BÚVÍSINDI
ICEL. AGR. SCI. *7, 1993:* 59–77

Behaviour and plant selection

ANNA G. THÓRHALLSDÓTTIR
Institute for Grassland and Animal Production, Wales Plant Breeding Station, Plas Gogerddan, Aberystwyth, Wales, U.K.
and
INGVI THORSTEINSSON
Agricultural Research Institute, Keldnaholt, IS-112 Reykjavík, Iceland

SUMMARY

The average Icelandic sheep learns initially from its mother what to graze on a cultivated pasture. In early summer it is driven on to native pastures with many different new plants. Here it follows its mothers grazing behaviour. At dawn it moves from its camping place into mires and semi-wet areas, grazing grasses, *Salix* spp. and *Carex* spp. until late afternoon. Before dusk it moves into drier areas, heather and moss ridges were it grazes grasses and forbs until dusk. During the light nights of summer it grazes in short bouts throughout the 24 hours. Later in the summer, when the nights are getting darker, it rests during the dark hours, starting grazing at sunrise and stopping at sunset. In fall, when nights are longer, it grazes for a short time during the middle of the night. In the fall it also grazes in the fens during the day, *Carex* spp. and *Calamagrostis neglecta*. At night it grazes *Vaccinium uliginosum* in the drier areas. Its average grazing time during the summer is 10 hours and 45 min.

Key words: behaviour, extrusa samples, grazing, plant selection, rumen samples.

YFIRLIT

Atferli og plöntuval sauðfjár

Í fyrsta hluta greinarinnar er greint frá íslenskum rannsóknum á plöntuvali sauðfjár sem fram fóru á árunum 1963–1982. Í öðrum hluta er greint frá rannsóknum á beitaratferli sauðfjár á afrétti sumarið 1982. Í síðasta hluta greinarinnar er fjallað um þær kenningar sem uppi eru um fæðuval og hvernig hægt er að skýra niðurstöður íslensku rannsóknanna með tilvísun í hinar ýmsu kenningar.

Niðurstöður plöntuvalsrannsóknanna eru sýndar í 1.–4. töflu og á 1.–16. mynd. Rannsóknirnar leiddu í ljós að plöntuval var verulega háð því hvaða plöntutegundir voru í boði á hverjum stað og tíma. Einnig kom í ljós allverulegur munur á plöntuvali einstakra kinda. Þrátt fyrir töluverðan breytileika eru niðurstöður plöntuvalsrannsóknanna frá mismunandi stöðum og tímum í meginatriðum samhljóða. Innan við tíu plöntutegundir eru alltaf bitnar í miklum mæli þar sem þær er að finna. Þær eru vinglar (*Festuca* sp.), língresi (*Agrosis* sp.), sveifgrös (*Poa* sp.), hálmgresi (*Calamagrostis neglecta*), stinnastör (*Carex bigelowii*), grávíðir (*Salix callicarpea*), kornsúra (*Polygonum viviparum*), möðrur (*Galium* sp.) og elftingar (*Equisetum* sp.). Þar eð einhverjar þessarra tegunda er að finna í flestum gróðurlendum landsins eru þær aðalfæða fjárins sumar og haust. Á veturna fá ýmsar trjákenndari tegundir aukið vægi í beitinni.

Rannsóknir á beitarferli sauðfjár voru fólgnar í því að skrá hve mikinn og hvaða tíma sólarhringsins féð notaði til beitar, gangs og hvíldar og hvaða gróðurlendi voru notuð til hverra athafna. Niðurstöður benda til að beitartíðni og lengd beitartímans sé háð daglengd. Meðan nætur eru bjartar bítur féð oft og allan sólarhringinn, en stutt í einu. Síðla sumars bítur það frá sólarupprás til sólseturs en hvílist meðan dimmt er. Að haustinu, er daginn tekur mjög að stytta, kemur fram stutt beitarlota á næturnar.

Beitar-atferlið virðist einnig breytast frá morgni til kvölds. Við sólarupprás flytur féð sig í votlendi, mýrar og hálfdeigjur þar sem það bítur fram eftir degi með styttri hléum. Fyrri hluta sumars er lengsta beitarhléið nálægt hádegi. Síðari hluta dags fer féð að flytja sig á þurrlendi þar sem það bítur fram eftir kvöldi, eða að sólsetri, og hvílist þar til í dögun að það flytur sig á ný í votlendið.

Með tilvísun til hins mikla breytileika sem fram kom í rannsóknunum milli einstaklinga á beit á sama stað og tíma eru færð rök fyrir því að plöntuval sé að miklu leyti lært atferli.

INTRODUCTION

Icelandic rangelands have been used for grazing since the time of settlement 1100 years ago. During this time, the rangeland has changed from extensive birch forests to less productive dry heathlands, mires and gravel ridges with little vegetative cover. These enormous vegetation changes can be assigned to a colder climate, unstable volcanic soils and the general activity of man. There is, however, little doubt that the grazing animal has been one of the main driving forces for these changes to occur.

Unlike the past, today very little winter grazing takes place by sheep, and grazing pressure on the native range is only for about three months in mid-summer. During these months, sheep roam freely over extensive areas of complex vegetation mosaics, often following the snow melt to higher areas as the summer progresses.

Because of the extensive summer ranges, detailed studies on plant selection and grazing behaviour must either restrict the animals with fencing or use methods adapted from wildlife studies. In the studies described below, both approaches have been taken.

PLANT SELECTION STUDIES

A number of studies have been conducted in Iceland on plant selection by sheep grazing native pastures. The first of these studies observed animals while grazing and recorded grazed plants in the sward (Thorsteinsson, 1964). Other studies have used oesophageal fistulated animals for data collection (Thorsteinsson and Ólafsson, 1965; Thorsteinsson and Ólafsson, 1967; Thorsteinsson and Ólafsson, unpublished data; Thórhallsdóttir and Thorsteinsson, unpublished data). In one study rumen contents of sacrificed animals and faecal samples from the same animals were analyzed (Thórhallsdóttir, 1981).

Studies using oesophageal fistulated animals

In the studies described below, extrusa from oesophageal fistulated sheep (Torrell, 1954; McManus, 1962) were collected and analyzed for botanical and chemical composition. The botanical composition of the samples was determined by a macrohistological analysis, using the point frame method described by van Dyne and Heady (1965). A subsample (200 ml) was immersed in a shallow tray of water under a 10–40× stereoscope (Gaare, 1968). The tray was moved systematically and the plant fragment under the middlepoint of the field was analysed. A total of 250 points were analysed in 1981, and 150 points in 1982. Plant fragments were identified to species when possible, or to family/group, i.e. *Equisetum* spp., *Juncus* spp., grasses, sedges, forbs etc. Usually, over 90% of the points were identified to species. The data are represented as percentage eaten of each plant species, defined as relative occurance of each species (points) in the sample analysed.

Potential sources of error with using oesophageal fistulated animals to estimate diet selection have been discussed by Langlands (1965, 1966, 1967), Hodgson (1969), Harniss *et al.* (1975), Hamilton and Hall (1975) and Thórhallsdóttir (1981).

Early studies with fistulated animals. The first study using fistulated sheep to estimate plant selection in Iceland was conducted in

Table 1. Botanical composition (% cover) of the enclosures in south-west Iceland in 1964 (Thorsteinsson and Ólafsson, 1965).
1. tafla. Gróðurþekja (%) í tilraunahólfum í Borgarfirði 1964.

Location	Grasses	Sedges	Woody species	Forbs	Moss
(1) Götuás					
Small shrub heath	17	12	50	8	13
Grassland	86	3	0	5	6
(2) Hestfjall					
Moss heath	6	5	45	2	40
Grassland	67	6	11	4	12
(3) Grímsá					
Bog	5	82	7	3	3
Grassland	85	6	5	4	0

Table 2. Plant selection (% grazed) of sheep in the study of 1964 (Thorsteinsson and Ólafsson, 1965).
2. tafla. Plöntuval sauðfjár (% bitið) í tilraunahólfum í Borgarfirði 1964.

Location	Grazing dates	Grasses	Sedges	Woody sp.	Other sp.
(1) Götuás	3/8–7/8	59.9	18.7	17.4	4.0
(2) Grímsá	10/8–14/8	68.2	21.4	6.7	3.7
(3) Hestfjall	17/8–21/8	69.4	17.9	5.4	7.3
(1) Götuás	31/8–4/9	72.6	12.8	11.9	2.7
(2) Grímsá	7/9–11/9	77.2	21.5	0.5	0.8
(3) Hestfjall	14/9–18/9	80.9	16.7	0.7	2.1

the summer of 1964. In the study, two sheep with oesophageal fistulae were grazed in three enclosures on a lowland native pasture in south-west Iceland (Thorsteinsson and Ólafsson, 1965). These enclosures were dry heath and grassland (1), moss tussock and grass tussock (2), and mire and grass tussock (3) (Table 1). The sheep grazed for two days in each enclosure before data was collected to become familiar with surroundings. Then they were grazed for five days, twice a day, for data collection. The results from these studies are shown in Table 2. Grasses were found to be the most important component in the diet, particularly later in the season. Sedges were not heavily grazed, even when in greatest supply (enclosure 3). In this study no statistical difference was found between the diet selected by the two sheep, or the time of day when the diet was selected.

The same overall picture was found in a later, more extensive study by the same researchers in the same area (Thorsteinsson and Ólafsson, 1967). In this study, three fistulated sheep were grazed in two enclosures; a grass tussock within a birch forest (1) and a grass tussock and mire (2), (Table 3), summer and winter. From June–September, grasses were most heavily grazed and continued to be the main diet component in the first enclosure (birch forest) throughout the winter. Only in April and May were grasses of lesser importance taken over by different dwarf shrubs (Table 4). The diet selected by the three sheep in this study was not significantly different.

A similar result was found in a study in 1979 where three oesophageal fistulated sheep were grazed in enclosures at three different altitudes; 100 m, 300 m and 500 m above sea

Table 3. Botanical composition (% cover) of the sward in two enclosures in south-west Iceland in 1965 and 1966 (Thorsteinsson and Ólafsson, 1967).
3. tafla. Þekja (%) undirgróðurs í tilraunahólfum í Borgarfirði 1965 og 1966.

Plant groups	Skorradalur (1) Dryland	Hesthals (2) Dryland	Bog
Moss	7	5	8
Grasses	33	30	13
Sedges	10	64	
Dicotyledons – forbs	36	5	15
Small shrubs	24	50	

Table 4. Plant selection (% grazed) of sheep in the study of 1965 and 1966 (Thorsteinsson and Ólafsson, 1967).
4. tafla. Plöntuval sauðfjár (% bitið) í tilraunahólfum í Borgarfirðii 1965 og 1966.

	1965								1966				
Location/Plant groups	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mar	May	Jun	Jul	Aug
(1) Skorradalur													
Grasses		36	56		62	60	52	64	58	71	38	42	52
Sedges		5	7		14	10	4	7	6	7	2	1	2
Small shrubs		24	4		6	28	43	26	34	7	29	9	10
Dicotyledons – forbs		35	33		18	2	1	3	2	15	31	48	36
(2) Hesthals													
Grasses	60	85	64	78	74	57	34	20	20				
Sedges	13	14	23	16	11	10	12	4	8				
Small shrubs	27		3		9	32	54	76	72				
Dicotyledons – forbs		1	10	6	6	1							

level on a mountain site in south-west Iceland (Thorsteinsson and Ólafsson, unpublished data). The sheep were grazed from the third week of July to the second week of October. The vegetation type in the enclosure at 100 m was grassland, at 300 m mire dominated by sedges and at 500 m moss heath. At 100 m and 500 m, the sheep grazed on average over the summer 83% and 76% grasses respectively. At 300 m, 25% of the diet on average consisted of grasses and 37% of sedges. Forbs were grazed 17%, 19% and 12% respectively at 100, 300 and 500 m. As the season progressed, consumption of forbs decreased, especially in the higher enclosures. At 300 m, there was an increase in sedge consumption later in the summer. On average, there was little difference in the diet selected by the three sheep in the study. There was, however, considerable difference in their diet selection on a daily basis.

Diet selection in five enclosures in east of Iceland. The most detailed information on diet selection by sheep on a summer grazing comes from studies in the east of Iceland in 1981 and 1982. In these studies sheep were grazed on a weekly basis in enclosures in five different areas throughout the summer season. Three of these enclosures were in the lowlands and two in the highlands. In the first year, two fistulated ewes were used,

and four the following year. These were from the same flock, though different ewes were used in each year.

Forest enclosure. The first enclosure was in an old birch (*Betula pubescens*) forest. Part of the enclosure had a very dense overstorey with sparse understorey, mainly consisting of *Equisetum pratensis*. In the more open parts where light reached the ground, the understorey was dominated by *Hierocloe odorata*, along with *Agrostis* spp., *Festuca* spp., *Poa* spp. and *Carex vaginata*. *Vaccinium uliginosum* was important in the understorey and forbs like *Campanula rotundifolia*, *Rubus saxatilis* and *Galium* spp. A total of 58 higher plants were found within the enclosure, of which 9 were grasses and 5 woddy species.

In both years of the study *Betula* leaves were heavily browsed by most of the sheep. In 1981 birch leaves comprised on average 35% of the total diet of the sheep, with a slight increase in consumption as the season progressed (Figure 1). The total average consumption was 19% the second year and the leaves were browsed in equal amounts throughout the season (Figure 2). More grasses were utilized by the sheep in 1982 than the first year, 30% versus 16% (Figure 1 and 2). The increase was mostly due to an increase in consumption of *Hierocloe odorata* by all the sheep. *Equisetum* spp. were grazed in early season in both years, the first year 4% on average by the two sheep and 7% on average the second year. Another important grazing plant was *Vaccinium uliginosum*. In 1981 the sheep consumed 23% bilberry leaves (Figure 1). In 1982 the average for the summer was 16% (Figure 2) and the consumption increased from early to late summer (Figure 3). Forbs were grazed on average 13% in both years. They were grazed to a variable

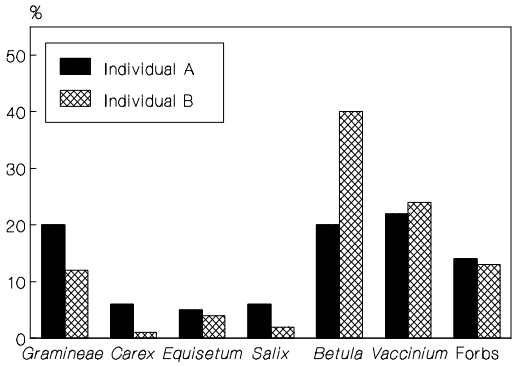

Figure 1. Plant selection (% grazed) of two sheep grazed in the forest enclosure in east Iceland in 1981 (Thórhallsdóttir, unpublished data).
1. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í Hallormsstaðarskógi 1981.

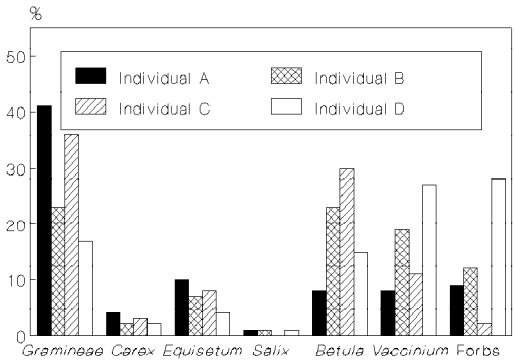

Figure 2. Plant selection (% grazed) of four sheep grazed in the forest enclosure in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
2. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í Hallormsstaðarskógi 1982.

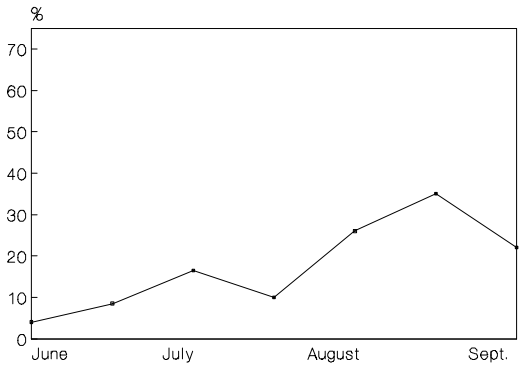

Figure 3. Relative amount (%) of bilberry (*Vaccinium uliginosum*) leaves in plant selection of four sheep in the forest enclosure in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
*3. mynd. Hlutfall (%) blaða af bláberjalyngi (*Vaccinium uliginosum*) í plöntuvali sauðfjár í tilraunahólfi í Hallormsstaðarskógi 1982.*

degree by the different individuals (Figure 1 and 2), when in season. *Campanula rotundifolia* was grazed on up to 15% on occasions in June and July. *Rubus saxatilis* was grazed heavily in August and September, often making up 20–40% of the diet. *Taraxacum* spp. were only eaten in early June and *Arctostaphylos uva-ursi* only in late season. In 1981 mushrooms appeared in late August and were eaten by both the sheep, up to 17% of total consumption on one occasion.

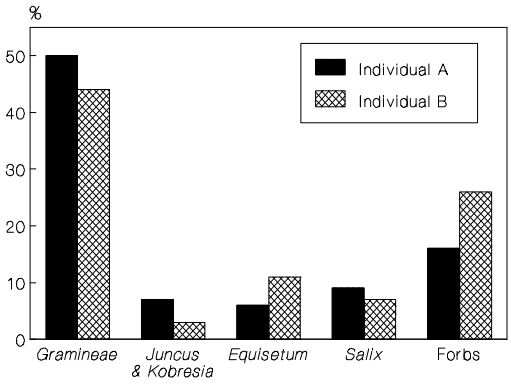

Figure 4. Plant selection (% grazed) of two sheep grazed in the larch plantation enclosure in east Iceland in 1981 (Thórhallsdóttir, unpublished data).
4. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í ungum lerkiskógi á Víðivöllum í Fljótsdal 1981.

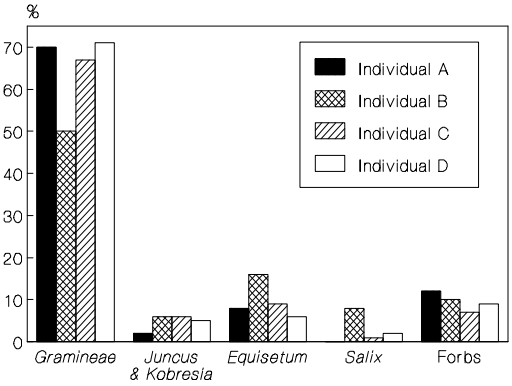

Figure 5. Plant selection (% grazed) of four sheep grazed in the larch plantation enclosure in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
5. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í ungum lerkiskógi á Víðivöllum í Fljótsdal 1982.

Larch plantation enclosure. The second enclosure was located in a reforested area with 12 year old larch trees of 2–3 metres height. The understorey was a grassland dominated by *Festuca rubra*, *Poa pratensis*, *Agrostis tenuis*, *Hierocloe odorata*, *Kobresia myosuroides* and *Carex bigelowii*. Forbs were dominated by *Galium* spp.

In this enclosure an average of 59% for both years were grasses with little changes from spring to fall (Figure 4 and 5). All grasses were grazed, with least utilization of *Hierocloe odorata*. *Equisetum* spp. were grazed more in early than late season (Figure 6), on average 9% for both years. *Kobresia myosuroides* and *Juncus* spp. had little utilization (Figure 4 and 5), but were grazed on occasions up to 17%, mostly in mid and late August. Forbs were utilized more in 1981 than 1982, 21% versus 10% (Figure 4 and 5). In both years, *Galium* spp., mainly *Galium boreale*, were consumed. Other forbs were heavily grazed on occasions, *Polygonum viviparum* up to 16% and *Trifolium repens* up to 17%, both by the same individual in 1981.

Sparse grassland enclosure. The third enclosure included in the study was located on a dry, sparse grassland. It was dominated

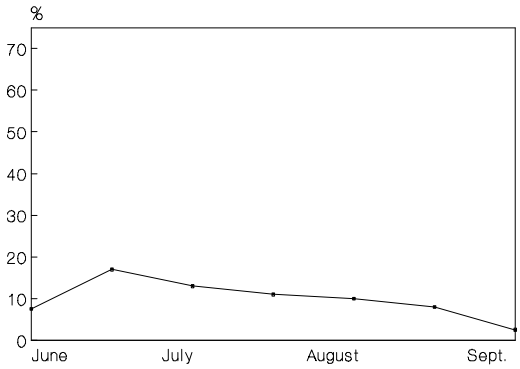

Figure 6. Relative amount (%) of horsetail (*Equisetum* spp.) in plant selection of four sheep in the larch plantation enclosure in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
*6. mynd. Hlutfall (%) elftingar (*Equisetum *spp.) í plöntuvali sauðfjár í tilraunahólfi í ungum lerkiskógi á Víðivöllum í Fljótsdal 1982.*

by *Kobresia myosuroides* with *Festuca rubra*, *Agrostis tenuis*, *Poa pratensis*, patches of *Juncus balticus* and *Trifolium repens*, and forbs like *Galium* spp., *Rhinanthus minor*, *Gentiana campestris*, *Achillea millefolium*, *Thymus arcticus* and *Cerastium fontanum*, many of which appear seasonally.

In both years grasses were the main diet, 46% in 1981 (Figure 7) and 43% in 1982 (Figure 8). The other main plant group utilized were forbs, 32% and 33% in 1981 and 1982 (Figure 7 and 8). Which forbs were grazed varied seasonally. *Trifolium repens* was available and grazed heavily throughout the season (up to 34%). *R. minor* and *A. millefolium* appeared later in the season and were grazed from mid August to mid September. On occasion, *R. minor* was utilized up to 48%, and *A. millefolium* 39%. *G. campestris* was also grazed in late summer, 16% on occasion. Though dominating in the sward *Kobresia myosuroides* was utilized less than 10% (Figure 7 and 8). *Juncus* spp. were mainly utilized by one sheep in 1982, up to 23% in early August.

Highland enclosure 1 (500 m). The enclosure at 500 m had a creek with a fen community dominated by *Eriophorum* spp. and tall *Carex* spp. like *C. rostrata* on both sides. Further from the creek the land was drier and dominated by *Carex bigelowii*, *Calamagrostis neglecta*, *Festuca rubra*, *Salix callicarpea*, *S. herbacea* and *Polygonum viviparum*. *Empetrum hermafroditum* and *Stereocaulon* spp. dominated on the driest ridges.

The sheep consumed 18% grasses (Figure 9) in 1981 and 26% the following year (Figure 10). In both years consumption of grasses increased as the season progressed. *Festuca rubra* was grazed earlier and *Calamagrostis neglecta* later in the season. *Carex* spp., mainly *Carex bigelowii*, were consumed in equal amounts in both years, 28% with a slight increase in late summer. *Salix callicarpea* and to a much lesser degree *S. herbacea* were browsed approx. 20% in both years. These were browsed in June and July, up to 62% on occasions, but by the middle of August the consumption had dropped markedly. In June and July over 30% of the diet selected by most of the sheep were *Salix* spp. *Polygonum viviparum* was important, especially for one individual in 1981 (Figure 9). The general picture was that individuals consuming much *Salix* spp. did not consume much *P. viviparum* and vice versa (Figure 9 and 10).

Highland enclosure 2 (600 m). The enclosure at 600 m also had a creek with a fen/mire community on both sides, dominated by

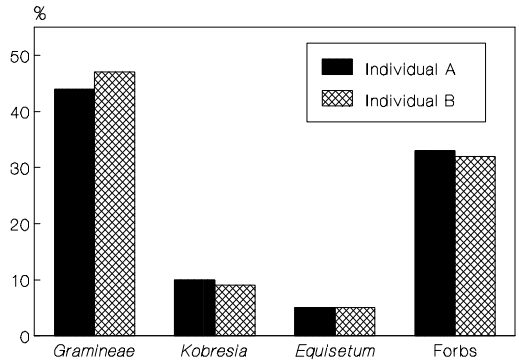

Figure 7. Plant selection (% grazed) of two sheep grazed in the sparse grassland enclosure in east Iceland in 1981 (Thórhallsdóttir, unpublished data). *7. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í þursaskeggsmóa á Skriðuklaustri í Fljótsdal 1981.*

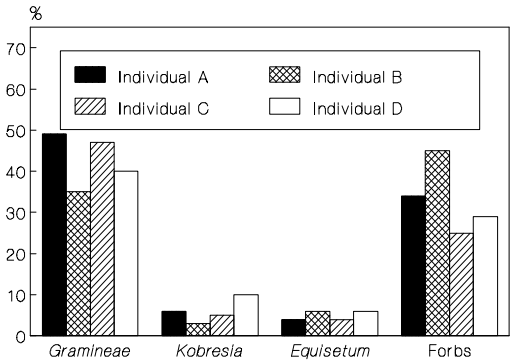

Figure 8. Plant selection (% grazed) of four sheep grazed in the sparse grassland enclosure in east Iceland in 1982 (Thórhallsdóttir, unpublished data). *8. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi í þursaskeggsmóa á Skriðuklaustri í Fljótsdal 1982.*

Carex rariflora, *C. nigra*, *C. saxatilis* and *Eriophorum* spp. Away from the creek there was a grass/sedge tussock dominated by *Carex bigelowii*, *Calamagrostis neglecta*, *Festuca rubra* and *Poa* spp., along with *Salix callicarpea*, *S. herbacea*, *Polygonum viviparum*, *Eriophorum boreale* and *Cardamine nymanii*. At each end of the enclosure there was a snow hollow with a number of plant species; *S. herbacea*, *Alchemilla filicaulis*, *Sibbaldia procumbens*, *Agrostis tenuis*, *Carex lachenalii* and *Equisetum arvense*.

In both years *Salix callicarpea* was heavily utilized, 35% in 1981 (Figure 11) and 33% in 1982 (Figure 12). As in the enclosure at 500 m, *Salix* spp. were mostly browsed in the early season (Figure 13). On occasions over 80% of grazed material consisted of *Salix* spp. Grasses were grazed 20% over the two years (Figure 11 and 12), and increased in consumption later in the season; the same pattern as seen in the enclosure at 500 m. Here, the increase was also due to an increase in consumption of *Calamagrostis neglecta*, which consisted of over 30% of grazed material for all the individuals in September 1982. Sedges, mainly *C. bigelowii* and, to much lesser degree, *C. saxatilis* were grazed on average 22% in both years (Figure 11 and 12). *Eriophorum* spp., though abundant, were only grazed 5%. The consumption was mainly in late season, and the last part of September one individual consumed 43% *Eriophorum* spp. on one occasion. *Polygonum viviparum* was an important grazing plant for the same individual here as in the enclosure at 500 m, grazed 20%, while grazed much less by the other sheep.

Analysis of rumen contents from sacrificed sheep

Analysis of rumen contents is a well known method when studying diet selection of wild herbivores. This method is, however, seldom used when studying domestic livestock because of the drawback that experimental animals have to be sacrificed. In Iceland the majority of the sheep population roam freely in extensive highland ranges during the summer season. Using fistulated animals on these ranges requires fencing and enclosures have to include a variety of plant communities. Methods developed for studying diet selection of wild herbivores, such as analysis of rumen contents or faeces are under these circumstances often more suitable. Analysis of rumen contents was used to study diet selection by reindeer in Iceland (Thorsteinsson *et al.*, 1970; Egilsson, 1983; Thórhallsdóttir, 1981), and to study diet selected by free

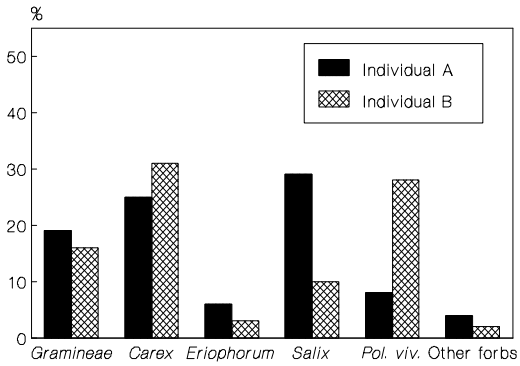

Figure 9. Plant selection (% grazed) of two sheep grazed in the highland enclosure 1 (500 m) in east Iceland in 1981 (Thórhallsdóttir, unpublished data). *9. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi við Bessastaðaá á Fljótsdalsheiði (500 m) 1981.*

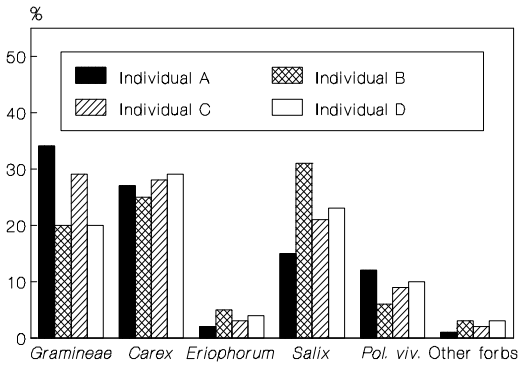

Figure 10. Plant selection (% grazed) of four sheep grazed in the highland enclosure 1 (500 m) in east Iceland in 1982 (Thórhallsdóttir, unpublished data). *10. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi við Bessastaðaá á Fljótsdalsheiði (500 m) 1982.*

roaming sheep on a mountain range (Thórhallsdóttir, 1981).

In a study by Thórhallsdóttir (1981) diets of reindeer and sheep grazing in the same area at the same time were compared to estimate whether these competed for the grazing resources. Seven sheep were sacrificed in July and seven again in early September. Before the animals were shot their grazing behaviour was monitored and the composition of the plant community in which they grazed for 30–45 min before recorded. Rumen contents were taken from all the animals and in addition samples of faeces from the colon for botanical analysis.

Analysis of rumen contents indicated that the sheep had eaten about equal amounts of grasses, sedges and willows in July (Figure 14). By August sedges had become the most important component in the diet (Figure 14). Grasses were eaten in equal amounts in July and August, while *Equisetum* spp. were grazed more in July than in August (Figure 14).

The results from the faecal samples differed from the rumen samples in both July and August. In July the faeces samples showed much more willow and less grasses and sedges than the rumen samples (Figure 15). In August the sedges dominated in the diet, while the amount of willows had decreased (Figure 15). Grasses were nearly absent in the faecal analysis from August.

Although the results from these two analysis differ, the main result they give is the same. Grasses, sedges and willows are the main plant groups according to both the analysis. Willows dominate in early season, sedges dominate in late season and grasses are found throughout the season (rumen samples).

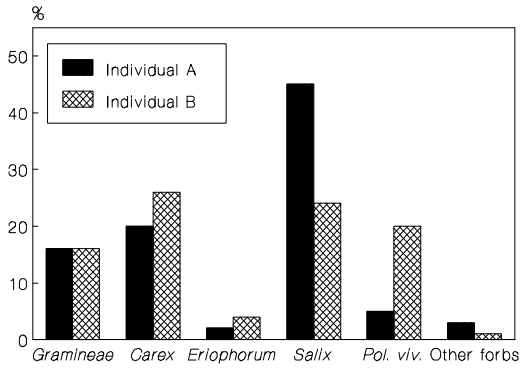

Figure 11. Plant selection (% grazed) of two sheep grazed in the highland enclosure 2 (600 m) in east Iceland in 1981 (Thórhallsdóttir, unpublished data).
11. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi við Grenisöldu á Fljótsdalsheiði (600 m) 1981.

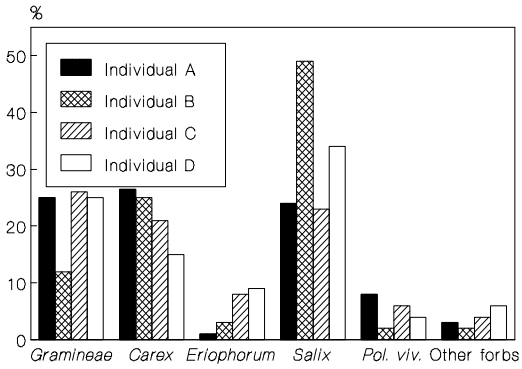

Figure 12. Plant selection (% grazed) of four sheep grazed in the highland enclosure 2 (600 m) in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
12. mynd. Plöntuval sauðfjár (% bitið) í tilraunahólfi við Grenisöldu á Fljótsdalsheiði (600 m) 1982.

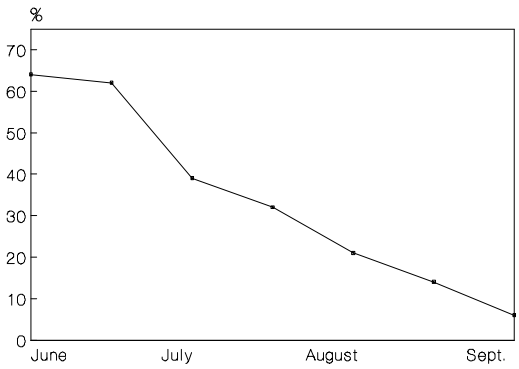

Figure 13. Relative amount (%) of willow (*Salix* spp.) in plant selection of four sheep in the highland enclosure 2 (600 m) in east Iceland in 1982 (Thórhallsdóttir, unpublished data).
*13. mynd. Hlutfall (%) víðis (*Salix *spp.) í plöntuvali sauðfjár í tilraunahólfi við Grenisöldu á Fljótsdalsheiði (600 m) 1982.*

Of plant fragments identifiable to a species level from the rumen samples, *E. variegatum* dominated in July while *E. arvense* dominated in August. The main willow found throughout the season was *S. callicarpea*, with a fraction of *S. herbacea*. Of the grasses, *C. neglecta* dominated, especially in August. *C. bigelowii*, *C. rariflora* and *E. angustifolium* were found in all the samples; *E. angustifolium* comprised 24% and 33% in two samples. *P. viviparum* was the main forb in the samples, with lesser amounts of *Bartsia alpina*, *Thalictrum alpinum*, *Cardamine nymanii*, and *Armeria maritima*.

Discussion on plant selection

Although the studies outlined above were conducted in different locations containing a variety of plant communities, using different individuals and methods, the overall results which emerged were the same. The same species were selected; *Festuca rubra*, *Calamagrostis neglecta*, *Agrostis* spp., *Poa* spp., *Carex bigelowii*, *Salix callicarpea*, *Polygonum viviparum*, *Galium* spp. and *Equisetum* spp., and the seasonal changes of that selection followed the same pattern. Grant *et al.* (1987) studying diet selection by sheep on native pastures in Scotland also found that the main diet selected by sheep consisted of a few species; grasses, *Carex* spp., *Vaccinium* spp., and *Juncus* spp.

In the Icelandic studies from the sixties, grasses were found to be of major importance in the diet of sheep grazing lowland pastures. The studies from 1979 and 1981–1982 with fistulated animals and from 1980 analysing rumen contents showed grasses of major importance where available in lower and drier areas. The only exception were the faecal samples from 1980 which showed very little grass content (for discussion on problems with faeces samples see Rice *et al.*, 1971; Vavra *et al.*, 1978; Thórhallsdóttir, 1981). Seasonal changes in grass consumption were observed in the studies from the sixties on lowland pastures and from 1981–1982 on highland pastures. There, consumption of grasses increased later in the season. These changes were not observed on the lowland pastures in the 1981–1982 study and the rumen analysis study on the highlands in 1980, where grasses were consumed in more or less equal amounts throughout the season. In both the studies analysing species composition, *Festuca rubra* was found to be consumed early and *Calamagrostis neglecta* late in the season.

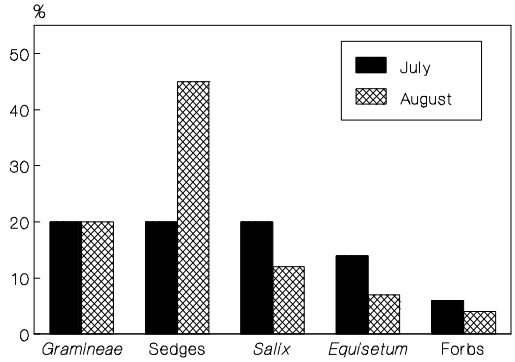

Figure 14. Results of rumen content analysis from 14 sheep (n=7) sacrificed in east Iceland 1980 (Thórhallsdóttir, 1981).

14. mynd. Niðurstöður gróðurgreininga á vambarsýnum 14 áa (n=7) sem skotnar voru á Vesturöræfum 1980.

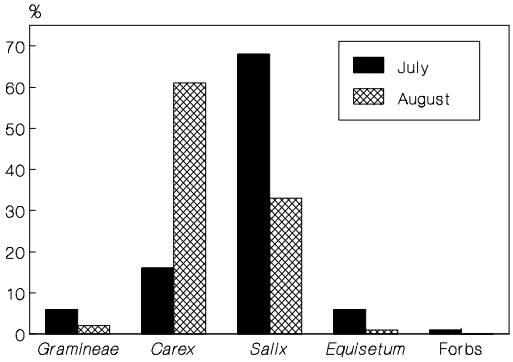

Figure 15. Results of feacal content analysis from 14 sheep (n=7) sacrificed in east Iceland 1980 (Thórhallsdóttir, 1981).

15. mynd. Niðurstöður gróðurgreininga á saursýnum 14 áa (n=7) sem skotnar voru á Vesturöræfum 1980.

In areas where sedges were abundant in the highlands and on the lowland mires *Carex bigelowii* was consumed in considerable amounts, and its intake increased later in the season. *C. bigelowii* was found to be of major importance for sheep grazing highlands in Norway (Vigerust, 1936; Selsjord, 1966); Wales (Milton, 1953); Scotland (Grant *et al.*, 1987) and for reindeer in Greenland (Holt, 1980) and Alaska (White and Trudell, 1980). *Eriophorum* spp. were not grazed to any degree, as observed by Grant *et al.* (1976) in Scotland.

The consumption of *Salix* spp. and *Equisetum* spp. varied with the season. In the highlands, *S. callicarpea* was consumed in large amounts until late summer when the intake dropped markedly. Thing (1980) in Greenland and Skogland (1974) in Norway reported that reindeer grazed *S. callicarpea* in the earlier part of the season. *Equisetum* spp. were also grazed in early season, as observed for reindeer in Alaska by Kuropat and Bryant (1980) and Spitzbergen by Holand *et al.* (1981).

The sheep were very opportunistic when grazing forbs, consuming what was in season, like *Rubus saxatilis*, *Rhinanthus minor* and *Gentiana campestris*. *Polygonum viviparum* was available for a long period of time and consumed more than any other forb. This species was found to be heavily grazed by reindeer in Spitzbergen (Punsvik *et al.*, 1980).

Differences in the diet consumption were considerable between some individuals in the studies described above. These differences were more pronounced in the consumption of forbs, where one individual might graze a particular species heavily, while it was not touched by another individual grazing at the same time and place.

In the study by Thórhallsdóttir (1981) an attempt was made to estimate plant preference by comparing demand, i.e. intake from rumen and faecal samples, and supply, i.e. the plant species cover in the community the animal grazed for the last 30–45 min. Estimated preference, or "forage ratio" was calculated as log FR = log r/p = log r + log p, with r = intake and p = supply (Jacobs, 1974). The estimated preference index D (= log FR) was found for each plant group for each animal.

The results from July showed a great variation in grazing preference of the different individuals. The D for *Salix* spp. was slightly positive for two individuals while negative for the remaining five. Grasses had a positive D in all the samples. The sedges had negative D in two samples and a positive in five (Figure 16).

In August the estimated preferences had changed and the overall estimated preference was calculated to be closer to zero, indicating less selective grazing (Figure 16). Skogland (personal communication) working with reindeer found that when the supply of green, lush forage went down, i.e. later in the season, selective grazing decreased and was taken over by a more generalized grazing. Redhead and Tyler (1988) analysing optimal foraging behaviour in patchy environments concluded that animals foraging in bad, stable environments (all equally bad; here in the fall) should stay longer at each patch, i.e. be less selective.

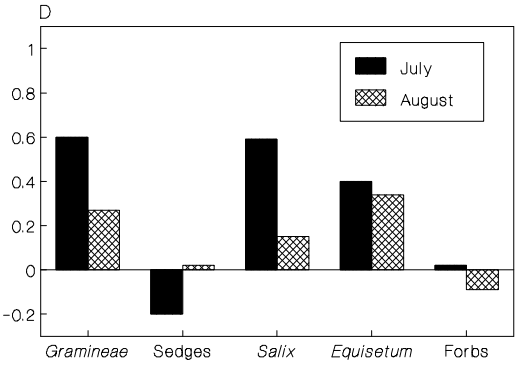

Figure 16. Estimated preference index (D) from results of rumen content analysis and plant composition on offer in east Iceland in 1980 (Thórhallsdóttir, 1981).
16. mynd. Reiknaður plöntuvalsstuðull (D) út frá niðurstöðum gróðurgreininga á vambarsýnum og gróðurþekju á beitarblettum á Vesturöræfum 1980.

BEHAVIOUR STUDIES

Grazing areas

In Iceland most of the sheep population grazes native pastures during the summer, and only a small fraction graze on cultivated or semi-cultivated pastures. The majority of the population on the native pasture roam freely over extensive highland and mountain ranges. On these ranges a complex mosaic of different plant communities exists, from wet fens and mires to dry heath and moss hummock.

The utilization of different plant communities by free roaming grazing sheep on a highland range was studied in north Iceland in the summer of 1982 (Thórhallsdóttir, unpublished data). Within a highland range, two locations of about 200 ha each were chosen, within which typical vegetation communities of the area were represented. Both locations had fens and bogs in depressions and dry heath and moss hummocks on ridges. With the help of a telescope, numbers of sheep in each plant community were counted every hour and their activity recorded; i.e. grazing, lying or walking. Records were taken for 3×24 hours in each location in July and from dawn to dusk, approximately 5 am to 9 pm, for another 3 days in each location in early September. For comparison of plant community utilization relative density index (Q) was calculated from the records as Q = (SP/PT) / (ST/TT), where SP = sheep in a plant community X at time X, PT = size (ha) of plant community X, ST = total sheep counted in the area at time X and TT = total size (ha) of area.

Area 1. In area 1, six different plant communities were represented. The main area was covered with a dry heath, dominated by *Betula nana*, *Kobresia myosuroides* and different grasses. Along a creek, running through the location was a sparse grassland, dominated by grasses, mostly *Calamagrostis neglecta*. Further from the creek the land was drier with a moss hummock dominated by *Racomitrium* spp. and *K. myosuroides*. A fen covering about 15% of the area was dominated by *Carex rostrata*, *C. rariflora* and *Eriophorum angustifolium*. Two mires covering together about 15% were dominated by *Carex bigelowii* and *E. angustifolium* and *Salix phylicifolia* respectively. The third mire in the area only covered 2% and was dominated by *C. bigelowii* and *C. rariflora*.

In July the main mires were most utilized with an average utilization index Q=1.44, followed by the fen, Q=1.12, and the dry heath, Q=0.94. There was a diurnal pattern to the utilization. From very early morning (4–5 am) there was a higher density of sheep in the mires than later in the day. The picture was reversed for the dry heather, where the sheep were found in highest densities from late night to early morning. Most of the sheep were found in the fen during the day, with few sheep at night and early morning. The utilization of the other three plant communities, the small mire, the sparse grassland and the moss hummock, did not show a distinctive diurnal pattern in July.

In September the fen had taken over with highest densities, Q=2.82, followed by the dry heather, Q=0.97. The mires were much less utilized than earlier in the season, Q=0.72, while the other communities were used about the same. The density of sheep remained high throughout the day in the fen, and did not change much during the hours of daylight. The utilization of the dry heather had the same general pattern as in July, with higher densities at dawn and again in late afternoon and early evening.

Area 2. In area 2 a fen dominated by *Carex rostrata* and *Eriophorum angustifolium* covered over 50% of the area. Surrounding the fen were ridges of dry heather dominated by *Betula nana*, *Kobresia myosuroides* and different grasses and *Racomitrium* heath with dwarf shrubs. Between the fen and the dryland there was a tussock community dominated by *Carex bigelowii* and lichens.

Table 5. Total grazing time (min) of five lactating ewes grazing a lowland drained mire in south-west Iceland in 1982 (Thórhallsdóttir, unpublished data).
5. tafla. Heildarbeitartíðni (mín) fimm áa á framræstri mýri á Hesti í Borgarfirði 1982.

Date	Ewes 1	2	3	4	5	Average
July	640	655	637	574	667	635
August	718			703	671	697
September	538		713	606	570	607
Average	632	(655)	675	628	636	645

In this area, the tussock community had by far the highest density of sheep in July with Q=2.84, followed by the dry heath with Q=1.12 and the fen with Q=0.53. The *Racomitrium* heath was, in general, very little utilized. Here again the sheep spent the middle of the day in the fen and late night and early morning in the dry heather. The sheep density was high during the 24 hours in the tussock community.

In September the utilization of the plant communities in the area had changed remarkably. Few sheep were found in the tussock community, Q=0.62, while the fen had the highest densities, Q=1.27. The dry heath had a density of Q=0.83. Here, as earlier, the sheep spent the day in the fen, from dawn until early evening (1900–2000 hours), then moving up to the dry heather community.

Grazing time

Total grazing time. In 1982 grazing time was measured with vibrarecorders fitted on five lactating ewes in two areas; a lowland drained mire and a highland dry heather community. Measurements were taken for 2–6 days in July, August and September. Average grazing time in the lowland was 645 min (Table 5), (10 hours and 45 min), and in the highland 668 min (11 hours and 8 min). In the lowland, the grazing time in early July, early August and mid September was on average 635 min, 697 min and 607 min re-

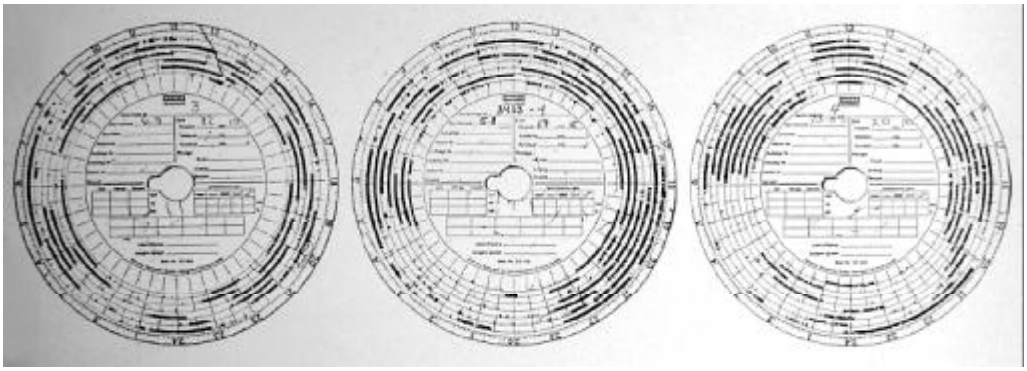

Figure 17. Chronographs from vibrarecorders fitted on sheep grazing a lowland mire in south-west Iceland in 1982. Broad black lines mark grazing periods (Thórhallsdóttir, unpublished data).
17. mynd. Spjöld úr síritum sem settir voru á sauðfé á Hesti í Borgarfirði 1982. Svartar, breiðar línur sýna beitarlotur.

spectively (Table 5). In the highland measurements were only taken in the middle of July and late August or early September. In July the sheep grazed on average for 657 min (10 hours and 57 min). In August/September the grazing time was 679 min (11 hours and 19 min).

Time of grazing. During the light nights in July animals grazed throughout the 24 hours. A bout could last from 1/2–3 hours, but usually 1–2 hours, with a 1/2–2 hours interval between (Figure 17). In August with darkening nights the sheep changed their grazing behaviour. They did not graze during the dark hours, but started just before sunrise and grazed until after sunset (4–5 am to 11 pm) (Figure 17). During the day the bouts were longer than in July, with shorter intervals between. In September the sheep also started grazing around dawn (6 am), and grazed in long bouts with short intervals between until dusk (8 pm). They would, however, often graze for 1–2 hours during the night, frequently around midnight (Figure 17).

Discussion on grazing behaviour

In the observations reported above, sheep showed marked preferences for different plant communities, and these preferences changed with the time of day and the season. Diurnal variation in diet selection has been reported earlier (Arnold and Dudzinski, 1978; van Dyne and Heady, 1965; Langlands, 1965, 1967; Kothmann, 1966). In Iceland the sheep stayed in the mires from early morning until mid or late afternoon, when they moved on to the dry heath and ridges. The wetland communities produce much more biomass than the dryland communities, especially the dry ridges (Thorsteinsson, 1981), and there is also more litter in the wetlands. Animals have a high intake rate on pastures with high biomass (Hodgson and Milne, 1978; Penning, 1986) and prefer grazing from patches of high biomass (Arnold, 1987). Arnold and Dudzinski (1978) stated that the hungry animal was less selective and looked for quantity rather than quality. In the mornings the animals are more hungry than in the afternoons, which might explain the grazing pattern observed.

Another factor influencing the diurnal movements of the sheep in the area could be ambient temperature. The wetlands are generally located in depressions in the topography. These cool down more during the night as the cold air sinks into the depressions. Sheep prefer camping in dry, warm places and thus frequently camp on roads. The observation that the wetlands had higher sheep densities in the fall than in the summer is in agreement with increased consumption of sedges found in the plant selection studies, discussed earlier.

Time spent grazing in the above discussed studies was 10–11 h/day. Grazing time by sheep was reported to be 6.5–15.5 h/day (Hodgson, 1986). Pasture level and physiological stage will influence grazing time (Arnold and Dudzinski, 1978; Arnold, 1981). Penning *et al*. (1989) found average grazing time for four different sward heights to be 11.12 h/day, from 12.33 h/day at low sward heights to 10.15 h/day for tall swards. In Iceland the grazing time was longest in early August, and shortest in mid September on the lowland pasture. This result can be explained as a function of pasture quality and nutritional demand. In early July when the ewes are lactating and the nutritional value of the pasture is high intermediate grazing time is observed. In early August the ewes are still lactating and the quality of the pasture is decreasing, which results in an increased grazing time. By mid September the pasture quality is still lower but the ewes are no longer lactating, so the grazing time is down again.

The grazing periods in Iceland clearly followed the seasons, from dawn to dusk. This diurnal patter of grazing is commonly observed in grazing studies (Arnold and Dudzinski, 1978). In warmer climates grazing

usually takes place at dawn and dusk with a resting period during the hottest time of the day (Arnold and Dudzinski, 1978). In Iceland no clear main midday resting period was observed, but many shorter resting periods during the course of the day. A short grazing period during the middle of the night was also reported by Arnold and Dudzinski (1978).

GENERAL DISCUSSION

Although the same plant species were represented in the diet in most of the studies the proportions of these differed and the diet between individual sheep varied considerably.

Diet selection has been explained in different ways by researchers with different backgrounds. Animal physiologists explain diet selection as a function of the morphology and physiology of the animal (Demment and van Soest, 1985; Hofmann, 1988). Because of their greater gut capacity (αW^{1}) and relatively lower energy requirements ($\alpha W^{0.75}$), larger ruminants can afford to retain the cell wall fraction longer, allowing for more extensive digestion (Demment and van Soest, 1985; Illius and Gordon, 1990). Large ruminants can thus survive on more fibrous, lower quality diet than small ruminants (Illius and Gordon, 1990). Mouth size and the dental morphology also sets constraints on the ability of the grazing animal to select from the sward. Selection of individual plants and plant parts is easier for animals with a narrow and pointed incisors arcade, than for those with a broad and flattened incisors arcade (Hofmann, 1988; Gordon and Illius, 1988). Another constraint upon diet selection are secondary compounds (e.g. tannins) found in plants and thought to be feeding deterrents (Provenza *et al.*, 1990). The ability to utilize forages high in secondary compounds varies among mammalian herbivores (Howe *et al.*, 1988; McCabe and Barry, 1988; Distel and Provenza, 1991). It has been related to the size of the salivary glands (Hofmann, 1988) and their ability to produce salivary proteins that interact with the deterrents (i.e. tannins: mice – Mehansho *et al.*, 1985; deer – Robbins *et al.*, 1987). Other species may have evolved different mechanisms to cope with secondary compounds (Distel and Provenza, 1991).

Behaviour ecologists explain diet selection as an optimum process, i.e. optimal foraging theory (Stephens and Krebs, 1986) where the animal is assumed to select diet to maximize gain and minimize cost. The measurement of optimality is usually observed foraging behaviour against a calculated economic optimum. The aim of using an optimality model is not to test whether the animals are optimal, but to test whether the particular optimality criterion and constraints used give a good description of the animal's behaviour (Krebs and Davis, 1987). Optimal foraging theory can thus rather be considered as a tool to study constraints on foraging behaviour than explaining diet selection.

Both of the above models, the morpho-physiology model and the optimal foraging model, give functional explanations on diet selection, i.e. why the observed diet selection occurs. The causal aspect, i.e. how the diet selection is accomplished is, however, less addressed. How does the small ruminant "know" that it has to eat more nutritious food than a larger one, or a moose what ratio of aquatic to terrestrial plants to eat to gain enough energy and sodium (Belovsky, 1978). Further, these models do not allow for interspecific plasticity in diet selection. Individuals of the same species under the same constraints should have the same diet selection.

In the Icelandic studies discussed above there was great variation in the diet selected by individual sheep grazing at the same time and place. This variation can, however, be explained by the learning mechanisms model (Provenza and Balph, 1988), adapted from behaviour psychology. Decades of studies on the development of dietary preferences in laboratory animals have confirmed the importance of learning; trial and error (Booth,

1985; Garcia, 1989) and social learning (Galef, 1981) on diet selection. Laboratory animals like rats, rely on older members of the group, especially the mother, to guide them to safe and edible foods (Galef, 1971). When ingested, foods are rated as preferred and less preferred based on their nutritional quality, detected post-ingestionally (Braveman and Bronstein 1985). Foods that have been experienced as poisonous are readily rejected (Garcia *et al.*, 1985) while nutritious foods become preferred (Bolles *et al.*, 1981; Booth, 1985). Experiments have shown that the same general model applies to sheep (Thórhallsdóttir *et al.*, 1987, 1990abc; Burritt and Provenza, 1989). Initially lambs learn from their mothers what foods to eat and what foods to avoid (Thórhallsdóttir *et al.*, 1990ab). Later they develop their diet preferences based on post-ingestional consequences of ingested feeds (positive and negative feedback). Foods ingested and followed by discomfort (negative feedback) are rejected in future trials (Thórhallsdóttir *et al.*, 1987) while foods which are followed by nutrient release in the rumen (positive feedback) become preferred (Thórhallsdóttir, unpublished data). The degree of the positive feedback experienced by the animal may depend on its physiological status and needs (Thórhallsdóttir, unpublished data).

The three models discussed are complementary rather than mutually exclusive. The physiology and morphology of the animal sets the constraints on the learning and the way the animal experiences the food. Animals that have the physiological and morphological ability to detoxify certain secondary compounds can utilize the nutrients associated with these and experience positive nutritional feedback. Others lacking the ability to detoxify these same compounds may only experience the negative consequences from eating these foods. An animal in nutritional deficit may experience a stronger positive feedback from ingesting a given feed than animals in nutritional balance.

Although the animal may prefer one food to another it may not express that preference in a foraging situation. Environmental factors like availability, density and ease of harvest of preferred species within the sward, predators and even social facilitation may influence diet selection. Within the constraints of the morpho-physiology of the animal, its previous dietary experience, its needs and the food on offer the animal tries to balance its dietary intake at any given time. Only by taking all these factors into consideration can we expect to understand diet selection in ruminants; how and why we have the observed diet selection.

REFERENCES

Arnold, G.W., 1981. Grazing behaviour. In: *World Animal Science, B1, Grazing Animals* (ed. F.H.W. Morley). Amsterdam Elsevier: 79–104.

Arnold, G.W., 1987. Influence of the biomass, botanical composition and sward height of annual pastures on foraging behaviour by sheep. *Journal of Applied Ecology* **24**: 759–772.

Arnold, G.W. & M.L. **Dudzinski**, 1978. *Ethology of Free-ranging Domestic Animals*. Amsterdam Elsevier: 197 pp.

Belovsky, G.E., 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* **14**: 105–134.

Bolles, R.C., L. **Hayward** & C. **Crandall**, 1981. Conditioned taste preferences based on caloric density. *Journal of Experimental Psychology. Animal Behavior Processes* **7**: 59–69.

Booth, D.A., 1985. Food-conditioned eating preferences and aversions with interoceptive elements: conditioned appetites and satieties. In: *Experimental Assessments and clinical Applications of Conditioned Food Aversions* (eds N.S. Braveman & P. Brons). New York Academic Science: 22–42.

Braveman, N.S. & P. **Bronstein** (eds), 1985. *Experimental Assessments and Clinical Applications of Conditioned Food Aversions*. New York Academic Science: 441 pp.

Burritt, E.A. & F.D. **Provenza**, 1989. Food aversion learning: ability of lambs to distinguish safe from harmful foods. *Journal of Animal Science* **67**: 1732–1739.

Demment M.W. & P.J. **van Soest**, 1985. A nu-

tritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist* **125**: 641–672.

Distel, R.A & F.D. **Provenza**, 1991. Experience early in life affects voluntary intake of blackbrush by goats. *Journal of Chemical Ecology* **17**: 431–450.

Egilsson, Kristbjörn, 1983. *Fæða og beitilönd íslensku hreindýranna*. OS-83073/VOD-07, Reykjavík, Iceland.

Gaare, E., 1968. Prøver av vominnhold i studiet av villreinens konsumption i vinterhalvåret. In: *Foredrag holdt under den nordiske viltbiologi kongress i Oslo 24–26.10 1968. Viltstell and viltforskning i Norge. Statens viltundersøkelser*: 23–25.

Galef, B.G., 1971. Social effects in the weaning of domestic rat pups. *Journal of Comparative Physiological Psychology* **75**: 358–362.

Galef, B.G., 1981. Development of flavour preference in man and animals: the role of social and nonsocial factors. In: *Development of Perception: Psychobiological Perspectives* (eds N.R. Aslin, J.R. Alberts & M.R. Peterson). Academic Press, New York: 411–431.

Garcia, J., 1989. Food for Tolman: Cognition and cathexis in concert. In: *Aversion, Avoidance and Anxiety* (eds T. Archer & L. Nilsson). Hillsdale, New Jersey: 45–85.

Garcia, J., P.A. **Lasiter**, F. **Bermudez-Rattoni** & D.A. **Deems**, 1985. A general theory of aversion learning. In: *Experimental Assessments and Clinical Applications of Conditioned Food Aversions* (eds N.S. Braveman & P. Bronstein). New York Academic Science: 8–12.

Gordon, I.J. & A.W. **Illius**, 1988. Incisor arcade structure and diet selection in ruminants. *Functional Ecology* **2**: 15–22.

Grant, S.A., W.I.C. **Lamb**, C.D. **Kerr** & G.R. **Bolton**, 1976. The utilization of blanket bog vegetation by grazing sheep. *Journal of Applied Ecology* **13**: 857–869.

Grant, S.A., L. **Torvell**, H.K. **Smith**, D.E. **Suckling**, T.D.A. **Forbes** & J. **Hodgson**, 1987. Comparative studies of diet selection by sheep and cattle: Blanket bog and heather moor. *Journal of Ecology* **75**: 947–960.

Hamilton, B.A. & D.G. **Hall**, 1975. Estimation of the botanical composition of the oesophageal extrusa samples. 1. A modified microscope point technique. *Journal of the British Grassland Society* **30**: 229–235.

Harniss, R.O., D.A. **Price** & D.C. **Tomlin**, 1975. Number of fistula samples needed for determination of sheep diet on sagebrush-grass range. *Journal of Range Management* **28**: 417–419.

Hodgson, J., 1969. The use of sheep fitted with oesophageal fistulae in grazing studies. *Journal of the British Grassland Society* **24**: 325–332.

Hodgson, J., 1986. Grazing behaviour and herbage intake. In: *Grazing* (ed. J Frame). British Grassland Society, Occasional Symposium No. 19: 51–65.

Hodgson, J. & J.A. **Milne**, 1978. The influence of weight of herbage per unit area upon the grazing behaviour of sheep. In: *Proceedings of the 7th General Meeting, European Grassland Federation, Ghent*: 4.31–4.38.

Hofmann, R.R., 1988. Anatomy of the gastrointestinal tract. In: *The Ruminant Animal: Digestive Physiology and Nutrition* (ed. D.C. Church). Prentice Hall, New Jersey: 14–44.

Holand, Ø., A.B. **Leifseth** & E. **Persen**, 1981. *Nyetablering av rein på Brøggerhalvøya – Svalbard, en beiteøkologisk undersøkelse*. Cand. Agric. thesis. Agricultural University of Norway, Ås: 196 pp.

Holt, S., 1980. Vegetation pattern and effects of grazing on caribou ranges in the Søndre Strømfjord area, West Grønland. In: *Proceedings of the 2nd International Reindeer/Caribou Symposium. Røros, Norway, 1979* (eds E. Reimers, E. Gaare & S. Skjenneberg). D.F.V. Trondheim, Norway: 57–63.

Howe, J.C., T.N. **Barry** & A.I. **Popay**, 1988. Voluntary intake and digestion of gorse (*Ulex europeus*) by goats and sheep. *The Journal of Agricultural Science, Cambridge* **111**: 107–114.

Illius, A.W. & I.J. **Gordon**, 1990. Constraints on diet selection and foraging behaviour in mammalian herbivores. In: *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes). NATO ASI Series, Vol. G 20. Springer-Verlag, Berlin Heidelberg: 369–393.

Jacobs, J., 1974. Quantitative measurement of food selection. A modification of the forage rate and Ivlev's electivity index. *Oecologica* **14**: 413–417.

Kothmann, M.M., 1966. Nutrient content of forage ingested in the morning compared to evening. *Journal of Range Management* **19**: 95–96.

Krebs, J.R. & N.B. **Davis**, 1987. *An Introduction*

to Behavioural Ecology. 2nd edn. Blackwell Scientific Publications: 389 pp.

Kuropat, P. & J.P. **Bryant**, 1980. Foraging behaviour of cow caribou on the Utukok calving grounds in north-western Alaska. In: *Proceedings of the 2nd International Reindeer/Caribou Symposium. Røros, Norway, 1979* (eds E. Reimers, E. Gaare & S. Skjenneberg). D.F.V. Trondheim, Norway.

Langlands, J.P., 1965. Diurnal variation in the diet selected by free-grazing sheep. *Nature* **207**: 666–667.

Langlands, J.P., 1966. Studies on the nutritive value of the diet selected by grazing sheep. I. Differences in composition between herbage consumed and material collected from oesophageal fistulae. *Animal Production* **8**: 253–259.

Langlands, J.P., 1967. Studies on the nutritive value of the diet selected by grazing sheep. II. Some sources of error when sampling oesophageally fistulated sheep at pasture. *Animal Production* **9**: 167–175.

McCabe, S.M. & T.N. **Barry**, 1988. Nutritive value of willow (*Salix* spp.) for sheep, goats and deer. *The Journal of Agricultural Science, Cambridge* **111**: 1–9.

McManus, W.R., 1962. Oesophageal fistulation studies in the sheep. *Australian Veterinary Journal* **38**: 85–91.

Mehansho, H., S. **Ciements**, B.T. **Sheares**, S. **Smith** & D.M. **Carlson**, 1985. Induction of proline-rich glycoprotein synthesis in mouse salivary glands by isoproterenol and by tannins. *Journal of Biological Chemistry* **260**: 4418–4423.

Milton, W.E.J., 1953. The palatability of herbage on undeveloped grasslands in west-central Wales. *Empire Journal of Experimental Agriculture* **21**: 116–122.

Penning, P.D., 1986. Some effects on sward conditions on grazing behaviour and intake by sheep. In: *Behavioural Mechanisms of Food Selection* (ed. R. N. Hughes). NATO ASI Series, Vol. G 20. Springer-Verlag, Berlin Heidelberg: 227–237.

Penning, P.D., A.J. **Parsons**, G.E. **Hooper** & R.J. **Orr**, 1989. Responses in ingestive behaviour by sheep to changes in sward structure. In: *XVI International Grassland Congress, Nice, France*: 791–792.

Provenza, F.D. & D.F. **Balph**, 1988. The development of dietary choice in livestock on rangelands and its implications for management. *Journal of Animal Science* **66**: 2356–2368.

Provenza, F.D., E.A. **Burritt**, T.P. **Clausen**, J.P. **Bryant**, P.B. **Reichardt** & R.A. **Distel**, 1990. Conditioned flavour aversion: A mechanism for goats to avoid condensed tannins in blackbrush. *The American Naturalist* **136**: 810–828.

Punsvik, T., A. **Syvertsen** & H. **Staaland**, 1980. Reindeer grazing in Adventdalen, Svalbard. In: *Proceedings of the 2nd International Reindeer/ Caribou Symposium. Røros, Norway, 1979* (eds E. Reimers, E. Gaare & S. Skjenneberg). D.F.V. Trondheim, Norway.

Redhead, E. & P.A. **Tyler**, 1988. An experimental analysis of optimal foraging behaviour in patchy environments. *Quarterly Journal of Experimental Psychology* **40B**: 83–102.

Rice, R.W., D.R. **Cundy** & P.R. **Weyerts**, 1971. Botanical and chemical composition of esophageal and rumen fistula samples of sheep. *Journal of Range Management* **24**: 121–125.

Robbins, C.T., S. **Mole**, A.E. **Hagerman** & J.A. **Hanley**, 1987. Role of tannins in defending plants against ruminants: Reduction in dry matter digestion. *Ecology* **68**: 1601–1615.

Selsjord, I., 1966. Vegetasjons- og beitegranskinger i fjellet (Vegetation and pasture investigations in mountain districts of Norway). *Forskning og forsøk i landbruket* **17**: 325–381.

Skogland, T., 1974. *Villreinens habitatatferd. Hardangervidda 1970–1973*. Norsk IBP. D.V.F. Viltforskningen, Trondheim, Norway: 133 pp.

Stephens, D.W. & J.R. **Krebs**, 1986. *Foraging Theory*. Princetown University Press, Princetown, New Jersey: 248 pp.

Thing, H., 1980. Preliminary studies of habitat use and food selectivity of West Grønland caribou. In: *Proceedings of the 2nd International Reindeer/Caribou Symposium. Røros, Norway, 1979* (eds E. Reimers, E. Gaare & S. Skjenneberg). D.F.V. Trondheim, Norway.

Thórhallsdóttir, Anna G., 1981. *Beitevalg hos sau og rein på Vesturøræfi – Island*. Cand. Agric. thesis. Agricultural University of Norway, Ås: 107 pp.

Thórhallsdóttir, Anna G., F.D. **Provenza** & D.F. **Balph**, 1987. Food aversion learning in lambs with and without a mother: Discrimination, novelty and persistance. *Applied Animal Behaviour Science* **18**: 327–340.

Thórhallsdóttir, Anna G., F.D. **Provenza** & D.F. **Balph**, 1990a. The role of the mother in the

intake of harmful foods by lambs. *Applied Animal Behaviour Science* **25**: 35–44.

Thórhallsdóttir, Anna G., F.D. **Provenza** & D.F. **Balph**, 1990b. Ability of lambs to learn about novel foods while observing or participating with social models. *Applied Animal Behaviour Science* **25**: 25–33.

Thórhallsdóttir, Anna G., F.D. **Provenza** & D.F. **Balph**, 1990c. Social influences on conditioned food aversions in sheep. *Applied Animal Behaviour Science* **25**: 45–50.

Thorsteinsson, Ingvi, 1964. Plöntuval sauðfjár. *Freyr* **60**: 194–201.

Thorsteinsson, Ingvi, 1981. Gróðurskilyrði, gróðurfar, uppskera gróðurlenda og plöntuval búfjár. *Íslenzkar landbúnaðarrannsóknir* **12(2)**: 85–99.

Thorsteinsson, Ingvi & Gunnar **Ólafsson**, 1965. Plöntuval sauðfjár og meltanleiki beitarplantna. *Freyr* **61**: 157–163.

Thorsteinsson, Ingvi & Gunnar **Ólafsson**, 1967. Fjárbeit í skóglendi og úthaga. *Ársrit Skógræktarfélags Íslands* **1967**: 6–14.

Thorsteinsson, Ingvi, Arnthór **Gardarson**, Gunnar **Ólafsson** & Gylfi M. **Gudbergsson**, 1970. Íslensku hreindýrin og sumarlönd þeirra. *Náttúrufræðingurinn* **40**: 145–170.

Torrell, D.T., 1954. An oesophageal fistula for animal nutrition studies. *Journal of Animal Science* **13**: 878–884.

van Dyne, G.M. & H.F. **Heady**, 1965. Botanical composition of sheep and cattle diets on a mature animal range. *Hilgardia* **36**: 465–492.

Vavra, M., R.W. **Rice** & R.M. **Hansen**, 1978. A comparison of oesophageal fistula and faecal material to determine steer diets. *Journal of Range Management* **31**: 11–13.

Vigerust, Y., 1936. Starrvekstene (*Carex*) og deres betydning i fjellbeitene. *Årbok for beitebruk i Norge* **12**: 42–64.

White, R.G. & J. **Trudell**, 1980. Patterns of herbivory and nutrient intake of reindeer grazing tundra vegetation. In: *Proceedings of the 2nd International Reindeer/Caribou Symposium. Røros, Norway, 1979* (eds E. Reimers, E. Gaare & S. Skjenneberg). D.F.V. Trondheim, Norway.

Manuscript received 11 November 1992.