MECHANISMS OF COEXISTENCE IN VULTURES: UNDERSTANDING THE PATTERNS OF VULTURE ABUNDANCE AT CARCASSES IN MASAI MARA NATIONAL RESERVE, KENYA

CORINNE KENDALL[1,2,5], MUNIR Z. VIRANI[2,3], PAUL KIRUI[4], SIMON THOMSETT[2], AND MWANGI GITHIRU[2]

[1]*Department of Ecology and Evolutionary Biology, 113 Eno Hall, Princeton University, Princeton, NJ 08544-2016*
[2]*Ornithology Section, Department of Zoology, National Museums of Kenya, P. O. Box 40658-00100, Nairobi, Kenya*
[3]*The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709*
[4]*Kenya Professional Safari Guides Association, P. O. Box 24397-00502, Nairobi, Kenya*

Abstract. Because of the high, albeit seasonal, availability of carcasses, the Mara-Serengeti ecosystem, Kenya, has a high diversity of scavengers, leading to considerable competition between species. From patterns of occurrence of vultures at 163 carcasses over an 8-year period in the Masai Mara National Reserve, we were able to identify some mechanisms that may reduce competition. Species are associated on the basis of similar dietary needs and beak morphology, and they are highly interdependent, showing little evidence of disassociation. Social vultures (genus *Gyps*) dominated the vulture scene at the reserve; they were more abundant at carcasses when migratory ungulates were present in the dry season, when more carcasses are likely to be available, than when migratory ungulates were absent. In addition, regardless of the predator's identity, presence of a predator reduced the number of vultures, suggesting that vultures prefer carrion not killed by predators where available. Comparisons between past and current counts of carcasses suggest a substantial shift in *Gyps* vultures with an increase in the relative abundance of Rüppell's Vulture (*G. rueppellii*) with respect to that of the White-backed Vulture (*G. africanus*). In addition, our findings suggest that as changing land use in the Mara-Serengeti ecosystem leads to reductions of large ungulates, social vultures will be the most adversely affected.

Key words: *aggregation, coexistence, competition, food availability, resource partitioning, scavengers, vulture.*

Mecanismos de Coexistencia de los Buitres: Entendiendo los Patrones de Abundancia de los Buitres en las Carcasas en la Reserva Nacional Masai Mara, Kenia

Resumen. Debido a la alta, aunque estacional, disponibilidad de carcasas, el ecosistema de Mara–Serengeti, Kenia, tiene una alta diversidad de carroñeros, generando una competencia considerable entre especies. A partir de los patrones de ocurrencia de los buitres en 163 carcasas a lo largo de un período de 8 años en la Reserva Nacional de Masai Mara, fuimos capaces de identificar algunos mecanismos que pueden reducir la competencia. Las especies están asociadas en base a las necesidades similares de dieta y a la morfología del pico y son altamente interdependientes, mostrando poca evidencia de disociación. Los buitres sociales (género *Gyps*) dominaron la escena de los buitres en la reserva; fueron más abundantes en las carcasas durante la migración de los ungulados, cuando es más probable que exista disponibilidad de carcasas, que cuando los ungulados no están migrando. Adicionalmente, sin tener en cuenta la identidad del depredador, la presencia de los depredadores redujo el número de buitres, sugiriendo que los buitres prefieren carroña que no haya sido matada por un depredador. Las comparaciones entre conteos pasados y actuales de carcasas sugiere un cambio sustancial en los buitres del género *Gyps*, con un incremento en la abundancia relativa de *G. rueppellii* con respecto a la de *G. africanus*. Adicionalmente, nuestros resultados sugieren que los cambios en el uso de la tierra en el ecosistema de Mara–Serengeti que conlleven a la reducción de los grandes ungulados afectarán más negativamente a los buitres sociales.

INTRODUCTION

In ecosystems where carcasses are readily available, such as the Mara–Serengeti, the ranges of scavengers overlap more and facultative scavengers use carrion more, which leads to high diversity of scavengers and intense interspecific competition (Petrides 1959, Kruuk 1967). Understanding the factors that enable species' coexistence in such diverse guilds is an important question in community ecology (MacArthur 1958, May and MacArthur 1972). Resource partitioning has been used to explain the coexistence of ecologically similar species and can arise through differences in diet or through

spatial and temporal segregation of resource use (Ilse and Hellgren 1995, Kronfeld-Schor and Dayan 2003). In addition, it has been proposed via the aggregation model of coexistence that in guilds using widely distributed and ephemeral resources such as carrion or dung, intraspecific aggregation with interspecific disassociation can enable coexistence (Atkinson and Shorrocks 1981). By considering the influence of spatio-temporal factors on patterns of vulture abundance at carcasses as well as levels of association and aggregation, we can better understand the mechanisms underlying coexistence in scavenger guilds in east Africa and more broadly.

Resource partitioning by vultures may be influenced by many factors, both behavioral and extrinsic (Selva et al. 2005). In east Africa, Kruuk (1967) suggested that vultures minimized aggressive encounters and interspecific competition through differences in beak morphology, which enable variation in which body parts are consumed at large carcasses. Body size also appears to have a strong influence on dominance hierarchies and thus resource partitioning in several guilds of scavengers (Petrides 1959, Kruuk 1967, Wilbur and Jackson 1983, Gomez et al. 1994). Mundy et al. (1992), however, suggested that the primary difference between vulture species is in diet. In particular, the size, though not species, of a carcass often has a significant effect on the number and proportions of vultures occurring at it (Gomez et al. 1994, Selva et al. 2005, Hunter et al. 2007).

Spatio-temporal partitioning of resources by scavengers has been assessed through studies of differences in habitat use and resource dispersion. Bamford et al. (2009a) assessed the effects of vegetation structure on the Cape Vulture (*Gyps coprotheres*) and White-backed Vulture (*G. africanus*) and found differences in carcasses exploited on the basis of the birds' abilities to take flight in the habitat. Kirk and Houston (1995) assessed the habitat use and foraging strategies of migrant and resident Turkey Vultures (*Cathartes aura*) and found a significant influence of social dominance on habitat preference of each group. Houston (1974a) found that density of vultures, particularly of the genus *Gyps*, increased in areas of high wildlife density. In addition, resource distribution, whether aggregated or scattered, appears to be important in determining the community composition of scavengers at ungulate carcasses in temperate-zone ecosystems (Wilmers et al. 2003, Blázquez et al. 2009). Competition with predators at carcasses may also influence scavengers and lead to variations in scavengers' community structure at carcasses killed by predators or not (Selva et al. 2005).

For species feeding on divided and ephemeral resources such as carrion, it has been predicted that aggregation of a single species can reduce interspecific competition (Atkinson and Shorrocks 1981, Rosewell et al. 1990, Hartley and Shorrocks 2002). Recent studies provide evidence for this in communities of scavengers as intraspecific aggregation of subordinate species with high recruitment at temporally or spatially aggregated resources led to resource partitioning of scavengers between aggregated and dispersed resources (Wilmers et al. 2003, Blazquez et al. 2009). This is due primarily to large groups of subordinate species being able to outcompete dominant species (Houston 1974b, Gomez et al. 1994, Kirk and Houston 1995, Buckley 1996). However, Atkinson and Shorrocks (1981) predicted that, in addition to intraspecific aggregation, disassociation of species is necessary for this to be an effective mechanism of coexistence (Shorrocks et al. 1990). Currently the role of aggregation and association among avian scavengers has not been assessed.

In this study, we investigate how six species of vultures use animal carcasses to assess possible mechanisms of their coexistence. In particular, we investigate how carcass size, predator presence, season, and year influence the number and composition of avian scavengers at a carcass. Given the dependence of *Gyps* vultures on social dominance to feed effectively, we predicted that these social species should be more concentrated at large carcasses than at small ones. In addition, social vultures should be more abundant during ungulates' migration season, when the availability of carcasses is high, than outside the migration season. Finally we expected fewer vultures of all species at carcasses with predators than at those without mammalian predators.

Avian scavengers are declining rapidly throughout Africa, including east Africa, and establishing the cause of these declines is essential (Thiollay 2007, Ogada and Keesing 2010, Virani et al. 2011). Loss of vultures from Kenya's prestigious Masai Mara National Reserve is likely to have significant ecological and economic ramifications, as has occurred elsewhere (Sekercioglu et al. 2004, Sergio et al. 2005, Sekercioglu 2006, Markandya et al. 2008). Transects have already revealed a decline of vultures in the reserve (Virani et al. 2011), but the species of *Gyps* were aggregated in past counts, making it impossible to assess differences in the rate of decline of the White-backed and Rüppell's (*G. rueppellii*) Vultures. Here we make the first attempt to assess changes in the relative abundance of these two species, by comparing current carcass counts with past numbers. In addition, understanding interspecific differences in food choice and foraging strategies will help in assessing the susceptibility of vultures to threats such as increased human disturbance, reduced and/or altered food availability due to land-use change, and poisoning, all of which are major problems affecting wildlife in east Africa (Ogutu et al. 2005, 2009, Kissui 2008, Murn and Anderson 2008, Bamford et al. 2009b, Virani et al. 2011).

METHODS

STUDY SITE

Masai Mara National Reserve (MMNR) is a savanna habitat in southwestern Kenya. It is approximately 1530 km^2 in size and is surrounded by Masai pastoral lands to the north, east, and west. To the south, it is bordered by the larger Serengeti National Park of Tanzania, and combined the two reserves

cover nearly 25 000 km^2. MMNR is an important area for avian scavengers because of the high density of ungulates and large herds of the migratory Blue Wildebeest (*Connochaetes taurinus*), Burchell's Zebra (*Equus burchelli*), and Thomson's Gazelle (*Gazella thomsonii*) that frequent the area from July to October each year (Boone et al. 2006). Rainfall is bimodal, with the long rains falling from March to June and the short rains from November to December (Ogutu et al. 2008). The Mara–Serengeti ecosystem is arguably one of the most important areas for scavengers in Africa, supporting high densities of many species of scavengers (Houston 1979, 2001). Throughout MMNR, we recorded patterns of vultures' occurrence primarily at large mammalian carcasses. Observations were made throughout the year both during and outside ungulates' migration seasons.

STUDY SPECIES

Six species of vultures are found in the Mara–Serengeti ecosystem. When classified by beak morphology and feeding technique, they are usually grouped into three subsets (Kruuk 1967) (Table 1). The Lappet-faced Vulture (*Torgos tracheliotus*) and White-headed Vulture (*Trigonoceps occipitalis*) have large beaks and use a tearing technique, allowing them to open carcasses and eat skin, tendons, and joints (Mundy et al. 1992). The Lappet-faced is dominant over all other vulture species (Kruuk 1967, Houston 1975, Mundy et al. 1992). Rüppell's Vulture (*Gyps rueppellii*) and the White-backed Vulture (*G. africanus*), often termed the *Gyps* vultures, are gregarious, have long necks and medium-sized beaks, and tend to feed on the viscera of the carcass (Houston 1974b, Mundy et al. 1992). *Gyps* vultures are believed to rely extensively on homo- and heterospecific facilitation to find carrion and then to compete with other species. Individually these species are generally subordinate to the larger vultures, but in large groups they are able to outcompete larger species (Mundy

et al. 1992, Jackson et al. 2008). Finally, the smaller Egyptian Vulture (*Neophron percnopterus*) and Hooded Vulture (*Necrosyrtes monachus*) have a more varied diet, using several food sources other than carrion, but when feeding at a carcass tend to peck on scraps.

VULTURE NUMBERS

We recorded data over 8 years in total from 1997 to 2006, 2000 and 2003 excluded for logistical reasons. We counted vultures during daylight hours while driving within MMNR. Initial trends indicated that searching for carcasses along specific routes only would yield too few observations. Therefore, we located carcasses opportunistically either by sight, by following vultures, or through communication with tour guides who had located carcasses previously. Although we did not quantify the spatial or temporal distribution of carcasses over our study area, their density was likely to be considerably higher during the dry migration season when wildlife density in MMNR is higher and mortality is also higher (Houston 1989).

For every carcass encountered, we recorded the number of each vulture species present, species of the carcass (from which we categorized the carcass by size), and the presence and identity of predators. We recorded carcasses of 18 species, the most common being Burchell's Zebra, Blue Wildebeest, Thompson's Gazelle, and African Buffalo (*Syncerus caffer*) (see Appendix 1, available at http://dx.doi.org/10.1525/cond.2012.100196, for the complete list). We considered predators present at the carcass if they were feeding at or within 20 m of it. We verified the identity of the predator that killed the animal, regardless of presence, by previous reports from tour guides or by the manner in which the animal had been killed and consumed. Predators recorded at carcasses included Lions (*Panthera leo*), Spotted Hyenas (*Crocuta crocuta*), Common Leopards (*Panthera pardus*), and Cheetahs

TABLE 1.   Characteristics of the species of vultures occupying the Masai Mara National Reserve, Kenya[a]

Species	Dominance	Level of specialization on carrion	Order of arrival	Feeding tactic
White-headed (*Trigonoceps occipitalis*)	Middle	Middle; some predation	Early	Tear
Lappet-faced (*Torgos tracheliotus*)	High (individually)	Middle; some predation	Late; occasionally early	Tear
Rüppell's (*Gyps rueppellii*)	High (in groups)	High; obligate scavenger	Middle	Pull
White-backed (*Gyps africanus*)	High (in groups)	High; obligate scavenger	Early/middle	Pull
Hooded (*Necrosyrtes monachus*)	Low	Low	Early at predator kills; late at natural carcasses	Peck
Egyptian (*Neophron percnopterus*)	Low	Low	Early at predator kills; late at natural carcasses	Peck

[a]Adapted from Mundy et al. (1992).

(*Acinonyx jubatus*). For leopard kills we only included carcasses that were either on the ground or in short open trees such as *Gardenia* sp., where vultures still had access to the meat.

In addition to year, we categorized each carcass by season: June–October (encompassing the Mara–Serengeti ungulate migration) (Estes and East 2009) and November–June (reflecting the nonmigration season). These seasons also roughly coincide with the pattern of rainfall in the MMNR region, the migration season being largely during the dry season and nonmigration during the wet (Ottichilo et al. 2001). Using a vehicle as a blind, we made all observations 20–50 m from the carcass. Observations were generally short, lasting only as long as needed for a count of all birds present at the carcass.

DATA ANALYSIS

We used a chi-squared test to compare our data on the proportion of each vulture species seen at carcasses with records from the 1960s and 1970s by Mundy et al. (1992), assuming the historical data for each species as the expected proportions. Historical data involved counts of vultures at carcasses in Amboseli and Serengeti national parks, Tanzania, primarily by David Houston, rather than in MMNR. Recent studies using GSM-GPS telemetry and wing tagging show that an individual *Gyps* vulture can range over these three areas—MMNR, Amboseli, and Serengeti—which are less than 100 km apart (Kendall and Virani 2012). Populations in this region therefore appear to be linked, and abundance and behavior at carcasses should be similar throughout, making these counts useful for historical comparisons.

We used a principal factor analysis as a classification method for detecting structure in the vulture dataset, in order to check whether certain vultures were more commonly seen together at a carcass than were others. PFA was done across the year and also by season to see if any differences in vulture associations occurred within the year. We used a principal-components extraction technique with the varimax rotation in Statistica (StatSoft 2001). We considered factor loadings (correlations between the factors and the original variables) >0.32 significant and interpreted them (Alsobrook et al. 1999). To assess aggregation of each vulture species we used an index of dispersion (for the migration and nonmigration seasons separately) calculated by dividing the variance by the mean number of individuals of a given species at a carcass (Lloyd 1967). A dispersion index >1 suggests that the species aggregates at carcassWe square-root-transformed the raw counts and used the transformed data as the response variable in a generalized nonlinear model [GLZ] (assuming a Poisson distribution, and using the log-link function) with five categorical explanatory variables: season (migration and nonmigration), carcass size (three classes: 1–100, 101–1000, and >1000 kg), identity of predator (cheetah, hyena, leopard, lion, none, unknown), and species (White-backed, Rüppell's, Lappet-faced, White-headed, Hooded, and Egyptian vultures). We considered year

as a random effect and included all four two-way interactions involving species. Because our primary objective was to identify the most parsimonious model, we then undertook an exploratory and sequential modeling approach involving all nine effects (five main, four interactions) that allows unsupported variables to be eliminated without further reporting (Devries et al. 2008). We thus excluded all models with uninformative parameters (i.e., Akaike weights of zero) from the table of the models' rankings (Arnold 2010).

For model building and selection we used the Best Subsets option based on the Akaike information criterion in Statistica (StatSoft 2001) corrected for small sample size (AIC_c). In addition to being within two AIC_c units of the top model, we considered a model competitive for inference only if the covariates in the lowest AIC_c model were not a subset of covariates in the competing model (Burnham and Anderson 2002, Devries et al. 2008, Arnold 2010, McClure et al. 2011). We also computed the Akaike weights (w_i) of the five top-ranked models, which provided a measure of evidence (probability) that z model was the best (Johnson and Omland 2004, Devries et al. 2008). There was no evidence of overdispersion in our dataset, with the deviance of the global model being 0.78; likewise, the residuals did not deviate significantly from expectation based on the Poisson distribution.

RESULTS

VULTURE NUMBERS

Over the 8-year period, at 163 carcasses, we counted 6840 individual vultures of which close to 90% were *Gyps* vultures. The relative abundance of vulture species per carcass in the current and historic data differed significantly, most notably in the greater relative abundance of Rüppell's Vulture in current counts (χ^2 = 96.2, p = 0.0001), suggesting a marked change in species composition within the vulture guild (Fig. 1).

VULTURE ASSOCIATIONS AND AGGREGATIONS

Using a Scree plot, we extracted three factors accounting for 77.8% of the total variance. On the basis of factor loadings (Table 2), we identified three associations in the overall sample: factor 1: White-backed–Rüppell's–Lappet-faced Vultures; factor 2: Hooded–Egyptian Vultures; factor 3: White-headed–Lappet-faced Vultures. Factors 1 and 3 remained the same throughout the year. Factor 2 was the same during the migration season but changed to White-headed–Egyptian outside of the migration.

The *Gyps* vultures were more aggregated at carcasses during ungulate migration (index of dispersion 20 for the White-backed Vulture, 15 for Rüppell's Vulture) than outside of the migration (index of dispersion 11 and 4 for the White-backed and Rüppell's Vulture, respectively). The level of aggregation of the Hooded Vulture was low during both seasons with an index of dispersion of 2 for both. Lappet-faced
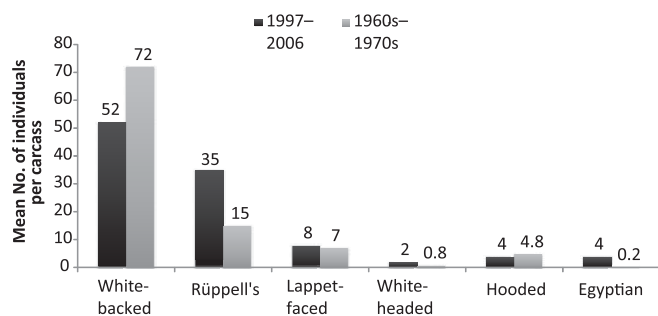
FIGURE 1.   Mean number of each vulture species per carcass on the basis of data from Serengeti National Park, Tanzania, 1960s–1970s (with an overall mean of 100 individuals/carcass) and from Masai Mara National Reserve, Kenya, 1997–2006 (overall mean of 105 individuals/carcass).

Vultures were aggregated only during the nonmigration season. Aggregation of the White-headed and Egyptian Vultures was also limited with an index of dispersion <2 for both seasons.

FACTORS INFLUENCING VULTURE NUMBERS AT CARCASSES

There were no models within two AIC_c units of the top model that were not hierarchically nested in it (Table 3). Thus none was competitive and we assumed the model with the lowest AIC_c was the best. This model was also considerably more probable than the others, with a 65% probability of being the best (Table 3). It had four significant main effects (species, carcass size, predator, and year) and one significant interaction (species × season). From the significant interaction, the White-backed and Rüppell's Vultures, which were the most abundant species at carcasses during both seasons, also showed greater variation across seasons than did the other species (Fig. 2). Vultures occurred in larger numbers at larger carcasses (small: mean = 3 ± 0.4, n = 38; medium: mean = 8 ± 0.6, n = 119; large: mean = 21 ± 12.8, n = 5), as well as at carcasses where there was no predator attendant (Fig. 3). Last, the year effect indicated that numbers of vultures at carcasses fluctuated significantly temporally, over and above the seasonal variations in carcass number driven by ungulate migration and associated changes in rainfall.

DISCUSSION

VULTURE ABUNDANCE, ASSOCIATIONS, AND AGGREGATION

The White-backed was the most common vulture at carcasses in the MMNR throughout the year and is probably resident. The mean number of Rüppell's Vulture was higher during the migration season, and its relative abundance increased significantly when migratory ungulates were present. Because of their nesting on cliffs and large home ranges, these species may be able to respond acutely to changes in wildlife density (Mundy et al. 1992).

Overall we found associations between (1) the White-backed, Rüppell's, and to a lesser extent Lappet-faced Vultures, (2) the Hooded and Egyptian Vultures, and (3) the White-headed and Lappet-faced Vultures. The White-backed, Rüppell's, and Lappet-faced Vultures associated regardless of season, suggesting that shifts in carcass and vulture density do not affect vulture interactions strongly. This is probably due to the increase in vulture abundance that tends to accompany, and compensate for, the increase in carcass density during the migration season (Houston 1979, 2001). Interestingly, these associations involve species that are also the most similar in their feeding ecology and so expected to compete most intensely (Houston 1974b, Mundy 1982, Mundy et al. 1992). Associations among White-backed, Rüppell's, and Lappet-faced Vultures may be explained in part by species using each other to find carcasses or by similarities in their preferences, which may in turn relate to similarities in their beak morphology and behavioral adaptations such as high social or individual dominance. Because the associations between these three species did not change even as carcass availability increased, vulture populations may be limited by food availability and competition between species may remain high throughout the year.

In some guilds of scavengers, high levels of aggregation have been found to reduce interspecific competition, but only

TABLE 2.   Factor loadings for the three extracted principal factors (PF), overall and by season. The factors represent vulture associations, with the loadings in **bold** font indicating the species that associate with one another under that PF.

Species	Overall			During ungulate migration			Outside ungulate migration		
	PF 1	PF 2	PF 3	PF 1	PF 2	PF 3	PF 1	PF 2	PF 3
White-backed	**0.96**	0.06	−0.08	**0.95**	0.09	−0.11	**0.90**	−0.13	0.02
Rüppell's	**0.93**	−0.07	−0.05	**0.95**	−0.06	0.01	**0.75**	−0.14	0.18
Lappet-faced	**0.62**	0.23	**0.46**	**0.77**	0.24	0.19	**0.80**	0.27	−0.24
White-headed	−0.06	−0.04	**0.94**	0.02	−0.07	**0.98**	0.12	**0.90**	0.10
Hooded	0.02	**0.79**	0.12	0.31	**0.78**	0.06	0.02	0.04	**0.96**
Egyptian	−0.08	**0.82**	−0.11	−0.10	**0.88**	−0.14	−0.26	**0.59**	−0.31

TABLE 3.   Summary of model-selection results for numbers of vultures at carcasses in Masai Mara National Reserve, Kenya, 1997–2006. Models are listed beginning with the best-fitting model and sorted by ΔAIC_c. The AIC_c weight indicates the relative likelihood of each model within the model set and sums to 1.

Model	K^a	Deviance	ΔAIC_c [b]	AIC_c weight
Species + carcass size + predator + year + season × species	24	1866.7	0.00	0.65
Species + season + carcass size + predator + year + season × species	25	1866.4	1.82	0.26
Species + carcass size + predator + year + season × species + carcass size × species	34	1850.4	5.01	0.05
Species + season + carcass size + predator + year + season × species + carcass size × species	35	1848.9	5.64	0.04
Species + carcass size + predator + season × species	17	1895.1	13.86	0.00

[a]Number of parameters.
[b]Difference between the AIC_c value for the current model and the model with the lowest AIC_c The lowest AIC_c score in the analysis was 1917.9.

if levels of association between species are low (Atkinson and Shorrocks 1981). As found previously, the *Gyps* vultures were the most highly aggregated of the species studied, especially during the migration season. However, the two species were also highly associated, so other mechanisms must operate to enable coexistence (Atkinson and Shorrocks 1981, Rosewell et al. 1990, Shorrocks et al. 1990, Hartley and Shorrocks 2002). Associations between similar vulture species suggest a high level of interdependence between those species, possibly related to one species facilitating another in discovering or opening carcasses or in reducing competition between avian and mammalian scavengers (Travaini et al. 1998).

FACTORS AFFECTING VULTURE COUNTS

As reported by Houston (1974a, b), all six species of vultures were less abundant at carcasses with predators than at those without predators, although we confirmed only six carcasses as not killed by predators and further investigation is merited. The predator's identity was generally not important, though vulture abundance was particularly low at leopard kills. In Serengeti, Houston (1974b) found that little food is typically available for vultures at predator kills and estimated that vultures consume 88% of their diet at carcasses not killed by predators, where competition with mammalian predators and scavengers is greatly reduced.

The annual fluctuations we found in vulture abundance at carcasses may be caused by changes in other factors that affect carcass availability within MMNR and thus influence vulture abundance overall. Variation in rainfall influences the breeding of many scavenging birds and may also affect their foraging behavior (Virani et al. 2012). In particular, vulture abundance should increase in years of low rainfall when ungulate mortality is higher. Declines in overall wildlife density or changes in the pattern of ungulate migration, so the animals spend less time in MMNR, as appears to be occurring, could also affect carcass availability in the study area and therefore lead to reductions in vulture abundance (Ogutu et al. 2011). Unfortunately, during this study no data on the level of annual variation in these factors were recorded.

The greater abundance of vultures at carcasses during the migration season was driven largely by higher numbers of the *Gyps* species. White-backed Vultures generally fledge
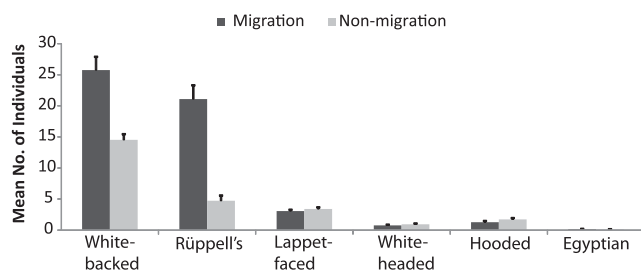

FIGURE 2.   Mean number of vultures of each species per carcass during (86 carcasses) and outside (76 carcasses) the season of ungulate migration at the Masai Mara National Reserve.
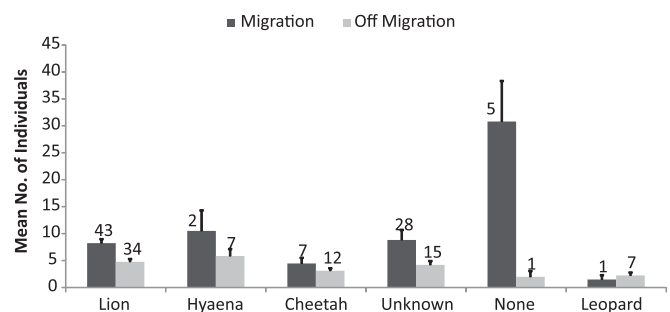

FIGURE 3.   Mean number (±SE) of vultures of all species per carcass at carcasses with different predators attendant at the Masai Mara National Reserve; sample sizes refer to number of carcasses.

during the migration season, while the timing of Rüppell's Vulture nesting is more variable (Houston 1989, Virani et al. 2010, 2012). It is unknown if vultures' foraging radius differs when the birds are nesting, but given their large home range and soaring flight, which allows for high mobility at a low energetic cost, nesting is unlikely to be related to foraging behavior (Pennycuick 1972, 1979). It is likely that more carcasses are available during the migration when the influx of ungulates increases their density in MMNR is high and their mortality is high because of the lack of forage and water brought on by the dry season (Houston 1989, Mduma et al. 1999). Our findings thus support the prediction that the concentration of both *Gyps* species at carcasses should be higher when more food is available, as during the migration. This is consistent with findings in other areas where social species are more prevalent at aggregated carcasses or in areas of high carcass density (Houston 1974b, Gomez et al. 1994, Wilmers et al. 2003, Blazquez et al. 2009). These social species, like other scavengers, rely on social facilitation to find food and then to compete with larger species, so they may be particularly sensitive to the quantity of meat available in a given area. There may even be a threshold density of these species that must be reached for them to forage most effectively (Jackson et al. 2008).

CONFOUNDING FACTORS

Although we did not record the amount of food remaining, carcasses generally decompose through the day, so the most intact carcasses are available in the morning (Mduma et al. 1999). Our observations were made throughout the day to reduce bias in oversampling a carcass at any one stage. In addition, because vultures often remain at the carcass long after they have finished feeding (Mundy et al. 1992), even if our sample were biased towards later-stage carcasses, the data should still give us accurate information about which species are using the carcass. Preliminary data from continuing studies in which carcass stage has been recorded suggest that the data are generally only slightly skewed to the later stages and that differences between different carcass sizes in the distribution of amount of meat remaining are not significant (CK, unpublished data). In addition, we see no reason to believe that our sample may be biased in terms of carcass age by season or year. The amount of meat remaining may differ by whether or not a carcass is a predator kill, but these differences are ultimately caused by the mortality factor itself, one of the variables we tested. These findings from similar surveys suggest it is unlikely that our data are biased in terms of carcass age in relation to any of the other explanatory variables considered. An experimental study that recorded the composition of scavengers at carcasses of various sizes over an extended period would provide greater insight into these potential biases.

CONSERVATION IMPLICATIONS

Counts at carcasses have been and continue to be used to assess vultures' abundance (Petrides 1959, Attwell 1963, Kruuk

1967, Houston 1974a, b, Anderson and Horwitz 1979, Mundy 1982). When compared to the counts by Mundy et al. (1992) at carcasses in east Africa in the 1960s and 1970s, ours showed a lower relative abundance of the White-backed Vulture, a 20-fold increase in the relative abundance of the Egyptian Vulture, and doubling of the relative abundance of Rüppell's Vulture from 15 to 35% and of the White-headed Vulture from 0.8 to 2%.

Virani et al. (2011) reported a 52% decline in *Gyps* vultures in MMNR over the last 30 years but were unable to differentiate between the two *Gyps* species because of limitations in past surveys. Changes in the two species' relative abundance at the carcasses seem most consistent with a steeper decline in the White-backed than in Rüppell's Vulture and are cause for concern. Reasons for a shift between the *Gyps* species over the last three decades, favoring the Rüppell's Vulture, could relate to increased human disturbance at tree nests of the semicolonial White-backed Vulture, differences in sensitivity or exposure to poisoning, or reported reductions in populations of ungulates resident in MMNR, which would be more likely to affect the resident White-backed Vulture than the Rüppell's Vulture (Ottichilo et al. 2001, Bamford et al. 2009b, Ogutu et al. 2009). In particular, continued fire and elephant damage to trees may be affecting the nesting success of White-backed Vultures (PK, pers. obs.).

Because of their high mobility, vultures respond readily to the increase in food availability as the ungulate migration comes to MMNR each year (Pennycuick 1979). However, as scavengers, vultures are also extremely sensitive to long-term trends in wildlife density and abundance (Houston 1974a). The number of *Gyps* vultures at carcasses was more sensitive to seasonal changes in carcass availability and carcass size than was that of other species, possibly because of their dependence on large groups for effective feeding. Given continued threat of wildlife declines due to poaching, livestock encroachment, and intensification of agriculture in and around the MMNR, vultures are at risk of reduced food supply (Ottichilo et al. 2000, 2001, Ogutu et al. 2009). Given their greater sensitivity to changes in the availability of carcasses, if the numbers of large ungulates were to decline, *Gyps* vultures should be the most affected, possibly with positive repercussions for the other species due to reduced interspecific competition.

High levels of association between species, even those with similar ecological traits, suggest that there may be both strong competitive and facilitative interactions between the species within this guild. Understanding these interspecific interactions as well as interactions between vultures and other ecological factors, such as food availability, predator density, and variations in climate, is crucial for conserving this important assemblage and for identifying which species are most susceptible to human-mediated environmental changes. Future research should consider the role of interspecific

interactions in these patterns of occurrence and the effects of other spatio-temporal environmental factors on vultures' density, movement, and habitat use.

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LITERATURE CITED

ALSOBROOK, J. P. II, J. F. LECKMAN, W. K. GOODMAN, S. A. RASMUSSEN, AND D. L. PAULS. 1999. Segregation analysis of obsessive-compulsive disorder using symptom-based factor scores. American Journal of Medical Genetics (Neuropsychiatric Genetics) 88:669–675.

ANDERSON, D. J., AND R. J. HORWITZ. 1979. Competitive interactions among vultures and their avian competitors. Ibis 121:505–509.

ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

ATKINSON, W. D., AND B. SHORROCKS. 1981. Competition on a divided and ephemeral resource—a simulation model. Journal of Animal Ecology 50:461–471.

ATTWELL, R. I. G. 1963. Some observations on feeding habits, behavior, and inter-relationships of Northern Rhodesian vultures. Ostrich 34:235–247.

BAMFORD, A. J., A. MONADJEM, AND I. C. W. HARDY. 2009a. An effect of vegetation structure on carcass exploitation by vultures in an African savanna. Ostrich 80:135–137.

BAMFORD, A. J., A. MONADJEM, AND I. C. W. HARDY. 2009b. Nesting habitat preference of the African White-backed Vulture Gyps africanus and the effects of anthropogenic disturbance. Ibis 151:51–62.

BLÁZQUEZ, M., J. A. SÁNCHEZ-ZAPATA, F. BOTELLA, M. CARRETE, AND S. EGUÍA. 2009. Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. Acta Oecologica 35:645–650.

BOONE, R. B., S. J. THIRGOOD, AND J. G. C. HOPCRAFT. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87:1987–1994.

BUCKLEY, N. J. 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. Auk 113:473–488.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

DEVRIES, J. H., L. M. ARMSTRONG, R. J. MACFARLANE, L. MOATS, AND P. T. THOROUGHGOOD. 2008. Waterfowl nesting in fall-seeded and spring-seeded cropland in Saskatchewan. Journal of Wildlife Management 72:1790–1797.

ESTES, R. D., AND R. EAST. 2009. Status of the wildebeest (Connochaetes taurinus) in the wild 1967–2005. Wildlife Conservation Society Working Paper 37.

GÓMEZ, L. G., D. C. HOUSTON, P. COTTON, AND A. TYE. 1994. The role of Greater Yellow-headed Vultures Cathartes melambrotus as scavengers in neotropical forest. Ibis 136:193–196.

HARTLEY, S., AND B. SHORROCKS. 2002. A general framework for the aggregation model of coexistence. Journal of Animal Ecology 71:651–662.

HOUSTON, D. C. 1974a. Food searching behavior in Griffon Vultures. East African Wildlife Journal 12:63–77.

HOUSTON, D. C. 1974b. The role of Griffon Vultures Gyps africanus and Gyps rueppellii as scavengers. Journal of Zoology 172:35–46.

HOUSTON, D. C. 1975. Ecological isolation of African scavenging birds. Ardea 63:55–64.

HOUSTON, D. C. 1979. The adaptations of scavengers, p. 263–286. In A. R. E. Sinclair and M. N. Griffiths [EDS.], Serengeti, dynamics of an ecosystem. University of Chicago Press, Chicago.

HOUSTON, D. C. 1989. A change in the breeding season of Rüppell's Griffon Vultures Gyps rueppellii in the Serengeti in response to changes in ungulate populations. Ibis 132:36–41.

HOUSTON, D. C. 2001. Vultures and condors. Colin Baxter Photography Ltd., Grantown-on-Spey, Scotland.

HUNTER, J. S., S. M. DURANT, AND T. M. CARO. 2007. Patterns of scavenger arrival at cheetah kills in Serengeti National Park, Tanzania. African Journal of Ecology 45:275–281.

ILSE, L. M., AND E. C. HELLGREN. 1995. Resource partitionig in sympatric popultions of collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76:784–799.

JACKSON, A. L., G. D. RUXTON, AND D. C. HOUSTON. 2008. The effect of social facilitation on foraging success in vultures: a modelling study. Biology Letters 4:311–313.

JOHNSON, J. B., AND K. S. OMLAND. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

KENDALL, C., AND M. VIRANI. 2012. Assessing mortality of African vultures using wing tags and GSM-GPS transmitters. Journal of Raptor Research 46:135–140.

KIRK, D. A., AND D. C. HOUSTON. 1995. Social dominance in migrant and resident Turkey Vultures at carcasses: evidence for a despotic distribution? Behavioral Ecology and Sociobiology 36:323–332.

KISSUI, B. M. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conservation 11:422–432.

KRONFELD-SCHOR, N., AND T. DAYAN. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

KRUUK, H. 1967. Competition for food between vultures in east Africa. Ardea 55:171–193.

LLOYD, M. 1967. Mean crowding. Journal of Animal Ecology 36:1–30.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MARKANDYA, A., T. TAYLOR, A. LONGO, M. N. MURTY, S. MURTY, AND K. DHAVALA. 2008. Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. Ecological Economics 67:194–204.

MAY, R. M., AND R. H. MACARTHUR. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences USA 69:1109–1113.

MCCLURE, C. J., N. D. BURKETT-CADENA, R. A. LIGON, AND G. E. HILL. 2011. Actual or perceived abundance? Interpreting annual survey data in the face of changing phenologies. Condor 113:490–500.

MDUMA, S. A. R., A. R. E. SINCLAIR, AND R. HILBORN. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology 68:1101–1122.

MUNDY, P. J. 1982. The comparative biology of southern African vultures. Vulture Study Group, Johannesburg.

Mundy, P. J., D. Butchart, J. A. Ledger, and S. E. Piper. 1992. The vultures of Africa. Acorn Books, Randburg, South Africa.

Murn, C., and M. D. Anderson. 2008. Activity patterns of African White-backed Vultures *Gyps africanus* in relation to different land-use practices and food availability. Ostrich 79:191–198.

Ogada, D. L., and F. Keesing. 2010. Decline of raptors over a three-year period in Laikipia, central Kenya. Journal of Raptor Research 44:129–135.

Ogutu, J. O., N. Bhola, and R. Reid. 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. Journal of Zoology 265:281–293.

Ogutu, J. O., N. Owen-Smith, H. P. Piepho, and M. Y. Said. 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. Journal of Zoology 285:99–109.

Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. Reid. 2009. Dynamics of Mara–Serengeti ungulates in relation to land use changes. Journal of Zoology 278:1–14.

Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. Rainfall influences on ungulate population abundance in the Mara–Serengeti ecosystem. Journal of Animal Ecology 77:814–829.

Ottichilo, W. K., J. de Leeuw, and H. H. T. Prins. 2001. Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Masai Mara ecosystem, Kenya. Biological Conservation 97:271–282.

Ottichilo, W. K., J. de Leeuw, A. K. Skidmore, H. H. T. Prins, and M. Y. Said. 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. African Journal of Ecology 38:202–216.

Pennycuick, C. J. 1972. Soaring behavior and performance of some east African birds, observed from a motor-glider. Ibis 114: 178–218.

Pennycuick, C. J. 1979. Energy costs of locomotion and the concept of "foraging radius," p. 166–184. *In* A. R. E. Sinclair and P. Arcese [eds.], Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago.

Petrides, G. A. 1959. Competiton for food between five species of east African vultures. Auk 76:104–106.

Rosewell, J., B. Shorrocks, and K. Edwards. 1990. Competition on a divided and ephemeral resource—testing the assumptions 1. Aggregation. Journal of Animal Ecology 59:977–1001.

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology & Evolution 21:464–471.

Sekercioglu, C. H., G. C. Daily, and P. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences USA 101:18042–18047.

Selva, N., B. Jedrzejewska, W. Jedrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83:1590–1601.

Sergio, F., I. Newton, and L. Marchesi. 2005. Top predators and biodiversity. Nature 436:192–192.

Shorrocks, B., J. Rosewell, and K. Edwards. 1990. Competition on a divided and ephemeral resource—testing the assumptions 2. Association. Journal of Animal Ecology 59:1003–1017.

Statsoft, I. 2001. STATISTICA (data analysis software system). StatSoft, Inc., Tulsa, OK.

Thiollay, J.-M. 2007. Raptor population decline in west Africa. Ostrich 78:405–413.

Traviani, A., J. A. Donazar, A. Rodríguez, O. Ceballos, M. Funes, M. Delibes, and F. Hiraldo. 1998. Use of European hare (*Lepus europaeus*) carcasses by an avian scavenging assemblage in Patagonia. Journal of Zoology 246:175–181.

Virani, M., P. Kirui, A. Monadjem, S. Thomsett, and M. Githiru. 2010. Nesting status of African White-backed Vultures *Gyps africanus* in the Masai Mara National Reserve, Kenya. Ostrich 81:205–209.

Virani, M., A. Monadjem, S. Thomsett, and C. Kendall. 2012. Seasonal variation in breeding Ruppell's Vultures (*Gyps rueppelli*) at Kwenia, southern Kenya, with implicatons for conservation. Bird Conservation International, in press. DOI: 10.1017/S0959270911000505.

Virani, M. Z., C. Kendall, P. Njoroge, and S. Thomsett. 2011. Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. Biological Conservation 144:746–752.

Wilbur, S. R., and J. A. Jackson [eds.]. 1983. Vulture biology and management. University of California Press, Berkeley.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in greater Yellowstone, USA. Ecology Letters 6:996–1003.