ALTERNATIVE STRATEGIES IN AN AVIAN SCAVENGER GUILD AND THEIR CONSERVATION IMPLICATIONS

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Abstract

This dissertation examines the alternative strategies used by a diverse eight species avian scavenger guild and how these enable their coexistence in Masai Mara National Reserve, Kenya. Methods include roadside transects, counts and behavioral observations of scavenger species at both natural and experimental carcasses, and a movement study using GSM-GPS telemetry. Findings suggest high association among species with similar beak morphology at natural carcasses demonstrating that resource partitioning is insufficient to explain coexistence. Instead, a series of alternative behavioral strategies occur across spatial and temporal gradients in resource availability, that occur seasonally, locally, daily, and regionally. Seasonally, social species move to areas of high food availability. As a result, higher competition caused by these social species appears to offset increases in food availability during the dry season, forcing solitary species to search throughout the day. On a local scale, trade-offs between individual dominance versus social dominance and search efficiency versus competitive ability enable socially dominant species and species with high search efficiency to use the best quality habitats, typically areas with high wildlife density. Across regional scales, variation in habitat use among Gyps vultures enables coexistence. In general, movement of competitively dominant vulture species is linked to prey mortality rather than abundance.

An understanding of alternative strategies employed by different avian scavengers has important implications for their conservation. All avian scavenger species except Bateleurs are found to be declining dramatically within and around Masai Mara National Reserve, Kenya. Poisoning, the primary threat to vultures, is expected to cause regional declines for species, such as Lappet-faced and Gyps vultures, whose ranges extend beyond protected areas. Subordinate species with
low search efficiency, such as Hooded vultures and Tawny eagles, disproportionately use areas of poor quality, such as those of high human settlement density and are thus at greatest risk of poisoning. Social species, such as *Gyps* vultures, depend on high ungulate mortality rates and are thus most likely to be impacted by on-going wildlife declines. Management actions to prevent poisoning and continued monitoring of vulture populations in Masai Mara National Reserve will be critical steps in the conservation of avian scavengers.
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CHAPTER 1

Introduction

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Using alternative strategies to understand mechanisms of coexistence

One of the major goals of community ecology is to understand the patterns, processes, and mechanisms that structure communities (Morin, 1999). Mechanisms of coexistence enable us to understand patterns of diversity; these are based on the assumption that competition is an important driving force in ecology and generally involve understanding how species divide up an ecosystem into their different niches (MacArthur, 1958). Several mechanisms have been proposed including resource partitioning, the aggregation model of coexistence, spatial and temporal segregation in resource use, and alternative strategies, which are mediated by trade-offs in species traits, such as competition-defense or competition-colonization (Viola et al., 2010, Bonsall et al., 2002, MacArthur and Levins, 1967, May and MacArthur, 1972, Rosewell et al., 1990, Kronfeld-Schor and Dayan, 2003, Blazquez et al., 2009, Cortes-Avizanda et al., 2010).

A focus on species’ traits and trade-offs provides generality and predictability within community ecology and is thus more useful than focusing on species identities (McGill et al., 2006). By assessing differences in the relative competitive advantage of various traits along resource gradients, it has been possible to assess alternative strategies used by species within a community and to generate general principles about the mechanisms that shape interspecific interactions and community composition (Schamp and Aarssen, 2009, McGill et al., 2006, Tilman, 1987, Tilman, 1988). Various traits have been considered, including body size, activity, vulnerability to predators, microhabitat use, competitive ability, tolerance to disturbance, feeding type, gregariousness, and numerous life history characteristics and the trade-offs between these traits have been assessed in several studies (Wellborn et al., 1996, Wallgren et al., 2009, Bertness and Leonard, 1997, Ilse and Hellgren, 1995, Kneitel and Chase, 2004). In particular, it has been argued that understanding variations in trade-offs that occur along environmental gradients could
enhance our mechanistic understanding of the factors that structure communities (McGill et al., 2006, Schamp and Aarssen, 2009, Kneitel and Chase, 2004).

Many studies of community ecology have been limited to pair-wise interactions or a local scale (Wilson and Keddy, 1986). However, in nature, a given species is typically faced with many interspecific interactions, which may be hierarchically distributed and asymmetrical (Wilson and Keddy, 1986) and multiple interactions among multiple species need to be considered to grasp the full complexity of community ecology. In addition, ecological patterns and processes, including alternative strategies used by competing species, may differ at varying spatial scales, necessitating studies across multiple spatial scales (Lavorel and Garnier, 2002, Levin, 1992, Bertness and Callaway, 1994). Studies considering only a single scale, particularly only a local scale, may miss important interactions and processes that are best understood through multi-scale studies (Bertness and Callaway, 1994, Leibold et al., 2004, Kneitel and Chase, 2004). Studies of meta-communities have attempted to bring together understanding of local and regional scale dynamics to provide a more complete picture of communities (Leibold et al., 2004).

In this study, I use avian scavengers to assess several mechanisms of coexistence at multiple spatial scales. This study assumes that food is an important limiting factor within this guild. The division of roles and diverse life history, behavioral, and morphological traits that has already been documented in vultures demonstrate the importance of competition. The avian scavenger guild in the Mara-Serengeti ecosystem is an ideal study system for assessing the mechanisms of coexistence that structure communities for many reasons. First, particularly high abundance of carcasses in the Mara-Serengeti ecosystem has allowed for a diverse community of avian scavengers to persist at high densities (Houston, 1975). In addition, this diverse community
exists in a system with a spatial and temporal gradient of resource availability, due to the migratory ungulates, leading to a complex set of possible alternative strategies among avian scavengers (Kruuk, 1967). Second, there are large variations between species in functional traits, such as body size, diet breadth, gregariousness, range size, and nesting behavior (Mundy et al., 1992). These differences enable comparisons among species and thus allow a greater understanding of trade-offs among traits that may exist. In addition, some scavengers have extremely large range sizes, which enable consideration of community structure across multiple spatial scales. Third, due to the nature of carcasses and the large groups of scavengers that congregate around them, behavioral observations can easily be conducted on individuals and their interactions (Kirk and Houston, 1995). Fourth, avian scavengers have few predators and generally are able to outcompete mammalian scavengers due to their soaring flight, which enables high carrion detection, large population size, and large ranges. Despite what is commonly thought, food availability for scavengers is not strongly affected by predators (Houston, 1974a). Together, these features simplify the study by limiting the number of interactions outside the guild that might affect community structure. Finally, avian scavengers are extremely sensitive to anthropogenic activities due to their affects on food availability, and thus they may be good indicators of how humans are altering ecosystem function (Murn and Anderson, 2008).

**Mara-Serengeti ecosystem of Kenya and Tanzania**

The Mara-Serengeti ecosystem is arguably one of the most important areas for scavengers in Africa, supporting high densities of a diverse set of scavenger species (Houston, 2001, Houston, 1979). Combined Masai Mara National Reserve, Kenya and Serengeti National
Park, Tanzania cover nearly 25,000 km\(^2\), primarily composed of a savannah habitat. Masai pastoral communities surround the protected areas. High, though seasonal, food availability for scavengers is created by the high density of ungulates and large migratory Blue Wildebeest (*Connochaetes taurinus*), Burchell’s Zebra (*Equus burchelli*), and Thomson’s Gazelle (*Gazella thomsonii*) herds that occur in the Masai Mara National Reserve from July to October and then move into Serengeti National Park from November to June each year (Boone et al., 2006). Rainfall is bimodal, with the long rains falling from March to June and short rains from November to December (Ogutu et al., 2008). As a result, carrion availability is also highly seasonal in the Mara-Serengeti ecosystem with greater abundance in the dry season (Mduma et al., 1999).

*Avian scavenger guild*

Scavengers are an understudied but important trophic guild and face a unique set of challenges due to their reliance on carrion, which is an ephemeral and sporadically dispersed resource (DeVault et al., 2003, Wilmers et al., 2003b). This study has focused on alternative behavioral strategies within the avian scavenger guild in Masai Mara National Reserve, Kenya, which consists of eight species. These species can be considered a guild due to their common use of a single resource – carrion. Avian species consume 70% of carcasses available and thus functionally represent the most important scavengers in this ecosystem (Houston, 1974b). Soaring flight, which enables carcass discovery from the air as well as large foraging radius, allows avian scavengers to frequently outcompete terrestrial ones and has enabled the evolution of obligate scavenging in *Gyps* vultures (Ruxton and Houston, 2004, Pennycuick, 1979). Species included in the study differ in several traits, including those related to life history and behavior,
which are expected to mediate their coexistence and have important consequences for their conservation (Table 1). Scavengers differ considerably in their body size, which determines individual dominance (Mundy et al., 1992). Species also vary in their sociality and only *Gyps* vultures are considered social. Early research on vultures has focused on resource partitioning and Kruuk (1967) categorized vultures as using either a tearing, pulling, or pecking feeding strategy based on beak strength (high, medium, low, respectively). In addition, most avian scavengers nest in trees (Mundy et al., 1992). However, Egyptian and Ruppell’s vultures utilize cliff-nesting sites, which may be widely dispersed and far from foraging areas (Houston, 1976). This has important implications for their movement patterns, habitat use, foraging ecology, and energetics (Ruxton and Houston, 2002). Finally, there exists a continuum of dependence within the guild on carcasses themselves. Vultures have been termed obligate scavengers, due to their heavy reliance on carcasses in their diet (Houston, 1975). In the case of African white-backed and Ruppell’s vultures – the most specialized of the vultures – these are most often the carcasses of large ungulates. Other species, such as Bateleurs and Tawny eagles, use a more generalist strategy and can opportunistically switch between scavenging and hunting depending on food availability (Steyn, 1980, Wichmann et al., 2004, Boshoff et al., 1981, Watson, 2000).

**Conservation concerns**

Avian scavengers are one of the most rapidly declining avian groups in the world. India suffered declines of up to 95% for important scavengers, the *Gyps* vultures, in the last decade (Anderson et al., 2005), primarily due to the veterinary use of diclofenac, which causes renal failure in vultures (Oaks et al., 2004). Similar declines in avian scavengers have been noted throughout Africa, but the causes are less clear as diclofenac is not widely used in Africa.
Scavengers play a critical role in decomposition and disease control and these losses are likely to have huge effects on ecosystem services provided by vultures and other avian scavengers and in some cases, lead to major economic losses as well (Mundy et al., 1992, Sekercioglu, 2006, Sekercioglu et al., 2004, Whelan et al., 2008, Ogada et al., 2012, Markandya et al., 2008).

The primary threats to vultures in East Africa are poisoning and land use change. Carbofuran poisoning for predators, often in retaliation for livestock depredation, has led to accidental poisoning of vultures. Poisoning has killed over 500 vultures in recent years in Kenya with most poisoning incidents occurring outside protected areas (Kissui, 2008, Otieno et al., 2010a). Land use change, particularly agricultural intensification, around Masai Mara National Reserve and throughout Kenya has led to rapid declines in resident wildlife (Western et al., 2009, Ogutu et al., 2011). Avian scavengers rely on high wildlife density. Reduced food availability in Europe, caused by changes in carcass disposal processes, has had significant impacts on scavengers and is likely to affect scavengers in Africa as well as food supplies continue to dwindle (Donazar et al., 2009, Margalida et al., 2011). Finally, human disturbance has been shown to have detrimental affects on scavengers in many ecosystems (Bamford et al., 2009b, Skagen et al., 1991). Given that the human population around Masai Mara National Reserve is growing, there is potential for increasing issues of disturbance.

Study design

This study has focused on understanding the alternative strategies employed by avian scavengers and how these enable coexistence of such a diverse guild. In addition, efforts have
been made to consider how the strategies that species employ may affect their conservation with particular focus on the main threats of poisoning, declining food supply, and human disturbance. Research methods used include roadside transects, counts of scavenger species and behavioral observations at both natural and experimental carcasses, and a movement study using GSM-GPS telemetry on White-backed, Ruppell’s, and Lappet-faced vultures.

Outline of dissertation chapters

Chapter 2 documents the drastic declines that have occurred in avian scavengers in Masai Mara National Reserve over the last thirty years. Declines occurred in all species except the Bateleur; Egyptian vultures appear to be locally extirpated. Declines occurred both within and outside of the protected area, demonstrating the importance of poisoning in causing the declines. Declines for Gyps vultures were higher during the dry season when this wide-ranging species concentrates in Masai Mara National Reserve, suggesting declines at a regional scale.

Chapter 3 assesses possible mechanisms of coexistence among vulture species in relation to their use of carcasses. Species with similar traits tend to aggregate at carcasses, making resource partitioning an unlikely mechanism of coexistence. Results also confirmed that social species were more abundant in periods of high food availability (i.e. the dry season) and all vulture species avoided carcasses with predators.

Chapter 4 outlines the effects of two possible trade-offs in species traits in avian scavengers on habitat use: one between individual dominance and social dominance and the other between dominance and search efficiency. Findings suggest that both trade-offs operate in avian scavengers. Smaller, social species are able to outcompete larger ones when they are able to reach large group sizes. In addition, search efficiency appears to compensate for dominance,
given that subordinate species with high search efficiency have greater abundance in habitats of high quality.

Chapter 5 considers the temporal segregation of resource use across time of day as a possible mechanism of coexistence. Findings document the ability of social species to dominate in periods of high food availability, particularly early morning and the greater foraging success of social species overall. As a result, the ability of solitary species to coexist appears to be more tied to high food availability in periods of overlap with competitors rather than with differences in temporal resource use.

Chapter 6 considers regional scale patterns of habitat use in three species: White-backed, Ruppell’s, and Lappet-faced vulture. Habitat use in vultures appears to be linked to differences in ungulate mortality rather than density, and vultures only overlapped with migratory ungulate herds during the dry season. Differences in regional scale habitat use may be key to the coexistence of the two species of Gyps vulture.

Chapter 7 summarizes the overall conservation implications of this work. Avian scavengers in Masai Mara National Reserve have declined precipitously, and it is clear that poisoning is a major threat, particularly for wide-ranging species and subordinate species that preferentially use areas outside the reserve. Wildlife declines are also likely to impact vultures, particularly Gyps species, in the long term. Recommendations are given for future management and monitoring priorities that will be key to preserving avian scavengers in Kenya.
<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>IUCN Red list status (2012)</th>
<th>Average body size (kg)</th>
<th>Sociality</th>
<th>Beak strength</th>
<th>Nesting behavior</th>
<th>Level of specialization on carrion</th>
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<tr>
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<td>Low</td>
<td>Tree</td>
<td>Least</td>
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<td>2.0</td>
<td>Solitary</td>
<td>Low</td>
<td>Cliff</td>
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<tr>
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<td>2.2</td>
<td>Solitary</td>
<td>High</td>
<td>Tree</td>
<td>Middle; some predation</td>
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<tr>
<td>Tawny Eagle</td>
<td><em>Aquila rapax</em></td>
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<td>Solitary</td>
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<td>Tree</td>
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Literature Cited


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CHAPTER 2

Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya

AUTHORS: Munir Z. Virani, Corinne Kendall, Peter Njoroge, and Simon Thomsett.

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Abstract

Vulture population declines have been noted in West and Southern Africa, but have not been assessed in East Africa. Roadside transects conducted in 1976 and 1988 were compared with surveys done from 2003-2005 in and around Masai Mara National Reserve, Kenya. Staggering declines in abundance were found for seven of eight scavenging raptors surveyed. No Egyptian vultures were seen during recent transects. We compared trends between the ungulate migration and non-migration season among three land use types (reserve, buffer, and grazed) and among the species surveyed to establish the causes of declines in scavenging raptors. Large declines during the ungulate migratory period suggest that most scavenging raptor species are declining well beyond the area of study. For all species, except Hooded Vultures, land use changes around Masai Mara National Reserve, appear to have reduced raptor abundance. In addition, significant declines of populations of *Gyps* species in the reserve itself, especially during the migration season, provide evidence that human activities occurring in other parts of the species’ range such as poisoning of carcasses may be causing their decline. Declines found in this study suggest that at a minimum African white-backed, Rüppell’s, and Hooded vultures should be relisted as Vulnerable. Management actions that limit land use change around the reserve combined with a countrywide ban on carbamate pesticides will be important for conserving keystone members of the scavenging guild. Future research should further examine possible causes of these declines and quantify the effect of reduced scavenging raptor abundance on scavenging efficiency.

Keywords: vulture, scavenger, Masai Mara, land use, poisoning

Introduction
Ecosystems the world over are being dramatically changed by human activities resulting in massive impacts on biodiversity. Globally, vultures are one of the fastest declining groups of birds and declines, especially outside of protected areas, have been documented in West and Southern Africa (Thiollay, 2007b, Thiollay, 2007a, Anderson, 2000, Herremans and Herremans-Tonnoeyr, 2000, Thiollay, 2006a, Brandl et al., 1985, Thiollay, 2006b, Thiollay, 2006c). The Mara-Serengeti ecosystem is known to be a hotspot for vultures due to the wildebeest migration, which provides considerable food for scavengers, with vultures consuming almost 70% of the available meat, but little is known about the status of scavenging raptors in this important ecosystem or in East Africa in general (Houston, 1974a, Houston, 1974b).

Several known threats to scavenging raptors have become prevalent in East Africa (Virani and Muchai, 2004). Food shortage, caused by land use change and wildlife declines, has been suggested as a major cause of decline in raptors in West Africa and is also occurring in East Africa (Thiollay, 2007b, Thiollay, 2007a). Wildlife declines have been noted throughout Kenya’s protected areas, including within Masai Mara National Reserve (MMNR) (Western et al., 2009). In particular, MMNR and the surrounding areas have undergone significant land use change in the last several decades (Homewood et al., 2001, Serneels and Lambin, 2001, Serneels et al., 2001). These changes have primarily come in the form of increasing settlements, a growing wheat agriculture, more livestock, and a prolific tourist industry both within and around the reserve (Lamprey and Reid, 2004). As a result of land use changes and poaching throughout the Mara ecosystem, resident ungulate populations have declined considerably during the last thirty years with up to 80% declines in resident wildebeest (Ogutu et al., 2009, Ottichilo et al., 2001, Ottichilo et al., 2000). However, large migratory ungulate populations that travel between Masai Mara National Reserve and Serengeti National Park each year have remained relatively
stable during the last three decades, due to land preservation of most important migratory routes (Thirgood et al., 2004).

In addition, poisoning of carcasses and persecution for body parts have become major causes of vulture decline in Southern and Western Africa and have been reported in East Africa as well (Thiollay, 2007a, Allan, 1989). Throughout East Africa, Furadan, a carbamate-based pesticide, has been widely used on carcasses primarily to kill hyenas (Kissui, 2008). While poisonings events causing the mortality of many lions, hyenas, and vultures have been recorded throughout East Africa, the extent of this issue and its effects on wildlife are yet to be fully understood (Watts and Holekamp, 2009, Ogada and Kibuthu, 2008). In the Mara ecosystem, as settlements and pastoralism increase and move closer to the reserve, human-wildlife conflict has escalated (Newmark et al., 1994). This conflict, particularly livestock depredation by lions and hyenas, has led to retaliatory killings by pastoral and farming communities close to the MMNR (Watts and Holekamp, 2009). However, hyena populations within MMNR have remained stable, suggesting that poisoning is minimal inside the reserve (Ogutu et al., 2005).

Finally, loss of nest sites and anthropogenic disturbance at nests have been important causes of decline elsewhere (Bamford et al., 2009b, Monadjem and Garcelon, 2005). However, no major declines in nest availability have been documented at important vulture nesting sites in Kenya, although the number of nesting birds has dropped in some areas, presumably due to overall population declines (Virani, M., unpublished data). In addition, deaths due to electrocution have been recorded for several raptor species, especially in Southern Africa, but given current limited prevalence of powerlines around MMNR and throughout East Africa, these are not currently likely to be a major threat, but need to be monitored (Ledger and Annegarn, 1981, Virani and Harper, 2009).
Roadside surveys were conducted in an early period from 1976 and 1988 and repeated from 2003 to 2005 during both the ungulate migration and non-migration seasons in three different land use types in and around Masai Mara National Reserve, Kenya. Based on these surveys, we document changes in abundance for six vulture species, which includes African White-backed *Gyps africanus* (AWBV), Rüppell’s *Gyps rueppellii* (RV), White-headed *Aegypius occipitalis* (WHV), Lappet-faced *Aegypius tracheliotos* (LFV), Hooded *Necrosyrtes monachus* (HV) and Egyptian *Neophron percnopterus* (EV) – and two species of scavenging eagles - Tawny *Aquila rapax* (Tawny) and Bateleur *Terothopius ecaudatus*. All raptors surveyed are known to consume carrion for a considerable portion of their diet, though their dependence on carcasses varies (Anderson and Horwitz, 1979, Houston, 1975, Watson and Watson, 1985, Herholdt et al., 1997, Steyn, 1980, Boshoff et al., 1981). Comparing trends in abundance between these eight species with similar foraging ecology provides useful insights into the possible causes of declines. In addition, we compare abundances indices for each species between periods (early and recent), season (when migratory wildebeest are present and absent), and land use type (reserve, buffer, and grazed) to assess the differences in susceptibility to human activities between the eight species.

**Materials and Methods**

**Study area**

The Masai Mara region in southwestern Kenya forms the northern part of the Serengeti ecosystem and encompasses an area of about 5560 km² of which about 1500 km² forms the Masai Mara National Reserve (MMNR) and the remaining area is made up of community group ranches (Sinclair and Arcese, 1995) (Figure 1). The region, a UNESCO designated World
Heritage Site, is globally famous for its great concentrations of large herbivores and their attendant predators. The reserve also is a globally recognized Important Bird Area (Bennun and Njoroge, 1999). More than 500 species of birds are known to occur in the reserve, of which 53 are birds of prey.

We divided the Masai Mara region and its environs into three major land use types, each with a characteristic habitat type: (i) Reserve: Masai Mara National Reserve (MMNR) is mainly open grasslands of *Themeda triandra*, riverine forests, swamps, non-deciduous thickets and *Acacia*, *Croton* and *Tarconanthus* scrub (Bennun and Njoroge, 1999). The reserve harbours a high concentration of large wild mammals, primarily ungulates that migrate into the reserve each year from July to October from the Serengeti National Park in Tanzania. (ii) Buffer: Previously part of the MMNR dispersal area, this region comprises several group ranches and is composed of *Themeda triandra* grasslands with *Acacia xanthophloea* trees. Masai pastoral communities live in *Manyattas* (traditional Masai homesteads) with moderate livestock grazing and medium to small settlements. (iii) Grazed: The area lying on either side of the 84 km stretch of road between the towns of Mai Mahiu (0° 58’ 55.88” S and 36° 35’ 11.32”E) and Narok (1° 04’ 19.78” S and 35° 51’ 37.7” E). Large cattle ranches interspersed with rural settlements, wheat farms and tracts of subsistence agricultural patches occupy this area. It is characterised by overgrazed grassland meadows consisting of *Acacia drepanolobium*, *Tarconanthus camphoratus* and *Acacia xanthophloea* trees. In general, it has fewer wild mammals than both the MMNR and the Group Ranches. Formerly sparsely populated, this area is rapidly turning into a densely human populated region.

*Road counts*
We conducted eight road counts on a quarterly basis between 2003 and 2005, totaling 3400 km along a survey route that provided access to all three land-use areas. Each survey consisted of six sections and took three days to complete. Section 1 was from Mai Mahiu to Narok (grazed, 84 km), Section 2 - Narok to Sekenani (buffer, 83 km), Section 3 - Sekenani to Ol-Kiombo (reserve, 50 km); Section 4 - Ol-Kiombo to Musiara (reserve, 50 km); Section 5 – Aitong plains (buffer, 74 km); Section 6 - Narok to Mai Mahiu (grazed, 84 km). Counts were made during July and September (2003 and 2004) coinciding with the presence of migratory herbivores and during January and May (2004 and 2005) during their absence. Numerous studies have shown that the annual migration of wildebeest and zebras from the Serengeti National Park takes place in the MMNR consistently from the beginning of July and ends in October when they move back into the Serengeti (Thirgood et al., 2004, Boone et al., 2006, Pennycuick, 1975, Sinclair and Arcese, 1995). J.M. Thiollay used the same methods to count diurnal raptors during the non-migratory season in December 1976 and during the migratory season in August 1988. He conducted three transects in each year, including one along Section 1 in the grazed area, one along Section 2 in the buffer area, and one through the reserve, giving a total transect length of 525 km from 1976 and 1988 combined. We used these data for comparison with our findings.

Road-side counts enable observers to cover large areas and record significant numbers of low-density species but they are sensitive to various factors that affect the spotting and identification of species (habitat openness, species’ conspicuousness, vehicle speed, weather, time of day, season, and number and experience of counters) (Thiollay, 2006a). However the random records during road counts tend to offset each other over long distances and we ensured each transect was at least 50 km long to average stochastic variations of detections and to maximize the likelihood of observing raptors.
We drove the survey route at 15-50 km per hour in a four-wheel drive vehicle. When raptors were observed, we momentarily stopped the vehicle to identify species. All raptor species observed perched or flying within view on either side of the roads were counted. Two species – the African White-backed *Gyps africanus* and Rüppell’s vultures *G. rüppelli* – that are difficult to distinguish over great distances in the field were counted under one group, *Gyps* vultures, in Thiollay’s surveys, but were separated when possible in recent surveys. MZV and ST conducted all recent counts using the same vehicle. Transect lengths were measured using the vehicle odometer. Villages and small towns were included but we excluded centers of towns at the ends of transects.

*Data analysis*

Analyses include the eight species of scavenging raptors. Replicate transects conducted in the same year and period were not significantly different and mean of replicate transects was used for all analyses. Abundance (Fuller and Moser, 1987, Bibby et al., 1992), expressed as the number of birds per 100 km for each species by transect (Thiollay, 2006a, Woffinden and Murphy, 1977), was calculated from roadside counts.

A Generalized Linear Model (GZLM) was used to investigate the relationship between the response variable, abundance index, and three explanatory variables: periods (early (1976/1988) and recent (2003-2005)), season (migration and non-migration), and land use type (reserve, buffer, and grazed) for each species. A GZLM was run for AWBV and RV separately to assess the effect of season and land use in the recent period only. In addition all two-way interactions between explanatory variables were examined. Models used a log-link function and Poisson distribution as the data were non-normal. Data that were highly aggregated were square-
root transformed. No GZLM was run for the Egyptian vulture as there was no variation in the recent period, during which no EVs were seen. All analyses were done in JMP 8.0 (SAS Institute Inc., 2009).

Results

523 and 1190 scavenging raptors were counted during the early (1976 and 1988; total 525 km) and recent (2003 to 2005; total 3400 km) surveys respectively. On average, raptor abundance (based on birds/100 km) was 100 in the early period and 35 in the recent period. Numbers of all scavenging raptors per 100 km declined considerably over the last thirty years – HV (62%), Gyps vultures (52%), LFV (50%), WHV (44%), Tawny eagle (28%), except Bateleurs, which have increased by 20%. Twenty-two EV were seen in the early period, but none were seen during the recent surveys.

Across species, the abundance index was generally higher during the migration season for both early and recent counts and declines between the periods were greater in the migration than non-migration season (Table 1). Gyps species were the most common across periods and seasons.

Effect of period, land use type, and season on scavenging raptor abundance

GZLMs were run for each species to assess the effect of season, land use type, and period on abundance (Table 2). All GZLMs were significant at the 0.05 level except for the Tawny Eagle. For GZLMs done separately for AWBV and RV during the recent surveys, land use and the interaction between land use and season was significant for AWBV and land use was significant for RV (Table 3).
Significant declines were found for HV, *Gyps* vultures, and LFV. For *Gyps* vultures, two-way interactions between land use-season and land use-period were significant. For *Gyps* vultures, greater declines occurred during the migration period and large declines occurred in all areas, including the reserve (Figure 2). *Gyps* vultures, and RV in particular, are more widely dispersed during the non-migration season, but have a considerably higher abundance in the reserve versus other areas during the migration season. Land use impacted Bateleurs, *Gyps* vultures, LFV, WHV, AWBV, and RV with more individuals being seen in the reserve.

**Discussion**

Significant recent and, in some cases, continuing declines in vulture populations have been documented in Asia, Europe, and West and Southern Africa (Anderson, 2007, Brown, 1991, Thiollay, 2007b, Donazar et al., 2009, Gilbert et al., 2006). Based on our findings, the number of vultures, and Tawny eagles, has declined dramatically over the last fifteen to thirty years in the Masai Mara ecosystem. Egyptian vultures have been locally extirpated from the Masai Mara ecosystem. Bateleur abundance has increased, though not significantly, and higher abundances were only found in the MMNR itself indicating the value of large protected areas as important breeding and foraging grounds for these species. Because recent surveys were repeated more often, driven more slowly, and conducted with two observers rather than one in relation to historical surveys, it is likely that the declines documented here represent an underestimate of actual population losses.

The Mara-Serengeti ecosystem is arguably one of the most important areas for avian scavengers in Africa (Houston, 1975, Houston, 2001). During the ungulate migration season when food availability increases, vulture abundance in the Masai Mara ecosystem increases
significantly (Houston, 1974a, Houston, 1974b, Houston, 1989). In this study, significantly higher abundance during both early and recent period counts were recorded during the migration season for all species, except HV during the recent counts. On-going research using GSM-GPS transmitters on three vulture species (AWBV, RV, and LFV) in MMNR provides evidence that these seasonal increases in vulture abundance are due to an influx of vultures from throughout Kenya and Tanzania (Kendall, C., unpublished data). Declines in abundance for all vulture species were greatest during the migration season, but migratory ungulate populations are known to have remained stable (Thirgood et al., 2004). It is thus likely that declines in MMNR may be representative of declines in vultures across the wider East African region.

Understanding the reasons for declines in avian scavenger species is critical for the conservation of this important guild. Globally, several possible causes of vulture declines, and avian scavenger declines more generally, have been proposed, including poisoning, persecution for body parts for cultural purposes, food shortage, electrocution on and collision with power lines, and loss of nesting sites (Monadjem and Garcelon, 2005, Bamford et al., 2009b, Margalida et al., 2008, Allan, 1989, Anderson, 2007, Bamford et al., 2009a, Kissui, 2008, Murn and Anderson, 2008, Thiollay, 2007b, Wichmann et al., 2004, Thiollay, 2007a, Anderson et al., 2005, Mundy et al., 1992, Virani and Harper, 2009).

While no data were collected on these threats directly, patterns in avian scavenger decline across land use types and seasons, and between species, suggest that both land use change and poisoning are important. Over the last fifteen to thirty years, significant changes in land use have been recorded outside MMNR with increased livestock and human abundance and increased wheat cultivation (Serneels and Lambin, 2001, Serneels et al., 2001). These changes, in combination with poaching, have led to significant declines in resident ungulate species in and
around the MMNR (Ogutu et al., 2009, Ogutu et al., 2005, Ottichilo et al., 2001, Ottichilo et al., 2000). Differences in land use among reserve, buffer, and grazed sites, significantly impacted the abundance of WHV, LFV, Bateleur, and *Gyps* vultures with higher abundances for all species inside the reserve. Based on our findings of significant interactions between land use and period, land use changes outside the reserve appear to be an important cause of decline for *Gyps* species. Extirpation of EV may also be related to land use change as the grazed area where EV was found in early surveys has undergone extensive changes over the last three decades. Over time, *Gyps* vultures have significantly reduced their use of non-protected areas, especially during the non-migration season. Bateleurs and Tawny eagles have increased in the reserve by 52% and 33% respectively, which could be caused by shifts in distribution due to land use change or increased population growth in the reserve itself, possibly caused by decreased competition with vultures for food and nesting resources. Given their smaller ranges and similar diet, increases in Tawny and Bateleur abundance inside MMNR provide evidence that declines in the larger-ranging vulture species’ abundance recorded in MMNR may relate to other human activities occurring at the regional scale (Watson, 2000, Pennycuick, 1983, Pennycuick, 1979, Pennycuick, 1972, Bamford et al., 2007).

While land use change may be an important reason for declines in many avian scavenger species, it is unlikely to be the cause of the 52% decline in *Gyps* species, a larger portion of which occurred during the migration season inside the reserve. Within MMNR there have been minimal land use changes (Serneels and Lambin, 2001, Serneels et al., 2001) and the migratory ungulate population has remained stable (Thirgood et al., 2004) over the last thirty years. Instead this pattern of decline is most consistent with trends caused by poisoning. During the last ten years, there has been an increase in the use of poisons to kill generalist predators, such as lions
and hyenas, often in retaliation for livestock predation in East Africa (Kissui, 2008, Kolowski and Holekamp, 2009, Watts and Holekamp, 2009, Ogada and Kibuthu, 2008). Carbofuran poisons are one of the most readily available and have been implicated in several wildlife poisoning events in Kenya (Martin and Kahumbu, 2010). While poisoning events are difficult to document due to their illegal nature documented incidents have killed as many as 187 vultures on a single poisoned carcasses (Thomsett, S., personal observation). Several poisoning incidents have been recorded inside and around MMNR and poisoning is known to occur throughout Kenya particularly in unprotected areas (Mijele, 2009, Otieno et al., 2010b). Certain life history traits and patterns of habitat use may make some scavenging species more susceptible to poisoning. LFV and *Gyps* vultures, particularly AWBV, appear to alter their land use patterns by season, moving outside the reserve during the non-migration season. Such behavior may make these species particularly susceptible to poisoning which appears to occur predominantly in non-protected areas during the non-migration season (Mijele, 2009, Otieno et al., 2010a, Kolowski and Holekamp, 2006). Sociality and large range size also appear to make *Gyps* species particularly susceptible to poisoning (Houston, 1974a, Houston, 1974b). Large declines in *Gyps* vulture populations have been observed elsewhere even with relatively low levels of poisoning; in southeast Asia, annual mortality rates of 22-50% in *Gyps* vultures could be explained by diclofenac poisoning in less than 1% of carcasses (Green et al., 2004).

Although population declines in vultures outside protected areas are known to be widespread, this study also documents significant population declines in far-ranging vulture species inside a protected area (MMNR), suggesting regional population declines caused by the widespread use of poisons (Brandl et al., 1985, Anderson, 2000, Herremans and Herremans-Tonnoeyr, 2000, Thiollay, 2006a). The magnitude of population declines documented in this
study urgently warrants a reassessment of the conservation status of the scavenging raptor species studied. *Gyps* vultures, HV, and LFV, have declined by over 2% per year over the last twenty-five years and have shown catastrophic population crashes of over 50% in the last twenty-five years and should be up-listed, at a minimum, to Vulnerable by the IUCN Red List (Mace and Lande, 1991). Continued population monitoring and research on the causes of avian scavenger declines in East Africa will be an essential feature of their conservation.

Research needs to assess differences among species in their susceptibility to different threats through a greater understanding of their movement, habitat use, and feeding behavior and should examine the consequences of vulture population declines and food shortage on avian scavenger interspecific interactions to assess possible Allee effects (Jackson et al., 2008). Vultures provide important ecosystem functions, such as waste removal, disease control, and nutrient cycling; rapid declines can have significant ecological and economic effects, as occurred in Southeast Asia with population declines in three *Gyps* vultures (Whelan et al., 2008, Sekercioglu, 2006, Sekercioglu et al., 2004, Markandya et al., 2008). Studies should assess the impact of vulture population declines throughout Africa on these ecosystem functions. Efforts to ban Furadan and other carbamates, currently used to poison wildlife in Kenya are underway and will be an essential step for the vulture conservation, particularly *Gyps* species, in East Africa. In addition, continued anti-poaching efforts and the establishment of more wildlife conservancies around MMNR will help to buffer the reserve and limit the effects of land use change and wildlife declines on this keystone guild.

**Acknowledgments**
This study is part of The Peregrine Fund’s Pan African Raptor Conservation Program and was funded by grants from The Peregrine Fund. We are indebted to the Narok County Council and the staff of the Masai Mara National Reserve in particular the wardens Mr Sindiyo and Mr Minis for their assistance and permission to conduct vulture research in the reserve. We also thank Mr Koikai and Mr Lenjirr for their help. We are grateful for the support accorded by the Mara Conservancy and neighboring group ranches – Koiyaki, Lemek, Siana and Olaro Orok; plus logistical help accorded by Heritage Hotels, Mada Hotels and Africa Eco-camps. We are thankful to Kenya Wildlife Service and the National Museums of Kenya. We would also like to thank Jean-Marc Thiollay for contribution of the survey data from 1976 and 1988.
Figure 1: Map of the Masai Mara Ecosystem showing the transects and the three land-use areas

Figure 2: Mean abundance index (±SD) for Gyps vultures by land use and period (N = 26)
Gyps vulture abundance by land use and period

![Graph showing Gyps vulture abundance by land use and period]

- **Grazed**
- **Buffer**
- **Reserve**

- **Mean abundance index (birds/km)**
  - **Early**
  - **Recent**
Table 1: Mean number of individuals recorded per 100 km (±SD) for each avian scavenger species for ungulate non-migration and migration season during the early and recent periods (N = 6 for 1976&1988, N = 20 for 2003-2005)

<table>
<thead>
<tr>
<th>Species</th>
<th>Years</th>
<th>Non-migration Season</th>
<th>Migration Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bateleur</td>
<td>1976&amp;1988</td>
<td>3.04 (± 1.61)</td>
<td>6.84 (± 5.41)</td>
</tr>
<tr>
<td><em>Terathopius ecaudatus</em></td>
<td>2003-2005</td>
<td>4.10 (± 3.75)</td>
<td>7.78 (± 8.27)</td>
</tr>
<tr>
<td>Egyptian Vulture</td>
<td>1976&amp;1988</td>
<td>0.40 (± 0.70)</td>
<td>7.23 (± 11.49)</td>
</tr>
<tr>
<td><em>Neophron percnopterus</em></td>
<td>2003-2005</td>
<td>0 (± 0)</td>
<td>0 (± 0)</td>
</tr>
<tr>
<td></td>
<td>2003-2005</td>
<td>21.27 (± 14.24)</td>
<td>46.10 (± 78.63)</td>
</tr>
<tr>
<td>Hooded Vulture</td>
<td>1976&amp;1988</td>
<td>2.17 (± 0.86)</td>
<td>7.21 (± 6.36)</td>
</tr>
<tr>
<td><em>Necrosyrtes monachus</em></td>
<td>2003-2005</td>
<td>2.30 (± 3.56)</td>
<td>1.26 (± 2.27)</td>
</tr>
<tr>
<td>Lappet-faced Vulture</td>
<td>1976&amp;1988</td>
<td>4.96 (± 5.00)</td>
<td>14.16 (± 16.32)</td>
</tr>
<tr>
<td><em>Aegypius tracheliotus</em></td>
<td>2003-2005</td>
<td>4.43 (± 4.30)</td>
<td>5.23 (± 6.25)</td>
</tr>
<tr>
<td>Tawny Eagle</td>
<td>1976&amp;1988</td>
<td>6.19 (± 5.09)</td>
<td>8.30 (± 4.03)</td>
</tr>
<tr>
<td><em>Aquila rapax</em></td>
<td>2003-2005</td>
<td>5.93 (± 4.55)</td>
<td>4.43 (± 2.74)</td>
</tr>
<tr>
<td>White-headed Vulture</td>
<td>1976&amp;1988</td>
<td>1.83 (±2.21)</td>
<td>1.87 (± 3.23)</td>
</tr>
<tr>
<td><em>Aegyptiusoccipitalis</em></td>
<td>2003-2005</td>
<td>1.36 (± 2.47)</td>
<td>0.70 (± 1.49)</td>
</tr>
</tbody>
</table>
Table 2: Individual effects on mean abundance (bird/100 km) for avian scavengers (bold text indicates significance at 0.05 level) (N = 26)

<table>
<thead>
<tr>
<th>Factor</th>
<th>D</th>
<th>F</th>
<th>Bat</th>
<th>Gyps</th>
<th>HV</th>
<th>LFV</th>
<th>WHV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X^2</td>
<td>p</td>
<td>X^2</td>
<td>p</td>
<td>X^2</td>
<td>p</td>
<td>X^2</td>
</tr>
<tr>
<td>Overall</td>
<td>9</td>
<td>83.9</td>
<td>&lt;0.0</td>
<td>101.9</td>
<td>&lt;0.0</td>
<td>24.8</td>
<td>&lt;0.0</td>
</tr>
<tr>
<td>Period</td>
<td>1</td>
<td>2.63</td>
<td>0.10</td>
<td>21.90</td>
<td>&lt;0.0</td>
<td>6.71</td>
<td>&lt;0.0</td>
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<tr>
<td>Season</td>
<td>1</td>
<td>0.66</td>
<td>0.42</td>
<td>4.29</td>
<td>&lt;0.0</td>
<td>1.87</td>
<td>0.17</td>
</tr>
<tr>
<td>Land use</td>
<td>2</td>
<td>7.83</td>
<td>&lt;0.0</td>
<td>17.59</td>
<td>&lt;0.0</td>
<td>3.45</td>
<td>0.18</td>
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<tr>
<td>Season*Land use</td>
<td>2</td>
<td>3.94</td>
<td>0.14</td>
<td>22.81</td>
<td>&lt;0.0</td>
<td>1.12</td>
<td>0.57</td>
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<tr>
<td>Period*Land use</td>
<td>2</td>
<td>5.56</td>
<td>0.06</td>
<td>11.03</td>
<td>&lt;0.0</td>
<td>3.62</td>
<td>0.16</td>
</tr>
<tr>
<td>Period*Season</td>
<td>1</td>
<td>0.64</td>
<td>0.42</td>
<td>3.21</td>
<td>0.07</td>
<td>1.86</td>
<td>0.17</td>
</tr>
</tbody>
</table>
Table 3: Individual effects on mean abundance (bird/100 km) for avian scavengers (bold text indicates significant at 0.05 level) (N = 20)

<table>
<thead>
<tr>
<th>Factor</th>
<th>DF</th>
<th>AWBV</th>
<th>RV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$X^2$</td>
<td>p</td>
</tr>
<tr>
<td>Overall</td>
<td>5</td>
<td>39.25</td>
<td>$&lt;0.01$</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>2.16</td>
<td>0.14</td>
</tr>
<tr>
<td>Land use</td>
<td>2</td>
<td>24.82</td>
<td>$&lt;0.01$</td>
</tr>
<tr>
<td>Season*Land use</td>
<td>2</td>
<td>6.73</td>
<td>$&lt;0.05$</td>
</tr>
</tbody>
</table>
Literature Cited


CHAPTER 3

Mechanisms of coexistence in vultures: Understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya

AUTHORS: Corinne Kendall, Munir Z. Virani, Paul Kirui, Simon Thomsett, and Mwangi Githiru.

REFERENCE: Accepted by Condor (February 2012).
Abstract

Due to high, albeit seasonal, carcass availability, the Mara-Serengeti ecosystem has high scavenger diversity, leading to considerable competition among species. By determining patterns of occurrence in vulture species at 163 carcasses over an eight-year period in the Masai Mara National Reserve (MMNR), we were able to identify some possible mechanisms that lead to reduced competition. Our findings indicate that species are associated based on similar dietary needs and beak morphology, and that they are highly interdependent, showing little evidence of disassociation. Social vultures’ (Gyps species) dominated the vulture scene at the MMNR; their abundance was higher at carcasses during the ungulate migration when carcass availability was likely to be higher than during the periods without migration. In addition, vulture abundance was detrimentally affected by predator presence regardless of predator identity, suggesting that vultures prefer non-predator-killed sources of carrion where available. Comparisons between historic and current carcass counts suggest a substantial shift in Gyps vultures with an increase in the relative abundance of Rüppell’s vultures compared to White-backed vultures. In addition, our findings suggest that as land use changes in the Mara-Serengeti ecosystem lead to reductions in large ungulate species, social vultures will be most adversely affected.

Keywords: aggregation, coexistence, competition, food availability, resource partitioning, scavengers, vulture

INTRODUCTION

In ecosystems with high carcass availability, such as the Mara-Serengeti ecosystem, there is a concomitant higher degree of range overlap among scavengers and greater use of carrion by
facultative scavengers which leads to large scavenger diversity 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 coexistence of ecologically similar species and can occur through differences in diet or through spatial and temporal segregation of resource use (Kronfeld-Schor and Dayan, 2003, Ilse and Hellgren, 1995). In addition, it has been proposed via the aggregation model of coexistence that in guilds using highly 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 in vultures may be influenced by many factors, both behavioral and extrinsic (Selva et al., 2005). In East Africa, early work 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 (Kruuk, 1967). Body size also appears to have a strong influence on dominance hierarchies and thus resource partitioning in several scavenger guilds (Gomez et al., 1994, Kruuk, 1967, Petrides, 1959, Wilbur and Jackson, 1983). However, others have suggested that the primary difference between vulture species is in diet (Mundy et al., 1992). In particular carcass size, though not carcass species identity, often has a significant impact on the number and proportion of vultures occurring at a given carcass (Gomez et al., 1994, Selva et al., 2005, Hunter et al., 2007).
Spatio-temporal partitioning of resources in 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 Cape Vulture (*Gyps coprotheres*) and White-backed Vulture (*G. africanus*) and found differences in carcasses exploited based on take-off abilities. Kirk and Houston (1995) assessed habitat use and foraging strategies of migrant and resident Turkey Vultures (*Cathartes aura*) and found significant influence of social dominance on habitat preference of each group. Houston (1974a) found that vulture density, particularly for the *Gyps* vultures, increased in areas of high wildlife density. In addition, resource distribution, whether aggregated or scattered, appears to be important in determining scavenger community composition at ungulate carcasses in temperate ecosystems (Wilmers et al., 2003b, Blazquez et al., 2009). Competition with predators at carcasses may also influence scavengers and lead to variations in scavenger community structure at predator and non-predator-killed food sources (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, Hartley and Shorrocks, 2002, Rosewell et al., 1990). Recent studies provide evidence that this may be occurring in scavenging communities 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 (Blazquez et al., 2009, Wilmers et al., 2003b). This is primarily due to the fact that subordinate species are able to outcompete dominant species when they occur in large groups (Houston, 1974b, Gomez et al., 1994, Buckley, 1996, Kirk and Houston, 1995). However, Atkinson and Shorrocks (1981) predicted that in addition to intraspecific aggregation, there would also have to be disassociation
among species 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 avian scavenger use animal carcasses to assess possible mechanisms of coexistence among vultures. 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 there will be a higher concentration of these social species at large carcasses than at small. In addition, the abundance of social vultures should be higher during the ungulate migration season, when carcass availability is high, than during the non-migration season. Finally we expected fewer vultures of all species at carcasses with predators than at those where mammalian predators do not occur.

Avian scavengers are known to be declining rapidly throughout Africa, including East Africa, and establishing the cause of these declines is essential (Thiollay, 2007b, Ogada and Keesing, 2010, Virani et al., 2011). Loss of vultures in Kenya’s prestigious Masai Mara National Reserve would be likely to have significant ecological and economic ramifications as has occurred elsewhere (Markandya et al., 2008, Sekercioglu, 2006, Sekercioglu et al., 2004, Sergio et al., 2005). Declines of vultures in MMNR have already been recorded based on transects (Virani et al. 2011), but *Gyps* vultures were aggregated in historic counts, making it impossible to assess differences in level of decline between White-backed and Rüppell’s Vultures. Here we provide the first attempt to assess changes in relative abundance between these two species, by comparing current carcass counts with historic numbers, providing important insights about their relative declines. 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 (Kissui, 2008, Murn and Anderson, 2008, Bamford et al., 2009b, Ogutu et al., 2005, Ogutu et al., 2009, Virani et al., 2011).

METHODS

STUDY SITE
Masai Mara National Reserve (MMNR) is a savannah habitat in south-western Kenya. It is approximately 1,530 km² 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 km². MMNR is an important area for avian scavengers due to the high density of ungulates and large migratory Blue Wildebeest (*Connochaetes taurinus*), Burchell’s Zebra (*Equus burchelli*), and Thomson’s Gazelle (*Gazella thomsonii*) herds 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 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 scavenger species (Houston, 2001, Houston, 1979). Patterns of occurrence in vultures were recorded at primarily large mammalian carcasses throughout MMNR. Observations were made throughout the year during both the ungulate migration and non-migration seasons.

STUDY SPECIES
Six vulture species are found in the Mara-Serengeti ecosystem. When classified by beak morphology and feeding technique, the six vulture species studied are usually grouped into three
subsets (Kruuk, 1967) (Table 1). Lappet-faced Vulture (*Torgos tracheliotos*) 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). Lappet-faced Vultures are dominant over all other vulture species (Mundy et al., 1992, Kruuk, 1967, Houston, 1975). Rüppell’s Vulture (*Gyps rueppellii*) and White-backed Vulture (*Gyps africanus*), often termed the *Gyps* vultures, are described as gregarious, have long necks and medium-sized beaks, and tend to feed on the innards of the carcass (Mundy et al., 1992, Houston, 1974b). *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 are able to outcompete larger species when found in large groups (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 non-carrion food sources, but tend to use a pecking technique to feed on scraps when feeding at a carcass.

**VULTURE NUMBERS**

Data were collected over eight years in total from 1997 to 2006, but excluding 2000 and 2003 when no data were gathered due to logistical reasons. Vulture counts were conducted during daylight hours while driving within MMNR. Initial trends indicated that sole use of specific routes for carcass detection would result in too few observations. Thus, carcasses were found 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 throughout our study area, carcass density was likely to be considerably higher during the migration season when wildlife density in MMNR is higher and
For every carcass encountered, we recorded: the number of each vulture species present, carcass (species) identity (based on which the carcass was assigned a size category), and the presence and identity of predators. Carcasses recorded were from 18 different species with the most common being Burchell’s Zebras, Blue Wildebeest, Thompson’s Gazelle, and African Buffalo (*Syncerus caffer*) (see Appendix for the complete list). Predators were considered to be present at the carcass if they were feeding at or within 20 m of the carcass. The identity of the predator that killed the animal, regardless of presence, was verified 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 (*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, a season variable was also ascribed to every carcass sighting: June-October (encompassing the Mara-Serengeti ungulate migration) (Estes and East, 2009) and November-June (reflecting the non-migration season). This season category also roughly coincides with the known rainfall pattern in the MMNR region, with the migration season being largely during the dry season and non-migration during the wet (Ottichilo et al. 2001). All observations were conducted 20-50 m away from the carcass using a vehicle as a hide. Observations were generally short, lasting as long as was needed to complete a count of all birds present at the carcass.

DATA ANALYSIS
Current data on the proportion of each vulture species seen at carcasses were compared with historical records taken in the 1960-70s from Mundy et al. (1992) using a chi-squared test, assuming the historical data for each species as the expected proportions. Historical data involved counts of vultures at carcasses in Amboseli and Serengeti National Park, Tanzania, primarily by David Houston, rather than in MMNR. Recent movement studies using GSM-GPS telemetry and wing tagging show that an individual *Gyps* vulture can range across these three sites – MMNR, Amboseli, and Serengeti, which are less than 100 km apart (Kendall and Virani In press). Populations therefore appear to be linked between these sites and abundance and behavior at carcasses are expected to be similar throughout this region, making these counts useful for historical comparisons.

A Principal Factor Analysis (PFA) was used 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 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). Factor loadings (correlations between the factors and the original variables) greater than 0.32 were deemed significant and interpreted (Alsobrook II et al., 1999). Aggregation for each vulture species was assessed using an index of dispersion (for the migration and non-migration 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 greater than one suggests that the species aggregates at carcasses.

Raw vulture count data were square root-transformed and used as the response variable in a Generalised Non-linear Model [GLZ] (assuming a Poisson distribution, and using the Log link
function) with five categorical explanatory variables: Season (migration and non-migration), Carcass size (three classes: 1-100, 101-1000 and >1000 kg), Predator ID (Cheetah, Hyena, Leopard, Lion, None, Unknown), and Species (White-backed, Rüppell’s, Lappet-faced, White-headed, Hooded and Egyptian vultures). Year (8 years: 1997-2006 excluding 2000 and 2003) was considered as a random effect. All four two-way interactions involving Species were also included. Among the 511 candidate models resulting from all possible combinations of these independent variables, we selected the set of best-fitting models that minimized the second-order Akaike information criterion ($\text{AIC}_c$) (e.g., Maestre et al. 2012). Because our primary objective was to identify a most parsimonious model, we followed an exploratory modeling approach, excluding all models with uninformative parameters (i.e., Akaike weights of zero) from the table of model rankings (Arnold 2010).

Model building and selection were performed using the Best Subsets option based on the Akaike Information Criterion in STATISTICA (StatSoft 2001) corrected for small sample size ($\text{AIC}_c$). In addition to being within two $\text{AIC}_c$ units of the top model, we considered a model competitive for inference only if the covariates in the lowest $\text{AIC}_c$ 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 ($w_i$) for each of the top-five ranked models, which provided a measure of evidence (probability) that the particular model was the best model (Johnson and Omland 2004, Devries et al. 2008). There was little evidence of over dispersion in our dataset, with the deviance of the global model being 0.78; likewise, the residuals did not show significant deviation from expected based on the Poisson distribution.

RESULTS
VULTURE NUMBERS

Over the eight-year period, we counted 6840 individual vultures at 163 carcasses, of which close to 90% were *Gyps* vultures. There were significant differences in relative abundance of vulture species per carcass between current and historic data, most notably with Rüppell’s vultures having greater relative abundance in current counts ($\chi^2 = 96.2, p = 0.0001$), suggesting a marked change in species composition within the vulture guild (Figure 1).

VULTURE ASSOCIATIONS AND AGGREGATIONS

Using a Scree plot, three factors were extracted accounting for 77.8% of the total variance. Based on factor loadings (Table 2), the following three vulture associations for the overall sample were identified: Factor 1: White-backed-Rüppell’s-Lappet-faced Vultures; Factor 2: Hooded-Egyptian Vultures; and Factor 3: White-headed-Lappet-faced Vultures. Factor 1 remained the same throughout the year. Factor 2 was the same during the migration season, but changed to White-headed-Egyptian during the non-migration. Factor 3 found no associations when considered by season.

The *Gyps* vultures appear to be highly aggregated at carcasses during the migration (index of dispersion was 20 for White-backed Vulture and 15 for Rüppell’s Vulture) and to a lesser extent non-migration season (index of dispersion was 11 and 4 for White-backed and Rüppell’s Vulture, respectively). Hooded Vultures showed low levels of aggregation during both seasons with an index of dispersion of 2 for both seasons, and Lappet-faced Vultures were only aggregated during the non-migration season. White-headed Vultures and Egyptian Vultures also showed limited aggregation with an index of dispersion less than 2 for both seasons.
FACTORS INFLUENCING VULTURE NUMBERS AT CARCASSES

There were no models within two AICc units of the top model that were not hierarchically nested to it (Table 3). Thus, none was considered competitive and we assumed the lowest AICc model as the best model. This model was also considerably more probable than the others, with a 65% probability of being the best model for these data (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 the other species (Figure 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 carcasses where there was no predator attendant (Figure 3). Lastly, 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 Vulture was the most common vulture species at carcasses in the MMNR throughout the year and is probably resident. Mean number of Rüppell’s Vultures was higher during the migration season and their relative abundance increased significantly when migratory ungulates were present. Due to their cliff-nesting and large range size, these species may be able to respond acutely to changes in wildlife density (Mundy et al., 1992).

Overall three associations were found between: 1) the White-backed, Rüppell’s, and to a lesser extent Lappet-faced Vultures; 2) Hooded and Egyptian Vultures; and 3) White-headed and
Lappet-faced Vulture. Associations between White-backed, Rüppell’s, and Lappet-faced Vultures occurred regardless of season suggesting that shifts in carcass and vulture density do not heavily impact vulture interactions. 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 thus would be expected to have the highest interspecific competition (Houston, 1974b, Mundy, 1982, Mundy et al., 1992). Associations among White-backed, Rüppell’s, and Lappet-faced Vultures may be explained in part by networking between species 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. Given that the associations between these three species did not change even as carcass availability increased, we would expect that vulture populations may be limited by food availability and that competition between species remains high throughout the year.

In some scavenger guilds, high levels of aggregation have been found to reduce interspecific competition, but only if there are low levels of association between species (Atkinson and Shorrocks, 1981). Similar to previous findings, Gyps species were the most highly aggregated of the species studied, especially during the migration season. However, Gyps vultures also showed high levels of association between the two species and thus other mechanisms must operate to enable coexistence (Atkinson and Shorrocks, 1981, Hartley and Shorrocks, 2002, Rosewell et al., 1990, Shorrocks et al., 1990). Associations between similar vulture species suggest a high level of interdependence among species, possibly related to
facilitative interactions between species in carcass discovery, in opening carcasses, or in reducing competition between avian and mammalian scavengers (Travaini et al., 1998).

**FACTORS AFFECTING VULTURE COUNTS**

Similar to previous studies (Houston, 1974a, Houston, 1974b), vulture abundance at predator kills was lower than at carcasses without predators across all six vulture species, although only six carcasses were confirmed to be non-predator kills and further investigation is merited. Predator identity was generally not important though leopard kills had particularly low vulture abundance. In Serengeti, Houston (1974b) found little food is typically available for vultures at predator kills and estimated that vultures consume 88% of their diet at non-predator killed carcasses, where competition with mammalian predators and scavengers is greatly reduced.

Annual fluctuations in vulture abundance at carcasses found in this study may be caused by changes in other factors which affect carcass availability within MMNR and thus influence vulture abundance overall. Rainfall variation is known to influence breeding of many scavenging birds and may also affect foraging behavior (Virani et al. In press). In particular, vulture abundance would be expected to increase in years with low rainfall when ungulate mortality is higher. Declines in overall wildlife density or changes in the pattern of ungulate migration with less time spent in MMNR as appears to be occurring could also lead affect carcass availability in the study area and therefore lead to reductions in vulture abundance (Ogutu et al. 2011).

Unfortunately no data were gathered on the level of annual variation in these factors during this study.

Vulture abundance at carcasses was higher during the migration season than during non-migration, driven largely by higher numbers of the *Gyps* species. White-backed Vultures
generally fledge during the migration season while the timing of Rüppell’s Vulture nesting is more variable (Virani et al., In press-a, Houston, 1989, Virani et al., 2010). It is unknown if nesting status affects the foraging radius of vultures, but given their large range sizes and soaring flight, which allows for high mobility and low energetic cost, it is unlikely to be related to foraging behavior (Pennycuick, 1972, Pennycuick, 1979). It is likely that carcass availability is higher during the migration when ungulate density in Masai Mara National Reserve is high due to the influx of migratory ungulates and high ungulate mortality due to the lack of forage and water brought on by the dry season (Houston, 1989, Mduma et al., 1999). Findings thus support predictions that there would be a higher concentration of both Gyps species at carcasses during periods with higher food availability, such as the migration. This is consistent with findings from other areas where social species are more prevalent at aggregated carcasses or in areas of high carcass density (Wilmers et al., 2003b, Blazquez et al., 2009, Gomez et al., 1994, Houston, 1974b). These social species, as in other scavenger systems, rely on social facilitation to find food and then to compete with larger species and may thus 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 the amount of food remaining was not recorded, carcasses generally decompose throughout the day with the most intact carcasses being available in the morning (Mduma et al., 1999). Observations were conducted throughout the day to reduce bias in over-sampling a carcass at any one particular 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 to be biased
towards later stage carcasses, the data should still give us accurate information about who is using the carcass. Preliminary data from on-going studies where carcass stage has been recorded have found that data is generally only slightly skewed to later stages, and that there do not appear to be significant differences between different carcass sizes in the distribution of amount of meat remaining (CK, unpublished data). In addition, we see no reason to believe that our sample would be biased in terms of carcass age by season or year. There may be differences in amount of meat remaining based on whether a carcass came from a predator kill or non-kill, but these differences are ultimately caused by the mortality factor itself (which is one of the variables that we are testing). Based on these findings from similar surveys, it appears unlikely that our data would be biased in terms of carcass age in relation to any of the other explanatory variables considered. An experimental study that recorded scavenger composition at carcasses of various sizes over an extended period would provide greater insight as to these potential biases and should be conducted in the near future.

**Conservation Implications**

Vulture counts at carcasses have been and continue to be used to assess vulture abundance (Anderson and Horwitz, 1979, Attwell, 1963, Houston, 1974a, Houston, 1974b, Kruuk, 1967, Mundy, 1982, Petrides, 1959). When compared to previous vulture counts at carcasses done in East Africa in the 1960s and 70s (Mundy et al., 1992), carcass counts from this study showed lower relative abundance of White-backed vulture with a 20-fold increase in relative abundance of Egyptian Vulture and doubling of relative abundance of Rüppell’s Vulture from 15 to 35% and White-headed Vultures from 0.8 to 2%.
Previous studies have reported a 52% decline in *Gyps* vultures in MMNR over the last thirty years, but were unable to differentiate between the two *Gyps* species due to limitations in historic surveys (Virani et al. 2011). Changes in relative abundance between these two species at the carcasses seem most consistent with a larger decline in White-backed vultures than Rüppell’s vultures and are cause for concern. Reasons for a shift between the *Gyps* species over the last three decades, favouring the Rüppell’s Vulture, could relate to increased human disturbance at tree nests of semi-colonial White-backed vulture, differences in sensitivity or exposure to poisoning, or reported reductions in resident ungulate populations in MMNR, which would be more likely to impact resident White-backed Vulture than the Rüppell’s Vulture (Bamford et al., 2009b, Ogutu et al., 2009, Ottichilo et al., 2001). In particular, continued fire and elephant damage to trees may be affecting the nesting success of White-backed Vultures (PK, personal observation).

Due to their high mobility, vultures readily respond to the increase in food availability that occurs 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 showed greater sensitivity to seasonal changes in carcass availability and carcass size than for other species, possibly due to their dependence on large groups for effective feeding. Given continued threat of wildlife declines due to poaching, livestock encroachment, and agricultural intensification in and around the MMNR, vultures are at risk of reduced food supply (Ogutu et al., 2009, Ottichilo et al., 2001, Ottichilo et al., 2000). Given their greater sensitivity to changes in carcass availability, if the numbers of large ungulates were to decline, *Gyps* vultures within this ecosystem would be
expected to 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 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 vulture density, movement, and habitat use.

ACKNOWLEDGEMENTS

This study is part of The Peregrine Fund’s Pan African Raptor Conservation Program and was funded by grants from The Peregrine Fund. We are indebted to the Narok County Council and the staff of the Masai Mara National Reserve in particular the wardens Mr Sindiyo and Mr Minis for their assistance and permission to conduct vulture research in the reserve. We also thank Mr Koikai and Mr Lenjirr for their help. We are grateful for the support accorded by the Mara Conservancy and neighboring group ranches – Koiyaki, Lemek, Siana and Olaro Orok; plus logistical help accorded by Heritage Hotels and Africa Eco-camps. We are thankful to Kenya Wildlife Service and the National Museums of Kenya. We also thank Keith Bildstein for his insightful comments on this manuscript.

LITERATURE CITED


FIGURES

**Figure 1:** Mean number of each vulture species per carcass for historical data collected in Serengeti National Park, Tanzania (with an overall mean of 100 individuals/carcass) and current data from Masai Mara National Reserve, Kenya (overall mean of 105 individuals/carcass)
Figure 2: Mean number of vultures of each species per carcass during the migration (number of carcasses n = 86) and non-migration (n = 76) seasons 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 shown refer to number of carcasses.
<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Dominance</th>
<th>Level of specialization on carrion</th>
<th>Arrival order</th>
<th>Beak morphology</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-headed</td>
<td><em>Trigonoceps occipitalis</em></td>
<td>Middle</td>
<td>Middle; some predation</td>
<td>Early</td>
<td>Tear</td>
</tr>
<tr>
<td>Lappet-faced</td>
<td><em>Torgos tracheliotos</em></td>
<td>Most (individually)</td>
<td>Middle; some predation</td>
<td>Late; occasionally early</td>
<td>Tear</td>
</tr>
<tr>
<td>Rüppell’s</td>
<td><em>Gyps rueppellii</em></td>
<td>Most (in groups)</td>
<td>Highest; obligate scavenger</td>
<td>Middle</td>
<td>Pull</td>
</tr>
<tr>
<td>White-backed</td>
<td><em>Gyps africanus</em></td>
<td>Most (in groups)</td>
<td>Highest; obligate scavenger</td>
<td>Early/Middle</td>
<td>Pull</td>
</tr>
<tr>
<td>Hooded</td>
<td><em>Necrosyrtes monachus</em></td>
<td>Least</td>
<td>Least</td>
<td>Early at predator kills; late at natural carcasses</td>
<td>Peck</td>
</tr>
<tr>
<td>Egyptian</td>
<td><em>Neophron percnopterus</em></td>
<td>Least</td>
<td>Least</td>
<td>Early at predator kills; late at natural carcasses</td>
<td>Peck</td>
</tr>
</tbody>
</table>

* Adapted from Mundy et al. (1992)
Table 2: Factor loadings for the three extracted Principal Factors (PF) overall and by season. The PFs represent vulture associations, with the loadings in **bold** font indicating the species that associate with one another under that PF.

<table>
<thead>
<tr>
<th>Species</th>
<th>Overall</th>
<th>Migration</th>
<th>Non-migration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PF 1</td>
<td>PF 2</td>
<td>PF 3</td>
</tr>
<tr>
<td>White-backed</td>
<td>0.96</td>
<td>0.06</td>
<td>-0.08</td>
</tr>
<tr>
<td>Rüppell’s</td>
<td>0.93</td>
<td>-0.07</td>
<td>-0.05</td>
</tr>
<tr>
<td>Lappet-faced</td>
<td>0.62</td>
<td>0.23</td>
<td>0.46</td>
</tr>
<tr>
<td>White-headed</td>
<td>-0.06</td>
<td>-0.04</td>
<td>0.94</td>
</tr>
<tr>
<td>Hooded</td>
<td>0.02</td>
<td>0.79</td>
<td>0.12</td>
</tr>
<tr>
<td>Egyptian</td>
<td>-0.08</td>
<td>0.82</td>
<td>-0.11</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>PF 1</th>
<th>PF 2</th>
<th>PF 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-backed</td>
<td>0.95</td>
<td>0.09</td>
<td>-0.11</td>
</tr>
<tr>
<td>Rüppell’s</td>
<td>0.95</td>
<td>-0.06</td>
<td>0.01</td>
</tr>
<tr>
<td>Lappet-faced</td>
<td>0.77</td>
<td>0.24</td>
<td>0.19</td>
</tr>
<tr>
<td>White-headed</td>
<td>0.94</td>
<td>0.02</td>
<td>-0.07</td>
</tr>
<tr>
<td>Hooded</td>
<td>0.31</td>
<td>0.78</td>
<td>0.06</td>
</tr>
<tr>
<td>Egyptian</td>
<td>0.88</td>
<td>0.14</td>
<td>-0.26</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>PF 1</th>
<th>PF 2</th>
<th>PF 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-backed</td>
<td>0.90</td>
<td>-0.13</td>
<td>0.02</td>
</tr>
<tr>
<td>Rüppell’s</td>
<td>0.75</td>
<td>-0.14</td>
<td>0.18</td>
</tr>
<tr>
<td>Lappet-faced</td>
<td>0.80</td>
<td>0.27</td>
<td>-0.24</td>
</tr>
<tr>
<td>White-headed</td>
<td>0.98</td>
<td>0.12</td>
<td>0.90</td>
</tr>
<tr>
<td>Hooded</td>
<td>0.88</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Egyptian</td>
<td>0.59</td>
<td>0.59</td>
<td>-0.31</td>
</tr>
</tbody>
</table>
Table 3: Summary of model selection results from generalized linear models examining vulture numbers at carcasses in Masai Mara National Reserve, Kenya, 1997-2006. Models are listed beginning with the best-fitting model, and sorted by $\Delta AIC_c$. The $AIC_c$ weight indicates the relative likelihood of each model given the model set and sums to 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>No. of Parameters</th>
<th>Deviance</th>
<th>$\Delta AIC_c^a$</th>
<th>$AIC_c$ weight</th>
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</thead>
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<td>1866.7</td>
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<td>1895.1</td>
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$^a$ This is the 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.
Appendix: Complete list of species identity for all carcasses observed

<table>
<thead>
<tr>
<th>Carcass common name</th>
<th>Carcass scientific name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cheetah</td>
<td><em>Acinonyx jubatus</em></td>
</tr>
<tr>
<td>Blue Wildebeest</td>
<td><em>Connochaetes taurinus</em></td>
</tr>
<tr>
<td>Spotted Hyena</td>
<td><em>Crocuta crocuta</em></td>
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<tr>
<td>Burchell’s Zebra</td>
<td><em>Equus burchelli</em></td>
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<tr>
<td>Thompson's Gazelle</td>
<td><em>Eudorcas thomsonii</em></td>
</tr>
<tr>
<td>Lion</td>
<td><em>Panthera leo</em></td>
</tr>
<tr>
<td>African Buffalo</td>
<td><em>Syncerus caffer</em></td>
</tr>
<tr>
<td>Olive Baboon</td>
<td><em>Papio anubis</em></td>
</tr>
<tr>
<td>Domestic Cow</td>
<td><em>Bos primigenius</em></td>
</tr>
<tr>
<td>Common Eland</td>
<td><em>Taurotragus oryx</em></td>
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<tr>
<td>Elephant</td>
<td><em>Loxodonta africana</em></td>
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<tr>
<td>Giraffe</td>
<td><em>Giraffa camelopardalis</em></td>
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<tr>
<td>Hippo</td>
<td><em>Hippopotamus amphibius</em></td>
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<tr>
<td>Impala</td>
<td><em>Aepyceros melampus</em></td>
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<tr>
<td>Ostrich</td>
<td><em>Struthio camelus</em></td>
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<tr>
<td>Topi</td>
<td><em>Damaliscus korrigum</em></td>
</tr>
<tr>
<td>Common Warthog</td>
<td><em>Phacochoerus africanus</em></td>
</tr>
<tr>
<td>Waterbuck</td>
<td><em>Kobus ellipsiprymnus</em></td>
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CHAPTER 4

Alternative strategies in avian scavengers: How subordinate species foil the despotic distribution

AUTHOR: Corinne J. Kendall.

Abstract

Trade-offs in species’ traits can mediate competition and enable coexistence. A key challenge in ecology is understanding the role of species’ trade-offs in maintaining diversity and evolutionary trade-offs between the abilities of competing species are best understood by considering how competitive advantages change along an environmental gradient. Previous studies of such trade-offs are generally limited to two-species systems and a single trade-off. In this study, I consider the effect of trade-offs in search efficiency and competitive abilities on habitat use patterns among a diverse avian scavenger guild. I hypothesize that species’ dominance status and search efficiency will both be correlated with patch quality. Using counts of searching birds in areas that vary in habitat quality in terms of both wildlife and human settlement density and observations at experimental carcasses, I assess the competitive ability, search efficiency, and habitat use of seven avian scavenger species in Masai Mara National Reserve, Kenya. Findings support the hypothesis with Bateleurs, a species with high search efficiency, and Ruppell’s, Lappet-faced, and White-backed vultures, species with high individual or social dominance, preferentially exploiting habitats of high quality, while Tawny eagles and Hooded vultures, species with low search efficiency and competitive ability, preferring habitats of low quality. This paper demonstrates the importance of considering multiple strategies for assessing the effect of competition on habitat use within complex communities.

Keywords: interspecific competition, dominance, habitat use, producer-scrounger, vultures

Introduction
A key challenge in ecology is understanding the role of species’ trade-offs in enabling coexistence (Tilman, 1987). Coexistence mechanisms can be defined through considerations of trade-offs among species in a heterogeneous environment (Brown et al., 1994). Studies of trade-offs are often limited to consideration of one trade-off at a time and to two species interactions, but overall community structure is likely to be shaped by multiple strategies among multiple species (Tilman, 1987). In this study, I consider the effect of multiple trade-offs on the habitat use patterns of a multi-species guild.

The avian scavenger guild in East Africa is incredibly diverse and thus represents an ideal system for studying coexistence (Mundy et al., 1992). These scavengers differ on a number of important species’ traits, including body size, beak strength, and nesting behavior. Previous studies of vultures have focused on differences in beak morphology, which affects feeding behavior and it is proposed that vultures can be divided into three subsets, each using a different feeding technique and thus focusing on a different part of the carcass (Kruuk, 1967, Hertel, 1994). While such differences explain resource partitioning patterns as a carcass is broken down (Carrete et al., 2010), they are unlikely to explain differences between species in their habitat use.

Several theories have been proposed to explain the distribution of individuals across environmental gradients, and these can also be used to understand habitat use patterns across competing species. The ideal free distribution assumes similar competitive abilities across species, and thus, that species will use patches based on habitat quality (Fryxell and Lundberg, 1997). However, vultures are known to differ in their competitive abilities based on body size with larger species generally winning agonistic interactions against smaller ones (Kruuk, 1967).
Thus a despotic distribution predicts that where competitive asymmetries exist, dominance status will distribute species across habitats in relation to patch quality (Parker and Sutherland, 1986).

However, across this diverse guild, collective action at the carcass may trump solitary competitive ability, and search efficiency may offset competitive ability (exploration-exploitation trade-off). Thus it is likely that multiple alternative strategies are possible, reducing the likelihood that a despotic distribution alone will be sufficient to explain carcass and habitat use patterns. To test for the impact of these trade-offs on habitat use, I observed interspecific interactions among scavenger species across habitats of varying quality. Using experimental carcasses, I established the dominance hierarchy between species and their search efficiency. First, I predict that dominance will generally be determined by body size, but that for social scavengers, dominance will increase with group size as has been found in other scavenging systems (Carrete et al., 2010, Kruuk, 1967, Kirk and Houston, 1995). As a result, species can gain dominance via either large body size or large group size. Second, arrival order is known to vary considerably among avian scavenger species (Mundy et al., 1992). Theoretical models of producer-scrounger games predict that small, non-social species are more likely to discover a food resource (i.e. be a producer) (Barta and Giraldeau, 1998). I predict that effective producers, species that reliably arrive first at a food resource, may reduce competitive interactions and undermine a despotic distribution. As a result, search efficiency in addition to dominance (both individual and group) will be necessary to explain habitat use among this diverse guild. Therefore dominance status and search efficiency of a species are expected to correlate with patch quality.

In addition, differences in habitat use may relate to differences in level of declines seen within the avian scavenger guild. All avian scavengers in East Africa are experiencing rapid
declines except Bateleurs (Virani et al., 2011). The major threat to scavengers in Africa, intentional poisoning of carcasses, is known to be more common in areas near human habitation (Otieno et al., 2010a, Kendall and Virani, In press). Given that threats vary across habitats, understanding interspecific differences in habitat use may be useful in explaining varying rates of decline seen among avian scavenger species.

This paper has two primary objectives. First, using behavioral observations at experimental carcasses, I determine differences in competitive ability and search efficiency among eight common avian scavenger species in Masai Mara National Reserve, Kenya. Second, I test the hypothesis that dominance status – of individuals and groups – and search efficiency are both correlated with patch quality by recording searching birds and observing scavenging behavior at experimental carcasses in habitats of varying quality. I consider two variables affecting habitat quality: wildlife density, which increases food availability and thus improves quality and human settlement density, which increases disturbance and thus reduces quality (Speziale et al., 2008, Skagen et al., 1991).

Methods

Study area

Avian scavenger abundance and diversity is high in Masai Mara National Reserve, Kenya, due to its high though seasonal wildlife density. Masai Mara National Reserve is approximately 1530 km² in size and primarily composed of savannah habitat. It is surrounded to the north, east, and west by Masai pastoral lands. Large herds of migratory wildebeest, zebra, and Thomson’s gazelle herds move between Masai Mara National Reserve and Serengeti National Park, Tanzania to the south and are most commonly found in Masai Mara National
Reserve from July to October. During this period, which coincides with the dry season, Masai Mara National Reserve experiences a significant increase in wildlife density (Ogutu et al., 2008). In addition, mortality rates of ungulates are considerably higher in the dry season when forage is scarce, leading to greater carcass availability (Mduma et al., 1999).

Masai Mara and the surrounding areas have undergone considerable changes in the last several decades, leading to habitat degradation. Agricultural intensification to the north, particularly in Loita plains has led to substantial declines in resident ungulate populations (Ottichilo et al., 2001, Ottichilo et al., 2000). Pastoral encroachment into the reserve, increased human population growth around the reserve, and poaching also have contributed to severe declines in resident ungulate populations (Ogutu et al., 2009). In order to kill predators, people place poisons, particularly carbofurans, on carcasses, which continues to threaten all scavengers in the area and occurs primarily outside protected areas during the wet season (Kissui, 2008, Otieno et al., 2010a, Otieno et al., 2010b).

**Study species**

Seven avian scavenger species occur in Masai Mara National Reserve and were included in the study: Bateleurs (Terathopius ecaudatus), Tawny eagle (Aquilla rapax), Lappet-faced vulture (Torgos tracheliotos), White-headed vulture (Trigonoceps occipitalis), African white-backed vulture (Gyps africanus), Ruppell’s vulture (Gyps rueppellii), and Hooded vulture (Necrosyrtes monachus) (Table 1). Three mammalian scavengers – Black-backed jackal (Canis mesomelas), Spotted hyena (Crocuta crocuta), and domestic dog (Canis familiaris) – are common in MMNR and were considered when they occurred at experimental carcasses. All mammalian scavengers are larger than and dominant to avian scavengers (Mundy et al., 1992).
For purposes of this study, mammalian scavengers were included as one group and I did not differentiate between species.

Habitat measurements

Carcass experiments and transects were conducted inside and outside Masai Mara National Reserve in areas that varied in habitat quality due to differences in human settlement density and wildlife density (Figure 1). The study site is divided into four sections with similar characteristics. Mara Middle (MM) included the central part of Masai Mara National Reserve, which was primarily open grassland with high wildlife density in areas of low grass height. Mara East (ME) was also inside the reserve, but has lower wildlife density as described in Ogutu et al. (2008) and (2009). Other than tourist lodges, human habitation is not allowed in the reserve. Two community areas on the border of the reserve were included: Koiyaki (KK) and Siana (SA). Human settlement density was higher in Siana than Koiyaki and wildlife density was higher in Koiyaki than Siana.

To quantify differences in habitat quality among the sites, wildlife density and human settlement density were measured along sixteen transects (four per section) with six replicates of each, except for four transects (two in MM, one in ME, and one in KK) that were only replicated five times for logistical reasons. Transects were conducted in two seasons that vary in wildlife density – three replicates in the wet season (February to May 2010) and three in the dry season (July to September 2010), when carcass availability is higher. Each transect varied in length from 13.2 to 38.3 km. Transects were treated as lines and the distances measured with the vehicle odometer. Habitat assessments were made continuously every two kilometers along the transect for an area extending 250 m on either side of the road, giving a total area of 1 km² for each
measurement when calculating density. Wildlife abundance, which included individuals of all mammal species greater than 50 kg, was estimated to the nearest 10 animals and settlement abundance was estimated based on number of bomas or clusters of houses, giving a count of one for each boma and ten for each larger town area (Lamprey and Reid, 2004).

Roadside surveys

Along the same set of transects used for habitat assessments, counts of searching birds were conducted to establish abundance of scavenger species in each site. Transects were driven along main roads and other paths, traveling at 15-50 km/hour. Two observers conducted all transects and windows and sunroof were kept open to maximize observations. All transects were completed between 9 AM and 4:30 PM, which are the peak activity periods for most scavenging raptors especially vultures (Mundy et al., 1992). Roadside counts were restricted to days of little or no rain. No more than three transects were conducted per day, and only one transect was conducted per section per day. Along transects, only raptors and Marabou storks were counted. When accurate identification was not possible, African white-backed and Ruppell’s vultures were categorized as *Gyps* vultures and were excluded from analyses on individual species.

Experimental carcasses

In order to assess foraging behavior and quantify presence and absence of each scavenger species at food sources in areas of varying habitat quality, behavioral observations were conducted at experimental carcasses placed in each of the four sites. Experimental carcasses were arranged to look like intact carcasses and consisted of a head, organs, and 2 kg of leg meat from a goat or sheep. Smaller carcasses intensify competitive interactions, allow for rapid
turnover between species, facilitate precise quantification of scavenger arrival and behavior, and are frequented by all members of the scavenger guild studied (Travaini et al., 1998). Use of small carcasses ensures that species cannot rely solely on differences in beak morphology by dividing up the carcass by body parts, but instead must compete for common resources, making subtle differences between species more evident.

Carcass set-up followed techniques used in similar studies of scavenging raptors (Bamford et al., 2009a, Carrete et al., 2010). All carcasses were put out at 8:00 AM. Observers watched from a stationary vehicle 50 m from the carcass using binoculars. Due to the high tourist density in the area, scavengers tend to ignore vehicles and, at this distance the vehicle did not appear to impact species landing or behavior. No carcasses were put out if rain had continued past 7 AM as this might impact the activity of the birds. Specific places where carcasses were used were selected in advance and marked with GPS (Garmin eTrex Legend C, Olathe, Kansas, accuracy < 15 feet). Observers then randomly selected from these carcass waypoints to determine where a carcass would be placed on a given day. The order of placement among sections was randomized without repetition to avoid bias, but the same section was never used two days in a row. Carcass points were always open (Bitterlich less than 15) with short grass (grass height less than 40 cm), at least 200 m from the nearest boma (i.e. settlement with surrounding cattle fence), and at least 1 km from the next carcass point. Putting carcasses in open areas with short grass increases the ease of observation and the probability of carcass detection by avian scavengers. Forty experimental carcasses were observed during the wet season (February to May 2010) with 10 in each section. Twenty of these were repeated in the same location during the dry season (July to September 2010) with 10 in each of the sections inside the reserve.
During carcass observations, abundance of species and behavior were quantified as follows. For each carcass, the total abundance of each species that occurred at the carcass (defined as being on the ground within 50 m of it) over the entire observation period was recorded. Five minute scan samples were used to determine number and behavior of all individuals of every species on the ground within 50 m of the carcass (Altmann, 1974). Activity was categorized as feeding (actively pecking at carcass) or standing (any other behavior). Order of species’ arrival was recorded based on the order in which at least one individual of each species landed within 50m of the carcass. Behavioral observations ceased one hour after all meat was consumed, one hour after all birds left if meat remained, or at 1 PM if no birds landed, whichever occurred first.

Data analysis

Sociality and search efficiency of each species was assessed. To assess sociality, mean crowding was calculated for each species across all scan samples during which the species was present across all experimental carcasses following Lloyd (1967), where a mean crowding value greater than two demonstrates high levels of sociality. To assess search efficiency, I considered the number of carcasses discovered by a species, taking into account the number of carcasses at which a given species occurred (see Figure 2).

Data on feeding behavior was used to quantify competitive ability. Using a Wilcoxon Signed Rank Test in JMP, I identified cases of displacement (i.e. when one species leaves the carcass due to arrival of another species) by comparing species composition at the carcass the time step before and after a given species left. In R, a binomial GLMM with whether or not a given species was feeding during a given scan sample as the response variable was used to assess
competitive interactions. For this model, the following fixed effects were considered: occurrence of other species feeding, group size of other species (if they were found to be social based on mean crowding), intraspecific group size, mammal presence at the carcass, whether or not a given species had been feeding in the previous time step, and elapsed time since carcass discovery (which was calculated as the time since the first bird of any species landed within 50 m of the carcass). Carcass ID was included as a random effect. For all analyses done as part of this study, all mammalian scavenger species were lumped into one category.

Habitat characteristics for each site were quantified and related to species abundance from transects and at carcasses. Habitat variables in relation to settlement and wildlife were averaged across a given transect or across a given section by season. Changes in wildlife density explain seasonal differences and for the purpose of analysis, data from both seasons studied (wet and dry) are combined.

Data from the roadside counts and the carcasses were analyzed to assess the habitat use of scavenging birds. For carcass analysis, a measure of conspecific abundance in the section was included and was determined as an average of species’ abundance for all transects within a given section taken from the average of abundance from each transect divided by transect length. Species abundance across the experimental carcasses was analyzed using a generalized linear model with a poisson or negative binomial distribution while considering average wildlife density per section, average settlement density per section, and abundance of conspecifics per section. A separate model was run for each species. Results from undiscovered carcasses were excluded from analysis. For use in figures (see Fig. 3), wildlife density was divided into three categories – low (0-25 individuals/km²), medium (26-90 individuals/km²), and high (90-100 individuals/km²) and related to an average abundance of birds per carcass in those areas.
For searching birds, a general linear model with a poisson distribution was conducted for each species in relation to average wildlife density, average settlement density, and time of day. Transects were categorized as morning or afternoon, depending on whether they started before or after 12:00 PM (Munday et al., 1992). Route number was included as a random factor and the logarithm of the length of each transect was used as an offset to account for variation in transect length. In all models including those used for competitive ability analysis and for habitat patterns, I selected for the model with the lowest AIC value using forward method. Analyses were conducted in R 2.7.2 (R Development Core Team 2008) using the MASS (Venables and Ripley, 2002) package to fit the general linear models and lme4 to fit generalized linear models.

**Results**

*Differences in competitive ability and search efficiency among avian scavengers*

Behavioral observations were used to quantify species competitive ability and search efficiency. Body size as well as group size determined competitive ability while foraging at carcasses (Table 2). Likelihood of feeding for most species, including Hooded vulture, Tawny eagle, White-backed vulture, and Ruppell’s vulture was negatively affected by the presence of larger species, including mammalian scavengers and Lappet-faced vulture. Bateleurs’ feeding behavior was also negatively affected by presence of Tawny eagles and Ruppell’s vultures. Bateleurs were displaced (i.e. left the carcass entirely) by larger competitors, particularly Lappet-faced and African white-backed vultures (n = 16, z = 13, p = 0.04; z=31.5, p <0.01, respectively). However, Lappet-faced vulture feeding was negatively affected by Hooded vultures and Bateleurs. White-backed vulture presence had a negative effect on Tawny eagles.
Only two species were considered social based on a mean crowding value greater than two – White-backed vulture (12.8) and Ruppell’s vulture (3.9). The feeding activity of White-backed vultures at the carcass had a negative affect on the feeding of Lappet-faced vultures only when the group size of White-backed vultures was considered. Although Ruppell’s vultures were also found to be social, group size was not important for feeding and did not effect competitive interactions.

Several other variables influenced the likelihood of feeding for several species and reinforce existing competitive interactions. Tawny eagle presence had a positive effect on White-backed vultures, increasing their likelihood of feeding. Lappet-faced vultures group size had a positive effect on the ability of Lappet-faced vultures to feed. Feeding occurrence increased for White-headed vultures and decreased for Ruppell’s and Lappet-faced vultures with the time since initial carcass discovery (by any species). The effect of feeding in previous time step, which was included as a control, made continued feeding more likely for most species (Hooded vulture, White-backed vulture, Ruppell’s vulture, and Lappet-faced vulture).

In general, smaller species discovered a larger proportion of carcasses than larger species. Accounting for the presence of a species at a given carcass, proportion of carcasses detected first by a given species, i.e. search efficiency, varied considerably (Fig. 2). Bateleurs discovered the largest percentage of carcasses and never occurred at a carcass after another species. Ruppell’s vultures never arrived first to a carcass (but occurred at 35% of experimental carcasses).

Effect of patch quality on habitat use patterns among avian scavengers

Avian scavenger abundance at carcasses was related to wildlife density for most species, but unaffected by human settlement density, although wildlife and settlement density were
inversely correlated (n = 92, Spearman’s $\rho = -0.46$, p < 0.001) (Table 3). At experimental carcasses, Bateleur and Ruppell’s vulture abundance increased while Tawny eagle and Hooded vulture abundance decreased with wildlife density (Fig. 3). White-backed vulture abundance at carcasses was only affected by the site abundance of White-backed vultures, which were calculated from transects. Presence of mammals at carcasses did not relate to wildlife or settlement density.

Similar patterns of habitat use were found for searching birds (Table 4). Searching bird abundance was affected by time of day, wildlife density, and settlement density. Bateleurs, White-backed, Ruppell’s, and Lappet-faced vultures abundance were all positively affected by wildlife density while Tawny eagle abundance was negatively correlated with wildlife density. Bateleurs, White-backed, White-headed, and Lappet-faced vulture abundances were also negatively affected by settlement density. Bateleurs, White-backed vultures, and Lappet-faced vultures were more abundant in the morning.

In addition to the seven avian scavengers studied, four other species occurred – African fish eagle (*Haliaeetus vocifer*), Augur buzzard (*Buteo augur*), White-necked ravens (*Corvus albicollis*), and Marabou stork (*Leptoptilos crumeniferus*) at some of the experimental carcasses, but generally infrequently (less than 10% of carcasses for all species except Marabou storks). Five carcasses (8% of total used), all of which occurred outside protected areas, were undiscovered by either mammalian or avian scavengers.

**Discussion**

*The effect of competitive ability on feeding behavior*
Consistent with previous studies, I found that body size generally determined dominance hierarchy among scavenger species in relation to feeding behavior (Mundy et al., 1992, Kruuk, 1967, Petrides, 1959). In particular, large species, such as Lappet-faced vultures and mammalian scavengers, had a negative effect on the feeding behavior of all other species, except White-headed vultures, with which they rarely overlapped at the carcass. However, when two of the smallest species, Hooded vultures and Bateleurs, were feeding the likelihood of feeding for Lappet-faced vultures declined. Measurements of competitive interaction used in this study are fine-scale. Given the huge differences in body size and beak morphology between these two smaller species and Lappet-faced vultures, one could expect that the consumption of meat by Hooded vultures and Bateleurs will have only a minimal effect on Lappet-faced vultures, in terms of total food consumption. During behavioral observations conducted as part of this study, Lappet-faced vulture were seen to hesitate to feed upon arrival at the carcass, which may confounded the effect of Hooded vultures and Bateleurs.

For social species, feeding behavior was also influenced by group size. In particular, I found that for White-backed vultures, intra-specific group size increased the likelihood of feeding. White-backed vultures have long necks, serrated tongues, use a pulling feeding technique, and focus on soft tissues, that enables feeding even when in large numbers (Mundy et al., 1992). In addition, White-backed vultures were able to outcompete Lappet-faced vulture when they occurred in large groups. Observations suggest that the large beak, tearing feeding technique, and short neck of Lappet-faced vultures may be inappropriate for feeding with large Gyps aggregations. It is worth noting that Lappet-faced vultures were seen to feed on all types of meat, including soft tissues, when not in the presence of other species. Rather than being limited
by the type of meat that they can consume, Lappet-faced vultures feeding strategy appears to be ineffective when in large groups of birds.

Although Ruppell’s vultures were also found to be social, group size did not affect their dominance. Due to their large body size, Ruppell’s vultures may confer dominance without large group sizes. White-backed vultures were also more likely to land at carcasses in areas with high conspecific abundance, suggesting an important role of social information in food finding. For both Gyps species, sociality may serve a function in food finding as well as competitive interactions (Jackson et al., 2008, Buckley, 1996). Although not found to be social in this study, Lappet-faced vultures were more likely to be feeding in the presence of conspecifics. Lappet-faced vultures tend to feed in pairs and may benefit from these social interactions, but this was not explicitly tested here.

Feeding behavior was also influenced by facilitative interactions. White-backed vultures were more likely to feed in the presence of Tawny eagles, which are smaller, more solitary raptors. Throughout the study, Tawny eagles were observed to arrive at carcasses and begin feeding more quickly than White-backed vultures. On several occasions, large groups of African white-backed vultures waited next to a carcass and only began feeding after a Tawny eagle had landed and started feeding, suggesting an important facilitative relationship between these two species, which is supported by findings.

**Differences in search efficiency and timing between species**

In general, I found that small avian scavenger species arrived first at a larger proportion of carcasses than large species. Bateleurs showed exceptional search efficiency as the only species that discovered 100% of the carcasses at which they occurred. Reasons for difference in
search efficiency may be related to interspecific variation in visual acuity or flight height, which in turn are mediated by variation in wing-loading (Pennycuick, 1972). Differences in flight height within avian scavengers have been noted before, and Bateleurs are known to fly lower than other avian scavengers, which may increase their ability to independently locate carcasses while reducing their ability to use public information (Mundy et al., 1992, Watson, 2000). This possible correlation between flight height and search efficiency is further supported by the fact that Ruppell’s vultures, which did not discover any carcasses, tend to fly highest and may thus be more reliant on social information (Mundy et al., 1992). On-going studies of visual acuity in raptors may provide additional insights as to how differences in vision between species may relate to search efficiency (Martin et al., 2012).

The one exception to this pattern was the medium-sized White-backed vulture, which discovered a similar proportion of carcasses to the smaller Tawny eagles and Hooded vultures. This higher than expected search efficiency for White-backed vultures can be explained by differences in abundance; across transects conducted as part of this study, White-backed vultures were nearly eight times more abundant than Tawny eagles and thirty-five times more abundant than Hooded vultures. Given their higher abundance, White-backed vultures can be expected to find more carcasses based on chance alone, which may lead them to discover a similar number of carcasses as other smaller species, despite lower search efficiency on a per capita basis.

Search efficiency is also likely to affect the time since discovery, which was defined as the time since the arrival of the first individual of any species at the carcass. Time since discovery had a significant effect on the feeding behavior for White-headed, Lappet-faced, and Ruppell’s vultures. Possibly due to their large beak size and lower dominance, the likelihood of
White-headed vultures feeding increased with time since carcass discovery. As suggested by the work of Kruuk (1967), White-headed vultures’ chance of feeding may increase as the number of scavengers able to feed on more difficult parts of the carcass declines. For Lappet-faced and Ruppell’s vultures, likelihood of feeding decreased with time since discovery. This may indicate that there is a cost to late arrival for these species even though they are dominant, and at least in the case of Lappet-faced vultures, can use their large beak to consume even the tougher parts of the carcass. This is not surprising given that food available at the carcass will decrease after discovery, so that regardless of body or beak size, late arrivers will have fewer opportunities to feed.

The effect of search efficiency on the despotic distribution

Results presented here from counts of searching birds and abundance at experimental carcasses support the hypothesis that species’ dominance status and search efficiency are both correlated with patch quality. Bateleurs, which had the highest search efficiency, and all large or socially dominant species – Ruppell’s, Lappet-faced, and White-backed vultures – showed preferences for patches of high quality whether the quality was due to high wildlife density or low settlement density. In contrast, Hooded vultures and Tawny eagles, which have low competitive ability and search efficiency, were more common in poor quality patches, particularly those of low wildlife density. This study demonstrates the need to consider multiple trade-offs in explaining habitat use within a diverse guild.

Another strategy that may effectively increase search efficiency is to have greater activity in the morning when carcass availability is highest. Wildlife mortality is highest overnight and thus carcasses tend to be most available in the early morning and are then consumed throughout
the day (Houston, 1974a). I found higher abundance of searching birds in the morning for Bateleur, White-backed, and Lappet-faced vultures. This higher activity in the morning may increase their opportunities for carcass discovery or early arrival. Although Lappet-faced vultures have high competitive ability, late arrival did appear to reduce their ability to feed and thus greater morning activity may increase the likelihood of early arrival. Although feeding behavior was also negatively affected by time since discovery for Ruppell’s vultures, this species did not show a preference for morning activity. Because this species nests in cliffs far from the foraging grounds (Pennycuick, 1983), there may be limits to their ability to reach foraging areas in the early morning. Further investigation as to how carcass use by avian scavengers varies with time of day would provide a greater understanding of differences in activity pattern as a plausible alternative strategy that may also confer important advantages within this guild.

Conservation implications

Avian scavengers did not occur at five of the experimental carcasses, all of which occurred in areas of high settlement density, often within a few kilometers of a large settlement area. Avian scavengers were seen flying over all carcasses, but they never landed at these five carcasses, demonstrating, as found in other studies, an important role of human disturbance in scavengers’ foraging ability (Skagen et al., 1991, Speziale et al., 2008).

Over the last thirty years, all scavenging raptors have declined in Masai Mara, but at different rates (Hooded vultures by 62%, Tawny eagles by 28%, White-headed vultures by 44%, Gyps vultures by 52%, Lappet-faced vultures by 50%), except Bateleurs, which have increased by 20%, (Virani et al., 2011). Given that poisoning occurs primarily outside of protected areas (Otieno et al., 2010a, Kolowski and Holekamp, 2006), habitat use patterns may partially explain
these differences in rates of decline. Bateleur’s ability to preferentially use high quality areas, due to high search efficiency, may explain the lack of decline seen in this species. Two species, Tawny eagle and Hooded vulture, showed a preference for areas outside MMNR and may be at greatest risk of poisoning. Hooded vultures are the fastest declining species in this system and Tawny eagles have shown significant declines. In addition Egyptian vultures, which were historically found primarily outside of protected areas, were the first scavenging species to disappear from this ecosystem (Virani et al., 2011). This suggests that use of habitats of low quality, a strategy employed by these species, may put them at greater risk of extinction given the spatial distribution of on-going human-mediated threats such as poisoning.

Acknowledgements

Research was conducted in collaboration with The Peregrine Fund’s Pan African Raptor Conservation Program. Funding for this study was provided by Princeton University, Hawk Mountain Sanctuary, The Peregrine Fund, and The Explorer’s Club. Advice and comments from Keith Bildstein and my advisor, Daniel Rubenstein, and committee members – Andy Dobson, Henry Horn, Simon Levin, Munir Virani, and David Wilcove were incredibly helpful as was the statistical support of Charles Yackulic. Field assistance was provided by Wilson and Jon Masek. I would like to thank Narok County Council, the staff of Masai Mara National Reserve, particularly Mr. Minis and Mr. Sindiyo for their assistance and permission to conduct this research as well as the neighboring group ranches and conservancies and Africa Eco-Camps for their support. I’m thankful to Kenya Wildlife Service and the National Museums of Kenya.
### Figures and Table

Table 1: Avian scavenger species characteristics. V stands for vulture. Adapted from Mundy et al. (1992).

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Average body size (kg)</th>
<th>Sociality</th>
<th>Beak strength</th>
<th>Nesting behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hooded V</td>
<td><em>Necrosyrtes monachus</em></td>
<td>1.9</td>
<td>Solitary or small groups</td>
<td>Low</td>
<td>Tree</td>
</tr>
<tr>
<td>Bateleur</td>
<td><em>Terathopius ecaudatus</em></td>
<td>2.2</td>
<td>Solitary</td>
<td>High</td>
<td>Tree</td>
</tr>
<tr>
<td>Tawny Eagle</td>
<td><em>Aquila rapax</em></td>
<td>2.3</td>
<td>Solitary</td>
<td>High</td>
<td>Tree</td>
</tr>
<tr>
<td>White-headed V</td>
<td><em>Trigonoceps occipitalis</em></td>
<td>4.3</td>
<td>Solitary</td>
<td>High</td>
<td>Tree</td>
</tr>
<tr>
<td>White-backed V</td>
<td><em>Gyps africanus</em></td>
<td>5.6</td>
<td>Social</td>
<td>Middle</td>
<td>Tree</td>
</tr>
<tr>
<td>Lappet-faced V</td>
<td><em>Torgos tracheliotos</em></td>
<td>6.8</td>
<td>Solitary or pairs</td>
<td>High</td>
<td>Tree</td>
</tr>
<tr>
<td>Ruppell’s V</td>
<td><em>Gyps rueppellii</em></td>
<td>7.6</td>
<td>Social</td>
<td>Middle</td>
<td>Cliff</td>
</tr>
</tbody>
</table>
Table 2: Binomial GLMM model for feeding behavior of each species ordered from smallest to largest by body size in relation to feeding of other species and other variables. Parameter estimate (and standard error) given for significant variables only. Negative values are shaded. Values for random factor “carcass” are not shown.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hooded V</th>
<th>Bateleur</th>
<th>Tawny E</th>
<th>White-headed V</th>
<th>White-backed V</th>
<th>Lappet-faced V</th>
<th>Ruppell’s V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-0.39 (0.25)</td>
<td>1.54 (0.45)</td>
<td>3.12 (0.48)</td>
<td>-3.95 (1.25)</td>
<td>-0.97 (0.35)</td>
<td>0.50 (0.44)</td>
<td>2.97 (0.81)</td>
</tr>
<tr>
<td>Competitive Interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammals</td>
<td>-1.11 (0.34)</td>
<td>-4.16 (0.72)</td>
<td>-1.52 (0.31)</td>
<td>-2.78 (0.35)</td>
<td>-1.92 (0.64)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hooded V</td>
<td></td>
<td></td>
<td></td>
<td>-1.01 (0.53)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bateleur</td>
<td></td>
<td></td>
<td>-1.41 (0.61)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tawny E</td>
<td>-1.78 (0.74)</td>
<td></td>
<td>0.86 (0.41)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-backed V</td>
<td>-1.99 (0.59)</td>
<td>-2.61 (0.54)</td>
<td>-0.63 (0.23)</td>
<td>-1.37 (0.51)*</td>
<td>-2.74 (0.48)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lappet-faced V</td>
<td>-1.66 (0.38)</td>
<td>-2.17 (0.54)</td>
<td>-0.63 (0.23)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ruppell's V</td>
<td>-2.39 (0.78)</td>
<td>-1.78 (0.48)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other variables</td>
<td></td>
<td></td>
<td></td>
<td>1.37 (0.53)</td>
<td>-0.01 (0.00)</td>
<td>-1.24 (0.28)</td>
<td></td>
</tr>
<tr>
<td>Time since discovery</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conspecific group size</td>
<td></td>
<td></td>
<td></td>
<td>0.66 (0.34)</td>
<td>0.40 (0.15)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding in previous time step</td>
<td>1.65 (0.31)</td>
<td></td>
<td></td>
<td>1.25 (0.21)</td>
<td>2.27 (0.28)</td>
<td>1.43 (0.36)</td>
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<tr>
<td>Model details</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual deviance</td>
<td>274.2</td>
<td>83.7</td>
<td>148.1</td>
<td>71.6</td>
<td>589.5</td>
<td>386.8</td>
<td>232.8</td>
</tr>
<tr>
<td>Number of carcasses</td>
<td>22</td>
<td>16</td>
<td>36</td>
<td>11</td>
<td>41</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td>Number of scan samples</td>
<td>265</td>
<td>80</td>
<td>197</td>
<td>69</td>
<td>531</td>
<td>522</td>
<td>254</td>
</tr>
</tbody>
</table>

*White-backed vulture feeding behavior was only significant when White-backed vulture group size also included in the model.
Table 3: GLM model for abundance at carcasses by species ordered from smallest to largest by body size in relation to habitat variables and site abundance of conspecifics using a negative binominal distribution with logistic link, excluding undiscovered carcasses. N = 54 carcasses. Parameter estimate (and standard error) given for significant variables only. Negative values are shaded. Settlement density was included in the model but was not significant. Models for White-headed V or Lappet-faced V were not significant.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hooded V</th>
<th>Bateleur&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Tawny E&lt;sup&gt;a&lt;/sup&gt;</th>
<th>White-backed V</th>
<th>Ruppell’s V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.23 (0.28)</td>
<td>0.11 (0.11)</td>
<td>2.54 (0.30)</td>
<td>1.48 (0.47)</td>
<td>-1.27 (0.36)</td>
</tr>
<tr>
<td>Wildlife density</td>
<td>-0.01 (0.01)</td>
<td>0.01 (0.00)</td>
<td>-0.01 (0.01)</td>
<td></td>
<td>0.03 (0.01)</td>
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<td>Conspecific site abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.07 (0.03)</td>
</tr>
<tr>
<td>Residual deviance</td>
<td>55.1</td>
<td>18.7</td>
<td>129.9</td>
<td>68.4</td>
<td>78.7</td>
</tr>
<tr>
<td>df</td>
<td>52</td>
<td>52</td>
<td>52</td>
<td>52</td>
<td>52</td>
</tr>
</tbody>
</table>

<sup>a</sup>Poisson distribution was used.
Table 4: GLMM model for searching birds by species ordered from smallest to largest by body size in relation to habitat variables and time of day using poisson distribution and logistic link with logarithm of transect length as an offset. Parameter estimate (and standard error) given for significant variables only. Negative values are shaded. Values for random factor “route” are not shown. N = 92 transects (across 16 routes).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hooded V</th>
<th>Bateleur</th>
<th>Tawny E</th>
<th>White-headed V</th>
<th>White-backed V</th>
<th>Lappet-faced V</th>
<th>Ruppell’s V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-2.63 (0.29)</td>
<td>-0.65 (0.17)</td>
<td>-0.59 (0.14)</td>
<td>-2.98 (0.40)</td>
<td>1.19 (0.15)</td>
<td>-0.37 (0.18)</td>
<td>-2.71 (0.37)</td>
</tr>
<tr>
<td>Wildlife density</td>
<td>0.01 (0.00)</td>
<td>-0.01 (0.00)</td>
<td></td>
<td>0.01 (0.00)</td>
<td>0.01 (0.00)</td>
<td>0.01 (0.00)</td>
<td></td>
</tr>
<tr>
<td>Settlement density</td>
<td>-0.24 (0.07)</td>
<td>-0.88 (0.47)</td>
<td>-0.16 (0.05)</td>
<td>-0.23 (0.08)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time of day</td>
<td>0.62 (0.13)</td>
<td></td>
<td></td>
<td>0.30 (0.05)</td>
<td>0.37 (0.11)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual deviance</td>
<td>131.8</td>
<td>227.9</td>
<td>182.6</td>
<td>42.8</td>
<td>739.1</td>
<td>220.9</td>
<td>294.2</td>
</tr>
</tbody>
</table>
Figures
Figure 1: Map of Masai Mara ecosystem showing sections, transects, and experimental carcasses.
Figure 2: Number of experimental carcasses where a given species arrived first or was present shown in order of body mass from smallest to largest (n = 60)
Figure 3: Average abundance at experimental carcasses for four species, shown in order of body size for low (0-25 individuals/sq km), medium (26-90 individuals/sq km), and high average wildlife density (90-100 individuals/sq km) (n = 54)
Ethical Standards
Experiments conducted as part of this study comply with Kenyan laws and were covered under research permit NCST/5/002/R/448.

Literature Cited
Hertel F (1994) Diversity in body size and feeding morphology within past and present vulture assemblages Ecology 75 (4):1074-1084


Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability - Phenotype-limited ideal free models. Anim Behav 34:1222-1242. doi:10.1016/s0003-3472(86)80182-8

Pennycuick CJ (1972) Soaring behavior and performance of some East African birds, observed from a motor-glider. Ibis 114 (2):178-218


Petrides GA (1959) Competition for food between five species of East African vultures. Auk 76:104-106


CHAPTER 5

The effect of local enhancement and temporal segregation on foraging behavior and success

AUTHOR: Corinne J. Kendall.
Abstract

Reasons for coexistence of three large and dominant vulture species – Lappet-faced, Ruppell’s, and White-backed vultures – are not well understood. Competition between the species is expected to be particularly high during the dry season, when Ruppell's vultures’ local abundance increases. Because carcass availability is higher in the morning and in the dry season in Masai Mara National Reserve, Kenya, temporal segregation of resource use is a possible mechanism of coexistence. I predict that foraging success of social vultures will be higher in the dry season. It is known that Lappet-faced vultures’ abundance of searching birds is higher in the morning but only during the dry season, and I therefore predict that Lappet-faced vultures preferentially use carcasses in the morning to reduce competition. I assess whether temporal segregation in resource use between social and solitary Lappet-faced vultures occurs across time of day and season in Masai Mara National Reserve, Kenya by studying foraging behavior and success. Contrary to predictions, I found that solitary species appear to forage throughout the day and have higher abundance at fresh carcasses in the afternoon, when the number of foraging social vultures has declined. Social species monopolize resources in the morning and dry season when food availability is high. During the dry season, temporal segregation of resource use does not appear to enable coexistence. Instead coexistence of these three species appears to be dependent on high food availability that allows social species to become satiated early in the day, leaving Lappet-faced vultures to use large beak size and longer foraging period to make use of the carrion resources remaining. Social species have higher foraging success than solitary species. In addition, social vultures had higher foraging success in the dry season, when
conspecific and food availability are high, suggesting the importance of local enhancement among social scavengers.

**Introduction**

The maintenance of high levels of biodiversity is best understood through mechanisms of coexistence. Considerable evidence exists for resource partitioning and spatial and temporal segregation in resource use as important mechanisms of coexistence (Bonsall et al., 2002, MacArthur and Levins, 1967, May and MacArthur, 1972, Kronfeld-Schor and Dayan, 2003, Blazquez et al., 2009, Cortes-Avizanda et al., 2010). For species dependent on divided and ephemeral resources, such as carrion, competitively inferior species can reduce competition through aggregation at food resources and avoidance of competitors (Hartley and Shorrocks, 2002, Rosewell et al., 1990, Shorrocks et al., 1990, Atkinson and Shorrocks, 1981). In addition, alternative strategies, which are mediated by trade-offs in species traits, such as competition-defense or competition-colonization, can be important in diverse guilds (Tilman, 2004, Tilman, 1990, Tilman, 1987, Viola et al., 2010).

Eight avian scavengers coexist in Masai Mara National Reserve (MMNR), Kenya (Attwell, 1963). For most species, coexistence patterns can be explained by resource partitioning, spatial segregation in resource use, and trade-offs in arrival time and competitive ability, with competitively inferior species arriving at food patches first (Kruuk, 1967, Kendall et al., In press, Kendall, In review). However, for three species – Lappet-faced (*Torgos tracheliotos*), Ruppell's (*Gyps ruppellii*), White-backed vultures (*Gyps africanus*) – reasons for coexistence remain unclear.
These three vulture species share most ecological traits – large body size, high individual or group dominance, soaring flight, and dependence on carrion from large ungulates for the bulk of their diet (Mundy et al., 1992, Ruxton and Houston, 2004). While differences in beak structure exist (Kruuk, 1967), these three species tend to aggregate at carrion resources with similar characteristics, which should limit opportunities for resource partitioning (Kendall et al., In press). In addition, these species appear to associate with each other at food patches, limiting potential benefits of aggregation and disassociation which may enable coexistence in other scavengers (Kendall et al., In press, Hartley and Shorrocks, 2002, Rosewell et al., 1990, Shorrocks et al., 1990, Atkinson and Shorrocks, 1981). Opportunities for spatial segregation of resource use among these three species appears to be limited, at least based on local scale study within MMNR (Kendall, In review). Finally, arrival rates at carcasses for these three species are highly variable (Mundy et al., 1992). While Ruppell’s vultures tend to arrive at carrion after Lappet-faced and White-backed vultures, differences in search efficiency are also insufficient to explain the high levels of overlap between these species (Kendall, In review).

Because these species are similar in body size, dominance, search efficiency, and habitat use patterns, a potentially important difference between these species, which may mediate competition, is sociality: White-backed vulture (*Gyps africanus*) and Ruppell’s vulture (*Gyps ruppellii*), are highly social, and Lappet-faced vultures (*Torgos tracheliotos*), are primarily solitary (Mundy et al., 1992). For Old World vultures, which rely extensively on sight, a primary benefit of sociality is local enhancement, which should lead to greater foraging efficiency (Houston, 1974b, Houston, 1974a, Houston, 1979, Beauchamp, 1998). Local enhancement can be defined as the use of conspecifics to provide information about
the position of food (Thorpe, 1963, Krause and Ruxton, 2002, Hoppitt and Laland, 2008). Benefits of local enhancement are likely to be greatest when food resources are ephemeral and clumped (Baird et al., 1991, Benkman, 1988), as is the case for carrion resources on which vultures rely (DeVault et al., 2003). Through local enhancement, individuals are expected to use public information and social cues to increase detection of food sources and thus reduce searching time (Baird et al., 1991, Galef Jr and Giraldeau, 2000). *Gyps* vultures enhance their use of public information by flying at high altitudes, which may in turn limit their ability to find carrion independently (Pennycuick, 1972). As a result, some subordinate solitary species, such as Bateleurs (*Terathopius ecaudatus*), are able to arrive at carcasses sooner than *Gyps* vultures, but this trade-off in arrival time and competitive ability does not appear to occur between *Gyps* and Lappet-faced vultures (Kendall, In review).

These three species show high levels of overlap in MMNR during the dry season, when local abundance of Ruppell's vultures increases (Houston, 1974a). *Gyps* species have higher competitive ability than Lappet-faced vultures when in large groups enabling them to outcompete Lappet-faced vultures while at large food patches (Carrete et al., 2010, Kendall, In review, Clark and Mangel, 1986). Given that in MMNR *Gyps* vulture abundance increases in the dry season but Lappet-faced abundance remains the same, the mechanisms enabling the solitary Lappet-faced vulture to persist in the presence of these dominant social competitors are unclear (Virani et al., 2011, Kendall, In review). Carrion availability varies temporally with greater abundance in the morning (Houston, 1975, Mduma et al., 1999). From counts of vultures along roadside transects, it is known that the abundance of searching Lappet-faced vultures is higher in the morning than in the afternoon, but only in
the dry season (Kendall, In review). Therefore it appears that Lappet-faced vultures may increase searching activity in the morning when food availability is highest, in response to greater competition from Gyps species during the dry season. I thus propose temporal segregation in resource use plays a key role in coexistence among these three vulture species. To test for the existence of temporal segregation in resource use and its effect on competition, I examine the effect of time of day on the foraging behavior and success of these three vulture species throughout the year in MMNR. I hypothesize that Lappet-faced vultures should occur at higher abundance at carcasses in the morning than in the afternoon during the dry season.

With local enhancement, models have demonstrated that carrion detection by social vultures increases with both food and conspecific abundance (Jackson et al., 2008), the impact of local enhancement on foraging success is yet to be measured in the field. I assess how foraging efficiency and success of these three species varies by season. During the dry season, food availability is high due to the seasonal influx of migratory herds, which also suffer high mortality rates due to low forage availability (Mduma et al., 1999). I predict that social Gyps vultures will have higher foraging success during the dry season while solitary Lappet-faced vultures should have lower foraging success in the dry season. This study will provide important insights about use of temporal segregation in vultures to enable coexistence and the effect of local enhancement on foraging success.

**Methods**

**Study site**
The Mara-Serengeti ecosystem is arguably one of the most important areas for scavengers in Africa, supporting high densities of many scavenger species (Houston, 2001, Houston, 1979). MMNR is a savannah habitat in southwestern Kenya. It is approximately 1,530 km² in size and is surrounded by Masai pastoral lands to the north, east, and west and the larger Serengeti National Park of Tanzania to the south. Large herds of Blue wildebeest (*Connochaetes taurinus*), Burchell’s zebra (*Equus burchelli*), and Thomson’s gazelle (*Gazella thomsonii*) move between MMNR and Serengeti National Park, Tanzania (Boone et al., 2006). During the dry season, which runs from July to October, herds enter MMNR (Ogutu et al., 2008). During this period, carcass availability in MMNR is high due to the presence of the migratory herds and high mortality rates which occur in the dry season when forage is scarce (Mduma et al., 1999).

**Study species**

Lappet-faced vultures, Ruppell’s vultures, and White-backed vultures are the three most numerous species within the East African avian scavenger guild and are dominant over other species due to high individual or group dominance (Kruuk, 1967). In addition, White-backed vultures are able to dominate Lappet-faced vultures when in large groups (Kendall, In review). Lappet-faced vultures show a greater preference for smaller carcasses than *Gyps* vultures, but all three feed primarily on the carrion of large mammals (Kendall et al., In press, Mundy et al., 1992). Species differ in sociality, beak structure, and nesting behavior, but are similar in other aspects of their ecology (Table 1).
Table 1: Vulture species characteristics*

<table>
<thead>
<tr>
<th>Vulture species</th>
<th>Scientific name</th>
<th>Sociality</th>
<th>Beak structure</th>
<th>Nesting behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-backed</td>
<td>Gyps africanus</td>
<td>Social</td>
<td>Medium</td>
<td>Tree</td>
</tr>
<tr>
<td>Rüppell's</td>
<td>Gyps rueppellii</td>
<td>Social</td>
<td>Medium</td>
<td>Cliff</td>
</tr>
<tr>
<td>Lappet-faced</td>
<td>Torgos tracheliotos</td>
<td>Solitary or pairs</td>
<td>Large</td>
<td>Tree</td>
</tr>
</tbody>
</table>

*Adapted from Mundy et al. (1992)

**Scavenger abundance at carcasses**

Efforts were made to discover carcasses with scavengers actively feeding by driving around MMNR. Carcass surveys were conducted from 7 AM to 5 PM during both wet and dry seasons during five field seasons from May 2009 to October 2011. Due to logistical constraints, effort varied across years with most observations coming from 2011. Carcasses were found by sight, by talking with tour guides, and by following vultures. Characteristics of the carcass were recorded including size, decomposition level, amount of the carcass remaining, and presence of mammalian competitors, including lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), Black-backed jackal (*Canis mesomelas*), and feral dogs (*Canis lupus*) (Table 2). In addition, the season and time were also recorded. The species and number of individuals at carcasses was recorded upon carcass discovery. Level of decomposition was determined based on smell and texture of skin following similar studies (Houston, personal communication). Carcasses were considered intact when no entry wounds from carnivores or scavengers were seen. Only carcasses in open areas with low grass height were included in this study to ensure accuracy of scavenger counts and carcass characteristics. Observations of the carcass characteristics and counts of scavengers were done by a single observer using 10 x 50 binoculars from a vehicle at least 50 meters away. Due to tourism in
this region, scavengers tend not to respond to vehicles until they approach closer than 50 meters.

Table 2: Carcass characteristics included in this study

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size</td>
<td>Greater than or less than 10 kg</td>
</tr>
<tr>
<td>Decomposition level</td>
<td>Fresh</td>
</tr>
<tr>
<td></td>
<td>One day old</td>
</tr>
<tr>
<td></td>
<td>More than one day old</td>
</tr>
<tr>
<td>Amount of meat remaining</td>
<td>Intact</td>
</tr>
<tr>
<td></td>
<td>76-100% and opened</td>
</tr>
<tr>
<td></td>
<td>51-75%</td>
</tr>
<tr>
<td></td>
<td>26-50%</td>
</tr>
<tr>
<td></td>
<td>&lt;25% bones/skull only</td>
</tr>
<tr>
<td>Year</td>
<td>2009-2011</td>
</tr>
<tr>
<td>Time of Day</td>
<td>7 AM to 5 PM, binned every two hours</td>
</tr>
<tr>
<td>Season</td>
<td>Dry (June to October)</td>
</tr>
<tr>
<td></td>
<td>Wet (November to May)</td>
</tr>
<tr>
<td>Presence of Mammalian</td>
<td>Mammal seen within 50 m of carcass or not</td>
</tr>
<tr>
<td>competitors</td>
<td></td>
</tr>
</tbody>
</table>

**Foraging behavior across time of day**

Experimental carcasses were arranged to appear as intact carcasses and consisted of a head, organs, and 2 kg of leg meat from a goat or sheep. Carcass set-up followed techniques used in similar studies of scavenging raptors (Bamford et al., 2009a, Carrete et al., 2010, Kendall, In review). All experimental carcasses were placed during the dry season, when local abundance of Ruppell’s vultures in MMNR is highest (Kendall et al., In press). In 2011, a total of 20 experimental carcasses were used with 10 in the morning and 10 in the afternoon. The order of placement between morning and afternoon was randomized to avoid bias.
To assess foraging behavior across time of day, behavioral observations were conducted at experimental carcasses. Experimental carcasses were placed in the same location once in the morning at 8 AM and once in the afternoon at 12 PM on separate days at least three days apart. Specific places where carcasses were placed were selected in advance and marked with GPS (Garmin eTrex Legend C, Olathe, Kansas, accuracy < 15 feet). Carcass points were always open (Bitterlich less than 15) with short grass (grass height less than 40 cm), at least 200 m from the nearest boma (i.e. settlement with surrounding cattle fence), and at least 1 km from the next experimental carcass point. Putting carcasses in open areas with short grass increases the ease of observation and the probability of carcass detection by avian scavengers. Observers randomly selected from these points to determine where a carcass would be placed on a given day. Carcasses were placed only when it was possible to be at least 1 km from another known natural carcass with scavengers actively feeding and on days with no rain.

During observations of carcasses, the total abundance of each species that occurred at the carcass (defined as being on the ground within 50 m of it) over the entire observation period was recorded. Similar to natural carcasses, observers watched from a stationary vehicle 50 m from the carcass using binoculars. Observations ended when all birds left or when no meat remained.

Assessment of crop status

Crops are hollow structures of the esophagus, which act as food storage sites and are visible as sacks below the neck of the bird (Houston, 1976). The fullness of the crop can be determined in Old World vultures by visual inspection using binoculars and is an
accurate measure of the quantity of food consumed in a given twenty four to thirty hour period (Houston, 1976, Mundy et al., 1992). Crop status was categorized as either empty (no visible bulge in crop) or full (prominent bulge extending beyond the chest). Vultures observed were categorized as either adult or juvenile based on beak and plumage coloration (Mundy et al., 1992). Observers searched for roosting vultures throughout the day during both wet and dry seasons in 2011 and crop status of roosting vultures was assessed.

**Data analysis**

The effect of carcass characteristics on the abundance of Lappet-faced, White-backed, and Ruppell’s vultures at carcasses was assessed using a Generalized Linear Model with a negative binomial distribution and forward stepwise process. All parameters from Table 2 were included in the model. Models with the lowest AIC value and difference in AIC of at least two from other models were selected. The effect of time of day on abundance of the three study species at experimental carcasses was assessed using a paired t-test.

Crop status was used to measure foraging success in relation to age, season, species, and time of day. A logistic regression examined the effect of age (adult or juvenile), season (dry or wet), and time of day (7:00 to 8:59, 9:00 to 10:59, 11:00 to 12:59, 13:00 to 14:59, and 15:00 to 16:59) on crop status (full or empty). Separate models were run for each species and models with lowest AIC value were selected using a forward method. A two-sample proportion test was used to look at interactions between categories of time of day or between seasons and between species in relation to their effect on proportion of
individuals with a full crop. Analyses were conducted in R 2.7.2 (R Development Core Team 2008) using the MASS (Venables and Ripley, 2002) package.

**Results**

*Foraging behavior by time of day and carcass characteristics*

Across natural carcasses, the abundance of vultures was influenced by temporal factors, the amount of carrion remaining, and the level of carcass decomposition, but not by the presence of mammals or carcass size (Table 3). Both White-backed vulture and Ruppell’s vulture abundance was influenced by the time of day, season, and year. Both *Gyps* species were more abundant in the morning. Ruppell’s vulture abundance also was high from 13:00 to 15:00. Ruppell’s vultures were more abundant in MMNR in the dry season, preferred carcasses with a larger proportion of meat remaining, preferred fresher carrion, and increased from 2009 to 2011. White-backed vultures were more abundant in the wet season and decreased annually from 2009 to 2011. Lappet-faced vulture abundance varied only by the proportion of the carcass remaining with a preference for less remaining, and the level of decomposition with greater abundance at fresh carcasses.

At experimental carcasses, vulture abundance was influenced by time of day. White-backed and Ruppell’s abundance was higher in the morning (*t* = 2.04, df=9, *p* = 0.04; *t*=2.07, df=9, *t* = 0.03) whereas Lappet-faced vulture abundance was higher in the afternoon (*t* = -2.39, df = 9, *p* = 0.02) (Figure 1).
Table 3: GLM model for abundance at carcasses by species in relation to carcass characteristics. Variable estimate (and standard error) given for all variables included in the model. Significant values are shown in bold. N = 220 carcasses

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>WHITE-BACKED V</th>
<th>RUPPELL'S V</th>
<th>LAPPET-FACED V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.75 (0.46)</td>
<td>-2.46 (0.64)</td>
<td>1.15 (0.12)</td>
</tr>
<tr>
<td>Year (2010)</td>
<td>-0.30 (0.44)</td>
<td>1.05 (0.59)</td>
<td></td>
</tr>
<tr>
<td>Year (2011)</td>
<td>-0.87 (0.35)</td>
<td>1.49 (0.45)</td>
<td></td>
</tr>
<tr>
<td>Time (9 to 11)</td>
<td>-0.39 (0.22)</td>
<td>-0.40 (0.24)</td>
<td></td>
</tr>
<tr>
<td>Time (11 to 13)</td>
<td>-0.56 (0.23)</td>
<td>0.08 (0.25)</td>
<td></td>
</tr>
<tr>
<td>Time (13 to 15)</td>
<td>-0.27 (0.24)</td>
<td>0.66 (0.27)</td>
<td></td>
</tr>
<tr>
<td>Time (15 to 17)</td>
<td>-0.97 (0.30)</td>
<td>-0.10 (0.32)</td>
<td></td>
</tr>
<tr>
<td>Season (dry)</td>
<td>-0.49 (0.29)</td>
<td>2.58 (0.40)</td>
<td></td>
</tr>
<tr>
<td>Remaining (&lt;25%)</td>
<td>0.54 (0.23)</td>
<td>-0.43 (0.19)</td>
<td></td>
</tr>
<tr>
<td>Remaining (25-50%)</td>
<td>0.82 (0.27)</td>
<td>-0.68 (0.24)</td>
<td></td>
</tr>
<tr>
<td>Remaining (50-75%)</td>
<td>0.66 (0.32)</td>
<td>-0.64 (0.28)</td>
<td></td>
</tr>
<tr>
<td>Remaining (76-100%)</td>
<td>1.37 (0.40)</td>
<td>-0.92 (0.36)</td>
<td></td>
</tr>
<tr>
<td>Remaining (intact)</td>
<td>1.11 (0.30)</td>
<td>-1.11 (0.30)</td>
<td></td>
</tr>
<tr>
<td>Decomposition (one day old)</td>
<td>0.05 (0.21)</td>
<td>-0.06 (0.17)</td>
<td></td>
</tr>
<tr>
<td>Decomposition (more than one day old)</td>
<td>-1.19 (0.35)</td>
<td>-1.06 (0.33)</td>
<td></td>
</tr>
</tbody>
</table>

Figure 1: Average abundance of vultures at the carcass varied by time of day (N = 20 carcasses)
Foraging success by season and time of day

Foraging success was measured by examining crop fullness in relation to time of day and season. Ruppell’s vultures were only observed roosting in MMNR during the dry season. Ruppell's vultures had the higher foraging success (76% of birds seen had full crops, n = 388) than White-backed vultures (59% of birds seen had full crops, n = 526) ($\chi^2=27.5$, df = 1, $p < 0.001$). White-backed vultures also had higher foraging success than Lappet-faced vultures (29% of birds seen were full, n = 127) ($\chi^2=35.3$, df = 1, $p < 0.01$).

White-backed vulture foraging success was related to time of day and season (Table 4). The proportion of White-backed vultures with full crops was higher in the dry season and increased with time of day (Figure 2). In the dry season all time categories were significantly different from the 7:00 to 9:00 period ($\chi^2=15.7$, df = 1, $p < 0.01$; $\chi^2=61.1$, df = 1, $p < 0.01$; $\chi^2=52.3$, df = 1, $p < 0.01$; $\chi^2=65.0$, df = 1, $p < 0.01$ for 9:00 to 11:00, 11:00 to 13:00, 13:00 to 15:00, and 15:00 to 17:00 respectively). In the wet season, only the 13:00 to 15:00 and 15:00 to 17:00 periods were different from the 7:00 to 9:00 period ($\chi^2=6.71$, df = 1, $p < 0.01$; $\chi^2=16.1$, df = 1, $p < 0.01$, respectively). Thus the proportion of White-backed vultures with full crops reached a plateau around 9:00 in the dry season at an average of 72% and around 13:00 at an average of 68% in the wet season. In addition, higher proportion of White-backed vultures were full in the 9:00 to 11:00 time period and in the 11:00 to 13:00 period in the dry season versus the wet season ($\chi^2=3.71$, df = 1, $p = 0.05$; $\chi^2=4.34$, df = 1, $p = 0.03$ respectively), but difference in proportion full by season was not significant for any other time category. The proportion of Ruppell’s vultures with full crops increased with time of day. The proportion of Ruppell’s vultures with full crops at 7:00 to 9:00 was not different than the proportion full at 9:00 to 11:00, but was different
from all later time categories ($\chi^2=49.3, \text{df} = 1, p < 0.01; \chi^2=23.7, \text{df} = 1, p < 0.01; \chi^2=46.2, \text{df} = 1, p < 0.01$ for 11:00 to 13:00, 13:00 to 15:00, and 15:00 to 17:00 respectively). In Ruppell’s vultures, proportion of individuals with a full crop reached a plateau at an average of 81% around 11:00 during the dry season. The proportion of Lappet-faced vultures with full crops was unaffected by time or season. Age did not have a significant effect on the proportion of full vultures for any of the species considered.

Table 4: Logistic regression for crop status in relation to time of day, season, and age. Variable estimates (and standard errors) given for significant variables only. Models for Lappet-faced vultures were not significant.

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>WHITE-BACKED V (N = 526)</th>
<th>RUPPELL'S V (N = 388)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-2.26 (0.43)</td>
<td>-1.39 (0.65)</td>
</tr>
<tr>
<td>Time (9:00 to 11:00)</td>
<td>0.87 (0.65)</td>
<td>0.29 (1.32)</td>
</tr>
<tr>
<td>Time (11:00 to 13:00)</td>
<td>2.54 (0.54)</td>
<td>3.51 (0.89)</td>
</tr>
<tr>
<td>Time (13:00 to 15:00)</td>
<td>2.60 (0.49)</td>
<td>2.67 (0.82)</td>
</tr>
<tr>
<td>Time (15:00 to 17:00)</td>
<td>2.03 (0.42)</td>
<td>1.91 (0.70)</td>
</tr>
<tr>
<td>Season</td>
<td>0.84 (0.32)</td>
<td></td>
</tr>
</tbody>
</table>

Figure 2: White-backed vultures reach a maximum proportion of individuals with full crop earlier in dry season than wet season

Discussion
Temporal segregation in resource use among vultures does not explain coexistence

Whereas resource partitioning and habitat use patterns may explain coexistence among some scavenger species in MMNR, mechanisms of coexistence for Lappet-faced vultures, Ruppell’s vultures, and African white-backed vultures have not been explained. Temporal segregation in resource use among species was examined as a possible mechanism of coexistence, given that carrion availability is higher in the morning. Findings suggest that temporal segregation in resource use exists. However contrary to predictions, *Gyps* vultures showed greater abundance at carcasses in the morning than in the afternoon. Despite greater abundance of searching Lappet-faced vultures in the morning, Lappet-faced vulture abundance at natural carcasses remained the same throughout the day. These findings suggest that *Gyps* vultures, which are highly social, have greater foraging efficiency in the morning and in the dry season when food availability is highest, most likely due to local enhancement. Lappet-faced vulture abundance remains the same at natural carcasses throughout the day, suggesting that these solitary birds must search continuously to access sufficient resources.

Experimental carcasses were used to examine behavior at new food resources. Lappet-faced vultures increase in abundance at experimental carcasses in the afternoon, while *Gyps* abundance decreases. This suggests that fresh carcasses that only become available in the afternoon could represent competitive refugia for solitary scavengers. Based solely on abundance patterns at carcasses, this would have suggested that Lappet-faced vultures have higher foraging efficiency than *Gyps* vultures in the afternoon, when food availability is lower. But based on patterns of crop fullness throughout the day, this appears to be a less likely explanation. Instead, findings on crop fullness demonstrate that
Gyps vultures become satiated early in the day, which is a more likely explanation for their lower abundance at carcasses in the afternoon. In particular, proportion of individuals with full crops of *Gyps* vultures generally reached a plateau early in the day, suggesting that these individuals become full by about 11:00. It would appear that coexistence of these three species is made possible by the extremely high food availability during the dry season. As a result, Lappet-faced vultures are still able to feed, primarily in the afternoon, even though they have lower competitive ability and lower foraging efficiency throughout the day. Findings demonstrate that Lappet-faced vultures are only able to effectively access carrion resources when *Gyps* vulture abundance decreases. Foraging success of Lappet-faced vultures is unaffected by time of day. This demonstrates that even though *Gyps* vulture abundance at carcasses decreases in the afternoon, the reduced competition doesn't compensate for the foraging opportunities that were forgone by the Lappet-faced vultures in the morning when food is most abundant.

Lower foraging efficiency and lower competitive ability of Lappet-faced vultures at natural carcasses may be partially offset by beak morphology. Lappet-faced vultures have a larger beak than *Gyps* vultures and tend to use a tearing feeding method, focusing on tougher pieces of carrion such as ligaments and muscles (Mundy et al., 1992, Kruuk, 1967). Results suggest that Lappet-faced vultures preferentially use carcasses with less carrion remaining, which may be less suitable for *Gyps* vultures; this ability of Lappet-faced vultures to use carcasses with less meat remaining may be essential given that *Gyps* vultures have higher foraging efficiency and are able to outcompete Lappet-faced vultures at the carcass when in large groups (Kendall, In review).
Ruppell’s vulture abundance at carcasses was generally higher in the morning but also increased in the mid-afternoon from 13:00 to 15:00. This second peak in abundance may be related to Ruppell’s vultures’ cliff-nesting behavior, which may affect the local abundance of this species in MMNR during the dry season. There are no cliff-nesting sites for Ruppell’s vultures in MMNR and the closest cliff nests are about 100 km away (Pennycuick, 1983). Although many Ruppell’s vultures appear to stay in MMNR for several days at a time even when breeding, some Ruppell’s vultures using MMNR to forage will travel back and forth between the foraging grounds and cliff nests every few days (Kendall, unpublished data). From counts of vultures along roadside transects, White-backed and Lappet-faced vultures, unlike Ruppell’s vultures, are known to have higher abundance of searching birds in the morning than in the afternoon (Kendall, In review). For Lappet-faced vultures, this effect is particularly significant in the dry season. Findings related to foraging behavior thus mirror what had been seen in relation to searching birds, with some Ruppell’s vultures arriving later at foraging grounds. While energetic costs of long distance travel for large soaring birds are minimal, Ruppell’s vultures may suffer a temporal cost of cliff-nesting, leading to slower arrival times in areas of high food availability for some individuals (Pennycuick, 1972, Pennycuick, 1979). This suggests that differences in nesting behavior between cliff and tree nesting birds may impact foraging behavior in addition to breeding success (Ruxton and Houston, 2002).

While findings demonstrate that high food availability in the dry season may enable coexistence of Lappet-faced vultures and Gyps vultures, the coexistence of White-backed vultures and Ruppell’s vultures merits further study. Results indicate that the White-backed vultures and Ruppell’s vultures vary in abundance both seasonally and annually.
Ruppell’s vultures were more abundant in Masai Mara National Reserve in the dry season and in the wetter years (2011 and 2010 had higher rainfall than 2009), while White-backed vultures had highest abundance in wet season and in 2009. These findings provide evidence that larger scale movement patterns may differ between the species in part due to differences in nesting behavior, enabling coexistence. On-going studies of movement ecology of *Gyps* vultures should provide insights as to the level of this difference (Kendall et al., in review). Finally, lower abundance of White-backed vultures at carcasses in recent years mirror long-term patterns at carcasses of lower relative abundance of White-backed vultures in relation to Ruppell’s vultures and may relate to current declines in vulture species due primarily to poisoning (Virani et al., 2011, Kendall et al., In press).

**Social species have higher foraging success, especially when food availability is high**

Results support findings from mathematical models showing that for social species, foraging success is greater when food availability and conspecific density is higher (Jackson et al., 2008). White-backed vultures had higher foraging success in the dry season and were able to reach crop fullness earlier in the dry season. Whether their foraging success is heightened simply by greater food availability or by local enhancement possibly via benefits from the increased abundance of the Ruppell’s vulture is unclear. In addition, social species had considerably higher foraging success than solitary species throughout the year, suggesting an important role of local enhancement for social scavengers. The foraging success of the solitary Lappet-faced vultures did not vary with season. Seasonally the limiting factor affecting foraging success for Lappet-faced vultures may shift and
compensate for each other, going higher competition from Gyps vultures in the dry season to lower food availability in the wet season.

**Acknowledgements**

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**Literature Cited**


CHAPTER 6

Vultures don’t follow migratory herds:
Evidence that scavenger habitat use is
mediated by prey mortality rates rather than
prey density

AUTHORS: Corinne J. Kendall, Munir Z. Virani, Grant
Hopcraft, and Dan Rubenstein.
Abstract

Little is known about the factors that mediate scavenger habitat use, in particular the importance of prey density versus prey mortality rate. In Mara-Serengeti ecosystem, migratory ungulate herds represent the greatest prey density available throughout the year, but suffer higher mortality rates in the dry season. Vultures are the only obligate scavenging vertebrates. Through soaring flight vultures are able to maintain a large foraging radius, and previous work on African vultures has suggested that these scavengers will track migratory ungulate herds throughout the year. We predict that vultures will follow migratory herds, with particularly close associations during the dry season, that vultures will use areas with high ungulate mortality, and that due to high wing-loading and tree-nesting, White-backed vultures will have higher association with migratory herds than the other two species. We used data from an emerging technology, GSM-GPS transmitters, to assess the relationship between three species of vulture – White-backed, Ruppell’s, and Lappet-faced – and migratory wildebeest in the Mara-Serengeti ecosystem. Vultures only showed preferential use of the migratory herd during the dry season, when the migratory herd experiences their highest mortality rates. In addition, Ruppell’s and Lappet-faced vultures selected for drier areas, based on Normalized Difference Vegetation Index, during the wet season. White-backed vultures showed the greatest preference to be near wildebeest herd and preferred wetter areas during the wet season. Differences in habitat use between the species may thus mediate coexistence. In general, results suggest that prey mortality rate rather than prey abundance may be more significant for determining scavengers’ habitat use. The reliance on vultures of non-migratory herds during the non-dry seasons has important conservation implications for vultures given on-going declines in non-migratory wildlife.
**Keywords:** movement, seasonality, coexistence, Mara-Serengeti, GSM-GPS telemetry

**Introduction**

The study of animal ecology has focused on herbivores, predators and parasites and thus has overlooked an important trophic level – scavengers (DeVault et al., 2003). Unlike herbivores, whose ecology is often governed by the interplay of predation risk and forage availability (Hopcraft et al., 2011) or predators, whose habitat use may be determined more by prey accessibility than abundance (Hopcraft et al., 2005), scavengers face a unique set of challenges, and their ecology is likely to be mediated by other ecological factors. In many ways scavengers provide an extreme example of a meta-community, one that assembles, competes, and disassembles over short periods of time as a carcass is broken down (Leibold et al., 2004). Scavengers must overcome the spatial and temporal challenges of feeding on carrion, a resource which is ephemeral, generally patchily distributed, and may be utilized by a large number of potential competitors, including predators (DeVault et al., 2003). Foraging success for scavengers depends on the ability to search across wide areas and rapidly detect carrion before it decomposes or is consumed by competitors (Shivik, 2006). Scavengers generally experience limited predation and thus food availability, predictability, and accessibility have generally been found to be the key factors determining scavenger habitat use and distribution (Wilmers et al., 2003b, Wilmers et al., 2003a, Blazquez et al., 2009). For scavengers, unlike predators, food availability is a factor of not just prey density but also prey mortality rate, which will vary both spatially and temporally. Differences in the relative importance of and interactions between prey density and mortality are likely to determine scavenger habitat use, but have not been tested.
In Europe and Asia, livestock has become the primary source of carrion for many scavenging species (Donazar et al., 2009, Margalida et al., 2011, Green et al., 2006). In addition, vulture restaurants, where livestock carcasses are routinely dumped, have been set up in Europe, Asia, and Southern Africa to supplement vulture populations and reduce exposure to poisons or veterinary medicines, such as diclofenac, but are known to alter scavenger behavior (Cortes-Avizanda et al., 2010, Donazar et al., 2010, Gilbert et al., 2007). East Africa has high wildlife densities and few human-mediated sources of carrion, making it an ideal study system in which to investigate natural scavenger behaviors. The Mara-Serengeti ecosystem is unique because it maintains one of the few ungulate migrations remaining in the world (Wilcove and Wikelski, 2008, Dobson et al., 2010).

The only obligate vertebrate scavengers are the vultures (Ruxton and Houston, 2004). Vultures feed primarily on carrion sources from non-predator mortalities, such as deaths from starvation and disease (Houston, 1979). Through their soaring flight, vultures can maintain extremely large foraging radii, even during breeding periods, and thus effectively utilize migratory ungulate herds throughout the year (Pennycuick, 1972, Ruxton and Houston, 2004). In the Mara-Serengeti ecosystem, migratory herds of Western white-bearded wildebeest (Connochaetes taurinus) represent the highest density of prey. East Africa has a distinct and steep rainfall gradient with considerable asynchrony in rainfall patterns across the region (Hills, 1979). Migratory ungulates utilize this rainfall gradient to maintain super-abundance by maximizing intake of seasonally available grasses and minimizing exposure to predation, primarily by following rainfall gradients (Fryxell et al., 1988, Boone et al., 2006, Norton-Griffiths et al., 1975). As a result, most adult wildebeest mortality occurs in the dry season with generally high survivorship through the rest of the year (Mduma et al., 1999). However, neonatal
mortality accounts for the highest numeric loss in migratory wildebeest and is not related to dry season forage availability (Mduma et al., 1999). Twenty-five percent of the 250,000 wildebeest calves die within their first year and thus represent a substantial food resource for scavengers.

Previous studies on vultures with marked individuals and radio telemetry suggest that these scavengers follow migratory herds, but results have been limited by small sample sizes, limited re-sightings, and short duration of telemetry devices used (Houston, 1974b, Pennycuick, 1983). Studies of aerial scavengers in Mara-Serengeti find that the distribution of aerial scavengers is higher in areas near the migration and have thus presumed that these scavengers follow migratory herds (Pennycuick, 1972). Houston (1974a, 1974b) also suggested that vultures may be better able to compete with mammalian scavengers by searching over larger areas with migratory ungulate herds where food density and prey to predator ratios will be particularly high. In addition, Houston (1974b) suggested that genus of *Gyps* vultures may have evolved as scavengers of migratory ungulate populations. Lappet-faced vultures preferentially feed on small carrion sources, including calves of large mammals and are believed to rely heavily on migratory herds, particularly in the wet season when calving occurs (Mundy et al., 1992).

In this study we use data collected from GSM-GPS transmitters attached to Lappet-faced, White-backed and Ruppell's vultures in the Mara-Serengeti ecosystem to examine how prey density and prey mortality rate mediate vulture movements. Based on the theory of ideal free distribution, we expect scavengers to select foraging areas where they are the most likely to find carrion (Fryxell and Lundberg, 1997). Following previous work on vultures, we predict that vultures will follow migratory herds. Overlap between vulture movement and migratory ungulate herds is expected to be greatest during the dry season, because migratory wildebeest suffer greatest rates of mortality during the dry season when forage availability is low (Mduma et al.,
We also consider the relationship between vultures and ungulate mortality rates and expect vultures to seek areas with high ungulate mortality, caused by low forage availability. Currently the mechanisms enabling coexistence of Lappet-faced, White-backed vultures and Ruppell’s vultures are not well understood, given similarities in use of carrion resources (Kendall et al., In press). Coexistence of the two Gyps vultures is particularly difficult to explain given the similarity in their feeding strategies (Kruuk, 1967, Kendall et al., In press, Kendall, In review) and their sociality, which enables local enhancement and higher competitive ability when in large groups (Jackson et al., 2008, Kendall, In prep). An understanding of the differences in movement patterns between the species may thus be key for determining the factors that enable coexistence between these species. Because White-backed, Ruppell’s, and Lappet-faced vultures differ in their flight abilities (Mundy et al., 1992), we expect to see differences in habitat use among the species. Lappet-faced vultures (Torgos tracheliotos) have lower wing-loading ratio, which reduces their ability to disperse long distances (Pennycuick, 1972). Conversely, Gyps vultures, such as White-backed (Gyps africanus) and Ruppell’s vultures (Gyps rueppellii) have high wing-loading and are expected to search larger areas than Lappet-faced vultures. While White-backed and Lappet-faced vultures frequently nest in trees in Mara-Serengeti area, Ruppell’s vultures are cliff-nesting, and cliffs are generally far from migratory herds (Pennycuick, 1983). Thus we predict that White-backed vultures will show the greatest association with migratory wildebeest movements followed by Ruppell’s vultures and then Lappet-faced vultures, which may have to specialize on more localized food supplies, due to lower wing-loading.

African vultures are declining rapidly and declines in Masai Mara National Reserve have been substantial (Virani et al., 2011, Thiollay, 2007b). Currently in East Africa, poisoning of
carrion resources, typically done by pastoralists to kill predators, is believed to be the primary threat, but declines in food availability have led to rapid losses in vultures elsewhere (Kendall and Virani, 2012, Donazar et al., 2009). Given that non-migratory ungulate populations are also declining in Kenya (Western et al., 2009, Ogutu et al., 2011), understanding how vultures use these resident wildlife populations has important conservation implications. A greater understanding of the interaction between scavengers and prey density, particularly migratory herds, will significantly expand existing knowledge about the factors that influence scavenger habitat use, help explain coexistence of these similar vulture species, and aid in their protection.

**Methods**

**Study area**

The Mara-Serengeti ecosystem is home to the largest ungulate migration in the world, with 1.3 million Western white-bearded wildebeest, 180,000 Bruchell’s zebra (*Equus burchelli*), and 250,000 Thomson’s and Grant’s gazelle (*Eudorcas thomsonii* and *Nanger granti*) moving between Serengeti National Park, Tanzania, and Masai Mara National Reserve, Kenya, each year. As a result the Mara-Serengeti ecosystem is arguably one of the most important areas for scavengers in Africa, supporting high densities of vultures of many species (Houston, 2001). Rainfall is generally seasonal, with the long rains falling from early February to the end of April, and short rains from November to December (Ogutu et al., 2008). Across the region there is a steep rainfall gradient which increases from southeast to northwest (approximately 400mm to 1200 mm of rain/year) (Norton-Griffiths et al., 1975).

**Study species**
Although six species of vultures are found in the greater Mara-Serengeti ecosystem, we focused on the three largest species for this study, due to the limitations imposed by the weight of the GSM-GPS transmitters (Houston, 1975). Ruppell’s vultures and White-backed vultures (collectively termed *Gyps*) are known for their gregariousness and rapid consumption of soft tissues (Houston, 1974a, Houston, 1974b). They have high wing-loading making them efficient soaring fliers (Pennycuick, 1972, Ruxton and Houston, 2004). Lappet-faced vultures have lower wing loading than other *Gyps* vultures and tend not to follow other vultures, making them efficient at searching a smaller area (Pennycuick, 1972). They are known to focus on the tougher pieces of the carcass, including tendons, skin, and joints using their large powerful beak (Kruuk, 1967). In addition, they have only a limited capacity for predation on small or immature animals (Mundy et al., 1992), and tend to prefer smaller carcasses. Lappet-faced vultures and White-backed vultures nest in trees, with particularly high densities of the latter nesting along riverbanks in the Mara-Serengeti ecosystem (Virani et al., 2010). Ruppell’s vultures nest on cliff ledges some of which are more than 100 km from the Mara-Serengeti ecosystem, including those at Lake Kwenia and Hell’s Gate National Park, Kenya, and the Gol Mountains in Tanzania (Pennycuick, 1983).

**Unit deployment**

Trapping was conducted in the Masai Mara National Reserve (01°05’ S, 34°50’ E) and all trapping procedures were approved by the IACUC committee at Princeton University under protocol number 1751. Vultures were trapped using nooses, set up as grids or in a line, along carcasses (Watson and Watson, 1985). Noose grids were made entirely of 90-kg-strength monofilament fishing line. Noose on noose lines were made of coated wire cord or
monofilament, and the noose line was made of parachute cord. Nooses were 10-15 cm in
diameter. Noose grids were generally staked into the ground using tent stakes, whereas noose on
noose lines were tied to carcasses and staked into the ground using 5-cm nails for added stability.
Grass or carrion was used to help hold the nooses upright to increase the chance of a capture.
Noose lines and grids consisted of 10 to 20 nooses. Once a bird was captured, processing took
approximately 30 minutes; birds’ eyes were covered to reduce stress and the handler restrained
both feet and head. The majority of vultures used in this study were adults, but due to trapping
constraints, particularly for Lappet-faced vultures, juvenile and subadult birds were also
included. Age was determined based on coloration following Mundy et al. (1992).

Forty-one battery-powered GSM-GPS transmitters (16 from Africa Wildlife Tracking,
Pretoria, South Africa and 25 from Savannah Tracking Ltd., Nairobi, Kenya) were attached as
backpacks using 11-mm Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, U.S.A.).
Fourteen transmitters were deployed in 2009 from May to August, 21 in 2010 from April to
October, and 3 in March 2011. These deployments include three re-deployments that occurred
after units were recovered (Kendall and Virani, In press). Units weighed between 100 and 160 g,
approximately 2% to 3% of the body mass of a given vulture. Units from African Wildlife
Tracking (primarily deployed in 2009) were programmed to record locations four times per day
(3, 11, 13, 15 hours) and were expected to last 12 months; units from Savannah Tracking Ltd
recorded six points a day (every two hours from 7 AM to 5 PM) and lasted an average of 8
months. Backpacks used to attach transmitters were designed to fall off within a few years, as
recapture of tagged individuals is generally infeasible. Individually numbered plastic wing tags
were attached to the patagium of one wing using cattle ear tags following Wallace et al. (1980).
Where possible both wing tags and transmitters were attached to aid with the visual identification of individuals in the field.

**Spatial analysis**

Analyses were focused on mid-day points (11, 13, and 15 hours) when vultures are most likely to be foraging. Nest sites were established for each individual based on consistent use of an area within a 50m radius across several months with at least 50 locations in the area. When possible for tree nests, nest sites were confirmed in the field by locating the tagged bird on the actual nest. Days where birds were on the nest during a mid-day point were then removed from analysis. To ensure independence, a single point was used for each day, which was calculated as the centroid of three mid-day points using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California, USA). Data for which these three points were not available in a given day, due to missed points, were excluded.

To assess the relationship with prey density, we relate vulture movement to migratory ungulate movement based on 75% kernel polygons representing the distribution of migratory wildebeest from movement data collected over a five-year study for four separate seasons (Wet – January to April, Wet to dry – May to June, Dry – July to October, Dry to wet – November to December) (Hopcraft et al., In press). Proximity between the centroid of the vulture day range and the wildebeest polygons were calculated such that overlapping points were given a value of zero and the nearest distance between boundary of wildebeest polygons and centroid was determined. In addition a random set of points was also generated for each individual bird within the minimum convex polygon of its overall range (calculated using Hawth’s tools in ArcGIS 9.3).
and proximity between these points and the wildebeest polygons was also measured in the same way as the actual points (Beyer, 2004).

To assess the relationship with prey mortality rate, we relate vulture movement to a Normalized Difference Vegetation Index (NDVI). NDVI values were extracted for centroids of the day range of vulture points and a random set of points from within the minimum convex polygon of each individual’s range in ArcGIS 9.3. Information on vegetation indices from MOD13Q1 were obtained from http://lpdaac.usgs.gov/get_data maintained by the NASA Land Processes Distributed Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota in January 2012. These data provide 16-day composites of vegetation indices at 250-meter spatial resolution. NDVI is a reliable measure of greenness or wetness and is linked to forage availability for ungulates (Boone et al., 2006, Ogutu et al., 2008). However, high NDVI values can be indicative of either high tree cover or high grass cover. Data points were also related to tree cover using data from Guan et al. (In press). Given that high tree cover will not be related to forage availability for ungulates, all points with greater than 60% tree cover were excluded from analysis.

Statistical analysis

To determine habitat selectivity in relation to wildebeest, values were averaged across month to reduce issues of pseudo-replication. A t-test for each species and each season was run comparing the true proximity of vultures to wildebeest herds and the proximity of randomly generated values to wildebeest herds. To determine habitat selectivity in relation to NDVI, a t-test for each species and each season was run comparing NDVI values for vulture day range centroids and randomly generated points. Both analyses of habitat preference follow Johnson’s
(1980) third order of selection, where habitat availability is determined based on home range size.

If a difference was detected, a linear mixed effects model was conducted to further assess patterns of vulture habitat use. Two models were run – one for wildebeest and one for NDVI. For both models, the dependent variable was calculated as the real values minus the randomly generated values of either proximity to wildebeest or NDVI. Models included season (dry, dry to wet, wet, or wet to dry), species (Ruppell’s, White-backed, or Lappet-faced vulture), and breeding status of the individual (used nest or did not use nest) as fixed factors with unit id as a random factor to account for differences between individuals using lme4 package (Pinheiro and Bates, 2000). AIC values were used to select the best model in a forward stepwise method. All statistical analyses were preformed in R 2.7.2 (R Development Core Team 2008). Means and standard error are given.

Results

Data included in the analysis came from 39 individual vultures with an average of 149 days of data per individual (Table 1). Only 21 of 39 birds studied appeared to use a nest and 962 days were excluded due to birds being on the nest for at least one of the mid-day points. On average, the centroids of daytime vulture locations overlapped with wildebeest migratory herds 30.9% (± 0.01%) of the time. The proportion of days in which vultures overlapped with wildebeest was highest during the dry season (60.0% ± 0.01%).
Table 1: Sample size by species

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>INDIVIDUALS</th>
<th># OF JUVENILES</th>
<th>DAYS</th>
<th>DAYS PER INDIVIDUAL (AVERAGE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruppell's vulture</td>
<td>15</td>
<td>1</td>
<td>1800</td>
<td>120</td>
</tr>
<tr>
<td>White-backed vulture</td>
<td>12</td>
<td>4</td>
<td>2276</td>
<td>190</td>
</tr>
<tr>
<td>Lappet-faced vulture</td>
<td>12</td>
<td>6</td>
<td>1747</td>
<td>146</td>
</tr>
</tbody>
</table>

All three species of vulture showed a preference to be closer to wildebeest herds than random only in the dry season based on the comparison of real and randomly generated points ($t = -6.67$, df = 37, $p < 0.001$; $t = -3.90$, df = 73, $p < 0.001$; $t = -5.55$, df = 33, $p < 0.001$ for White-backed, Ruppell’s, and Lappet-faced vultures respectively) (Figure 1).

Figure 1: Selectivity of vultures to migratory wildebeest herds (based on the proximity between random points and wildebeest minus the proximity between real vulture points and wildebeest) by species and season

In addition, all three species of vultures studied used areas where migratory ungulates never occur and *Gyps* vultures in particular frequented a number of areas beyond the Mara-Serengeti.
ecosystem including both Tsavo National Parks in Kenya and parts of Northern Kenya (Figure 2). Interestingly one Ruppell’s vulture spent three months in the Boma-Jonglei area in Sudan-Ethiopia, where a separate migratory ungulate population is known to occur.
Figure 2: The overlap between vultures and migratory wildebeest herds varies by season. Vultures remain near the wildebeest herds for most of the dry season (C), but range widely and show little overlap during the rest of the year (A, B, and D).
All three species preferred greener areas than random in the dry season (t = 8.12, df = 1161, p < 0.001; t = 5.36, df = 932, p < 0.001; t = 8.68, df = 1198, p < 0.001 for White-backed, Ruppell’s, and Lappet-faced vultures respectively). White-backed vultures selected greener areas in the wet and dry to wet seasons (t = 4.06, df = 1602, p < 0.001; t = 3.36, df = 979, p < 0.001) (Figure 3). Ruppell’s vultures and Lappet-faced vultures selected browner areas in the wet season (t = -3.22, df = 1219, p = 0.001; t = -5.67, df = 1030, p < 0.001 respectively).

Figure 3: Selectivity of vultures in relation to NDVI (based on NDVI values of real vulture points minus NDVI values of random points) by species and season

Selectivity of vultures to be near migratory wildebeest herds and in relation to NDVI was significantly affected by season, species, and breeding status (Table 2). White-backed vultures showed the greatest selectivity for wildebeest, followed by Ruppell’s, and Lappet-faced vultures. White-backed vultures also showed less selection for brown or dry areas than Lappet-faced and
Ruppell’s vultures. Breeding vultures tended to be farther from the herds and in browner or drier areas than non-breeding adults or juveniles.

Table 2: GLMM model for habitat selectivity in relation to proximity to wildebeest and NDVI. Variable estimate (and standard error) given for all variables included in the model.

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>WILDEBEEST (AIC = 74462)</th>
<th>NDVI (AIC = 101156)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-16.5 (21.3)</td>
<td>210.7 (149.45)</td>
</tr>
<tr>
<td>Season (Wet to dry)</td>
<td>-17.2 (7.0)</td>
<td>195.6 (82.8)</td>
</tr>
<tr>
<td>Season (Dry)</td>
<td>-78.4 (4.9)</td>
<td>661.6 (58.9)</td>
</tr>
<tr>
<td>Season (Dry to wet)</td>
<td>-13.4 (5.2)</td>
<td>219.6 (62.3)</td>
</tr>
<tr>
<td>Species (Ruppell’s)</td>
<td>10.8 (24.4)</td>
<td>-476.7 (170.9)</td>
</tr>
<tr>
<td>Species (Lappet-faced)</td>
<td>41.4 (25.8)</td>
<td>-325.5 (177.9)</td>
</tr>
<tr>
<td>Breeding Status (breeding)</td>
<td>7.4 (21.1)</td>
<td>-333.0 (147.3)</td>
</tr>
<tr>
<td>Number of individuals</td>
<td>39</td>
<td>38</td>
</tr>
<tr>
<td>Number of days</td>
<td>5823</td>
<td>5708</td>
</tr>
</tbody>
</table>

**Discussion**

*Vulture habitat use is driven by prey mortality rates rather than density*

Carcass availability is mediated by both prey density and prey mortality rates, but the mechanisms governing scavenger habitat use have been unknown. Findings demonstrate that in vultures, an obligate scavenger, habitat use is driven by ungulate mortality rates rather than prey density. Evidence for this comes from three key points. First, vultures showed limited selection to be near migratory herds and the overlap between vultures and wildebeest migratory herds was limited (less than 30%), contrary to previous predictions (Pennycuick, 1972, Houston, 1974b). Estimates of overlap are conservative given that only one vulture foraging point was used per day and wildebeest herd location was taken from estimates across multiple years. Due to soaring flight, vultures are physiologically capable of following wildebeest herds at very low energetic costs (Ruxton and Houston, 2004, Pennycuick, 1979) and findings from movement studies verify that day range of vultures can often be greater than 100 km, making it possible for even cliff-nesting species to access herds throughout the year (Kendall, unpublished). Migratory wildebeest
herds consistently represent the greatest prey abundance in this landscape, yet vultures use them only seasonally. Second, as predicted, vultures showed greater use of migratory herds during the dry season, when mortality rates are high (Mduma et al., 1999). Abundance of migratory herds is stable throughout the year, but there are dramatic shifts in mortality rate depending on season. The fact that the dry season was the only period when vultures showed selectivity to be near migratory herds strongly suggests vulture habitat use, and selection to be near the herds, is more affected by prey mortality rate than prey abundance. Finally, two vulture species – Lappet-faced and Ruppell’s vultures – preferentially use dry or brown areas during the wet season, based on NDVI. Rainfall and forage availability are known to have major impacts on ungulate survival (Ogutu et al., 2008). Drier areas should lead to higher mortality rates in ungulates, but are unlikely to affect ungulate density. The selection of dry areas during the wet season and lack of selection of migratory herds is thus consistent with prey mortality rates being more important than prey density in driving scavenger habitat use.

**Differences in habitat use between the species may enable coexistence**

Differences in habitat use between these three species could potentially enable coexistence. As predicted, Lappet-faced vultures showed less selection for migratory wildebeest than *Gyps* vultures, likely due to differences in wing-loading and carrion preferences (Pennycuick, 1972, Houston, 1974b). Ruppell’s vultures showed slightly lower use of migratory herds than White-backed vultures, which may be due to differences in nesting behavior. Because Ruppell’s vultures nest in cliffs which may be hundreds of kilometers from the wildebeest migration, use of other resources of similar or lesser quality but in closer proximity may be preferred. However, it is worth noting that Ruppell’s vultures still frequently used wildebeest
herds during the nesting period, which typically coincides with the dry season (Houston, 1989, Virani et al., In press-b).

White-backed vultures selected for greener areas, based on NDVI, during the wet season, unlike Lappet-faced and Ruppell’s vultures. This suggests that different factors may drive movement in White-backed vultures than in the other two species, but reasons for this difference are unclear. White-backed vultures may use slightly different foraging strategies than the other two species, perhaps with closer dependence on ungulate density, as evidenced by their higher selectivity to be near migratory herds. This difference in large-scale habitat use may be critical for the coexistence of the two *Gyps* species, particularly during periods of low food availability, such as the wet season.

*Conservation implications*

Vultures are likely dependent on the persistence of both migratory herds, during the dry season, and resident ungulates, during the wet season. Although there is some variability, vultures generally fledge chicks during the dry season (Virani et al., 2010, Virani et al., 2012). Given that fledgling success is highly dependent on food availability, declines in migratory herds could have dramatic impacts on vultures (Houston, 1976, Mundy et al., 1992). On-going threats to migratory herds, and changes in their dry season range, could thus have important consequences on the survival of avian scavengers (Ogutu et al., 2011, Dobson et al., 2010). In addition, food availability may be an important limiting factor during the wet season, when ungulate mortality rates are low (Mduma et al., 1999). While the effect of important human-mediated habitat factors, such as protected areas, human settlement density, and powerlines, on vulture movement was not considered here, on-going research suggests that vultures
preferentially use protected areas throughout the year (Kendall, unpublished data). Combined
with findings that current livestock management practices in Kenya limit the availability of
livestock carrion to scavengers, this suggests that vultures are using primarily resident wildlife
populations for carrion during the non-dry season (Reson & Kendall, unpublished data). Given
that resident wildlife populations are declining dramatically throughout Kenya (Western et al.,
2009), particularly in Masai Mara National Reserve (Ogutu et al., 2011, Ogutu et al., 2009), food
availability could become a major issue for vulture survival in the near future as has occurred in
Europe (Donazar et al., 2009).

The concentration of vultures on migratory herds during the dry season may offer a
significant opportunity for monitoring practices. Because all vultures used in this study
frequented the wildebeest herds throughout the dry season, roadside counts done in this area
during this period may give the most accurate and cost-effective account of the population status
of Gyps vultures in eastern Africa. Given rapid declines in these species and difficulties in
assessing population status of wide-ranging vertebrates, monitoring efforts for Kenya’s Gyps
vultures in the Mara during the dry season should be continued (Virani et al., 2011).

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Literature Cited


CHAPTER 7

Conservation Implications

AUTHOR: Corinne J. Kendall.
**Vulture declines and causes**

Findings from this research as well as other on-going studies have led to the up-listing of three vulture species – Hooded, Ruppell’s, and White-backed vulture – to Endangered by the IUCN (pending). Comparisons of roadside surveys from 1976 and 1988 with recent surveys from 2003-2005 have demonstrated drastic declines in all avian scavenger species except the Bateleur in and around Masai Mara National Reserve, Kenya. Egyptian vultures appear to be functionally extinct and few were seen throughout the course of the study. Over the last thirty years, declines have varied by species with greatest losses occurring for the Hooded vulture (62%) followed by the *Gyps* vultures (52%), Lappet-faced vulture (50%), White-headed vulture (44%), and Tawny eagle (28%). *Gyps* vultures were not differentiated during historical surveys and thus declines of Ruppell’s and White-backed vultures can not be delineated based on the transect data. However, vulture abundance at carcasses in Masai Mara National Reserve demonstrate that the relative abundance of Ruppell’s vultures has increased in relation to White-backed vultures. In addition, during intensive carcass surveying, which occurred from 2009 to 2011, White-backed vulture abundance declined while Ruppell’s vulture abundance increased.

Declines documented from the transects were particularly drastic during the dry season, when vulture density tends to be high due to large-scale movements, suggesting that declines in vulture populations are not limited to Masai Mara National Reserve itself. Findings from GSM-GPS transmitters confirm that vultures have large range sizes, which go beyond Masai Mara National Reserve, which is only 2,500 km². Home range size of White-backed, Lappet-faced, and Ruppell’s vultures are estimated as 68,000, 22,000, and 168,000 km² respectively (Kendall, unpublished data, based on minimum convex polygons). Given such large movement patterns, declines observed are likely to document declines in vulture populations throughout Kenya.
For both wide and small ranging species, declines were documented both inside and outside the reserve, suggesting that causes of the decline go beyond the significant land use change that has occurred outside the park. Poisoning of vultures, primarily at carcasses laced with carbofuran that are used to kill mammalian predators, has been reported and is likely the major cause of mortality for vultures. Evidence from GSM-GPS telemetry studies has confirmed that poisoning is a serious problem. During the first year of the movement study, 25% of tagged Lappet-faced and White-backed vultures were killed with all deaths suggesting poisoning, based on presence of multiple dead birds at mortality site, reports, or circumstances (Kendall and Virani, 2012). As in other studies in East Africa, the majority of poisoning incidents appear to occur outside protected areas.

Other threats to vultures

While the primary cause of declines in vultures in East Africa is currently poisoning, other threats to vultures exist. In particular, this study has demonstrated that vultures only rely on migratory wildebeest herds during the dry season and are using other sources of carrion throughout the rest of the year. Given the precipitous declines in wildlife, particularly in Masai Mara National Reserve, that are occurring across East Africa, (Western et al., 2009, Ogutu et al., 2011, Ogutu et al., 2009), it is likely that wildlife declines will have a significant impact on vultures at some point in the near future. These impacts are expected to have the greatest effect on dominant, social scavenger species, such as White-backed and Ruppell’s vultures, whose foraging success is dependent on high conspecific abundance and high food availability. Human disturbance was also shown to have a significant effect on avian scavenger behavior. Disturbance may limit the ability of scavengers to feed successfully and likely exacerbates on-going declines.
Differences between species mediate declines

Studies on the habitat use of avian scavengers indicate that subordinate species with low search efficiency, such as Tawny eagles and Hooded vultures, preferentially use areas outside the reserve. Large dominant species, such as Lappet-faced vultures, Ruppell’s vultures, and White-backed vultures, as well as species with high search efficiency, such as Bateleurs, use areas of high wildlife density and low settlement density. Given that most poisoning events occur in settlement areas, these findings suggest that Hooded vultures and Tawny eagles are at greater risk of poisoning. Hooded vultures have experienced the most rapid declines of all the scavenger species, but Tawny eagles have shown the lowest declines. Part of the discrepancy in rates of decline may be explained by differences in range sizes. Declines of Tawny eagles have been more localized with rapid declines occurring outside protected areas, but with numbers remaining stable in the reserve. This is consistent with Tawny eagles having considerably smaller ranges than Hooded vultures, which should limit the proportion of the population exposed to poisoning and thus explain why Tawny eagles have not declined as rapidly despite their habitat use patterns. Egyptian vultures have a similar life history to Hooded vultures and similar habitat use patterns; the extirpation of Egyptian vultures may thus be explained in part by their habitat use and higher risk of exposure to poisoning events.

Larger scale studies of habitat use using GSM-GPS telemetry suggest that wide-ranging species, such as Lappet-faced, Ruppell’s, and White-backed vultures, spend a significant amount of time outside protected areas across the course of a year and these species may also be at risk of frequently encountering poisoning events due to their large range size. In general, the large home range sizes of *Gyps* and Lappet-faced vultures, and likely of other vulture species as well,
mean that conservation efforts limited to the protected area networks will be insufficient. Ecosystem level conservation efforts that involve local communities and deal with systemic conservation problems will be critical to the long-term survival of these wide-ranging species.

**Interspecific interactions and the potential for intraguild cascades**

Behavioral studies have demonstrated that scavengers exert both competitive and facilitative effects on one another when foraging. Most competitive interactions are marked by a dominance hierarchy, which is determined by body size. In addition, White-backed vultures are able to exert greater dominance through large group size. Foraging success was measured for three species – Lappet-faced, White-backed, and Ruppell’s vulture – through assessment of crop status. For these three species, competitive interactions are significant and coexistence in the dry season appears to be contingent upon high food availability. In terms of facilitative interactions, Tawny eagles appear to have a positive effect on the feeding of White-backed vultures. In addition, mammalian scavengers appear to use vultures to find carcasses not killed by mammals.

While the effect of interspecific interactions on population dynamics for scavengers is still unclear, this work suggests that scavenger species are highly dependent on each other and thus that declines in one species may lead to declines in others. Loss of vultures will likely impact foraging success of mammalian scavengers as well.

**Recommendations**

Vultures are long-lived birds with low fecundity. If poisoning in East Africa continues at its current rates, vultures are likely to go extinct in the near future. Better management of human-wildlife conflict is urgently needed to reduce the incentive to poison as are bans on particularly
lethal and misused pesticides. Educational efforts to teach people about the serious negative impacts that poisoning has on the environment are also needed. In addition, land use changes which are leading to wildlife declines, including overstocking of cattle and agricultural expansion, need to be addressed if the integrity of Masai Mara National Reserve and the species within it are to be maintained.

Moving forward, a critical step in vulture conservation is monitoring. Without proper monitoring, the severity of the problem and the success of conservation efforts cannot be measured. Findings from this study suggest that wide-ranging species, particularly White-backed and Ruppell’s vultures, can be best monitored by conducting roadside counts in Masai Mara National Reserve during the dry season when the vulture populations concentrate in this area. Continued counts during this period should give a good snapshot of the health of vulture populations that concentrate in Mara-Serengeti during the dry season, but annually range through most of Kenya and Northern Tanzania.

**Literature Cited**