



The early bird gets the carcass: Temporal segregation and its effects on foraging success in avian scavengers

Author: Kendall, Corinne J.

Source: The Auk, 131(1) : 12-19

Published By: American Ornithological Society

URL: <https://doi.org/10.1642/AUK-13-201.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



RESEARCH ARTICLE

The early bird gets the carcass: Temporal segregation and its effects on foraging success in avian scavengers

Corinne J. Kendall

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA
Ornithology Section, Department of Zoology, National Museums of Kenya, Nairobi, Kenya
Current address: Columbia University, New York, New York, USA
cjk2113@columbia.edu

Received October 14, 2013; Accepted October 21, 2013; Published January 2, 2014

ABSTRACT

Temporal segregation is known to be an important mechanism of coexistence in many foraging guilds but has not been examined in avian scavengers. Given that carrion availability is higher in the morning than in the afternoon and that differences in wing-loading and nesting behavior may limit morning activity in some species, there is potential for temporal segregation in resource use to play an important role in the coexistence of avian scavengers. I predicted that Lappet-faced Vultures (*Torgos tracheliotos*), which have lower wing-loading and lower competitive abilities, would have higher abundance at carrion resources in the morning than White-backed Vultures (*Gyps africanus*) and Rüppell's Vultures (*G. rueppellii*). In addition, I predicted that differences in activity patterns among vulture species would affect foraging success. Using experimental carcasses, I examined the effect of time of day on foraging behavior. I quantified foraging success in roosting birds, measured as the proportion of individuals with a full crop. Contrary to predictions, during the dry season White-backed and Rüppell's Vultures were more abundant at carcasses in the morning and Lappet-faced Vultures were more abundant in the afternoon. In the afternoon a large proportion of the *Gyps* individuals appeared to be satiated and densities were lower at carcasses, perhaps creating a temporal competitive refugium in the afternoon during which Lappet-faced Vultures could feed. However, Lappet-faced Vultures have lower foraging success than White-backed and Rüppell's Vultures. These results demonstrate that temporal segregation occurs, but may not reduce competition, in this scavenging guild.

Keywords: activity patterns, coexistence, competition, foraging success, vulture

El ave que madruga consigue el cadáver: Segregación temporal y sus efectos sobre el éxito de forrajeo en aves carroñeras

RESUMEN

La segregación temporal es reconocida por su importancia como mecanismo de coexistencia en muchos gremios de forrajeo, pero no ha sido examinado en aves carroñeras. Ya que la disponibilidad de carroña es mayor en la mañana que en la tarde, y diferencias en carga alar y comportamiento de nidificación pueden limitar la actividad matinal de algunas especies, existe la posibilidad de que la segregación temporal en el uso de recursos juegue un rol importante en la coexistencia de aves carroñeras. Predigo que *Torgos tracheliotos*, el cual tiene una carga alar menor y habilidades competitivas inferiores, sería más abundante que miembros del género *Gyps* en recursos de carroña durante la mañana. Además, predigo que las diferencias en patrones de actividad entre especies de buitres afectará el éxito de forrajeo. Utilizando cadáveres experimentales, examiné el efecto de hora del día sobre el comportamiento de forrajeo. Cuantifiqué el éxito de forrajeo de aves en dormitorios midiendo la proporción de individuos con el buche lleno. Contrario a mis predicciones, durante la época seca, *Gyps africanus* y *Gyps rueppellii* fueron más abundantes en cadáveres en la mañana y *Torgos tracheliotos* fue más abundante en la tarde. En la tarde, una proporción importante de *Gyps* parecía estar saciada y se observaron a bajas densidades en los cadáveres, lo cual podría crear un refugio competitivo temporal durante la tarde, durante el cual los *Torgos tracheliotos* pueden alimentarse. Sin embargo, los *Torgos tracheliotos* tienen un éxito de forrajeo menor al de los *Gyps*. Estos resultados demuestran que la segregación temporal ocurre, pero tal vez no reduce la competencia en este gremio de carroñeros.

Palabras clave: buitre, coexistencia, patrones de actividad, éxito de forrajeo, competencia

INTRODUCTION

Mechanisms of coexistence are critical for maintaining biodiversity. Considerable evidence supports the impor-

tance of resource partitioning and spatial and temporal segregation in resource use as mechanisms of coexistence (MacArthur and Levins 1967, May and MacArthur 1972, Scheuring et al. 2000, Bonsall et al. 2002, Kronfeld-Schor

and Dayan 2003, Blázquez et al. 2009, Cortés-Avizanda et al. 2010). Among species that depend on widely dispersed and ephemeral resources such as carrion, competitively inferior species can reduce competition through aggregation at food resources and avoidance of competitors (Atkinson and Shorrocks 1981, Rosewell et al. 1990, Shorrocks et al. 1990, Hartley and Shorrocks 2002). In addition, alternative strategies, which are mediated by tradeoffs in species' traits (e.g., body size and sociality), can be important in maintaining diverse guilds (Tilman 1987, 1990, 2004; Viola et al. 2010).

For most avian scavengers in the Masai Mara National Reserve (MMNR), Kenya, coexistence patterns can be explained by spatial segregation in resource use, resource partitioning, and tradeoffs in arrival time and competitive ability, with competitively inferior species arriving at food patches first (Kruuk 1967, Kendall et al. 2012, Kendall 2013). However, for some species, such as Rüppell's Vulture (*Gyps rueppellii*), White-backed Vulture (*G. africanus*) (Figure 1; hereafter, "Gyps" denotes these two species), and Lappet-faced Vulture (*Torgos tracheliotos*), the mechanisms of coexistence remain unclear. These three vulture species share most ecological traits, such as large body size, soaring flight, and dependence on carrion from large ungulates for the bulk of their diet (Mundy et al. 1992, Ruxton and Houston 2004). In addition, these three species show high levels of spatial overlap in MMNR, particularly during the dry season (Houston 1974a). Habitat-use studies have demonstrated that spatial segregation of resource use does not occur among these three species (Kendall 2013).

The three study species differ in feeding preference and beak morphology: Lappet-faced Vultures have a larger beak than Rüppell's and White-backed Vultures and tend to use a tearing feeding method, focusing on tougher pieces of carrion such as ligaments and muscles (Kruuk 1967, Mundy et al. 1992). However, these three species tend to aggregate at carrion resources with similar characteristics, which should limit opportunities for this kind of resource partitioning (Kendall et al. 2012). In addition, these species appear to associate with each other at food patches, limiting potential benefits of aggregation and disassociation that may enable coexistence in other scavengers (Atkinson and Shorrocks 1981, Rosewell et al. 1990, Shorrocks et al. 1990, Hartley and Shorrocks 2002, Kendall et al. 2012). Despite these differences in feeding preferences, there remains a cost to late arrival, in that Rüppell's and Lappet-faced Vultures are less likely to feed as time since carcass discovery by other scavengers increases (Kendall 2013). White-backed Vultures have higher search efficiency and are more likely to discover carcasses than either Rüppell's or Lappet-faced Vultures (Kendall 2013).



FIGURE 1. Rüppell's (left) and White-backed Vulture (right) with empty crops. Photo credit: Corinne Kendall

In addition, White-backed Vultures are dominant over Lappet-faced Vultures once they reach a certain group size (Kendall 2013). Thus, although Lappet-faced Vultures' larger body size confers dominance when they are one-on-one with *Gyps* (Mundy et al. 1992), individuals or pairs of Lappet-faced Vultures are generally outcompeted by large groups of *Gyps* at large carrion resources (Clark and Mangel 1986, Carrete et al. 2010, Kendall 2013). Despite this, Lappet-faced Vulture abundance remains stable throughout the year in MMNR, even when *Gyps* abundance increases in the dry season (Virani et al. 2011, Kendall 2013).

Carrion availability varies temporally with higher abundance in the morning because most ungulate mortality occurs overnight (Houston 1975, Mduma et al. 1999). Temporal segregation in resource use may thus play an important role in the coexistence of scavengers. In particular, a tradeoff could exist in which species with both lower search efficiency and lower competitive ability, such as Lappet-faced Vultures, forage earlier in the morning to reduce competition with dominant birds such as *Gyps*.

Physiological differences in wing-loading and differences in nesting behavior may further explain differences in temporal segregation of resource use. The two *Gyps* species' high wing-loading (90 N m^{-2} for Rüppell's Vulture and 77 N m^{-2} for White-backed Vultures) makes them dependent on thermals, which are weaker in the early morning, for lift and flight (Pennycuik 1972, Mundy et al. 1992, Ruxton and Houston 2004). Lappet-faced Vultures have lower wing-loading (63 N m^{-2}) than the *Gyps* species, which allows them to start flying earlier in the morning, before thermals are present (Pennycuik 1972, Mundy et al. 1992). Given this anatomical difference, one would predict that Lappet-faced Vultures would be more active in

early morning, when the flight ability of *Gyps* is limited. In addition, White-backed and Lappet-faced Vultures nest locally in trees (Virani et al. 2010), whereas Rüppell's Vultures nest on cliff ledges, some of which are >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 (Pennycuik 1983). As a result, Rüppell's Vultures may arrive later on foraging grounds during the breeding season, which tends to overlap with the dry season (Houston 1976, Virani et al. 2012). On the basis of nesting behavior, one would predict that the abundance of Rüppell's Vulture would be higher at carcasses in the afternoon.

Counts of vultures along roadside transects in MMNR demonstrate that the abundance of foraging Lappet-faced Vultures is higher in the morning than in the afternoon, but only in the dry season (Kendall 2013). White-backed Vulture abundance is also higher in the morning than afternoon throughout the year, but Rüppell's Vulture abundance is unaffected by time of day. Findings from transect data suggest that differences in activity patterns exist, but the effect of these differences on temporal segregation of carrion use is unclear (Kendall 2013). I predicted that if food is a limiting resource and temporal segregation in carrion use acts as a mechanism of coexistence among these three species, then Lappet-faced Vultures would feed primarily in the morning, when food availability was highest. This pattern would be particularly prominent in the dry season, when competition from *Gyps* is highest because of their increased local abundance.

I also predicted that if temporal segregation in resource use is important for coexistence, then the foraging success of these three species would vary in relation to time of day and season. Foraging success can be measured as the proportion of individuals with full crops (Houston and Cooper 1975). Satiation is defined as the time at which the proportion of the population with a full crop reaches a plateau. In addition, foraging success can be used to demonstrate that food availability is a limiting resource. If not all individuals are able to feed and become satiated, food may be limited. I hypothesized that if Lappet-faced Vultures fed earlier in the day, they would reach satiation before *Gyps*.

However, social *Gyps* may still have a higher foraging success (i.e. a higher proportion of individuals with a full crop at satiation) than solitary Lappet-faced Vultures, particularly during the dry season. In scavengers, a primary benefit of sociality is local enhancement, which can lead to greater foraging success (Houston 1974b, 1974a, 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). With local enhancement, mathematical models have predicted that carrion detection

by social vultures should increase with both conspecific and food abundance (Jackson et al. 2008). In MMNR, both conspecific and food abundance are higher in the dry season as the numbers of *Gyps* increase and as higher mortality in migratory herds, due to low forage availability, increases the availability of carrion (Mduma et al. 1999). As a result, I predicted that social *Gyps* would reach a higher satiation plateau in the dry season than in the wet season.

To test for the existence of temporal segregation in resource use and its effects on foraging success and satiation in avian scavengers, I examined the effect of time of day on (1) abundance at experimentally placed carrion sources during the dry season and (2) proportion of individuals of a given species with full crops in MMNR. This is the first field study on the effects of time of day and season on foraging success and satiation in avian scavengers, and the results provide important insights about temporal segregation as a mechanism of coexistence.

METHODS

Study Site

The Mara–Serengeti ecosystem is one of the most important areas for scavengers in Africa, supporting high densities of many scavenger species (Houston 1979, 2001). MMNR is a savannah habitat in southwestern Kenya. It is ~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*) migrate from Serengeti National Park to MMNR in the dry season (July–October; Boone et al. 2006). Food availability and local abundance of vultures are significantly greater during this period (Mduma et al. 1999, Kendall et al. 2012).

Foraging Behavior across Time of Day

Experimental carcasses were arranged to mimic intact carcasses and consisted of a head, organs, and 2 kg of leg meat from a goat or sheep. Carcass setup followed techniques used in similar studies of scavenging raptors (Bamford et al. 2009, Carrete et al. 2010, Kendall 2013). 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). Smaller carcasses therefore make results more applicable to understanding the foraging behavior of all three species, particularly Lappet-faced Vultures, which may show a preference for smaller carcasses (Mundy et al. 1992). All experimental carcasses were placed during the dry season. In 2011, a total of 20

experimental carcasses were used, 10 in the morning (at 0800 hours) and 10 in the afternoon (at 1200 hours). The order of placement between morning and afternoon was randomized. Experimental carcasses were placed in the same location once in the morning and once in the afternoon on separate days ≥ 3 days apart.

Specific areas where carcasses were placed were selected in advance and marked with GPS (eTrex Legend C; Garmin, Olathe, KS, USA; accuracy < 5 m). Carcass points were always in open areas with short grass (grass height < 40 cm), ≥ 200 m from the nearest *boma* (i.e. settlement with surrounding cattle fence), and ≥ 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 (Kendall 2013). Observers randomly selected among these points to determine where a carcass would be placed on a given day. Carcasses were placed only when it was possible to be ≥ 1 km from another known natural carcass with scavengers actively feeding and only on days with no rain.

To assess foraging behavior across time of day, behavioral observations were conducted at experimental carcasses. During observations of carcasses, the total number of each species that occurred at the carcass (i.e. on the ground < 50 m from it) over the entire observation period was recorded. Observers watched, using binoculars, from a stationary vehicle 50 m from the carcass. Observations ended when all birds left or when no meat remained.

Assessment of Crop Status

Crops are hollow structures of the esophagus that act as food storage sites and are visible as sacs 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 24- to 30-hr 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 are assumed to begin the day with an empty crop, given that food within a full crop will be completely digested within 30 hr (Houston and Cooper 1975). The proportion of individuals with a full crop can be used as a measure of foraging success (Houston 1976). The proportion of individuals with a full crop is expected to plateau once most individuals of a given species have fed, and this point was defined as “population satiation.”

Vultures were categorized as either adult or juvenile on the basis of beak and plumage coloration (Mundy et al. 1992). Observers searched for roosting vultures throughout the day during both the wet and the dry season in 2011 and assessed their crop status. Searches were conducted opportunistically while driving around MMNR on 90 days,

45 during the wet season and 45 in the dry season, ~ 8 hr day^{-1} .

Data Analysis

The effect of time of day on abundances 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 (0700–0859, 0900–1059, 1100–1259, 1300–1459, and 1500–1659 hours) on crop status (full or empty). Separate models were run for each species, and models with the lowest Akaike’s Information Criterion values 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 version 2.7.2 (R Development Core Team, Vienna, Austria) using the MASS package (Venables and Ripley 2002).

RESULTS

Effect of Time of Day on Foraging Behavior

Vulture abundance at carcasses was influenced by time of day. White-backed and Rüppell’s Vulture abundances were higher in the morning ($t = 2.04$, $df = 9$, $P = 0.04$ and $t = 2.07$, $df = 9$, $P = 0.03$, respectively), whereas Lappet-faced Vulture abundance was higher in the afternoon ($t = -2.39$, $df = 9$, $P = 0.02$) (Figure 2).

Effects of Species, Season, and Time of Day on Foraging Success

Foraging success was measured by examining crop fullness in relation to time of day and season. Rüppell’s Vultures were observed roosting in MMNR only during the dry season; thus, data on crop fullness exhibited in Rüppell’s Vultures are limited to the dry season. Rüppell’s Vultures

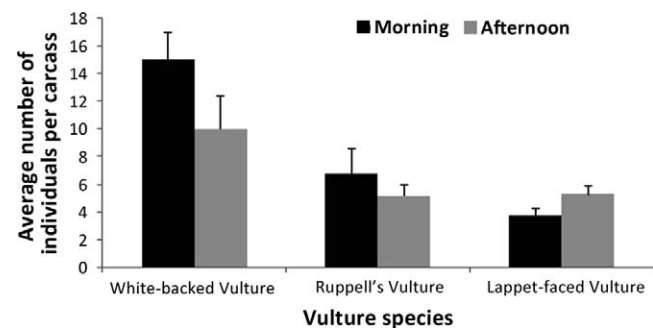


FIGURE 2. Average abundance of White-backed, Rüppell’s, and Lappet-faced Vultures at the carcass varied by time of day ($n = 20$ carcasses).

had 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 with full crops, $n = 127$; $\chi^2 = 35.3$, $df = 1$, $P < 0.01$). Age did not have a significant effect on the proportion of individuals that exhibited full crops in any of the species considered (57% of both adult and juvenile birds had full crops, $n = 1,041$; $\chi^2 = 0$, $df = 1$, $P = 1$).

The proportion of Lappet-faced Vultures with full crops was unaffected by time of day or season and never reached a plateau (Figure 3). White-backed Vulture foraging success was related to time of day and season (Table 1). The proportion of White-backed Vultures with full crops was higher in the dry season and increased with time of day (Figure 4). In the dry season, all time categories differed significantly from the period 0700–0900 hours, which was used as a reference point when the majority of birds would not yet have fed ($\chi^2 = 15.7$, $df = 1$, $P < 0.01$; $\chi^2 = 61.1$, $df = 1$, $P < 0.01$; $\chi^2 = 52.3$, $df = 1$, $P < 0.01$; and $\chi^2 = 65.0$, $df = 1$, $P < 0.01$ for 0900–1100, 1100–1300, 1300–1500, and 1500–1700 hours, respectively). In the wet season, only the periods 1300–1500 and 1500–1700 hours were different from 0700–0900 hours ($\chi^2 = 6.71$, $df = 1$, $P < 0.01$ and $\chi^2 = 16.1$, $df = 1$, $P < 0.01$, respectively). The proportion of White-backed Vultures with full crops reached a plateau (i.e. population satiation) around 0900 hours in the dry season (72% of all birds had full crops) and around 1300 hours in the wet season (68% of all birds had full crops).

The proportion of Rüppell's Vultures with full crops increased with time of day: The result for 0700–0900 hours did not differ from that for 0900–1100 hours but differed from the results for all later time categories (1100–

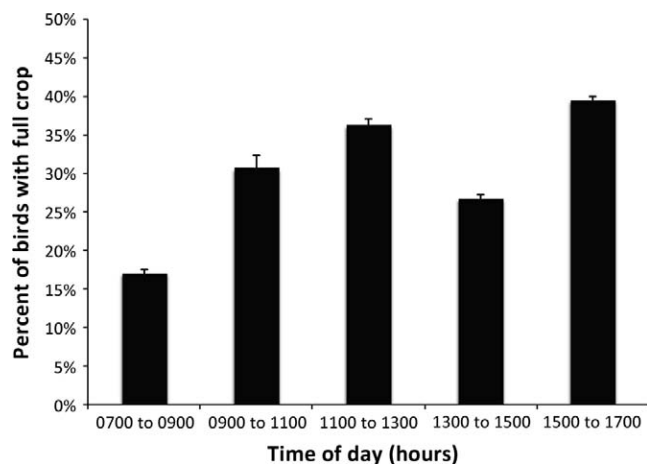


FIGURE 3. Percentage of Lappet-faced Vultures with full crop does not plateau in the afternoon. Data shown are for both seasons combined (error bars = SE).

TABLE 1. Logistic regression for crop status in relation to time of day, season, and age in White-backed Vultures and Rüppell's Vultures. Variable estimates (with SE in parentheses) are given for significant variables only. Models for Lappet-faced Vultures were not significant.

| Variables | White-backed ($n = 526$) | Rüppell's ($n = 388$) |
|------------------------|-------------------------------|----------------------------|
| Constant | -2.26 (0.43) | -1.39 (0.65) |
| Time (0900–1100 hours) | 0.87 (0.65) | 0.29 (1.32) |
| Time (1100–1300 hours) | 2.54 (0.54) | 3.51 (0.89) |
| Time (1300–1500 hours) | 2.60 (0.49) | 2.67 (0.82) |
| Time (1500–1700 hours) | 2.03 (0.42) | 1.91 (0.70) |
| Season | 0.84 (0.32) | |

1300 hours: $\chi^2 = 49.3$, $df = 1$, $P < 0.01$; 1300–1500 hours: $\chi^2 = 23.7$, $df = 1$, $P < 0.01$; 1500–1700 hours: $\chi^2 = 46.2$, $df = 1$, $P < 0.01$) (Figure 5). In Rüppell's Vultures, the proportion of individuals with a full crop reached a plateau at ~1100 hours in the dry season (81% of all birds had full crops).

DISCUSSION

I examined temporal segregation in resource use as a possible mechanism of coexistence for Lappet-faced, Rüppell's, and White-backed Vultures. The results suggest that (1) food is a limited resource, given the inability of many individuals to feed and, therefore, to get a full crop; and (2) temporal segregation in resource use exists but does not reduce competition.

Contrary to predictions, *Gyps* were more abundant at carcasses in the morning than in the afternoon during the dry season. This suggests that because of local enhancement, the social *Gyps* are better than solitary Lappet-faced Vultures at finding carcasses in the morning and in the dry season when food availability is highest. The *Gyps*

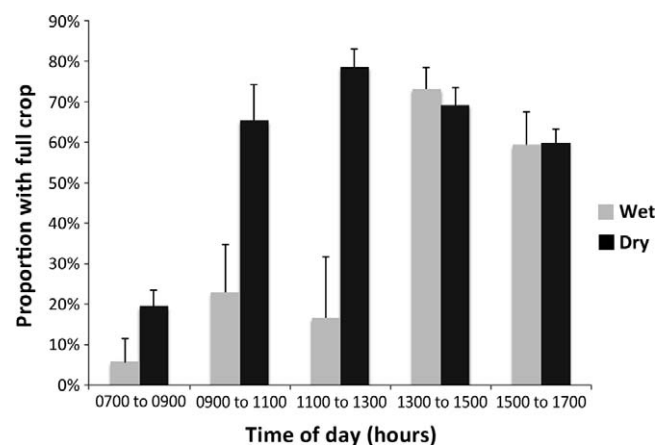


FIGURE 4. White-backed Vultures reach a maximum percentage of individuals with full crop earlier in the dry season than in the wet season (error bars = SE).

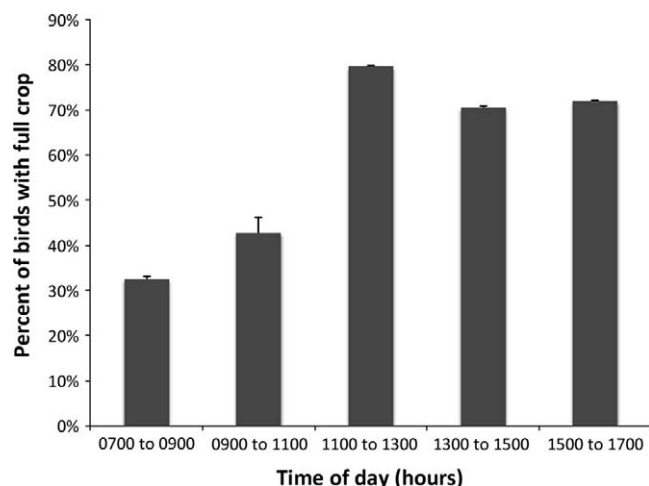


FIGURE 5. Rüppell's Vultures reach a maximum percentage of individuals with full crops by 1100 hours. Data shown are for dry season only (error bars = SE).

populations became satiated in the morning by 1100 hours, which may explain their low abundance at carcasses in the afternoon. Thus, high wing-loading of *Gyps* does not appear to limit early-morning foraging activity.

Despite higher abundance of foraging Lappet-faced Vultures in the morning along transects (Kendall 2013), their abundance was greater at experimental carcasses in the afternoon. The dominance of *Gyps* over Lappet-faced Vultures is contingent on group size of *Gyps*, which is greater at carcasses in the morning (Kendall 2013). Thus, Lappet-faced Vultures' foraging patterns suggest that fresh carcasses that only become available in the afternoon (as was the case with experimental carcasses used in the present study) could represent a temporal competitive refugium for these solitary scavengers, which have lower search efficiency and lower competitive ability when *Gyps* are in large groups.

Contrary to predictions, Lappet-faced Vultures did not reach population satiation before *Gyps*. Social *Gyps* had considerably higher foraging success than solitary Lappet-faced Vultures throughout the year, which suggests possible dominance of social foraging strategies within this guild. The inability of Lappet-faced Vultures to reach similar levels of satiation as *Gyps* demonstrates that even though *Gyps* abundance at carcasses is lower in the afternoon, the reduced competition may not compensate for the foraging opportunities forgone by Lappet-faced Vultures in the morning, when food is most abundant. The lower foraging success of Lappet-faced Vultures provides further evidence in support of Kendall's (2013) conclusion that lower search efficiency may be costly, particularly for species with low dominance. Seasonally, the limiting factors that affect Lappet-faced Vulture foraging success may shift and compensate for each other, going from

higher competition from *Gyps* in the dry season to lower food availability in the wet season. An important limiting factor for *Gyps* is likely to be seasonal food availability, but this requires further study.

Finally, my results support findings from mathematical models that foraging success is greater for social species when food availability and conspecific density are higher (Jackson et al. 2008). White-backed Vultures had higher foraging success and were able to reach satiation earlier in the day in the dry season than in the wet season. Whether their foraging success is heightened simply by greater food availability or by greater conspecific abundance via increased abundance of Rüppell's Vultures is unclear. In addition, Rüppell's Vultures reached satiation slightly later in the day than White-backed Vultures during the dry season. This pattern could be explained by higher search efficiency of White-backed Vultures compared with Rüppell's Vultures. Alternatively, because the dry season typically overlaps with breeding, the longer travel distances required to reach MMNR by cliff-nesting Rüppell's Vultures may limit their early-morning foraging activity compared with tree-nesting White-backed Vultures.

Conclusion

Carrion availability is higher in the morning than in the afternoon, which suggests that temporal segregation in resource use should be an important mechanism of coexistence among scavengers. In particular, subordinate species could reduce competition by feeding earlier in the morning, when food availability is highest. However, among the three vulture species considered, solitary species with lower competitive abilities were not able to use this temporal competitive refugium and appeared to pay a cost via lower foraging success. Instead, likely as a result of local enhancement, social species appear to have higher search efficiency and foraging success than solitary species, particularly when carrion resources are most abundant, as occurs in the morning. Sociality may thus be a particularly successful strategy for scavengers in periods of high food availability.

ACKNOWLEDGMENTS

Research was conducted in collaboration with The Peregrine Fund's Pan African Raptor Conservation Program. Funding was provided by the Pompeo M. Maresi Memorial Fund from Princeton University, Hawk Mountain Sanctuary, The Peregrine Fund, and The Explorer's Club. Advice and comments from my advisor, Daniel Rubenstein, and lab members were incredibly helpful. Field assistance was provided by W. Masek, J. Masek, and W. Kilong. I thank Narok County Council and the staff of Masai Mara National Reserve, particularly Mr. Minis and Mr. Sindiyo, for assistance and permission to conduct this research, as well as Africa Eco-Camps for their support. I am thankful to Kenya Wildlife Service and the

National Museums of Kenya. Experiments conducted as part of this study complied with Kenyan laws and were covered under research permit NCST/5/002/R/448. This is Hawk Mountain Sanctuary contribution to conservation science no. 228.

LITERATURE CITED

- Atkinson, W. D., and B. Shorrocks (1981). Competition on a divided and ephemeral resource: A simulation model. *Journal of Animal Ecology* 50:461–471.
- Bamford, A. J., A. Monadjem, and I. C. W. Hardy (2009). An effect of vegetation structure on carcass exploitation by vultures in an African savanna. *Ostrich* 80:135–137.
- Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews* 73:449–472.
- Blázquez, M., J. A. Sánchez-Zapata, F. Botella, M. Carrete, and S. Eguía (2009). Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. *Acta Oecologica* 35: 645–650.
- Bonsall, M. B., M. P. Hassell, and G. Asefa (2002). Ecological trade-offs, resource partitioning, and coexistence in a host-parasitoid assemblage. *Ecology* 83:925–934.
- Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft (2006). Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* 87:1987–1994.
- Carrete, M., S. A. Lambertucci, K. L. Speziale, O. Ceballos, A. Travaini, M. Delibes, F. Hiraldo, and J. A. Donazar (2010). Winners and losers in human-made habitats: Interspecific competition outcomes in two Neotropical vultures. *Animal Conservation* 13:390–398.
- Clark, C. W., and M. Mangel (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology* 30:45–75.
- Cortés-Avizanda, A., M. Carrete, and J. A. Donazar (2010). Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. *Biological Conservation* 143:1707–1715.
- Hartley, S., and B. Shorrocks (2002). A general framework for the aggregation model of coexistence. *Journal of Animal Ecology* 71:651–662.
- Hoppitt, W., and K. N. Laland (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior* 38:105–165.
- Houston, D. C. (1974a). Food searching behavior in griffon vultures. *East African Wildlife Journal* 12:63–77.
- Houston, D. C. (1974b). The role of griffon vultures *Gyps africanus* and *Gyps rueppellii* as scavengers. *Journal of Zoology, London* 172:35–46.
- Houston, D. C. (1975). Ecological isolation of African scavenging birds. *Ardea* 63:55–64.
- Houston, D. C. (1976). Breeding of White-backed and Rüppell's griffon vultures, *Gyps africanus* and *G. rueppellii*. *Ibis* 118:14–40.
- Houston, D. C. (1979). The adaptations of scavengers. In *Serengeti: Dynamics of an Ecosystem* (A. R. E. Sinclair and M. Norton-Griffiths, Editors). University of Chicago Press, Chicago, IL, USA. pp. 263–286.
- Houston, D. C. (2001). Vultures and Condors. Colin Baxter, Grantown on Spey, Scotland.
- Houston, D. C., and J. E. Cooper (1975). The digestive tract of the white-back griffon vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases* 11:306–313.
- Jackson, A. L., G. D. Ruxton, and D. C. Houston (2008). The effect of social facilitation on foraging success in vultures: A modelling study. *Biology Letters* 4:311–313.
- Kendall, C. (2013). Alternative strategies in avian scavengers: How subordinate species foil the despotic distribution. *Behavioral Ecology and Sociobiology* 67:383–393.
- Kendall, C., M. Z. Virani, P. Kirui, S. Thomsett, and M. Githiru (2012). Mechanisms of coexistence in vultures: Understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. *The Condor* 114:523–531.
- Krause, J., and G. D. Ruxton (2002). *Living in Groups*. Oxford University Press, Oxford, UK.
- Kronfeld-Schor, N., and T. Dayan (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics* 34:153–181.
- Kruuk, H. (1967). Competition for food between vultures in East Africa. *Ardea* 55:171–193.
- MacArthur, R. H., and R. Levins (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–387.
- May, R. M., and R. H. MacArthur (1972). Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences USA* 69:1109–1113.
- Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn (1999). Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology* 68:1101–1122.
- Mundy, P. J., D. Butchart, J. A. Ledger, and S. E. Piper (1992). *The Vultures of Africa*. Acorn Books and Russel Friedman Books, Randburg, South Africa.
- Pennycuik, C. J. (1972). Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* 114:178–218.
- Pennycuik, C. J. (1983). Effective nest density of Rüppell's griffon vulture in the Serengeti–Rift Valley area of northern Tanzania. In *Vulture Biology and Management* (S. R. Wilbur and J. A. Jackson, Editors). University of California Press, Berkeley, California, USA. pp. 172–184.
- Rosewell, J., B. Shorrocks, and K. Edwards (1990). Competition on a divided and ephemeral resource: Testing the assumptions. I. Aggregation. *Journal of Animal Ecology* 59:977–1001.
- Ruxton, G. D., and D. C. Houston (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228:431–436.
- Scheuring, I., G. Károlyi, Á. Péntek, T. Téi, and Z. Toroczka (2000). A model for resolving the plankton paradox: Coexistence in open flows. *Freshwater Biology* 45:123–132.
- Shorrocks, B., J. Rosewell, and K. Edwards (1990). Competition on a divided and ephemeral resource: Testing the assumptions. II. Association. *Journal of Animal Ecology* 59:1003–1017.
- Thorpe, W. H. (1963). *Learning and Instinct in Animals*, 2nd ed. Methuen, London, UK.
- Tilman, D. (1987). The importance of the mechanisms of interspecific competition. *American Naturalist* 129:769–774.
- Tilman, D. (1990). Constraints and tradeoffs: Toward a predictive theory of competition and succession. *Oikos* 58:3–15.
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA* 101:10854–10861.

- Travaini, A., J. A. Donázar, A. Rodríguez, O. Ceballos, M. Funes, M. Delibes, and F. Hiraldo (1998). Use of European hare (*Lepus europaeus*) carcasses by an avian scavenging assemblage in Patagonia. *Journal of Zoology* 246:175–181.
- Venables, W. N., and B. D. Ripley (2002). *Modern Applied Statistics with S*, 4th ed. Springer, Berlin, Germany.
- Viola, D. V., E. A. Mordecai, A. G. Jaramillo, S. A. Sistla, L. K. Albertson, J. S. Gosnell, B. J. Cardinale, and J. M. Levine (2010). Competition–defense tradeoffs and the maintenance of plant diversity. *Proceedings of the National Academy of Sciences USA* 107:17217–17222.
- Virani, M. Z., C. Kendall, P. Njoroge, and S. Thomsett (2011). Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biological Conservation* 144:746–752.
- Virani, M. Z., P. Kirui, A. Monadjem, S. Thomsett, and M. Githiru (2010). Nesting status of African White-backed Vultures *Gyps africanus* in the Masai Mara National Reserve, Kenya. *Ostrich* 81:205–209.
- Virani, M. Z., A. Monadjem, S. Thomsett, and C. Kendall (2012). Seasonal variation in breeding Rüppell's Vultures *Gyps rueppellii* at Kwenia, southern Kenya and implications for conservation. *Bird Conservation International* 22:260–269.