

Temporal resource partitioning of wildebeest carcasses by scavengers after riverine mass mortality events

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Abstract. Scavengers play an important role in nutrient recycling and disease control, and this role may be particularly critical after mass mortality events, such as those caused by epidemics, culling, or natural disasters. Current work on scavenger ecology has focused on use of single carcasses, but behaviors are likely to be different at mass mortality events, in which high resource abundance can prolong the spatial and temporal availability of carcasses. Little is currently known about how scavengers respond to large die-offs and understanding scavenger use and succession patterns at mass mortality events has important implications for disease ecology. We used photographic time series and river-side surveys of scavengers using carcasses to investigate scavenger use and succession on wildebeest carcasses that resulted from annual mass drownings in the Mara River, Kenya. In addition, we used telemetry data for tagged avian scavengers to assess individual use of mass drownings. Density of avian scavengers per carcass was almost two orders of magnitude lower at mass drownings than has been documented previously for single carcasses on land. Scavengers demonstrated patterns of temporal resource partitioning, with large-bodied avian scavengers more common initially, followed by small-bodied avian scavengers, and then by insectivorous birds and non-avian scavengers. Avian scavengers also differed in daily activity patterns, with marabou storks more common in the morning and late afternoon and white-backed and Rüppell's vultures more common mid-day. Telemetry data indicated that approximately half of tagged vultures used mass drowning events but only spent a small proportion of their time there, suggesting that competition still plays an important role in scavenger dynamics at mass mortality events and that the rewards of such abundant resources may be offset by the risk of foraging in the river. Further research on scavenger behavior during mass mortality events is needed to better understand the role of scavengers in decomposition of carcasses and disease control during these events.

Key words: carrion use; decomposition; Mara Serengeti; marabou stork; mass mortality; river; scavenger; succession; vulture; wildebeest.

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INTRODUCTION

Scavengers play critical roles in ecosystem processes by recycling nutrients, promoting the flow

of energy throughout food webs, and controlling the spread of disease (DeVault et al. 2003, Wilson and Wolkovich 2011, Ogada et al. 2012a). However, studies of scavengers are under-represented

in ecological literature (DeVault et al. 2003, Kendall et al. 2014), and scavengers tend to be an over-looked link in food webs around the world. Most food webs focus on predator–prey relationships and ignore the complexity of added detrital and scavenger pathways (Moore et al. 2004), although scavenging processes can be involved in almost half of all food web linkages (Wilson and Wolkovich 2011) and may be critically important to ecosystem function and health (DeVault et al. 2003, Buechley and Şekercioğlu 2016).

Avian scavengers are unique and important components of the scavenger community because their ability to fly paired with acute vision and olfactory senses allow them to access carcasses quickly over a large spatial extent (DeVault et al. 2003). Carcasses tend to be unpredictable in time and space, and more unpredictable resources increase biodiversity and maintain functionality of the scavenger guild (Wilmers et al. 2003, Cortés-Avizanda et al. 2012). Vulture scavenging abilities decrease the time it takes carcasses to decompose and therefore can decrease disease transmission between mammalian species by reducing the opportunity for contact (Ogada et al. 2012*b*). However, the majority of vulture species are in danger of extinction (Ogada et al. 2012*a*). Understanding factors that allow coexistence among scavenger species can be important for understanding the impact of changing resource availability on scavenger community dynamics.

High diversity of avian scavenger species within a single ecosystem suggests the need for spatial and temporal partitioning of carrion resources (Kendall 2013). Scavenger dominance creates succession patterns in the use of carrion with interspecific dominance determined partially by body mass (Wallace and Temple 1987). Smaller, solitary avian scavengers, such as Bateleurs (*Terathopius ecaudatus*), assist in locating carrion (Kendall 2013). Small-bodied vultures depend on the presence of large-bodied vultures to facilitate feeding by opening up carcasses (Hunter et al. 2007). Scavenger species that nest further away from carcass sites, particularly those relying on cliff-nests, may take longer to arrive at carrion resources than closer-dwelling, tree-nesting species (Kendall 2014). Overall, interspecific competition remains high regardless

of the season because individuals are able to move large distances, responding to influxes in carrion abundance (Kendall 2013).

Most scavenger literature focuses on competitive scavenger interactions at the single carcass level (Wallace and Temple 1987, Hunter et al. 2007, Ogada et al. 2012*b*). Such carcasses typically do not last for longer than a day, and thus, current studies are confined to scavenger succession patterns on a resource of extremely limited quantity and temporal availability. Mass mortality events can lead to the occurrence of many carcasses on the landscape (Fey et al. 2015), which can provide the opportunity to study scavenger succession at longer time scales and upon less limited resources. Mass mortality events can result from natural disasters, extreme weather events, culling associated with management actions, disease epidemics, or as part of regular seasonal movements or breeding behaviors (Newton 2007, Fey et al. 2015, Subalusky et al. 2017). These events lead to a large amount of carcass biomass on the landscape, which can become an important part of the diet of many scavengers and alter food web dynamics (Hewson 1995, 2002, Shardlow and Hyatt 2013, Tomberlin et al. 2017, Baruzzi et al. 2018, Lashley et al. 2018*b*, Fey et al. 2019). The longer duration of carrion availability associated with mass mortality events may lead to different scavenger successional patterns than those typically seen in consumption of a single carcass over one day and may be informative in understanding the impact of scavengers on disease dynamics during an epidemic.

The Serengeti Mara Ecosystem (SME) is home to the largest remaining overland migration of 1.3 million wildebeest (*Connochaetes taurinus*; Hopcraft et al. 2013). Approximately 200,000 wildebeest die each year during the migration (Mduma et al. 1999), and these carcasses provide an important resource to avian scavengers throughout the region (Houston 1974, Kendall et al. 2012). One cause of mortality is through mass drownings that occur on a nearly annual basis as the wildebeest cross the Mara River while moving between dry season feeding grounds (Subalusky et al. 2017). These drownings contribute a mean of 6,250 wildebeest carcasses every year into the Mara River, which likely provide an important resource for a range

of scavenger species in the ecosystem. These carcass inputs occur in large pulses, with a mean of 4.6 drowning events per year and a mean of 1,360 carcasses per drowning. The magnitude of these events suggest avian scavenger communities might respond differently than to single carcasses on the landscape. The location of carcasses in the river may also influence the avian scavenger response, as foraging in the river poses risks for avian scavengers, including getting their feathers wet (which limits their ability to fly), drowning, or being predated by Nile crocodiles (*Crocodylus niloticus*). Access for scavengers to the meat within a given carcass in the river may also be more limited than when the carcass is on land, due to orientation of the carcass among the rocks and in the water, which could affect how these resources are used by scavengers.

Here we quantify the avian scavenger community composition on wildebeest carcasses in the Mara River after multiple mass drownings and analyze temporal resource partitioning at both daily time scales and throughout the decomposition period. We use detailed surveys of photographic time series from camera traps at the river, visual surveys at the river reach scale (100–200 m of river length), and GSM-GPS telemetry of three different vulture species to count avian and non-avian scavengers using carcasses after mass drownings and to quantify succession patterns in the scavenger community during these events.

METHODS

Study site

This research was conducted on the Mara River in the Maasai Mara National Reserve (MMNR) in Kenya, which is in the northern portion of the Serengeti Mara Ecosystem (SME; Fig. 1). Wildebeest cross the Mara River frequently during movements between dry season feeding grounds while in the northern portion of their range. There are 11 major crossing sites located along the Mara River, and mass drownings have been documented at four of these sites (Subalusky et al. 2017). Data from this study span four different drowning events across four years, which occurred at two different sites on the Mara River—Serena Lunch Spot (1.538583° S, 35.028681° E) and Cul de Sac Crossing (1.374229° S, 34.996873° E).

Camera trap photographs

We counted scavengers on carcass aggregations using an automated camera trap (Trophy Cam HD Max Black LED, Bushnell, Kansas City, Missouri, USA) placed on two different aggregations of wildebeest carcasses after drownings. In 2012, there was a drowning of an estimated 3,100 wildebeest on 5 November followed by a drowning of 400 wildebeest on 13 November. An average wildebeest carcass is 175 kg (wet mass; Subalusky et al. 2017); thus, these drownings contributed 612,500 kg of carcass biomass to the river. The camera trap was deployed on an aggregation of 16 carcasses (2800 kg carcass biomass) on 18 November 2012, which was 13 d after the first drowning and 5 d after fresh carcasses entered the river. In 2013, there was a series of drownings of an estimated 2110 wildebeest on 25 September, 1850 wildebeest on 26 September, and 1500 wildebeest on 27 September (a total of 955,500 kg carcass biomass). The camera trap was deployed on an aggregation of 39 carcasses (6825 kg) on 1 October 2013, which was 4–6 d after fresh carcasses entered the river. In both years, the camera was programmed to take a picture every 15 min, and species identification and number of individuals were recorded every hour from November 18 to 30 in 2012 (days 5–17 after the last drowning occurred; 1273 photographs) and from October 1 to 18 in 2013 (days 4–21 after the last drowning occurred; 1802 photographs; Fig. 2). The camera was removed once carcasses had decomposed to an advanced stage.

For each picture analyzed, we identified and counted both avian and non-avian scavenger species present. 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*). Changes in lighting throughout the day made some species identifications difficult, particularly differentiation of juvenile white-backed vultures and Rüppell's vultures, which have similar coloring and markings. Vultures that could not be identified to species were counted as unknown vultures. Individuals of these 4 species accounted for 87% of all species (avian and non-avian) observed in 2012 and 88% in 2013. A preliminary data

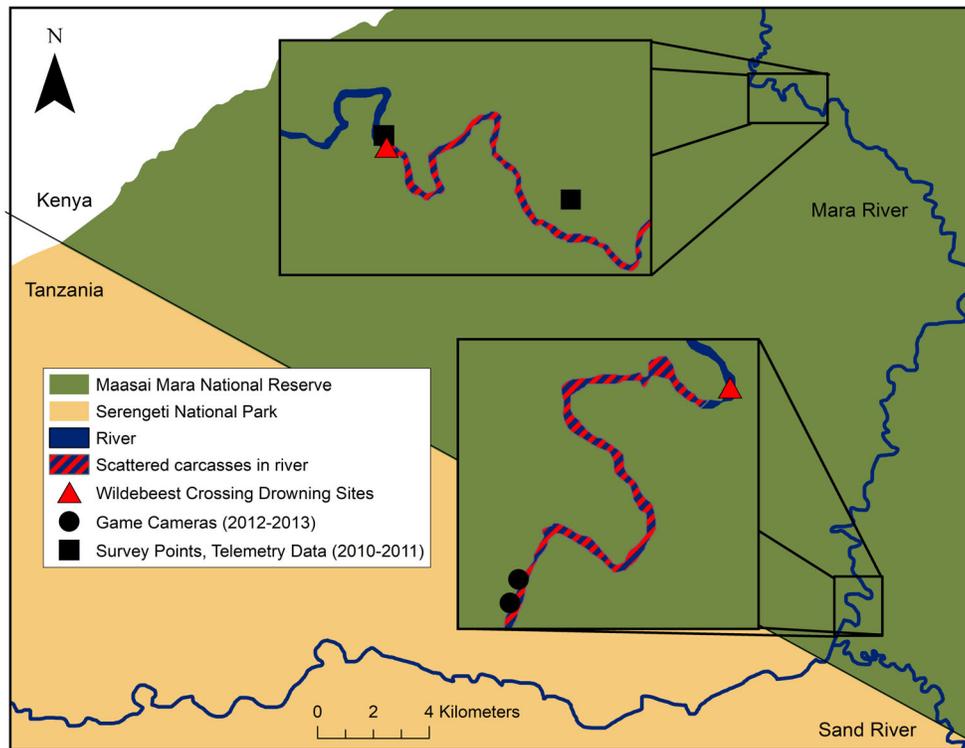


Fig. 1. A map of the Mara River inside the Maasai Mara National Reserve showing the location of wildebeest (*C. taurinus*) drowning sites, focal surveys with camera traps and river reach-scale surveys with visual observations.

analysis conducted on the first two days of the photograph series showed there was little variation in the species and number of common scavengers counted every fifteen minutes as compared to every hour. Thus, we only counted the four most common avian species in photographs taken on the hour for every hour of the photograph series. Less common avian species [lappet-faced vultures (*Torgos tracheliotos*), African sacred ibis (*Threskiornis aethiopicus*) and helmeted guinea fowl (*Numida meleagris*)] and non-avian species [crocodile (*Crocodylus niloticus*), Nile monitor (*Varanus niloticus*), banded mongoose (*Mungos mungo*), dwarf mongoose (*Helogale parvula*), slender mongoose (*Galerella sanguinea*), and spotted hyena (*Crocuta crocuta*)] were counted in every picture in which they appeared. Hippopotamus (*Hippopotamus amphibius*) were observed in several photographs but were not observed using the carcasses, so they were not counted.

We analyzed the correlations through time between carcass availability and scavenger species. We quantified the relative surface area of carcass material available in one photograph for each day throughout the time series, or when the number of carcasses changed for any reason. We analyzed images in ImageJ (Schneider et al. 2012), and we calculated the total area of visible carcass material in pixels using the freehand selection tool. We calculated the relative change in carcass surface area over time by dividing the measure of area on each day by the measure of area on the first day of the photograph series. We calculated the daily maximum number (the maximum number of individuals counted at any single time point on a given day) of each avian and non-avian species, and analyzed changes in the scavenger community over the duration of the photograph series by conducting a correlation analysis in the corrplot package in R (Wei and Simko 2017). We analyzed correlations between



Fig. 2. Sample camera trap photographs of wildebeest carcass aggregations on the Mara River from the first and last day of the photograph series in 2012 and 2013: (a) 18 November 2012, (b) 30 November 2012, (c) 1 October 2013, and (d) 18 October 2013.

carcass availability and abundance of marabou storks, white-backed vultures, Rüppell's vultures, hooded vultures, sacred ibis, and non-avian scavengers. We used $\alpha < 0.05$ to indicate statistical significance.

We calculated the proportion of each avian scavenger species (Marabou storks and vultures) directly using the carcasses as the maximum number of individuals of a given species counted at any one time over the duration of the photograph series divided by the sum of the maximum count for all taxa. This approach minimized double counting of individuals and allowed comparison of carcass use by species that may peak in numbers on different days. These proportions were compared to estimates from the literature for observations of avian scavengers on single carcasses.

We examined daily carcass use by the four most common avian scavenger species by calculating the mean number of individuals counted at each hour over the duration of the photograph series in 2012 and 2013. We analyzed daily activity curves by using the data across all days to

develop probability density functions for each species, and we analyzed the degree of overlap in activity curves using the overlap package in R (Ridout and Linkie 2009, Lashley et al. 2018a). We calculated a coefficient of overlap (using the λ_4 estimator for larger datasets), which is a continuous variable between 0 and 1, where 1 indicates identical curves. All analyses were conducted in R version 3.6.1 (R Core Team 2018), and data and R code are provided in the Mendeley Data Repository.

Scavenger counts

We conducted river reach-scale surveys of avian scavengers at wildebeest drowning sites at multiple time points after a drowning occurred in both 2010 (6 time points) and 2011 (4 time points). We selected a vantage point with a clear view of the wildebeest carcasses in the river, and we counted all the carcasses and avian scavengers within a 200 m radius of the river, including the river and riparian area. We counted all individuals of the following species: marabou storks, white-backed vultures, Rüppell's

vultures, hooded vultures, and lappet-faced vultures. We examined the number of individuals of each avian scavenger species over time, although we did not know the exact date of either drowning event. These data are of limited temporal resolution, but they complement the camera trap photographs in characterizing community patterns over time since drowning by providing a larger spatial scale perspective on scavenger use of carcasses.

GSM-GPS telemetry

As part of a larger study on vulture movement patterns in the region (see Kendall et al. 2014 for more details on study and unit attachment methods used), 18 vultures were being tracked with GSM-GPS tags (Africa Wildlife Tracking, Pretoria, South Africa and Savannah Tracking, Nairobi, Kenya) during the time when the migration was near the Mara River in 2010–2011. These included 6 white-backed vultures, 8 Rüppell's vultures and 4 lappet-faced vultures. During this tracking period, there were two mass drowning events. We examined vulture use of the river region in which drownings were observed to occur during those two events. We assumed an individual was using a mass drowning if they were located within 2 km of the river along the river section where drownings were observed to occur and within 30 d of when the drowning occurred. Four to six locations were recorded every day for each individual, so these criteria were designed to include individuals that may be using the drowning but for which a location was not captured at the precise moment they were at the river. This approach could have resulted in the inclusion of individuals located near the river but not using the carcasses, or the exclusion of individuals that used the carcasses for a brief period before relocating >2 km away.

We assessed individual vulture use of mass drowning sites by looking at the behavior of tagged vultures. Data coverage during a given drowning period was not complete for all individuals, so we calculated the total number of days each individual was tracked during a given drowning period. We then quantified the proportion of time a given individual used the drowning as the number of days they were at the river divided by the number of days tracked during a drowning event and took an average for each

species across the two events. Some individuals used both drowning events and were thus included twice. To determine the proportion of individuals of a given species using mass drownings, we divided the number of tracked individuals of a given species that used the drowning for either the first or second event by the total number of individuals of that species being tracked for either the first or second drowning event. These data provide us with an understanding of landscape-level choices vultures are making in their foraging behavior as they provide information on both which species are at the wildebeest carcasses along the river and how an individual used the mass mortality event over time.

RESULTS

Camera trap photographs

Carcasses decomposed substantially over the period of the study. There were 8–16 carcasses throughout the period of observation in 2012, with changing numbers caused by carcasses floating downstream in or out of view of the camera trap, and carcass loss through decomposition. On day 1 of the photograph series, there were both fresh carcasses from the drowning that occurred 5 d prior and some partially decomposed carcasses from an earlier drowning that occurred 13 d prior. By day 4 of the photograph series, rib bones were showing on fresh carcasses. Carcasses were almost entirely skeletal by the end of the photograph series, with 16% of the initial surface area remaining (Fig. 2a). There were 30–40 carcasses throughout the period of observation in 2013. On day 1 of the photograph series, all carcasses were fresh from the recent series of drownings that had occurred 4–6 d prior. Rib bones began showing at day 11 of the photograph series. At the end of the photograph series, some carcass material was still present, with 37% of the initial surface area remaining (Fig. 2b).

The majority of individuals observed in both photograph series were avian, which accounted for 95% of individuals in 2012 and 98% of individuals in 2013. The number of avian scavengers changed over time as the carcasses decomposed (Fig. 3). In 2012, the number of marabou storks and vultures was high at the beginning of the photograph series and declined in concert with

carcass availability (Fig. 3a). The ratio of marabou storks and vultures (based on the maximum number per species per day) to carcasses was 1.7 ± 1.0 (mean \pm SD) over the entire period of observation, and it ranged from 0.3 to 3.3. In 2013, the number of marabou storks and vultures did not peak until the middle of the photograph series and declined before carcasses reached the same stage of decomposition (Fig. 3b). The ratio of vultures to carcasses was 1.0 ± 0.6 over the entire period of observation, and it varied between 0.3 and 2.1.

Scavenger community composition changed through time in both years, with larger-bodied avian scavengers (marabou storks, white-backed vultures, and Rüppell's vultures) more abundant in the early to middle portion of the photograph series and smaller-bodied avian scavengers (hooded vultures), sacred ibis (which feed on insects that colonize the carcasses), and non-avian scavengers (primarily spotted hyena, Nile

crocodile, and banded mongoose) more abundant later (Fig. 4). In 2012, marabou storks, white-backed vultures, and Rüppell's vultures were significantly positively correlated with % carcass remaining and with one another (Fig. 5a). Hooded vultures, sacred ibis, and non-avian scavengers were negatively correlated with percentage of carcass remaining, and with marabou storks, white-backed vultures and Rüppell's vultures, although only the negative correlation between sacred ibis and the other birds was significant. In 2013, marabou storks, white-backed vultures, and Rüppell's vultures again were significantly positively correlated with one another, although the correlation with percentage of carcass remaining was much less strong (Fig. 5b). Hooded vultures were still negatively correlated with percentage of carcass remaining, but they were positively correlated with the marabou storks and *Gyps* vultures. Sacred ibis and non-avian scavengers were negatively correlated with

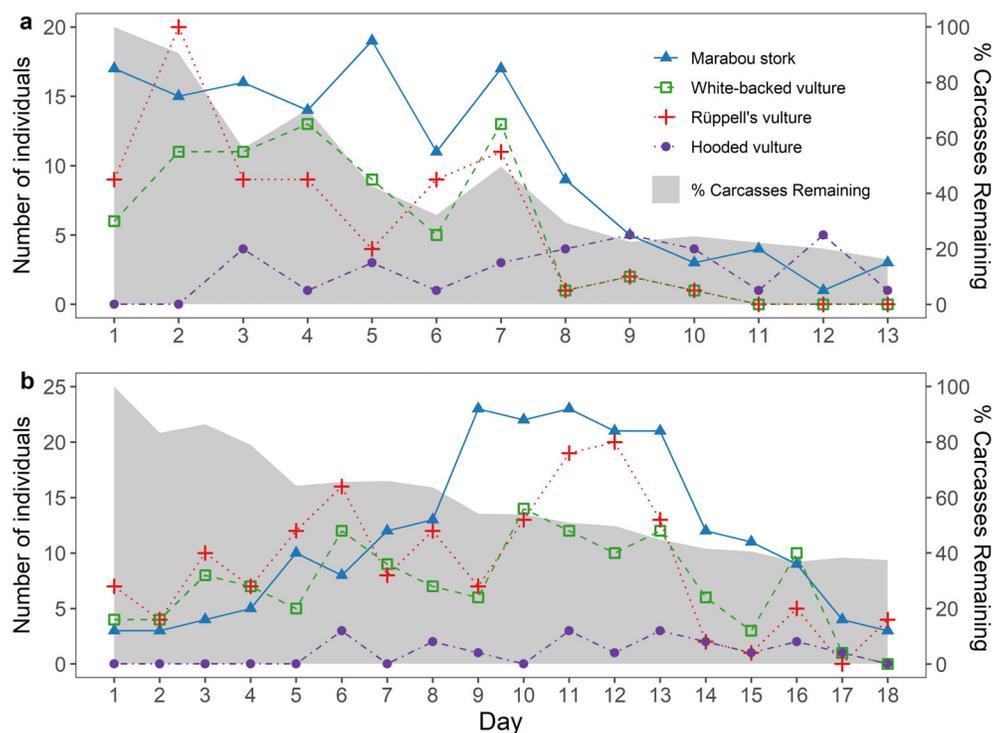


Fig. 3. The percentage of carcass remaining (in terms of relative surface area) and the maximum number per day of observation of the four most common avian scavengers surveyed from camera trap images on an aggregation of (a) 16 wildebeest carcasses in November 2012 and (b) 39 carcasses in October 2013 after mass drownings in the Mara River, Kenya.

percentage of carcass remaining, marabou storks, and *Gyps* vultures, although most correlations were not significant.

Marabou storks were the most common avian scavenger species observed in both 2012 and 2013, comprising 30–34% of all avian scavengers, followed by Rüppell's vultures (29–32%) and white-backed vultures (21%; Table 1). This pattern was very different than that observed for single carcasses in terrestrial habitats, in which marabou storks only comprised 2–4% of total avian scavengers. Unknown vultures only accounted for 4–5% of total avian scavenger species. In both years, lappet-faced vultures were only seen four times at the carcass sites.

The dominant avian scavengers showed variation in their daily use of carcasses that was consistent in 2012 and 2013 (Fig. 6). Species' activity curves in 2012 had high overlap values with curves in 2013: marabou storks, $\lambda = 0.869$; white-backed vultures, $\lambda = 0.881$; Rüppell's vultures, $\lambda = 0.772$; hooded vultures, $\lambda = 0.854$. Thus, we

combined data for each species across years and compared overlap values between species pairs (Fig. 7). White-backed and Rüppell's vultures, which both used the carcasses more in mid-day (10:00–13:00), had high overlap in activity curves ($\lambda = 0.924$). They both had relatively low overlap with marabou storks (0.757 and 0.705, respectively), which used the carcasses more frequently in the morning (7:00–9:00) and late afternoon (15:00–17:00). Hooded vultures were observed throughout the day and had intermediate overlap values with the other species (0.761–0.841), although hooded vultures were less commonly observed compared to other species.

Scavenger counts

At the river reach scale, the number of vultures generally followed the same pattern as the number of carcasses during 2010 and 2011 (Fig. 8). We could not quantify the number of days since the drowning for these observations, but observations from the 2010 drowning likely began on

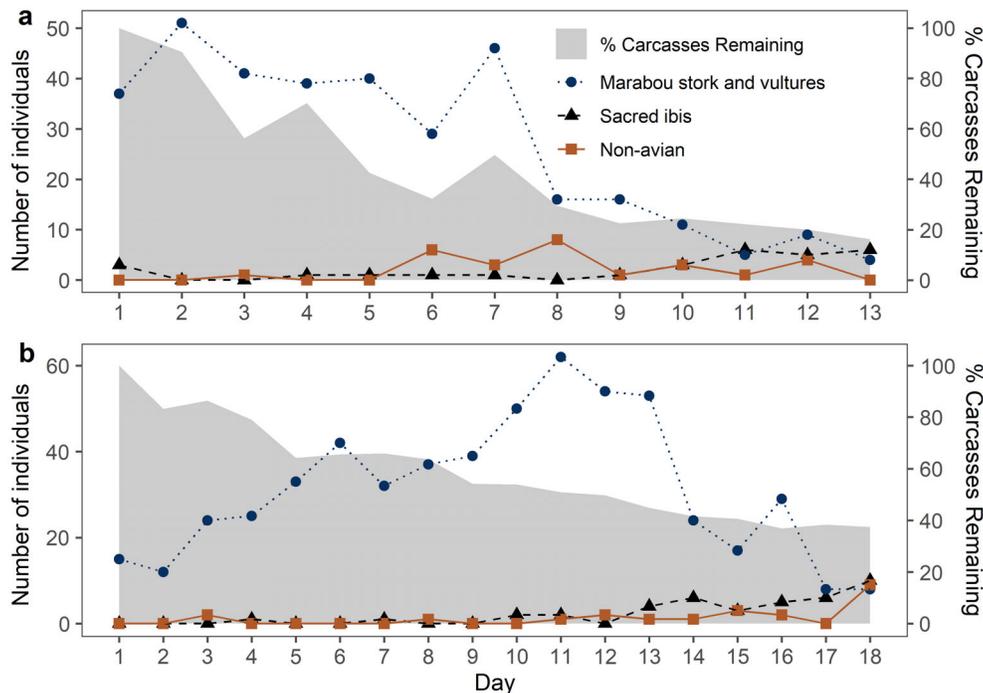


Fig. 4. The percentage of carcass remaining (in terms of relative surface area) and the maximum number per day of observation of marabou storks (*L. crumenifer*) and vultures, sacred ibis (*T. aethiopicus*), and non-avian scavengers, surveyed from camera trap images on (a) 16 wildebeest carcasses in November 2012 and (b) 39 carcasses in October 2013 after mass drownings in the Mara River, Kenya.

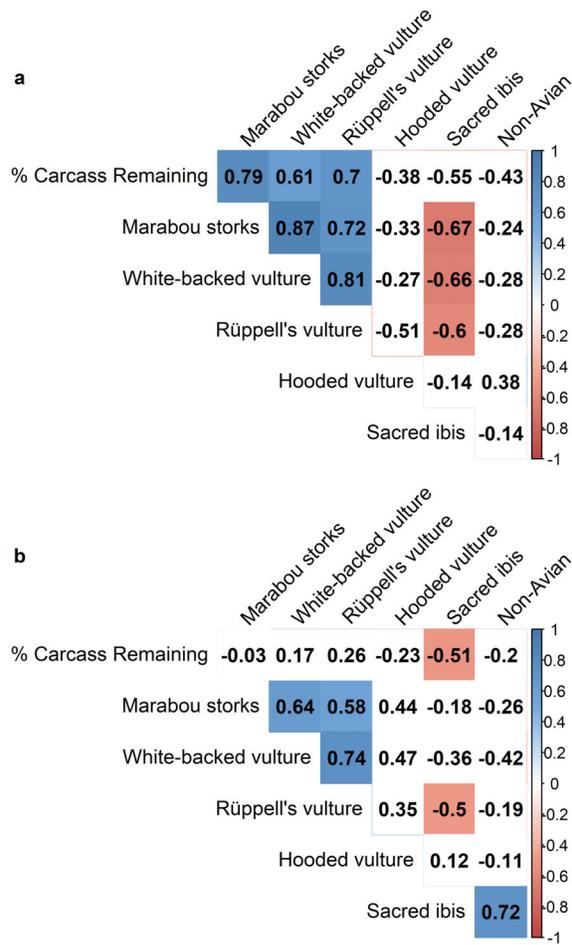


Fig. 5. Correlation matrix for percentage of carcass remaining (in terms of relative surface area) and the maximum number per day of observation of marabou storks (*L. crumenifer*), white-backed vultures (*G. africanus*), Rüppell's vultures (*G. rueppelli*), hooded vultures (*N. monachus*), sacred ibis (*T. aethiopicus*), and non-avian scavengers surveyed from camera trap images on wildebeest carcasses in (a) November 2012 and (b) October 2013 after mass drownings in the Mara River, Kenya.

a date near the actual drowning event, and observations from the 2011 drowning likely began slightly after the actual drowning event, as carcass and vulture numbers were already high on the first day of observation. In 2010, the number of carcasses increased from 30 to 232 within the first week of observation as carcasses floated and aggregated downstream (Fig. 8a), and in

2011 the number of carcasses increased to a maximum of 650 carcasses on day 2 of observation (Fig. 8b). The total number of vultures increased in the first week of observation and then declined rapidly by the second week of observation in both 2010 and 2011. After approximately three weeks, both vultures and carcasses disappeared. The ratio of marabou storks and vultures to carcasses was 2.5 ± 2.5 in 2010 and 1.4 ± 0.5 in 2011, similar to what we observed from the photograph time series.

The composition of avian scavengers utilizing wildebeest carcasses was similar in 2010 and 2011. In 2010, Rüppell's and white-backed vultures were most common, and there were very few hooded vultures and no lappet-faced vultures. Marabou storks were present but only at very low numbers (never more than 20 individuals on any given day). In 2011, again Rüppell's and white-backed vultures were most common, and there were fewer hooded vultures. There were, however, a number of lappet-faced vultures and many more marabou storks (a maximum of >100 on day 5) present in 2011 than in 2010.

GSM-GPS telemetry

Vulture use of the river during mass drownings varied greatly by species and individual (Table 2). Vultures used the river during mass drownings a mean of 14% of the time they were being tracked, with white-backed vultures and Rüppell's vultures using the drownings a similar amount of time (18–19%), and lappet-faced vultures scarcely using the drownings at all (1%).

There was a great deal of individual variability within each species regarding use of the drownings. Sixty percent of the white-backed vultures used the drowning, and those that visited the drowning used it on $30 \pm 32\%$ of the days they were tracked. Similarly, 64% of the Rüppell's vultures using the drowning, and those that visited the drowning used it on $30 \pm 18\%$ of the days on which they were tracked. Lappet-faced vultures used drownings much less frequently, with only 25% of individuals using drownings on only $5 \pm 2\%$ of the days they were tracked. Vultures that were tracked during drowning events but did not use the river were located a mean distance of 28 km from the river.

Table 1. Proportion of avian scavenger species at mass mortality events (MME) (data from this study) and individual carcasses (data from the literature).

Study	Marabou storks (<i>Leptoptilos</i> <i>crumenifer</i>)	White-backed vulture (<i>Gyps</i> <i>africanus</i>)	Rüppell's vulture (<i>Gyps</i> <i>ruppellii</i>)	Hooded vulture (<i>Necrosyrtes</i> <i>monachus</i>)	Lappet-faced vulture (<i>Torgos</i> <i>tracheliotos</i>)
2012 wildebeest MME (this study; Mara)	0.30	0.21	0.32	0.08	0.02
2013 wildebeest MME (this study; Mara)	0.34	0.21	0.29	0.04	0.03
Single wildebeest carcass (Anderson and Horwitz 1979; Amboseli)	0.03	0.75	0.11	0.09	0.02
Single wildebeest or zebra carcass (Kendall unpublished data; Mara)	0.02	0.57	0.32	0.02	0.08
Single, small (<5 kg) experimental carcass (Kendall 2013; Mara)	0.04	0.59	0.07	0.04	0.14

DISCUSSION

We observed a total of nine avian species at the carcasses in the Mara River, but marabou storks, white-backed vultures, Rüppell's vultures, and hooded vultures were the dominant avian scavengers. A large number of individuals of these species were observed at the mass drownings. Our reach-scale counts exceeded 700 avian scavengers in a day in both years (Fig. 8). Despite these high numbers, the mean ratio of vultures to carcasses across both focal- and reach-scale observations (1.6:1) was almost two orders of magnitude lower than that observed for single carcasses on land during surveys conducted from 1997 to 2006 in the same region (105:1; Kendall et al. 2012). While vulture populations in the area have declined in recent years, this is unlikely to explain the difference in carcass use between mass drownings and single terrestrial carcasses. Instead, data suggest that greater resource availability during mass drownings decreases scavenger density per carcass. The elevated risk of in-stream foraging and reduced access to carcasses (due to portions being covered by water) also likely contributed to the lower ratio of vultures per carcass.

This significantly lower per carcass utilization by avian scavengers probably contributes to the longer duration of carcasses in the river, which can remain for several weeks, as compared to carcasses on land, which usually persist for less

than a day (Houston 1974). Longer duration of carcasses in turn enabled observations of successional patterns in scavenger community composition. Despite the lower ratio of avian scavengers per carcass, we still observed body posturing and displacement of individuals, suggesting competition still plays a role in community succession patterns on mass mortality events despite the high availability of resources and lower densities of scavengers on the carcasses.

Differences between our two photograph series suggests that avian scavengers may not reach their peak until one to two weeks after a mass drowning occurs. In 2012, the number of avian scavengers was highest at the beginning of the photograph series, 5 d after the most recent drowning, but they may have already been present in the river in response to a large drowning event that occurred 13 d before the start of the photograph series. There were also four other drownings that occurred earlier that season and resulted in nearly 6,000 carcasses in the river between August and October, and it is possible these earlier drownings influenced the response of avian scavengers to the latter event. In 2013, the number of avian scavengers did not peak until the middle of the photograph series, 16–18 d after drownings occurred, and they declined more quickly than in 2012. There had been only three other drownings in the river before the start of the 2013 photograph series,

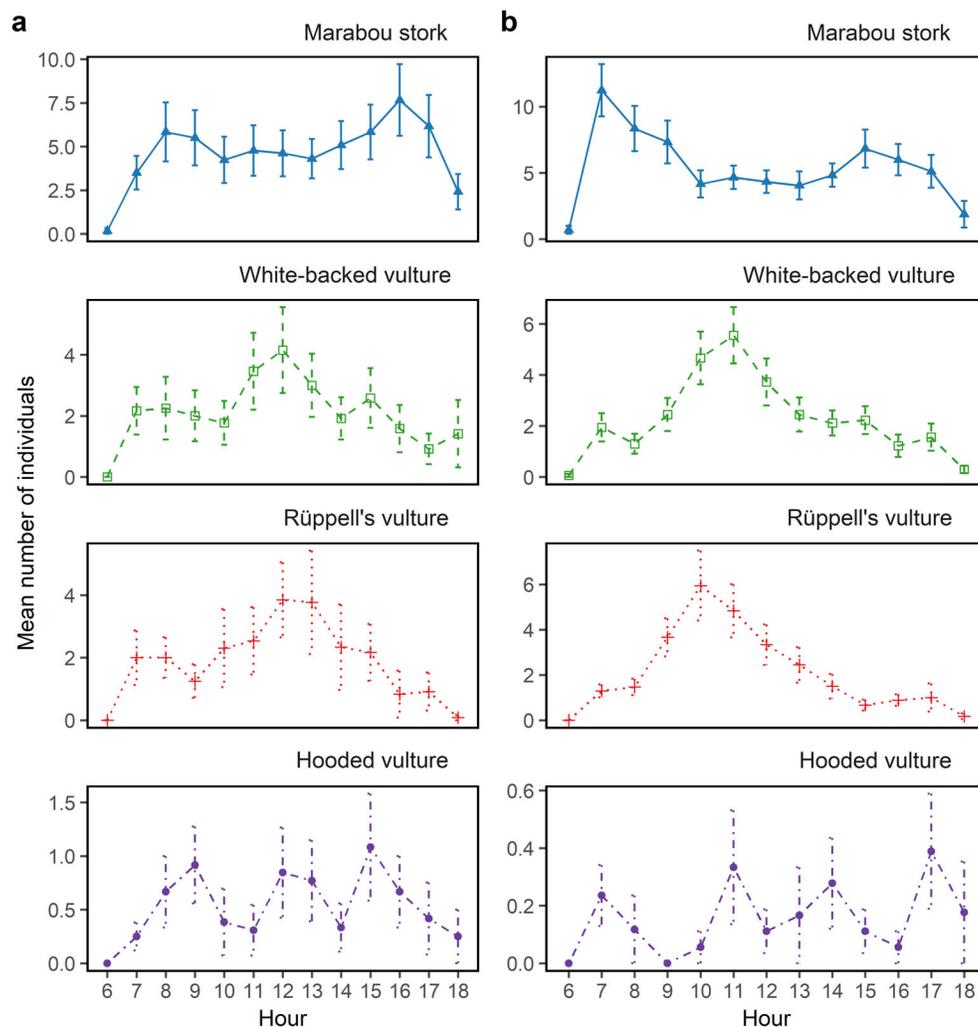


Fig. 6. Diel activity patterns (mean \pm SE number of individuals per hour) of the four most common species of avian scavenger on wildebeest carcasses after mass drownings in the Mara River in (a) 2012 and (b) 2013.

resulting in 1,500 carcasses in the river, and all occurred more than a month prior.

At the focal carcass sites monitored with camera traps, the most common avian scavengers were marabou storks, comprising 30–34% of individuals, which likely reflects their enhanced ability to forage in aquatic habitats (Kahl 1966). Marabou storks typically are not included in surveys of avian scavengers feeding on terrestrial carcasses due to their low abundance, as they comprise only 3–4% of individuals (Table 1), suggesting the habitat in which mortality occurs is of fundamental importance in determining its attendant scavenger community. Marabou storks

have limited ability to tear meat, sometimes relying on vultures to pull off pieces of meat that the storks then steal (Attwell 1963, Houston 1975), and the longer period of carcass decomposition in water may benefit marabou storks in their feeding style. In contrast, in surveys along river reaches near the mass drownings, the most common avian scavengers were white-backed and Rüppell's vultures, suggesting these species congregate in higher numbers along the riverbanks. The large number of *Gyps* vulture individuals (up to several hundred) resting along the riverbanks between feeding bouts may be due to the need to dry out wings after feeding in the river,

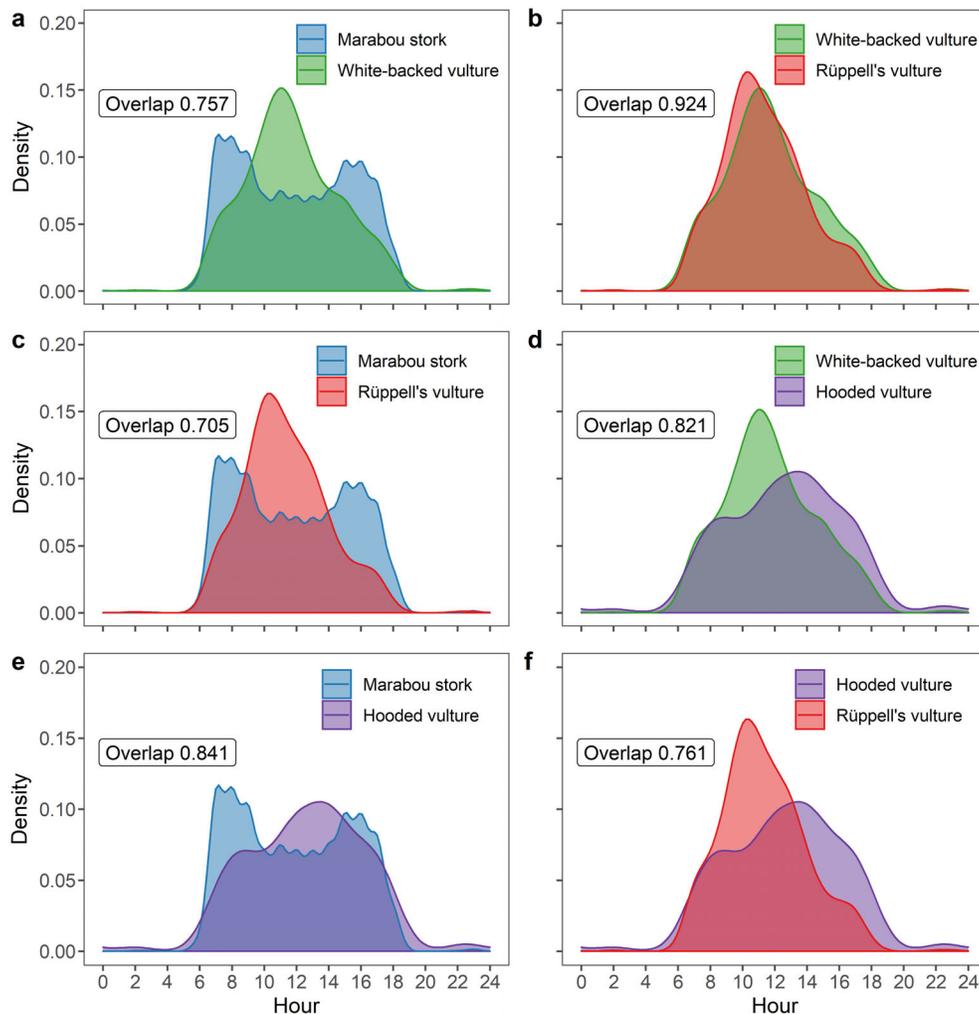


Fig. 7. Overlap plots of the combined activity curves from 2012 and 2013 of (a) marabou storks and white-backed vultures ($\lambda = 0.757$), (b) white-backed vultures and Rüppell's vultures ($\lambda = 0.924$), (c) marabou storks and Rüppell's vultures ($\lambda = 0.705$), (d) white-backed vultures and hooded vultures ($\lambda = 0.821$), (e) marabou storks and hooded vultures ($\lambda = 0.841$), and (f) hooded vultures and Rüppell's vultures ($\lambda = 0.761$) on wildebeest carcasses in the Mara River, Kenya.

or to other social or behavioral reasons. These riparian aggregations have implications for nutrient transport to riparian zones as well as intra- and interspecific social interactions. Such waiting or resting behavior is seen when vultures feed at single carcasses on land, but it occurs at a much larger scale after mass drownings. White-backed and Rüppell's vultures were also the most common avian scavenger species and were highly associated with one another in studies of vulture use of single carcasses in this region

(Table 1), suggesting mechanisms that enable their coexistence may apply across a range of carcass availability (Kendall et al. 2012). However, the number of individuals per carcass was far lower in this study, again suggesting the importance of carcass location, that is, in the water as opposed to on land (Kendall et al. 2012, Kendall 2014). Lappet-faced vultures were rarely documented in this study, although they were documented in greater numbers at the river reach scale. Differences in their foraging ecology, with

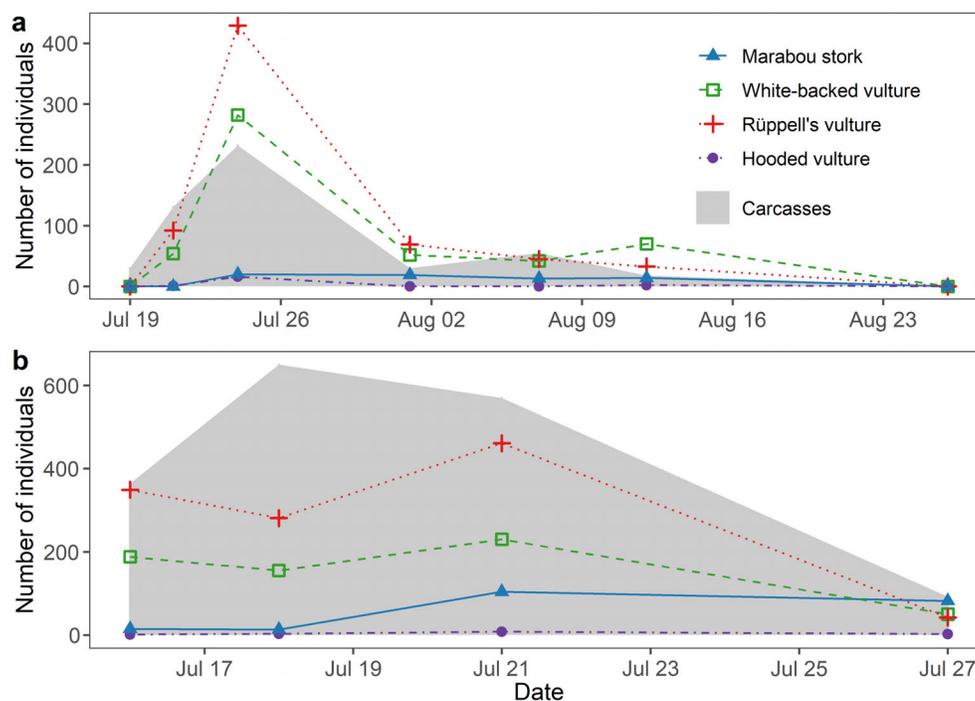


Fig. 8. The number of carcasses and the total number of the four most common avian scavengers surveyed during visual observations of wildebeest carcasses at a section of the Mara River, Kenya, in (a) July 2010 and (b) July 2011.

Table 2. Vulture use of the Mara River following two wildebeest mass drownings in 2010 for three different species, as indicated by tracking with GSM-GPS tags.

Species	Age	No. days at river	No. days tracked	Percentage of time tracked at river	Mean distance from river (km)
White-backed vulture (<i>Gyps africanus</i>)	3 J, 3 A	3.6 (4.9)	17.6 (13.2)	18.0 (28.7)	26.9 (13.9)
Lappet-faced vulture (<i>Torgos tracheliotos</i>)	2 J, 3 A	0.4 (0.7)	15.6 (12.9)	1.3 (2.5)	28.7 (14.2)
Rüppell's vulture (<i>Gyps ruppellii</i>)	1 J, 7 A	3.8 (4.5)	19.4 (11.6)	19.2 (20.5)	45.0 (52.7)

Note: Age is given as number of juveniles (J) and adults (A). Means are presented with SD in parentheses.

a preference for smaller carrion sources, need to reduce competition with white-backed and Rüppell's vultures, and preference for feeding in smaller aggregations, may explain the low number of lappet-faced vultures around large carcass aggregations (Houston 1976, Kendall et al. 2014).

The larger-bodied avian scavengers declined as carcass decomposition progressed. In concert with this decline, smaller-bodied avian species increased, such as hooded vultures, which forage

on the carcasses, and sacred ibis, which forage on insects that have colonized the carcasses. Non-avian scavengers, including hyenas, crocodiles, and mongoose, also increased during the later stages of decomposition. These changes in community composition likely reflect both interspecific competition and resource partitioning. Smaller-bodied vultures like hooded vultures are often dependent on larger-bodied vultures to tear open carcasses and make them available for

consumption, and they also may be out-competed by larger-bodied vultures during preferred feeding times due to their small body size (Kendall 2013). Sacred ibis and mongoose preferentially feed on smaller-bodied prey such as insects and are therefore likely responding to the large number of insect larvae available on the carcasses. These larvae may be more accessible in later decomposition stages due to increased access to the inner portions of carcasses and decreased activity by larger-bodied avian scavengers (Baruzzi et al. 2018, Lashley et al. 2018b). This feeding guild is not likely to benefit as substantially from single carcasses, which are largely consumed within a 24-hour period and leave little material to host insect larvae. The increased presence of crocodiles later in the decomposition stage reflects their preferred use of rotten tissue, which is easier to manipulate with their jaws. Their relatively low numbers in our surveys support earlier estimates that crocodiles consume a small number of carcasses from mass drownings (Subalusky et al. 2017). Use of carcasses by terrestrial scavengers, including mongoose and hyenas, was largely limited to carcasses located next to the riverbank, and falling water levels throughout both camera photograph series made these carcasses more accessible to terrestrial scavengers in the later stages. Thus, carcass availability and decomposition stage were confounded through time, and it is possible that hyenas would have been more abundant early in the time series if low water levels had allowed them easier access to carcasses. However, hyenas' unique ability to use the carcass bones as a resource may make them less sensitive to decomposition stage (Wambuguh 2008). This study did not address carcass use by aquatic consumers, such as aquatic macroinvertebrates and fishes, although other research has suggested the carcasses might provide a substantial resource for them (Subalusky et al. 2017, 2020).

We also observed diel patterns in avian scavenger carrion use. Marabou storks used the carcasses more frequently in the morning and late afternoon, while both white-backed and Rüppell's vultures used the carcasses more in mid-day. Prior research in this region on single carcasses on land found similar temporal patterns of higher carcass use in mid-day for Rüppell's vultures, which was attributed to

nesting behavior (Kendall 2014). Rüppell's vultures nest on cliff ledges during this time of year, and some of these are located >100 km away from the Serengeti Mara Ecosystem, suggesting they make more frequent long-distance flights to take advantage of carcass resources and would not arrive at the river until mid-afternoon. This behavior also suggests Rüppell's vultures are likely transporting carcass resources back to their nest sites, which could result in nutrient transport from the river to distant terrestrial ecosystems. White-backed vultures, which nest locally in trees and have higher search efficiency (Virani et al. 2010, Kendall 2013), typically arrive at carcasses in the early morning to maximize foraging ability, which is what was observed on single carcasses on land (Kendall 2014). However, the large availability of carcasses in the river may have made early morning foraging less important than under normal conditions. It is also possible that risks due to foraging in the river made it preferable to wait until later in the day when air temperatures were higher and vultures could dry their wings more quickly. Marabou storks may have been more active in the mornings and late afternoons, which are normally preferable activity times due to cooler temperatures, because their adaptation to feeding in aquatic habitats allowed them to take advantage of this temporal niche (Kahl 1966). Thus, marabou storks may have a competitive advantage in the case of drowning deaths that they do not normally have for carcasses on land.

Despite the large number of avian scavengers observed at the carcasses, telemetry results suggest many vultures in the area do not use carcasses from mass drownings and that the time each individual spent at a mass drowning sites was limited. For both white-backed and Rüppell's vultures, approximately two-thirds of individuals being tracked used the carcasses during one-third of their time. Only one-quarter of lappet-faced vultures used the drownings at all, and those only visited the river during 5% of their time. Given the majority of individuals were within a sufficiently close range (<30 km) and that carcasses from mass drownings are present for several weeks, it is likely that vultures would have observed carcass aggregations and been aware of attendant vultures (Houston 1974, Cortés-Avizanda et al. 2014), but chose to avoid

or make limited use of the available carrion. The low use of carcasses may be due to the riskiness of foraging in the river, difficulty accessing floating carcasses, competition for accessible carcasses, and/or the prevalence of other carcasses in preferable habitats on the landscape during this time. Combined with the low number of individuals observed per carcass, these data suggest that local enhancement is less important for mass mortality events than for a single carcass (Jackson et al. 2008). These data also support findings from earlier studies on both landscape-scale movements of vultures and the influence of supplemental feeding stations (i.e., vulture restaurants) that food availability is not the only factor mediating vulture foraging behavior (Cortés-Avizanda et al. 2009, Phipps et al. 2013, Kendall et al. 2014). This variation in use of the river and associated carcasses may further reflect differences in carcass and habitat use exhibited by vulture species that helps to mediate their coexistence (Kendall et al. 2014). For instance, Rüppell's vultures occurred at similar proportions at mass drownings and single large terrestrial carcasses whereas white-backed vultures had lower prevalence at mass drownings. Similar to what has been found at vulture restaurants, larger aggregations of carrion may benefit dominant species, such as Rüppell's vultures, who can more effectively monopolize known food sources (Cortés-Avizanda et al. 2012).

This research shows that a suite of scavenger species responds to carcasses from mass drownings, but the abundance of carcasses in conjunction with their location in the river influence scavenger use and succession patterns. Scavenger use of wildebeest mass drownings likely plays an important role in nutrient cycling and transport from these events. The declining populations of most African vulture species suggest carrion from mass mortalities such as these may persist for even longer on the landscape and not be transported away from mortality hotspots. Furthermore, the longer persistence of carcasses on the landscape could increase the abundance of and contact between facultative mammalian scavengers, which could increase potential for disease transmission (Ogada et al. 2012*a, b*). It is unclear the degree to which these scavenger species rely upon mass drownings to supplement their annual energy budget. The relatively low

proportion of individuals and low proportion of time that avian scavengers spent near the river after mass drownings suggest the challenges associated with foraging in the river do not outweigh the benefits of abundant resources; however, mass drownings may provide an important resource pulse during a time when most avian scavenger species are nesting. The general decline of large migrations and associated mass mortality events could negatively influence scavenger species in other parts of the world. The relative predictability of mass drownings in the Mara River allows us to study the influence of these mass drownings on scavenger succession patterns, which can inform our understanding of other mass mortality events that may result from starvation during drought, disease mortality during anthrax or brucellosis outbreaks, or culling during management interventions. Our research suggests the location of carcasses and life history and behavioral characteristics of available scavenger species are critical determinants of carcass utilization by scavengers.

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applicable institutional and/or national guidelines for the care and use of animals were followed. Author contributions: All authors conceived the idea. Katherine S. Handler, Amanda Subalusky, Christopher Dutton, and Corinne J. Kendall collected and analyzed the data. Katherine S. Handler, Amanda Subalusky, and Corinne J. Kendall wrote the paper; other authors provided editorial advice. Data availability: All data and analysis code has been deposited in the Mendeley Data Repository and be accessed at <http://dx.doi.org/10.17632/g9z8vc km5y1>.

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