How large herbivores subsidize aquatic food webs in African savannas

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Mass migration—the periodic, synchronized movement of large numbers of animals from one place to another—is an important part of the life cycle of many species. Such migrations are variously a means of avoiding climatic stress, escaping food and water scarcity, and satiating predators (thereby reducing individuals' risk of being eaten). They are among the most spectacular of natural phenomena, and also among the most threatened: by building walls and dams, disrupting the climate, and decimating wildlife populations, people have steadily diminished and extinguished many of the huge migrations known from historical records (1, 2). Although tragic on purely aesthetic grounds—nobody today knows the music of several million American bison (*Bison bison*) snuffling and shuffling across the Great Plains—the extinction of great migrations also poses a profound threat to the functioning of ecosystems. In PNAS, Subalusky et al. (3) show how one of the world's last vast overland migrations, the seasonal movement of ∼1.2 million wildebeest (*Connochaetes taurinus*) through East Africa's Serengeti–Mara Ecosystem, couples terrestrial and aquatic food webs. Each year, thousands of wildebeest drown while trying to cross the Mara river, injecting the water with massive doses of carbon, nitrogen, phosphorus, and other nutrients, much of which is taken up by aquatic organisms. When wildebeest sleep with the fishes, the fishes feast.

The Serengeti wildebeest, along with more than 200,000 zebra (*Equus quagga*) and 400,000 gazelles (*Eudorcas thomsonii*), follow the rains in a clockwise loop from the southern part of Tanzania's Serengeti National Park into Kenya's Maasai Mara National Reserve, and back again (Fig. 1). The river crossings that they must undertake to complete this annual cycle are dramatic events that attract thousands of tourists, who watch as animals fling themselves into the water (and occasionally into the jaws of lurking crocodiles). It had been observed that some wildebeest also drown while trying to cross, but Subalusky et al. (3) provide the first quantitative multiyear accounting of this phenomenon, and of what happens to the nutrients that drowned wildebeest carry into the river in their bodies. The numbers involved are staggering: mass drownings occurred in the Kenyan portion of the Mara almost every year from 2001 to 2015, on average four to five times per year, resulting in a mean annual total of 6,250 wildebeest carcasses. These carcasses contribute more than 1,000 tons of biomass into the river—equivalent to roughly 10 blue whales—comprising dry mass of 107 tons carbon, 25 tons nitrogen, and 13 tons phosphorus.

Subalusky et al. (3) conducted a suite of detailed measurements and calculations to track the fate of these nutrients. By combining photographic surveys of carcasses with an energetic model for vultures, they estimate that avian scavengers consume 4–7% of the carbon and nitrogen, much of which is transported back to land (Fig. 1*C*). Unscavenged soft tissues—such as skin, muscle, and internal organs, which together make up 56% of each carcass—decompose rapidly within 70 d, saturating the water with nutrients that are either assimilated locally by biofilms (algae, bacteria, fungi) or else transported downstream (Fig. 1*E*). The remaining 44% of each carcass is bone, which decays slowly; thus, 95% of the phosphorus, 25% of the nitrogen, and 29% of the carbon present in wildebeest carcasses ends up in a kind of extended-release capsule, slowly infusing the river with nutrients over a period of 7 y (Fig. 1*F*). Collectively, these pathways account for around half of the carbon and nitrogen and the vast majority of phosphorus entering the river via wildebeest carcasses. The remainder flows into two as yet unquantified pathways: atmospheric loss (e.g., CO_2 and N_2 produced during microbial breakdown of tissues) and in-stream consumption by aquatic animals (Fig. 1 *G*–*I*). Although it therefore remains to be determined what overall fraction of wildebeest-derived nutrients actually enters the riverine food web, the contribution is substantial: stable-isotope analyses revealed that wildebeest account for between 34% and 50% of the assimilated diet of three fish species when carcasses are present, and between 7% and 24% (derived from biofilm growing on bones) after soft tissues decomposed (3).

The nutrient budget assembled by Subalusky et al. (3) provides valuable insights into the ecological functioning not just of rivers, but also of the larger landscapes

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Fig. 1. Subsidies linking terrestrial and aquatic food webs in African savannas. (*A*) Large herbivores visit water to feed and drink, and their excretions wash into the river. (*B*) Hippopotami graze on land at night and spend their days partially submerged, showering dung and urine into the river (13). Drowned wildebeest carcasses provide food for (*C*) vultures, which move nutrients back to land, and (*D*) crocodiles. (*E*) Uneaten soft tissue decomposes rapidly, releasing large pulses of carbon and nitrogen (3). (*F*) Bones take years to decay, slowly leaching nutrients (notably phosphorus) and a providing a substrate where biofilms grow and are grazed by aquatic consumers. Nutrients in the water column can enter aquatic food chains via consumption by (*G*) zooplankton, (*H*) insects and crustaceans, and (*I*) fishes, or be conveyed back into the riparian zone by (*J*) floods, which fertilize the plants eaten by herbivores (*A* and *B*). (*Inset*) Map of the Serengeti wildebeest migration; triangles indicate major river crossings. Figure designed by TerraCommunications.

in which they are embedded. The fluxes of energy and nutrients that link terrestrial and aquatic food webs, known as allochthonous inputs, play a crucial role in structuring and stabilizing these coupled systems (4, 5). Perhaps the best known and most celebrated example of such fluxes involves the migration of Pacific salmon (*Oncorhynchus* spp.) from the ocean into their nutrient-poor natal streams and lakes, where they spawn and die in their thousands (6). This attracts bears (*Ursus* spp.), wolves (*Canis lupus*), and other terrestrial carnivores and scavengers, which kill as many as 40–50% of the salmon (7, 8) and transport the marine-derived nutrients onto land in the form of urine, feces, and uneaten fish scraps. These inputs have transformative effects on riparian ecosystems, supplying up to a quarter of the nitrogen budget, enriching the foliage, increasing plant growth rates, shifting the species composition of vegetation assemblages (6–8), and perhaps even locally depressing the densities of moose by inflating the number of wolves (9).

The work of Subalusky et al. (3) shows that the wildebeest migration plays a very similar functional role: wildebeest are the salmon of the Serengeti, but in reverse, transferring terrestrial-derived nutrients into the river and subsidizing fish. However, wildebeest are not alone in vectoring terrestrial resources into African rivers and lakes (10–12); astonishingly, given the numbers quoted above, they do not even rank first in the Mara River! Another recent study by the Subalusky et al. research team (13) estimated that the Mara's 4,000 hippos (*Hippopotamus amphibius*), which graze nightly on land and return daily to water, contribute 1,277 tons of carbon, 180 tons of nitrogen, and 18 tons of phosphorus to the river each year via dung and urine (Fig. 1*B*). More mundanely, permanent water sources in African savannas attract diverse wildlife species to drink and forage on riparian vegetation that stays green year-round (Fig. 1*A*), concentrating dung and urine inputs, some of which enter the water. Even the vertical structure of riparian vegetation can serve as a source of subsidies, as gravity-assisted downward movement of tree-dwelling insects makes prey available to predators in lower habitat strata (14).

These diverse inputs of terrestrial-derived resources may be particularly important for sustaining Africa's freshwater food webs.

Many of these waters are highly turbid, due to high sediment loads (not to mention enormous quantities of hippo feces and moldering antelope corpses), which reduces the availability of light needed for photosynthesis and in situ (autochthonous) production. Consequently, the abundance of fish and other high-level consumers in these systems likely depends on the regular influx of energy and nutrients assimilated by terrestrial animals in sun-drenched savanna grasslands.

So what would happen if the great wildebeest migration were sapped of its wildebeest and all its greatness, or blocked by an ill-situated highway (15), or if the hippo pods and elephant herds were hunted and harried into oblivion? In the Serengeti, at least, the short-term future seems secure; in fact, its wildebeest, hippo, and elephant populations have all increased in recent decades (3, 16, 17). The same cannot be said for other once-great animal migrations. The biomass of spawning salmon, and associated nitrogen and phosphorus transfers, are down by 93% relative to historical levels throughout the northwestern United States (6). American bison, although no longer in danger of extinction, are also in no danger of returning to their 18th-century range and migration patterns. The migratory saiga antelope (*Saiga tatarica*) of the Asian steppe declined from more than a million individuals in 1993 to fewer than 50,000 in 2008 (2) and remain critically endangered. The disintegration of these migrations has undoubtedly reconfigured nutrient transport and allochthonous fluxes, but reconstructing the details is difficult because there are few reliable baseline data with which to measure change.

Instead, the most promising route to understanding the ecological and biogeochemical consequences of mass animal movements (and their loss) is to focus on extant migrations, as Subalusky et al. (3) have done. Their study raises multiple fascinating questions in need of further research. Now that we know the astounding frequency and ecological significance of wildebeest mass drowning, we need to know why wildebeest mass drown. Subalusky et al. hypothesize that mass drownings result from complex interactions between geomorphology, river discharge, herd size, and tourist behavior; elucidating the role of this last factor, in particular, is of paramount importance for management. Exactly how much of the wildebeest-vectored nutrient load ends up as atmospheric loss and how much as aquatic biomass, and what pathways do the nutrients follow up the food chain? What is the fate and role of other elemental inputs—what of potassium, calcium, iron, molybdenum? And to what extent, if any, do these and other large-herbivore–vectored subsidies bolster the fisheries relied upon by people downstream (18)?

Ecologists are justifiably preoccupied with the specter of species extinction. But as studies like that of Subalusky et al. (3) remind us, the biodiversity of interactions and processes also merit urgent conservation attention: they are what knit ecosystems together and they are easily lost. However, the continuing vibrancy of the Serengeti migration, a century after its devastation by the great rinderpest pandemic, also affirms that nature's great spectacles can, with a little help from their friends, reconstitute themselves. With a concerted global effort to expand protected areas (19) and conserve migration corridors (2), perhaps even some of the storied migrations of yesteryear can be resurrected.

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