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Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission

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Abstract: *Vultures (Accipitridae and Cathartidae) are the only known obligate scavengers. They feed on rotting carcasses and are the most threatened avian functional group in the world. Possible effects of vulture declines include longer persistence of carcasses and increasing abundance of and contact between facultative scavengers at these carcasses. These changes could increase rates of transmission of infectious diseases, with carcasses serving as hubs of infection. To evaluate these possibilities, we conducted a series of observations and experimental tests of the effects of vulture extirpation on decomposition rates of livestock carcasses and mammalian scavengers in Kenya. We examined whether the absence of vultures changed carcass decomposition time, number of mammalian scavengers visiting carcasses, time spent by mammals at carcasses, and potential for disease transmission at carcasses (measured by changes in intraspecific contact rates). In the absence of vultures, mean carcass decomposition rates nearly tripled. Furthermore, the mean number of mammals at carcasses increased 3-fold (from 1.5 to 4.4 individuals/carcass), and the average time spent by mammals at carcasses increased almost 3-fold (from 55 min to 143 min). There was a nearly 3-fold increase in the mean number of contacts between mammalian scavengers at carcasses without vultures. These results highlight the role of vultures in carcass decomposition and level of contact among mammalian scavengers. In combination, our findings lead us to hypothesize that changes in vulture abundance may affect patterns of disease transmission among mammalian carnivores.*

Keywords: carcass decomposition, carnivore, hyena, jackal, Kenya

Efectos de la Declinación de Buitres sobre Carroñeros Facultativos e Implicaciones Potenciales para la Transmisión de Enfermedades a Mamíferos

Resumen: *Los buitres (Accipitridae y Cathartidae) son los únicos carroñeros obligados que se conocen. Se alimentan de cadáveres en descomposición y son el grupo funcional de aves más amenazado del mundo. Los efectos posibles de las declinaciones de buitres incluyen una mayor persistencia de cadáveres y el incremento de la abundancia de y contacto entre carroñeros facultativos en esos cadáveres. Estos cambios podrían incrementar las tasas de transmisión de enfermedades infecciosas, con los cadáveres funcionando como focos de infección. Para evaluar estas posibilidades, realizamos una serie de observaciones y pruebas experimentales de los efectos de la extirpación de buitres sobre las tasas de descomposición de cadáveres de ganado y*

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mamíferos carroñeros en Kenia. Examinamos sí la ausencia de buitres cambiaba el tiempo de descomposición de cadáveres, el número de mamíferos carroñeros visitando los cadáveres, el tiempo utilizado por mamíferos en los cadáveres y la potencial transmisión de enfermedades en los cadáveres (medida por cambios en las tasas de contacto interespecífico). En ausencia de buitres, las tasas medias de descomposición de cadáveres incrementaron 3 veces (de 1.5 a 4.4 individuos/cadáver), y el tiempo promedio invertido por mamíferos en los cadáveres incrementó casi 3 veces (de 55 min a 143 min). Hubo un aumento de casi tres veces en el número promedio de contactos entre mamíferos carroñeros en cadáveres sin buitres. Estos resultados resaltan el papel de los buitres en la descomposición de cadáveres y del nivel de contacto entre mamíferos carroñeros. En combinación, nuestros resultados nos llevaron a plantear la hipótesis de que cambios en la abundancia de buitre pueden afectar los patrones de transmisión de enfermedades entre mamíferos carnívoros.

Palabras Clave: carnívoro, chacal, descomposición de cadáveres, hiena, Kenia

Introduction

As obligate scavengers, vultures (Accipitridae & Cathartidae) are highly specialized to rapidly consume large carcasses, and their scavenging contributes to nutrient cycling and limits the spread of diseases (Houston & Cooper 1975; DeVault et al. 2003). In birds, increased specialization is highly correlated with increased probability of extinction (Sekercioglu et al. 2004). Avian scavengers have the highest percentage of extinction-prone species among avian functional groups (Sekercioglu et al. 2004). Drivers of vulture declines worldwide are poisoning (Pain et al. 2003; Hernández & Margalida 2008), food scarcity, hunting, and land-use changes (Rondeau & Thiollay 2004). Sharp declines in the abundance of vultures have occurred in West Africa (Rondeau & Thiollay 2004; Thiollay 2006) and southern Asia (Prakash et al. 2003; Oaks et al. 2004). In East Africa, vulture abundance in the Masai Mara National Reserve, Kenya, has declined over 50% since the 1970s (Virani et al. 2010), and from 2001 through 2003 there was a 70% decline in central Kenya (Ogada & Keesing 2010). A decade ago, none of the 8 species of vultures that occur in Kenya were on the International Union for Conservation of Nature (IUCN) Red List. Currently, 6 of 8 species are on the IUCN Red List, and populations continue to decline (e.g., Ogada & Buij 2011).

Little is known about the effects of the widespread decline in abundance of vultures (Sekercioglu et al. 2004; Sekercioglu 2006). Facultative scavenger communities in a Polish forest are highly structured, meaning scavengers do not visit carcasses randomly (Selva & Fortuna 2007). Less specialized scavengers do not scavenge carcasses unless highly specialized scavengers have done so first (Selva & Fortuna 2007). This suggests that specialized scavengers, such as vultures, may affect the composition of and interactions within the scavenger community. Vultures can search widely for carrion because they fly and have keen eyesight (Houston 1974; Ruxton & Houston 2004), which enable them to locate food more easily than terrestrial scavengers. Vultures also are resistant to and possibly can detoxify bacterial toxins in rotting flesh (Houston & Cooper 1975). Highly acidic secretions ($pH = 1$) in their stomachs destroy almost all microbial organisms, which greatly reduces the chance of infection from a carcass (Houston & Cooper 1975). It has been suggested, but rarely evaluated empirically, that vultures spread pathogenic organisms through contamination of their feet or feathers (but see Houston & Cooper [1975]).

In regions where vultures have declined to such low levels that they no longer provide measurable ecosystem services or functions (i.e., they have been functionally extirpated), such as in India, the absence of vultures at carcasses appears to have driven increases in the abundances of feral dogs and rats (*Rattus rattus*) (Pain et al. 2003; Prakash et al. 2003). These increases suggest that facultative mammalian scavengers that can locate and consume carcasses before decomposition may serve an equivalent ecological role to vultures (Sekercioglu et al. 2004). Thus, vulture extirpation may lead to increases in abundance of other scavengers (Selva & Fortuna 2007). In African savannas, species most likely to increase in abundance in the absence of vultures are hyenas (*Crocuta crocuta*, *Hyaena hyaena*) and jackals (*Canis mesomelas*) (Kruuk 1972; Kingdon 1997).

In addition to altering the composition and relative abundance of the scavenger community, the absence of vultures may also affect disease transmission. Decomposing carcasses may serve as incubators for many pathogens, and animals that come into contact with rotting carcasses may be exposed to infectious agents (Wobeser 2002; Butler et al. 2004; Jennelle et al. 2009). Carcasses may also be hubs for interactions between potential hosts of infectious agents (Mills 1993; Ragg et al. 2000) because the number of contacts between individual animals of the same or different species at carcasses is relatively high. Furthermore, because contacts at carcasses are likely aggressive in nature, due to competition for food, there may be high rates of close contact between individuals. Close contact is particularly relevant for the transmission of directly transmitted infectious diseases. In India small predators that appear to increase in abundance when vultures are absent are well-known disease reservoirs (e.g., rats, feral dogs) (Pain et al. 2003). Similarly, hyenas and jackals host a number of pathogens that infect a wide range of other wild and domesticated species (Alexander et al. 1994; Harrison et al. 2004). Two major diseases that affect African carnivores, rabies and canine distemper, spread through direct contact between infected and susceptible individuals, and carnivores often interact closely at carcasses (Mills 1993; Roelke-Parker et al. 1996; Butler et al. 2004). Thus, vulture declines may lead to increases in the frequency of such contact between terrestrial scavengers.

We hypothesized that in the absence of vultures, decomposition rates of carcasses increase and abundances of facultative scavengers at carcasses and time in close proximity to carcasses also increase. We also measured the number of contacts between conspecific mammals at a carcass which could potentially facilitate disease transmission.

Methods

Study Site

The study was conducted at Mpala Research Centre in Laikipia District of central Kenya (0°17′N, 37°53′E). Mpala Research Centre, located on Mpala Ranch, covers 20,000 ha of wooded savanna. The ranch, which is lightly stocked (0.15 head of livestock/ha) with cattle, sheep, and camels, contains high-quality habitat for large native herbivores such as elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), and Grevy's zebras (*Equus grevyi*). Large scavenging carnivores on the ranch include lions (*Panthera leo*), leopards (*P. pardus*), spotted hyenas (*Crocuta crocuta*), and striped hyenas (*Hyaena hyaena*). Smaller mammalian scavengers include black-backed jackals (*Canis mesomelas*) and Egyptian mongooses (*Herpestes ichneumon*). Vultures present on the ranch during our study included palm-nut (*Gypohierax angolensis*), hooded (*Necrosyrtes monachus*), white-backed (*Gyps africanus*), Rüppell's (*G. rueppellii*), and lappet-faced (*Torgos tracheliotus*) Vultures. In the past 10 years there have been fewer than 5 sightings of Egyptian (*Neophron percnopterus*) and white-headed vultures (*Trigonoceps occipitalis*) (D.L.O., personal observation). Besides vultures, major avian scavengers include tawny eagles (*Aquila rapax*), fan-tailed Ravens (*Corvus rhipidurus*), steppe eagles (*A. nipalensis*), and Marabou Storks (*Leptoptilos crumeniferus*).

Study Design

We placed carcasses of goats and cows at 54 abandoned bomas (temporary corrals) or other open sites (i.e., areas without tree cover) in the southern half (approximately 10,000 ha) of Mpala Ranch. We used open sites to reduce the likelihood that high rainfall and resulting thick vegetation would make the carcasses more difficult for scavengers to locate. We reused 7 sites, and carcasses at these sites were spaced at least 1 month apart.

We used 2 methods to test whether number of vultures was associated with carcass decomposition rates, abundance of facultative scavengers, and number of contacts between facultative scavengers. First, we placed 11 large and 50 small carcasses at separate locations. We did not place these carcasses so as to attract or deter vultures. Small carcasses were goats (35–62 kg, mean = [SE] 47.3 [0.94]), whereas large carcasses were cows (150–340 kg, mean = 184.1 [16.4]). We skinned all areas of each animal except the legs and head to provide avian scavengers with access to the flesh and organs. Each small carcass was secured to the ground with six 60-cm iron stakes to prevent large scavengers, particularly hyenas, from dragging the carcass away. Large carcasses were secured with eight 60-cm iron stakes. Second, we placed 14 pairs of small carcasses, 1 of which was fully exposed in open grass to attract vultures and 1 of which was under tree cover to experimentally mimic the absence of vultures. We placed the first carcass in each pair in the open. The day after the edible parts of the carcass were fully consumed and the remainder of the carcass (e.g., bones, fur) was removed by scavengers, we placed another carcass under tree cover within 50 m of the open area to visually obscure it from vultures. The carcass under the trees effectively excluded vultures because Old World vultures find carcasses only by sight (Mundy et al. 1992). Carcasses were skinned and staked as described earlier.

Data Collection

We deployed 73 carcasses at dawn (06:15–07:20) to maximize detection by vultures; peak foraging times of vultures are between 09:00 and 14:00 (Butler & du Toit 2002). Two large carcasses were deployed at 10:15 and 18:50. Vultures did not come to these 2 carcasses, but the arrival times of mammals at these 2 carcasses fell within the 25th to 75th percentile of arrival times at carcasses deployed at dawn. We used a camouflaged night-vision video camera to continually record activity at all carcasses. The camera was mounted on a tree branch and was checked at dusk and dawn. It was removed after 10% or less of flesh remained on the carcass.

For each individual animal visiting the carcass we recorded species, time of arrival, length of stay, and the number of direct contacts with conspecifics. The majority of scavengers were spotted and striped hyenas and jackals, individuals of which could be differentiated by stripe and spot patterns. For these species, we recorded the number of individuals at each carcass. For mammalian scavengers that lacked unique individual fur patterns (e.g., lions and mongooses), we recorded abundance on the basis of unique identifying characteristics, such as scars for lions and behavior patterns for mongooses. Mongooses have small territories, so the probability of more than 2 individuals visiting a carcass at a given time was low. We also recorded the presence of scavenging birds other than vultures, but because of the difficulty in identifying individual birds, we recorded the maximum number of each species seen at the carcass at any one time.

We measured carcass decomposition time in seconds from the time of arrival of the first scavenger until the carcass was >90% consumed. We recorded arrival time as the number of minutes that elapsed prior to arrival of the first vulture or mammal at a carcass. The number of mammals at a carcass was calculated as the sum of the number of individuals of all species that visited the carcass. The amount of time spent by mammals at the carcass was the sum of the number of seconds spent at the carcass by all individuals of all species until over 90% of the carcass was consumed. We counted the number of times 2 individual mammals of the same species made physical contact (individual contacts). As a measure of the total number of contacts for each carcass, we summed all contacts until >90% of the carcass was consumed. We did not record interspecific contacts because individuals of different species rarely fed at a carcass simultaneously and never came into direct contact with each other.

Data Analyses

For analyses of observations at unpaired carcasses, we treated carcass size as a categorical variable, small (35–62 kg) or large (150–340 kg). We used 2-sample Wilcoxon signed rank tests to assess whether carcass size was associated with 6 response variables: decomposition time, number of mammals and contacts between mammals, time spent by mammals at the carcass, and numbers of vultures and scavenging birds. Given significant effects of carcass size on decomposition time, number of mammals, contacts between mammals, and time spent by mammals at the carcass, we used multivariate generalized linear models (GLMs), controlling for carcass size, to examine associations between the numbers and effects of vultures and the response variables. Covariates included in the model for decomposition time were carcass size, number of vultures, number of mammals, arrival times of vultures, and arrival time of mammals.

We used a GLM to test the effect of vulture occurrence and carcass size class on carcass decomposition time. We did this because carcass decomposition time was not significantly correlated with either the number of vultures or numerical size of carcasses (i.e., continuous variables). Since vulture occurrence had a significant effect on carcass decomposition time, we included decomposition time as a covariate in subsequent analyses to test whether the effects of other covariates were occurring independently of increased decomposition time. Carcasses that decompose more slowly may attract more mammals.

We included 5 covariates in the models for time spent by mammals at the carcass and number of contacts between mammals: carcass size, number of vultures, number of mammals, decomposition time, and the interaction between number of mammals and carcass size. We used an exponential distribution for the GLM and evaluated whether covariates fit this distribution by testing whether deviance residuals for each GLM were normally distributed. Significance was assessed at alpha = 0.05. We confirmed that variance inflation factors (VIFs) were <10 prior to fitting GLMs (O'Brien 2007). The highest VIF (9.0) was between the number of mammals and the time mammals spent at the carcass. All other VIFs were below 1.2.

For analyses of observations at the paired carcasses, we used paired Wilcoxon signed rank tests to determine whether vulture absence was associated with carcass decomposition time, number of mammals, time spent by mammals at the carcass, and the number of contacts. We used the same test to examine whether vulture absence was associated with the number of individual mammals at the carcass (hyenas and jackals). We also used a GLM with an exponential distribution to test whether the number of vultures was associated with carcass decomposition time.

Results

Observations

Vultures fed on 35 of 61 carcasses (57%), and the number of vultures per carcass ranged from 19 to 151 (mean [SE] = 43.5 [4.3]). We recorded 1009 vultures at carcasses. Ninety-five percent of these were *Gyps* spp., 4% were lappet-faced vultures, and 1% were hooded vultures. We observed 544 animals that were not vultures scavenging on carcasses. The majority of these were tawny eagles (47%), spotted hyenas (15%), steppe eagles (10%), striped hyenas (8%), and black-backed jackals (5%). Spotted and striped hyenas and black-backed jackals were the highest proportion of observed mammalian scavengers. Leopards, lions, mongooses, and genets (*Genetta genetta*) also scavenged on carcasses. At carcasses without vultures, mean species richness was 3.6 (SE 0.3), whereas at carcasses scavenged by vultures mean species richness was 2.9 (0.3).

Carcass size was associated with most response variables. Decomposition of large carcasses was slower than that of small carcasses (Wilcoxon signed rank test: $Z = 2.74$, $p < 0.01$). At large carcasses there were more individual mammals ($Z = 4.25$, $p < 0.001$), mammals stayed longer ($Z = 4.06$, $p < 0.001$), and the number of contacts between mammals was higher ($Z = 4.27$, $p < 0.001$). The number of vultures and scavenging birds was not significantly associated with carcass size (vultures: $Z = 1.42$, $p = 0.16$; scavenging birds: $Z = 0.97$, $p = 0.33$).

Table 1. Covariates associated with changes in scavenger composition and probability of disease transmission at observed carcasses ($n = 61$)[a].

	Independent variable[b]						
Dependent variable	*carcass size (kg)*	*number of vultures*	*number of mammals*	*arrival time of vultures (min)*	*arrival time of mammals (min)*	*decomposition time (sec/kg)*	*carcass size × number of mammals*
Decomposition time	0.01	0.01	0.05	0.12	2.17	–	–
Number of mammals	27.55^{***}	12.21^{***}	–	–	–	0.02	–
Time spent by mammals at carcasses (sec)	17.87^{***}	3.56	10.18^{**}	–	–	1.70	23.58^{***}
Number of contacts between mammals	79.27^{***}	10.44^{**}	38.93^{***}	–	–	3.02	53.80^{***}

[a] *Observed carcasses were not manipulated to attract or deter vultures.*

[b] *Results are based on multivariate general linear models with an exponential distribution. Numbers are chi-square values and significance is denoted as* $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Therefore, we controlled for carcass size in all subsequent analyses of observations.

Carcass decomposition time was not significantly associated with any of the variables we examined (Table 1). However, analyses with categorical variables showed decomposition time was significantly higher at carcasses without vultures (GLM: $X^2 = 11.24$, $p < 0.001$) and was not associated with carcass size (GLM: $\chi^2 = 2.90$, $p = 0.09$). The number of mammals at carcasses was strongly associated with carcass size and number of vultures (Table 1). Larger carcasses had more mammals and there was a negative relationship between the numbers of mammals and vultures at carcasses. In addition, the time spent at carcasses by mammals increased as carcass size and abundance of mammals increased. The interaction term between carcass size and number of mammals was also significantly associated with time spent at the carcass (Table 1). The number of contacts between mammals at carcasses increased as carcass size and number of mammals increased. The number of contacts between mammals was a negative function of the number of vultures (Table 1). The interaction between carcass size and number of mammals was also significantly associated with the number of contacts (Table 1).

Experiment

Vultures visited 50% of 14 paired carcasses, and number of vultures at each carcass ranged from 22 to 89 (mean 50.4 [SE 6.2]). We recorded 707 vultures at experimental carcasses: 94% *Gyps* spp., 4% lappet-faced vultures, and 2% hooded vultures. We observed 1 palm-nut vulture. We observed 176 scavengers that were not vultures, including tawny eagles (65%), spotted hyenas (13%), black-backed jackals (8%), striped hyenas (4%), and steppe eagles (2%). Leopards, mongooses, and genets also scavenged these carcasses. At carcasses without vultures, mean species richness was 2.6 species (SE 0.3), compared with 1.4 species (0.2) at carcasses scavenged by vultures.

Carcass decomposition time was slower in the absence of vultures (paired Wilcoxon signed rank test: $n = 28$, $Z = 41.50$, $p < 0.01$). The number of mammals ($Z = 45.50$, $p < 0.001$), the amount of time they spent at carcasses ($Z = 51.50$, $p < 0.001$), and number of contacts between mammals ($Z = 14.00$, $p = 0.02$) were also greater in the absence of vultures (Fig. 1). At carcasses without vultures the abundance of spotted and striped hyenas increased significantly (spotted: $n = 28$, $Z = 35.50$, $p < 0.01$; striped: $n = 28$, $Z = 18.00$, $p < 0.01$) (Fig. 2). However, there was no significant difference in number of jackals ($n = 28$, $Z = 5.00$, $p = 0.12$) at the 6 carcasses they visited (Fig. 2). Carcass decomposition time was significantly and negatively correlated with abundance of vultures ($X^2 = 10.72$, $p = 0.001$).

Discussion

The absence of vultures at carcasses was associated with longer carcass decomposition times, more individual mammals at carcasses, mammals spending more time at carcasses and mammals coming into contact with one another more frequently, which could facilitate disease transmission between mammalian scavengers at carcasses.

Vultures consume carcasses quickly, and their absence was associated with significantly slower decomposition times. By contrast, our results suggested mammalian scavengers did not play a significant role in carcass decomposition. However, the role of mammals in the decomposition of carcasses may be greater than our results indicate because we deployed carcasses at dawn, when vultures are more likely to forage than mammals. We believe mammalian scavengers may serve a functionally equivalent role to vultures in terms of their ability to rapidly locate and consume carcasses at night (e.g., Butler & du Toit 2002).

The total number of facultative mammalian scavengers and the time they spent at carcasses increased in the

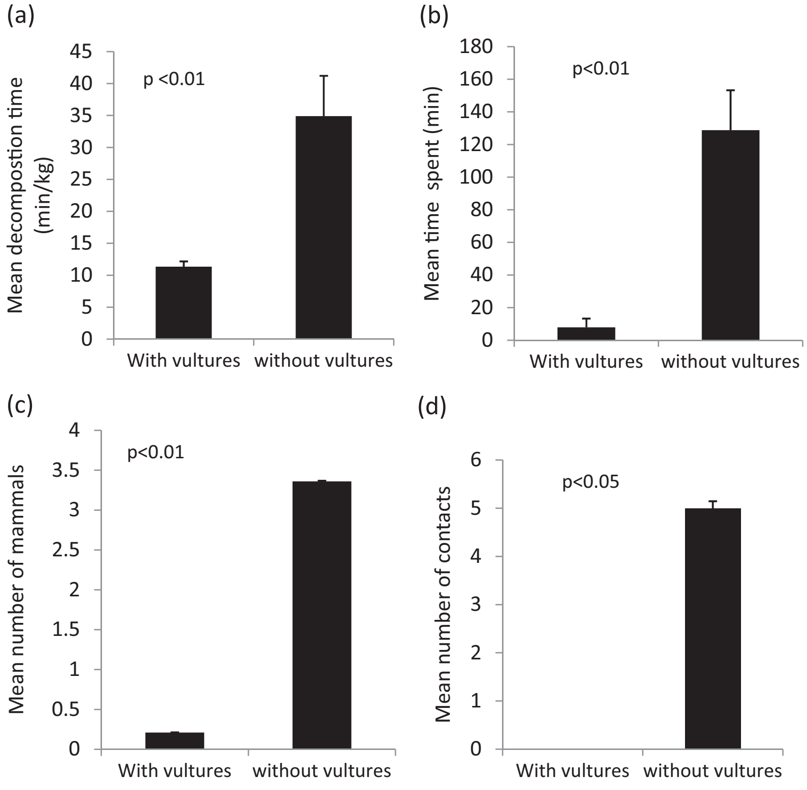

*Figure 1. Effects of vulture absence on (a) carcass decomposition time, (b) time mammalian scavengers spent at carcasses, (c) number of mammals at carcasses, (d) contact between mammals at carcasses and at experimental carcasses (*n = *14 pairs). Experimental carcasses were paired. One carcass was placed in the open to encourage vultures to scavenge and the second was placed under trees to deter vultures.*

absence of vultures. Although changes in scavenger composition and abundance have been proposed as an effect of declines of top-level scavengers (e.g., Pain et al. 2003; Sekercioglu et al. 2004; Jones et al. 2007), to our knowledge ours is the first study to provide quantitative data supporting this claim. Changes in species composition may be driven by a number of factors, including competition between top-level scavengers, temporal availability of carcasses, and carcass origin (e.g., natural death, predator kill, or hunter bycatch) (Wilmers et al. 2003; Selva & Fortuna 2007). At the individual carcasses we deployed, the number of spotted and striped hyenas increased by 87% and 100%, respectively, when vultures were absent. Similarly, facultative scavengers including dogs, eagles, and foxes effectively locate and consume carcasses in the absence of specialized scavengers (e.g., Hiraldo et al. 1991; Butler & du Toit 2002; Blázquez et al. 2009). Increases in numbers and time spent by facultative scavengers at carcasses did not reflect longer persistence times of carcasses in the absence of vultures. This suggests that vultures and hyenas may indirectly compete for the same resource and that the lack of vultures may facilitate use of this food source by mammals. This idea is consistent with results from Butler and du Toit (2002), who found that in unprotected areas in Zimbabwe, where vultures were absent or wary of human activities, domestic dogs consumed the largest portion of experimental carcasses.

In our study, the change in species composition of scavengers at carcasses without vultures was a function of both larger carcasses and a lack of vultures that facilitated an increase in the abundance of mammals at carcasses. Larger carcasses influence competition among vertebrate scavengers (DeVault et al. 2004). However, our results that show carcass size was associated with scavenger composition should be treated as preliminary because our sample size of large carcasses was small.

For hyenas and jackals the mean number of contacts between conspecifics increased nearly 3-fold in the absence of vultures. We considered the number of contacts between individuals an indicator of potential disease transmission at carcasses because close contact between individuals is a likely source of pathogen transmission for a number of carnivore diseases, including rabies and canine distemper (Murray et al. 1999). We observed only intraspecific contacts, and these were mainly in spotted hyenas and jackals. Both of these species are well-known hosts of a number of carnivore diseases (Alexander et al. 1994; Craft et al. 2008), and because rates of disease transmission depend on the number of susceptible individuals with which an infected individual interacts (McCallum et al. 2001), aggregation and intraspecific contact at carcasses could facilitate pathogen transmission.

Because of the social nature of spotted hyenas, it is possible that the contacts we observed at carcasses were be-

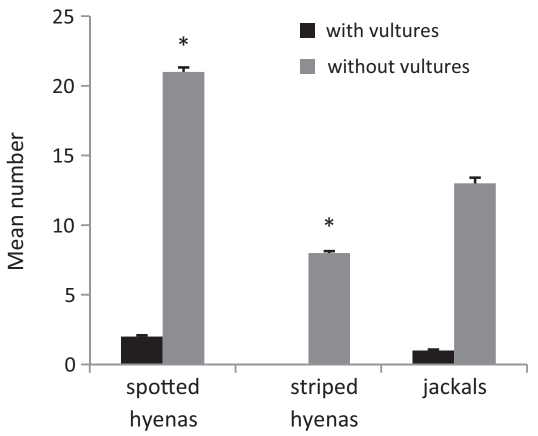

Figure 2. Effects of vulture absence on mammalian scavenger abundance at experimental carcasses ($n = 14$ pairs). Experimental carcasses were paired. One carcass was placed in the open to encourage vultures to scavenge and the second was placed under trees to deter vultures ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

tween individuals who regularly come into contact with one another (e.g., members of the same clan). Therefore, the contacts we observed may not reflect a significant increase in the net number of contacts experienced by any one individual. Contact rates within spotted hyena clans are determined by social status. For example, adult females have the highest number of oral contacts (open-mouth licking) with clan members (East et al. 2001). However, it is also possible that contacts between individuals from distinct clans occur frequently at carcasses, increasing the probability of both primary transmission at the carcass and secondary transmission to other group members when individuals return to their respective dens. We believe the transmission of directly transmitted carnivore diseases at carcasses may increase as vultures decline or are extirpated. Although we focused on mammals, changes in abundance of avian scavengers (tawny eagles) were the most pronounced in the absence of vultures. Abundant avian scavengers such as crows may transmit diseases at carcasses as vulture abundance declines. For example, in Bangladesh, a region with substantial declines in vulture abundance, dead crows have tested positive for the highly pathogenic influenza virus (H5) (Giasuddin et al. 2009). However, compared with African mammals, very little work has focused on diseases of avian scavengers, including vultures.

As vulture abundance declines or vultures are extirpated, the number of facultative mammalian scavengers consuming carcasses is likely to increase, which may lead to carcasses becoming hubs of disease transmission for mammalian scavengers. Transmission of carnivore diseases via domestic dogs, which forage on carcasses alongside hyenas and jackals in areas where vultures are absent (Butler & du Toit 2002), is well documented (Alexander & Appel 1994; Cleaveland et al. 2000; Lembo et al. 2008). However, the extent to which pathogenic organisms are spread at carcasses is unknown.

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