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Serengeti Ungulates: Feeding Selectivity Influences the Effectiveness of Plant Defense Guilds

Abstract. Association of Themeda triandra, a palatable grass species, with less palatable plants protected it from grazing by two comparatively unselective herbivores, wildebeest and African buffalo. Grazing on T. triandra by two more selective herbivores, Thomson's gazelle and zebra, was not related to the relative abundance of less palatable plants. The differential effectiveness of plant defense guilds against different ungulates may contribute to the high species diversity of the East African grazer fauna.

Consumption of palatable forage plants by domestic ungulates is reduced when the palatable species are spatially associated with unpalatable plants in pastures (1). Atsatt and O'Dowd (2) proposed that such functional interdependence among plant species constitutes plant defense guilds. This report presents the first evidence, from studies in the Serengeti ecosystem, that such defense guilds may influence consumption by large wild herbivores. However, the protection from grazing afforded to a palatable species by association with unpalatable plants was not sustained as herbivore feeding selectivity increased.

East African ecosystems are well known for high biomasses and diversities of large, wild, grazing ungulates (3). The proportion of net above-ground primary productivity consumed by these herbivores is higher than has been reported for any other terrestrial grazing food web (4). This suggests that herbivore impact upon forage plants is intense, and places a premium on effective strategies of plant "escape" from grazing. In addition, the general ungulate fauna is one of substantial antiquity (5), suggesting a long period of plant-herbivore coevolution that might distinguish relations between animals and their food plants in these ecosystems from those involving domestic ungulates and their food plants. To examine the effectiveness of plant defense guilds in such an ecosystem, experiments were done in Tanzania's Serengeti National Park and Kenya's Masai-Mara Game Reserve during the dry seasons of 1974 and 1975. Forage quality falls below maintenance requirements of the animals during the dry season (6), and therefore acceptable forage should be strongly sought after by grazers during this period. Consumption of a highly palatable (7) grass, Themeda triandra Forsk., was determined in stands where



Fig. 1. Relation between relative abundance of unpalatable plants in a grassland and the percentage of Themeda triandra that was eaten by four herbivore species: (top) wildebeest (•) and buffalo (\Box); (bottom) zebra (\circ) and Thompson's gazelle (*). r_p is the partial correlation coefficient with T. triandra relative abundance held constant. Each point is the mean of four replicate samples in a single study stand.

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the proportion of such less palatable (7) species as Cymbopogon excavatus (Hochst.) Stapf, Loudetia kagerensis (K. Schum) Hutch., and Pennisetum mezianum Leeke varied. An exclosure was erected in a test stand, and consumption was estimated by comparing fenced and unfenced areas before and after standard grazing periods ranging from 4 to 14 days, depending on grazing intensity (8). Although genotypic variations in palatability within plant species are well known (9), I assume that unpalatable genotypes of T. triandra were not preferentially associated with other plant species of generally low palatability.

I studied four species of large grazing ungulates: wildebeest (Connochaetes taurinus albojubatus Thomas), Thomson's gazelle (Gazella thomsonii Gunther), zebra (Equus burchelli Gray), and African buffalo (Syncerus caffer Sparrman). These species constitute the vast majority of the grazing biomass in the Serengeti ecosystem (10). Spatial segregation between these grazers during the dry season is pronounced (11), and hence study stands were isolated where grazing was confined to a single animal species (12). Previous studies suggest that zebra and Thomson's gazelle are more selective feeders than wildebeest and buffalo (13). I calculated feeding selectivity directly from randomly placed study sites, rather than those utilized in this experiment, as

$$S = \Sigma |p_{\rm s} - p_{\rm c}| / 2$$

where p_s was the proportional abundance of a plant species in fenced control areas, $p_{\rm c}$ was the proportional abundance of that species in consumption by a given herbivore population (8), and the absolute value of the differences are summed for all plant species. This index will be zero if animals consume species in the same proportions as their abundances in the plant community, and will approach one as consumption becomes the inverse of species relative abundance. I found mean dry season selectivities to be 0.189 for wildebeest, 0.215 for buffalo, 0.315 for zebra, and 0.335 for Thomson's gazelle ($F_{3,14} = 10.470$ for P < .001). The least significant difference for a three-way comparison (P =.05) was .036. So, during the dry season, the species fall into two groups, the less selective species being wildebeest and buffalo, and the more selective species being zebra and Thomson's gazelle. Therefore, I combined data for analyses of the effect on consumption of T. triandra of association with unpalatable plants.

One potentially serious design defect in studies of defense by association is the

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problem of changing relative abundance in the plants studied as the abundance of associates changes, either through vegetation differences or through experimental manipulation. For instance, if an unpalatable species is merely removed differentially from different parts of a pasture, without controlling overall plant density, the relative abundance of palatable plants de facto increases. And in my studies an increase in the proportion of less palatable species in a grassland generally was accompanied by a decline in T. triandra relative abundance. I controlled for this by applying the partial correlation coefficient (r_p) , statistically removing the effect of variations in T. triandra relative abundance.

The proportion of T. triandra eaten by the two less selective grazers decreased as the relative abundance of unpalatable plants in the stand increased (Fig. 1). The best-fit line indicates that about 80 percent of the T. triandra present initially was eaten when there were no unpalatable plants present, and none of it was eaten when unpalatable associates reached about 95 percent of the initial grassland biomass. This was not merely a reflection of lower total consumption by these grazers as the proportion of unpalatable forage plants increased. For instance, in the stand where wildebeest consumption of T. triandra was zero, total consumption was 28 percent of the initial forage biomass (t = 2.855 for P < .01, with d.f. = 8, in comparison of fenced and unfenced areas).

Behavioral manifestations of changes in wildebeest feeding patterns were obvious. Large concentrations of animals moved slowly through grasslands with a low representation of unpalatables, feeding relatively continuously. As the proportion of palatable plants diminished, both the number of animals and the rate of their movement were influenced. Fewer wildebeest fed in stands where unpalatable forage was concentrated, and individuals moved rapidly through such stands, stopping only occasionally for brief grazing periods. Buffalo are much more wary than wildebeest in these study areas and also feed at night to a considerable extent during the dry season (14), and hence changes in feeding behavior were not observed.

For the more selective grazers, such as Thomson's gazelle and zebra, the proportion of T. triandra consumed was not related to the proportion of less palatable forage plants in a stand (Fig. 1). Rather, the pattern was completely chaotic. Thus, zebra consumption of T. triandra

was none and 82 percent in two stands, both with a high representation of less palatable forage plants.

The relation between herbivores and their food plants is complex, involving whole suites of plant properties and animal behavior patterns. The degree of complexity may be considerable in large ungulates, since feeding selection operates at several different levels. These animals may select geographic regions in their migratory movements (15), grassland stands within those regions (11), and plant species (13) and plant parts (16)within a given stand. My experiments indicate that plant defense guilds may protect palatable forage plants from less selective grazers, but are ineffective against grazing by more selective feeders. The mechanisms of these differences are undoubtedly complicated, involving specific search images (17), learning of plant distribution patterns (18), and modifications of food preferences according to availability (19).

One of the remarkable features of the large ungulates of East Africa is the unparalleled species diversity. I have shown previously that wildebeest grazing facilitates energy flow into the gazelle population during the dry season because of stimulation of above-ground productivity and production of a grass growth form more favorable for gazelle grazing (20). The data presented here provide additional definition to our understanding of the mechanisms of species coexistence in this fauna by providing evidence that plant defense guilds are differentially effective against different ungulates. Such mechanisms of resource partitioning (21) represent subtle interactions among grassland properties and foraging behaviors of the grazers, undoubtedly a consequence of the long coevolutionary history of this ecosystem.

S. J. MCNAUGHTON

Biological Research Laboratories,

Syracuse University, Syracuse,

New York 13210, and

Serengeti Research Institute,

P.O. Seronera, via Arusha, Tanzania

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- < .001) 12. Spatial < .001). Spatial segregation among herbivores documented in (11) allowed such experiments to be done. However, before a stand was characterized as, say, a "zebra-grazing" stand, three criteria had to be met: (i) A given herbivore had to be observed on the site in large and preponderant (>95 percent of total) numbers. (ii) Such preponderance of numbers by a single ungulate species had to be observed on several seulate species had to be observed on several sequential visits to a site. (iii) Dung of another spe-
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