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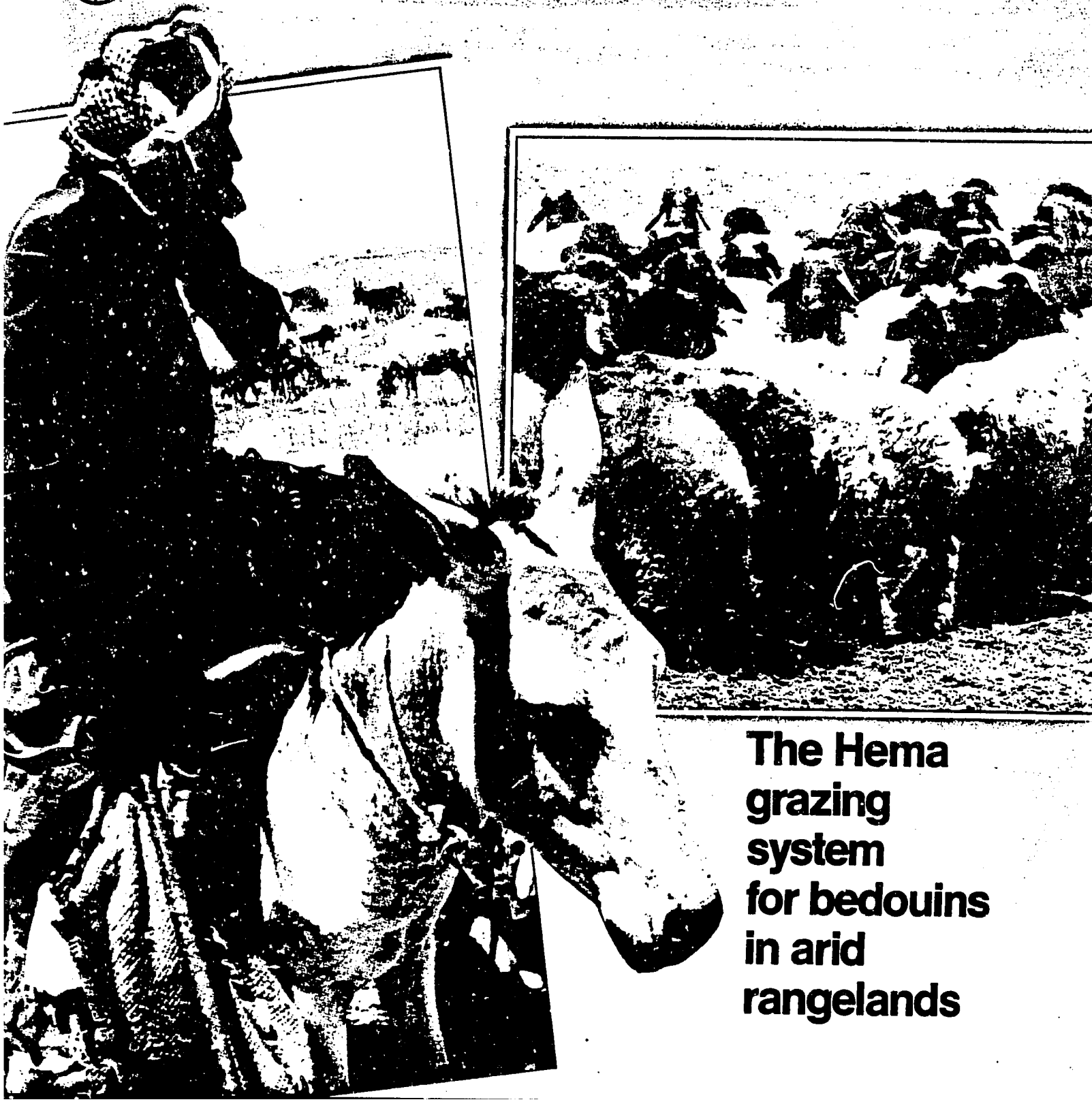
ISN 24459

WORLD
animal
REVIEW a quarterly journal on animal health, production and products —1983 47



The Hema grazing system for bedouins in arid rangelands

FEEDING BEHAVIOUR AND NUTRITION OF GOATS ON RANGELANDS

• J.C. Malechek and F.D. Provenza

During recent years there has been a steadily increasing interest in the goat. As the article states, however, probably less is known about this animal in relation to its numbers and economic importance than any other livestock species.

The capacity of the goat to thrive and produce under poor environmental conditions and its potential for improvement are increasingly becoming recognized.

This article is a valuable contribution to the knowledge of goats on rangelands and to the research necessary in order to improve productivity in this type of environment.

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The authors wish to acknowledge the contribution of ideas and information from Dr Hamid Narjisse, Ecole nationale d'agriculture, Meknes, Morocco and Mr James Pfister, Small Ruminants CRSP Project, CNPC/EMBRAPA, Sobral, Ceara, Brazil.

DAN-1282-G-SS-0282-00

The majority of goats in the world exist on rangelands. Over 90 percent of the world's estimated 400 million head are located in the less developed countries (Fitzhugh *et al.*, 1978). Their husbandry and management are based in large part on traditions passed down from generation to generation. In some situations, exquisitely designed and effective management systems have evolved. However, with increasing human and animal population pressures, diminishing grazing resources, and changes in traditional social systems in many pastoral cultures, the need for scientific management is becoming critical. Of the important domestic animal species, probably less is known about the goat in relation to its numbers and economic importance than any other livestock species.

On the other hand, no other domestic animal species has been subjected to so much myth, malignment and misunderstanding as the goat (French, 1970). A possible extreme in this regard was the campaign mounted by some countries to eradicate the goat because it gained the reputation (unjustly in the authors' opinion) as a despoiler of forests and rangelands. Fortunately for the large number of poor people who depend mainly on the goat for survival, none of these campaigns succeeded. An awakening has apparently occurred during the past decade to the fact that overgrazing is the result of *excessive animal numbers* and that all domestic grazing animals have the capacity to overgraze if not managed intelligently (Owen, 1979; Norris, 1982).

There also seems to be a growing realization that the goat, simply because it is often the last species in a progression of ruminants (both wild and domestic) to be displaced from severely deteriorated areas, is not always the sole culprit in overgrazing. While its adaptability to harsh conditions makes the goat an ideal candidate as a food-producing animal in marginal areas, it does emphasize the great need for information on how best to utilize its traits and particularly how to manage it in ecologically sensitive environments.

Feed selection by goats on rangelands

In contrast to stall-fed animals that receive their rations in amounts and proportions dictated by the husbandman, range animals are free to choose their diets from the complex variety of forage plants available in most native plant communities. Man exerts only limited managerial control through such decisions as season and location of grazing, stocking rates, and herd composition. The diet ultimately selected in a particular situation is a function of many interacting and poorly understood plant- and animal-related factors. Certainly, characteristics of individual plants which broadly influence their acceptance or rejection play a major role. These characteristics determine the plant's palatability (Heady, 1964). Then there are also the unique morphological, physiological and behavioural traits of a particular animal species that interact to determine the animal's feeding strategy, or the approach used in exploiting the available feed resource. The aggregate effect of all these is

Figure 1. *Meraz goats, Iraq*

manifested in the feeding behaviour termed "selectivity": the response of the animal in choosing one or more plant species (and plant parts) from an array.

Palatability and diet selection processes

Factors that relate to a plant's palatability include its chemical make-up, particularly the presence of so-called "secondary" plant metabolites such as tannins, volatile oils, alkaloids and others. Commonly recognized nutritional fractions such as crude protein, fibre and fat are also related to plant palatability, but probably only in a correlative sense. Arnold and Hill (1972) pointed out that the receptors involved in the senses of taste (gustation) and smell (olfaction) can detect chemical substances only at the molecular level and animals have no means of recognizing such proximate components as "crude protein" or "fibre" *per se*, since such components are complex mixtures of many chemical compounds. Anatomical features of plants, such as thorns, awns, prickles, dense pubescence and textural features also affect a plant's palatability, but their importance is not clear and would certainly affect goats differently from cattle, for example.

The selectivity by grazing animals of certain plant species in relation to others is in part determined genetically, in part by prior experience or conditioning, in part by the animal's prevailing nutritional and physiological state, and in part by environmental circumstances, including the relative availability of various plants from which the choice is made. Both palatability and selectivity as the terms are commonly used are relative, being influenced by the array of choices available in a given situation.

Some evolutionary ecologists consider animals' dietary habits to be expressions of optimization processes involving time and effort spent in relation to energy harvested in the process of feeding (Emlen, 1966). Others (Westoby, 1974; Pulliam, 1974) consider grazing selectivity as an optimization of total nutrient balance. The implication of both schools of thought is that natural selection, in the evolutionary sense, will favour those genotypes which are the most efficient feeders in a given environment. The original work on this theory has been based primarily on insects, birds and small mammals. Only recently has consideration been given to wild native ungulates (Jarman

and Sinclair, 1979) and domestic animals (Zahorik and Houpt, 1977). The strict application of this theory to domesticated species is questionable where man's intervention is longstanding. However, it offers, at least, a framework for experimentation and hypothesis testing that has not previously existed in domestic animal research. It also offers a theoretical basis for explaining the broad differences commonly observed in the kinds of foods selected by various ruminant species. Upon this basis, Van Soest (1982) has classified goats as "intermediate feeders", preferring forbs or browse to bulkier roughages consumed by larger herbivores such as cattle.

Gustation and olfaction in the goat

Sensory thresholds for particular chemicals are one of the major genetically determined features that influence animal dietary selection. Church (1979) reported sensory thresholds for goats and other ruminants relative to the four basic taste sensations: sweet, salty, bitter and sour (acid). His data indicated that goats were intermediate in ranking with respect to cattle, sheep and deer in both their sensitivity to and rejection of sweet, salty and sour taste sensations. However, they were both more sensitive to and more tolerant of bitter substances than were the other animals tested (see Table 1). High sensitivity indicates that a particular compound can be detected at very low molecular concentrations, whereas high tolerance indicates that a particular compound will be accepted at relatively high concentrations. Hafez (1968) credited the browsing habit of goats to the evolutionary development of taste receptors with high thresholds to bitter substances, implying that browse plants contain higher concentrations of such chemicals than do other forage species. This, in general, agrees with current theory on evolution of chemical defences by plants, in that certain secondary compounds such as alkaloids and tannins tend to evoke bitter sensations (Arnold and Hill, 1972). In the case of tannins, however, uncertainty exists as to whether the sensation is one of bitter taste or the result of astringent action upon the mucosal epithelium of the mouth which could be interpreted as a touch rather than taste sensation (McLeod, 1974).

Genotypic variation within the species (*Capra hircus*) is undoubtedly important in determining sensory thresholds. For example, Church's (1979) findings (see Table 1) indicate a breed difference between "pygmy goats" and "normal goats". Researchers in Texas (Merrill and Taylor, 1976) observed that the Angora goat tended to be a less effective browser than the Spanish goat when the two breeds foraged on common range, but the implication was that this resulted from a generally "stronger constitution" of the Spanish goat rather than genetic differences in selectivity patterns. In contrast, Bryant, Kothmann and Merrill (1979) found no dietary differences between Spanish and Angora goats that indicated true differences in selectivity. Both genotypes were equally effective in exploiting the forage resource for crude protein and digestible energy (Bryant, Kothmann and Merrill, 1980). More recently, Warren, Ueckert and Shelton (1982) presented preliminary evidence indicating that Angora goats selected appreciably more grass and less browse than did Spanish goats while grazing on common ranges. Averaged over three separate plant communities, the diets of Angora goats contained 54 percent grass and 33 percent browse, compared to 33 percent grass and 55 percent browse in the case of Spanish goats.

TABLE 1. **Relative sensitivity to and tolerance of a bitter-tasting substance by different ruminant species**

Compound	Rank
Quinine *HCl*	
☐ Sensitivity	Pygmy goats = normal goats > deer > sheep = cattle
☐ Tolerance	Pygmy goats > normal goats > deer > sheep = cattle

Source: Church (1979).

Variation among individual animals in a particular flock of goats is not well documented, but it is probably large. Arnold and Hill (1972) indicated that much variability existed among individual sheep of a breed in response to flavour threshold tests. They attributed ecological significance to this variation because the individual animal is not restricted in its food selection by rigid preferences and aversions. When this variability is considered on a flock or population basis, the significance would be greater, i.e. the likelihood of direct competition for food is greatly reduced. Moreover, grazing pressure on the range is extended over a broader array of plant species, reducing the probability of plant community successional changes. Notwithstanding these advantages, animal variation is a major problem confronting the scientist who researches feeding behaviour and diets, as high variation implies a need for large sample numbers to detect differences between treatments. More attention is needed in quantifying individual animal variation in goat diet studies and more effort should be directed toward explaining its occurrence.

Little is known about olfactory responses in grazing ruminants in general, and almost nothing about goats in particular. Arnold and Hill (1972) conducted experiments on sheep which indicated that the sense of smell was critically involved in food selection, probably in a complex interrelation with the sense of taste. In a recent work, Arnold, de Boer and Boundy (1980) showed that sheep confronted with an array of pure chemical solutions in an odour preference test initially rejected cedarwood oil, tannic

Figure 2. *Bipedal stance of goat*

acid, propionic acid, and amyl alcohol, but later adapted to these odours. In taste preference tests, tannic acid and gramine reduced consumption of a basal diet; both also reduced *in vitro* digestibility. Comparisons of anosmic sheep and goats (i.e. animals lacking a sense of smell) by Narjisse (1981) suggested differences in sensory modes in the two species. Goats tended to reject mixtures of monoterpene hydrocarbons based on their taste while sheep made the rejection based primarily on odour.

Whether animals reject plants containing aversive compounds because of their potential malnutritional consequences or simply because they dislike the taste (or smell) remains uncertain. Rhoades (1979) pointed out that taste and smell are evolved responses to chemical compounds that have either noxious or beneficial qualities. Arnold (1970) maintained that evidence was insufficient to reject the hypothesis that grazing animals are *hedyphagic* feeders, i.e. they seek to maximize pleasurable sensations. The counter-hypothesis was that grazing animals exercise *euphagia*, i.e. nutritional wisdom. Probably, a clear distinction between the two modes will never be possible. Through co-evolution of plants and animals, correlative relationships between taste preferences and nutritional consequences presumably developed. Man's genetic selection in domestic animals for numerous reasons other than as a means of survival has probably masked many of these relationships to the point where they may no longer be evident except in extreme cases. Nonetheless, this is an area where well-designed research might enhance our knowledge of such practical problems as poisonous plant management and selective breeding of animals for utilization of particular kinds of plants.

Morphological features of adaptation

Several morphological factors related to foraging behaviour apparently contribute to the goat's successful adaptation to a broad variety of environmental conditions. These include a mobile upper lip and the ability to assume a bipedal stance in feeding (see Fig. 2). Among domestic ruminant species, goats alone appear to possess this latter trait. However, no research is available, as far as the authors know, that has specifically tested whether a bipedal stance would confer a competitive advantage on goats. Intuition suggests that the ability to forage overhead would in-

Figure 3. *Angora goat with oesophageal fistula used for collections of representative dietary samples from the range*

crease the biomass of forage available in woodlands and shrublands, provided the overhead species were palatable. Probably the greatest advantage would occur during dry seasons when ground-layer forage is either dry or depleted from grazing and decomposition. The tendency of some deep-rooted trees and shrubs to maintain persistent leaves during drought periods would seem to offer a nutritional advantage to a herbivore capable of utilizing such forage. Specific research is needed to document this hypothesis and to quantify the advantages, if any. A situation where sheep and goats graze together would be appropriate for such experiments.

Arnold (1970) stated that grazing sheep move in a horizontal plane but select food in a vertical plane. Crocker-Bedford and Crocker-Bedford (1977) reported that on rangelands in southern Tunisia where sheep and goats grazed together, goats tended to select the tallest species while sheep grazed the shorter ones. In this situation, however, the tallest plant did not exceed 2 m in height, and most were shrubs of 1 m or less. Even in this situation, where overhead browsing was not a major consideration, the tendency for sheep and goats to stratify their forage selection in horizontal planes is interesting and needs investigation. It also points to the limitations of studies where interspecific competition is evaluated entirely on considerations of dietary overlap. Squires (1982) addressed this point in his recent paper on dietary overlap between sheep, cattle and goats grazing in common. Even though diets may be similar, competition is not important if animals partition the food resource spatially.

Diet studies in perspective

During the past two decades, considerable information has accumulated in the literature on animals' dietary habits. Most of this information provides a listing, by species or plant groups (i.e. grasses, forbs and shrubs), of plants eaten by various animals under different environmental conditions. Usually the contribution of a particular plant species or group to the diet is expressed as a percentage of the whole diet. Numerous techniques have been employed to gain this information, but the following list, after Van Dyne *et al.* (1983), includes the most common:

- observation of free-roaming or tethered animals, using bite counts or feeding minutes to quantify the relative amounts of different species selected;
- use of oesophageally and ruminally fistulated animals to collect samples of grazed forage, followed by laboratory analysis of the ingesta samples (see Fig. 3);
- killing of animals followed by botanical examination of their rumen contents;
- microscopic examination of faeces collected from rangelands, with analysis based on undigested cuticular residues.

The relative utility, advantages and disadvantages of these (and other) methodologies were reviewed by Theurer, Lesperance and Wallace (1976).

Generalizations from these so-called "diet studies" are difficult, because virtually all have been conducted under conditions of different plant availabilities. Consequently, the results tend to be site-specific and offer little, if any, basis for formulating principles of diet selection. Despite such limitations, these studies, when applied to the site from which the data originated, have provided range managers with a partial basis for making management decisions and

ecologists with a first approximation for explaining plant community relationships as affected by grazing.

Relatively few such studies have been conducted on goats. Van Dyne *et al.* (1980) recently published the most comprehensive review available on dietary habits of large, free-grazing herbivores. Their review covered some 668 separate entries, including 43 animal species worldwide. Only 21 data entries were reported on the diets of goats, compared to 110 for sheep and 119 for cattle.

A summary of their findings for sheep and goats is provided in Figure 4. This includes only studies that reported diets on a year-long basis, so that the number of data points is a subset of the 21 data entries for goats cited above. Generalizations from these graphs are that goats select about 60 percent shrubs, 30 percent grass and 10 percent forbs, compared to sheep which select about 20 percent shrubs, 30 percent forbs and 50 percent grass.

Summaries of data such as those in Figure 4 are valuable only in a general way, since they obscure seasonal variability and offer no insight into the particular plant species or plant parts consumed. Most studies show large seasonal variations in diets selected by goats. The knowledge that animals depend, for example, on a certain class or species of forage during a critical season is more important in managing those animals than merely knowing their average yearly diets. Taking this argument one step further, Harrington (1978) correctly stated that considering dietary data as forage classes (grasses, forbs, shrubs) also obscures the important fact that animals "select their diets on a plant species basis irrespective of the type of plant". Therefore, future studies should give paramount consideration to analysing and reporting diets at the species level. Equally important is a detailed, quantitative description of the available forage. However, in the meantime, such information as does exist should be used to the fullest extent of its inferential value, but certainly with care and caution.

Seasonal variation. Several dietary studies reviewed were designed to show important temporal variation, either seasonally or monthly. However, the patterns of variation differ greatly from study to study because of the differences in prevailing forage conditions. Even under similar pasture conditions, year-to-year climatic differences can cause major departures in dietary trends. For example, Bryant, Kothmann and Merrill (1979) and

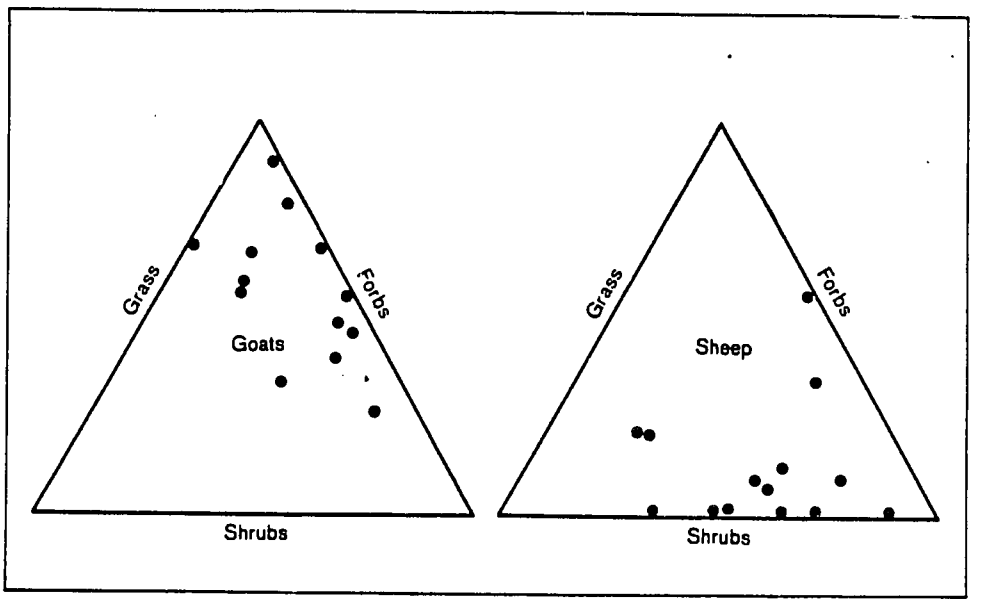

Figure 4. *Summary of botanical composition of diets of sheep and goats on a year-long basis (Van Dyne* et al., *1980). In reading these triangular coordinate graphs, the magnitude of a variable increases the further that data point is located from the axis where it is listed. A point located on any margin has the value of 0 percent for the component listed on that margin*

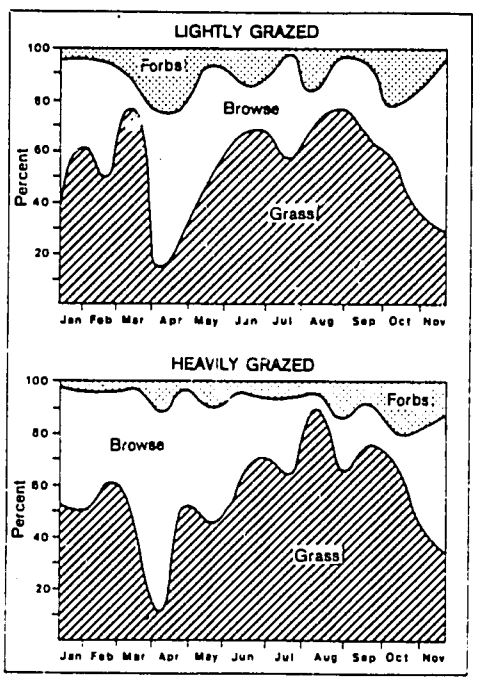

Figure 5. *Diets of Angora goats on lightly and heavily grazed range, Texas (Malechek and Leinweber, 1972a)*

Malechek and Leinweber (1972a) studied diets of Angora goats on the Texas A & M University Ranch Experiment Station in the Edwards Plateau region of Texas. Although the specific pastures utilized in the two studies were different, vegetational conditions were similar. Both studies reported remarkably similar annual means for grass (48 percent vs. 50 percent), browse (40 percent vs. 39 percent), and forbs (12 percent vs. 11 percent), and both reported a heavy reliance (generally > 50 percent) on browse during winter (December, January and February). Malechek and Leinweber (1972a) observed increased selection for browse again in April on both lightly and heavily stocked pastures (see Fig. 5) when the deciduous oak species *Quercus pungens* var. *vaseyana* leafed out. In contrast, Bryant, Kothmann and Merrill (1979)

did not report elevated dietary levels of *Quercus* or any browse species during this period. Their animals selected only about 30 percent browse in April. The major differences in the two studies were that drought conditions in the winter and spring of Malechek and Leinweber's study were particularly severe and by early April only 10 percent of the diet was green grass. When oak leaves appeared, they were sought avidly even though they are not generally considered highly palatable. In contrast, the Bryant, Kothmann and Merrill (1979) study was conducted during a year when winter and spring growing conditions were conducive to grass production and animals selected a diet of almost 50 percent grass in April.

Another interesting feature of both the Malechek and Leinweber (1972a) and the Bryant, Kothmann and Merrill (1979) studies was the heavy reliance upon grass during the summer and autumn months: roughly 60 percent for the June-October period in the former study and about 50 percent for the latter study. Browse species were generally available to animals in both situations, but the summer and early autumn periods corresponded to the time when major growth of warm-season perennial grasses normally occurs. Thus, goats apparently preferred the new growth of these grasses to the browse species. Nge'the and Box (1976), working in southern Kenya, found greater yearly use of the grass *Digitaria milanjiana* than any of the browse species on their site. These studies cast considerable doubt on the notion that goats are obligatory browsers and that grasses are not important, at least seasonally.

Seasonal dietary shifts can be abrupt, particularly in areas having distinct wet and dry seasons. The nutritional consequences of these shifts are probably great. For example, Griego (1977) reported that in southern Tunisia during late spring and early summer, winter-growing annual grasses and forbs quickly dry due to rapidly increasing temperatures and declining humidity. Dry material remaining from these plants is rapidly weathered and much of it is blown away by the wind. By midsummer, the available forage consists largely of shrubs, primarily *Rhanterium suaveolens* and *Artemisia campestris*. Over a four-week period during the spring-summer transition, annuals in the diet declined from about 74 percent to 4 percent for goats grazing alone (see Fig. 6). The decline was less for goats grazing in a mixed flock with sheep (from 32 percent to 4 percent), because a palatable shrub (*Retama raetam*) was present in the mixed flock pasture and contributed significantly to the diet while annuals were still available. Sheep were equally responsive to rapidly changing forage conditions (see Fig. 6). Crude protein levels in diets of both sheep and goats declined from about 12.5 percent to about 9.5 percent over this period. A similarly rapid dietary shift was described for goats in western Afghanistan by McArthur and Harrington (1978). There, the shift was from annual species to the shrub *Artemisia herba-alba* which, along with plant litter, provided the major summer forage. In northern Kenya, Schwartz and Said (1981) reported that flowers and fruits of *Acacia* spp. contributed up to 40 percent and 20 percent respectively to diets of goats during dry seasons. They maintained that these were important nutritional supplements to the otherwise meagre dry-season diet of browse.

Increased attention is warranted to the goat's ability rapidly to switch its diet in order to accommodate food items that may be highly ephemeral yet nutritionally important. This holds for items that may be seasonally available on a relatively regular basis, such as the fruits and flowers mentioned above by Schwartz and Said (1981), as well as items such as annual forbs which may occur only in response to unpredictable rains. For example, Harrington (1982) reported that feral goats living mainly on a browse diet in South Australia came into oestrus after rains promoted a flush of growth in ephemeral herbs.

Variation due to stocking rate. The particular grazing management programme employed can influence dietary botanical composition and, consequently, nutrition of grazing animals. Though such information is limited for goats, some indications are available. For example, Malechek and Leinweber (1972a) compared light stocking (2.5 ha per goat per year) and heavy stocking (0.9 ha per goat per year) and found no significant differences for grasses, forbs and

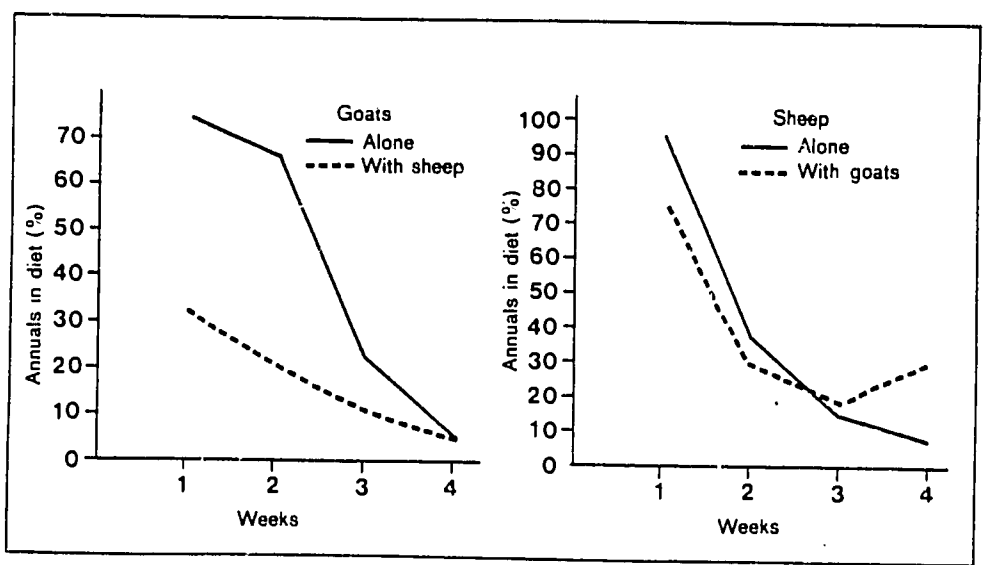

Figure 6. *Annual plant species in the diets of goats and sheep on the rangelands of southern Tunisia (Griego, 1977)*

shrubs in average year-long diets. However, a major short-term difference occurred in individual species selected during March (see Fig. 5) when drought conditions caused goats foraging on heavily stocked pasture to consume relatively large quantities of *Juniperus* sp. and *Opuntia* sp., both considered species of poor palatability. Meanwhile, goats foraging on lightly stocked pastures consumed dead grass remaining from the previous growing season.

In summary, goats appear to be extremely flexible and opportunist in their dietary habits, as suggested by numerous investigators. However, they are also fastidiously selective, being able to select particular leaves or parts of individual plants. They select more browse than do sheep, but often utilize considerable amounts of grass, particularly during the height of the growing season. The probability is large for major dietary overlap with other grass-eating species at this time, and competition may be of concern in mixed grazing schemes if forage on the pasture is generally scarce (Squires, 1982). Perennial forbs rarely contribute more than 20 percent to diets, and this quantity is apparently reduced by heavy stocking. However, the relatively minor botanical contribution by preferred forbs can often belie their nutritional importance, particularly with respect to nitrogen (Malechek and Leinweber, 1972b). Annual forbs are eaten avidly during spring in areas with a Mediterranean-type climate or whenever they happen to be available, following rains in other areas. Consumption of browse increases (dramatically in some cases) during the dry period in areas characterized by distinct wet and dry seasons. Effects of managerial measures differ from place to place but generally as stocking rate increases, goats increasingly rely upon species of poor palatability. However, even conditions of extreme forage scarcity will usually not be sufficient to force significant use of the very unpalatable species. Wilson, Molham and Leigh (1976) observed this in the case of turpentine bush (*Eremophila sturtii*) in New South Wales, Australia, and the authors observed it in the case of sagebrush (*Artemisia tridentata* subsp. *tridentata*) in west-central Utah, USA (Narjisse, 1981). Contrary to myth, there are plant species that goats virtually refuse to eat. This is a crucial point in planning schemes in which the goat is to be used as an agent in biological bush manipulation or control.

Figure 7. *Angora goats browsing tannin-containing blackbrush plants in south-western Utah. Note the compact, densely branched spinescent growth form of blackbrush. Black marks on animals' muzzles are spots where hair has been abraded from reaching into shrub canopy to obtain basal twigs*

Chemical defence in browse plants: a case study

A growing body of theory in evolutionary ecology holds that many plant species have developed complex systems of chemical defence against native herbivores (often invertebrate species). This theory offers hypotheses and approaches that may be useful in answering practical questions relating to utilization of these plants as livestock forage.

One school of thought (Rhoades, 1979) classifies native plants in two general categories based on the type of so-called secondary chemicals they employ in defence and the probability of discovery by a herbivore. *Unapparent plants* (or plant parts) include annual species, early successional species, young leaves and deciduous leaves. *Apparent plants* (or plant parts) are those with a high probability of being encountered by a herbivore and include such items as woody perennials, climax species, mature leaves, bark, stems and evergreen leaves. Chemical defences of unapparent plants and plant parts are generally present in low concentrations and act through antibiosis (i.e. they are toxic). An example is the alkaloid group. In contrast, chemicals that defend apparent plants and plant parts are generally present in high

concentrations and tend to reduce the digestibility of ingested plant tissue. Tannins and related phenolic compounds are an example of this type.

The authors have employed theory on plant defence chemistry in their studies of goat browsing in the blackbrush (*Coleogyne ramosissima*) plant community type (Provenza and Malechek, 1982). Blackbrush is a low (< 1 m) shrub that occurs in extensive and nearly monospecific stands in the southwestern United States. It contains high levels of tannins and, based on the criteria listed above, can be classified as an "apparent" plant.

The terminal twigs of blackbrush branches tend to die back for several centimetres from the tip, resulting in a spinescent growth form (see Fig. 7). Death of terminal twigs suppresses apical dominance and allows lateral twig development. As a result, blackbrush plants have a dense, diffusely branched growth form. Removal of the spinescent twigs stimulates the growth of basal and axillary buds and results in increased production of new twigs, which are more available to browsing herbivores than spinescent material on unbrowsed plants.

Goat browsing was introduced by the authors on blackbrush ranges with the objective of modifying the morphology of the shrubs so that more of their twigs would be available for cattle that commonly occupy these ranges during winter. Goat browsing began in 1977 and continued until 1979. Pastures were browsed while the plants were dormant (from January to the end of March) at three stocking intensities.

TABLE 2. **Stocking rates and utilization levels for blackbrush pastures browsed by goats in 1979**

Pasture	Stocking rate [1]	Percent utilization	
		Terminal twigs	Basal twigs
Heavy	2.0	39[a]	67[b]
Moderate	1.0	29[a]	30[a]
Light	0.5	11[a]	14[a]

[1] Animal-unit-months per hectare. Animal units were computed on a weight basis with a 454-kg cow equal to one animal unit. — [a b] Means in the same row with a different letter are significantly different (P > 0.05).

Post-browsing twig utilization was measured on two types of branches: terminal branches (on the outer edges of the plant canopy) and basal branches (sprouts and small branches growing within the shrub canopy). Ample moisture combined with heavy goat utilization during 1977 and 1978 prompted abundant twig production during 1979, especially in the heavily browsed pastures. Goats showed no differential preference for terminal or basal twigs in the lightly and moderately stocked pastures where an excess of blackbrush browse was available (see Table 2). However, they definitely preferred basal twigs in the heavily stocked pastures where total forage was limiting.

Hand-plucked blackbrush twigs which simulated material consumed by goats were assayed for tannins by the method of Hagerman and Butler (1978). This analysis confirmed that twigs produced by terminal branches of browsed plants were considerably higher in tannins than twigs produced by basal branches grown on the same plant (see Fig. 8). Goats effectively discriminated between the two types.

Just as browsing increased tannin levels, rest from browsing led to a reduction in tannins (see Fig. 8). With one year of rest from browsing, terminal twigs contained no more tannins than did basal twigs. However, even with three years of rest after one year of browsing, both kinds of twigs still contained about 60 percent more tannins than twigs on plants that had never been browsed. The change in tannin levels was largely due to a decrease in the proportion of new to older twigs. The "disappearance" of tannins as twigs aged is probably due to polymerization to compounds of high molecular weight

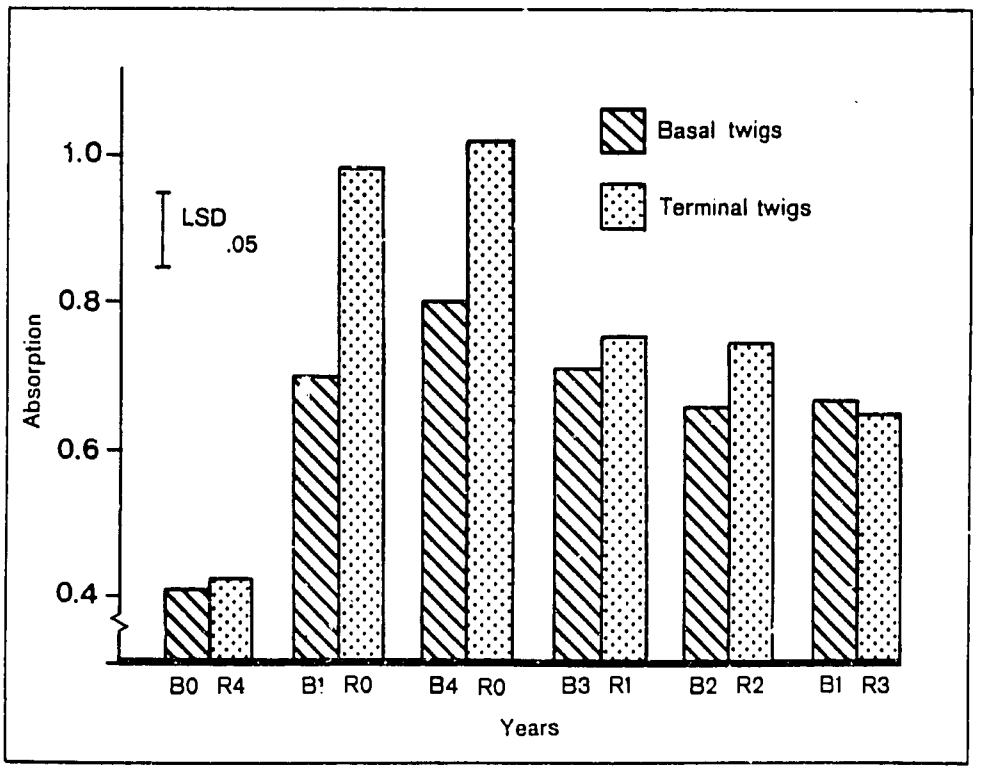

Figure 8. *Relative concentrations of tannins in the terminal and basal twigs of blackbrush plants.* B *and* R *refer to* browsed *and* rested *respectively and the numerals denote the number of years browsed or rested from browsing (Provenza and Malechek, 1982)*

that are non-astringent (Goldstein and Swain, 1963).

These findings have implications in goat production and range management where "apparent" plants are the dominant food resources as, for example, in tropical environments. New twigs, while supposedly more nutritious than older material as determined in standard chemical tests (e.g. Kjeldahl *N*, fibre analysis), are not always as palatable as older twigs. Goats, while reputedly more tolerant than other livestock species to such "bitter" components, persistently discriminated among potential feeds based on their content of tannins. Treatments (e.g. heavy browsing, lopping) that stimulate production of new plant material may be counter-productive in the short run if they result in reduced utilization of the plants. The apparently effective chemical defence system in blackbrush reduces its risk of being overbrowsed.

These findings also have important implications in studies where nutritional tests (e.g. digestion-balance trials, chemical analyses, *in vitro* digestibility) are conducted on hand-harvested browse. Results from such tests may provide only a dim picture of what the free-grazing animal would experience if it were able to use its complete repertoire of behavioural capabilities in selecting its diet in the rangeland setting. The set of hypotheses discussed in the study of blackbrush may have applicability in research on other tannin-containing browse species.

Research needs

The large and growing importance of goats reared on the world's rangelands is not reflected by a commensurate amount of scientific information on their biology, ecology and management. The following are research needs identified as justifying high priority.

Diets and feeding behaviour. Improved and more detailed research is needed on environmental and management-related factors that influence diets selected by the free-grazing animal. Given the reputation of goats as opportunist yet highly selective feeders, attention should be given to evaluating the occurrence and nutritional importance of so-called "minor" feeds such as fruits, flowers and ephemeral forbs. The ability to exploit quickly such feeds when available may provide goats with a key advantage over other livestock species. This will necessitate the use of intensive sampling designs and such technology as the oesophageal fistula (see Fig. 3) which is expensive but superior to other methods. Analysis should be at the level of plant species (and parts) rather than at broad plant groups.

Secondary phytochemicals. The effects of these compounds, particularly tannins, on diet selection and animal nutrition need clarification. Particular attention should be given to tannins and nitrogen nutrition, considering that those plants often considered valuable sources of dry-season dietary protein (i.e. evergreen trees and shrubs) are also the most likely to contain high levels of tannins. Tannins can make a significant impact on the nitrogen nutrition of goats (Nastis and Malechek, 1981).

Diet selection and nutrition. Better information is needed at all levels on how dietary botanical composition affects the nutrition of goats. However, a particularly glaring void in the literature relates to mineral nutrition. Improved sampling methodology is needed to overcome the limitation on use of the oesophageal fistula imposed by salivary mineral contamination of samples.

Grazing management. Such basic questions of applied management as proper stocking rates and effectiveness of mixed-species grazing schemes require answers in most goat-producing areas. However, statistically valid grazing trials are very expensive in land, labour and animals, and are necessarily long-term. Smaller-scale experiments that address specific hypotheses on plant-animal relationships offer high potential in yielding information that can form the basis of true principles, and often with a much smaller economic investment. This kind of research necessitates the use of theories and hypotheses from the ecological sciences, integrated with the techniques and approaches of the familiar animal production sciences.

Conclusions

Goats differ fundamentally from sheep and other livestock in their sensory physiology and in several morphological traits that appear to render them particularly well adapted to utilization of leaves, buds and fruiting bodies of woody plants. They are highly flexible in their feeding habits and seem particularly responsive (opportunist) in exploiting ephemeral types of feed. Grasses and forbs are often important dietary items during periods when they are growing rapidly. Secondary phytochemicals, particularly tannins, are apparently more tolerated by goats than by other livestock species, but are none the less important feeding deterrents and perhaps important nutritional liabilities. Range management programmes should capitalize upon the opportunist feeding habits of goats. This means maintaining plant communities that are highly diverse in botanical structure. □

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