Multispecies Grazing: The Ecological Advantage

John W. Walker

Summary
Grazing of several species of herbivores on the same area typically results in more efficient utilization of forage resources and increases sustainable production. These benefits are the result of different dietary habits of the animals because plants avoided by one kind of livestock may be relished by another. Differences in dietary habits are related to the physical limitation on the ability to select and the physiological limitation on the ability to detoxify forage phytotoxins. Compared to cattle, sheep diets usually have more forbs and less grass. Sheep can graze lower in the forage canopy, have a greater ability to select from a fine-scale mixture and have a more varied diet than cattle. As available forage decreases, dietary overlap between sheep and cattle tends to decrease because cattle shift their diet to lower quality but more available forage while sheep can continue to select their preferred diet. Averaged across a wide range of studies, multispecies grazing increased meat production by 24% compared to cattle-only grazing and by 9% compared to sheep-only grazing. This advantage is usually caused by both increased individual animal performance and increased carrying capacity. Despite the potential increases in economic and biological efficiency, multispecies grazing is not widely practiced. This valuable management practice should be promoted based on its ability to meet societal goals for more environmentally sound agricultural production practices. Compared to single species grazing, multiple species of animals use vegetation resources more uniformly, which can enhance ecosystem stability.

Key words: sheep, cattle, goats, diet selection, diet overlap, foraging behavior, sustainable agriculture.

Introduction
Multispecies grazing refers to the use of more than one species of large herbivores to graze a common forage resource. The grazers may be either domestic or wild and grazing by the different species of animals may occur concurrently or at different times. Multispecies grazing, the norm for wild ungulates, probably originated in domestic livestock when sheep and cattle used the same resource area for the first time. Evidence that mixed grazing is a long-standing practice is demonstrated by 19 occurrences of the words sheep and cattle (and often goats and camels) within the same verse of the Old Testament. Furthermore, multispecies grazing has been advocated since the inception of range science (Jardine and Anderson, 1919; Sampson, 1952; Stoddart and Smith, 1943). The idea that sheep and cattle are incompatible is a product of the settlement of the western United States. However, the reason for the conflict between cattle and sheep graziers was economic. It was caused by competition for a limited forage resource in the unfenced west (O'Neal, 1989).

The basic principles of grazing management are control of: 1) intensity of grazing (stocking rate); 2) timing of grazing; 3) kind and class of herbivore; and 4) distribution of grazing (Stoddart et al., 1975; Heitschmidt and Taylor, 1991; Vallentine, 1990). It can be argued that other grazing management practices, such as grazing systems, should not be implemented until these factors are properly controlled (Hart et al., 1993). Multispecies livestock grazing directly addresses the important principle of kind and class of livestock. The presence of multiple species of large herbivores is the typical condition of grassland and savanna ecosystems. Grazing by a diverse assemblage of large herbivores increases ecosystem stability and results in more uniform utilization of the vegetation resource (Bell, 1971; Hirst, 1975; Dunbar, 1978; McNaughton, 1985; Du Toit, 1990;)

1 USDA/ARS, U.S. Sheep Experiment Station, Dubois, ID 83423.
Ben-Shahar, 1991; Rejmanek, 1992). Multispecies grazing can increase the efficiency of forage harvest and therefore increase production on a land area basis (Briske and Heitschmidt, 1991).

Basic Ecological Principles
The overriding principle favoring multispecies grazing is that intraspecific (between individuals of the same species) competition is always greater than interspecific (between different species) competition. This is a corollary to the ecological principle that a niche defines the ultimate distributional unit and no two species living in the same area can occupy the same niche (Grinnell, 1917). Each species of animal, whether domestic or wild, will tend to exploit different portions of a common environment. Thus competition for limiting resources has led ungulates in a given area to occupy different dietary niches and to develop complementary forage preferences and grazing habits (Kay et al., 1980). Niche separation may be achieved by spatial or temporal differences in habitat use or by different dietary preferences among sympatric (joint fatherland — animals that occupy the same range) herbivores.

Bell (1971) described a succession of herbivores in the Serengeti plain of East Africa that not only reduced competition among different herbivore species but also enhanced the foraging environment for subsequent herbivores. During the seasonal movements of ungulates transversing the Serengeti, grasses and animals interact to create a grazing patterns wherein each species of ungulate follows another in characteristic sequence. The principal migratory species (wildebeest, zebra, Thompson’s gazelle) have physiological reasons for seeking different food items and tend to move on when the preferred forage becomes scarce. Changes in the availability of the plant tissues determines the order of movement of the animals (zebra move first, followed by wildebeest and then Thompson’s gazelle).

At the end of the wet season the herb layer presents a series of levels of different food value and accessibility to herbivores. The top level consists of low-protein grass culms. Below this level are the stems and leaves of the taller grasses, lower still are the leaves of the smaller grasses, young shoots and forbs. The result is that the highest concentration of protein is in the lowest level, which is relatively inaccessible to grazers because of the dense grass stems and culms above it. Zebra graze in the upper canopy and consume a diet highest in cell-wall constituents. Wildebeest ingest a higher protein diet from the leafy levels below and gazelle select the high-protein fruits from the ground. The activity of zebra, the first species in the succession of grazers, breaks down and opens up the dense stands of stems and culms by grazing and trampling; therefore, of great assistance to the later members (wildebeest followed by gazelle) of the succession.

Objectives
The objective of this paper is to show that, from both a theoretical and practical perspective, multispecies grazing is one of the soundest grazing management practices. I will review what is known about the biological, ecological, economic and managerial aspects of multispecies grazing. Then I will try to determine why this practice has not received widespread acceptance by livestock producers in this country and suggest strategies to encourage the use of multispecies grazing.

Rolston (1979) articulated society’s current paradigm concerning nature and agriculture in the following statement: “We direct nature round to our goals; yet, if we are intelligent, we use only those disruptions that nature can absorb, those appropriate to the resilience of the ecosystem under cultivation.” Thus, I will try to demonstrate the ecological logic for multispecies grazing as an environmentally friendly management practice.

Morphophysiological Explanation of Grazing Habits
Niche separation in sympatric herbivores is accompanied by morphological and physiological adaptations. These adaptations have been used to categorize ruminants into concentrate selectors, intermediate feeders and grass/rougahage feeders (Hofmann, 1988). Species in these different groups form a continuum of adaptations in all portions of the gastro-intestinal tract (Table 1). Ruminant concentrate selectors (40% of ruminants) evolved early and adapted to their food plants before the radiation (i.e., evolution and dispersal) of grasses in the Miocene (26 million years before present). Animals in this group select plants or plant parts rich in easily digestible and highly nutritious plant cell contents such as starch, protein and fat (Hofmann, 1988). Roughage selectors (25% of ruminants) evolved later and utilize grasses and other fibrous forage high in cell-wall content. Intermediate feeders (35% of ruminants) can opportunistically adapt to varying forage conditions.

According to Hofmann (1988), concentrate selectors differ from grass/rougahage feeders by having narrower, more pronghose muzzles; larger salivary (particularly parotid) glands; smaller mass of gastro-intestinal tract relative to body weight; and larger livers. These morphophysiological differences enable concentrate selectors to quickly pass forage through the alimentary tract, resulting in rapid digestion of cell solubles and passage of undigested cell walls. In contrast, grass/rougahage feeders have slower rates of passage and digest cell walls more completely. Concentrate selectors eat smaller more frequent meals compared to roughage selectors.

Other factors that affect diet selection include body size and type of digestive system. Large body size animals can meet their nutrient requirement with lower quality forage, but they must consume a higher total amount of forage within the same time.
constraints as smaller body size animals. This allows smaller animals more time per unit of intake to select the high quality food items from the environment. Thus, where forage quantity is limiting, small body size is advantageous; where forage quality is limiting, large body size is advantageous (Bell, 1971; Hanley and Hanley, 1982; Demment and Van Soest, 1985).

The foraging niche is further defined by the type of digestive system; that is, foregut (ruminant) versus hindgut (cecal) fermentors. Ruminants can digest a greater proportion of forage cell walls because they break their food into smaller particle size as part of the rumination process and because the products of microbial digestion in the foregut are available for gastric digestion and absorption further down the gastro-intestinal tract. However, this more complete digestion has a cost in terms of slower rates of passage and consequently lower intakes relative to body weight. Thus, in a manner somewhat analogous to the effect of body size on diet selection it can be generalized that where forage quantity is limiting, a ruminant digestive system is advantageous; whereas where forage quality is limiting, a cecal digestive system is advantageous (Bell, 1971; Janis, 1976; Hanley and Hanley, 1982; Demment and Van Soest, 1985).

Based on morphophysiological differences, horses, cattle and sheep are classified as grass/roughage eaters. Goats are classified as intermediate feeders showing a preference for cell contents but a limited capacity to digest cellulose (Hofmann, 1988). Vallentine (1990) takes issue with Hofmann (1988) on the classification of sheep as grass/roughage eaters. Vallentine argues that sheep should be classified as intermediate feeders because of their versatility and ability to utilize high proportions of forbs and browse.

Within the three broad classifications, species differences in diet selection exist. Because they are cecal fermentors and have both upper and lower incisors, horses can subsist in habitats that have both lower quality and lower availability of herbage than cattle. Hanley and Hanley (1982) described sheep as very well adapted to producing on poor quality rangeland because: 1) their small body size and ruminant digestive system minimize the time/energy constraints and provide a relatively large amount of time to forage selectively; 2) the large rumen volume enables it to exploit the relatively abundant sources of fermentable carbohydrates; and 3) the small mouth size enables it to be highly selective of species and plant parts. This agrees with surveys that show, in comparisons of either sheep to cattle (Oesterheld et al., 1992) or small to large native herbivores (Demment and Van Soest, 1985; McNaughton, 1985), that body size increases as forage biomass increases.

**Foraging Behavior**

Diet selection and overlap are the processes that determine the effect of

<table>
<thead>
<tr>
<th>Table 1. Comparison of morphological and physiological differences between ruminants classified as concentrate selectors versus grass/roughage eaters.*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Organ</strong></td>
</tr>
<tr>
<td><strong>Prehensile organs:</strong></td>
</tr>
<tr>
<td>lips</td>
</tr>
<tr>
<td>oral cavity</td>
</tr>
<tr>
<td>hard palate, palatine ridges</td>
</tr>
<tr>
<td>tongue</td>
</tr>
<tr>
<td>salivary glands, parotid</td>
</tr>
<tr>
<td>rumen volume-to-BW ratio, liter/kg</td>
</tr>
<tr>
<td>relative size of compartments</td>
</tr>
<tr>
<td>ruminal papillae distribution</td>
</tr>
<tr>
<td>mucosal surface</td>
</tr>
<tr>
<td>reticulo-omasal orifice</td>
</tr>
<tr>
<td>omasal laminae</td>
</tr>
<tr>
<td>body length-to-intestine length ratio</td>
</tr>
<tr>
<td>small intestine-to-large intestine ratio</td>
</tr>
<tr>
<td><strong>Hindgut:</strong></td>
</tr>
<tr>
<td>cecum proportion of intestinal length</td>
</tr>
<tr>
<td><strong>Associated organs:</strong></td>
</tr>
<tr>
<td>liver % BW</td>
</tr>
</tbody>
</table>

*a* Hofmann (1988).
multispecies grazing on carrying capacity and pasture composition. Diet selection is a function of post-ingestive consequences, the animal's ability to discriminate between alternate plant species and the ability to physically select among alternative choices (Marinier and Alexander, 1991; Provenza and Balph, 1990). The relative importance of these different processes will depend in part on the forage resource grazed as it relates to the most prevalent grazing resistance mechanism in the assemblage of plants that comprise the community.

Grazing resistance refers to the ability of plants to survive grazing and is usually separated into avoidance and tolerance components. Avoidance mechanisms reduce the probability and severity of plant defoliation; tolerance mechanisms facilitate growth following defoliation (Briske, 1991). Tolerance mechanisms are generally more prevalent in monocots than dicots while the reverse is true for avoidance mechanisms (McArthur et al., 1991). In environments where most forages plants use a tolerance mechanism to resist defoliation, the animal's physical limitations on ability to selectively consume plants may be the primary factor causing differences in diet selection among different herbivores. This situation is typical of improved pastures and true prairies. However, in ecosystems where many plants use avoidance mechanisms to resist grazing, diet selection will often be determined by the animal's ability to detect and defoliate plant chemical defenses or avoid physical defenses such as thorns. Avoidance strategies to defoliation are most common in desert and savanna ecosystems. Regardless of the ecosystem, the morphological and physiological differences between different species of livestock will allow multiple species to use a wider array of the available vegetation than a single species.

Morphological differences in the mouth parts of sheep, cattle, horses and goats determine to a great extent the degree to which they can selectively graze. Cattle have no upper incisors and use their tongues as prehensile organs. The herbage is swept into the mouth with the tongue then pinched between dental pad and the lower teeth and torn off. Because of the structure of the lower jaw, cattle can seldom graze less than 12 mm from the soil (Leigh, 1974). Sheep have a cleft upper lip which permits them to graze closer to the soil surface than cattle. The lips, the lower incisor teeth and the dental pad are used in grazing rather than the tongue as in cattle. The animal bites the forage to be grazed and jerks its head slightly forwards and upward. The goat has a mobile upper lip and a prehensile tongue and thus can graze herbage as short as can sheep. Because of its ability to climb and to stand on its hind legs, the goat can take browse not normally eaten by other herbivores (Maher, 1945).

In a study on improved grass/clover pastures, Dudzinski and Arnold (1973) reported that sheep had a higher proportion of clover in their diets than cattle when there were small amounts of live vegetation and abundant stem. When green forage was abundant this relationship tended to reverse and sheep had less clover in their diets than cattle. Cattle always ate a higher proportion of stem, but the difference relative to sheep decreased at the amount of preferred live forage increased.

Dudzinski and Arnold (1973) concluded that most of the results seem to be logically explained in terms of differences in the mechanics of grazing between sheep and cattle. Sheep can graze closer to the ground and on short pastures where clover is prostrate; cattle have less chance of harvesting it than sheep. The stronger jaws of cattle and the jerking action of the head in grazing enable cattle to harvest stem more readily than sheep. Because sheep choose to graze closer to the ground than cattle, they are likely to pick up more litter than cattle when feed is abundant, since this fraction is on the soil surface. When food is short, cattle are forced to graze close to the ground and, being mechanically less able to select, probably cannot avoid picking up more litter than sheep.

In contrast to most studies that show sheep prefer clover over grass (see Newman et al., 1992) Norton et al. (1990) found that sheep preferred grass leaves while cattle and goats preferred clover. They postulated that this deviation from expected preferences was the result of differences in plant growth habit and behavioral differences. They suggested that sheep prefer to graze from the lower strata while cattle and goats prefer to graze initially from the top of the sward. In this study on tropical pasture, the trailing legumes are mainly in the uppermost parts of the sward; whereas, in temperate clover pastures, the legume is in the lowest strata. Thus, Norton et al. (1990) postulated that the propensity of sheep to graze in the lower strata of the sward explains the lack of legumes in their diets under the conditions of the study.

Botanical Composition

During spring, when vegetation is actively growing and forbs are most abundant, sheep diets on western U.S. ranges have a slightly higher percentage of forbs than grass while cattle diets are reported to average 70% grass (Thetford et al., 1971; Hanley and Hanley, 1982; Ralphe et al., 1986; Kirby et al., 1988). As the growing season progresses and forbs senesce, grass content of sheep and cattle diets increases to 60 and 80%, respectively. Shrub contents are about equal between the two species and average 10 and 5% in the spring and summer, respectively. Dietary overlap is lowest in the spring (55%) and increases to 75% in the summer and fall.

In a series of studies on natural plant communities in Scotland, Grant et al. (1985, 1987) found sheep diets were more variable than cattle diets. Sheep diets contained more forbs and less grass stem in the summer and generally contained more live plant tissue than cattle diets. However, seasonal differences in preference for certain plant species in certain vegetation communities resulted in cattle having a higher percentage of live components in their diets. As available forage declined, cattle shifted to less preferred species more readily than sheep, similar to results presented by Ralphe et al. (1986) for
U.S. rangelands. Grant et al. (1985) attributed the reluctance of sheep to shift preference to lower quality components in the vegetation to their greater ability to physically manipulate and select their preferred diet. Differences between sheep and cattle diets were explained by: 1) a difference in the height animals grazed in relation to differences in the distribution of plant species within the sward canopy (agrees with Norton et al., 1990); 2) greater ability of sheep to select from fine-scale mixtures (agrees with Dudzinski and Arnold, 1973); and 3) greater readiness of cattle to graze tall, more fibrous components.

Sheep, but not cattle, were able to increase the proportion of certain components in their diets compared with the proportion in the sward, even when the components were introduced into the diet by selective grazing for certain components in the vegetation it was either because they non-selectively grazed the upper canopy or because they preferentially grazed small areas where the component was more abundant. Though the proportions of most dietary components differed significantly between sheep and cattle in at least one period, it was clear that there were no significant differences in the proportion of dead material that were selected or avoided in common by sheep and cattle. Cattle diets contained more dead material than sheep diets in all seasons.

On semi-arid western U.S. rangeland, the ability to physically select desired plants may be of fairly minor importance because biomass production is low; consequently, plants are not closely intermingled. In these situations, post-ingestive consequences may be the overriding factor determining dietary preference (Provenza and Balph, 1990). It is well documented that many plants that are toxic to cattle do not harm sheep, such as larkspur (Ralphs et al., 1991), leafy spurge (Kronberg et al., 1993), tansy ragwort (Craig et al., 1992) and pine needles (Short et al., 1992). Though not documented, there are presumably many other forbs which although not overtly toxic to cattle may cause gastrointestinal upset in this species and yet be innocuous to sheep. This sheep may demonstrate a higher preference for native forbs because of their greater ability to neutralize phytochemicals. While less is known about goats, this same argument presumably applies to them.

There is general agreement that, from a single plant, sheep and cattle eat leaf in preference to stem and green in preference to dry material (Arnold and Dudzinski, 1978). Furthermore, sheep, cattle and goats selectively graze pastures in such a way that while green leaf is usually sought by all, different plants in a pasture are often preferred by each species (Arnold, 1980). Summarizing data from over 200 studies, from the world literature Van Dyne et al. (1980) concluded that, on a year-long basis, sheep, cattle and goats consume about 50, 70 and 30% grass; 30, 15 and 10% forbs; and 20, 15 and 60% browse, respectively (Table 2). However, there is wide fluctuation around these means caused by season and plant community. Based on these gross averages it can be seen that cattle and sheep have the greatest degree of similarity while cattle and goats have the least.

Differences in botanical composition of diets result in differences in nutrient composition as well. The smaller mouth size of sheep and goats and the resultant greater ability to selectively consume forage results in a higher quality diet for these two species compared to cattle. Averages over nine studies on natural or improved pastures sheep compared to cattle diets were 3.9 and 6.5 percentage units higher in crude protein and in vitro digestibility, respectively. Because of their similar ability to selectively graze, sheep and goat diets tend to have relatively similar nutrient concentrations (Bryan et al., 1980; Pfister and Malechek, 1986). However, the higher preference for browse by goats compared to sheep has resulted in diets with higher crude protein but lower digestibility (Wilson et al., 1975; Norton et al., 1990).

**Table 2. Diets and Overlaps of Common Domestic Livestock.**

<table>
<thead>
<tr>
<th></th>
<th>Botanical Composition, %</th>
<th>Dietary Overlap, %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grass</td>
<td>Forbs</td>
</tr>
<tr>
<td><strong>Yearlong:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheep</td>
<td>50</td>
<td>30</td>
</tr>
<tr>
<td>Cattle &amp; Horses</td>
<td>70</td>
<td>15</td>
</tr>
<tr>
<td>Goat</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td><strong>Spring:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheep</td>
<td>50</td>
<td>29</td>
</tr>
<tr>
<td>Cattle</td>
<td>71</td>
<td>12</td>
</tr>
<tr>
<td><strong>Summer:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheep</td>
<td>44</td>
<td>38</td>
</tr>
<tr>
<td>Cattle</td>
<td>68</td>
<td>19</td>
</tr>
<tr>
<td><strong>Fall:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheep</td>
<td>62</td>
<td>30</td>
</tr>
<tr>
<td>Cattle</td>
<td>75</td>
<td>13</td>
</tr>
<tr>
<td><strong>Winter:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheep</td>
<td>54</td>
<td>14</td>
</tr>
<tr>
<td>Cattle</td>
<td>70</td>
<td>13</td>
</tr>
</tbody>
</table>

* After Van Dyne et al. (1980).
defoliation more uniformly across all plant species in the community (Figure 1). While a high degree of dietary overlap does not necessarily indicate interspecific competition, a low level of overlap indicates reduced potential for competition. Generally, it is thought that dietary overlap and interspecific competition will increase as grazing pressure increases or plant community diversity decreases (Janis, 1976; Collins and Nicol, 1986; Taylor, 1986; Vallentine, 1990; Huston and Pinchak, 1991; Walker, 1991). However, this has not been rigorously tested. To test this hypothesis, I calculated the correlation between either forage biomass or plant species diversity and dietary overlap. Data were obtained from ten published studies located on three continents. Across the studies, analysis indicated no relationship for dietary overlap between sheep and cattle with biomass (74 observations) or diversity (80 observations). However, on a within-study basis, dietary overlap between sheep and cattle had a significant positive relationship with diversity in five (Dudzinski and Arnold, 1973; Rector, 1983; Ralhs et al., 1986; Grant et al., 1987; Norton et al., 1990) of

Figure 1. Diagram representing the concept of dietary overlap.

Shaded circles represent botanical composition of diet of different herbivores, surrounding area represents composition of available forage. Areas shared by two or more species indicate potential for competition while areas used by only one species indicate potential for greater resource utilization due to complementarity of diets.
eight studies analyzed and with biomass in three of the studies. These results contrast with the generally held hypothesis that dietary overlap should decrease as biomass or plant species diversity increases. However, they are in agreement with the hypothesis that sympatric herbivores should reduce competition by filling different food niches and diet overlap should decrease with decreasing food resources (Schwartz and Ellis, 1981). The apparent reason is that, when available forage becomes limiting, cattle shift their diet to the lower quality but more available forage resources while sheep are apparently capable of continuing to select their preferred diet. Furthermore, this agrees with the generally accepted opinion that sheep are more selective grazers than cattle (Dudzinski and Arnold, 1973; Grant et al., 1985; Hodgson et al., 1991).

A significant positive correlation between diversity and dietary overlap was also found between cattle and horses (Krysl et al., 1984). Across studies, however, this relationship was significantly negative for dietary overlap between sheep and goats and nonsignificant but negative for dietary overlap between cattle and goats (Squires, 1982; Rector, 1983; Norton et al., 1990). This is consistent with the lower dietary overlap between goats and either sheep or cattle reported by Van Dyne et al. (1980; Table 1). When grazed in common, goats apparently deplete a different forage resource than that consumed by sheep or cattle until high grazing pressure causes increased dietary overlap and greater interspecific competition. The difference in how competitive relationships and dietary overlap vary between sheep and cattle compared to the relationship of these species with goats supports Hofmann’s (1988) classification of sheep and cattle as roughage eaters and goats as intermediate selectors.

Diet selection, dietary overlap and competition among multiple species of livestock are important because this determines the appropriate number and combination of livestock for a given forage resource. Theoretically, the proper mix and number of animals is a function of: 1) livestock dietary preferences; 2) animal forage demand; 3) botanical composition and production of forage resources; and 4) proper use factors for key forage species (Cook, 1964; Smith, 1965; Hobbs and Carpenter, 1986). Available forage is allocated to different herbivores grazing the same range based on the anticipated dietary botanical composition of each herbivore and the botanical composition of the vegetation. Maximum combined stocking rate is determined by the full allowable use of key forage species (Smith, 1965). Smith (1965) states that when two species of animals graze the same key species and one herbivore species is better suited for the range, then maximum production is obtained when the range is fully stocked with the animal more suited for the range. However, it is not possible to predict how the interaction of several species of herbivores will affect total forage demand and empirical evidence indicates that multispecies grazing always increases carrying capacity.

**Replacement Ratios**

Maximum benefit from multispecies grazing will occur when the proper substitution ratio of one livestock species for another is used. Biologically, this is dependent upon the degree of overlap in demand for limiting resources and the production efficiency of different species. Economically, the price ratio of the products is also important (Hopkins, 1954; Hamilton, 1975; Connolly and Nolan, 1976).

Replacement ratios of 5 sheep, 6 goats or 1.2 horses per cow are commonly used and are based on relative differences in forage consumption (Valentine, 1990). Animal unit equivalence based on either a body weight basis or body weight raised to the 0.7 to 0.8 power have also been used. Substitution ratios that adjust for dietary overlap have been suggested as well. This approach uses animal equivalency on a metabolic body weight basis divided by the dietary overlap of the two species to determine animal unit equivalents (AUE; Flinders and Conde, 1980; Botha et al., 1983).

Equation 1:

\[
AUE = \frac{1000^{.75}}{(LW_i^{.75} \times \% \text{ dietary overlap})}
\]

where: 1000^{.75} = 1 Animal Unit

\[LW_i^{.75} = \text{metabolic body weight of } i^{th} \text{ species of herbivore.}\]

Using this method the standard 5-to-1 replacement ratio for sheep to cows becomes 14, 7, 5 and 3 sheep per cow for dietary overlaps of 25, 50, 75 and 100%, respectively.

A common rule of thumb for moderately stocked rangelands is one ewe can be added per cow without affecting cattle production (Umbarger et al., 1984; Glimp, 1988). The ratio of sheep to cattle affects the response of each species of livestock and total system production. As the proportion of one species of livestock in the mix increases individual animal performance by that species declines while performance of the other livestock species improves (Nolan and Connolly, 1977; 1989). Because of the complex interactions among different species of livestock and the forage resource, proper stocking rates and replacement rate can only be determined empirically by grazing at different ratios and stocking rates and solving for the maximum production per unit land area (Connolly et al., 1974; Connolly and Nolan, 1976; Connolly, 1986; Nolan and Connolly, 1989). Equivalence between different livestock species is relative; thus Connolly and Nolan (1976) found that if one steer (305 kg) was removed it could be replaced by 4.2 lambs (4 months old) without affecting lamb performance. Similarly, replacement of one steer by 10 lambs held the performance of the remaining steers constant. Nolan and Connolly (1989) reported that at 3 to 5 ewes per steer, about 13% more area would be required to produce the same outputs if they were grazed.
separately compared to grazing in combination. Thus, forage allocation is a complex biological problem without simple, objective solutions (Valentine, 1990).

Individual Animal Performance

Complementary use of resources by mixed species of livestock result in benefits accrued from increased carrying capacity and consequent increased production per unit of land area, as well as increased individual animal performance by at least one and often all of the species grazed in combination. Data in Table 3 show that multispecies grazing benefits individual performance of sheep more than cattle. Sheep grazed in combination with cattle had gains that averaged 30% higher (range: 12 to 126%) than sheep grazed alone. Cattle grazed in combination with sheep had gains that averaged 6% higher than cattle grazed alone; however, the range (-3 to 21%) showed that, in some studies, combination grazing depressed cattle performance. This indicates that when forage availability is low, sheep are more competitive for the limiting resource than cattle. This is a result, as discussed previously, of their ability to graze both closer to the soil surface and more selectively from the total forage standing crop. This greater competitive ability of sheep compared to cattle is undoubtedly the reason sheep were inappropriately considered to spoil the range in Old West mythology.

Production per Unit Area

Table 3 shows that multispecies grazing always increases total animal product per unit area compared to cattle-only grazing (24% average increase) and usually increased production compared to sheep-only grazing (9% average increase). Compared to sheep-only grazing, multispecies grazing did not always increase total production of animal product per unit area because of the higher relative growth rate of lambs compared to calves and because of the higher prolificacy of ewes compared to cows (Matthews et al., 1986; Wilson and Graetz, 1980). The studies reviewed showing a decline in total production in multispecies grazing compared to sheep only grazing indicate that these studies did not cover the necessary range of stocking rates and replacement ratios. Because of complementarity of diet selection among different species of livestock, it is theoretically possible to find a stocking rate/replacement ratio combination that will produce more total gain per unit area by multispecies grazing than by any species grazed alone.

Multispecies Management

Little has been written about management of multispecies of herbivores. From the pastoralist perspective, the critical issue is numbers of each species of livestock. As discussed previously, the optimal solution to this problem will require empirical research for each major vegetation type. However, it is possible to develop rules of thumb that will serve as a starting point which, over time, can be adjusted to obtain near-optimal combinations for the conditions. The addition of one ewe per cow or conversely one cow per five ewes is a conservative starting point for moderately natural plant communities (Umberger et al., 1983; Cook, 1985; Glimp, 1988; Valentine, 1990). Nolan and Connolly (1989) found that on perennial ryegrass monocultures, carrying capacity could be increased about 10% in mixed-species compared to single-species grazing. Thus, 10% would be the lowest expected increase in carrying capacity from multispecies grazing. Using the adjustment for dietary overlap in Equation 1 (Flinders and Conde, 1980; Botha et al., 1983) and the average dietary overlap reported by Van Dyne et al. (1980; Table 1) indicates that carrying capacity can be increased 25% by mixed grazing of sheep and cattle compared to either species singly. Expanding this logic to the mixed grazing of goats with sheep or cattle shows a potential increased carrying capacity of about 70% under mixed compared to single grazing.

Mixed grazing from the perspective of animal management does not appear to offer any problems beyond those encountered under single species grazing of any of the livestock species under consideration. However, it does appear to add the additional management challenge of learning additional husbandry skills required for the new species of livestock being considered. Although Valentine (1990) recommended separating ewes and does from cattle at lambing and kidding, this is primarily a problem under intensive management where animals are concentrated. At the U.S. Sheep Experiment Station, ewes have been lambed under extensive conditions in pastures with cattle and had no apparent difficulties. Taylor (1986) recommended using creep gates for sheep and goats to allow separate access to water away from cattle and horses in areas of livestock concentration associated with intensive grazing systems. However, I have watered ewes and lambs from a common trough with yearling cattle under continuous grazing and observed no adverse interaction. Under these conditions, sheep and cattle were often found resting together around the water at midday. Adverse interactions between large and small livestock species will normally only be a problem during crowding or times of commotion.

Economics of Multispecies Grazing

It is difficult to predict what the effect of multi-versus single-species grazing will be on net ranch income because this will be affected by the proportion of each species of livestock, variable cost of production for different species and relative value of the products (Hopkins, 1954). A definite advantage of multispecies grazing is that by increasing stocking rate, fixed cost per animal unit is decreased. Thus, a 20% increase in carrying capacity of a ranch that is obtained by multispecies grazing would result in a reduction in fixed cost per animal unit of 17%, assuming no capital improvements were necessary to add the second species of livestock. The assumption of no additional capital outlays indicates that it is easier to
<table>
<thead>
<tr>
<th>Author</th>
<th>Geographic location</th>
<th>Vegetation type</th>
<th>Kind of animal</th>
<th>Change in individual animal performance, mixed versus single</th>
<th>Gain per hectare acre: mixed versus single species by:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sheep</td>
<td>Cattle</td>
</tr>
<tr>
<td>Hamilton et al., 1970</td>
<td>Victoria, Australia</td>
<td>ryegrass, clover</td>
<td>ewe/lamb, steer</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>Connolly et al., 1976</td>
<td>Ireland</td>
<td>ryegrass, clover</td>
<td>lamb, steer</td>
<td>29</td>
<td>10</td>
</tr>
<tr>
<td>Nolan et al., 1989</td>
<td>Ireland</td>
<td>ryegrass</td>
<td>ewe/lamb, steer</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Boswell et al., 1978a</td>
<td>New Zealand</td>
<td>ryegrass, clover</td>
<td>wethers, steers</td>
<td>126</td>
<td>-3</td>
</tr>
<tr>
<td>Dickson et al., 1981b</td>
<td>Ayshire, Scotland</td>
<td>fertilized ryegrass</td>
<td>ewe/lamb, steer</td>
<td>-</td>
<td>21</td>
</tr>
<tr>
<td>Heinemann, 1970c</td>
<td>Washington, USA</td>
<td>orchardgrass, alfalfa</td>
<td>ewe/lamb, steer</td>
<td>-</td>
<td>17</td>
</tr>
<tr>
<td>Rynolds et al. 1971d,e</td>
<td>Maryland, USA</td>
<td>fertilized orchardgrass, alfalfa</td>
<td>wethers steers</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Bennett et al., 1970f</td>
<td>New South Wales, Australia</td>
<td>phalaris, subterranean clover</td>
<td>ewe/lamb, steer</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Van Keuren, 1970</td>
<td>Ohio, USA</td>
<td>birdsfoot trefoil, Kentucky bluegrass</td>
<td>lamb, steer</td>
<td>28</td>
<td>2</td>
</tr>
<tr>
<td>Abaye, 1992</td>
<td>Virginia, USA</td>
<td>white clover, Kentucky bluegrass</td>
<td>ewe/lamb, cow/calf</td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td>Brelin, 1979</td>
<td>Southern Sweden</td>
<td>fertilized oldfield</td>
<td>ewe/lamb, cow/calf</td>
<td>27</td>
<td>5</td>
</tr>
<tr>
<td>Peart, 1961s</td>
<td>Chevoit Hills, Scotland</td>
<td>hill pasture, mixed grass, forb, shrub</td>
<td>ewe/lamb, cow/calf or heifer</td>
<td>27</td>
<td>-</td>
</tr>
<tr>
<td>Matthews et al., 1986</td>
<td>Utah, USA</td>
<td>mountain range, mixed grass, forb &amp; shrub</td>
<td>ewe/lamb, cow/calf</td>
<td>8</td>
<td>-2</td>
</tr>
<tr>
<td>Walker et al., 1990</td>
<td>Idaho, USA</td>
<td>sagebrush, steppe</td>
<td>ewe/lamb, heifer</td>
<td>5</td>
<td>8</td>
</tr>
</tbody>
</table>

---

* Based on forage production and utilization.
* No sheep-only controls.
* Control was cattle-only (no sheep-only comparison). Animals were rotationally grazed with sheep following cattle.
* Increased individual animal performance at 5:1 sheep-to-cattle ratio only.
* Increased production per unit area at 1:1 sheep-to-cattle ratio only.
* Mixed grazing increased weight gains of ewes at higher stocking rates but exact increase could not be determined from data presented.
* Added cattle to sheep grazed pastures. Comparison to cattle only or on production per unit area not possible.
change from small ruminants to mixed grazing than from cattle to mixed grazing because fences that will contain sheep and goats will also contain cattle, but the reverse is not true (Conner, 1991). Connolly and Nolan (1976) demonstrated the effect of relative price of sheep compared to cattle on the ratio of sheep to cattle to obtain maximum income. They reported the economic optimum was met by mixed grazing of sheep and cattle as long as the ratio of sheep to cattle prices were between 2.13 and 0.61. When the ratio was above or below these extremes, maximum income was obtained by sheep only or cattle only, respectively. Meyer and Harvey (1985) stated that, in New Zealand, multispecies grazing results in the highest overall returns even though one species in the system may appear considerably less profitable than another. An economic analysis of multispecies grazing in Virginia indicated that, by grazing sheep and cattle together at a ratio of one sheep per cow, stocking rates could be increased 20% and net income increased 29% when steer prices were about 20% above lamb prices (Umberger et al., 1983). Other economic advantages of multispecies grazing include improved cash flow caused by marketing various products at different times and reduced risk due to more diversified enterprises.

Obstacles to Multispecies Grazing

While the case for multispecies grazing can be effectively argued from both an ecological and economic perspective, outside of a few areas the practice is uncommon. The reasons commonly cited for the low implementation rate of multispecies grazing are: 1) predation losses of sheep and goats (Gee et al., 1977; Merrill, 1985; Etchepare, 1985); 2) resistance by public land management agencies to issuance of multispecies grazing permits (Hopkins, 1954; Bowns, 1985; Valentine, 1990); 3) education voids by producers (Byington, 1985); and 4) traditional prejudices about different species of livestock (Valentine, 1990). However, except for the predator problem, I believe the reasons are of minor importance at least among sheep producers. This is demonstrated by the fact that two-thirds of the commercial sheep producers in the western states also raise cattle (Gee and Magleby, 1976).

While the predator problem will probably continue to be the major factor limiting the expansion of small ruminant numbers, I believe there are three other major obstacles to widespread implementation of multispecies grazing. First, profit maximization is not the only motive that drives the decision-making process. In the hierarchy of man's goals, our society currently provides for biological survival and its place as a prominent goal is overtaken by more advanced goals such as social status or self-actualization (Maslow, 1954; Conner, 1991). Thus, livestock producers that have met their standard of living goals may not want to invest the additional capital and managerial resources necessary to implement multispecies grazing because it would require them to sacrifice more advanced goals. Second, rather than assess current management in terms of the basic principles of grazing management that were discussed at the start of this essay (intensity, kind, season, distribution) there is a strong tendency toward implementing grazing systems as the first step in grazing management (Sanford, 1983; Malecheck, 1984; Walker, 1993; Valentine, 1990). A third impediment to multispecies grazing is the trend toward larger agricultural production units coupled with a trend toward specialization (Beus and Dunlap, 1990). Thus, the trend is toward a contraction of enterprises rather than an expansion as implied by multispecies grazing.

I do not believe greater implementation of multispecies grazing will be achieved by countering the factors listed above that are thought to restrict its implementation. Rather, a different approach must be used. That approach is indicated in the title of this review: the ecological advantage. Thus the environmental benefits that can accrue from grazing multiple compared to single species of livestock must be promoted.

Producers, that would not adopt multispecies grazing for economic reasons may do so for environmental ones. Government agencies that promote implementation of grazing systems to counter the adverse environmental affects of livestock grazing may adopt multispecies grazing because it can enhance the environment.

Multispecies grazing should be promoted because, while there are many factors that affect plant community dynamics and composition, the one factor that man has the most control over is how livestock are grazed. A major impact of livestock on plant communities is that by preferentially grazing some species and avoiding others, livestock impact plant succession (Davidson 1993). Wooton (1908) noted that "Stock eat the valuable forage plants and leave the poor ones, thus giving the latter undue advantages in the struggle for existence." By using multiple species of livestock, each with their unique dietary preferences, the impact of grazing will be more evenly distributed across the botanical community and thus reduce the impact of a single species of livestock on its preferred forage plant. This should result in plant communities that are more resistant not only to grazing but also to other factors that affect ecosystem stability, such as drought.

Literature Cited


Smith, A.D. 1965. Determining common use grazing capacities by application of the key species concept. J. Range Manage. 18:196-201.


