Supporting Information

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SI Materials and Methods

Drowning Occurrences and Carcass Numbers. We documented wildebeest crossings and mass drownings in the Kenyan portion of the Mara River from 2001 to 2015 from two sets of historical reports and from field surveys. We collected information on the occurrence of mass drownings from Mara Conservancy monthly newsletters from September 2001 through December 2014. We also collected information from 2003 to 2014 from Governor's Camp monthly newsletters from June through December (the period overlapping the wildebeest migration).

From 2011 to 2015, we worked with Mara Conservancy rangers to collect historical and current locations for wildebeest crossing sites (Fig. 1), and we actively monitored mass drownings during field seasons (2011, June–August; 2012, July–December; 2013–2015, August–December) through direct observation, communication from reserve rangers, and observation of carcass aggregations (Table S1). Field seasons did not always encompass the full period when the migration was present in the Mara region, but they did cover most of the time when river crossings were occurring in every year except 2011. In 2011, discussions with rangers and management staff suggest we did not miss any mass drowning events, but our counts may be an underestimation for that year. We counted the number of carcasses floating downstream from a stationary location if we were present when the drowning occurred, or we counted carcasses as soon as possible after the drowning by walking the riverbank and counting all carcasses until the carcasses became sufficiently scarce that spot checks could be conducted by vehicle at river bends. Final carcass counts were rounded to 10s. When our counts were artificially abbreviated by the Tanzanian border, we estimated the total number of wildebeest drowned by working with reserve rangers who had observed either the drownings or carcass aggregations downstream of the border. These estimations were rounded to 100s. On July 21, 2011, 7 d after a mass drowning at the uppermost crossing site, we mapped carcass locations in the river using handheld maps and a global positioning system unit (Oregon 300; Garmin International, Inc.) and imported data into ArcGIS (Fig. 1*C*).

Carcass Composition. Carcass composition was measured by collecting freshly drowned wildebeest carcasses from the river (1 adult male and 1 subadult male in 2012, and 1 adult female in 2013), dissecting them into their primary components, and weighing each component (Table S2). The percentage of dry mass was measured on triplicate subsamples of each component for the adult female and used to estimate dry mass for components of all carcasses. Triplicate subsamples of each carcass component from each individual were analyzed for C, N, and P composition. Samples were dried at 72 °C (to meet US Department of Agriculture permit import regulations) and finely ground using a cryogenic ball mill. C and N composition was measured using a Costech Elemental Analyzer (Costech Analytical Technologies, Inc.). P composition was measured by digesting preweighed combusted material using 1 M HCl at 80 °C for 2 h, treating with an ammonium molybdate color reagent, and analyzing on a spectrophotometer at 885 nm. Average wildebeest mass values were taken from the literature (21). We estimated a herd to be composed of one-third juveniles (145-kg female, 159-kg male) and two-thirds adults (165-kg female, 210-kg male), with equal sex ratios, giving us an average mass of 175 kg per individual (175 kg·individual^{-1}).

Microbial Decomposition. We measured the decay rate of carcass components due to microbial decomposition by placing subsamples of muscle, intestine, skin, and bone in fine-mesh bags, which were secured inside a metal cage in the river (Table S2). Triplicate samples of muscle, intestine, and skin were collected at five different time points that were predetermined using data from a preliminary decomposition experiment (muscle, days 2–16; intestine, days 4–38; skin, days 8–49). After collection, samples were weighed, dried, and reweighed to measure the percentage of dry mass. Due to the large variability across bone types, triplicate subsamples of leg, rib, scapula, and vertebrae were placed in fine-mesh bags inside the metal cage in the river. Wet weight was measured at five time intervals (days 48–216), and samples were replaced in the bags after weighing. The percentage of dry mass of bone was measured for the final time interval. The decay rate was calculated in R using a single exponential decay function, with a fixed intercept of 100% remaining at time step 0 (44). Days to 95% biomass loss were calculated by dividing ln(0.05) by k (decay rate) (45). The decay rate was calculated using dry mass for muscle, intestine, and skin, and using average wet mass across the different types of bone.

Discharge Data. We collected discharge data for the Mara River from 2011 to 2014, which were used in estimations of nutrient flux and uptake. Discharge was measured at Purungat Bridge, at the lower reach of our study region on the border between Kenya and Tanzania. Stage height data were measured every 15 min from June 2011 through November 2012 using a Rugged TROLL 100 depth transducer corrected with a BaroTROLL barometric pressure logger (In-Situ, Inc.). From December 2012 through December 2014, stage height data were measured every 15 min using a depth transducer probe connected to a Manta2 sonde (Eureka Water Probes).

Stage heights were converted to discharge using a rating curve we developed by measuring discharge on multiple days using the area-velocity method. We measured depth using a handheld staff gauge or weighted measuring tape and velocity using a velocimeter, or we measured depth and velocity with a HydroSurveyor (SonTek/Xylem, Inc.) (46). Discharge was measured 10 times in 2011 and one time in 2014. Due to the bedrock substrate at the channel reach, the channel geomorphology appeared to be consistent over this time period. Three outliers were removed from the rating curve because they fell outside the 95% CI and were collected during the rising or falling limb of a flood, when it is not appropriate to collect data for rating curves. The final rating curve had an adjusted $R^2 = 0.95$.

Nutrient Uptake. After a mass drowning of 5,000 wildebeest on July 14, 2011, we measured nutrient uptake length (S_w), uptake velocity (v_f), and aerial uptake (U) using the carcasses as a high-input nutrient source and declines in concentration downstream as an indication of nutrient uptake in the river (27, 28, 47) (Table S3). Although nutrient uptake is often measured using additions of inorganic nutrients accompanied by a conservative tracer (48), a high-input source and downstream declines have been used to measure nutrient uptake downstream of wastewater treatment plants (27, 28). Measurement of a conservative tracer (Cl^- or Fl^-) is often still used in this approach to detect any influence of dilution. However, discharge data showed this portion of the river received minimal inputs of water from other sources during this time, so we assumed there was no dilution over the study reach.

Water samples were collected directly upstream of the carcasses and at five points downstream of the carcasses, ranging from 5.0–36.9 km, on days 8, 16, and 26 after the drowning occurred. Although this distance is longer than commonly used in

studies of nutrient uptake length, we anticipated that uptake lengths would be long in a river of this size with this level of nutrient loading. NH_4^+ and SRP concentrations were analyzed as described in the section below. For NH_4^+, we accounted for changes in background NH_4^+ concentrations (31.6–60.9 μg NH_4^+-N·L^{-1}) throughout the duration of the sampling period (26 d) by subtracting upstream values from downstream values. We then measured the decline of the corrected values. For SRP, upstream concentrations did not change significantly over the sampling period (29.4–36.8 μg·L^{-1}). Furthermore, upstream values were higher than the furthest downstream values in some cases, possibly due to elevated rates of nutrient uptake. We used non–background-corrected SRP values and simply investigated declines in concentration. DOC concentrations did not decrease steadily downstream of carcasses, so we were not able to calculate DOC uptake.

We used the following equation to estimate nutrient uptake length for each of these three time periods:

$$\ln C_x = \ln C_0 - k_c x,$$

where C_x is the background-corrected nutrient concentration x kilometers from the top of the sampling reach (just downstream of the majority of the carcasses), C_0 is the background-corrected nutrient concentration at the top of the sampling reach, and k_c is the per meter nutrient uptake rate (27, 47). Nutrient uptake length, which is the average distance downstream a nutrient molecule travels before being removed from the water column, is calculated as k_c^{-1} (47).

We calculated nutrient v_f, which is a measure of the speed at which a nutrient molecule moves from the water column to an uptake compartment, using the following equation:

$$v_f = Q\, w^{-1} S_w^{-1},$$

where Q is discharge [cubic meters per day (m^3·d^{-1})], w is wetted width (measured in meters), and S_w is measured in meters (27, 55). We measured w every ∼0.15 km along the river length using Google Earth version 7 (Google) and satellite imagery (DigitalGlobe).

We calculated total U, which is the total flux of nutrient from the water column to the stream bottom, expressed on the basis of stream bottom area, as

$$U = v_f C_b,$$

where v_f is measured as meters per day (m·d^{-1}) and C_b is the background concentration of the nutrient [milligrams per cubic meter (mg·m^{-3})] (55). In a nutrient addition experiment, C_b would be the nutrient concentration in the river reach before the experiment. For this study, C_b could be approximated as the nutrient concentration upstream of the carcasses. However, v_f is calculated for an extended period of elevated nutrient concentrations rather than the upstream level. Therefore, we calculated a range of U values from minimum (U_{min}; based on upstream nutrient concentrations) to maximum (U_{max}; based on the highest measured nutrient concentrations during the sampling period). Actual aerial nutrient flux values will fall somewhere in this range. We calculated both U_{min} and U_{max} values for NH_4^+ and SRP on days 8, 16, and 26 after the drowning. We calculated total aerial uptake over this time period (assuming equal aerial uptake from the beginning of the drowning to day 8) for the 6.5-km reach in which the majority of carcasses were located by measuring the area under the curve in Sigmaplot 12.0 (Systat Software, Inc.). We compared these amounts with the total amount of N and P loaded by the 4,820 carcasses within this reach.

Nutrient Flux. We measured the flux of total and dissolved inorganic nutrient levels and DOC upstream and downstream of carcasses for six different drowning events in 2011, 2012, and 2013. For three of these events, we were able to measure flux for at least 25 d after the drowning, after which carcasses were no longer visibly present in the river and downstream nutrient values had generally returned to baseline levels. We used flux estimations from these three drownings to estimate total downstream transport of carcass nutrients (Table S4). Measurements were taken every 0.5–7 d for a period of 25–29 d per drowning, for a total of 34 sampling days across the three drownings. Water samples were collected for nutrient analysis upstream and downstream of the majority of carcasses from a drowning. The distance between upstream and downstream samples ranged from 3.1 to 5.0 km.

Water samples were kept refrigerated after collection and processed as soon as possible. For DOC analysis, samples were filtered through a glass fiber filter (Whatman GF/F; GE Healthcare Bio-Sciences), acidified with sulfuric acid to pH < 2 for preservation, and analyzed on a total organic carbon analyzer (Shimadzu Scientific Instruments). For TN and TP analysis, unfiltered samples were acidified for preservation, diluted to acceptable sediment levels (<150 mg·L^{-1}) to avoid interference with colorimetric measurements, digested using an alkaline potassium persulfate digestion reagent, and analyzed on an Astoria Analyzer (Astoria-Pacific).

Inorganic nutrient samples were filtered after collection and either analyzed in the field or preserved and analyzed in the laboratory. NH_4^+-N was analyzed in the field using fluorometric methods in 2011–2012 (56, 57) and using the gas exchange method on a portable flow injection analyzer in 2013 (58). Nitrate (NO_3^--N) was analyzed in the laboratory using cadmium reduction on an Astoria Analyzer in 2011 and in the field using zinc reduction on a portable flow injection analyzer in 2012–2013 (59, 60). SRP was analyzed using the molybdate blue method in the laboratory in 2011 and on a portable flow injection analyzer in 2012–2013 (61).

Nutrient concentrations were multiplied by average hourly discharge for the time the sample was collected, and were scaled to estimate nutrient flux in kilograms per day (kg·d^{-1}). Upstream flux was calculated over this time period to compare with carcass loading. Net nutrient flux from the carcasses was calculated by subtracting upstream values from downstream values. Total flux was estimated by measuring the area under the curve in Sigmaplot 12.0 (Systat Software, Inc.). Flux values were compared with total carcass loading levels for C, N, and P, which were quantified by multiplying the number of carcasses between water sampling points by the percentage of C, N, and P composition of a carcass (described above) (Table S2).

Terrestrial Transport via Scavengers. We used game cameras and metabolic models to estimate the use of wildebeest carcasses and fate of nutrients and C consumed by scavengers. We estimated scavenger abundance using a game camera (Trophy Cam HD Max Black LED; Bushnell) placed on two different aggregations of wildebeest carcasses after drownings: one aggregation of 16 carcasses in November 2012 and one aggregation of 40 carcasses in October 2013. The camera was programmed to take a picture every 15 min, and species identification and abundance were recorded every hour from days 5–17 after the drowning occurred in 2012 and days 4–21 in 2013. The majority of scavengers were avian, and the most common species observed were Marabou storks (*Leptoptilos crumenifer*), white-backed vultures (*Gyps africanus*), Rüppell's vultures (*Gyps rueppellii*), and hooded vultures (*Necrosyrtes monachus*) (all referred to below as vultures for ease of description). Individuals of these four species accounted for 80% of all scavengers observed in 2012 and 86% in 2013.

We developed a metabolic model for vulture consumption of carcasses (Table S5) based on estimations of daily energy expenditure (kilojoules per day) of free-living Cape vultures (*Gyps*

coprotheres) of 826.7 $kJ \cdot d^{-1} * kg^{0.61}$ (49). We used this equation and average mass estimations (50) for our four most common species to estimate total energy required daily. We divided this estimation by vulture mean energy assimilation efficiency (86%) to estimate the total daily energy intake required, and we divided that amount by carcass energy content (based on literature estimations of 26 $kJ \cdot g^{-1}$ of ash-free dry mass) to estimate the total dry mass of carcass consumed daily (49). We multiplied this mass by the mean percentage of C, N, and P of wildebeest soft tissue (excluding bone) to estimate total C, N, and P consumed.

We multiplied individual consumption rates by the maximum number of vultures documented daily at each carcass aggregation. We assumed that avian scavengers were obtaining 100% of their energy during this time period from the carcasses, so we used the maximum number of individuals recorded at any point in time each day for each species as our estimation of the number of vultures. Our photographs began on days 4 and 5 after the drowning. We assumed there were no vultures feeding on the first day and a linear increase in vultures to the number present on the first day of photographs. The maximum number of vultures counted on any given day ranged from two to 46 for the 2012 photograph series and from four to 57 for the 2013 photograph series. This number could be a very conservative estimation if vultures only spend several hours feeding at the river and then leave to be replaced by different individuals; thus, we could be underestimating total vulture consumption. We summed the daily consumption of C, N, and P by vultures and compared it with the total amount of C, N, and P loaded by the number of carcasses present in the photographs.

Assimilation by Aquatic Consumers. We used analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to quantify assimilation of wildebeest carcass by fish. We collected basal resources and fish samples in November 2013 (1 mo after a series of large wildebeest mass drownings) and February 2014 (4 mo after the last drowning). Basal resources included biofilm, coarse particulate organic matter (CPOM), and wildebeest tissue. We collected biofilm from rocks and wildebeest bones, which were the dominant substrates in the river, by scraping the surface of the substrate and filtering the slurry onto a precombusted glass fiber filter (Whatman GF/C). We collected a composite CPOM sample by holding a 1-mm mesh net in a well-mixed portion of the river to collect suspended material, which we subsampled for analysis. There is no emergent vegetation in this region of the river and minimal riparian vegetation, and CPOM reflects the majority of terrestrial vegetation that has entered the river, which is predominantly grass loaded by hippos (62). We collected muscle tissue from three recently drowned wildebeest carcasses (one adult male and one subadult male in 2012, and one adult female in 2013). Consumers included three common taxa of fish. *Bagrus docmak* [$n = 3$ in November (125- to 156-mm standard total length) and $n = 3$ in February (147–265 mm)] is largely predacious, consuming insects, crustaceans, and fishes, although debris and vegetative matter are also consumed (34, 35). *Labeobarbus altianalis* [$n = 10$ in November (69–318 mm) and $n = 5$ in February (132–311 mm)] is a generalist consumer, with a diet including molluscs, insects, plants, and crustaceans as well as, to a lesser extent, fishes (34). *Labeo victorianus* [$n = 9$ in November (71–333 mm) and $n = 8$ in February (81–233 mm)] largely feeds on epilithic and epiphytic algae (34). We captured fish using gillnets and an electroshocker, and collected tissue plugs from the lateral muscle near the dorsal fin. Fish muscle tissue typically has a turnover rate of several weeks to months, so it provides an integrated signal of diet at a time scale relevant to the occurrence of carcasses in the river and the timing of our sample collection (63). All samples were kept frozen until they could be dried at 60 °C, ground into a fine powder, and analyzed for $\delta^{13}C$ and $\delta^{15}N$ on a Costech Elemental Analyzer.

We estimated the contribution of basal resources to the fish tissue assimilation using Bayesian mixing models in MixSIAR (51, 52). For trophic enrichment factors, we used 0.4 ± 1.3 for $\delta^{13}C$ (53) and 4.3 ± 1.5 for $\delta^{15}N$ (54), which incorporate variability in trophic structure for these omnivorous fish. In November 2013, when carcasses were present in the river, the isotopic signature of bone biofilm was very similar to wildebeest tissue, so we only included wildebeest tissue as a potential source. For basal resource end members, we used CPOM ($\delta^{13}C = -14.3 \pm 0.3$, $\delta^{15}N = 3.1 \pm 0.5$; $n = 3$), wildebeest tissue ($\delta^{13}C = -11.0 \pm 0.5$, $\delta^{15}N = 7.3 \pm 0.4$; $n = 3$), and rock biofilm ($\delta^{13}C = -23.4 \pm 2.0$, $\delta^{15}N = 6.8 \pm 2.2$; $n = 3$). In February 2014, wildebeest tissue had not been present in the river for 4 mo, so we replaced wildebeest tissue with bone biofilm as a potential source. Our basal resource end members were CPOM ($\delta^{13}C = -14.1 \pm 0.5$, $\delta^{15}N = 4.7 \pm 0.3$; $n = 3$), bone biofilm ($\delta^{13}C = -15.2 \pm 2.3$, $\delta^{15}N = 11.2 \pm 1.8$; $n = 3$), and rock biofilm ($\delta^{13}C = -19.2 \pm 0.6$, $\delta^{15}N = 13.0 \pm 1.2$; $n = 3$). Fish may have retained some of the isotopic signal from wildebeest tissue even after carcasses were gone; however, we estimated the average isotopic half-life for muscle tissue from fish in our study was 71 d (63), suggesting that signal would be largely gone by February. Furthermore, the bone biofilm signature in February 2014 was distinct from the wildebeest tissue signature. Visual analysis of isospace plots confirmed that consumer data were within the minimum convex polygon of source data, suggesting we were not missing any major diet sources (64).

We estimated consumption of carcasses by Nile crocodiles (*Crocodylus niloticus*) using literature and field estimations. Captive adult Nile crocodiles (2–4 m long) fed to satiation consumed, on average, 1–3 kg of fish per day (37). During two carcass surveys, we counted 33–41 Nile crocodiles in the 3.5 km of river in which the majority of mass drownings occurred. If all individuals ate to satiation throughout the average 172-d period when the wildebeest migration is in the Mara region, they would consume 21,160 kg of carcass (wet mass), which is equivalent to the total mass in 120 carcasses and the soft tissue mass in 150 carcasses.

All data used in these analyses will be made available on the Dryad Digital Repository.

Table S1. Number and elemental composition of wildebeest carcasses entering the Mara River from 2011 to 2015

Year	No. of mass drownings	No. of carcasses	Carcass dry mass,* 10^3 kg	Average aerial loading,† g of DM per m^{-2}	C, 10^3 kg	N, 10^3 kg	P, 10^3 kg
2011	3	8,000	385	590	137	32	16
2012	6	9,400	453	250	161	37	19
2013	7	7,750	373	360	133	31	16
2014	4	2,700	130	640	46	11	5
2015	3	3,400	164	140	58	13	7
Mean (SD)	4.6 (1.8)	6,250 (3,000)	301 (144)	400 (210)	107 (51)	25(12)	13(6)

DM, dry matter.
*Total carcass biomass assuming a mean biomass of 175 kg of wet mass and 48 kg of dry mass per carcass.
†Average aerial loading for mass drownings, where detailed carcass counts could be conducted over a spatially explicit area (12 of 23 mass drownings).

Table S2. Elemental composition and decomposition rates of wildebeest carcass components

Carcass element	Percentage of carcass,* mean (SD)	C/N/P†	Decay rate, $k \cdot d^{-1}$ (95% CI)	Days to 95% biomass loss, mean days (95% CI)
Stomach contents	12.4 (2.9)	69.2:3.3:1.0		
Muscle	25.7 (0.7)	152.0:45.7:1.0	−0.188 (−0.168 to −0.208)	16 (14–18)
Internal organs‡	7.2 (1.7)	96.4:21.2:1.0	−0.068 (−0.047 to −0.089)	44 (38–63)
Skin	10.9 (2.0)	215.5:72.5:1.0	−0.043 (−0.038 to −0.048)	70 (63–80)
Bone	43.7 (3.7)	2.6:0.5:1.0	−0.001 (−0.0013 to −0.0009)	2,709 (2,285–3,327)
Total carcass	100.0	8.5:2.0:1.0		

*Based on dry mass.
†C/N/P ratio is shown by mass.
‡Percentage of carcass and stoichiometry averaged across all internal organs; decay rate based on intestine.

Table S3. Nutrient cycling in the Mara River after a drowning of 5,000 wildebeest

	NH_4^+				SRP			
Days after drowning	S_w,* km	V_f,† $m \cdot d^{-1}$	U_{min},‡ $mg \cdot m^{-2} \cdot d^{-1}$	U_{max},§ $mg \cdot m^{-2} \cdot d^{-1}$	S_w, km	V_f, $m \cdot d^{-1}$	U_{min}, $mg \cdot m^{-2} \cdot d^{-1}$	U_{max}, $mg \cdot m^{-2} \cdot d^{-1}$
8	34.4	0.5	31.2	164.6	35.6	0.5	18.2	25.9
16	72.5	0.3	13.0	115.8	51.6	0.5	16.6	16.6
26	69.9	0.3	10.9	42.7	103.1	0.2	6.9	8.4

*Nutrient uptake length.
†Nutrient uptake velocity.
‡Minimum aerial uptake, based on upstream nutrient concentration.
§Maximum aerial uptake, based on peak nutrient concentrations measured within the sampling reach.

Table S4. C and nutrient flux upstream and downstream of wildebeest carcass aggregations

Date	No. of carcasses	Average Q, $m^3 \cdot s^{-1}$	Upstream DOC flux, kg	Total carcass C loading, kg	Soft tissue C loading, kg	Net DOC flux, kg	Upstream TN flux, kg	Total carcass N loading, kg	Soft tissue N loading, kg	Net TN flux, kg	Upstream TP flux, kg	Total carcass P loading, kg	Soft tissue P loading, kg	Net TP flux, kg
7/4/2011	3,380	9.7	30,310	57,900	40,800	−1,290	17,080	13,400	10,000	1,270	1,510	6,800	320	50
11/5/2012	990	15.6	96,270	17,000	12,000	3,480	64,290	3,900	2,900	−180	6,450	2,000	90	−40
9/25/2013	1,610	16.6	10,8490	27,600	19,400	8,350	60,720	6,400	4,700	2,240	6,250	3,300	150	−210
Mean (SD)	1,990 (1,240)	13.9 (3.7)	78,360 (42,060)	34,200 (21,300)	24,100 (15,000)	3,510 (4,820)	47,370 (26,290)	7,900 (4,900)	5,900 (3,700)	1,110 (1,220)	4,740 (2,790)	4,000 (2,500)	190 (120)	−65

All fluxes were calculated over a period of 25–29 d. Q, discharge; TN, total nitrogen.

Table S5. Metabolic model for avian scavenger consumption of wildebeest carcasses

Species	Average mass, kg	Daily energy expenditure, $kJ \cdot d^{-1}$	Daily energy consumed, $kJ \cdot d^{-1}$	Daily dry mass consumed, $g \cdot d^{-1}$	Daily C consumed, $g \cdot d^{-1}$	Daily N consumed, $g \cdot d^{-1}$	Daily P consumed, $g \cdot d^{-1}$
Maribou stork	6.45	2,577	2,990	115	51	13	0.4
White-backed vulture	5.43	2,321	2,692	104	46	11	0.4
Rüppell's vulture	7.40	2,803	3,251	125	56	14	0.4
Hooded vulture	2.04	1,277	14,812	57	25	6	0.2