STOCKING RATES AND CARRYING CAPACITIES FOR UNGULATES ON AFRICAN RANGELANDS

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ABSTRACT. — The principles in calculating and setting stocking rates for African ungulates are considered. Stocking rates should be calculated using estimated energy consumption, not biomass. The capacity of rangelands to support ungulates is high for large sized and largely grazing species, and low for small sized and largely browsing species. The former type of animal appears an inefficient converter per unit mass of intake, but efficient per unit mass of primary production; the opposite holds for the latter type of animal. The methods of agriculturists to calculate an economically optimal stocking rate are applicable to wild ungulate production systems, and avoid the difficulties inherent in the classical ecological methods involving the intrinsic rate of natural increase, and ecological efficiency ratios. The agriculturists' method may be extended to determine an economically optimal proportional animal species composition. Previous protagonists of game ranching have overemphasized the 'wild' vs. 'domestic' animals, under-emphasized the 'one or two species community' vs. 'complete community', paid insufficient attention to mixing compatible domestic and wild ungulates to create a complete community, and have misunderstood or ignored the effects of the properties of different ungulates, and of the system of management on animal production and range condition.

INTRODUCTION

Following the early studies of African big-game ecosystems it was surmised that on the large areas of land unsuitable for intensive agriculture, a complete community of wild ungulates used a broader spectrum of the available plants, could be stocked safely at a higher level, and would be more productive than one or two domestic species (Talbot et al. 1965). Despite the wealth of scientific publications on African ungulates that has emerged in the past two decades, little attention has been paid to the question: at what rate wild ungulates should be stocked, how a stocking rate is best calculated, and what production can be expected?

The purpose of this paper is to discuss these questions by considering (1) the nutritional requirements of the animals, (2) methods of calculating stocking rates, (3) complications introduced by interspecific differences in feeding preferences, (4) the relative abundance of different types of food, (5) the expected and observed carrying capacities of rangelands, (6) the general inverse relationship between stocking rate and animal production per animal, and (7) the relative productive efficiencies of different ungulates.

NUTRITIONAL REQUIREMENTS

The nutritional requirements of African ungulates have been little studied. It is possible therefore only to apply cautiously the principles that have emerged largely from the study of domestic species.

The basal metabolism, or rate of energy consumption of an animal at rest, is nonlinearly related to live mass. Consumption at rest is greater per unit live mass for small than large homeotherms (Brody 1945). While there are age and sex differences, and individuals vary, the mean standard basal metabolism of a variety of mammals was given by Kleiber (1975) as

\[ 70 \times W^{0.75} \text{ kcal day}^{-1} \]  

(1)

where \( W \) is the live mass in kilograms. The increment in energy consumption of an active animal over that of an individual at rest varies according to physiological and reproductive status, level of activity and weather conditions (Blaxter 1962; Moen 1973). While the interspecific variation in the proportion of this increment has not been studied exhaustively, data on a variety of wild ruminants reviewed by Moen (1973) indicate that the average energy consumption of the average free-ranging animal does not usually exceed twice the basal metabolism. Assuming, for purposes of discussion, that the average metabolism of free-ranging animals is 1.33 times the basal metabolism, the absolute daily energy consumption and the daily energy consumption per unit live mass may be plotted against live mass (Fig. 1). Small ungulates have low absolute but high relative expenditures of energy.
Since the nutrient requirements for all mammals are, within small limits, likely to be similar when expressed in proportion to the metabolisable energy (Crampton 1964), live mass and in turn energy metabolism are the bases for estimating nutrient requirements.

**CALCULATING STOCKING RATES**

Stocking rates or standing crops of ungulates are a measure of the amount of ungulates per unit area of land. This section deals with the alternative units that might be used to express the amount of ungulates.

The total number of animals per unit area is a poor index of stocking rate. Most wild ungulate communities in Africa comprise several species differing widely in live mass and therefore in food requirement. The species composition of ungulate communities also varies regionally, thus invalidating regional comparisons of stocking rates based simply on population densities. Popular means of overcoming such difficulties have been to calculate biomass either as mass per unit area of land

\[(W_a \times N_a) + (W_b \times N_b) + ... + (W_i \times N_i) \text{ kg. km}^{-2} \ldots (2)\]

where \(W_a, W_b,..., W_i\) are the live masses in kg of average individuals of species \(a, b,..., i\), respectively, and \(N_a, N_b,..., N_i\) are the population sizes of species \(a, b,..., i\), respectively, on the area of land, \(A\), measured in km\(^2\) or as energy per unit area of land

\[
\frac{(W_a \times N_a \times 1.5) + (W_b \times N_b \times 1.5) + ... + (W_i \times N_i \times 1.5)}{A} \text{kcal.m}^{-2} \ldots (3)
\]

where \(W_a, W_b, W_i, N_a, N_b, N_i\) and \(N_i\) are as above, the area of land. \(A\) is measured in m\(^2\), and 1.0 g live mass is equivalent to 1.5 kcal.

Because of the nonlinear relationship between live mass and energy consumption, the latter has also been used to express stocking rates. The absolute energy consumption may be estimated by

\[
(70 \times W_a^{0.75} \times c \times N_a) + (70 \times W_b^{0.75} \times c \times N_b) + ... + (70 \times W_i^{0.75} \times c \times N_i) \text{kcal day}^{-1} \ldots \text{ha}^{-1} \ldots (4)
\]

where 70 \(\times W_a^{0.75}, 70 \times W_b^{0.75}, ..., 70 \times W_i^{0.75}\) are the daily basal metabolisms of average individuals of \(W_a, W_b,..., W_i\) kg of species \(a, b,..., i\) respectively, \(c\) is the proportion by which the free-ranging individual exceeds the energy consumption at rest, and \(N_a, N_b,..., N_i\) are the population sizes of species \(a, b,..., i\) respectively, on the area of the land, \(A\), measured in ha. Alternatively, the relative energy consumption of the populations of the different species present may be expressed using an arbitrarily chosen unit, with the stocking rate of the community given by

\[
\left( \frac{W_{au}^{0.75} \times N_a}{W_a^{0.75}} \right) + \left( \frac{W_{bu}^{0.75} \times N_b}{W_b^{0.75}} \right) + ... + \left( \frac{W_{iu}^{0.75} \times N_i}{W_i^{0.75}} \right) \text{AU ha}^{-1} \ldots (5)
\]

where the notation is as for expression (4), \(W_{au}\) is the live mass (455 kg) of an average steer (commonly called one animal unit or 1 AU), and the factor, \(c\), in expression (4), above is assumed to be the same for different species.

The differences between expressing a stocking rate in terms of energy consumption rather than as a biomass have been stated previously to be small (Lamprey 1964, Eltringham 1974). There are no large differences in the proportionate contributions by individual species. However, particularly where small animals are involved, biomass underestimates the real situation. The point is emphasized by taking impala \((Aepyceros melampus)\) as an example. On a biomass basis, there are 11.1 impala (41 kg mean individual live mass) to 1 AU, whereas on an energy consumption basis there are only 6.1 impala.

Table 1, adapted from Mentis and Duke (1976), presents stocking rates on 12 areas using biomass and energy consumption expressed as a percentage of the carrying capacity for cattle. Because ungulates smaller than cattle were involved in all cases, the 'energy consumption' estimate was consistently higher than the 'biomass' estimate, and, more importantly, the differences between the two types of estimate varied between areas.

<table>
<thead>
<tr>
<th>Example</th>
<th>Stocking rate as a percentage of capacity</th>
<th>Proportion by which estimate (B) exceeds estimate (A)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td>Energy consumption</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(A)</td>
<td>(B)</td>
</tr>
<tr>
<td>1</td>
<td>124</td>
<td>191</td>
</tr>
<tr>
<td>2</td>
<td>203</td>
<td>300</td>
</tr>
<tr>
<td>3</td>
<td>113</td>
<td>183</td>
</tr>
<tr>
<td>4</td>
<td>147</td>
<td>231</td>
</tr>
<tr>
<td>5</td>
<td>249</td>
<td>316</td>
</tr>
<tr>
<td>6</td>
<td>75</td>
<td>92</td>
</tr>
<tr>
<td>7</td>
<td>71</td>
<td>84</td>
</tr>
<tr>
<td>8</td>
<td>65</td>
<td>96</td>
</tr>
<tr>
<td>9</td>
<td>24</td>
<td>31</td>
</tr>
<tr>
<td>10</td>
<td>127</td>
<td>222</td>
</tr>
<tr>
<td>11</td>
<td>124</td>
<td>148</td>
</tr>
<tr>
<td>12</td>
<td>161</td>
<td>170</td>
</tr>
</tbody>
</table>

For comparative purposes, therefore, estimates of stocking rates based on energy consumption (expressions (4) and (5)) are superior to those based on biomass (expressions (2) and (3)). Nevertheless, estimates based on energy consumption rely more on textbook formulae than on measurements of the metabolic rates of the specific wild ungulates involved. Rogerson (1968) and du Plessis (1972) observed in wildebeest \((Connochaetes taurinus)\), eland \((Taurotragus oryx)\) and blesbok \((Damaliscus dorcas)\) higher basal metabolisms than predicted by Kleiber's (1975) generalisation (expression (1)). Allowance could be made in expressions (4) and (5) in situations where any of these three species occur, but perhaps the observed high basal metabolisms arise from stresses suffered in confinement and in handling by these non-domesticated species.
The respective merits of the absolute (expression (4)) and the relative (expression (5)) estimates of energy consumption are determined by the purpose of study. The former is necessary in studies of energy transfers, although it has been used to express stocking rates (Lamprey 1964, Elfring and 1974), but the relative measure is useful in the applied field. Energy transfers in terrestrial ecosystems in Africa have been little explored, in few instances have basal metabolisms been measured and the intra- and inter-specific variability of the factor, e. (expression (4)) is not known. However, at least in southern Africa, agriculturalists can, through experience, estimate indices of usable primary production in the herb layer. These indices are carrying capacities for domestic livestock expressed as the number of hectare required to support one animal unit. To wildlife managers, these indices are a guide to carrying capacities for grazing animals, but the indices must be used cautiously (see under Carrying capacity) (Mentis and Duke 1976).

**FEEDING PREFERENCES**

It is necessary to distinguish between bodily or metabolic energy and nutrient requirements on the one hand and, on the other hand, what the composition of the food should be. While requirements may be estimated from function (1) or some modification of it, for reasons now to be discussed ungulates employ different feeding strategies to satisfy their needs, and consequently some species can survive on poorer quality food than can other species.

Small ungulates are faced with a higher relative energy and nutrient need than are large ungulates (Fig. 1). To accommodate this they must have a relatively high intake, or ingest relatively high quality food, or achieve some compromise situation of intermediate intake and food quality.

Among non-ruminants, a high requirement or a decline in the quality of food available can be met at least partly by an increase in food intake (McDonald, Edwards and Greenhalgh 1973). However, while non-ruminants do possess this facility to vary intake over a wide range, the small animal, as opposed to the large, has a low absolute requirement and therefore has the opportunity in terms of time per unit mass of intake to feed selectively, and to ingest concentrated, highly digestible food.

In ruminants, food intake increases with the digestibility of the food since appetite is stimulated by a decrease in 'rumen-load' (Blaxter 1962). For any given quality of food, then, ruminants have an upper limit to intake determined by the rate at which that food can be digested, and by the capacity of the stomach. Thus, small ruminants might adjust for their high relative requirement either by having capacious stomachs or by eating concentrated food. Observation favours the latter alternative as a general principle. Using the data of Hofmann (1973: Tables 3-7), I calculate that, per unit metabolic mass, small ruminants have less not more capacious rumeno-ricueta than large ruminants, the regression of metabolic mass/fore-stomach capacity (X) on metabolic mass (Y) being

\[ Y = 81.75 - 22.98X (P < 0.01) \]  

To generalise, then, small ungulates tend to have a higher quality intake than do their larger counterparts. This is possible by virtue of the low absolute requirement of small ungulates, the favourable relationship between time and unit mass of intake, and therefore the opportunity to feed selectively. That small ungulates do indeed eat concentrated food is supported by Bell (1970) and Blankenheim and Qvortrup (1974). However, this inverse relationship between live mass on the one hand, and the quality of intake and degree of selective feeding on the other, is complicated by specialisations for diets of particular quality. Hofmann (1973) showed that the classical division of African ruminants into grazers, browsers and mixed feeders is poor descriptive terminology, a more appropriate classification being

(i) Bulk and roughage eaters, characterised by capacious stomachs filled to capacity with relatively low quality food composed mostly of grass.

(ii) Concentrate selectors, characterised by small stomachs filled only to 50-60% of their capacity with concentrated food composed mostly of the leaves, flowers and fruits of forbs, shrubs and trees.

(iii) Intermediate feeders, characterised by an ability to adapt in different seasons and areas towards one or other of the above two feeding types.

Placing non-ruminants in the above system is perhaps artificial. However, since the classification is based on specialisation for different qualities of food, or the capacity to adapt to varying food quality, non-ruminants, with their ability to adjust intake relatively freely, might be classed as intermediate feeders.

**FOOD QUALITY AND QUANTITY**

It is well known that the digestibility of foods by ungulates is inversely related to the fibre content, the degree of lignification or the proportion of structural material in the food (e.g. McDonald et al. 1973). High quality items of browse from trees and shrubs tend to be concentrated at the apical meristems. Lignification increases and digestibility by the ungulate decreases with age and with distance from the apical meristem. Other factors, such as the build up to tannins and other substances as plant parts mature, prevent or inhibit digestion by and growth of herbivores (Feeny 1968, Feeny and Bostock 1968, Oh, Jones and Longhurst 1968, Varley 1970). Consequently, ungulates concentrate their browsing of trees and shrubs on young growth. Although such choice items of browse have a high protein content (Field and Blankenheim 1973, Field and Ross 1976), these items tend to be widely spaced and scarce on African rangelands.

In grasses, and probably in non-grass herbs too, the distribution in time and space of available energy and nutrients is uneven (Weinmann 1955). The proportion of structural material increases with age, and is greater for naturally tall than naturally short growing plants. Leaves have a higher nutrient content and a lower fibre content than stems. There are additional factors, by no means well known, which affect acceptability to or digestibility by the ungulate. Although grass is of generally low quality, on African rangelands it is a superabundant food resource for those ungulates which can tolerate fibrous foods.

**CARRYING CAPACITY**

In view of the general inverse relationship, modified by feeding specialisations, between live mass of ungulates and the quality of preferred diet, and in view of the scarcity of concentrated food on African rangelands, the capacity of a given area of rangeland to
Few data are available on carrying capacities for concentrate selectors and intermediate feeders which prefer to browse rather than graze. Many such ungulates are small, non-gregarious, secretive and difficult to census. However, the contribution such ‘browsing’ animals make to total stocking rates has been recorded as small (Lamprey 1965, Mentis 1970, Eltringham 1974). Even if population densities of these animals have been under-estimated, the general conclusion is hardly likely to be affected, because many of the ‘browsers’ are small, and extremely high densities would be required to affect the total stocking rate appreciably.

It might be thought that the views expressed in this paper assume that food is the factor limiting wild ungulate populations. Sinclair (1974) has shown such limitation to be important for at least some ungulate species. Perhaps food is not universally a proximate limiting factor, but this need not alter the relationships in Fig. 2 from which it is suggested that food is a likely ultimate factor limiting population growth. It has yet to be shown whether the so-called ‘sensitive’ species such as roan antelope (Hippotragus equinus), sable antelope (H. niger) and common reedbuck (Redunca arundinum) require any special conservation measures after the stocking rate has been trimmed and balanced in accord with the provisions stated so far in this paper.

**STOCKING RATE AND ANIMAL PRODUCTION**

In ecology, the inverse relationship, above a certain population density, between stocking rate and animal production per animal is implicit in the logistic equation

\[
\frac{dN}{dt} = rN \left( \frac{K - N}{K} \right)
\]

where \( N \) is the number of animals at time \( t \), \( r \) is the intrinsic rate of natural increase, and \( K \) is the asymptotic value of \( N \). \( K \) is termed the carrying capacity and represents an equilibrium level at which limiting factors prevent further sustained population increase (Odum 1971). It is widely conceded that the population growth curve often does not follow the logistic equation, and \( N \) may exceed \( K \) on occasions. Regarding the latter point, an alternative definition of carrying capacity is desirable where the upper level of stocking is that which can be

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**FIG. 2. Diagrammatic representation of carrying capacities of grasslands and woodlands for African ruminants expressed in relation to live mass of animal, relative requirement for concentrated food, and selectivity in feeding. BRE = bulk and roughage eaters; IF = intermediate feeders; and CS = concentrate selectors.**
maintained indefinitely without damage to the veld (e.g. Booyzen 1967). Nevertheless, ecologists have used the logistic model in discussing relationships between ungulates and their habitats (Watson 1969, Laws 1969). Further, it has been suggested that the optimal density of animals, providing the maximum harvestable yield, corresponds to the point of inflection of the growth curve (i.e. where the rate of population growth per unit time begins to decrease) (Dasmann 1964: 193) (Fig. 3).

There are methodological and theoretical objections to the above approach to ungulate production.

Regarding the former objections, if population growth does not accord with the logistic equation, the values of r for values of N outside those observed can only be guessed. If population increase does approximate to the logistic equation, the only practicable means of ascertaining r for most wild ungulate populations is to measure the rate at which a newly established population increases initially, or to fit a curve to the growth of a population after its density has been reduced artificially (Caughley and Birch 1971). Both these methods depend on non-interference of the populations during observation. But the purpose of finding the optimal density is to maximise yield, and harvesting the yield is interference. Harvesting is likely to alter the age distribution and therefore r, and more importantly, harvesting is likely to introduce compensatory mortality such that at least some animals that would have died naturally are harvested.

The theoretical objection to the optimal density perceived by Dasmann (1964) is that it tacitly assumes that maximum sustained yield per unit area of land is the goal. In reality, it is economics which will, within limits, dictate the optimal stocking rate. Where such an optimum is defined as the stocking rate yielding maximum percentage return on costs, it may be determined from the nature of the relationship between stocking rate and animal production per animal (or per unit area of land), and from the relative costs of land, animals, development and management (Booyzen, Tainton and Foran 1975).

To illustrate the implications of the economic factors in determining the optimal stocking rate, observations on the production of blesbok run with cattle and stocked in four paddocks at four different levels are considered (Table 2, Fig. 4). In this example, development costs were regarded as nil, since such facilities (fencing and water troughs) were provided for cattle, the primary crop on the land. The analysis deals only with blesbok, but clearly they and the cattle must be considered jointly if the profitability of a mixed cattle-blesbok system were to be examined. Two economic environments were chosen, namely, expensive land and inexpensive animals, and inexpensive land and expensive animals.

After inspection, second degree polynomials were fitted to the relationships between stocking rate and animal production per animal, and animal production per unit area of land. The respective equations were (Fig. 4):

\[ p = 16.28 + 12.1s - 290s^2 \ (r = 0.8334; P < 0.05) \] (8)
\[ g = 0.225 + 17s - 29s^2 \ (r = 0.8193; P < 0.05) \] (9)

where p is the production per animal expressed as the daily gain in kg of saleable carcass per day, g is the production per unit area of land expressed as the annual gain in kg of saleable carcass per ha, and s is the stocking rate expressed in equation (8) in ha/blesbok, and in equation (9) in blesbok/1 ha.

Since the fit of both curves to the data is tolerably good, the maxima of production per animal and per ha may be calculated readily. In the generalised second degree polynomial

\[ Y = A + BX - CX^2 \] (10)

The peak of the inverted parabola occurs where

\[ \frac{dY}{dX} = 0 \]

Since

\[ \frac{dY}{dX} = B - 2CX, \]

the point where change in X brings no change in Y is ascertained by solving for X.

\[ B = 2CX = 0 \]
\[ X = \frac{B}{2C} \]

Accordingly, the stocking rates at which maximum production per animal and per ha are achieved are 0.209 and 0.293 blesbok/ha respectively.

Although not a necessary consequence of the logistic equation (7), in the present example, production per animal was low at very low stocking rates, increased with stocking rate, and then declined as the stocking rate increased to high levels. This pattern has been observed previously in domestic cattle (Carew 1976). Because of this particular relationship between stocking rate and production per animal, the transformation of the data to production per ha results in the fitted parabola being displaced to the left of the data themselves (Fig. 4). For this reason, the stocking rate yielding the maximum percentage return on costs was calculated by an iterative method, substituting values of s and solving for p in equation (8). The value of s corresponding to the maximum percentage return on costs (or to the minimum percentage loss on costs), y, is then found by substituting the solved values of p in the equation...
TABLE 2. Production of blesbok per animal and per hectare, and costs in relation to stocking rate for two arbitrarily chosen economic environments (Case 1 and Case 2) where blesbok were stocked at four different levels in four separate paddocks.

<table>
<thead>
<tr>
<th>PADDOCKS</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>s = stocking rate (ha/blesbok) (blesbok/1 ha)</td>
<td>5.11</td>
<td>12.75</td>
<td>25.33</td>
<td>2.28</td>
</tr>
<tr>
<td>p = production per animal (kg/day)</td>
<td>0.1957</td>
<td>0.0784</td>
<td>0.0395</td>
<td>0.4386</td>
</tr>
<tr>
<td>g = production per ha (kg/ha/yr)</td>
<td>0.0292</td>
<td>0.0257</td>
<td>0.0205</td>
<td>0.0116</td>
</tr>
<tr>
<td>t = time period in days</td>
<td>2,0858</td>
<td>0.7354</td>
<td>0.2955</td>
<td>1,8570</td>
</tr>
<tr>
<td>h = cost of land (rand/ha)</td>
<td>365</td>
<td>365</td>
<td>365</td>
<td>365</td>
</tr>
<tr>
<td>a = cost of blesbok (rand/head)</td>
<td>200</td>
<td>200</td>
<td>200</td>
<td>200</td>
</tr>
<tr>
<td>r = price received (rand/kg)</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>v = management costs (rand/ha)</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
</tr>
<tr>
<td>d = development costs</td>
<td>nil</td>
<td>nil</td>
<td>nil</td>
<td>nil</td>
</tr>
</tbody>
</table>

For the present example, the optimal stocking rates for blesbok were 0.333 blesbok/ha (Case 1) and 0.243 blesbok/ha (Case 2). On pragmatic grounds, it is incongruous that the optimal stocking rate in case 1 exceeds the stocking level yielding maximum production per ha. However, it is suggested that the pragmatic grounds are correct, but, for reasons already stated, the curve from equation (9) is displaced unduly to the left of the actual relationship between animal production per ha and stocking rate. Clearly, once the relationships between stocking rate and animal production per animal and per ha have been ascertained, the nature of these relationships must be considered carefully so that an appropriate method of calculating the economic optimum can be decided. Of course, the economic criteria applied may not necessarily require a maximum return (or minimum loss) on costs. An alternative goal might be to maximise absolute nett profit, but here again calculations rest on the relationship between stocking rate and animal production (Booysen 1975).

The observations cited above on blesbok are not definitive, and do not necessarily reflect average production figures from blesbok stocked at different levels on the particular vegetation type (dry tall grass veld (Phillips 1973)) concerned. The data have been used here merely to illustrate principles and methods. The most important conclusion arising from these principles and methods is that economic optima do not necessarily coincide with maximal biological production. As the purchase costs of animals and the costs of development and management per animal rise in relation to the other costs so will the economically optimal stocking rate be depressed further and further below the stocking rate maximising secondary production.

As far as I am aware, for no African ungulate has the relationship between stocking rate and animal production...
TABLE 3. Herbivore efficiency ratios calculated in kilocalories per square meter per year, and compared to mean individual live mass.

<table>
<thead>
<tr>
<th>Efficiency ratios</th>
<th>Elephant (Loxodonta africana)</th>
<th>Cow (Bos taurus)</th>
<th>Moose (Alces alces)</th>
<th>Blesbok (Damaliscus dorcas)</th>
<th>Deer (Odocoileus virginianus)</th>
<th>Mouse (Microtus pennsylvanicus)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>0.059</td>
<td>0.115</td>
<td>0.25</td>
<td>0.29</td>
<td>0.5</td>
<td>2.5</td>
</tr>
<tr>
<td>2.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Assimilation/ food consumed</td>
<td>3.38</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food consumed/ standing crop</td>
<td>10.38</td>
<td>1.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth/food consumed</td>
<td>0.0057</td>
<td>0.060</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Assimilation/food consumed</td>
<td>0.326</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maintenance/food consumed</td>
<td>0.320</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth/assimilation</td>
<td>0.017</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean individual live mass (kg)</td>
<td>2 000</td>
<td>460</td>
<td>300</td>
<td>55</td>
<td>50</td>
<td>0.1</td>
</tr>
</tbody>
</table>

1. Laws, Parker and Johnstone (1975)
2. Petrides, Golley and Brisbin (1968)
3. du Plessis (1972)

The relative productive efficiencies of bulk and roughage eaters and concentrate selectors may be expected to parallel the efficiencies of large and small ungulates. Concentrate selectors select and ingest concentrated food which they are likely to digest and assimilate efficiently, but their absolute production will be limited by the scarcity of suitable food.

It has been claimed that African ungulates breed faster, grow quicker and are therefore more productive than domestic cattle (Talbot et al. 1965). However, domestic cattle are large bulk and roughage eaters while most wild ungulates are smaller than domestic cattle, and many wild ungulates are concentrate selectors or intermediate feeders. Accordingly, most wild ungulates may be expected to feed more selectively, and to ingest more concentrated food than domestic cattle. It is uncertain, therefore, to what extent these factors contribute to high fecundity and rapid maturation of wild ungulates, and to what extent individual wild ungulate species might indeed be superior to domestic cattle as secondary producers. In this context, any meaningful interspecific comparisons of secondary productivity must be related to total primary production. However, in practice the entrepreneur asks at what rate and in what proportion should which of a variety of ungulates be stocked to maximise return on costs. Efficiency ratios such as those in Table 3 do not provide a direct answer.

The respective merits of large or small, domestic or wild ungulates of the various feeding types might be determined by varying the total stocking rate and its proportionate animal species composition, and by monitoring animal production per 'animal unit', where one animal unit is defined as that biomass of ungulate consuming the same amount of energy per unit time as an average steer of 455 kg. The method of calculating...

be determined satisfactorily on any vegetation type. The technique is readily applicable to farmland in southern Africa where the popular game species, such as impala, blesbok and springbok (Antidorcas marsupialis) are either localised in habit or are readily contained by ordinary stock fences.

RELATIVE PRODUCTIVE EFFICIENCIES

Data on the productive efficiencies of a variety of mammalian herbivores are given in Table 3. Expressed either in terms of growth/standing crop or as growth/food consumed, efficiency increases with decrease in the size of the animal, cattle being an efficient exception as regards growth/food consumed.

Interspecific differences in assimilation and maintenance in relation to food consumed, and in growth in relation to assimilation, are relatively small. It appears therefore that the major interspecific differences in productive efficiency arise between the foraging and assimilation stages, as opposed to how efficiently an animal uses assimilated food. These major differences might result from the greater ability of small rather than large animals to select and ingest concentrated food which, by virtue of its ready digestibility, is digested quickly thus permitting a high intake relative to metabolic mass. However, despite the resulting apparent efficiency of small herbivores, high quality food is scarce on African rangelands. Small ungulates are therefore inefficient in that they are incapable of converting much of primary production. The point is emphasized by the relative position of the carrying capacity, $K$, for blesbok in Fig. 4. Although, as expected, $K$ exceeds any optimal stocking rate for blesbok, $K$ is only 40% of what is considered a carrying capacity for cattle (Mentis and Duke 1976).
the percentage return on costs is suggested in Table 4. Experiments to ascertain the relationships between species composition, stocking rate and animal production should be done in conjunction with monitoring range condition.

TABLE 4. Suggested method of calculating the percentage return on costs from a multiple species community of ungulates (after Booysen et al. 1975).

<table>
<thead>
<tr>
<th>Percentage return on costs, y</th>
<th>= 100 ( \frac{p t r - s (h + d + v) - a}{s (h + d + v) + a} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Where s</td>
<td>stocking rate in ha/AU, one AU being the biomass of ungulate consuming the same amount of energy per unit time as an average steer weighing 455 kg.</td>
</tr>
<tr>
<td>p</td>
<td>production per AU per day.</td>
</tr>
<tr>
<td>t</td>
<td>period of time in days.</td>
</tr>
<tr>
<td>h</td>
<td>costs of land per ha.</td>
</tr>
<tr>
<td>d</td>
<td>cost of development per ha.</td>
</tr>
<tr>
<td>a</td>
<td>cost of animals per AU.</td>
</tr>
<tr>
<td>r</td>
<td>price received per AU harvested.</td>
</tr>
<tr>
<td>v</td>
<td>management costs per ha.</td>
</tr>
</tbody>
</table>

DISCUSSION

The practical implications of the matters considered above relate firstly to measuring and expressing the standing crop of ungulates, secondly to deciding on the ideal size and species composition of the standing crop in relation to stated management goals, and thirdly to the meat production potential of African ungulates.

(i) Standing crop

The expression of stocking rate based on energy consumption is superior to estimates based on biomass or simple population size. The arbitrarily chosen 'animal unit' permits ready comparison of stocking rates between areas regardless of the species occurring, and it is a convenient base for calculating optimal stocking rates and combinations of species in the commercial exploitation of ungulates. It must not be thought, however, that use of energy consumption to express stocking rates necessarily implies that energy is an important factor in population limitation. Studies such as those of Bell (1970) and Sinclair (1974) suggest that, where food is a limiting factor, it is the availability of nutrients rather than of energy which is critical.

(ii) Management goals

Management goals for national parks (or game reserves) and game ranches differ. In a park, emphasis is on preserving the native biota and the natural order. On a ranch, there is financial incentive. In neither case is management necessarily directed at sustained maximum biological production. In a park, the desired stocking rate is likely to approximate to the carrying capacity above the inflection-point in Fig. 3. However, on a ranch the optimal stocking rate depends partly on economic considerations. The natural diversity of a park is not necessarily conducive to economically producing from a ranch the commodities to satisfy man's needs. Park and ranch managers therefore need not necessarily stock the same ungulate species, and even if they do, total stocking rates and relative contributions by different species are likely to differ.

(iii) Meat production potential

The validity of the early views on the meat production potential of African ungulates depends on the types of land to which the views are applied, and on what aspects of the views emphasis is laid.

There are areas unsuitable for domestic ungulates, for reasons of topography, aridity and disease. But many such areas are distant from markets, have in any case a low primary production, and the very character of the land does not facilitate ready harvesting. As the capacity of the land to support wild ungulates declines, and as the accessibility of the terrain to motor vehicle decreases, so the effort to harvest and market animals becomes increasingly uneconomic. It is unrealistic therefore to expect that marginal land can necessarily support more than a meagre subsistence economy.

Per unit metabolic mass, many wild ungulates are potentially more, not less, damaging to their habitats than are domestic cattle. The reason is that many wild ungulates are smaller and feed more selectively than domestic cattle (Mentis and Duke 1976). This contradicts the early views which were based on comparisons between wildlife sanctuaries and neighbouring 'tribal trust land' without considering the respective managerial competence and stocking rate history. Recently in South Africa there has been a tendency to enclose private properties with game fences and stock them with wild ungulates. Some of the properties have been stocked heavily, and in many cases small, selective grazers predominate. Managed under a confined continuous grazing system, the trend on such properties is, in the history of natural resource management in South Africa, retrogressive. Agriculturalists have suggested that these 'high stocking rate, continuous grazing systems' applied by the pioneering graziers were the cause of damage to vast areas of rangeland (Acocks 1964). The situation is aggravated by imbalances in large to small stock ratios, and Mentis and Duke (1976) believe that these imbalances are a root cause of grazing problems that bedevil the management of many wildlife areas.

Regarding the alleged productive and economic superiority of game compared to cattle ranching, Talbot et al. (1965) presented data on stocking rates and animal production without demonstrating the actual relationships existing between the two sets of phenomena. Dasmann and Mossman (1961) aimed to 'demonstrate quickly the economic potential of big game mammals'. Firstly, such intentions are spurious, since scientific method enables hypotheses to be falsified, not proved correct. Secondly, on the evidence given, their conclusion is falsifiable. Die-offs of zebra and other grazing species were reported, suggesting that the land was overstocked. In comparing cattle and game ranching, 'some years' of veld improvement were required for cattle but not for game ranching on the as yet undeveloped portion of the property. By implication, the game mammals caused the need for veld improvement, but the authors, in effect, advocate that the unsatisfactory circumstances of degraded or degrading habitat be perpetuated in the interests of preserving the native biota. While Johnstone (1975) came to the same conclusion as Dasmann and Mossman (1961), he did not consider the possibility that the combined effects of wild and domestic animals prior to initiating his game ranching operation might have resulted in cattle ranching being considered uneconomic. All three of the above mentioned publications lay
emphasis on the 'wild' versus the 'domestic' ungulates, rather than on the 'complete community' versus the 'one or two species'. Adopting the former rather than the latter emphasis appears to result from an ideal to preserve complete wild communities on the basis of a preconceived utilitarian merit of such communities. The preconceptions arise perhaps from speculation that climax communities exhibit maximum turnover of energy (Macladyen 1963), and that African ungulates are adapted to local conditions and must consequently be more productive than introduced exotic ungulates (Huxley 1961; Talbot et al. 1965). Overlooked are the points that it is the availability of nutrients, rather than of energy, which is important in the resource limitation of African ungulates (Sinclair 1974), and that, whereas domestic ungulates have been bred selectively for production, among wild animals natural selection favours those individuals leaving most surviving offspring (Moss 1975). Further, as already stated, the ideals of preserving complete wild communities (in parks) and of producing meat to maximise economic return (from ranches) are two separate objectives involving different maxims in selecting species and in setting stocking rates and the proportionate contributions of the various species.

Regarding the emphasis of 'complete community' versus 'one or two species', the complete community may be expected to be the more productive, provided interspecific competition is no more than partial. At least in South Africa there are reasons why a complete community need not comprise only wild ungulates if meat production is the goal. Firstly, for reasons of disease and lack of availability, some wild ungulates cannot be stocked on private land. Secondly, in the absence of large wild grazing ungulates like buffalo (Syncerus caffer) and zebra (Equus burchelli) there is only one practicable alternative filling the same niche, namely domestic cattle which have been bred selectively for production and for which the managerial technology is relatively well developed. Thirdly, there is nevertheless a variety of wild ungulates from which to choose species which are compatible with or supplementary to extensive farming with domestic livestock. Fourthly, a mixed domestic and wild ungulate system has merit in permitting the manager a measure of flexibility in shifting emphasis to one or other of the animal types depending on his experience, and on changing economic and other circumstances. Although the mixed system might enable a close approximation to the complete community, it is not as pleasing aesthetically to the wildlife preservationist as is the purely wild community. But it must be conceded that the mixed system, if popular, favours the survival of at least some wild species over that greater part of the subcontinent which is suitable for only extensive pastoral farming. In Natal, mixed systems are more popular among farmers than is game ranching with only wild ungulates (Natal Parks Board, unpublished records). Almost universally the motives of the landowners in managing wild ungulates with their domestic livestock are aesthetic and recreational. In some cases there is additional economic incentive.

While the above would appear to be the existing prospects which relate specifically to South Africa, it is emphasized that the fundamental relationships between stocking rate, species composition and animal performance per animal or per unit area of land have yet to be studied. The optimal stocking rate and combination of ungulates, wild or domestic or both, is therefore not known, and in any case a universal answer is unlikely because, given even a standard biological environment, socio-economic conditions vary in time and space.

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REFERENCES


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