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Ecology

# Carnivore dominance and herbivore coexistence in Africa

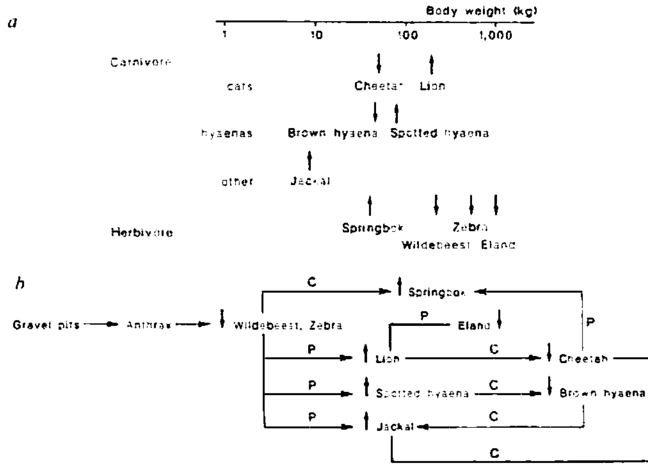
*from Jared M. Diamond*

Most concepts of temperate-zone ecology are derived from studies in Europe and North America, but are such concepts really appropriate to the temperate zone of southern Africa? This issue was debated at two meetings last year in South Africa: a symposium on competition and coexistence, held by the Zoological Society of South Africa at Pietermaritzburg (23–25 July, 1985); and a workshop on terrestrial ecology at Houw Hoek organized by the Foundation for Research Development (1–3 August, 1985). Two studies of large mammals discussed at these meetings illustrate some of the special problems of southern African ecology.

The first is an unintended natural experiment on a large scale (Hugh Berry, Etosha National Park: *Madoqua* **12**, 242, 255, 1981; **13** 151, 1982). The gravel pits excavated in Etosha during road construction produced entirely unexpected large-scale changes in the mammal community of the plains. The trophic relationships and size structure of this community are outlined in *a* in the figure. As a result of the seemingly modest disturbance there were crashes in the wildebeest and zebra populations; declines in cheetah, brown hyaena and eland; and increases in lions, spotted hyaenas, jackal and springbok.

Berry reconstructed the causal sequence of these changes as follows (*b* in the figure): rainwater standing in the alkaline gravel pits became a reservoir for anthrax bacteria, to which wildebeest and zebra are especially susceptible; and the resulting abundance of sick or dead prey more than offset the effects of the decline in healthy prey, causing a population surge of the two dominant and largest species of carnivores/scavengers, the lion and the spotted hyaena, which are immune to anthrax. The lions reduced the population of eland, which suffered little from anthrax but are a favourite alternative prey of lions. The lions and spotted hyaenas competitively suppressed the next largest species of cat and hyaenid, the cheetah and brown hyaena, respectively. Relief from competing cheetahs and brown hyaenas, together with the abundance of carcasses, permitted the next-largest carnivore/scavenger, the black-backed jackal, to increase. Competitive release was also seen among herbivores — the wildebeest and zebra crashes permitted the smaller and more anthrax-resistant springbok (which also profited from the decline of cheetah, its major predator) to increase.

Berry's work illustrates the unique insights that careful study of the natural environment can yield. Ecologists will never be permitted to kill 25,000 wildebeest out of curiosity, but the same result produced by anthrax has illustrated how predation and competition control population sizes of mammals on the Etosha plains.




*a*, Trophic relationships and size structure of mammals from the Etosha National Park. *b*, Inferred causal sequences of changes in the community. ↑, Increased abundance; ↓, decreased abundance; P, predator/prey interaction; C, competitive interaction.

The second study concerned species coexistence among Africa's diverse large herbivorous mammals, which include 78 species of bovids. Several species often feed right next to each other and Richard Emslie (University of Witwatersrand) has examined the niche specializations that permit this coexistence among five large grazers in Umfolozi Game Reserve — white rhinoceros, buffalo, zebra, wildebeest and impala, adding a new level of detail to previous analyses.

After individual animals had finished grazing, Emslie searched their feeding sites for freshly defoliated surfaces, measuring the vegetation available within a 0.25 $m^2$ hoop and recording what had been eaten and how it had been eaten. Every plant in the hoop was examined and every tiller (the unit of a grass tuft) of the two key grass species *Themeda trianda* and *Panicum coloratum* was measured. He also monitored the availability of vegetation over an area of 33.25 $km^2$ by measuring within each 25-hectare block. This yielded data on resource selection over a hierarchy of levels, ranging from 25-hectare areas to parts of individual plants.

At the coarsest level, buffalo selected areas (25 hectares) with a high biomass of tall grass, whereas the other four species chose areas of shorter grass. In the short grass areas, impala selected feeding patches dominated by *P. coloratum*, whereas wildebeest, often only a few metres away, sought patches with short *T. triandra*. Within feeding patches, the different species selected different tillers of the same grass species — the short erect tillers in the centre of *P. coloratum* plants grazed preferentially by wildebeest and white rhino, with their lawnmower-like wide muzzle and lips, and the longer, more prostrate tillers at the edge of tufts were eaten by the narrower-muzzled zebra and impala. Buffalo rejected tall *T. triandra* but selected medium-height tillers (40 – 75 cm), whereas wildebeest favoured short leafy tillers with no stem. Clearly, ecological studies that list only the species eaten omit considerations that are important to grazers.

Previous studies have revealed ecological differences among herbivores related to their differing body sizes and digestive anatomies (Bell, R. in *Animal Populations in Relation to Their Feeding Resources* ed. Watson, A. p. 111; British Ecological Society, 1970 and Jarman, P. *Behaviour* **48**, 215; 1974). Big animals cannot afford to be as selective about food as their related smaller species. On one hand, the non-ruminant zebra processes large quantities of low-quality plant matter quickly and inefficiently; on the other, ruminants process smaller quantities of higher-quality matter more slowly and efficiently. Emslie's studies now emphasize the importance of differing mouth anatomy as well. It is these differences that give rise to the familiar African scene of diverse large herbivores grazing next to each other, apparently in contempt of Gause's competitive exclusion principle but actually exploiting habitat heterogeneity at many scales. □

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## Corrigendum

The article by Jeremy Berg (*Nature* **319** 264; 1986), which discussed the repeated domains in the TFIIIA protein described by Miller *et al.* (*EMBO J.* **4** 1609; 1986), should have mentioned that the repeating nature of the TFIIIA sequence has been independently noted by R.S Brown and coworkers (Brown, R.S., Sander, C. & Argos, P. *FEBS Lett.* **186**, 271; 1985).