazers are under pressure to remain close together such as predation or a mating system with active herding (Estes 1976, Jarman 1974, Owen-Smith 1977).

The clumped dispersion pattern always evolved into the front dispersion pattern suggesting the latter to be more stable or alternatively large groups broke into smaller groups. Sheep were more affected by the dispersion pattern than cattle and broke into small groups or spread out as a front over short periods. This indicates a greater sensitivity to group size and its attendant foraging costs.

The dispersion pattern adopted over pastures strongly influenced the effect of group size on grazing speed and spacing. When spread out as a grazing front, group size had little effect on progression rates and nearest neighbour distances as new individuals added onto the group periphery. When clumped, grazing speeds increased proportionately with group size as extra individuals had potentially greater impacts on resources available.

The avoidance of grazed areas and subtle competition in cattle and sheep foraging groups is comparable to that observed in yellow baboons by Altmann (1974). The baboons deployed in a pattern where individuals moved parallel to each other in a line formation when feeding in open grasslands. In this way harvest per unit distance travelled was maximized. The maintenance of exclusive feeding swathes avoided areas covered by other group members preventing drops in foraging efficiency if swathes of other group members were encountered. For this reason, nearest neighbour distances were highest for both grazers on the LL pastures as larger areas to scan for the highly dispersed and poor quality forage items.

Group size did not have any effect on herbage intake or quality of forage and the higher resultant grazing speeds were not sufficient to depress forage intake appreciably. Long sampling periods, adversely affecting the fistulated animals, would have been necessary to quantify drops in forage intake with group size.

Spacing constraintment increased animal density, resources were depleted faster and there was more intimate contact between potential competitors. By moving away from each other, group members avoided interference in their foraging precipitating higher progression rates when spacing was reduced.

Group size affected spacing on the pastures along biomass lines with increased spacing on the high biomass pastures and reduced on the low biomass pastures. On the heterogeneous high biomass pastures cattle were selective in their foraging. Competition and interference were possible and were avoided by spacing apart. On the low biomass pastures, difficulties in herbage harvest made the grazers indifferent to their nearest neighbours as it was more limiting than competition.

Results obtained when group parameters were manipulated indicate that group membership does have a cost on members foraging and are comparable to those obtained in other studies. Edye et al (1978) found declines in live weight gain for cattle under high stocking densities. Prolonged grazing times found for cattle under heavy stocking rates implied that larger areas had to be covered to offset foraging shortfalls (Smith 1959). Larger primate troops have larger home ranges than smaller troops indicating feeding costs and larger areas are needed to compensate these foraging shortfalls (Takaski 1981, Stacey 1986).

As the model predicts group size does have an effect on the foraging performance of a grazer. The effects are, however, dependent on pasture attributes, group geometry and compensatory mechanisms aimed at offsetting negative impacts of group size on forage intake.

3.5 : Conclusions.

The optimal Grazing speed model is essentially a predictive model attempting to relate the grazing speed herbage on offer and group parameters. There were no attempts to make mathematical predictions on intake on different pasture and group sizes.

In attempting to predict the effect of grazing speed and group size on nutritional performance, several factors affecting intake were assumed constant. Factors such as palatability, rumen fill, breeding status and animal experience were not considered though they affect intake over long periods (Owen-Smith 1982). This study focused on instantaneous intake as a function of pasture attributes and group parameters. Factors affecting intake on a long term basis were set aside. Figures 18a, 18b and 18c show the optimal grazing speed model revised after the grazing experiments were performed. In the following section are the conclusions based on hypotheses accruing from optimal grazing speed model (1.4.2).

3.5.1 : Different grazing speeds over pastures.

The model postulated that grazing speeds would vary as a function of herbage on offer and animal requirements. As shown in Figures 18a, 18b and 18c, the quantity of potentially available food was a function of progression rate, implying that on low yielding pastures, animals would move faster to meet their intake requirements. Contrary to these, the two grazers used, had the lowest grazing speeds on low yielding pastures where forage harvest was more limiting. Grazing speed on the pasture varied as a function of pastures yield and thus the contention in the model that grazing speed would vary as

Figure 18. A reconstruction of the optimal grazing speed model after the grazing experiments were performed.

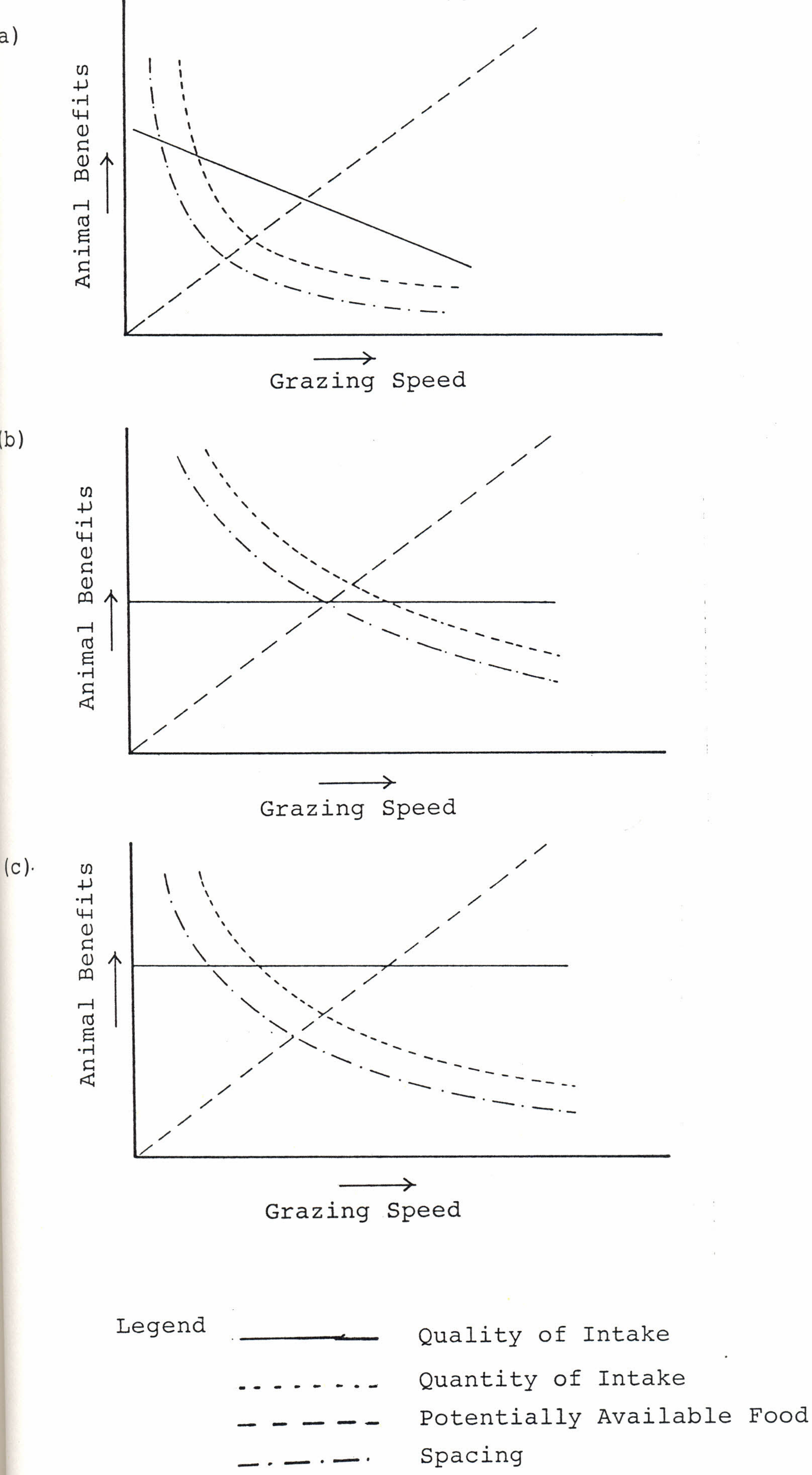
(a) Cattle on the low quality pastures (LL and LH).

(b) Cattle on the high quality low biomass pastures (HL).

(c) Sheep on the high quality low biOmass pastures (HL).

NB: Experiments for cattle on high quality high biomass were unsatisfactory and are not shown.

Foraging experiments with sheep on low quality pastures were abandoned after fistula failure during the dry season when such pastures were available.


a)
Animal Benefits
Grazing Speed
(b)
Animal Benefits
Grazing Speed
(c)
Animal Benefits
Grazing Speed
Legend
Quality of Intake
Quantity of Intake
Potentially Available Food
Spacing

a function of herbage yield and quality held. Raising grazing speed lowered the amount of forage intake and on low quality pastures forage of lower quality was harvested.

Body size dictates the selectivity regime adopted by a grazer and determines the movement rate over a pasture. Sheep moved proportionately faster than cattle over similar pastures showing that the dispersion of forage items is an important aspect of the grazing speed adopted by a grazer. A grazer with a highly selective feeding style have to cover large areas in search of high quality forage items. Large bodied herbivores with spacious guts enabling them subsist on low quality diets move slowly over pastures as bulk rather than quality is more important.

3.5.2 : Quality and quantity of forage intake.

The model postulated that quality of intake would vary as an inverse function of grazing speed. The amount of forage harvested was postulated to rise, level off and then decline as grazing speed increased. The observation was contrary to this and on the high quality pastures where the quality of intake remained constant for both grazers. The drops in the quality of intake on the low quality pastures for cattle did not display the postulated asymptotic decline but was rather linear with marked variations. The amount of herbage harvested similarly declined asymptotically with movement rate from the free settlement levels.

3.5.3 : Group size and forage intake.

Herd geometry rather than group size was found to be more important in affecting grazing speed. Group size *per se* did not have intake depressing effects when animals were deployed as a grazing front. The positioning of individuals with respect to each other is more important in determining competition pressure when grazers feed in a herd. It is only when grazers were prevented from adopting competition minimizing strategies that group size could potentially depress intake. In this kind of situation the animals moved faster over the pastures and this can depress the amount of herbage harvested. Potential competition is an important factor in group foraging as observed when spacing between individuals was constrained. The animals responded by moving faster over the pastures and this can be interpreted as an attempt to move away from potential competitors.

3.5.4 : Strategies aimed at group size effects.

Individuals have strategies aimed at counteracting the negative effects of group size such as deployment as a grazing front, spacing further apart as group size increases, movement of individual ahead of the group mass and group break up into smaller units. These responses were aimed at offsetting the subtle costs such as covering longer distances when in large groups.

3.5.5 : Suggested model refinements.

By assuming a few variables to be the sole determinants of foraging performance in grazers the model as it stands cannot be used to predict intake for these animals. The model can only hold if foraging were a continuous process, ceasing after requirements are fulfilled. Grazers however do not forage continuously but have a diurnal pattern, with periods of rumination, drinking and rest fitted into the daily grazing regime (Arnold 1981). Metabolism has also been observed to be depressed during dry periods of low feed availability (Western and Finch 1986). Pregnancy and lactation also affect the nutritive requirements of grazers and they would have to be taken into account.

If rumen turnover rates, digestibility coefficients of different feeds and the metabolic energy expenditure of a grazer can be determined along with pasture yield then the model can be an excellent tool in range management and wildlife habitat management.

3.6 : Possible application.

3.6.1 : Wild grazers.

Wild ruminant grazers nutrition is a complex process that involves herbage structure , digestive physiology, body size, animal physiology and the response of the animal to predator pressures, weather conditions as well as the social organisation of the species.

The model under test took a simplistic approach and assumed herbage structure and body size to be the only critical factors influencing forage intake. The results do indicate a general validity of the model in as much as herbage structure influence was concerned for the domestic grazers. The model may as well be applicable to wild grazers as group size is more adaptive to them than domestic grazers. Predation pressure and the need for individuals to be close together may amplify competition and hence play an important part in determining group size. Predation pressure is highest for animals at the group periphery (Estes 1976) but at the same time those in the middle are subject to intense forage competition pressure. The resolution of these two problems may be an important determinant of herd dynamics in the wild and their effects on foraging performance have to be taken into account.

3.6.2 : Pastoralism and ranching.

It was found that group size have effects that may make animals incur energetic expenses as group size increases. Large herds would entail unnecessary energy expenditure by animals hence lowering production. In ranches the paddock area should be considered with respect to group size with large herds provided with correspondingly large paddocks. Where animals are actively herded as in pastoral communities, moving animals over the pastures at grazing speeds above free ranging levels would lower animal productivity.

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Appendix 1. Grazing speeds, forage intake, crude protein content (C.P.) and energy (cal for cattle on low quality low biomass (LL) pastures.

Grazing speed (m/min)	Extruded forage (g/10min)	C.P. content (mg/g)	Energy value (cal)
5.0	159.00	62.5	340.00
5.4	113.33	57.8	106.19
6.0	92.00	35.0	158.74
6.3	60.73	46.6	119.69
6.5	171.00	36.7	299.87
6.5	162.60	39.9	298.14
6.6	257.50	27.0	337.52
6.6	203.00	30.0	246.66
6.9	102.22	50.0	206.45
7.2	128.89	71.7	282.42
7.2	108.20	80.1	240.86
7.4	251.60	43.1	480.56
8.3	164.33	36.2	286.27
10.5	160.00	38.9	290.46
10.9	107.00	36.9	188.26
11.5	91.84	53.3	119.69
12.0	218.00	49.1	437.78
12.0	114.00	48.1	227.33
12.6	58.66	65.8	126.77
12.8	187.50	39.9	345.07
13.0	126.13	49.1	253.23
13.7	50.50	30.0	96.5
13.9	64.00	71.0	175.98
15.8	81.00	38.6	146.41
15.8	141.00	38.7	255.23
17.1	166.93	35.5	286.33
17.1	124.26	34.5	208.97
17.3	117.00	38.1	197.37
17.3	120.00	37.8	203.11
17.3	76.00	37.6	135.71
18.2	108.60	25.4	129.93
18.2	126.50	37.0	222.97
19.9	52.00	40.8	96.80
19.9	131.00	29.5	191.50
19.5	43.40	39.5	79.44
19.6	33.05	35.8	-
21.2	76.00	33.6	125.24
21.3	111.00	35.2	189.32
28.5	86.90	47.0	171.87
28.5	65.00	36.1	142.44
30.8	50.50	47.8	113.12

Appendix 2. Grazing speed, forage intake, crude protein content and energy value of extruded forage of cattle on high quality low biomass (HL) pastures.

Grazing speed (m/min)	Extruded forage (g/10 min)	C.P. (mg/g)	Energy (kcal)
2.37	137.00	71.3	299.69
2.37	136.40	100.9	312.15
3.17	180.00	74.3	436.21
3.17	237.00	82.8	521.43
3.20	189.00	66.5	408.73
3.20	146.00	60.3	314.10
3.43	140.00	73.6	310.00
3.43	156.00	66.5	337.91
3.57	132.00	78.0	292.35
4.27	236.00	60.1	504.75
4.27	228.00	72.5	500.43
4.57	200.00	71.7	438.21
4.57	49.00	61.5	104.42
5.00	175.00	82.8	390.70
5.00	206.00	74.4	453.89
5.30	128.00	96.9	291.97
5.65	103.00	104.7	237.39
6.17	209.00	77.9	313.80
6.33	120.00	46.8	169.83
6.77	127.00	47.0	250.79
7.50	118.00	90.5	267.22
12.60	64.00	79.2	142.69
13.00	126.00	49.1	253.29
13.00	57.00	59.1	119.81
13.13	86.00	71.2	188.36
13.13	90.00	91.8	203.74
13.90	64.00	71.0	140.79
13.90	80.00	73.6	175.99

Appendix 3. Grazing speed, forage intake, crude protein content and energy value of forage extruded by cattle on low quality high biomass (LH) pastures.

Grazing speed (m/min)	Extruded forage (g/10 min)	C.P. content (mg/g)	Energy value (cal)
3.20	32.00	60.3	679.20
3.50	250.00	75.0	551.48
3.52	142.80	43.3	273.31
4.00	249.90	74.0	550.18
4.00	260.00	103.3	596.60
4.00	272.00	44.5	526.60
4.00	219.50	49.6	442.27
5.00	284.00	72.4	623.20
5.00	233.80	72.0	512.60
5.00	207.80	39.7	376.94
5.37	213.00	63.6	320.65
6.00	240.00	66.0	518.56
6.00	339.50	54.3	495.66
6.06	177.60	44.3	343.25
6.06	150.00	40.1	287.10
6.60	220.60	68.0	479.10
6.70	225.00	40.0	414.63
6.80	238.30	45.0	463.91
6.80	250.70	41.4	470.04
7.00	256.00	79.8	569.60
7.50	186.40	36.2	324.00
7.80	179.70	50.6	364.79
8.00	173.00	52.0	333.70
8.06	170.80	37.6	304.03
8.06	179.30	70.5	391.81
8.20	245.20	52.6	503.00
9.00	196.50	38.3	353.59
10.40	150.00	74.8	330.76
10.40	120.00	49.2	241.14
10.40	56.70	50.8	115.11
10.50	175.00	53.4	360.53
10.50	146.00	45.0	283.99
10.70	81.00	38.1	145.32
10.70	80.00	37.5	142.18
11.62	142.20	51.3	289.56
12.00	116.00	45.0	225.64
12.00	110.00	35.6	137.51
12.00	59.00	43.8	115.90
12.00	140.00	40.8	260.19
13.00	68.00	46.7	134.17
13.03	77.30	32.9	137.61

APPENDIX 3 CONTINUED

13.50	81.00	30.1	120.95
13.66	144.80	69.0	315.50
14.00	120.00	80.3	267.22
14.06	153.00	62.0	326.65
14.19	46.00	45.9	-
14.20	96.40	44.0	173.00
15.00	64.00	35.8	110.49
15.34	108.00	39.5	241.27
17.00	63.00	44.4	121.87
18.60	41.00	40.4	75.95
18.60	55.00	27.8	75.00
19.50	77.20	37.7	137.64
20.00	40.70	37.8	72.67
21.00	66.90	45.5	130.70
22.50	52.80	54.3	109.27

Appendix 4. Grazing speed, forage intake, crude protein content and energy value of forage extruded by cattle on high biomass high quality (HH) pastures.

Grazing speed (m/min)	Extruded forage (g/10min)	C.P. content (mg/g)	Energy value (cal)
4.50	220.00	112.6	106.61
5.30	270.00	108.0	146.87
7.40	265.00	109.3	151.04
8.00	280.00	113.0	209.53
9.60	197.33	53.3	405.67
9.60	219.00	74.4	482.53
10.00	158.67	82.4	354.57
10.00	241.00	92.1	545.67
11.00	179.00	75.0	394.86
11.00	175.00	65.6	365.90
12.00	260.40	92.0	589.64
12.00	144.08	85.6	323.46
12.00	200.78	72.4	440.58
12.00	393.40	84.4	881.56
12.70	316.67	86.0	711.33
12.70	254.00	96.0	573.20
13.70	210.30	63.3	452.63
14.00	217.00	55.9	452.80
14.80	236.20	102.0	541.19
15.80	246.80	137.0	586.82
15.80	229.60	79.2	510.34
19.00	172.40	75.1	380.36
19.00	99.73	98.7	227.65
20.80	150.10	93.5	340.52

Appendix 5. Grazing speeds, herbage intake selectivity and energy returns for sheep on high quality low biomass (HL) pastures.

Grazing speed (m/min)	Forage intake (g/10min)	C.P. (mg/g)	Energy value (cal)
1.80	32.0	171.4	65.15
2.00	16.3	191.3	42.58
2.60	21.00	193.0	53.02
3.23	10.80	126.9	25.14
3.30	36.00	231.5	96.50
3.47	20.70	153.0	50.69
3.57	29.9	100.4	68.38
3.80	28.80	153.9	69.67
4.00	16.70	121.8	39.07
4.50	10.80	168.3	26.61
4.70	30.00	145.3	71.97
4.70	30.20	147.1	69.97
5.00	12.50	119.5	29.18
5.50	16.80	153.9	40.69
5.85	24.80	175.9	61.68
5.90	29.40	100.0	68.38
6.00	26.80	161.8	65.52
6.00	21.70	135.9	51.60
6.00	21.00	186.6	52.93
6.00	22.00	-	-
6.00	16.00	193.0	40.67
6.40	27.00	130.0	63.71
6.40	10.00	129.7	23.59
6.40	20.30	145.0	48.69
6.40	15.70	203.6	40.48
6.40	14.00	165.0	34.35
6.60	31.80	160.1	77.58
6.80	20.80	154.8	50.46
6.83	20.00	161.8	48.90
6.83	16.70	128.0	39.32
7.20	11.60	142.6	27.75
7.50	25.50	188.2	64.41
7.50	10.10	158.9	24.61
7.50	15.00	181.8	37.58
8.00	36.00	135.0	85.41
8.90	19.00	144.8	45.56
9.00	18.80	136.4	44.67
9.00	17.50	147.0	42.07
9.00	10.00	156.1	24.28
9.55	16.00	193.0	40.67
9.80	18.70	180.0	40.67
10.15	12.80	150.8	30.90

Append 5 Cont'd.

10.30	21.00	150.0	50.65
10.30	8.80	157.5	21.40
10.50	14.20	133.1	23.59
10.67	16.70	162.2	10.79
11.30	13.00	157.5	31.62
11.40	8.00	251.4	22.10
11.67	14.30	104.0	52.83
12.00	11.18	147.3	28.37
12.00	14.00	120.0	32.70
13.40	11.00	122.9	22.85
13.50	16.00	176.1	39.80
14.40	9.70	139.4	23.12
14.40	23.00	155.0	59.36
16.00	10.90	134.8	25.86
16.20	26.00	137.5	61.28
21.50	2.50	145.2	25.49
21.60	10.80	130.8	5.99
22.00	5.60	137.4	13.52
22.50	3.10	135.4	7.35
28.50	4.40	135.9	10.92
30.20	1.80	136.0	4.27

Appendix 6. Group size, Nearest neighbour distances (N.N.D.) grazing speed of cattle on Low quality low Biomass (LL) pastures when clumped.

Group size	N.N.D. (m)	Grazing speed (m/min)
4	1.21	3.80
6	1.00	6.30
8	1.50	7.20
10	1.2	4.60
11	1.11	4.40
12	0.25	12.40
12	1.27	10.50
16	0.25	12.60
17	1.35	13.40
19	0.25	19.50
19	1.60	19.50
20	0.25	33.05
20	0.25	12.00
25	1.43	11.50
26	0.45	21.20
32	0.25	13.70
36	1.27	13.90
41	1.30	13.10
45	1.27	12.60
45	0.25	17.30
61	1.18	13.00
64	1.42	12.00
120	0.56	28.50
199	0.84	19.90
219	1.33	12.80
220	0.93	10.90
220	1.70	18.20

Appendix 7. Group size, nearest neighbour distances (N.N.D.) and grazing speeds for cattle on High quality Low biomass (HL) pastures when clumped on the pastures.

Group size	N.N.D. (m)	Grazing speed (m/min)
3	2.50	5.65
3	2.20	5.30
4	2.20	7.50
5	1.72	7.50
6	1.00	3.17
7	8.16	10.00
7	8.26	8.00
10	1.20	4.57
11	1.64	3.57
11	1.11	4.40
11	1.64	3.57
11	1.62	4.60
12	1.25	3.20
12	1.27	10.50
14	1.25	3.20
14	0.81	5.00
16	1.94	4.27
17	1.35	13.40
18	0.79	4.57
21	1.35	7.47
21	0.25	13.00
21	1.15	7.73
22	1.64	6.17
22	0.35	13.13
24	1.19	3.43
25	1.25	6.77
36	1.27	13.90
41	1.30	13.13
45	1.27	12.60
46	1.30	5.05
50	1.25	6.00
56	1.09	5.95
63	1.18	13.00
220	4.41	22.0

Appendix 8. Group size, nearest neighbour distances (N.N.D) and grazing speed of cattle on Low quality High biomass (LH) pastures when clumped.

Group size	N.N.D. (m)	Grazing speed (m/min)
3	1.57	10.70
4	1.20	9.00
6	1.62	6.06
8	1.17	10.50
10	2.42	5.20
10	1.50	8.06
12	1.50	8.06
14	1.61	10.00
15	1.15	7.00
15	0.98	4.06
16	1.34	5.00
17	0.25	13.53
18	2.40	3.52
19	1.50	13.50
21	1.20	3.73
21	0.25	13.00
30	1.31	8.20
30	0.25	13.66
33	1.08	10.40
39	0.93	10.40
39	0.50	10.70
40	2.42	7.50
43	0.59	15.00
45	1.14	10.40
45	0.30	14.00
53	0.35	13.20
54	1.23	7.80
56	0.25	19.50
59	2.50	15.00
63	1.40	11.30
74	1.46	14.00
80	0.50	16.00
90	0.83	14.30
96	1.00	18.60
100	0.79	21.00
100	0.56	21.50
120	2.85	14.00
120	1.36	17.00
120	0.45	12.00
120	2.56	11.62
220	0.69	20.00
200	2.83	11.00

Appendix 9. Group size, nearest neighbour distances (N.N.D.) and grazing speeds of cattle on high quality high biomass (HH) pastures.

Group size	N.N.D. (m)	Grazing speed (m/min)
5	0.30	12.00
5	1.31	11.00
10	1.48	14.00
14	0.25	19.00
21	1.37	25.00
21	1.95	9.60
22	1.82	5.30
22	1.34	6.20
24	1.68	5.30
24	1.14	4.22
27	1.24	10.00
27	1.95	9.60
28	1.10	7.50
29	1.08	4.50
29	1.21	9.80
35	1.14	6.80
35	1.08	3.80
36	1.35	6.00
43	0.30	14.00
43	1.20	6.40
57	0.91	7.00
57	1.26	6.50
60	1.00	7.40
84	0.40	13.70
84	1.06	5.50
90	0.25	15.80
200	1.16	12.00
200	2.24	12.70
220	0.50	15.80
220	1.42	13.00
220	1.39	14.80
220	1.30	11.00

Appendix 10. The effect of group flux on forage intake by cattle and sheep when grazing speed was manipulated resulting in some in instances in higher forage intake than would have been expected. This higher intakes were regarded as anomalous.

CATTLE	Grazing speed (m/min.)	Forage intake (g/10 min.)	CP content	Pasture
	4.5	367.0	3.52	LL
	12.0	218.0	4.91	LL
	17.3	117.0	3.81	LL
	21.2	118.0	3.52	LL
	19.5	220.5	3.80	LL
	16.3	256.0	7.98	LH
	16.0	260.0	10.33	LH
	19.8	225.0	4.00	LH
SHEEP	10.3	21.0	15.00	HL
	14.4	23.0	15.50	HL
	16.2	26.0	13.75	HL
	22.5	14.7	13.54	HL
	21.6	10.8	13.08	HL