

Finders' eaters: Increasing bush encroachment may shift carcass detection from diurnal avian to nocturnal mammalian scavengers

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Abstract

Bush encroachment is increasingly becoming a problem for biodiversity conservation in African savannas. While this invasion by woody vegetation may hamper avian scavengers such as vultures, which primarily search by sight, it may benefit mammalian scavengers that search by smell. This study aimed to examine the ability of nocturnal mammalian and diurnal avian scavengers to locate carcasses at increasing vegetation densities. We successively placed 27 impala (*Aepyceros melampus*) carcasses five days apart in a 2000 ha fenced game camp that offered an extensive range of woody plant densities. Scavenger arrivals and first feedings were recorded with camera traps. The avian scavengers, mainly white-backed Vultures (*Gyps africanus*), fed exclusively on carcasses during the day, and mammalian scavengers, predominantly brown hyenas (*Parahyena brunnea*), fed solely at night. The two guilds thus competed exploitatively without direct interaction between them. For vultures, the time taken to locate a carcass increased with woody plant density. The mean density of woody plants that avian scavengers located carcasses at was 2188 plants/ha, whereas mammalian scavengers located carcasses at appreciably higher densities of 5156 plants/ha. Resource managers need to understand the synergy between maintaining woody vegetation to benefit nocturnal mammalian scavengers and maintaining open savannas to benefit diurnal avian scavengers.

KEYWORDS

avian, digital cover photography, exploitative competition, mammalian, scavengers, woody plant density

Résumé

L'embroussaillage devient progressivement un problème pour la conservation de la biodiversité dans les savanes africaines. Si cet envahissement par la végétation ligneuse peut gêner les oiseaux charognards tels que les vautours, qui recherchent principalement par la vue, il peut profiter aux mammifères charognards qui recherchent par l'odorat. Cette étude visait à examiner la capacité des mammifères charognards nocturnes et des oiseaux charognards diurnes à localiser les carcasses à des endroits

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où les densités de végétation sont croissantes. Nous avons placé successivement 27 carcasses d'impalas (*Aepyceros melampus*) à cinq jours d'intervalle dans un camp de chasse clôturé de 2 000 ha offrant une large gamme de densités de plantes ligneuses. Les arrivées des charognards et les premiers repas ont été enregistrés à l'aide de pièges photographiques. Les oiseaux charognards, principalement des vautours à dos blanc (*Gyps africanus*), se nourrissaient exclusivement de carcasses pendant la journée, et les mammifères charognards, principalement des hyènes brunes (*Parahyena brunnea*), se nourrissaient uniquement la nuit. Les deux guildes se livraient donc à une concurrence d'exploitation sans interaction directe entre elles. Pour les vautours, le temps nécessaire pour localiser une carcasse augmentait avec la densité des plantes ligneuses. La densité moyenne de plantes ligneuses à laquelle les oiseaux charognards localisaient les carcasses était de 2 188 plantes/ha, alors que les mammifères charognards localisaient les carcasses à des densités sensiblement plus élevées de 5 156 plantes/ha. Les responsables de ressources doivent comprendre la synergie entre le maintien de la végétation ligneuse au profit des mammifères charognards nocturnes et le maintien des savanes ouvertes au profit des oiseaux charognards diurnes.

1 | INTRODUCTION

Africa is richly endowed with medium to large-bodied herbivores, which supports an assortment of opportunistic scavengers (Di Vittorio et al., 2018; Owen-Smith, 2013). The primary ecological role of scavengers in ecosystems is the consumption and, thus, recycling of otherwise wasted carrion and the speedy removal of dead animals (Buechley & Şekercioğlu, 2016; DeVault et al., 2003; Hugh-Jones & De Vos, 2002; Phipps et al., 2013; Selva & Fortuna, 2007). However, because the availability of carrion is unpredictable in time and space and searching for it can be energetically expensive, most vertebrate carnivores will only scavenge when a carcass is available (DeVault et al., 2003; Ruxton & Houston, 2004; Selva & Fortuna, 2007). The 22 obligate vertebrate scavengers, however, are all species of Old and New World vultures that are physiologically adapted to meet the costly energetic demands of scavenging (Benbow et al., 2015; Ruxton & Houston, 2004; Selva & Fortuna, 2007).

Hence, the scavenger group found in African savannas can be separated into two distinct guilds: the diurnal avian scavengers and nocturnal mammalian scavengers. The diurnal avian scavengers, primarily vultures, have exceptional soaring ability and excellent eyesight to search for ungulates and other mammal carcasses (Mundy et al., 1992). The second guild consists of nocturnal mammalian scavengers like spotted hyena (*Crocuta crocuta*), and brown hyena (*Parahyena brunnea*) (Skinner & Chimimba, 2005) (Figure 1). To find a carcass, these scavengers walk great distances searching for olfactory cues that are released upon the death of their ungulate prey, and once decomposition has been initiated (Forbes & Perrault, 2014; McWhorter, 2014; Mills, 1978, 1984).



FIGURE 1 A brown hyena (*Parahyena brunnea*) is feeding on the impala carcass in quadrat no. 2A10. Although not visible, the Canopy Cover recorded at this quadrat was the 5th highest at 64%, and the woody density at 32 plants/64 m² (4997 plants/ha). The image was taken with the motion detection camera.

In Africa's Savanna Biome, woody and herbaceous vegetation has been steadily increasing over the past few decades (Marston et al., 2017; Stevens et al., 2017; Trollope, 1980). This woody biomass invasion, or bush encroachment, is driven by escalating human impacts such as increasing atmospheric CO₂ concentrations, altering fire regimes, scale-dependent interactions between these variables and overgrazing (Buitenwerf et al., 2012; Staver et al., 2011).

Previous research has often indicated that a landscape-scale increase in tree density can compromise the ability of avian scavengers to locate a carcass during the day and even physically hamper vultures from gaining access to or departing from the carcass (Bamford et al., 2009; Gavashelishvili & McGrady, 2006; Kendall, 2014; Ogada et al., 2012; Schultz, 2007; Spiegel et al., 2013). However, for mammalian scavengers, bush encroachment has a completely different outcome, as in dense stands of trees and shrubs, under the cover of darkness it is the facultative mammalian scavengers, for example, the brown hyena employing olfactory cues that gain access to carrion (Jackson et al., 2020; Mundy et al., 1992; O'Brien et al., 2010).

However, our understanding of the relationship between vegetation structure and the ability of avian and mammalian scavengers to locate prey is still rudimentary (Bamford et al., 2009; Jones et al., 2015; Schultz, 2007).

This study, therefore, set out to investigate how the temporal placement of carcasses in increasing bush-encroached areas could impact the ability of the two scavenger guilds to locate carcasses. The first objective of the study was to examine if avian and mammalian scavengers exploit carcasses during different periods of the day, and if not, if there is a competitive relationship between the two guilds (Jones et al., 2015; Mundy et al., 1992). The second objective was to ascertain the relationship between vegetation structure, and woody plant density in particular, and the ability of avian and mammalian scavengers to locate carcasses (Bamford et al., 2009; Ogada et al., 2016; Schultz, 2007). We predicted that increased woody plant density would favour mammalian scavengers over avian ones.

2 | METHODS

2.1 | Study area

Pidwa Wilderness Reserve is a 12,000-ha privately-owned protected area located 20km south of Gravelotte, Limpopo Province, South Africa (centroid S24° 02.591'; E30° 35.241'). The dominant vegetation ranges from tall shrubland with few trees to somewhat dense low woodland, and the topography is flat to undulating, with seep lines and sandy soils (Granite Lowveld vegetation unit); The dominant trees were *Senegalia nigrescens*, *Combretum apiculatum* and *Colophospermum mopane*. The average annual rainfall is 633mm, with a winter mean monthly minimum temperature of 7°C and a summer mean monthly maximum of 30°C (Mucina & Rutherford, 2006).

The study was conducted within the Langa camp, which is a 2057-ha fenced-off camp located within the Pidwa Wilderness Reserve (Figure 2). The camp was surrounded by a standard 2.4m tall game fence that constricts the movement of medium to large-sized ungulates; however, small and large predators could jump over or burrow under it. The vegetation in the camp differs notably from the rest of the reserve, with relatively more bush-encroached habitats, which we assumed to be at densities

at which vultures would be unable to detect or take off from a carcass (Schultz, 2007).

2.2 | Carcass placements

We used impala (*Aepyceros melampus*) carcasses, which were supplied by Pidwa Wilderness Reserve as part of their culling management program. The impala carcasses were considered large enough ($\bar{x} \pm 1$ STD; 46 ± 4 kg; Skinner & Chimimba, 2005) to be visible to avian scavengers and release a *putrid odour* to attract mammalian scavengers (Mundy et al., 1983), even with the head removed (see below). This size of an impala carcass was also perceived as small enough to be consumed by a single or one gathering of scavengers. Mundy et al. (1992) estimated that a 45kg impala, with 30kg of meat, can fill the crop of a white-backed Vulture (*Gyps africanus*) with a 1kg capacity in 5 min.

Pidwa Wilderness Reserve supplied a head-shot impala on the afternoon before each placement. The following morning, the carcass was placed 1.5h after sunrise. The placement was conducted in the morning as most small antelope die during this period when temperatures are at their lowest (Mundy et al., 1992). The carcass was positioned lying side-down, with the head and neck removed to avoid lead-bullet fragments being ingested by scavenging animals (Knott et al., 2010; Watson et al., 2009). To place the carcasses at the selected sites, we obtained ethical clearance from the Tshwane University of Technology (AREC 2015/10/001). The Reserve conducted its independent culling program (17 February to 3 June 2016; 108 days) as part of its annual management plan, and the owners of the Pidwa Wilderness Reserve permitted the work in the Langa camp.

A 1:15,000 orthophoto of Langa was divided into 87, 548 × 460m quadrats to select placement sites for the carcasses. Fifty-two quadrats were deemed suitable as they fell inside the camp. Twenty-seven sites were chosen randomly (Figure 2) as the maximum number of carcass placements we could conduct within our placement schedule, in which four days were allocated to each carcass. The carcass was left at the placement site for a maximum period of three days and nights (see below), and on the morning of the fourth day, all remains were removed (including primarily skeletal bones and skin). During the remainder of this day, we made no other carcass available at this site to not habituate the scavengers to continuous scavenging opportunities.

Each carcass was placed in the centre of its randomly selected quadrat. The centroid of the quadrat was located with QGIS (QGIS Development Team, 2016), and the carcass was placed at the exact centre point, whether in the open, underneath a (thorny) shrub or against a tree. The Langa camp was also divided into four geographically separate sectors (A–D) to account for scavengers demonstrating a possible preference for one or more of these units. The plant community of sector A is dominated by *Dichrostachys cinerea*, and sector B has more *Commiphora* species and stonier quartzite terrain. Sector C is dominated by *Colophospermum mopane* and *Senegalia nigrescens* on sandy soil, and sector D by *D. cinerea* and *Combretum apiculatum* with sparsely interspersed with quartzite patches.

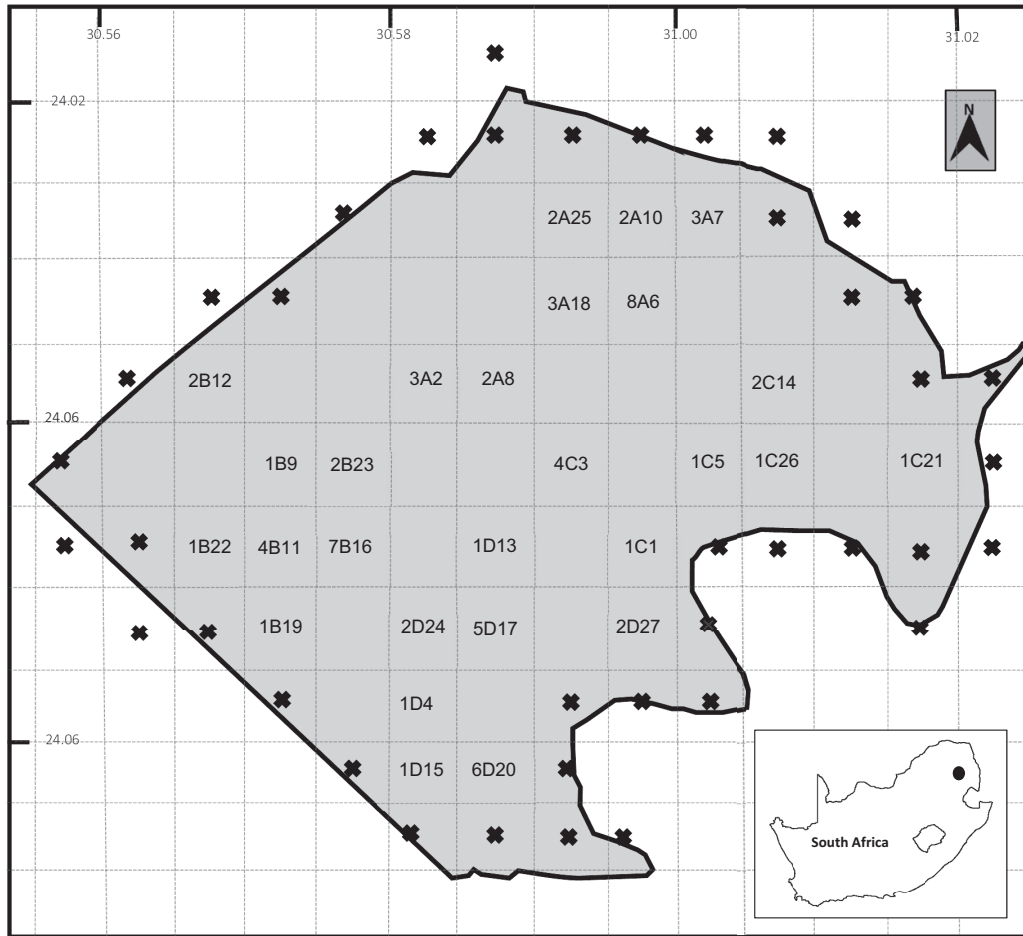


FIGURE 2 The Langa camp showing where the 27 experimental carcasses were placed. The first numerical number indicated the scavenger: African white-backed vulture (1), brown hyena (2), bateleur (3), leopard (4), African civet (5), tawny eagle (6), black-backed jackal (7) and honey badger (8). The alphabetical capital indicates the random sector (A–D) for the generalised mixed models allocated to each carcass. The second numerical number indicates the random number in which the carcasses were placed. For quadrat 1D4 for example, (1) the 1 indicates an African white-backed Vulture first fed on this carcass, (2) B was the random sector allocated for the generalised mixed models, and (3) 4 that this quadrat received an impala carcass fourth in the random sequence. The saltire crosses show the quadrats not considered for carcass placements as they partly fell outside the Langa camp. For scale, the quadrats were practically 548 × 460 m in size.

2.3 | Data collection

A scouting flash camera trap was used to record still images of the carcass throughout each placement. A time-lapse camera (Bushnell Trophy Cam HD Max) was placed 5 m from the carcass, with the carcass positioned diagonally in front of the camera. The time-lapse camera was set to capture an image every 30 s. The camera was attached to a tree or shrub trunk, metal stud or dropper pole and placed 1.2–1.7 m above the ground. The camera was also positioned with a clear view of the carcass, and the vegetation was not removed or altered to ensure the plant structure and cover remained unchanged around the carcass.

Because the camera traps were only aimed at and positioned relatively close to the carcass, we could not record which scavenger first detected the carcass outside this radius. Each carcass was checked to see if it was discovered and scavenged after 34 h of exposure and

once every 12 h after that. The camera traps did, however, make it possible to accurately record the time and scavenger species that arrived first within this radius and the scavenger that fed first. We then allocated the latter event to a circadian period (daylight or night-time) over three days and three nights. The two twilight periods, that is astronomical dawn and dusk (obtained from <http://www.timeanddate.com>), with associated poor light conditions, were added to the night-time. The camera was removed on the morning of the fourth day.

We recorded only which scavenger species was the first to arrive at the carcass and which scavengers fed first. The time it took for the carcass to be located was calculated from carcass placement to a scavenger arriving in the camera's field of view. The arrival of the first scavenger was assigned to a circadian period as either day or nighttime. The time it took for the carcass to be fed on was calculated from carcass placement to a scavenger feeding in the camera's field of view.

2.4 | Vegetation survey

To assess the vegetation structure at each sample site, we measured and calculated the growth form, canopy cover, and woody plant height and density (Edwards, 1983). In each of the 27 quadrats at which carcasses had been placed, and with the carcass placement site indicating the centre of the quadrat, an 8×8m sample site was demarcated using four dropper poles positioned in the four cardinal directions. All woody plants taller than 0.5m were classified as either a tree (single stem; 2→20m) or shrub (multi-stemmed; <0.5–5m) (Edwards, 1983). A 10m long extendable pole with a tape measure attached to the side was used to measure the height of each woody plant, and a mean and standard deviation of the plant height (in m) was calculated for the site. All woody plants within the sample site were counted to calculate the density of woody plants per 64 m² sample site.

Digital cover photography allows robust estimates of canopy cover, and this method is not influenced by variation in actual canopy cover or gap sizes within and between canopies (Chianucci, 2016; Chianucci et al., 2014; Poblete-Echeverría et al., 2015). The typical head posture of an avian scavenger flying over a carcass allows for a 45° field of view between the horizontal 0° and vertical 90°. Therefore, 45° photographs were necessary to estimate the relative vertical canopy cover above a carcass, that is, the reverse of what a vulture would see Martin et al. (2012). A 40cm tall tripod was positioned in the centre of the sample site at which the carcass was placed. A Pentax K100D (6 megapixels, 18–55mm Pentax lens) was orientated north, then

$$\text{model} = \text{glmer}(\text{Guild} \sim \text{Density} + \text{Height} + \text{Canopy} + \text{Shrub} + (1|\text{Sector}), \text{family} = \text{binomial}).$$

rotated vertically and levelled with a spirit level. Canopy cover photographs were taken in low light conditions as direct sunlight caused contrasting issues during image analysis (Chianucci, 2016). All photographs were captured with the lens set at 18mm zoom and focus set ∞

$$\text{model} = \text{glmer}(\text{Locating_time} \sim \text{Guild}/\text{Density} + \text{Guild}/\text{Height} + \text{Guild}/\text{Canopy} + \text{Guild}/\text{Shrub} + (1|\text{Sector}), \text{family} = \text{Gamma}(\text{link} = \text{"log"})).$$

(Martin et al., 2012). A vertical photograph was taken first; the camera was then angled 45° from vertical to take a fisheye photograph in each of the four cardinal directions.

Photographs were analysed with a scientific image-analysis program (ImageJ 1.50d) and then converted from RGB to 8-bit images (Nortjé et al., 2016; Schneider et al., 2012). The program combines the gaps within and between crowns and compares the pixel images with the leaf crown (Chianucci, 2016; Poblete-Echeverría et al., 2015). The image threshold, that is, partitioning the *image* into a foreground and background, was adjusted until the sky as background (= white) and foliage as foreground (= black) were visually separated. The number of black and total (black + white) pixels was then counted, and the % canopy cover was calculated as the fraction of black pixels over total pixels (Chianucci, 2016; Nortjé et al., 2016). The % canopy cover was calculated as the fraction of black pixels to fall upon scrub vegetation over total pixels.

2.5 | Data analysis

We labelled the (above) four vegetation parameters (mean and 1 std values) as Density (density of woody plants), Height (mean height of woody plants), Canopy (relative vertical canopy cover above a carcass) and Shrub (relative vertical shrub cover above a carcass). We then tested the effect of these four fixed (explanatory) variables on two response variables. In the first analysis, our response variable was binary, "Guild", consisting of diurnal or nocturnal scavengers, whichever first located the carcass. In the second analysis, it was a continuous variable, "Locating_time", which was the time taken for a scavenger to locate the carcass. We checked for collinearity between the vegetation variables using the R package *usdm* (Naimi et al., 2014). We calculated the Variance Inflation Factor (VIF) and retained any variables with VIF < 3. Since VIF values ranged between a minimum of 1.12 and a maximum of 2.66, we retained all four vegetation parameters. To assist with model convergence, we scaled all our vegetation variables using R's `scale()` function (McCleery et al., 2018).

Since our sites were relatively closely placed, they would have suffered from spatial autocorrelation. Furthermore, one response variable (Guild) was binary, and the other (Locating_time) was highly skewed. Therefore, we built generalised mixed models (GLMMs) in the R package *lme4* (Bates et al., 2015). In the first analysis (response variable guild), we built a logistic regression with "Sector" as a random variable. The full model was built as follows:

In the second analysis (response variable Locating time), we built a generalised linear mixed model fitted with a Gamma distribution and a log link function, again with the Sector as a random variable. The full model was built as follows:

We compared models within the two analyses using the corrected Akaike's Information Criterion (AICc) adjusted for a small sample size (Burnham et al., 2011). The Delta AICc (ΔAICc), Akaike weights (ω_i), and the Wald statistic "z" were calculated for each model. The best model was identified as the one with the smallest AICc value, and all models with $\Delta\text{AICc} \leq 2$ were considered to be competing models (Anderson & Burnham, 2002). Model selection and fitting were performed in R version 3.6.1 (R Core Team, 2019) using the *AICcmodavg* package (Mazerolle, 2023).

3 | RESULTS

3.1 | Scavenger guild

Fourteen carcasses were fed on during the day and 13 during the night. No carcasses were fed on both night and day (Table 1). Of

those scavenged during the day, 13 were on the first day and one on the second day. Of those scavenged during the night, eight were on the first night, four on the second night and one on the third night.

During the day, three avian scavengers, one vulture and two eagle species, were recorded at carcasses (Table 1). The white-backed vulture was the dominant scavenger to arrive first at the impala carcass (71%; 10 of 14 detections) (Figure 3), followed by three detections of Bateleur (*Terathopius ecaudatus*) and one detection of Tawny Eagle (*Aquila rapax*) (Table 1). In all daytime detections, the species that arrived first was the first to feed on the carcass.

During the night, five mammalian scavengers were recorded at carcasses, of which one species was exclusively nocturnal, and the rest were predominantly nocturnal (Table 1). A brown hyena (*Parahyena brunnea*) arrived first at the impala carcass during eight of 13 detections (62%) (Figure 4), followed by a leopard (*Panthera pardus*) and African civet (*Civettictis civetta*) on two occasions, and one black-backed jackal (*Canis mesomelas*) (Table 1). All the nocturnal scavengers were mammals, and no mammalian scavenger was recorded at any carcasses during the day. In two of the 13 night-time detections, the species that detected the carcass was replaced by a different mammal before it could scavenge: a black-backed jackal took over from an African civet, and a honey badger (*Mellivora capensis*) replaced a black-backed jackal.

3.2 | Vegetation parameters

There was a large amount of variation in the four vegetation parameters recorded at the 27 sites where impala carcasses were placed, with woody plant density varying from 0 to 93.5 plants/100 m²,

canopy cover from 4% to 81%, mean woody plant height from 0 to 8.8 m, and proportional shrub cover from 0 to 100%. On average, the percentage of canopy cover was 20% lower at carcasses located by diurnal scavengers than those found by nocturnal scavengers (Table 2). Similarly, the density of woody plants at carcass sites located by diurnal scavengers contained, on average, 31 fewer woody plants per 100 m² than those discovered by nocturnal scavengers. The top model included the density of woody plants and mean woody plant height (Table 2).

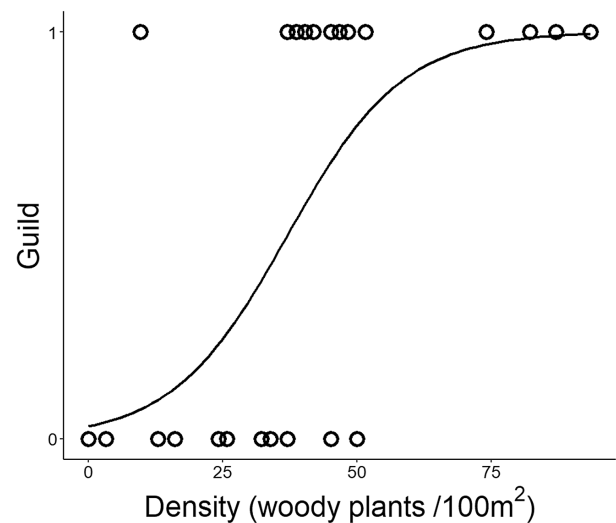


FIGURE 3 Predicted probability of either nocturnal (1) or diurnal (0) scavengers finding an impala carcass in relation to the density of woody plants, fitted with a logistic regression mixed model (see text for further details).

TABLE 1 Activity periods and scavengers' feeding preferences were recorded at Langa impala carcasses from 17 February to 7 June 2016 (IUCN, 2020; Piper, 2005; Simmons, 2005a, 2005b; Skinner & Chimimba, 2005).

Species	The first species to arrive	The first species to feed	Activity period	Carrion feeding preference	Conservation status	IUCN red list
<i>Diurnal avian scavengers</i>						
African white-backed vulture (<i>Gyps africanus</i>)	10	10	Diurnal	Obligate	Critically endangered	BirdLife International (2018b)
Bateleur (<i>Terathopius ecaudatus</i>)	3	3	Diurnal	Facultative	Near threatened	BirdLife International (2016)
Tawny eagle (<i>Aquila rapax</i>)	1	1	Diurnal	Facultative	Vulnerable	BirdLife International (2018a)
<i>Nocturnal mammalian scavengers</i>						
Brown hyena (<i>Parahyena brunnea</i>)	8	8	Nocturnal & crepuscular	Obligate	Near threatened	Wiesel (2015)
Leopard (<i>Panthera pardus</i>)	2	2	Largely nocturnal	Facultative	Vulnerable	Stein et al. (2020)
African civet (<i>Civettictis civetta</i>)	2	1	Nocturnal	Facultative	Least-concern	Do Linh San et al. (2019)
Black-backed jackal (<i>Canis mesomelas</i>)	1	1	All times	Facultative	Least-concern	Hoffmann (2014)
Honey badger (<i>Mellivora capensis</i>)	0	1	Mostly nocturnal	Facultative	Least-concern	Do Linh San et al. (2016)

FIGURE 4 A wake of African white-backed vultures (*Gyps africanus*) is feeding on the impala carcass in quadrat no. 1B9. For carcasses located by diurnal avian scavengers, the Canopy Cover recorded at this quadrat was the 12th highest at 57%, and the woody density at 28 plants/64 m² (4375 plants/ha). The photograph shows the 5-m time-lapse camera (30s) positioned directly behind the carcass.



TABLE 2 The four plant parameters were compared at sites first visited by diurnal (avian) versus nocturnal (mammalian) scavengers. The mean time to locate carcasses is means \pm STDs.

	Diurnal scavengers	Nocturnal scavengers	U test (p-value)
Mean (minimum and maximum times) time to locate carcasses (h)	6.5 \pm 6.66 (2.4, 28.7)	25.5 \pm 15.50 (11.7, 62.2)	
Proportion canopy cover (%)	40.2 \pm 18.95	60.0 \pm 13.99	39.5 (0.0133)
Density (woody-plants per 100 m ²)	22.04 \pm 15.98	53.60 \pm 23.89	23 (0.0010)
Woody plant height (m)	4.71 \pm 2.86	4.66 \pm 1.77	104 (0.5439)
Proportion shrub proportions (%)	64.5 \pm 29.89	73.2 \pm 15.69	85.5 (0.8080)

TABLE 3 Candidate models used to test differences in vegetation parameters at carcasses discovered by diurnal (avian) and nocturnal (mammalian) scavengers, using GLMM (family = binomial).

Rank	Models	k	AICc	Δ AICc	ω_i	L.L.
1	Density + Height	4	31.895	0.00	0.295	-11.04
2	Density + Canopy + Height	5	32.302	0.407	0.241	-9.72
3	Density + Shrub	4	32.846	0.952	0.183	-11.51
4	Density + Canopy + Height + Shrub (full)	6	34.088	2.193	0.099	-8.94
5	Density + Height + Shrub	5	34.264	2.369	0.090	-10.70
6	Density + Canopy + Shrub	5	34.285	2.390	0.089	-10.71
7	Null	2	41.732	9.837	0.002	-18.62

Note: The models are ranked in order of importance.

Abbreviations: AICc, Akaike's information criterion corrected for small sample size; k, number of parameters; L.L., log likelihood; Δ AICc, differences in Akaike's information criterion; ω_i , AICc weights.

There were two competing models: one that included density, height and canopy cover of woody plants, and one that included density of woody plants and proportion of shrub cover (Table 3). However, when examining the beta estimates for the variables in the three best models, only the density of woody plants was a relevant variable (Table 4), as the confidence intervals of the remaining variables all crossed zero (Table 5).

3.3 | Factors affecting locating time

Scavengers discovered all 27 carcasses, and either an avian or mammalian scavenger fed on them and none of the carcasses were visited or fed on by both guilds. The mean time taken to locate a carcass was 6.5 (\pm 4.3 STD) hrs for avian scavengers compared with 14.0 (\pm 7.8) hrs for mammalian ones (if the 11.5 hrs median daylight length

Models	Beta estimate	SE	z	Pr(> z)
Model 1				
Intercept	0.327	0.591	0.553	0.5802
Density	2.999	1.272	2.357	0.0184
Height	-0.951	0.818	-1.162	0.2453
Model 2				
Intercept	0.251	0.620	0.405	0.6855
Density	2.550	1.394	1.830	0.0673
Height	-2.125	1.273	1.422	0.1551
Canopy	1.810	1.390	-1.528	0.1264
Model 3				
Intercept	-0.059	0.533	-0.111	0.9118
Density	2.517	1.080	2.330	0.0198
Shrub	0.739	1.017	0.726	0.4678

Note: The bold shows significant variables and with confidence intervals of beta estimates that do not cross zero.

TABLE 5 Candidate models used to test the time taken to locate carcasses by diurnal (avian) and nocturnal (mammalian) scavengers, using GLMM (family=gamma).

Rank	Models	k	AICc	Δ AICc	ω_i	L.L.
1	Density+Height	8	419.035	0.00	0.727	-197.52
2	Density+Shrub	8	421.158	2.123	0.251	-198.58
3	Density+Canopy + Height	10	427.522	8.487	0.010	-196.89
4	Density+Height+Shrub	10	428.476	9.440	0.007	-197.36
5	Density+Canopy + Shrub	10	430.559	11.524	0.002	-198.40
6	Null	3	430.693	11.657	0.002	-211.82
7	Density+Canopy + Height+Shrub (full)	12	439.843	20.807	0.000	-196.78

Note: The models are ranked per order of importance.

Abbreviations: AICc, Akaike's information criterion corrected for small sample size; k, number of parameters; L.L., log likelihood; Δ AICc, differences in Akaike's information criterion; ω_i , AICc weights.

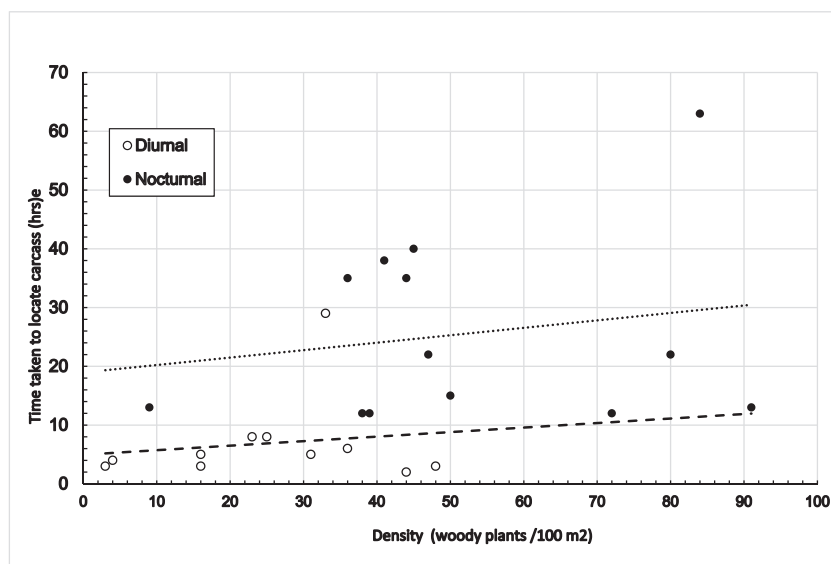


FIGURE 5 The relationship between the time taken to locate a carcass and the density of woody plants, plotted separately for diurnal (avian) and nocturnal (mammalian) scavengers. The top black dots and dotted line represents nocturnal scavengers and the bottom white dots and dashed line the diurnal scavengers.

during the study period is removed) (Figure 5). The top model was the one that included the density and mean height of woody plants (Table 5). There were no competing models. Within the top model,

only density was a relevant variable (with the 95% CI of its beta estimate not including zero), not height (95% CI of height did include zero) (Table 6).

TABLE 6 Beta estimates for fixed effects included in the top model (see Table 4) used to test the time taken to locate carcasses by diurnal (avian) and nocturnal (mammalian) scavengers, using GLMM (family = gamma).

Model 1	Estimate	SE	z	Pr(> z)
Intercept (diurnal)	5.884	0.2807	20.958	<0.001
Intercept (nocturnal)	7.180	0.3122	4.152	<0.001
Density (diurnal)	-0.0025	0.3595	-0.007	0.994
Density (nocturnal)	0.2322	0.1795	1.288	0.198
Height (diurnal)	0.2686	0.1693	1.587	0.112
Height (nocturnal)	0.2685	0.2024	1.327	0.185

Note: The bold shows significant variables and with confidence intervals of beta estimates that do not cross zero.

4 | DISCUSSION

4.1 | Nocturnal mammalian and diurnal aerial scavengers

During daylight hours, the quicker arrival of African white-backed vultures, and in greater numbers, compared to bateleurs or tawny eagles, was likely due to the vulture's larger non-sedentary population, which outnumbered the last two (BirdLife International, 2016, 2018a, 2018b). A soaring flock of African white-backed vultures can also extensively scan large areas for carcasses as multiple birds fly in an outstretched grid pattern while in visual contact with each other and other scavengers (Dermody et al., 2011; Jackson et al., 2008; Kane et al., 2014; Mundy et al., 1983; Piper, 2005). Of interest was that none of the smaller birds and mammals, which are typically used by avian scavengers as indicators, were first to arrive at a carcass (and recorded by the camera traps), for example, crows (*Corvus* spp.), kites (*Milvus* spp.), small cats (*Caracal caracal*, *Felis* spp.), mongooses (Herpestidae) and genets (*Genetta* spp.) (Jones et al., 2015; Schultz, 2007; Shaw et al., 2015).

Whereas avian scavengers employ visual clues to locate a carcass under cover of darkness, mammalian scavengers must principally wait for the decomposing odour to be released from the carcass before they can smell and find it (Kane et al., 2014; Selva et al., 2003). The brown hyena is particularly perceptive to the odour of decomposing carcasses; downwind, this species can smell carrion up to 4 km (Mills, 1978; Thorn et al., 2009). As the impala was culled the day before experimental placement, and with an 11 h 30 min median daylight length during the study period (12 April; Keisling, 1982), the cellular decomposition had ample time to start before placement of the carcasses (Crippen et al., 2015; Dekeirsschieter et al., 2009; Forbes & Perrault, 2014). In addition, removing the head from the carcass opened the body and thus enhanced the scent signature. Our fieldwork was also conducted during the late summer early winter period with maximum day temperatures ranging from 24 to 32°C (mean monthly rainfall 2–80 mm; Mucina & Rutherford, 2006), and these temperatures and moistures would have enhanced the microbial activity and invertebrate abundance that leads to higher decomposition rates (Braack, 1987; Jones et al., 2015; Richards et al., 2009).

We established that the temporal window in which avian scavengers can search for a carcass is not finite. Nocturnal mammalian

scavengers take over this role by the start of the first night. This mammalian–avian search pattern was reversed and repeated during each carcass deployment period for a maximum of three days until the experimental carcasses were located and eaten. Furthermore, the scavenger guild that discovers the carcass will inevitably devour it, which prevents the competing guild from benefiting from the food resource. It is thus clear that competition for impala carcasses took place indirectly between White-backed vultures and brown hyenas. There was also no physical contest between heterospecifics over a single food resource. Thus, a form of exploitative competition occurred where individuals of two guilds indirectly share a limiting resource in the same area (Amarasekare, 2002; Armstrong & McGehee, 1980; Bonaccorso et al., 2007). During this study, despite the avian diurnal scavengers given a head start to mimic the early morning death of small antelope (Mundy et al., 1992), the number of carcasses consumed by the two guilds was broadly similar, so there was no evidence of the one guild being superior to the other or removing the food from the inferior guild (Hardin, 1960).

Noteworthy was the finding that, although four of the five nocturnal mammalian scavengers recorded in this study are known to search for carrion during the day, especially the black-backed jackal (Hoffmann, 2014), the camera traps did not record these species at the carcasses during daylight hours. We thus found a clear separation in feeding periods between the diurnal multiscanning of the diurnal avian scavengers and the nocturnal prowling of the mammalian scavengers. The 27 carcasses placed out over 107 days probably provided enough food, that is, muscle, fat and bone, so that the two guilds did not have to scavenge outside their preferred or dominant activity period and thus compete directly with each other.

4.2 | Bush encroachment

In the Savanna Biome, woodlands and open grasslands are inversely related in space, providing essential ecosystem functions (Mograbi et al., 2015; Sankaran et al., 2005). The functionality of the Savanna transforms as the density of shrubs and small trees increases (Buitenwerf et al., 2012; Mograbi et al., 2015; Stevens et al., 2016). First, avian scavengers locate carcasses at a mean proportion canopy cover of 40%, and at this cover value, the fundamental ecosystem function of the savanna begins to fail (Archibald et al., 2009; Staver et al., 2011; Stevens et al., 2016). Second, avian scavengers located

carcasses at a mean woody density of 14 woody plants/64 m² (2188 plants/ha) and at densities of 12.8–16.0 woody plants/64 m² (2000–2500 woody plants/ha), the phytomass production of the Savannah grass layer and thus its grazing capacity becomes limited (Richter et al., 2001). When natural woody plants encroach into savannas during these two transformations, this biome loses its open canopy and avian scavengers.

On Langa, the woody plant density was positively related to the time it took for avian scavengers to locate a carcass. However, an unabated increase in woody plant density over a certain threshold will ultimately block avian scavengers from detecting carcasses (Bamford et al., 2009; Schultz, 2007). At low woody densities of 400–800 woody plants/ha (2.56–5.12 plants/64 m²) and with grazing capacity still intact (14–9 ha/Large Stocking Unit) (Richter et al., 2001), carcasses still tend to be highly detectable to avian scavengers. After all, for a white-backed vulture to locate a carcass from an altitude of 300 m, the carcass must be visible from the air and, per definition, located in an open area with minimal or no vegetation (Cardinal, 1998; Di Vittorio et al., 2018; Gavashelishvili & McGrady, 2006; Houston, 1974; Kane et al., 2014; Kendall, 2013; Selva et al., 2003). At Langa, the mean woody density for avian scavengers was 14 woody plants/64 m² (2188 woody plants/ha), appreciably higher than the 5.04 woody plants/64 m² (788 trees/ha) recorded for scavenging Cape vultures (*Gyps coprotheres*) at historic locations in the Waterberg, but still below the 16.64 woody plants/64 m² (2600 trees/ha) at which densities the latter vultures were unable to detect a carcass (Schultz, 2007). Bamford et al. (2009) found that Cape vultures were reluctant to land and take off 100 m from a carcass when the vegetation was 10.5 and 7 m tall, respectively, but the mean tree height at carcasses at Langa for avian scavengers with lower wing loadings was 4.7 m for all scavengers there, which is well within this limit.

For the nocturnal mammalian scavengers, bush encroachment had a completely different outcome, as this study provided evidence that under the shroud of Langa's dense stands of trees and shrubs, it was the facultative mammalian scavengers that had access to carrion. The dominant mammalian scavenger, the brown hyena, is more likely to be detected in scrub or woodland areas rather than grassland (Thorn et al., 2009; Wiesel, 2015).

Our mean value of 33 woody plants/64 m² (5156 woody plants/ha) is similar to that of woody densities recorded in other encroached savannas in southern Africa (Buitenwerf et al., 2012). These mammalian scavengers are also of conservation importance, for example, the leopard is listed as Vulnerable, and the brown hyena is Near Threatened (IUCN, 2020). Furthermore, if bush encroachment excludes aerial scavengers from the scavenging guild, the number of mammalian scavengers and their time at a carcass increase threefold (Ogada et al., 2012).

Managers of conservation areas in the African savanna biome, such as Langa, should, therefore, include a heterogeneous landscape that contains both densely wooded areas to enhance the retention of mammalian scavengers as well as open grassland to protect the Critically Endangered African white-backed vulture,

the Near Threatened bateleur and the Vulnerable tawny eagle (IUCN, 2020). These animals should not be regarded as mere scavengers present in an area, but conserving the ecosystem services of these scavengers is critical (Di Vittorio et al., 2018). Ultimately, habitat assessments for vultures should, at the outset, include an assessment of potential mammalian scavenger densities to understand how they, during daylight hours, compete and consort efficiently with avian scavengers.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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