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# Ecology: Megaherbivores Homogenize the Landscape of Fear

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**When herbivores avoid areas with high predation risk, the intensity of plant consumption and nutrient deposition is distributed unevenly across landscapes. Experimental work in African savanna ecosystems shows that the biggest herbivores, virtually immune to predators, smooth out these imbalances.**

In 1960, Hairston, Smith, and Slobodkin [1] sketched an idea that would exert a defining influence on ecology. Contending that ''cases of obvious depletion of green plants by herbivores are exceptions to the general picture, in which the plants are abundant and largely intact,'' they reasoned that herbivore populations are limited by predation and therefore do not compete for (or deplete) their food supply. This scenario, wherein predators indirectly benefit plants by keeping herbivore numbers in check, was later dubbed a 'trophic cascade' [2]; the label refers to the trickle-down effects of predators onto successively lower levels of the food chain. The Hairston *et al.* [1] paper seems almost designed to spark controversy: its tone was provocative, its scope sweeping, its implications profound, its premises debatable. The logic was appealing, but the authors did not present any hard data, nor did they acknowledge much in the way of nuance. Decades of debate, refinement, and elaboration ensued.

Fast-forward to 2018: evidence of trophic cascades has accumulated from a variety of ecological systems [3–5]. Studies have shown not only that predators frequently affect plant communities, but also that they can influence nutrient cycling and other ecosystem functions [6]. Among the refinements to the original concept, one has been particularly influential — predators need not consume prey to create trophic cascade [7,8]. Fear itself is often sufficient. For example, anxious grazers may avoid low-visibility habitats where predation risk is high, thereby converting dangerous places for herbivores into safe spaces for plants. Still, a fundamental question remains unanswered: how far can we generalize from the most conclusive analyses of trophic cascades (which derive from experiments on relatively small organisms in tractable model systems) and scale them up to the largest organisms in the largest landscapes (which have the greatest bearing on environmental policy)? The difficulty of manipulating big animals and the ubiquity of confounding variables have precluded the kind of mechanistic precision attained in smaller-scale systems, leaving uncertainty about how trophic cascades might operate in large-mammal assemblages [9]. A new study by Elizabeth Le Roux, Graham Kerley and Joris Cromsigt [10], published in this issue of *Current Biology*, sheds fresh light on this challenging problem.

African savannas, with their diversity of mammalian herbivores and carnivores spanning multiple orders-of-magnitude in body size, are a pivotal testing ground for trophic-cascade theory. Such diversity might dampen or conceal trophic cascades if different herbivore species respond to predation risk in contrasting ways. In these ecosystems, susceptibility to predation is a function of body size [11]. Smaller herbivores, such as antelopes, are eaten by a range of carnivores, and their populations tend to be limited by predation — just as postulated by Hairston *et al.* [1]. Larger species, however, are harder to bring down, and fewer carnivores are up to the task. The largest megaherbivores ($\geq$1000 kg), including rhinoceroses, hippopotamus, and elephant, are essentially invulnerable to predation as adults [12].

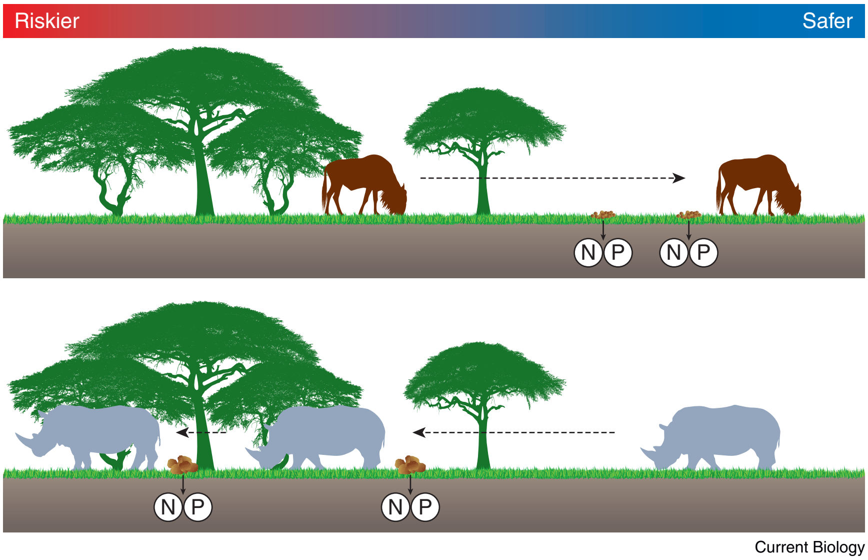


**Figure 1. Countercurrent nutrient exchange driven by differential risk sensitivity.**
Top: Mid-sized herbivores, such as wildebeest, graze and defecate disproportionately in high-visibility areas, which have lower predation risk, leading to nutrient accumulation in safer open areas. Bottom: Megaherbivores, such as white rhinoceros, consume large amounts of plant biomass and distribute nutrients more evenly across the landscape.

These disparities in size and security should generate a gradient of risk-avoidance behavior, and therefore in the outcome of fear-driven cascades. Grazing mesoherbivores, such as warthog, impala, and wildebeest, should congregate in open areas with high visibility and fewer places for carnivores to hide. By depositing dung and urine in these refuges, they should contribute to the accretion of nutrients and the local enrichment of soils. Megaherbivores, however, should be indifferent to this risk gradient and disperse nutrients broadly — a conveyor belt of organic material circulating fearlessly around the landscape.

Working in South Africa's Hluhluwe-iMfolozi Park, Le Roux and colleagues [10] set up an experiment to test this hypothesis. By removing trees and shrubs, they created open glades within the savanna matrix. (Similar experiments in Kenya have shown that mesoherbivores favor such clearings for their safety, irrespective of food availability [13,14].) Mid-sized grazers foraged slightly more frequently in high-visibility areas but deposited far more nitrogen and phosphorus in cleared plots than in bushy controls, suggesting that they both import and locally recycle nutrients. Megaherbivores, in contrast, foraged and defecated without regard for visibility and ate huge amounts of biomass wherever they went, apparently helping to export nutrients from open areas. Among the mesograzers, the smallest (read: most vulnerable) species responded most strongly to the habitat manipulation, adding weight to the idea of a size-biased risk-aversion continuum.

These results suggest a countercurrent exchange of nutrients across the landscape, powered by herbivores' differential sensitivity to predation risk (Figure 1). There remains some uncertainty in the accounting, as the authors were not able to fully balance the equations: the amount of dung that megaherbivores deposited in the experimental plots was not commensurate with the estimated amount of biomass they consumed, which might reflect constraints on the spatial scale of the manipulation. The mystery of this missing scat is partly illuminated by a series of larger-scale transect surveys, which revealed that elephant and white rhino dung was more plentiful in thicketed woodland than in open savanna, reinforcing the countercurrent hypothesis. Other mysteries remain to be worked out. Unlike the mesograzers, which eat mostly grass, mesobrowsers, such as kudu and nyala, which eat mostly woody plants, exerted greater herbivory pressure in low-visibility wooded areas. Although browsers were negligible consumers and nutrient-transporters in this system, they are more prevalent elsewhere and might function similarly to megaherbivores by

**Figure 2. Megaherbivores are relatively insensitive to predation risk.**
Elephants ignore a lioness while foraging in central Kenya.

dissipating the imbalances established by open-habitat grazers. Likewise, the potentially contrasting effects on nutrient distribution of predators with different attack modes [15], such as ambush-hunting leopards versus coursing wild dogs, warrant further investigation.

It is clear that top-down control in African savannas is strong, but not simple. The abundance and behavior of smaller grazers is constrained by apex carnivores [11,14], but not to the point of preventing them from depleting vegetation [16]; trophic cascades do occur [10,13], but not invariably [17]. Because megaherbivores are far less constrained by predators (Figure 2), they exert strong top-down control that can counteract, erase, or even outweigh the effects of trophic cascades involving smaller herbivores [10]. As a result of these countervailing forces, conventional predator-driven trophic cascades may occur simultaneously within multiple individual food chains yet be undetectable at the level of the entire food web. Classic theory holds that the effects of trophic cascades attenuate or switch sign depending on the number of trophic levels in the food chain [18], but functional and body-size diversity within herbivore guilds can generate similar outcomes in three-level food webs.

Le Roux and colleagues [10] put it more succinctly: ''trophic cascades work differently in a world of giants.'' This statement refers to more than just the distinctiveness of contemporary African food webs. In the Pleistocene, many ecosystems worldwide were similar to those in African protected areas today. In North America, for example, mammoths and mastodons are hypothesized [12] to have been functional analogs of white rhinos and elephants: consumers of enormous plant biomass, rarely depredated as adults (but see [19]), and perhaps counterbalancing the effects of trophic cascades involving American lions, saber-toothed cats, and mesoherbivore prey. When *Homo sapiens* went viral at the end of the Pleistocene, spearing megaherbivores into oblivion on four continents, they created a new, cleaner trophic cascade — one in which essentially all herbivores were susceptible to predation and the landscape of fear. Ironically, and perhaps not coincidentally, the view that inspired the original conception of trophic cascades — a green world in which plants are ''largely intact'' [1] — was itself shaped by a trophic cascade: a downsized world in which the dominant plant-depleters had already been depleted by human super-predators.

Today, megaherbivores persist only in small and shrinking pockets of Africa and Asia, which provide the last living windows into ecological prehistory. All are at risk of extinction, some imminently, and the human onslaught is far from finished. Even where megaherbivore populations cling on, their numbers are often insufficient to fulfill their unique ecological functions. In this regard, however, Hluhluwe-iMfolozi and several other African parks offer rays of hope. The white rhino population in Hluhluwe has rebounded from the brink of extinction, and elephants are thriving after having been reintroduced. Farther north, in Mozambique, the megafauna of Gorongosa National Park, nearly extirpated in the 1990s, has recovered dramatically over the past 15 years thanks to large-scale restoration [20]. Only by similarly reconstructing megaherbivore and apex-predator guilds in the many other places where they have disappeared can we restore the complementary functional roles of big animals that induce fear and even bigger animals that disregard it.

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