Effect of animal husbandry on herbivore-carrying capacity at a regional scale

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ALL significant properties of the herbivore trophic level, including biomass, consumption and productivity, are significantly correlated with primary productivity across a broad range of terrestrial ecosystems[1,2]. Here we show that livestock biomass in South American agricultural ecosystems across a 25-fold gradient of primary productivity exhibited a relationship with a slope essentially identical to unmanaged ecosystems, but with a substantially greater *y*-intercept. Therefore the biomass of herbivores supported per unit of primary productivity is about an order of magnitude greater in agricultural than in natural ecosystems, for a given level of primary production. We also present evidence of an increase in livestock body size with primary productivity, a pattern previously characterized in natural ecosystems[3]. To our knowledge this is the first quantitative documentation at a regional scale of the impact of animal husbandry practices, such as herding, stock selection and veterinary care, on the biomass and size-structure of livestock herds compared with native herbivores.

Our objectives were to assess the impact of human intervention on herbivore carrying capacity, to determine whether the close relationship between natural herbivore biomass and primary productivity observed across terrestrial habitats[1,2] reflects a limitation imposed by primary production, and to assess the impact of human intervention on the relationship between herbivore body size and primary productivity. We searched for a geographic region where (1) rangelands grazed by domestic herbivores are dominant, (2) primary production varies over a broad range, and (3) management practices are limited to elementary animal husbandry. The southern portion of South America meets those criteria. Together with the North American Great Plains, Asian grasslands and African savannas, it represents one of Earth's largest expanses of natural rangelands. South American rangelands encompass several vegetation types: desert, steppe, subhumid temperate grassland and subtropical savanna. They are used principally by domestic herbivores, cattle (*Bos indicus*) and sheep (*Ovis aries*). The technological level of husbandry practices is more developed than pastoralism, but does not reach the intensities of care characteristic of Europe or North America. Animals are rarely fed silage or grain, and management practices that tend to increase primary productivity, such as fertilization, irrigation and forage species replacement, are rare. But effort is devoted to the improvement of animal status: herds are organized by categories, ranches are subdivided in paddocks, water holes are abundant, veterinary care is intense, predators and parasites are controlled, and breed purity is highly appreciated.

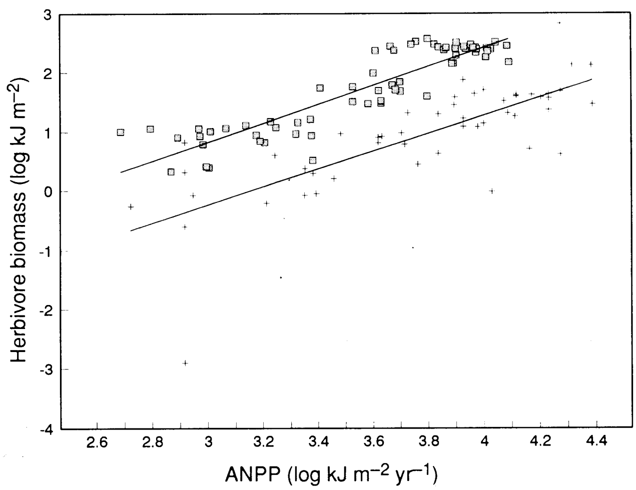

FIG. 1 Relationship between net above-ground primary productivity (ANPP) and herbivore biomass for natural (crosses) and agricultural (squares) ecosystems. The data set consisted of 67 agricultural points and 51 natural points. The latter were taken from refs 1 and 2. Logarithms are on a decimal base. Energy-biomass conversion units are 9,900 kJ per kg livestock fresh weight[20] and 16.76 kJ per gram of ANPP (ref. 21).

We compiled a data set of livestock biomass from censuses at the county level across Argentina and Uruguay[4,5]. Above-ground net primary productivity (ANPP) was estimated from annual rainfall data[6] using a linear model[7] that closely fits primary productivity data for 14 sites in South America[8]. Our data set was compared with recently published data on herbivore biomass, from insects to large ungulates, in natural terrestrial habitats[1,2].

Livestock biomass, B (kJ m^{-2}), was associated with ANPP (kJ m^{-2} yr^{-1}; $r^2 = 0.797$, $P < 0.000001$, d.f. = 65) by $\log B = 1.602 \log \mathrm{ANPP} - 3.98$. A comparison of this pattern with the best-fit line from natural ecosystems (Fig. 1) reveals similarity of slopes, but a significant difference in y-intercept. The slope for natural habitats was 1.52, not significantly different from the slope for agricultural ecosystems ($P = 0.706$, d.f. = 1, 114). The y-intercept for natural habitats was −4.79, significantly lower than that for livestock ($P < 0.00001$, d.f. = 1, 115). Livestock biomass supported per unit of primary production was about an order of magnitude greater than herbivore biomass in natural ecosystems.

In natural ecosystems, increasing herbivore biomass with primary productivity is accompanied by an increase in average herbivore body size[3]. A similar pattern was documented for livestock in our data set (Fig. 2). The proportion of sheep biomass decreased, whereas the proportion of cattle increased along the productivity gradient. This is not the result of compulsory management techniques. Therefore it must be the result of ecological constraints, but we are not certain about the ecological determinants of this pattern.

The results have four major implications for ecosystem theory and agricultural practice. First, the exponential relationship between livestock biomass and primary productivity described here provides a quantitative reference for those attempting to determine the long-term carrying capacity of a system, a key step in rangeland management[9].

Second, the data suggest that although herbivore biomass and primary productivity are closely related in natural ecosystems, primary productivity is not the only limiting factor (see ref. 10 and refs therein). Determining the factors influencing the carrying capacity of ecosystems has been a major concern of ecology since its beginnings[11,12], and is an obvious pursuit of range management. Elementary management techniques aimed at providing drinking water and minerals, regulating animal distribution and reducing parasitism, predation and disease have a large impact on ecosystem-carrying capacity. In agreement with our results, it has been shown that herbivore biomass and rainfall in African systems are related[13], and that agricultural and pastoral systems have greater herbivore biomass than their natural counterparts[13,14].

Third, the results can contribute to resolving a contradiction between suggestions that a high density of wild ungulates may improve forage resources[15] but a high density of livestock depletes them[16]. It has been proposed that grazing by herds of wild ungulates results in the formation of grazing lawns that favour forage intake due to higher forage concentration per unit volume, higher nutritional quality and reduced mastication time[15]. This claim is contradicted by evidence from agroecosystems showing that high herbivore density leads to a deterioration of forage resources[16]. Our results indicate that 'high density' has a very different meaning when comparing the two types of ecosystem as there is a tenfold difference in herbivore load between them.

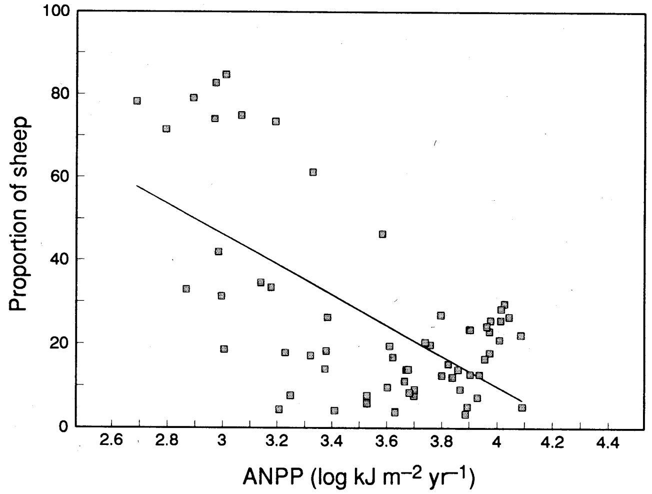

FIG. 2 Relationship between the angular-transformed proportion of sheep biomass and ANPP (kJ m^{-2} yr^{-1}) across a variety of rangeland agroecosystems in southern South America. Proportions were angularly transformed to homogenize variances. The best-fit line was $y = 155.9 - 36.51$ log ANPP ($r^2 = 0.38$, $P < 0.000001$, d.f. 65).

Finally, the results can explain the greater grazing effects on grassland species composition in South America compared with those in Africa. Subhumid grasslands of South America are invaded by exotic, mostly European, species when grazed by livestock and the importance of native grasses is drastically reduced[17]. In contrast, equivalent subhumid grasslands in East African game reserves are always dominated by native grasses, even under high grazing pressure[18]. A general model of the impact of grazing on community structure[19] attributed this difference to the longer evolutionary history of grazing in African grasslands and savannas compared with those in South America, whose grazer and browser fauna almost totally failed to survive the Pleistocene extinctions of large herbivorous mammals. Our results show that grazing evolutionary history is not the only major difference between these systems. The much higher herbivore load supported by South American agricultural grasslands over the past two centuries may contribute to their different response to grazing. □

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