

Hippopotamus dung inputs accelerate fish predation by terrestrial consumers

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1 | INTRODUCTION

Biologically mediated transfers of nutrients and energy from aquatic to terrestrial ecosystems can play an important role in shaping both the structure and functioning of recipient terrestrial ecosystems (Polis, Power, & Huxel, 2004; Sabo & Power, 2002). Given the ecological significance of these subsidies, it is critically important to better understand both the pathway and mechanisms that regulate the core dynamics of these aquatic to terrestrial transfers.

The common hippopotamus (*Hippopotamus amphibius*) has been shown to promote nutrient transfer from terrestrial to aquatic ecosystems by excreting terrestrial organic material in its aquatic refuges (McCauley et al., 2015; Subalusky, Dutton, Rosi-Marshall, & Post, 2015). During the dry season when river flow drops, or ceases, there is frequently excessive build-up of *H. amphibius*-vectored organic matter within riverine pools (Wolanski & Gereta, 1999). These *H. amphibius*-mediated additions of terrestrial organic matter can influence the structure and function of aquatic communities by shaping the feeding ecology of aquatic consumers, altering macroinvertebrate community structure and depressing microphytobenthic biomass (Dawson, Pillay, Roberts, & Perissinotto, 2016; Grey & Harper, 2002; McCauley et al., 2015). Furthermore, this build-up increases nutrient concentrations, which fuel bacterial respiration and decomposition, thereby substantially decreasing dissolved oxygen (DO) concentrations to near-anoxic levels (Dutton, Subalusky, Hamilton, Rosi, & Post, 2018; Stears et al., 2018). DO concentrations are lowest at the river bed where *H. amphibius* dung accumulates and microbial respiration is presumed to be the highest, resulting in a decrease in DO with an increase in depth (Mnaya, Mwangomo, & Wolanski, 2006; Wolanski & Gereta, 1999).

As a result of *H. amphibius*-mediated shifts in water chemistry, fish species, especially those that cannot tolerate low DO concentrations, become restricted to the upper water column where DO levels

are higher (Chapman, Kaufman, Chapman, & McKenzie, 1995). Depressed DO concentrations in aquatic systems can also increase the lethargy of fish (Chapman et al., 1995). This lethargic behaviour, coupled with the distribution of fish in the upper water column, may greatly increase the availability of these fish to terrestrial consumers.

We posit that *H. amphibius* not only transfer nutrients from terrestrial to aquatic systems, but will also promote a reciprocal transfer of nutrients from aquatic to terrestrial ecosystems by increasing the availability of fish to terrestrial consumers. To test this hypothesis, we compared the dry season numerical response of terrestrial consumers around high- and low-density *H. amphibius* river pools, which differed in DO concentrations. By testing this new hypothesis, we seek to better understand whether, and how, *H. amphibius*-mediated changes in aquatic systems may reshape dynamics in neighbouring terrestrial ecosystems.

2 | MATERIALS AND METHODS

We conducted this study during the peak dry season (November 2015) in Ruaha National Park, Tanzania (7°42'S, 34°54'E). Due to anthropogenic water abstraction, the Great Ruaha River does not flow during the dry season and only isolated pools remain (Mtahiko et al., 2006). Field sampling was conducted along a 50-km stretch of the river, and we used daily *H. amphibius* counts to divide pools into high- and low-density *H. amphibius* pools. *H. amphibius* density for each pool was calculated as the average number of *H. amphibius* in each pool divided by the pool volume. Average pool length and width measurements were calculated from three field measurements made using a laser rangefinder. Average pool depth was estimated from three depth measurements made along the midline of the pools using a remotely deployed sounding line. Volume was estimated from average length, width and depth measurements by assuming

pools approximate a hemisphere or semicylinder shape. Any density that fell above the 50% percentile was categorized as a “high-density *H. amphibius* pool,” and any value that fell below was a “low-density *H. amphibius* pool” (for further details, see Stears et al., 2018).

From these pools ($n = 6$ high-density *H. amphibius* pools, $n = 6$ low-density *H. amphibius* pools), we collected water samples (i.e. from the top 10 cm) to assess surface water DO concentrations. We collected two water samples from all high- and low-density *H. amphibius* pools and field-tested them immediately for DO using a hand-held, cross-calibrated multiparameter electronic meter (YSI Inc.). We monitored for terrestrial consumers at all pool sites using visual surveys in which we enumerated all terrestrial consumers fishing within ~2 m of the water's edge (see Table 1 for species list). Visual surveys were conducted from approximately 50 m away from pools using binoculars to ensure that we did not disturb terrestrial consumers at these pools. Water samples and terrestrial consumer counts were conducted every 5 days between 8:00 and 10:00 hours ($n = 5$ DO sampling periods and $n = 6$ terrestrial consumer surveys). During these surveys, we also noted the presence/absence of surface swimming and aerial respiration of fish. From a subset of these pools ($n = 2$ high-density *H. amphibius* pools, $n = 2$ low-density *H. amphibius* pools), we assessed weekly ($n = 4$) DO concentrations across a depth profile from two DO depth profiles per pool (collecting measurements every 30 cm from surface water to 210 cm depth). Additionally, in the two high-density *H. amphibius* pools, we assessed diel changes in surface water DO concentrations over a 5-day period using a HOBO data logger that analysed DO concentrations at 15-min intervals. *Hippopotamus amphibius* pools were physically and hydrologically similar to each other. Thus, differences in DO are likely influenced by *H. amphibius* density rather than physical differences between pools (e.g. the presence of a fringing wetland; Mnaya et al., 2006).

We used generalized estimating equations (GEEs) to compare (a) DO concentrations; and (b) the number of terrestrial consumers

TABLE 1 List of terrestrial consumers observed fishing around *Hippopotamus amphibius* pools

Species name	Common name
Mammalian consumers:	
<i>Papio cynocephalus</i>	Yellow baboon
Avian consumers:	
<i>Leptoptilos crumenifer</i>	Marabou stork
<i>Mycteria ibis</i>	Yellow-billed stork
<i>Pelecanus onocrotalus</i>	Great white pelican
<i>Ardea cinerea</i>	Grey heron
<i>Ardea alba</i>	Great egret
<i>Butorides striata</i>	Green-backed heron
<i>Haliaeetus vocifer</i>	African fish eagle
<i>Ephippiorhynchus senegalensis</i>	Saddle-billed stork

Note. Mammalian consumers were only observed fishing from high-density *Hippopotamus amphibius* pools, whereas avian consumers fished from both high- and low-density *Hippopotamus amphibius* pools.

across the two *H. amphibius* densities. We used GEEs because we assessed the same pools continually, so data were not independent across the sampling period. For the first model, we included DO as the dependent variable and pool as the subject of repeated measures. Pool treatment type (high- and low-density *H. amphibius* pool), sampling period and their interaction were included as independent variables. We used a gamma distribution with a log link function and an exchangeable correlation matrix. For the second model, we used the number of terrestrial consumers as the dependent variable and treatment, sampling period and their interaction were included as

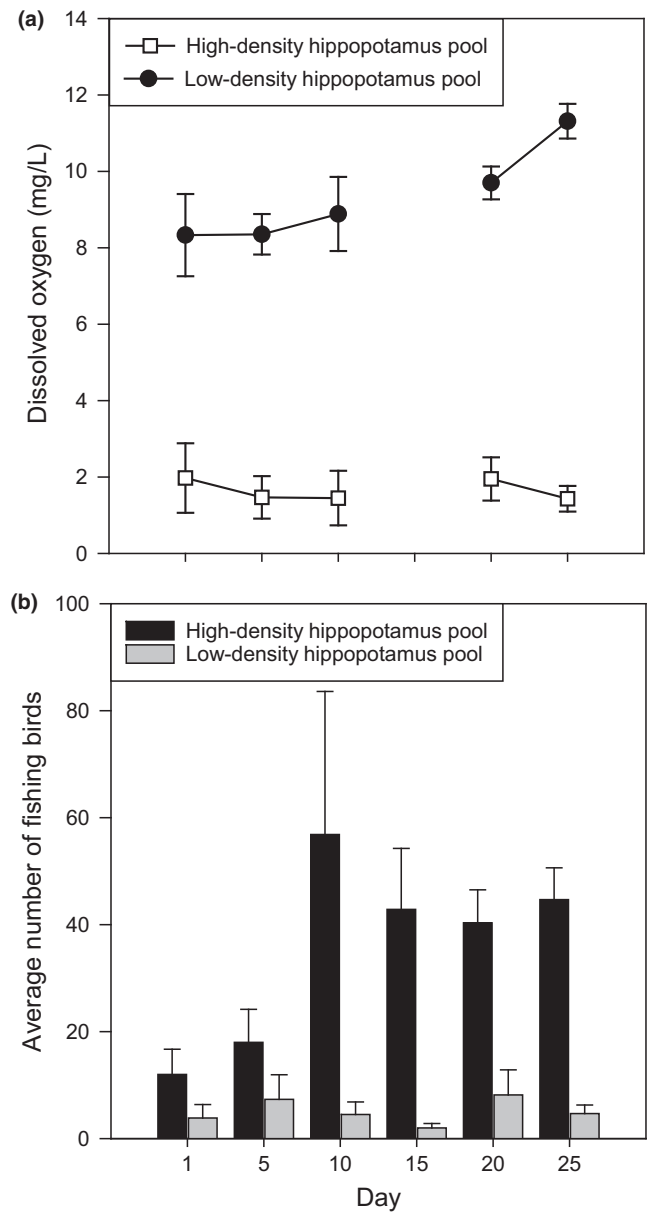


FIGURE 1 (a) Average dissolved oxygen (DO) concentration (mean \pm SE) of surface water across high- and low-density *Hippopotamus amphibius* pools for the different sampling days and (b) the average number of fishing birds (mean \pm SE) in high- and low-density *Hippopotamus amphibius* pools for the different sampling days in the Great Ruaha River, Tanzania

independent variables. Pool volume was included as a covariate. This model used a Poisson's distribution and log link function for count data. Data were back-transformed for graphical representation. All statistical analyses were run using SPSS version 25 (IBM).

3 | RESULTS

High-density *H. amphibius* pools had significantly lower surface water DO concentrations compared to low-density *H. amphibius* pools at every sampling period ($\chi^2 = 26.19$, $df = 4$, $p < 0.001$; Figure 1a). Furthermore, as depth increased, DO concentration decreased (Supporting Information Table S1). In high-density *H. amphibius* pools, above-lethal DO concentrations (>1 mg/L; Stickney, 2000) were only observed at the water surface. By contrast, in low-density *H. amphibius* pools, DO concentrations were much higher (>7 mg/L at water surface) and sublethal concentrations were never recorded.

Consequently, in high-density *H. amphibius* pools, we observed fish displaying aerial respiration and swimming close to the surface where the DO concentration was highest (Figure 2a). We recorded significantly higher abundances of fishing birds at high-density *H. amphibius* pools compared to low-density *H. amphibius* pools for all sampling periods throughout the dry season ($\chi^2 = 17.99$, $df = 5$, $p = 0.003$; Figures 1b and 2b), irrespective of pool volume ($\chi^2 = 0.023$, $df = 1$, $p = 0.878$). During all surveys, we observed yellow baboons (*Papio cynocephalus*), which are not normally associated with fishing, catching live fish from three high-density *H. amphibius* pools (Figure 2c,d; Supporting Information Video S1). This behaviour was only observed at high-density *H. amphibius* pools. This increase in terrestrial consumers around these pools only occurred in the morning because of the cyclical nature of DO concentrations (Supporting Information Figure S1). DO concentrations were lowest during the night and only started to increase by mid-morning (e.g. ~ 9 hr).

4 | DISCUSSION

Past research has highlighted the diverse impacts that *H. amphibius*-vectored organic matter can have on both the chemistry and ecology of aquatic ecosystems and food webs (Dutton et al., 2018; Grey & Harper, 2002; McCauley et al., 2015; Stears et al., 2018; Subalusky et al., 2015). Our results build from these previous observations and illuminate a novel pathway in which these influences of *H. amphibius* on aquatic systems can also serve to promote a reciprocal transfer of nutrients from aquatic to terrestrial ecosystems. We show that the depletion of dissolved oxygen in a riverine system caused by the decomposition of *H. amphibius* dung forces fish species to take refuge in more oxygen-rich surface waters where they are more susceptible to predation. This pulse of more accessible piscine resources appears to be created seasonally during periods of low flow, and is likely to be exacerbated, in hydrologically disturbed rivers. The oxygen-starved fish made vulnerable to predation subsidized typically nonpiscivorous yellow baboon (chacma baboons, *Papio ursinus*, feed on marine invertebrates, but no fishing has been observed; Lewis, West, & O'riain, 2018) as well as piscivorous birds, which were on average approximately seven times more abundant at high-density *H. amphibius* pools compared to low-density *H. amphibius* pools.

By definition, resource pulses are brief, infrequent events of high resource availability (Yang, 2004). However, because the Great Ruaha River has stopped flowing in the dry season since 1993, these subsidy pulses are temporally common and spatially predictable so that consumers are able to predict and track their occurrence. The tracking of resource pulses by consumers has been well documented; Kodiak brown bears (*Ursus arctos*) migrate between salmon runs (Deacy, Leacock, Armstrong, & Stanford, 2016), and tiger sharks (*Galeocerdo cuvier*) return to specific locations to take advantage of seasonally abundant albatross fledglings, *Phoebastria* spp. (Lowe, Wetherbee, & Meyer, 2006; Meyer, Papastamatiou, & Holland, 2010). With respect to our study, the migratory great white pelican

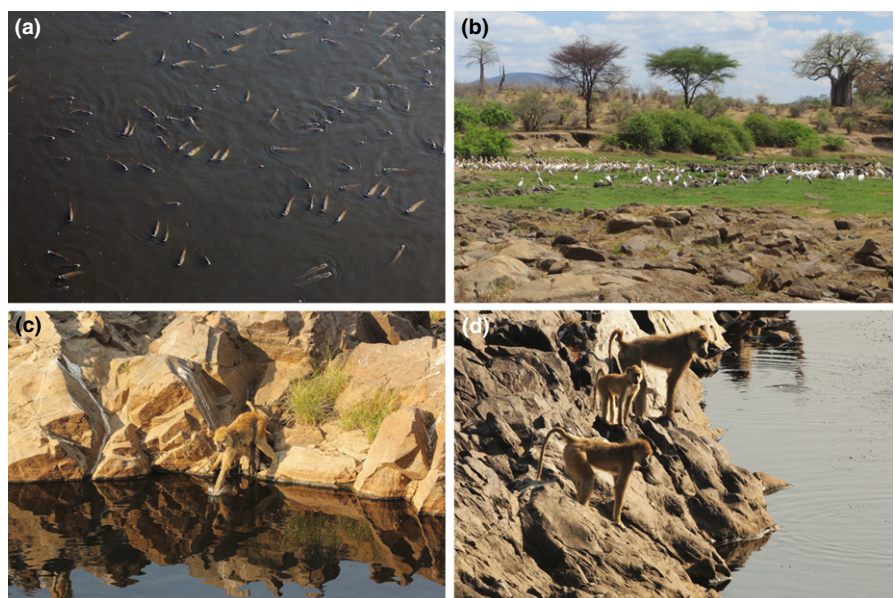


FIGURE 2 The low dissolved oxygen concentration in high-density *Hippopotamus amphibius* pools caused (a) a large number of fish (e.g. *Labeo* spp.) to exhibit aerial respiration in surface waters, (b) this behaviour attracted a large number of terrestrial consumers to these pools and (c,d) a rare phenomenon of baboons fishing and taking advantage of the easily accessible fish food source

(*Pelecanus onocrotalus*) only arrived en masse in Ruaha National Park towards the end of the dry season when DO concentrations were at their lowest and oxygen-starved fish were confined to surface waters.

The ecological consequences of resource pulses can persist long after the pulse has diminished such that the community assemblages and processes around these pools may be the result of “the ghost of resource pulses past” (sensu Yang, Bastow, Spence, & Wright, 2008). Long-term effects can occur when resource pulses propagate indirect effects over a community network (Yang et al., 2008). The exploitation of the piscine resource by opportunistic consumers may lead to higher encounter rates with additional food resources around river pools (e.g. Sabo & Power, 2002), thereby increasing predation on local resources through apparent competition (Schmitt, 1987). White-crowned lapwing populations (*Vanellus albiceps*) are declining within the park (Fox, 2004). These ground-nesting birds may experience increased predation from the terrestrial consumers that aggregate around high-density *H. amphibius* pools (e.g. baboon predation; Walters, 1990). In addition, the increase in the abundance of opportunistic terrestrial consumers could compete with consumers that rely on fish as a constant food source, such as the African fish eagle (*Haliaeetus vocifer*), by exploiting their primary food source. Population declines of this species have been noted in the park since the river has ceased flowing in the dry season (Fox, 2004). Finally, the fish themselves are predators of larval aquatic invertebrates and fish abundance indirectly facilitates terrestrial plant reproduction through cascading trophic interactions across ecosystem boundaries (Knight, McCoy, Chase, McCoy, & Holt, 2005). Because of the abovementioned community interactions, it is plausible that the resource pulse that we observed can contribute to the persistence of long-term ecological effects around these pools (Yang et al., 2008).

Stearns et al. (2018) found that within the same river pools, river flow prevented a build-up of *H. amphibius* dung and no observed differences in DO concentrations were observed between high- and low-density *H. amphibius* pools. Thus, the intensity and duration of the *H. amphibius*-mediated connectivity and subsidy of terrestrial consumers are strongly regulated by river hydrology (Stearns et al., 2018). These results extend our understanding of the ecological depth and reach by which *H. amphibius* affect ecosystems. Future study will facilitate improved understanding of how these *H. amphibius*-mediated aquatic to terrestrial linkages may shift in the rapidly changing environments of sub-Saharan Africa.

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SUPPORTING INFORMATION

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