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# The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa

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## SUMMARY

1. Hippopotami can play a significant role as ecosystem engineers and may play an important role as carbon and nutrient vectors from savanna grasslands to aquatic systems.

2. We coupled the results of a feeding study of captive hippopotami, faeces leaching/mineralisation experiments, hippopotamus consumption estimates and the stoichiometry of savanna grasses to calculate excretion and egestion rates of hippopotami. We then used time budgets and population estimates to calculate nutrient loading by hippopotami in the Mara River, Kenya.

3. In captivity, hippopotami consumed 11.0 g dry matter (DM) kg hippopotamus$^{-1}$ day$^{-1}$ (110.6 C; 6.8 N; 1.0 P) and egested 5.3 g DM kg$^{-1}$ day$^{-1}$. They excreted or egested 2.72 g C, 0.28 g N and 0.04 g P kg hippopotamus$^{-1}$ day$^{-1}$, and urine comprised 12% of C, 70% of N and 33% of P of total excretion and egestion.

4. By integrating data from previously published work on hippopotamus digestion with the data we collected in the field, we estimated an average hippopotamus in the Mara River would excrete or egest 1.93–3.58 g DM, 0.78–1.47 g C, 0.13–0.19 g N and 0.01–0.02 g P kg hippopotamus$^{-1}$ day$^{-1}$, and that half of this excretion/egestion would enter the river.

5. The hippopotamus population increased by 1500% inside the Maasai Mara National Reserve, Kenya, between 1959 and 2006. We estimate that hippopotami egest 36 200 kg faeces day$^{-1}$ into the Mara River (wet mass). Daily loading into the river by excretion and egestion equals 8563 kg DM, 3499 kg C, 492 kg N and 48 kg P, which is equivalent to 670% of CPOM, 15% of DOC, 27% of TN and 29% of TP of loading from the upstream catchment.

6. This research provides the first estimates for hippopotamus inputs to rivers that include both excretion and egestion and provides evidence that hippopotami are important resource vectors in sub-Saharan African rivers, even when compared to other sources of carbon and nutrients.

*Keywords*: allochthonous resource, animal subsidy, egestion, excretion, *Hippopotamus amphibius*

## Introduction

Animal movements can form substantial linkages between ecosystems through the transport of carbon (C) and nutrients across ecosystem boundaries (Kitchell *et al.*, 1979; Polis, Anderson & Holt, 1997; Vanni, 2002). These animal-mediated resource subsidies can strongly affect nutrient cycling (Kitchell *et al.*, 1999; Vanni, 2002), ecosystem productivity (Menninger *et al.*, 2008; Marcarelli *et al.*, 2011) and food-web structure and stability (Sabo & Power, 2002; Nowlin *et al.*, 2007; Leroux & Loreau, 2008) of the recipient system. However, the scale of these effects is determined by the quantity, quality, timing and duration of the inputs, which in turn are defined by characteristics of the animal vector and the recipient system (Chaloner *et al.*, 2007; Hocking & Reimchen, 2009; Richardson, Zhang & Marczak, 2010; Marcarelli *et al.*, 2011). The input of any materials (nutrients, carbon,

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organic matter, etc.) from one ecosystem into another – often referred to as loading or subsidies – can have substantial ecosystem effects, but inputs transported by biotic versus abiotic vectors are often higher quality resources more aggregated in space and time (McClain *et al.*, 2003; Marcarelli *et al.*, 2011).

One of the primary ways in which animals transfer subsidies across ecosystem boundaries is via feeding migrations, in which animals feed in a different habitat than the one in which they nest or rest. Subsidy transfer via daily feeding migrations has been documented in a diversity of animals, including geese (Post *et al.*, 1998), seabirds (Anderson & Polis, 1999), coral reef fish (Meyer & Schultz, 1985) and whales (Roman & McCarthy, 2010). The dispersal of animals into the feeding habitat and subsequent return and aggregation within the resting habitat can result in particularly large subsidies transferred from the feeding to resting habitat. These migrations are often seasonal, peaking in a given area during longer-distance migrations to distant breeding grounds (Post *et al.*, 1998), which can limit the temporal impact, but may permit larger animal aggregations than could be sustained year-round. Nutrient and C loading from feeding migrations by many animals occurs through excretion (urine), which is highly labile, and egestion (faeces), which requires mineralisation.

Hippopotami (*Hippopotamus amphibius*) make daily feeding migrations between terrestrial ecosystems where they forage (typically savanna grasslands) and aquatic systems where they rest (rivers, wetlands and lakes) (Field, 1970). This daily feeding migration is probably an important source of allochthonous subsidies to aquatic ecosystems in sub-Saharan Africa, particularly because the migration occurs year-round. Hippopotami travel 1–10 km inland during the night to feed, somewhat selectively, on grass (Field, 1970; Olivier & Laurie, 1974) and return by dawn to spend the day basking in and near the water (necessary due to their sensitive skin, rapid dehydration and large size). Through this daily migration, hippopotami probably contribute a substantial amount of excretion and egestion to aquatic systems during daytime resting hours. Productivity in these systems is often limited by high turbidity and low light, which can be further exacerbated by the hippopotami themselves (Dutton, 2012). Therefore, C and nutrient input by hippopotami to aquatic systems could play an important role in supporting primary and secondary productivity in sub-Saharan African rivers.

Hippopotami have significant impacts as ecosystem engineers. They can change the abundance and composition of grass species and overall plant community structure in grazing areas (Field, 1970), facilitate the presence of other herbivores (Verweij *et al.*, 2006; Kanga *et al.*, 2013), maintain open-water areas used by other species (Naiman & Rogers, 1997) and create paths that influence geomorphology, hydrology and ecosystem connectivity (McCarthy, Ellery & Bloem, 1998; Mosepele *et al.*, 2009). Researchers have hypothesised that hippopotami also play an important role in moving C and nutrients from terrestrial to aquatic systems, and several studies have made general estimates of loading (Payne, 1979; Heeg & Breen, 1982; Kilham, 1982; Grey & Harper, 2002; Naiman, Decamps & McClain, 2005). Here, we build on that literature by developing the first explicit model of hippopotamus excretion and egestion rates and by providing the first comparison of excretion and egestion stoichiometry. We also examine loading estimates in the context of changing hippopotamus populations and catchment loading, which may influence the ecosystem effects of these inputs.

Hippopotamus populations are declining across much of their range, and they are now listed as vulnerable by the International Union for Conservation of Nature (IUCN) (Lewison & Oliver, 2008; Kanga *et al.*, 2011). They congregate in pools during the day, and their aggregation sizes are a complex function of water level (group size increases during low flows) and behavioural interactions between individuals (which limit group size) (Karstad, 1984). Discharge in many aquatic systems in sub-Saharan Africa is increasingly influenced by hydropower development, agricultural extraction and altered precipitation associated with global climate change (McClain, 2013; McClain *et al.*, 2014). The coupled effects of declining hippopotamus populations and decreasing discharge may influence the ecosystem effects of hippopotamus loading through changes in hippopotamus aggregation sizes and/or concentration of inputs. At the same time, overall catchment loading of nutrients is increasing due to anthropogenic inputs, which may interact with the effects of loading by hippopotami.

Here, we estimated total excretion and egestion rates of captive hippopotami by comparing the mass and stoichiometry of food consumed with that of waste produced. We coupled experiments partitioning C, nitrogen (N) and phosphorus (P) loading from urine and faeces of captive hippopotami with estimates from the hippopotamus digestion literature (Field, 1970; Arman & Field, 1973; Clauss *et al.*, 2004, 2007; Schwarm *et al.*, 2006) and data from the field to estimate average loading by hippopotami into the Mara River, Kenya. Finally, we used historical and contemporary estimates of the hippopotamus population to estimate how loading has changed

over time and compare nutrient loading by hippopotami to loading from other sources in the Mara catchment.

## Methods

### *Excretion and egestion rates of captive hippopotami*

We estimated excretion and egestion of C, N and P by hippopotami at the Milwaukee County Zoo using three captive adult hippopotami – one adult male (2604 kg) and two adult females (1334 and 1353 kg). Although the hippopotamus habitat contains both indoor and outdoor components, the hippopotami were kept indoors for the 3 days of the study due to inclement weather. The indoor habitat consisted of several separate pens with concrete floors and walls, and a large pool (total volume = 99 700–109 900 L) to which the hippopotami had access nearly 24 h day$^{-1}$ (except during cleaning). Each morning, we washed and swept into the pool the surface of the adjacent concrete pens that had been used by hippopotami over the previous 24 h. Then, the hippopotami were moved into the farthest pens to be fed, allowing the pool to be sampled, cleaned and refilled with clean water. We estimated the final volume of the pool by measuring water depth and applying a series of volumetric calculations.

We collected measurements from the pool as soon as the hippopotami had departed, as their movement around and out of the pool helped mix the water column. To collect coarse particulate organic matter (CPOM, >1 mm), we used a 2-metre-long tube to collect a depth-integrated water sample, filtered 18.9 (day 1) to 37.8 (day 2–3) L of water through a 1-mm sieve and dried and weighed the sieved material. To collect total suspended organic matter (>0.7 μm), we filtered a known volume of water through a pre-weighed Whatman GF/F glass fibre filter and dried and reweighed the filter papers. Filters were not combusted to measure ash-free dry mass, but there was no source of suspended inorganic material, so we assumed all mass was organic. We collected water samples for nutrient and dissolved organic carbon (DOC) analysis and measured temperature, conductivity and dissolved oxygen with an YSI 556 MPS (Yellow Springs, Ohio, U.S.A.). We multiplied the concentrations of CPOM, total suspended organic matter, nutrients and DOC by the total volume in the pool to quantify total mass. Once the pool had been cleaned and refilled, we collected all samples and measurements again to provide before-hippopotamus data for comparison.

Water samples were processed immediately after collection and frozen until analysis. For total nitrogen (TN) and total phosphorus (TP) analysis, unfiltered samples were digested using an alkaline potassium persulfate digestion reagent and analysed on an Astoria-Pacific flow analyser. For total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) analysis, samples were filtered through 0.2-μm Supor filters (Metricel), digested as for TN/TP samples and analysed on an Astoria-Pacific flow analyser. For inorganic nutrient analysis, samples were filtered through 0.2-μm Supor filters (Metricel) and analysed on a portable flow injection analyser (Ellis *et al.*, 2003, 2011; Worsfold *et al.*, 2013). We analysed ammonium ($NH_4^+$-N) using the gas exchange method, soluble reactive P (SRP) using the molybdate blue method and nitrate ($NO_3^-$-N) using zinc reduction (APHA (American Public Health Association), 2006; Ellis *et al.*, 2011). Dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) were then obtained by subtracting inorganic nutrient levels from TDN/TDP levels. For DOC analysis, samples were filtered through Whatman GF/F filters and analysed on a Shimadzu total organic carbon (TOC) analyser.

After all samples were collected, we drained the pool through a 1-mm mesh sieve. Due to the large amount of organic matter in the pool, we put a single 9-cm$^2$ hole in the sieve to drain the pool in a reasonable amount of time. Although this probably allowed for the loss of some suspended hippopotamus faeces, it slowed the draining period sufficiently (*c.* 2 h) to allow most faeces to settle and remain on the bottom of the pool. After the pool was completely drained, we shovelled all the hippopotamus faeces into wheelbarrows, weighed the total mass and collected five subsamples to measure % dry mass. We added total suspended organic matter to this measurement and corrected for time spent in the pool to obtain an estimate for total faeces egested.

Hippopotami typically urinate and defecate simultaneously, mixing the urine and faeces together with rapid tail movements, making it difficult to collect pure samples of either one. Throughout the study period, we observed one instance in which the adult male hippopotamus defecated without urinating, allowing us to collect two subsamples of faeces uncontaminated with urine for C, N and P analysis.

We measured the total quantity of each food type consumed by the hippopotami each day (mass of food provided minus mass of food not consumed) during days 1–6 of the study. On days 4–6, we took subsamples of each food type (dried grass, pellets and produce comprised of apples, carrots and lettuce) and analysed these samples for % dry mass and C, N and P content. The hippopotami were fed a consistent diet throughout

the study, so we assumed the C, N and P content of the food types was the same for days 1–3. Previous diet tracer studies have found it takes approximately 71 h for particles to move through a hippopotamus's gut (Clauss *et al.*, 2004), so we collected data on hippopotamus excretion and egestion (described above) during days 4–6 and related this to the diet data from days 1–3. Results were standardised by the total time the hippopotami were in the pool or adjacent pens and by total kg hippopotamus mass.

We analysed the C, N and P content of both food and faecal samples collected during the zoo study. For the faecal samples, we used the two subsamples collected from the adult male that we believed were not contaminated with urine. All samples were finely ground using a cryogenic ball mill grinder with liquid nitrogen. For % C and %N, samples were weighed and loaded into tin cups and analysed on a Costech elemental analyser (Valencia, California, U.S.A.). For %P, samples were weighed, ashed in a muffle furnace at 550 °C, mixed for 5 min on a shaker table with 15 mL of 1 N HCl and digested in a drying oven at 80 °C. The acid was then filtered through a 45-μm filter and analysed on a Perkin-Elmer ICP-OES.

### *Mineralisation and leaching rates*

We used small chambers with faecal samples collected during the zoo study and in the field to estimate the leaching rates of C, N and P from hippopotamus faeces. For the zoo study, we placed 5 g (wet weight) of faeces uncontaminated with urine in 270-mL BOD bottles (four replicates), filled the bottles with tap water and placed them on a large shaker table. Although this led to a higher concentration of faeces in the bottles (18.5 g $L^{-1}$) as opposed to in the field study (4 g $L^{-1}$) and the zoo pool (1.6 g $L^{-1}$), this was the smallest amount of faeces for which we could obtain a representative subsample. We subsampled 10–20 mL from the bottles after 1, 4, 12 and 24 h. We analysed each sample for inorganic nutrients ($NH_4^+$, $NO_3^-$, SRP) and the 1- and 24-h samples for TN, TDN, DON, TP, TDP and DOC using previously described methods.

For the field study, we collected fresh hippopotamus faeces from five locations near the Mara River, Kenya, and mixed them together to create a composite hippopotamus faeces signature. We placed 20 g (wet weight; 23.7% dry mass) of faeces in 5-L bottles (three replicates), filled the bottles with river water and placed them in a large pool of water to maintain ambient temperatures. We subsampled the bottles after 24 h and collected samples for inorganic nutrients ($NH_4^+$, $NO_3^-$, SRP), TN, TP and DOC analysis (as described above). We analysed samples for $NH_4^+$ in the field using the fluorometric ammonium method (Holmes *et al.*, 1999; Taylor *et al.*, 2007), and samples were preserved with sulphuric acid and analysed in a laboratory at Yale University for the remaining variables. For both chamber studies, we calculated the net increase in C, N and P g faeces$^{-1}$.

For the zoo study, we used this mineralisation and leaching data to partition the proportion of dissolved loading in the pool due to faeces versus urine. We multiplied the DOC, TDN and TDP values from faeces after 24 h of leaching by the total amount of faeces in the pool to give us the portion of dissolved loading due to faeces. We then subtracted this portion from the total DOC, TDN and TDP levels measured in the pool to give us the portion of dissolved loading due to urine.

To quantify total loading from excretion and egestion, we added the C, N and P content of faeces (measured by % weight analysis of dried faecal samples) to the DOC, TDN and TDP from urine, with both faeces and urine estimates corrected for the amount of time hippopotami spent in the pool. We then divided total loading from excretion and egestion by total food intake to calculate the % of C, N and P that are excreted or egested.

### *Loading rates in the field*

We estimated hippopotamus loading rates in the field for the Mara River basin, upstream of and inside the Maasai Mara National Reserve (MMNR), Kenya. Because intake rates, nutritional content of food and seasonality were expected to differ in the field from the zoo study, we used literature and field data to augment our model as much as possible. We used literature estimates of the daily dry matter intake (DMI) of hippopotami, which were determined as a function of their body mass (BM), based on experimental measures of intake in captive hippopotami (Clauss *et al.*, 2004, 2007; Schwarm *et al.*, 2006).

$$\mathrm{DMI} = \mathrm{X} \times \mathrm{BM}^{0.75}$$

where DMI is measured in g, and BM is measured in kg. This equation scales DMI to body size and incorporates energy demand, energy content of food and assimilation efficiency into the equation's coefficient (X). For hippopotami on a diet of fresh grass, the coefficient was 28, and for hippopotami on a diet of grass hay (dried grass), the coefficient was 42. Because the Mara is a semi-arid area with a bimodal rainy season during approximately half of the year (Sept.-Nov., March-May),

we used 28 for the wet season and 42 for the dry season. We assumed a mean BM of 1500 kg for hippopotami in the Mara basin (Eltringham, 2010).

As the majority of the population in the Mara is composed of adults not growing significantly (Kanga *et al.*, 2011), we assumed hippopotami were in equilibrium and used the following equation to estimate the mass of excreted or egested (ex/eg) C, N and P:

$$\text{Mass of ex/eg}_{C,N,P} = \text{Mass Food Consumed (DMI)} \times \%\text{ex/eg}_{C,N,P} \times \text{content of food}_{C,N,P}$$

We measured the C, N and P content of savanna grass ($n = 5$) located near the river as examples of typical hippopotamus food in the field. For N and P, we assumed 100% of the consumed N and P was excreted or egested. For C, we used literature estimates showing that hippopotami on a grass diet excrete or egest 42% of organic matter, and hippopotami on a grass hay diet excrete or egest 53%. The latter value was close to our zoo study value of 55% C excreted/egested by hippopotami primarily on a grass hay diet. For dry matter, we used literature estimates showing hippopotami on a grass diet excrete or egest 43% and hippopotami on a grass hay diet excrete or egest 53% (close to our zoo study value of 48%). Similar to our estimates of DMI, we used grass diet values for wet season estimates and grass hay diet values for dry season estimates (Schwarm *et al.*, 2006).

Hippopotami defecate on both land and water, so we used time budgets to estimate the per cent of excretion and egestion occurring in the river. Hippopotami have a long mean gut retention time, averaging 71 h for particles and 26 h for fluids (Clauss *et al.*, 2004), so we assumed constant excretion and egestion through the day. Game camera photographs we collected at hippopotamus pools show hippopotami generally leaving the river at dusk and returning at dawn (Subalusky, personal observation) and spending approximately 12–18 h per day in or near the river. Although they may spend part of that time basking on the river bank, hippopotami are so close to the river that we assumed any excretion or egestion occurring during this time entered the river. For loading estimates in this paper, we used the conservative estimate that hippopotami spend 12 h a day in the river; therefore, we divided total per-hippopotamus excretion and egestion rates by 2 to obtain the per-hippopotamus rate of loading into the Mara River.

We estimated the total loading rates to the Mara River by multiplying the per-hippopotamus loading rate by hippopotamus population estimates collected in the Mara River in 1959, 1971, 1980 and 2006 (Darling, 1960; Olivier & Laurie, 1974; Karstad & Hudson, 1984; Kanga *et al.*, 2011). We mapped the spatial pattern of loading in the Mara using data from Kanga *et al.* (2011), who mapped hippopotamus aggregations in the Mara as ranges of individuals in four categories (1–5, 6–30, 31–60 and 61–132). We used the minimum and maximum of each category and multiplied it by our daily individual hippopotamus loading estimates for C, N and P.

We measured catchment loading levels of CPOM, DOC, TN and TP monthly from June – December, 2012 at one of our primary study sites in the river – site 1 (Emarti Bridge) – upstream of any hippopotami. Coarse particulate organic matter (CPOM) was collected with a 1-mm mesh net, and samples were corrected for the volume of water that passed through the net. Water samples were preserved with sulphuric acid in the field and analysed as described above. Concentrations were multiplied by the discharge at each site to quantify total flux. Discharge was measured using pressure transducer depth gauges placed at rated cross sections of the river.

## Results

### *Excretion and egestion rates of captive hippopotami*

Hippopotami significantly increased DOC levels, and total, organic and inorganic N and P concentrations in the zoo pool (Table 1, Fig. 1) and modified water quality variables (see Table S1, in Supporting Information). The ratio of inorganic N/P was 0.9:1 (by mass), but the ratio of TN/TP was 7.6:1, reflecting a large increase in dissolved organic nitrogen due to hippopotami. Although

**Table 1** Inputs of carbon and nutrients by hippopotami, based on increased concentrations in a hippopotamus habitat pool at the Milwaukee County Zoo before and after *c.* 21 h of use by three adult hippopotami. Results are given as means and standard deviations in parentheses

| | DOC | TN | TDN | $NH_4^+$-N | $NO_3^-$-N | DON | TP | TDP | SRP |
|---|---|---|---|---|---|---|---|---|---|
| Total increase in pool (g) | 1983 (193) | 1074 (87) | 993 (43) | 100 (8) | 8 (2) | 885 (38) | 141 (23) | 114 (8) | 122 (8) |
| Standardised loading estimate (g kg hippo$^{-1}$ day$^{-1}$) | 0.42 (0.03) | 0.23 (0.03) | 0.21 (0.02) | 0.02 (0.00) | 0.00 (0.00) | 0.19 (0.01) | 0.03 (0.01) | 0.02 (0.00) | 0.03 (0.00) |

Data for the water pool, not feces or urine

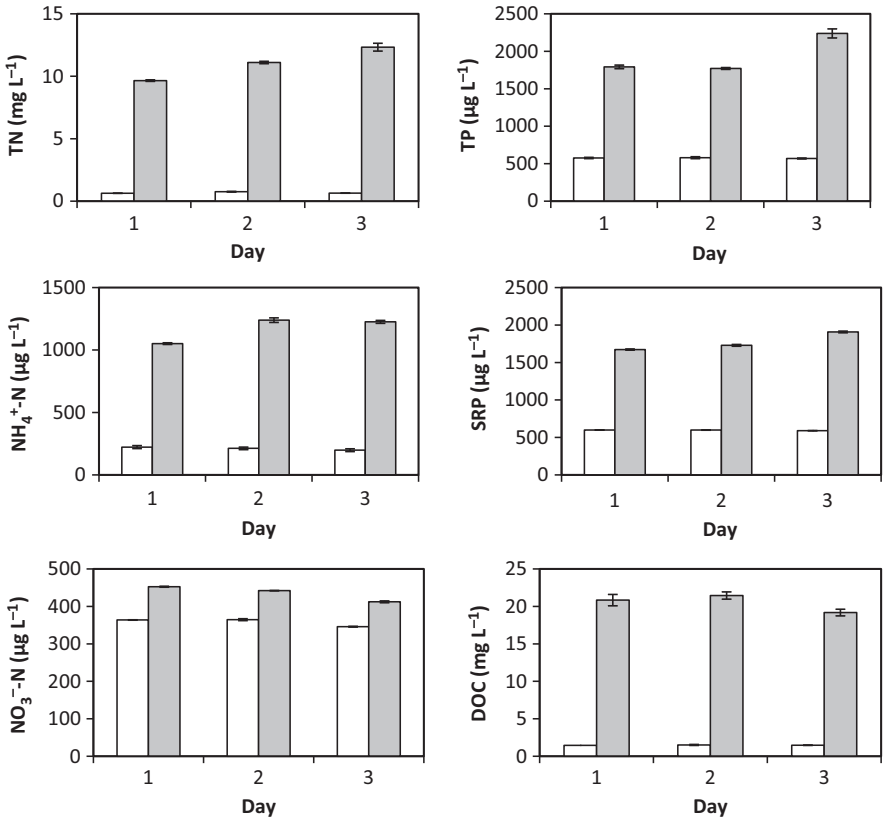


**Fig. 1** Total nutrient (TN, TP), inorganic nutrient ($NH_4^+$, SRP, $NO_3^-$) and dissolved organic carbon (DOC) loading in a hippopotamus habitat pool at the Milwaukee County Zoo before (unshaded) and after (shaded) *c.* 21 h of use by three adult hippopotami. Error bars are ± 1 SE.

TDN comprised 92.4% of TN, dissolved inorganic N ($NH_4^+$ and $NO_3^-$) accounted for only 10.0% of TN. In contrast, SRP was essentially equal to TP and TDP.

We measured mean suspended CPOM of 10.5 ± 5.8 mg $L^{-1}$ (dry mass ± 1 SD) for a total input of 1.2 ± 0.7 kg $day^{-1}$. Mean total suspended organic matter was 25.5 ± 2.0 mg $L^{-1}$, or 3.0 ± 0.2 kg $day^{-1}$. The mean total volume of wet hippopotamus faeces remaining after draining the pool was 168.9 ± 8.9 kg. Hippopotamus faeces were 13% dry mass, leading to a mean dry mass of 25.0 ± 3.3 kg $day^{-1}$. Adding total suspended organic matter gave an overall faeces dry mass of 28.0 ± 3.2 kg $day^{-1}$. Total suspended organic matter accounted for only 10.8% of the total faeces collected daily, suggesting 89% of faeces egested in a hippopotamus pool could be deposited on the bottom of the pool until a sufficient disturbance mobilises it into the water column. This also suggests our TN/TP measurements may be conservative, if a significant portion of organic matter was not included in our water samples for analysis.

The mass and C, N and P concentration of the hippopotamus diet was fairly consistent throughout the 6 days of the study (see Table S2). Although the produce and pellets were relatively high in N and P, the majority of diet mass (mean = 88%) was composed of grass. The overall stoichiometry of the zoo diet was 110.6 C: 6.8 N: 1.0 P (by mass). Hippopotami consumed an average of 11.0 g dry matter kg hippopotamus$^{-1}$ day$^{-1}$ and egested 5.3 g dry matter kg hippopotamus$^{-1}$ day$^{-1}$, or 48% of intake. These consumption and excretion/egestion values are higher than those we developed using literature on hippopotamus digestion (Clauss *et al.*, 2004, 2007; Schwarm *et al.*, 2006). This difference could be due to the fact that the zoo hippopotami were feeding only on dry grass (which requires a higher daily intake), or because they were not in metabolic equilibrium, as evidenced by their weight gain over the previous year (mean 10.2% increase). The overall stoichiometry of waste (excretion + egestion) produced by zoo hippopotami was 72.9 C: 7.6 N: 1.0 P.

### *Mineralisation and leaching rates*

The stoichiometry of field-collected faeces (222.8 C: 6.3 N: 1.0 P) differed from that of zoo faeces (96.5 C: 3.4 N: 1.0 P) although diet stoichiometry for both populations was similar (see Table S3), suggesting hippopotami in the wild may have higher assimilation efficiencies than those in captivity. These differences in stoichiometry were reflected in faeces leaching rates for

P, but not for N or C. Concentrations of DOC, TN, $NH_4^+$ and $NO_3^-$ after 24 h of leaching were very similar between the field and zoo study, but field values for TP and SRP were less than half of zoo values (Table 2). Values for $NO_3^-$ were actually negative for both studies, indicating a decline in values below the control values, possibly suggesting the presence of denitrifying bacteria in hippopotamus waste. Although both zoo and field faeces leached substantial amounts of dissolved organic C and total and dissolved N and P, these concentrations accounted for only a fraction of the elemental concentrations observed in the zoo pool (Table 1).

The dissolved fractions of N and P (TDN and TDP) constituted a lower percentage of TN and TP in the bottles than in the entire pool. It is possible the bottles became saturated with dissolved nutrients, and faeces were unable to leach nutrients to the same degree as they did in the pool. This would lead to an underestimation of dissolved nutrient leaching from faeces and an overestimation of the proportion due to urine. Leaching differences between the pool and the bottles could be due to the higher concentration of faeces in the bottles (18.5 g $L^{-1}$) as opposed to in the pool (1.6 g $L^{-1}$), although other data from the field experiment not presented here showed consistent levels of nutrient leaching per gram faeces across a low range of concentrations (1–4 g $L^{-1}$). Alternatively, settling of particulate faeces in the pool may have led to an underestimation of TN and TP values from the pool, as mentioned above.

In the zoo study, there was very little change in N and C concentrations between the 1- and 24-h samples, indicating that most of the leachable N and C leached out of faeces almost immediately. Additionally, there was a small decline for DON, $NH_4^+$ and $NO_3^-$, which could indicate volatilisation. In contrast, TP, TDP and SRP all increased by 60–70% from 1 to 24 h, suggesting that P takes longer to leach out of faeces and that our estimates of dissolved P due to faeces may be low.

The stoichiometry of urine was 25.8 C: 15.8 N: 1 P (by mass). Urine comprised 12% of C (although 76% of DOC), 70% of N and 33% of P of the total C, N and P excreted and egested. Dividing the total amount of C, N and P in excretion or egestion by the amount consumed in the diet showed that hippopotami excreted or egested 55.4 ± 6.0% of C, 93.7 ± 6.5% of N and 84.2 ± 8.9% of P that they consumed (mean ± 1 SD; Table 3).

### *Hippopotamus population in the Mara River*

The hippopotamus population within the MMNR grew from 120 to 1924 individuals between 1959 and 2006

**Table 2** Nutrient leaching over a 24-h period from hippopotamus faeces collected in the field in the Maasai Mara National Reserve, Kenya, and over a 1- and 24-h period from hippopotamus faeces uncontaminated with urine collected from an adult male hippopotamus at the Milwaukee County Zoo, Wisconsin, the U.S.A. Dissolved C, N and P from leaching of zoo faeces are scaled to the total amount of faeces in the pool after *c.* 21 h of use by three adult hippopotami. The difference between those levels and total dissolved levels in the pool (Table 1) is shown as dissolved nutrients due to urine. Results are given as means and standard deviations in parentheses

| Units | Time (hrs) | DOC | TN | TDN | $NH_4^+$-N | $NO_3^-$-N | DON | TP | TDP | SRP |
|---|---|---|---|---|---|---|---|---|---|---|
| Field: μg g faeces$^{-1}$ | 24 | 1947 (50) | 1082 (226) | - | 120 (22) | −33 (12) | - | 235 (12) | - | 115 (20) |
| Zoo: μg g faeces$^{-1}$ | 1 | 2741 (170) | 894 (107) | 486 (23) | 130 (0) | −3 (1) | 358 (23) | 307 (68) | 177 (29) | 174 (23) |
| Zoo: μg g faeces$^{-1}$ | 24 | 2519 (137) | 992 (121) | 404 (14) | 102 (3) | −3 (0) | 304 (14) | 500 (67) | 296 (7) | 282 (9) |
| Zoo: g total faeces$^{-1}$ | 21 | 477.3 (23.0) | | 76.6 (3.7) | | | | | 56.2 (2.7) | |
| Zoo: g total urine$^{-1}$ | 21 | 1505.9 (181.3) | | 916.1 (43.5) | | | | | 57.9 (10.1) | |

| Sample | Mass (g) | C (g) | N (g) | P (g) |
|---|---|---|---|---|
| Zoo consumption (g kg hippo$^{-1}$ day$^{-1}$) | 11.04 (0.40) | 4.92 (0.18) | 0.30 (0.01) | 0.04 (0.00) |
| Zoo faeces (g kg hippo$^{-1}$ day$^{-1}$) | 5.29 (0.61) | 2.40 (0.28) | 0.09 (0.01) | 0.02 (0.00) |
| Zoo urine (g kg hippo$^{-1}$ day$^{-1}$) | | 0.32 (0.03) | 0.20 (0.02) | 0.01 (0.00) |
| Zoo ex/eg (g kg hippo$^{-1}$ day$^{-1}$) | | 2.72 (0.30) | 0.28 (0.01) | 0.04 (0.00) |
| Ratio zoo ex/eg: zoo diet (%) | | 55.40 (5.95) | 93.68 (6.47) | 84.17 (8.95) |
| Field consumption (g kg hippo$^{-1}$ day$^{-1}$) | 4.50–6.75 | 1.85–2.78 | 0.13–0.19 | 0.01–0.02 |
| Field ex/eg (g kg hippo$^{-1}$ day$^{-1}$) | 1.93–3.58 | 0.78–1.47 | 0.13–0.19 | 0.01–0.02 |

**Table 3** Mass and C, N and P composition for zoo consumption and faeces (measured), zoo urine (estimated), the ratio of total excretion and egestion to consumption for the zoo study and our estimates of consumption and excretion/egestion for hippopotami in the field (ranges given for wet – dry season estimates). Results are given as means and standard deviations in parentheses

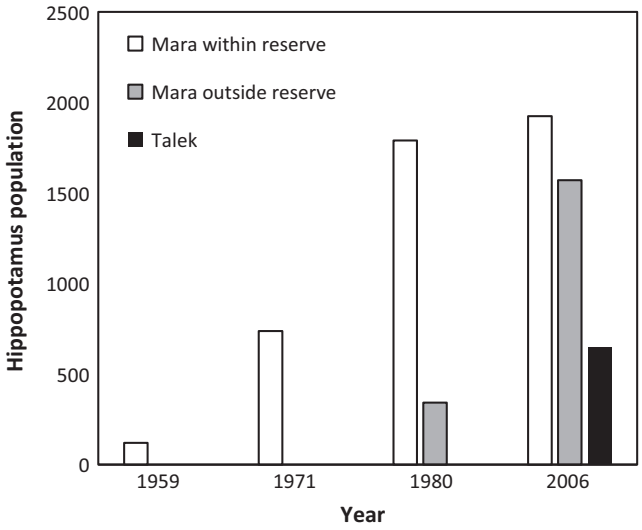


**Fig. 2** Hippopotamus populations in the Mara River between 1959 and 2006, within and outside the Maasai Mara National Reserve (the latter is only available for 1980 and 2006), and on the Talek River (only available for 2006) according to surveys published by Darling (1961), Olivier & Laurie (1974), Karstad & Hudson (1984) and Kanga *et al.* (2011).

(Fig. 2) (Darling, 1960; Olivier & Laurie, 1974; Karstad & Hudson, 1984; Kanga *et al.*, 2011). In 1980 and 2006, surveys that included hippopotami both within and outside the MMNR demonstrated that although the hippopotamus population inside the reserve increased by only 7.5%, suggesting they had reached a fairly stable population, the population outside the reserve increased by 359%, possibly due to increasing conservation measures in this region. In 2006, the total number of hippopotami in the Mara River and its tributaries was 4143, with a density of 36.1 and 34.4 per km of river, within and outside the reserve respectively (Kanga *et al.*, 2011). Kanga *et al.* (2011) included in these estimates surveys for the Talek River and its tributaries, which enter the Mara River inside the MMNR. These tributaries had only 648 hippopotami, but some of the highest densities (up to 48 hippopotami km river$^{-1}$).

Group size of aggregating hippopotami has also increased with increasing population size. The mean size of hippopotamus groups in the 1980 survey was 10.6 hippopotami, with very few groups exceeding 50 individuals (Karstad & Hudson, 1984). In contrast, in 2006, 95% confidence intervals for group size ranged from 20 to 32 individuals within and 17–28 individuals outside the reserve, with some groups having >100 individuals (Kanga *et al.*, 2011).

### *Loading rates in the field*

We estimate hippopotami in the Mara basin have a daily dry matter intake of 4.5 g DM kg$^{-1}$ in the wet season and 6.8 g DM kg$^{-1}$ in the dry season. Based on the composition of our savanna grass samples (41.2% C, 2.8% N and 0.3% P) and the proportion of dry matter, C, N and P hippopotami excrete or egest (43–53% DM, 42–53% C, 100% N, 100% P), we estimate that an average hippopotamus excretes or egests 1.93 g DM, 0.78 g C, 0.13 g N and 0.01 g P kg hippopotamus$^{-1}$ day$^{-1}$ in the wet season, and 3.58 g DM, 1.47 g C, 0.19 g N and 0.02 g P kg hippopotamus$^{-1}$ day$^{-1}$ in the dry season (Table 3). Overall stoichiometry by mass of hippopotamus excretion/egestion in the field is 70.1 C: 10.2 N: 1.0 P. Assuming hippopotami consumption is averaged over 6 months of wet season and 6 months of dry season, and that they spend 12 h in the water per day, we estimate the average hippopotamus loads 1.38 g DM, 0.56 g C, 0.08 g N and 0.01 g P kg hippopotamus$^{-1}$ day$^{-1}$ to the river. Using % dry mass estimates from hippopotamus faeces in the field (23.7% dry mass), we calculated that 1.38 g DM equals 5.8 g faeces (wet mass), thus an average hippopotamus (1500 kg) defecates 17.4 kg faeces (wet mass) every day, and 8.7 kg of that goes into the Mara River. Using population estimates from 2006, we estimated total loading for the hippopotamus population in the Mara River is 36 200 kg faeces (wet mass) every day. Total loading to the river from excretion and eges-

**Table 4** Average daily loading from hippopotami to the Mara River, Kenya, within and outside the Maasai Mara National Reserve, based on population surveys between 1959 and 2006

| Survey year | Hippo Population-Mara inside Reserve (km) | Hippo Population-Mara outside Reserve (km) | Hippo Population-Talek/ Olare Orok (km) | Dry Matter (kg day$^{-1}$) | C (kg day$^{-1}$) | N (kg day$^{-1}$) | P (kg day$^{-1}$) |
|---|---|---|---|---|---|---|---|
| 1959 (Darling, 1960) | 120 (?) | * | * | 248.0 | 101.4 | 14.3 | 1.4 |
| 1971 (Oliver & Laurie 1974) | 738 (60) | * | * | 1525.3 | 623.3 | 87.6 | 8.6 |
| 1980 (Karstad, 1984) | 1790 (74.2) | 342 (50.2) | * | 4406.5 | 1800.8 | 253.2 | 24.8 |
| 2006 (Kanga *et al.*, 2011) | 1924 (53.3) | 1571 (45.7) | 648 (56.3) | 8562.8 | 3499.4 | 492.0 | 48.2 |

*Data unavailable, which probably leads to underestimates of loading.

tion equals 8563 kg day$^{-1}$ DM, 3499 kg day$^{-1}$ TC, 492 kg day$^{-1}$ TN and 48 kg day$^{-1}$ TP (Table 4). To compare our estimates of hippopotamus loading of TC to our field measurements of DOC, we multiplied TC loading by the portion composed of DOC in our zoo study (15.6%), which yielded 545.9 kg day$^{-1}$ DOC.

Due to increases in the hippopotamus population from 1959–2006, daily hippopotamus loading in the Mara River increased substantially both within the MMNR and outside the reserve (Table 4). Using the average widths of the Mara River and its major tributary the Talek River, 20 and 10 m, respectively, hippopotami load a total of 1229 g DM, 502 g C, 71 g N and 6.9 g P m$^{-2}$ year$^{-1}$ across the system. In one tributary where hippopotamus densities are extremely high, the Olare Orok, hippopotami load 3624 g DM, 1481 g C, 208 g N, and 20 g P m$^{-2}$ year$^{-1}$.

Loading by hippopotami was a considerable proportion of the total C and N transported by the Mara at site 1 (Emarti Bridge) upstream of the range of hippopotami. We estimate that the daily loading rates at site 1 were 1283 ± 1840 kg day$^{-1}$ CPOM, 3601 ± 1704 kg day$^{-1}$ DOC, 1846 ± 1402 kg day$^{-1}$ TN and 165 ± 126 kg day$^{-1}$ TP (mean ± 1 SD). Hippopotami contribute nearly 6.7 times more CPOM (8563 kg day$^{-1}$ DM) than is transported by the Mara past site 1. This value may be somewhat elevated due to the large portion of organic material often present in rivers as fine particulate organic matter (FPOM), which we did not include here. Hippopotami also contribute 15% of the DOC (546 kg day$^{-1}$), 27% of the TN (492 kg day$^{-1}$) and 29% of the TP (48 kg day$^{-1}$) of the upstream catchment loading by the Mara.

## Discussion

Our study suggests that hippopotami play a major role in C and nutrient dynamics and influence the function of African rivers. According to our calculations, total loading by hippopotami into the Mara River is approximately 3125 metric tons of dry matter, 1277 metric tons of C, 180 metric tons of N and 18 metric tons of P every year. This loading from hippopotami is equivalent to 670% of CPOM, 15% of DOC and over 25% of the TN and TP loading from the upstream catchment of the river system. Although hippopotami are declining in many parts of their range, the population in the Mara River has increased by over an order of magnitude since the 1950s, resulting in a 1500% increase of hippopotamus loading to the river inside the reserve.

Hippopotami load C and nutrients through both urine and faeces, which differ in their stoichiometry, transport dynamics and lability, suggesting these waste products have different fates in the ecosystem. When compared to total elemental load produced by hippopotami, urine accounts for only 12% of C loading, but 76% of DOC inputs. Urine also accounts for 70% of TN, most of which is dissolved organic N, and 33% of TP. In contrast, an average hippopotamus contributes 754 kg year$^{-1}$ of faeces (dry mass), which are largely particulate C, with only 4% of C, 19% of N and 48% of P leaching out within 24 h. Inputs via urine are soluble and are probably transported with the current as solutes that can be readily taken up by primary producers or microbes. Conversely, hippopotamus faeces probably settle in depositional areas of the river, especially within hippopotamus aggregations, as they typically occur in low-current bends in the river and pools. Low-current bends may increase settling rates of faeces where they can be stored and slowly mineralised until flushing events move them through the system.

As mobile consumers, hippopotami act as a conveyor belt by moving resources from productive savanna grasslands to aquatic systems where these terrestrial inputs may influence new in-stream productivity. In the greater Serengeti Mara Ecosystem, which includes the MMNR, average annual aboveground productivity in grasslands is 664 g m$^{-2}$ year$^{-1}$, but can range from 200–1200 g m$^{-2}$ year$^{-1}$ due to seasonal and annual variations in precipitation, grazing, fire and other factors (McNaughton, 1985; Seagle & McNaughton, 1993). We estimate each hippopotamus consumes 0.26–1.54 ha of annual production. Based on our loading estimates, we estimate that each hippopotamus transfers 0.06–0.38 ha of annual production, and the entire hippopotamus population of the Mara River transfers 260–1563 ha of annual production, from the grasslands into the river every year. Variations in grassland productivity also influence the time hippopotami spend foraging and the distances they have to travel to consume sufficient forage, ranging from 2.5 km to 4 km during the wet and dry season in the Mara, respectively (Kanga *et al*., 2011). Changes in travel time in turn influence how much time hippopotami spend in the river and subsequent loading to the river ecosystem. In wet years, hippopotami may be able to consume most of their diet relatively close to the river, which would increase the amount of time spent in the river and total loading to the river system. In contrast, in dry years, hippopotami would need to travel further distances to consume a sufficient amount of vegetation, and total loading may decline as a result (Lewison & Carter, 2004).

The loading rates we estimate for hippopotami (71 g N and 6.9 g P m$^{-2}$ year$^{-1}$) are at the high end of estimates

that have been developed for other animal vectors. Alewife contribute 0.91 g N $m^{-2}$ $year^{-1}$ and 0.14 g P $m^{-2}$ $year^{-1}$ to lacustrine spawning sites through excretion, carcasses and gametes; however, historical nutrient loading levels prior to population declines were 17 and 14 times higher, for N and P, respectively, than modern-day levels (Walters *et al.* 2009; West *et al.*, 2010; Twining, West & Post, 2013). Historical alewife loading would have been in the same range as modern-day loading estimates for sockeye salmon, which contribute an average of 17.0 g N $m^{-2}$ $year^{-1}$ and 2.1 g P $m^{-2}$ $year^{-1}$ through carcass additions to spawning streams in south-western Alaska, the U.S.A., although inputs ranged from 0 to 57.2 g N and 0–7.1 g P $m^{-2}$ $year^{-1}$ (Moore *et al.*, 2007). Average salmon values were also similar to those for waterfowl wintering in New Mexico, the U.S.A., which load up to 17.5 g N and 2.2 g P $m^{-2}$ $year^{-1}$ through excretion into the wetlands where they roost (Post *et al.*, 1998). Nutrient loading levels for hippopotami in the Mara are at the upper end of these estimates because: a) as megaherbivores they consume large amounts of vegetation (Owen-Smith, 1988), b) the inputs happen daily throughout the year and c) hippopotamus populations have grown remarkably over the last five decades.

Increases in hippopotamus populations since the first surveys in the 1950s have caused a 1500% increase in C and nutrient loading by hippopotami into the Mara River. Hippopotamus numbers in the Mara in the 1950s may have been depressed because of legal and illegal hunting (hunting is now illegal in Kenya) and now recovered to natural levels, although densities and group sizes appear to be larger in the Mara than those recorded in other study systems (Field, 1970; Eltringham, 2010; Kanga *et al.*, 2011). It is also possible that hippopotamus populations have increased in response to decreased grazing competition with other ungulate species that are declining in the region due to land use change (Ogutu *et al.*, 2009, 2011). While the population in the Mara has increased, hippopotamus populations are declining or disappearing in many other aquatic systems in sub-Saharan Africa (Lewison & Oliver, 2008; Kanga *et al.*, 2011). Population declines or extirpations of hippopotami, as well as other mobile consumers, can significantly decrease nutrient transport across ecosystems and impact ecosystem function (Capps *et al.*, 2012; Twining *et al.*, 2013).

Where hippopotami occur, the large amount of C and nutrient loading they contribute probably has strong effects on aquatic ecosystem function and biogeochemical dynamics. Hippopotamus inputs, particularly via urine, are fairly high in N and P, which may fuel primary production in the system. However, hippopotamus inputs are primarily composed of C, which may drive microbial production, increase community respiration and fuel secondary production via the detrital food web. Which pathway is favoured probably depends on characteristics of the aquatic ecosystem, such as stoichiometry of catchment loading, turbidity and light limitation and discharge variability. In addition to increases in overall population size, hippopotamus aggregation sizes are also increasing. Mapping hippopotamus loading according to hippopotamus distribution in the Mara River in 2006 (Kanga *et al.*, 2011) illustrates the potential role of aggregation size in determining loading for a given reach of river (Fig. 3). These aggregations probably form biogeochemical hotspots in the river, which may influence the fate of inputs and nutrient cycling in the system (McClain *et al.*, 2003; McIntyre *et al.*, 2008), and if these processes are influenced by aggregation size, changes in average aggregation size could have broader ecosystem effects. Further, because aggregation of hippopotami varies with discharge – hippopotami crowd into pools during low flows and disperse across the landscape during high flows – there may be complex interactions between discharge and hippopotamus density.

Our final loading estimates were based on several assumptions about the rate at which hippopotami consume, assimilate and excrete or egest food. For example, the largest determinant of individual hippopotamus loading rates is daily consumption (daily mass intake, DMI). Although no estimates of hippopotamus metabolic rate are available, we based our consumption estimates on an equation that incorporates metabolic theory (by scaling intake to 3/4 of body mass) and has support both in field estimates (Field, 1970; Arman & Field, 1973; Clauss *et al.*, 2004) and comparative theory (Clauss *et al.*, 2007). The coefficient we used in the consumption equation was based on digestion studies that used captive hippopotami (Clauss *et al.*, 2004; Schwarm *et al.*, 2006). These values were more conservative than what we measured in our own captive study, but we believe their use was warranted by the weight gain we observed in our hippopotami; however, these consumption differences may also lead to differences in partitioning between urine and faeces. It is possible that including free-living costs would make daily consumption higher for hippopotami in the wild, which would make our loading estimates conservative. We also used assimilation values for C based on captive animals, although we assumed all N and P was excreted or egested. If wild animals have higher assimilation efficiencies than cap-

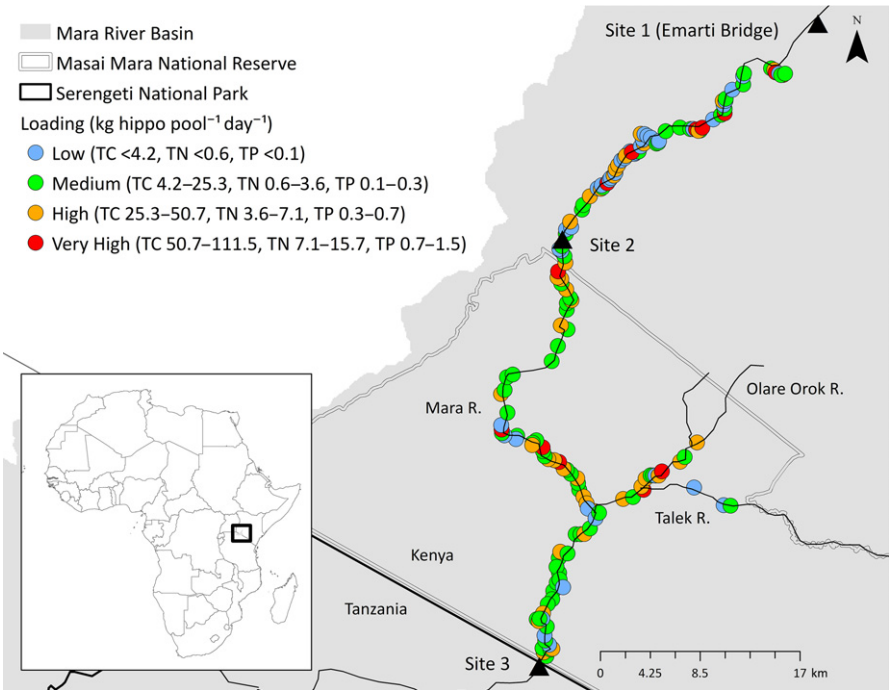


**Fig. 3** Estimated spatial distribution of TC, TN and TP loading by hippopotami into the Mara River, Kenya, based on the spatial distribution of hippopotami from Kanga *et al.* (2011).

tive ones (suggested by the difference in captive versus wild faecal C, N and P levels), our C loading estimates could be slightly high. However, we did apply assimilation efficiencies to the C and nutrient content of food from the field, rather than the zoo diet. For per-hippopotamus consumption and excretion and egestion estimates, we had to assume a mean hippopotamus mass. We used a value of 1500 kg, which is at the upper end of the range of adult female mass but the lower end of adult male mass (Eltringham, 2010). Assuming a fairly balanced sex ratio and a population largely composed of adults, this estimate is probably sound for the Mara, although it may vary in other populations.

Hippopotamus population size and structure also influence the contribution of hippopotami to nutrient dynamics in the Mara. In this study, we assumed the population was composed predominantly of adults, which is supported by data from the 2006 survey showing approximately nine calves for every 100 adult hippopotami (Kanga *et al.*, 2011); thus, we assumed that individual growth per hippopotamus was minimal. Not accounting for the N and P withheld by the small proportion of the population that is growing may have led to slightly elevated estimates of N and P loading to the river. To estimate population-level loading for the Mara, we assumed the population was fairly stable, which is supported by declining population growth within the reserve during the last two surveys, and similar densities both inside and outside the reserve in the last survey. However, the population has probably increased somewhat since the 2006 survey, which would make our estimates conservative. We also based our loading estimates on the conservative estimate that hippopotami spend only 12 h a day in the river; however, the time they spend in the river varies substantially, which has significant impacts on loading. For example, in situations where hippopotami spend only 6 h away from the river foraging, loading estimates would increase by *c.* 50%.

Our results provide estimates of loading by hippopotami to aquatic systems that are considerably lower than those provided by and used in previous studies (Heeg & Breen, 1982; Grey & Harper, 2002; Naiman *et al.*, 2005). Although none of these studies provided a detailed accounting of how they arrived at their estimates, they all appear to be based on an early estimate of hippopotamus intake of *c.* 18 kg day$^{-1}$ (Field, 1970). This intake estimate was based on stomach weights of culled hippopotami and an estimated mean retention time of 2 days; however, this intake estimate is not supported by the recent, more rigorous, digestion studies used here (Clauss *et al.*, 2004, 2007; Schwarm *et al.*, 2006). Additionally, the previously published loading estimates do not appear to account for maintenance costs (with the exception of Heeg & Breen, 1982) or time spent in the river versus on land grazing (i.e. estimated intake is presented as equal to potential loading to aquatic systems). Ours is the first study to explicitly

model hippopotamus loading to aquatic systems, and the general framework outlined here can be adapted to other systems in which hippopotamus mass, population structure, population numbers or time budgets are different.

Collectively, our data suggest that hippopotami probably play a major role in biogeochemical cycling and ecosystem function within this system. However, there are other loading sources in this region of the basin for which we have not accounted, including N fixation, dryland tributaries that enter downstream of site 1, other wildlife that congregate near the river and human inputs from settlements and tourism establishments. Although hippopotamus loading has increased in recent decades, upstream catchment loading has also probably increased due to increasing agricultural and urban development in the basin. In addition, hippopotamus inputs are now interacting with potentially altered flow levels (LVBC & WWF-ESARPO, 2010; McClain *et al*., 2014). In the Mara basin, these processes probably serve to amplify the effects of hippopotamus loading and may ultimately have undesirable ecosystem effects. In many other systems, in which hippopotami have declined or disappeared, the loss of hippopotamus loading could have negative impacts on secondary production or could be being replaced by anthropogenic inputs (Twining *et al*., 2013). The Mara River may be an end-member in our current understanding of the ways in which megafauna can impact aquatic ecosystem function and may improve our ability to understand some of the ecological implications of historical megafaunal extinctions (Lyons, Smith & Brown, 2004). To fully understand the dynamics of sub-Saharan aquatic ecosystems in which hippopotami play a major role, currently or historically, one must consider hippopotamus loading inputs and how these interact with changing characteristics of the recipient aquatic ecosystems.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Water quality variables in zoo hippopotamus pool measured before and after *c.* 21 h of use by three adult hippopotami.

**Table S2.** Hippopotamus food characteristics at the Milwaukee County Zoo over the 6-day study period.

**Table S3.** Per cent by weight of C, N and P in food and faecal samples collected from both the Milwaukee County Zoo and the Mara River, Kenya.

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