THE INFLUENCE OF LARGE ANIMAL DIVERSITY IN GRAZED ECOSYSTEMS

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Abstract

Field observations in the Serengeti National Park, Tanzania have revealed several modes of grazing system, including migration, sustained-yield grazing and grazing succession which contribute on the one hand to ecological separation of herbivores by habitat choice, but on the other hand to positive association of species on wet season pastures known as hot spots. Drawing from results of experimental field studies, we consider what is known about resource competition and facilitation, the two key ecological processes underlying these grazing systems, and specify the shape of the relationship between species richness and pasture height that is predicted depending on which process is dominating in the grazing system. We test between these alternatives by analysing for the first time data on herbivore distributions and vegetation condition from a series of 33 survey flights over the entire Serengeti ecosystem. Our preliminary results strongly support the importance of facilitation as a process structuring the herbivore community of the Serengeti Plains in the wet season. Resource competition may limit use of the shortest swards.

Keywords: Grazing ecosystem, species richness, herbivore biomass, resource competition, facilitation

Introduction

On surveying large herbivores in African savanna parks, ecologists have observed that each species may prefer certain habitats over others, giving rise to a degree of ecological separation (Lamprey 1963, Sinclair 1977); but conversely, a variety of species will sometimes concentrate in the same habitats giving rise to hot spots of species richness (McNaughton and Banyikwa 1995). Longer-term observation has revealed that these same herbivores may take part in extensive grazing patterns. Most notable are the long distance migrations of wildebeest, zebra and gazelle in the Serengeti-Mara ecosystem and of kob and tiang in southern Sudan (Bell 1971; Fryxell and Sinclair 1988; Howell et al 1989). Other examples include the grazing succession at the end of the wet season, in which the larger herbivores are first to move down the local catena from the short grass community at the top to the tall grasses at the bottom (Vesey-Fitzgerald 1965), and the occupation of new habitat by grazing ungulates following removal of the dominant grazer (Eltringham 1974). It is the aim of ecologists that study these diverse assemblages of large mammals to reveal the primary grazing processes. The question being addressed today is whether an underlying explanation, a kind of unified theory for grazing, can be developed to explain extensive grazing patterns and to predict the distributions of large herbivores across grassland habitats.

Much progress has been made in recent years towards an understanding of how the local biomass and structure of pastures influences the short-term or daily intake of herbivores of different species (Hodgson & Illius 1996), but relatively little is understood about the processes occurring in the grazing community at a larger scale. Research in the Serengeti National Park has shown how an integral part of these large-scale processes, is the modification of vegetation by the herbivores themselves. Which species remain on a particular site depends on how the vegetation has been modified (McNaughton 1976; Murray & Illius 2000). In combination with the stochastic nature of rainfall, disease and other external events, the modification of vegetation by herbivores contributes to the creation of a more dynamic grazing ecosystem.

Grazing processes in the serengeti ecosystem

Principal ecological features of the Serengeti ecosystem in Tanzania are the open grass plains covering an area of approximately 7,500 km^2 in the south and southeast, where rainfall is low (300-700mm per annum), and the open scrub and woodlands, together with smaller grassland plains in the remaining moister areas (up to 1200 mm rainfall), covering some 17,500 km^2 (map in Murray 1995). The gradient in rainfall and in growing conditions is exploited by the migratory wildebeest, which spend the wet season, nominally from November to May on the short grasslands to the southeast and the dry season in the woodlands. They share the ecosystem with some 14 other indigenous grazing ungulates, as well as cattle and other domestic species. The herbivores exploit a great variety of grass species of which more than 120 have been collected in Serengeti National Park. Important forage species are the mat-forming grasses of the southeast, including *Andropogon*, *Digitaria* and *Sporobolus* species and some of the common woodland grasses with erect growth form such as species of *Bothriochloa*, *Digitaria*, *Panicum*, *Pennisetum* and *Themeda*.

A number of effects of grazing can be discerned immediately following the passage of a herd. The height and biomass of swards are reduced and should grazing pressure be sufficiently intense, it may give rise to a ‘grazing lawn’ (Figure 1). If the herbivores specialise in selective feeding, there may be a significant reduction in the content of green leaf in the sward leaving a poor quality, stemmy pasture or ‘grazing stubble’ (Figure 2; Murray & Illius 2000). Over a period of a few days to several weeks, intensive grazing can also give rise to secondary effects in the production of new vegetative growth (McNaughton 1976). But whilst it may be obvious that selective grazing will modify the vegetation in these ways, it has not been known whether this modification would affect the intake of ungulates or whether it would have importance in structuring the ungulate community.

Two resource-based hypotheses have emerged from the studies of grazing ungulates in Serengeti to explain their community dynamics: one is based on competition and the other on facilitation. According to the competition hypothesis, low biomass swards such as grazing lawns will only support herbivores of small body size and/or wide mouths. So the consequence of grazing down a tall sward will be a reduction in the number of herbivore species utilising that sward due to grazing competition (Figure 3; Murray & Illius 2000). According to the facilitation hypothesis, heavy grazing of high biomass swards stimulates new production of more digestible food, creating forage that can be utilised by the smaller herbivore species, and so the overall number of herbivore species will increase (Figure 4).

In order to test these two hypotheses we have undertaken a preliminary analysis of a dataset of large mammal distributions compiled by the Serengeti Ecological Monitoring Programme (SEMP) from monthly aerial surveys of the Serengeti-Mara ecosystem over the period, July 1969 to August 1972. Each month several planes and crews took part in the survey of the entire ecosystem, recording information against a 5 X 5 km grid. Observations of the more common large animals (wildebeest, zebra, Thomson’s gazelle, Grant’s gazelle, topi, hartebeest, giraffe, rhino, elephant, buffalo, impala, eland and cattle) were recorded according to one of four abundance classes: 1-25; 26-250; 251-2500; 2501+. Observations of rare or low density species (roan, oryx, warthog, ostrich, lion, cheetah, leopard, reedbuck, kudu, waterbuck and bushbuck) were also noted, usually with an actual count of numbers seen. In the case of burnt ground, the state of grass regrowth was classified as bare ground, or in one of five height classes. The greenness of regrowth was assigned to one of five classes, varying from dry and parched to lush. On unburnt ground, the height and greenness of unburnt grass were also each assigned to one of five classes. In all, data from 33 reconnaisance flights were entered into the database by SEMP.

The combined biomass of large herbivores on the Serengeti Plains during the wet season was highest at an intermediate height of vegetation, indicating that food may have been limiting on the shortest grass swards, but quality may have been limiting on the tallest grass swards (Figure 5). However, species richness was maintained on the shorter swards, and only declined on the tallest pastures (Figure 6). This result suggests that facilitation of grazing may be enabling more species to utilise short pastures. In order to investigate this possibility further, an index of vegetation quality (q) was defined as: q = greenness class / height class. Thus, the highest values of quality were assigned to short green swards and the lowest to tall non-green swards. The quality index (q) predicted mean herbivore biomass with surprising accuracy (Figure 7). Species richness was also closely correlated with vegetation quality (Figure 8). These results further indicate that ungulates tend to congregate in large numbers on the high quality swards in the Serengeti Plains during the wet season, and that the overall interaction between herbivores and grasslands facilitates the formation of higher species richness in the herbivores.

Conclusion

Although our analysis of the 1969-1972 survey data is preliminary, these first results emphasise the importance of grazing pressure by large herds in creating pastures that can be utilised by many species, so confirming the early observations of Vesey-Fitzgerald (1965) and McNaughton (1976). The findings here relate solely to the Plains grasslands in the wet seasons, but the occurrence of hot spots of species richness in the woodlands area suggests that facilitation may be of widespread importance in the ecosystem (McNaughton 1988). In addition to this ecological process, the reduction in herbivore biomass that was evident on the shortest swards suggests that there are conditions on the Plains in which intake by herbivores may be constrained. This could lead to differential displacement of herbivore species because of differences in the threshold at which sward height and biomass begin to limit food intake (Murray & Illius 2000). The survey data reveal a low abundance of buffalo (the heaviest ruminant grazer) on the Plains, which may indicate the effect of resource competition. This would suggest that the overall pattern of community dynamics amongst grazing herbivores in the Serengeti ecosystem is being influenced by both competition and facilitation processes. There is a need for greater resolution in the methods used to study competition and facilitation so as to clarify their influence on large animal diversity.

Acknowledgements

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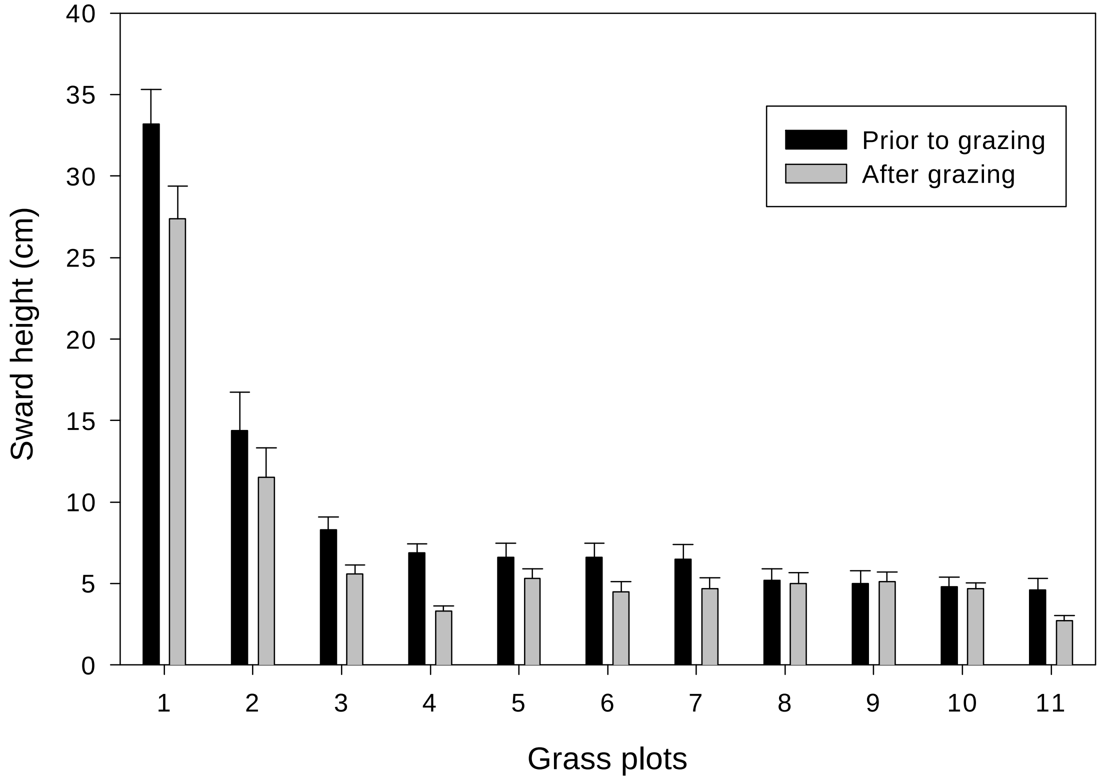


Figure 1 - Evidence for resource depletion during periods of foraging by topi and wildebeest: mean height of green leaf in the sward with standard errors are shown for experimental plots before and after grazing trials.

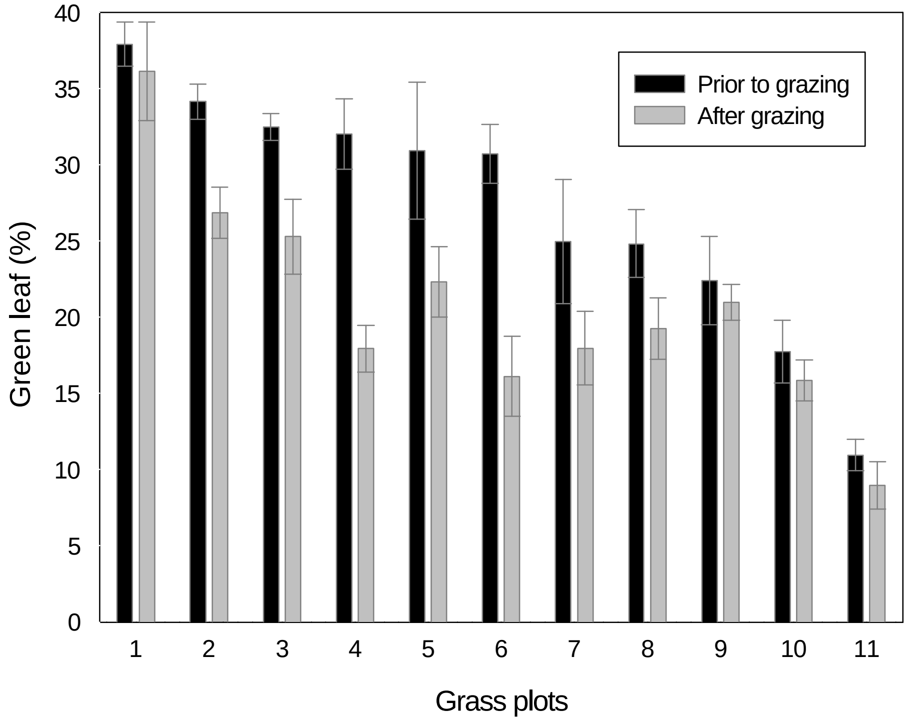


Figure 2 - Evidence for depletion of resource quality during periods of foraging by topi and wildebeest: mean proportion of green leaf in the sward with standard errors as measured in experimental plots before and after grazing.

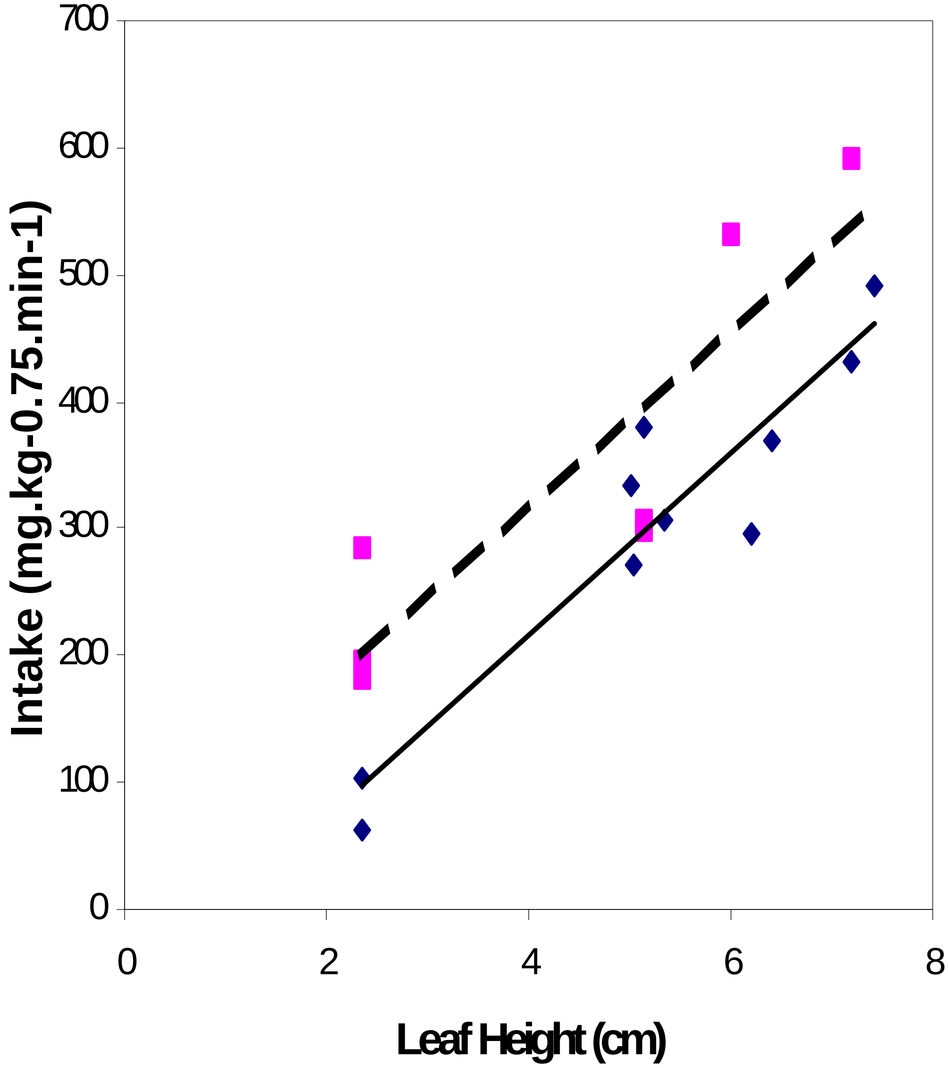
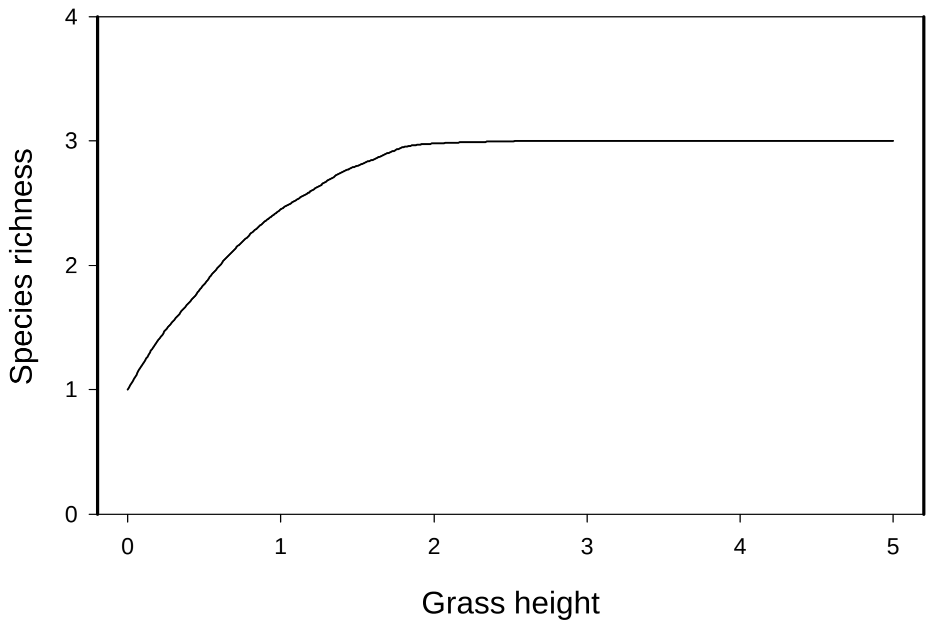
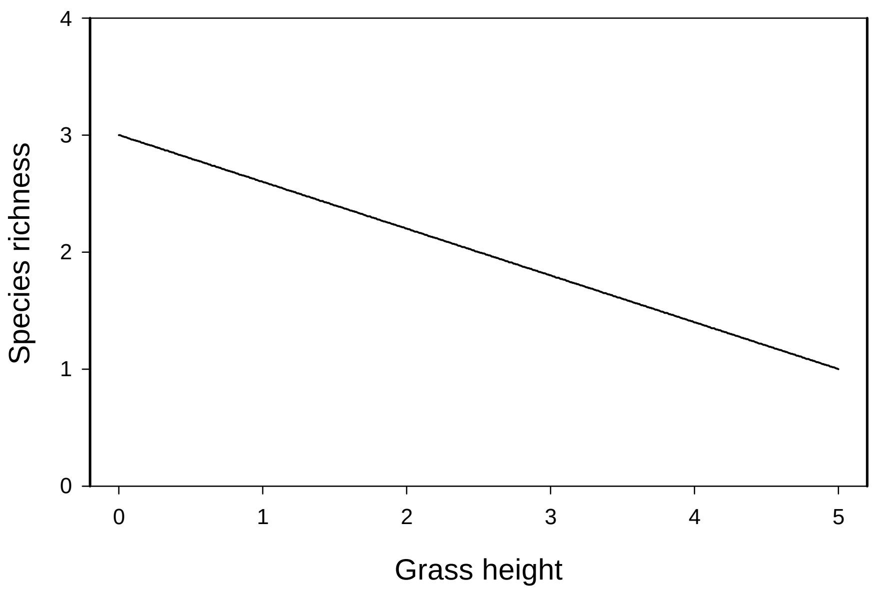


Figure 3 - Intake rate of yearling wildebeest (filled squares) and topi (filled diamonds) feeding on grass swards in an early vegetative growth stage within the Serengeti National Park.



a) Competition model



b) Facilitation model

Figure 4 - The relationship between herbivore species richness and the height of grass in savanna habitats, as predicted by a) a classical model of resource competition and b) a model of resource facilitation (see text for further details).

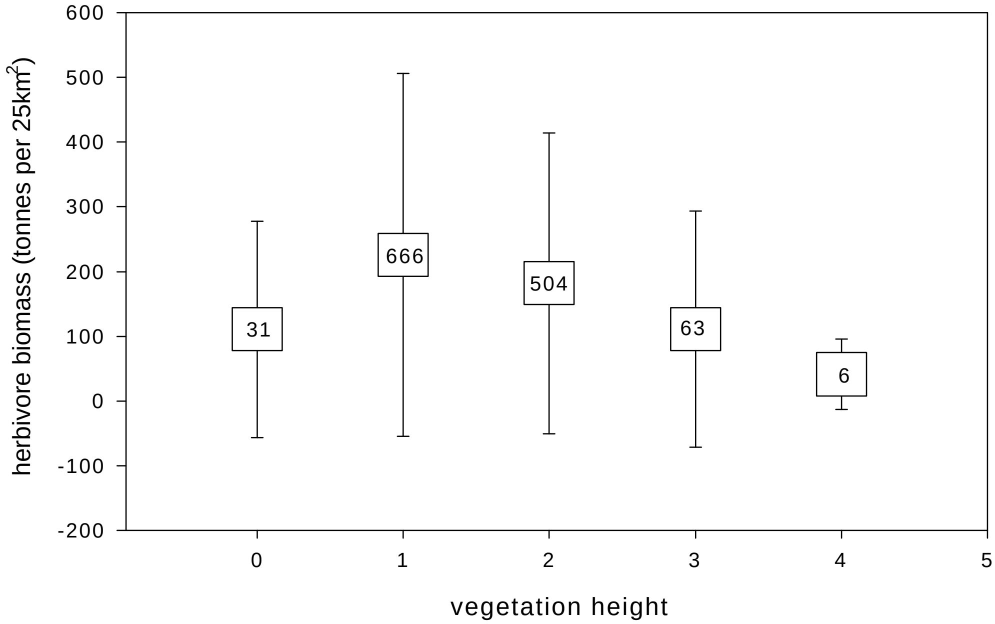


Figure 5 - Observed relationship between herbivore biomass (combined for all species) and grass height in the Serengeti Plains during the wet season months, January to May, based on survey flights from 1969-1972. Mean herbivore biomass is indicated by the boxes containing the sample size (i.e. the number of 5 X 5 km survey quadrats of that vegetation height); bars indicate the standard deviation.

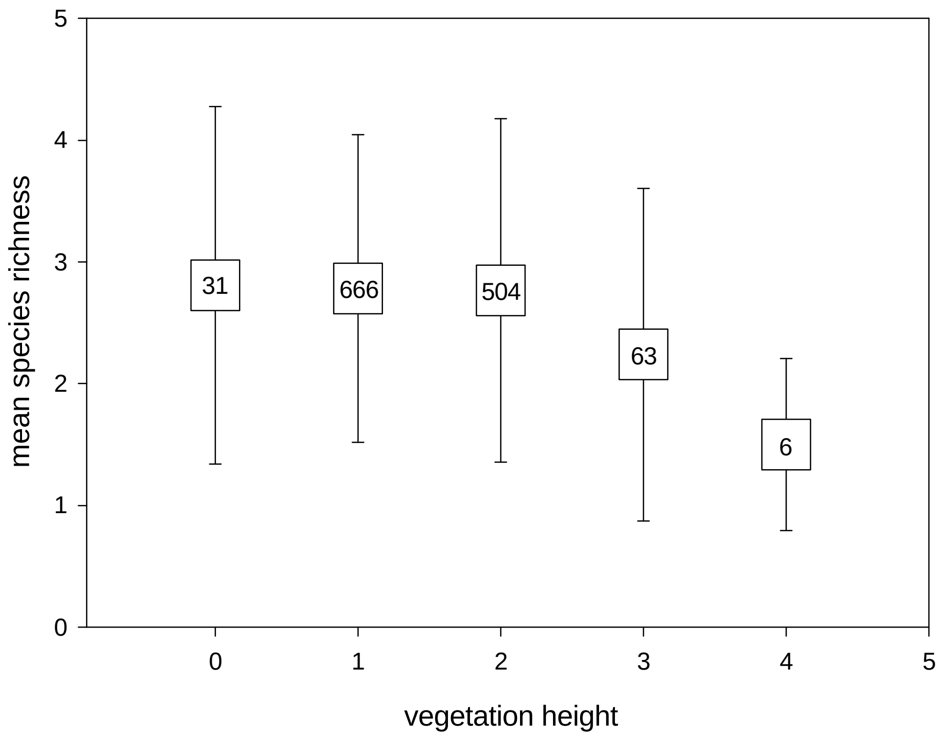


Figure 6 - Observed relationship between herbivore species richness and grass height in the Serengeti Plains during the wet season months, January to May, based on survey flights from 1969-1972. Mean species richness is indicated by the boxes containing the sample size (i.e. the number of 5 X 5 km survey quadrats of that vegetation height); bars indicate the standard deviation.

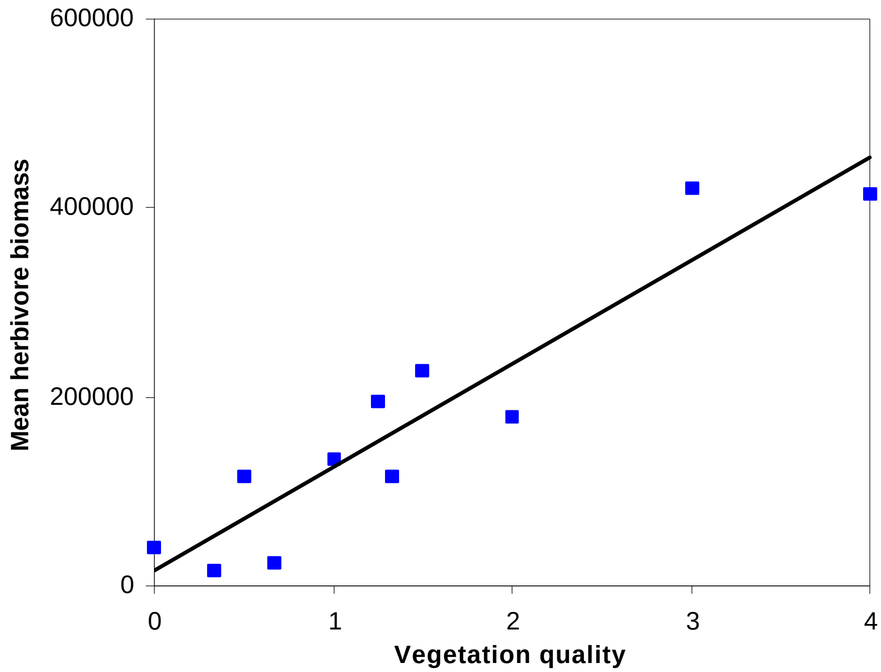


Figure 7 - Relationship between herbivore biomass (tonnes per 25 km^2) and the vegetation quality on the Serengeti Plains in the wet season (R^2 = 0.86, P<0.001).

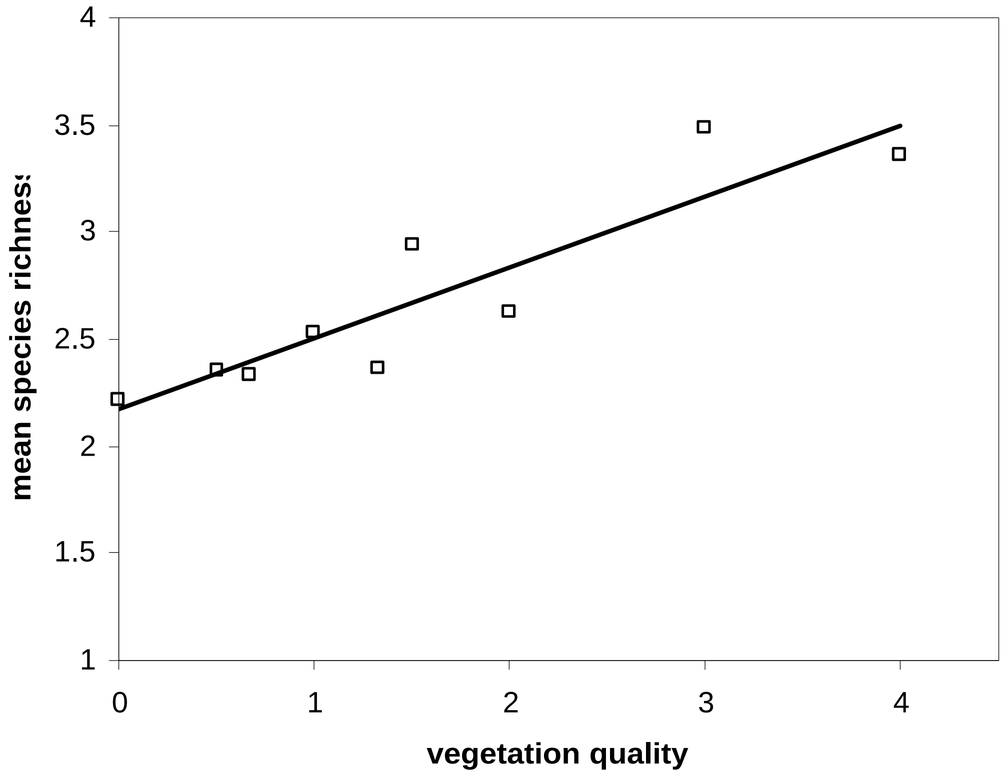


Figure 8 - Relationship between species richness of herbivores and the vegetation quality on the Serengeti Plains in the wet season (R^2 = 0.80, P<0.001).