SOME PRINCIPLES IN THE INVESTIGATION OF SELECTIVE GRAZING

(Invited Paper)

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I. INTRODUCTION

The grazing animal, in most natural situations, has a complex environment in which to live. Figure 1 illustrates the multitude of factors that can influence the selection and composition of any day's diet. Selective grazing by ruminants has been extensively reviewed by Arnold (1963) and Heady (1964). This review will indicate the present state of knowledge of the interactions between plant and animal characteristics in selective grazing.

Palatable, by definition, means "pleasant to the taste". The term palatability has been widely used to describe all the 'characteristics, not taste alone, that make a plant acceptable to the grazing animal. In this paper, the expression "acceptability" is used to describe the degree to which a plant is acceptable to an animal. The animal itself expresses preferences when presented with a number of species in a plant community; these preferences can be arranged in an order of relative acceptability, i.e. a preference ranking.

The reader is referred to Heady (1964) for a discussion on techniques used to study selective grazing.

There has been general agreement that sheep and cattle, at the single plant level, eat leaf in preference to stem (Arnold 1960, 1963; Cook and Harris 1950; Reppert 1960) and green (or young) material in preference to dry (or old) material (Arnold 1963; Cook, Stoddart and Harris 1956; Cowlishaw and Alder 1960; Milton 1953; Reppert 1960; Stapledon 1934). There may be exceptions to these basic rules, but they are rare. The material eaten, when compared to the material offered, is usually higher in nitrogen (Arnold 1960; Cook, Stoddart and Harris 1956; Harrison ***et al.*** 1954; Weir and Tore11 1959) phosphate (Cook, Stoddart and Harris 1956; Plice 1952; Staten 1949), and gross energy (Cook, Stoddart and Harris 1956), but lower in "fibre" (Hardison ***et al.*** 1954; Weir and Tore11 1959). Opinion varies on whether eaten material is higher in sugars and minerals.

Other questions remain largely unanswered. Are green material and leaf material eaten ***because*** they contain higher nitrogen, etc., or are the differences in chemical composition merely ***associated*** with physical characteristics of the plant parts? Is there definite motivated selection for this material and, if so, is this linked to a conscious nutritional wisdom? In this review, the available information on these questions is discussed, to illustrate the principles underlying investigations of selective grazing.

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ANIMAL

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Motor outflow

↓

Reflexes of attention, approach, examination and consumption or rejection

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Senses of sight, smell, touch and taste

↓

PLANTS

Plant species present and their chemical and physical characteristics and relative availability.

Modified by

↓

PLANT ENVIRONMENT

Soil type Soil fertility Plant community

Modified by

↓

PHYSICAL ENVIRONMENT

Topography (i.e. slope, aspect and site of a plant) Distance plant is from water Distance plant is from tracks or shade.

Modified by

↓

ANIMAL FACTORS

Animal species Animal individuality Physiological condition (food demand) Grazing behaviour
Social behaviour

Modified by

↓

PREVIOUS EXPERIENCE

↓

DIET COMPOSITION

Fig. 1.-Diet selection by the grazing animal.

II. PREFERENCES AND PLANT CHARACTERISTICS

Numerous experiments have been carried out to study the causes of preferences. These have been reviewed by Arnold (1963) and Heady (1964). Basically, preferences will be determined through the animal's special senses. Therefore, any characteristics of plants or plant communities must act through these senses. Neural responses to stimuli received will be partly innate and partly due to previous experience and physiological need of the animal; any intelligence (nutritional wisdom) on the animal's part will be reflected in the reaction to both previous experience and physiological need.

(a) Chemical composition and acceptability of different species

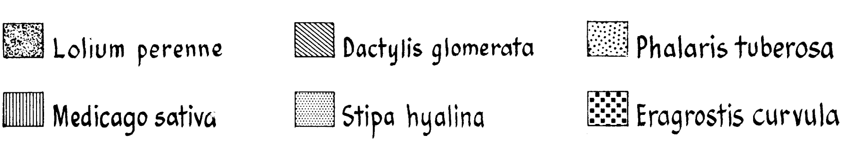
No single chemical constituent has been found to determine the acceptability when a number of herbage species are on offer. This is not surprising. In the first place, most workers have attempted to correlate proximate analysis data with acceptability, i.e. nitrogen, crude fibre or ether extract content. These are not chemical entities that could be recognised at the molecular level-a pre-requisite for the use of the senses of taste and smell. Secondly, one would expect few instances where differences in acceptability ***between species*** were determined by differences in a single chemical constituent because a large variation in concentration of a large number of constituents would be involved.

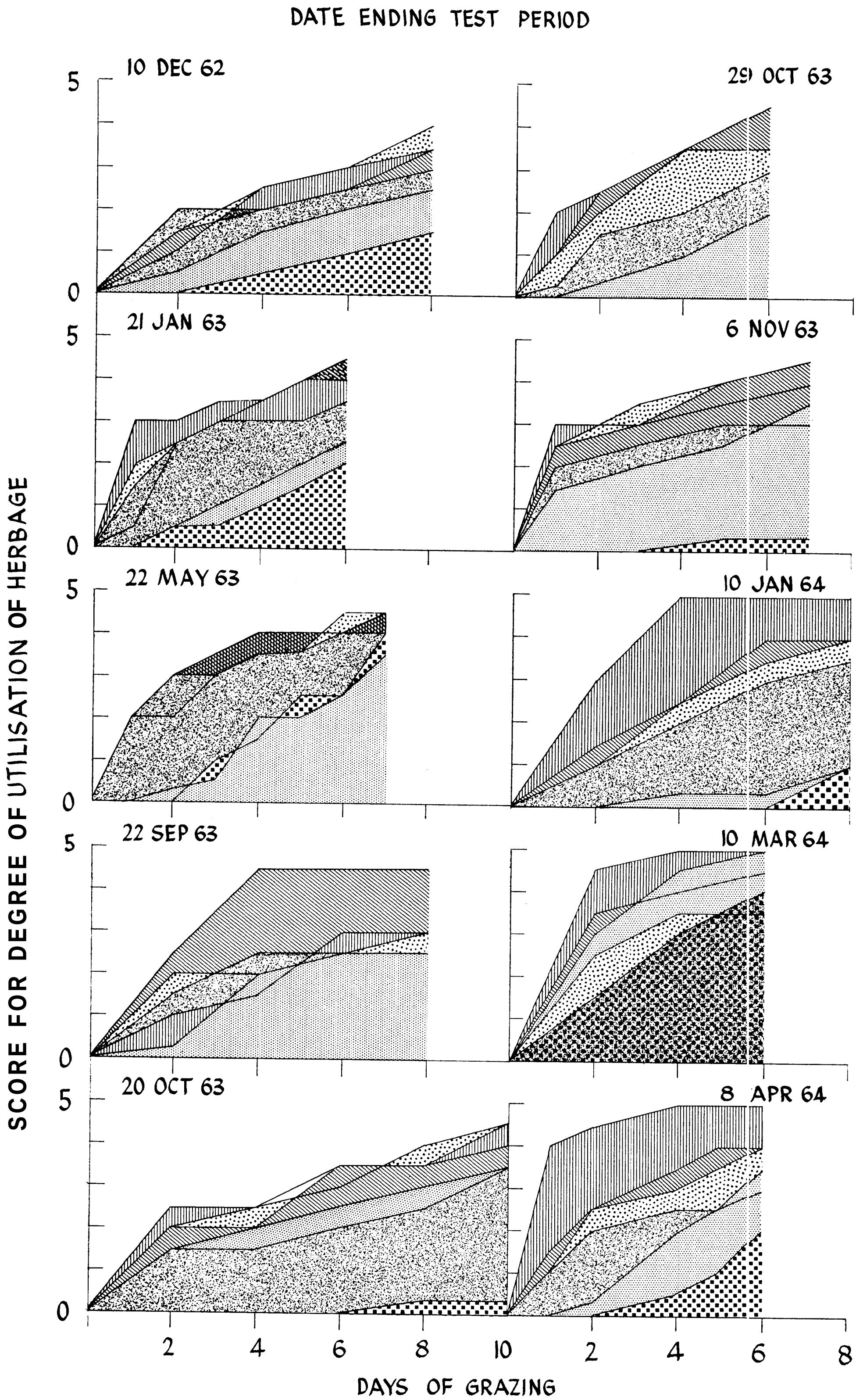
(b) Chemical composition and acceptability of strains of a species

When comparing ecotypes and cultivars of a single species for acceptability it is possible that variation in a single chemical constituent may dominate preference ranking. This has been found for reed canary grass-***Phalaris arundinacea*** (Brown 196 1) and perennial Lespedeza—***Lespedeza sericea*** (Donelly 1954). The successful breeding of more acceptable lines of species such as tall fescue—*Festuca* ***arundinacea*** (Buckner 1960) and P. ***arundinacea*** (Donelly 1954) has

Fig. 2.—GRAZING PRESSURE AND UTILIZATION OF HERBAGE. In each test, 6 sheep grazed on 1/6th ac containing eight equal areas of different species. Results are given for six species, four relatively acceptable and two relatively unacceptable. At the beginning of each test there was an abundance of feed and the most acceptable species were eaten, but as the feed supply declined, different species were eaten. Tests were carried out at different seasons of the year (periods 1-10). The three main points to emerge are (1) that preference ranking was altered little by grazing pressure, (2) that relative acceptability differences may be reduced between species at high grazing pressures, particularly within groups of high acceptability, (3) that when only a really disliked species is left to graze, sheep may prefer to starve. The stages of growth during periods 1-10 were:—

Period 1, 2 All flowering
3, 4, 5 All vegetative
6, 7 All vegetative
Period 8 All flowering
9 All vegetative except *Stipa hyalina* and *Eragrostis curvula* which were flowering
10 All vegetative




DATE ENDING TEST PERIOD
10 DEC 62
29 OCT 63
21 JAN 63
6 NOV 63
22 MAY 63
10 JAN 64
22 SEP 63
10 MAR 64
20 OCT 63
8 APR 64
SCORE FOR DEGREE OF UTILISATION OF HERBAGE
0
5
2
4
6
8
10
DAYS OF GRAZING

probably been achieved because acceptability differences between strains were linked with varying concentrations of a single chemical constituent.

(c) Physical characteristics of the individual plant

If a range of species that differ markedly in stage of growth is available, preferences will usually be for the species with the least mature herbage; this may be associated with degree of lignification in relation to ease of harvesting.

Hairiness, thorns, etc., on plants tend to depress acceptability just as glabrousness and crispness enhance acceptability (Davies 1925). However, there is no direct experimental evidence to show the extent to which such characteristics influence preferences.

Habit of growth can also influence preferences because it affects accessibility (Davies 1925; Elder 1959).

(d) Physical composition of the plant community

The "availability" of a species within a plant community will influence its acceptability. That is "availability" in terms of frequency of occurrence, relative

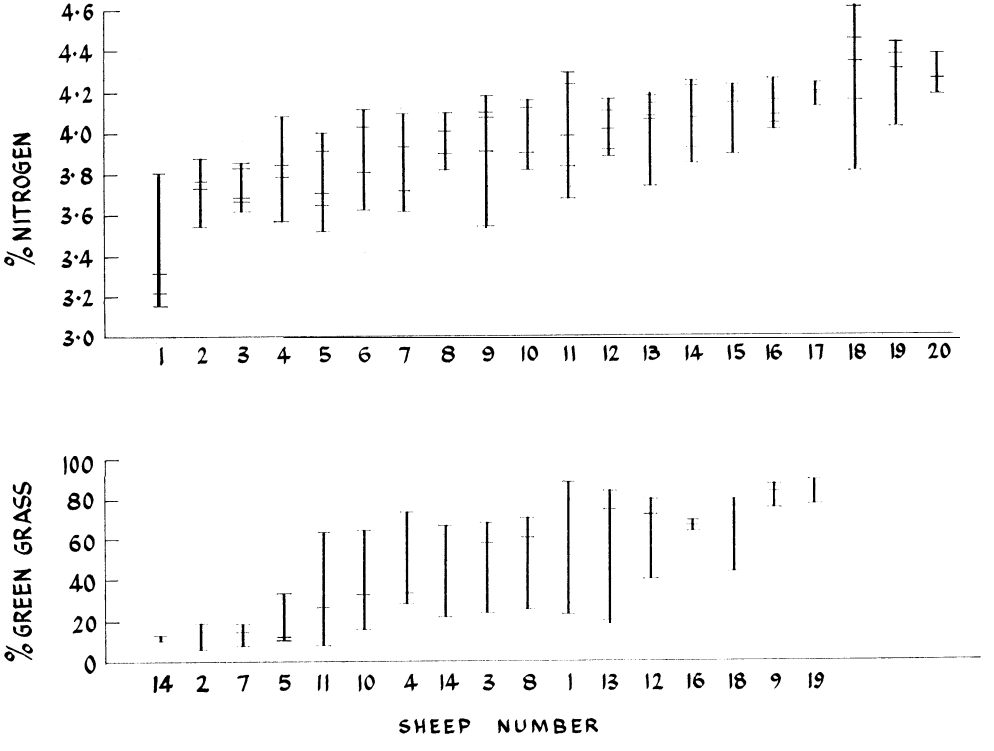


Fig. X-VARIATION IN DIET SELECTED BY SHEEP. A flock of sheep with oesophageal fistulae grazed on a pasture expected to produce a wide variation in diet composition between individuals. The pasture yield was 2500 lb dry matter per ac (2800 kg/ha) mainly of dry grass and dry clover, but with a "pick". of green grass. As the stocking rate was low, food availability changed little during the test of 7 days; diet samples were obtained up to five times during the 7 days. The horizontal bars represent the % nitrogen or % green grass in single samples. The vertical lines indicate the range of values in the individual sheep, numbered 1 to 20. The sheep are arranged in ascending order of mean values of % nitrogen and % grass.

yield and accessibility, and as influenced by the nature of surrounding plant material. Thus the acceptability of low preference ranking species is higher when there are few plants of the species in a community (Hooper 1962; Stoddart and Smith 1955; Tomanek, Martin, Alberston 1958). Also, the physical presence of a disliked species or the presence of dry material are detrimental to the consumption of species known to be acceptable under other conditions (Anon. 1955; Arnold 1963; Cowlishaw and Alder 1960; Glendening 1944; Milton 1933, 1953; Phillips and Pfeiffer 1958).

(e) Local environment

Soil fertility can considerably influence acceptability (Milton 1933; Hurd and Pond 1958; Cook 1959; Collett 1961; Beetle *et al.* 1961). A species with a high preference ranking in one pedological situation may have a lower ranking in another situation.

(f) Grazing pressure

Where there is an abundance of feed, the grazing animal can express its preferences freely. As the feed supply decreases, the animal must eat less acceptable plant material or starve. In effect, the animal appears to compromise so that whilst eating previously neglected species a high proportion of its total grazing time will still be spent on favoured species of low accessibility. This type of situation is illustrated in Figure 2.

(g) Summary

In selectively grazing, it appears likely that the animal balances favourable and unfavourable chemical and physical characteristics of all available material (or species) to determine relative acceptability of the components (or species) of

TABLE 1

Reactions of one year old Merino wethers, differing in experience, to eight plant species

Species	Score for Degree of Utilization†			
	Group 1‡	Group 2‡	Group 3‡	Group 4‡
Phalaris tuberosa	2·5	3·5	2·5	2·5
Medicago sativa	3·5	2·0	4·0	4·5
Trifolium subterraneum	3·5	4·0	3·5	3·0
Bromus mollis	1·0	1·0	1·0	1·0
Eragrostis curvula	1·0	1·0	2·5	2·5
Dactylis glomerata	2·5	2·5	4·0	3·5
Stipa hyalina	1·5	1·0	2·0	2·0
Lolium perenne	2·5	2·0	3·5	3·0

†The sheep were pen fed for three weeks after being brought from their rearing environments. They then entered the test area (see legend to Fig. 2) for the species preference test. Each species was scored daily for degree of utilization on a scale 0-5. This scale has been shown to be related linearly to percentage utilization of available dry matter (Arnold 1963).

‡Group 1. Reared at Trangie, N.S.W., on native pastures, improved annual pastures and lucerne. The pastures differed widely in physical and chemical characteristics.

Group 2. Reared on *Phalaris*-subterranean clover pasture. The sheep experienced seasonal changes in physical and chemical characteristics of only two species.

Group 3. Reared on irrigated pastures at Deniliquin, N.S.W. Sheep experienced only green herbage.

Group 4. Reared on dryland pastures at Deniliquin, N.S.W. Sheep experienced a large number of species which changed little in physical and chemical characteristics. Pasture structure was quite different from that experienced by groups 1, 2 and 3.

the plant community. Although numerous factors can influence the relative acceptability of a species, individual species will remain within broad groupings of high, medium or low acceptability.

III. ANIMAL CHARACTERISTICS AFFECTING PREFERENCES

(a) Individuality

Not only are there differences between species of grazing animals in selection preferences, but there is considerable variation between individuals of a flock or herd. This is illustrated in Figure 3. This figure shows how individuals may select from 10% to 80% grass in their diets when grazing together on the same small pasture (three acres). This sort of animai variation is always encountered and means that even though one species in a community is generally favoured in a particular season, there will usually be some consumption of other species.

(b) Previous grazing experience

Preference ranking of species can be strongly influenced by the previous grazing experience of the animals. This is illustrated in Table 1 which gives the immediate reactions of four groups each of six sheep, of identical breeding but differing in experience in the first year of life; eight species were presented. It has been found (Arnold, unpublished data) that differences in acceptability of generally liked species (perennial ryegrass-Lolium ***perenne,*** cocksfoot—*Dactylis glo-****merata,*** phalaris-Phalaris ***tuberosa,*** lucerne—*Medicago* ***sativa)*** between these groups of sheep disappear after two or three tests, but that differences in acceptability of generally disliked species (a speargrass-Stipa ***hyalina*** and African love ***grass-Eraqrostis*** *curvula*) persist until the sheep are forced to graze exclusively on the species for at least a month. Differences such as those shown in Table 1 canoccur by three months of age.

(c) Special senses

There is little work to show that the special senses are involved in selective grazing. Preliminary studies by the author- (Arnold 1963) have shown that sight allows the sheep to recognise plants it has experienced previously and to orientate itself within its environment. Sight plays only a minor role in determining either species of plants or plant parts eaten (Arnold 1963).

TABLE 2

Differences in acceptability of herbage species between normal and sense impaired sheep

Date	Sense Removed	No. of Species Showing Significant Changes Due to Sense Deprivation† Increased (+)	Decreased (—)	No Change (0)
6·11·62	smell	13	2	9
21· 1·63	smell	3	13	5
8·10·63	smell	12	6	19
27·11·63	smell	12	9	9
5· 9·63	touch	7	10	13

†The test area had microswards (36 sq ft or 3·34 sq m) of the different species set in red clover (*Trifolium pratense* L.). This allowed free choice of red clover or the species on offer. Species were scored for degree of utilization.

In the four tests with smell-deprived sheep there were 21 species common to each test. No species gave only (+), (—) or (0) in all four tests. Five species gave either (0 or +) and 4 species (0 or —). The remaining 12 species gave (0, + and —) in different periods.

TABLE 3

Changing acceptability of Medicago sativa during spring growth

Date	Normal	Relative Acceptability in Sense Deprived Sheep Smell Deprived	Taste Deprived	Touch Deprived
10· 9·63	25	100	50	25
16· 9·63	22	100	89	56
19·10·63	63	100	50	50
24·10·63	71	100	71	86
30·10·63	100	100	100	100

Each of the senses of smell, touch and taste is involved in selective grazing (Arnold 1963). Table 2 shows that the relative acceptability of a large number of species differs for sheep with or without either the sense of smell, or the sense of touch in the lips. Thus deprivation of a sense will result in increased acceptability of some species, decreased acceptability of others with no change in acceptability in a further group. This indicates that a sense is important in deciding the acceptability of some species, but not that of other species. In other words, some species have constituents producing favourable or unfavourable stimuli to the sense, others do not.

(d) Response of animal to changing plant composition

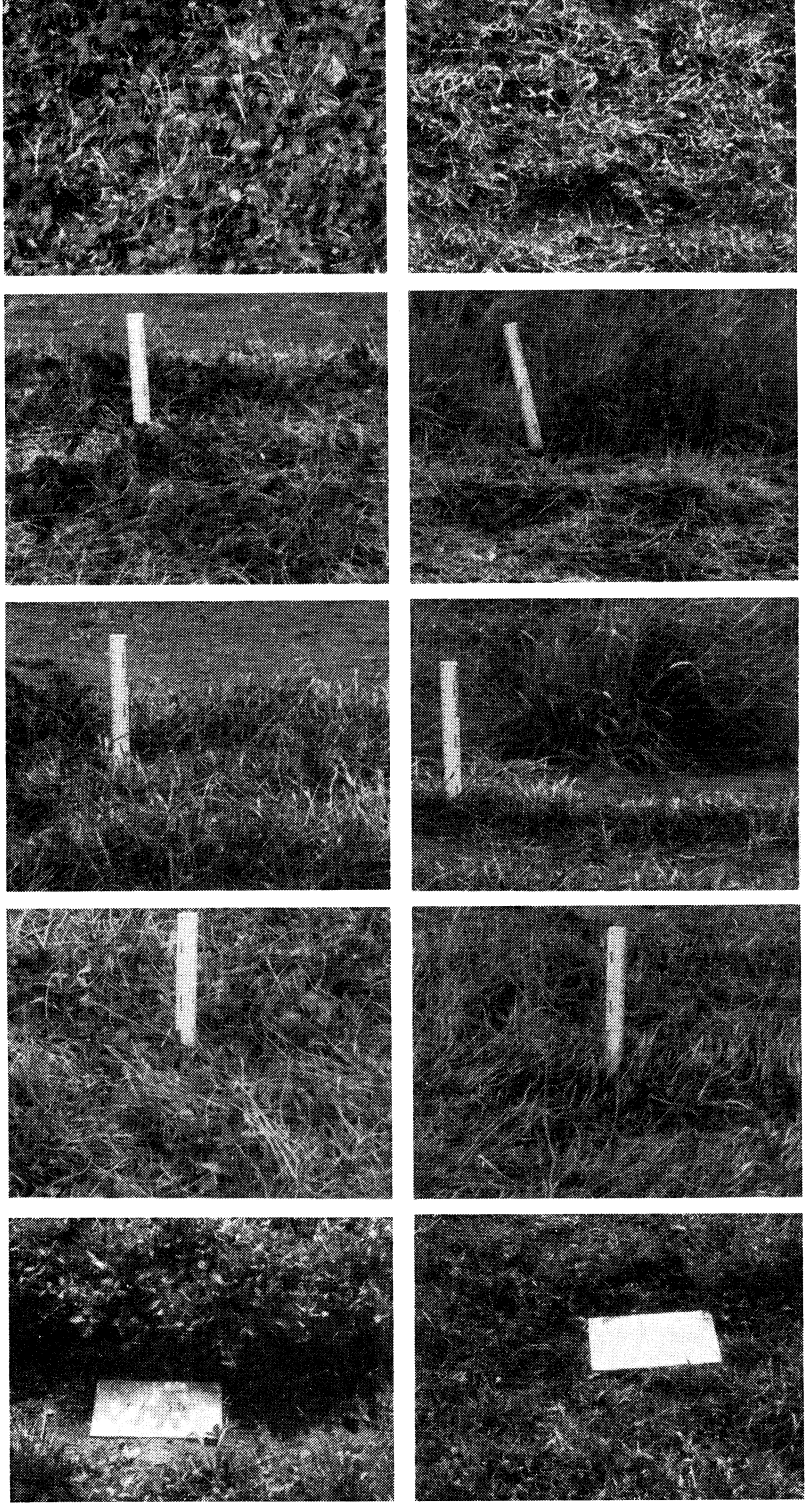
There is not a fixed reaction to a particular species, but changing reactions from season to season. This is shown in Table 2 where the proportion of species changing in acceptability consistently in one direction to smell-deprived sheep is low. It is illustrated more clearly in Table 3 which shows how the acceptability of *Medicago sativa* is low in early spring, due to an unfavourable smell, but that this changes with time until the species no longer gives an unfavourable smell-stimulus. by late spring. This trend is found in many legumes (Arnold 1963) and the magnitude of the effect is illustrated in Figure 4.

Current work should indicate the chemical constitutents of plants that are recognised by the senses of taste and smell. It is not proposed to consider how physiological need of the animal may modify preferences-mainly because of the paucity of evidence.

(e) Nutritional wisdom

There is a great deal of evidence in the literature to show that most mammals, exhibit very little nutritional wisdom. That is, numerous experiments have shown that animals will selectively eat a palatable but poor quality food in preference to an unpalatable nutritious food even to the point of death. There is very little evidence for grazing animals. It has been shown (Gordon and Tribe 195 1) that-sheep cannot select a diet adequate for bearing and rearing a lamb from basic milled foodstuffs and that grazing sheep and cattle fail to correct a phosphate deficiency when given the opportunity (Gordon, Tribe and Graham 1954).

On the other hand it has been shown by Denton and Sabine (1963) that Na^+ deficiency in sheep is rectified very precisely when Na^+ solutions are available.. Recently the author found that Na^+ deficient sheep will preferentially select those herbage species high in Na^+, independent of the normal preference ranking of the species (Table 4). Thus we return to the question of motivation in selective grazing. It would seem that innate reactions mainly determine selection by the:



1 *Trifolium repens*

2 *Trifolium subterraneum*

3 *Trifolium hybridum*

4 *Trifolium fragiferum*

5 *Trifolium pratense*

Grazed by normal sheep

Grazed by sheep without sense of smell

TABLE 4

Ability of Na+ deficient sheep to select Na+ rich species

Composition of Total Forage Eaten (%)† by Normal Sheep "N" and Na+ Deficient Sheep "P"‡

Period	*Dactylis glomerata* N	*Dactylis glomerata* P	*Stipa hyalina* N	*Stipa hyalina* P	*Eragrostis curvula* N	*Eragrostis curvula* P	*Phalaris tuberosa* N	*Phalaris tuberosa* P	*Lolium perenne* N	*Lolium perenne* P
(1) 19-23/10/63	17·6	13·9	11·7	16·7	0	0	17·6	16·7	9·8	11·1
(2) 24-29/10/63	21·1	12·1	7·9	8·0	0	0	15·8	28·0	15·8	24·0
(3) 30/10-6/11/63	15·8	6·9	13·2	0	0	0	18·4	31·0	10·5	17·2
Mean	18·2	10·9	10·9	8·2	0	0	17·3	25·2	12·0	17·4
Difference		—7·3		—2·7				+7·9		+5·4

Minerals in Leaf Material (%)

	Dactylis glomerata	*Stipa hyalina*	*Eragrostis curvula*	*Phalaris tuberosa*	*Lolium perenne*
Na	0·02	0·14	0·03	0·77	0·85
K	0·28	0·16	0·11	0·44	0·16
Ca	0·30	0·29	0·29	0·29	0·25
Mg	0·43	0·26	0·28	0·47	0·48

†Sheep had free choice of the five species and were moved to a new area for each period. Feed supply was never limiting. Composition of the forage eaten was calculated from the scores of utilization. Na+ supplement was withheld for 10 days from sheep with parotid fistulae, prior to period 1. As Na+ deficiency increased, the sheep grazed more on Na+ rich species.

‡P = sheep with parotid fistulae.

grazing animal and that these innate reactions have developed during the evolution of each species.

Sheep evolved in an environment where mature plant material was more frequently available than green herbage. Survival would depend on selection of readily digestible plant material containing adequate protein, i.e. material of low lignin content.

Results from recent studies, using sheep with oesophageal fistulae (Arnold 1963), show clearly that sheep are extremely selective for green herbage in preference to dry herbage. This, and the preference for leaf to stem, is nutritionally advantageous in many situations. However, on luxuriant improved pastures, selection in this direction, which always occurs, means that the sheep acquires a diet that is protein rich and low in readily fermentable carbohydrates (Arnold 1963). On the other hand, Arnold (1964) has shown that on dry herbage from an improved pasture of *Phalaris tuberosa* and *Trifolium subterraneum* the protein content of residual herbage *increases* with progressive defoliation. The sheep do not select the legume component at a time when this could be nutritionally advantageous.

The above evidence lends little support to the hypothesis that selection of a diet is motivated by nutritional wisdom in grazing animals. The example of selection of Na+ rich plants is a rare exception. Thus it may be that sheep actively

Fig. 4.—Change in grazing behaviour of sheep due to deprivation of sense of smell.

TABLE 5

Reaction of one year old Merino wethers to different pasture species

Pasture	Green Herbage† Per Unit Area (lb/ac)	Green Herbage as % of Total Available† (%)	Mean Leaf Length (mm)	Daily Organic‡ Matter Intake (kg)	Digestibility of Ingested Organic Matter (%)§	Daily Digestible Organic Matter (g)		Relative Preference Ranking$
Lolium perenne	1666	97·8	94	1·15	79·1	908	(100)¶	79
Dactylis glomerata	1469	82·6	93	1·12	79·4	809	(89)	89
Phalaris tuberosa	1875	86·8	118	0·93	77·5	719	(79)	79
P. tuberosa + Trifolium suberraneum	3771	94·1	103	0·92	78·5	769	(85)	—
T. subterraneum	2978	99·3	92	0·76	71·8	546	(60)	100
Medicago sativa	2801	92·5	234	0·93	77·0	713	(79)	100
Native pasture	586	36·6	110	1·01	65·6	665	(73)	—

†On dry matter basis (D.M.).

‡Intake test was of 4 days duration following a 7 day preliminary period.

§Digestibility of the diet and intake were estimated from the *in vitro* digestion of diet samples collected through oesophageal fistulae. The following equation was used for calculating intake:—

$$\text{Organic matter intake (OMI)} = \frac{\text{Organic matter output}}{100 - \text{Digestibility \% of diet}} \times 100.$$

$Preference ranking test based on free choice of eight species which included five of the species used — test conducted at the same time as the above intake test.

¶Relative digestible organic matter intakes.

select green plant material rich in protein and low in lignin. It is doubtful, however, that sheep can recognise "protein" and "lignin" ***per se,*** The selection of such material must be achieved through recognition of undefined chemical characteristics in the cell sap of plants. This selection is probably motivated through the special senses and it is suggested that these are innate reactions. Dove (1935) summed up the situation very well, many years ago, when he said-"Survival in the past has depended upon the nature of the choice of food. However, the instincts themselves are not always wise, i.e. do not always result in optimum results."

IV. PREFERENCE RANKING AND FOOD INTAKE

Grazing of any plant community will always result in the preferential selection of certain species at least during some part of the year. The animals will often continue to graze on preferred species even when "availability" is poor. There is a resultant reduction in intake and productivity. The question is whether the neglected species would be eaten if the preferred species were absent. In effect, we are asking whether preference ranking is related to voluntary consumption of the individual species when there is no free choice. This is a critical question and yet there is very little available information. Experimentally, this is difficult to test since other factors such as herbage yield, pasture structure and digestibility of the diet must be constant to all species under test.

Roe and Lambourne (personal communication) obtained significant differences in herbage intake for sheep grazing on different strains of ***P. arundinacea*** which ranked high or low in previous preference ranking tests.

Table 5 gives the food intakes of Merino sheep weighing 70 lb (30·2 kg) grazing seven pastures having yields which should not limit food intake. There were considerable differences in digestible organic matter intakes from pastures producing the same diet digestibility, e.g. ryegrass, cocksfoot, phalaris and lucerne. These differences could be said to reflect differences in acceptability. The ranking of species in intake does not agree with that from a free choice amongst the species.

The above example is given as an illustration of the problem of relating preference ranking of a species under a free choice situation to the relative food intake of that species where there is no choice. More evidence is required from similar tests.

V. CONCLUSION

It is apparent that selective grazing is a complex of interacting factors to which there is no single key. The progressive improvement of pasture and range management is closely linked with an appreciation of the basis on which the grazing animal chooses a diet.

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