RESEARCH ARTICLE

Carcass Density, Size and Visibility Do Not Significantly Differ Between Areas With and Without Spotted-Hyaenas (*Crocuta crocuta*), With Implications for Threatened Vultures

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ABSTRACT

Changes in predator guild composition can affect obligate scavengers through facilitation and competition dynamics. In Namibia, declines of spotted-hyaenas (*Crocuta crocuta*) may influence threatened vultures, either positively, via provisioning carcasses, or negatively, as dominant scavengers competing for carcasses. To examine potential mechanisms of influence of spotted-hyaenas on vultures, we compared carcass densities, carcass size (live weight estimated by species, age class and sex), and potential visibility of carcasses to vultures between sites with and without spotted-hyaenas across Namibia. We sampled thirteen private protected areas (PPAs), six with spotted-hyaenas present and seven where they were absent. Carcass densities were estimated for each PPA using line-transect sampling, recording a total of fifty-four carcasses. There were no significant differences in carcass density, carcass size or carcass distance to cover, as a proxy for visibility, between areas with and without spotted-hyaenas. These results do not indicate mechanisms of either strong facilitation or strong competition with vultures, suggesting that spotted-hyaena activity on these Namibian reserves is not detrimental to vultures, but equally may not result in increased carcass availability.

1 | Introduction

The on-going global declines in large carnivores (Wolf and Ripple 2017) may influence carcass availability for scavengers, such as threatened vultures. For example, predators facilitate scavengers by provisioning carcasses (Perrig et al. 2017; Wilmers et al. 2003), and their loss may cause linked declines in carcass-dependent scavengers (Nordli et al. 2024; Walker et al. 2018). Conversely, predators can also directly compete with scavengers by displacing them at carcasses and limiting their resource access (Hunter, Durant, and Caro 2007; Moleón et al. 2014). For

example, some predators may consume carcasses quickly due to their larger body size or social group structures, providing little facilitative benefit for scavengers (Henschel and Tilson 1988; Kruuk 1972; Macdonald 1983).

The decline of food availability for vultures is a threat to Old-World (Accipitridae) vultures (Botha et al. 2017). Production of carcasses suitable for vultures relies on several natural factors such as species densities, disease, stochastic events and for most prey species, predation (Pereira, Owen-Smith, and Moleón 2014). In some cases, wildlife mortality can be key in

determining habitat use by Old-World vultures, more so than wildlife density (Kendall et al. 2014). In this light, considering how wildlife mortality and carcasses are influenced by the presence, composition and density of predators may be crucial in identifying habitat suitability for vultures and targeting management practices to maintain it (Allen et al. 2015; Pereira, Owen-Smith, and Moleón 2014; Prugh and Sivy 2020).

Carcass availability and accessibility for obligate scavengers such as vultures can be spatially and temporally variable depending on predator presence, behaviour and the presence of cues needed for scavengers to detect carcasses (Moleón et al. 2019). Carcass visibility affects use by scavengers such as vultures (Hunter, Durant, and Caro 2007; Ogada et al. 2012; Pardo-Barquín, Mateo-Tomás, and Olea 2019; Smith, Laatsch, and Beasley 2017; Turner et al. 2017). Old-World vultures who live on the European, African and Asian continents are predominantly visual foragers, having poorly developed olfactory senses (Dermody, Tanner, and Jackson 2011; Ogada, Keesing, and Virani 2012; Oliva-Vidal, Sebastián-González, and Margalida 2022; Stager 1967), and tree cover can effectively exclude vultures from most carcasses (Malan, Walker, and Monadjem 2024; Ogada et al. 2012). Several environmental factors can influence the visibility and accessibility of a carcass to vultures including landscape and vegetation complexity (Bamford, Monadjem, and Hardy 2009; Malan, Walker, and Monadjem 2024; Oliva-Vidal, Sebastián-González, and Margalida 2022; Pardo-Barquín, Mateo-Tomás, and Olea 2019). Likewise, interspecific interactions and cues may also help vultures locate carcasses, such as visual and auditory signals used between vultures and predators (Jackson et al. 2020; Kane, Kendall, and Jackson 2017; Kruuk 1972). For example, an audio recording of spotted-hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) competing over a kill strongly attracted vultures even before mammalian facultative scavengers arrived (Jackson et al. 2020), suggesting coevolutionary interspecific ties.

In southern African savannah ecosystems, predation is a high cause of wildlife mortality (Pereira, Owen-Smith, and Moleón 2014). Spotted-hyaenas occur across many different biomes and vegetation densities and do not generally hide kills (Bohm and Höner 2015; Kruuk 1972), and thus may be particularly important in providing carcasses suitable for vultures. Spotted-hyaenas have a preferred wildlife prey weight range of 91–139+ kg (Clements et al. 2014; Hayward 2006; Owen-Smith and Mills 2008) and are able to subdue larger wildlife species (Kruuk 1972; Trinkel 2009b) such as wildlife in excess of 300 kg (Cooper, Holekamp, and Smale 1999; Kruuk 1972). Several studies highlight their aptitude for hunting over facultative scavenging (Cooper, Holekamp, and Smale 1999; Gasaway, Mossestad, and Standers 1991; Holekamp et al. 1997). With the availability of large carcasses being an important factor for some Old-World vultures (Hunter, Durant, and Caro 2007; Moleón et al. 2015; Naves-Alegre et al. 2022; Turner et al. 2017), this may make spotted-hyaena presence particularly important for vultures.

Spotted-hyaenas are declining (Bohm and Höner 2015; Jones et al. 2021) with an overall range reduction of 24% compared to their historical range (Wolf and Ripple 2017). Amongst the threats to spotted-hyaenas are persecution, road mortality and snaring. There is generally little conservation concern or

tolerance for spotted-hyaenas, and their densities are low within southern Africa (Hanssen et al. 2022; Lindsey et al. 2013).

Few studies have explored the mechanistic links between predators and subordinate scavengers such as vultures (Hunter, Durant, and Caro 2007). There are studies investigating the interactions among predators and scavengers at carcasses, but these have largely supplied their own experimental carcasses (Amorós et al. 2020; Moleón et al. 2015; Ogada et al. 2012), leaving the role of natural carcass facilitation largely unknown. This is important because the loss of predators like spotted-hyaenas may reduce large carcasses available to threatened vultures (Kruuk 1972). Alternatively, spotted-hyaenas readily scavenge and can consume large amounts of food in a single feeding bout (Henschel and Tilson 1988), sometimes leaving few remains for subordinate scavengers like vultures (Kruuk 1972). Therefore, we explored indications of whether spotted-hyaenas may facilitate or compete for natural carcasses.

In this study, we compare carcass availability between sites with and without spotted-hyaenas. To determine differences in carcass availability to vultures, we ask the following questions. Does spotted-hyaena presence affect the density of available carcasses? Specifically, is the density of large carcasses greater where spotted hyaenas are present due to their ability to hunt larger prey species, compared to similar-sized large carnivores? Second, does the distance of carcasses to cover, which could obscure the visibility of carcasses from above, differ between sites with and without spotted-hyaenas? Spotted-hyaenas tend not to hide their kills, but their presence may induce caching behaviour in other carnivores. We predicted that locations with spotted-hyaenas would support higher natural carcass densities, size and greater carcass visibility to vultures. The findings will aid our understanding of spotted-hyaena loss on carcass availability for vultures.

2 | Methods

2.1 | Study Sites

We sampled thirteen private protected areas (PPAs) across Namibia with sizes ranging from 64.6–730 km². Six of these PPAs (hereafter, 'sites') had resident spotted-hyaenas, and seven which did not (Figure 1). The Namibian climate is arid to semi-arid with two distinct seasons defined as wet (November–April) and dry (May–October), with an average annual rainfall across the study sites ranging from < 100 mm to 450 mm (Mendelsohn et al. 2022). The elevation extents of study sites ranged from 303 to 1822 m asl.

The different vegetation types represented across these sites included dwarf shrub desert transition, dwarf shrubland, acacia tree and shrub savanna, highland acacia tree and shrub savanna, thornbush shrubland and karstveld acacia tree and shrub savanna. The vegetation types can be further simplified into three distinct groups defined by the vegetation height: sparse, bushveld and acacia tree (Mendelsohn et al. 2022). These three groups were evenly represented amongst the sites between spotted-hyaena presence and absence. A summary of the terrain and vegetation structure at each site are shown in Table S1.
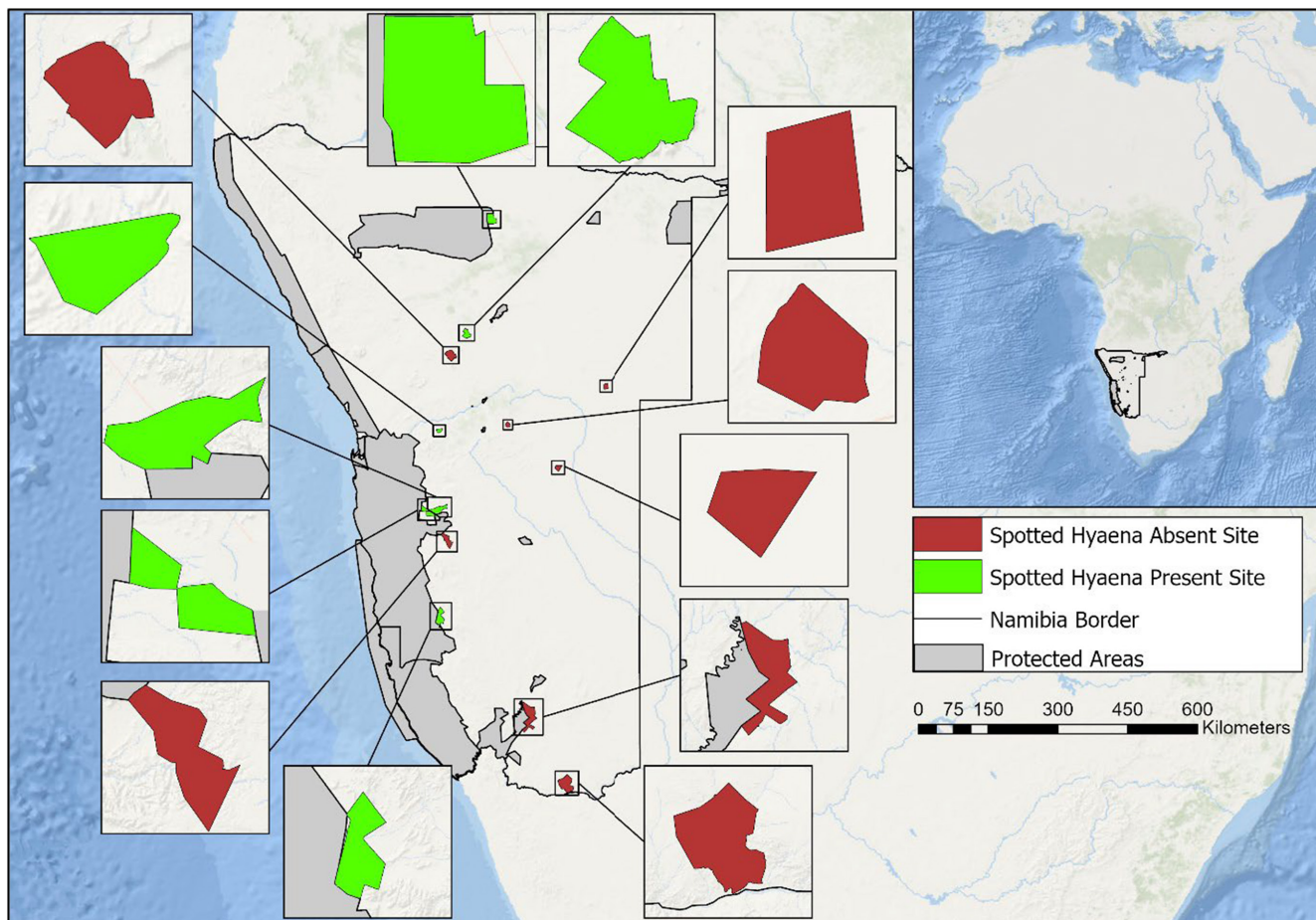
FIGURE 1 | Locations of the thirteen private protected areas (PPAs) sampled across Namibia.

TABLE 1 | Non-herbivorous wildlife species and livestock species presence divided between the six study sites with, and seven study sites without, spotted-hyaenas.

Species	Spotted-hyaena present sites	Spotted hyaena absent sites
Predators		
Lion *Panthera leo*	1	2
Leopard *Panthera pardus*	6	6
Cheetah *Acinonyx jubatus*	4	3
Brown hyaena *Parahyaena brunnea*	5	7
Black-backed jackal *Canis mesomelas*	6	7
Livestock		
Horse *Equus ferus caballus*	2	3
Donkey *Equus asinus*	0	2
Cattle *Bos taurus*	0	3
Vultures		
Lappet-faced vulture *Torgos tracheliotos*	6	7
White-backed vulture *Gyps africanus*	5	4
Cape vulture *Gyps coprotheres*	0	1

2.2 | Wildlife Communities

Each site was managed as a protected wildlife area with little to no introduced livestock present, and managers provided information about any livestock present (which were included under wildlife prey in this study) and the different free-roaming predator species and vultures that had been recorded at each site (Table 1). The diversity of wildlife prey species, defined as herbivores over an adult body weight threshold of 10 kg, ranged from one to two to >eight species (Table S2; Mendelsohn et al. 2022).

2.3 | Field Data Collection

Each site was visited for two to three weeks between February and mid-September 2023. This encompassed the late wet season and the majority of the dry season. This was done to capitalise on most wildlife having birthed and the juveniles offering an influx in prey densities and the dry season providing food limitations and higher disease probabilities to maximise natural carcass production opportunities (Pereira, Owen-Smith, and Moleón 2014).

To collect data on both available wildlife prey and carcasses, existing roads at each site were driven systematically as line transects at a slow continuous speed (10–30 km/h) for two to five hours per day for five consecutive days a week, searching for both carcasses and live wildlife prey species. Following line transect sampling techniques outlined by Karanth and Nichols (2017), a given road was not travelled more than once a day, and sampling was stopped when a transect neared the vicinity of a previously sampled transect from the same day. The distance between adjacent transects depended on the established road network at each site, and longer roads that varied in direction (> 45°) were separated into more than one transect. Transects had their start and end points randomised to avoid overlapping perpendicular areas (600 m on either side of a transect). To ensure all habitat types, when present at any given site, were sampled, roads that traversed different habitats were used instead of preferentially sampling only open habitats. Sampling occurred once to twice daily, depending on the study site size, within the time frames of 08:00–12:30, and/or 14:30–18:00. Distances travelled were measured using a Garmin eTrex10 handheld GPS. During transect surveys, all carcasses and individuals of wildlife prey species were recorded.

Carcasses were not included if they comprised only skeletal remains, highly desiccated carcasses with no soft tissues remaining or if within 1 km of 'bone pits' where carcasses of euthanised or otherwise human-killed animals were discarded. These exclusions ensured that no potential bias of anthropogenic facilitation arose, and because we were interested only in carcasses likely to be used by vultures during the sampling period, no signs of previous availability. Once carcasses fitting the selection criteria were located, the species was identified, and the percent of soft tissue already consumed was estimated. The approximate age and sex of the carcass were identified where possible to enable estimates of the live weight prior to death (Table S3; species-specific age and sex weights obtained from Estes (2012) and Hayward (2006)). The distance of the carcass from the transect being driven was also measured, to enable estimation of carcass density for each property accounting for differences in detectability. Reports of carcasses by field staff at sites were taken into account and occasionally altered route planning on given days.

At each carcass, surrounding environmental factors were measured. The distance in meters to the nearest feature cover high enough to obscure visibility from above was recorded using a laser range finder or satellite imagery from Google Earth when more appropriate for further distances in sparse areas (Figure 2). Features considered able to obscure carcasses included trees, large shrubs, rocky outcroppings and overhangs, and solid human structures (e.g., buildings or above-ground water tanks).

During the line transect surveys, in order to identify the potentially available wildlife prey, we recorded individuals of all potential wildlife prey within the typical size range preferred by large mammalian predators in Africa (Clements et al. 2014; Owen-Smith and Mills 2008), and the mean carcass size preferred by most vultures (Moleón et al. 2015). Wildlife prey species included all terrestrial vertebrates ≥ 10 kg adult body weight up to 550–1200 kg (adult giraffe, *Giraffa camelopardalis*, Table S3). Livestock species within the weight range, if present at sites, were included as available wildlife prey species. Similar-sized conspecifics or species belonging to the same genus (e.g., zebra spp. *Equus*, impala spp. *Aepyceros* and wildebeest spp. *Connochaetes*) were grouped. Species smaller than this size range (e.g., *Lagomorphs*) were omitted because they are usually wholly consumed when predated, leaving little to no carcass remains for scavengers.
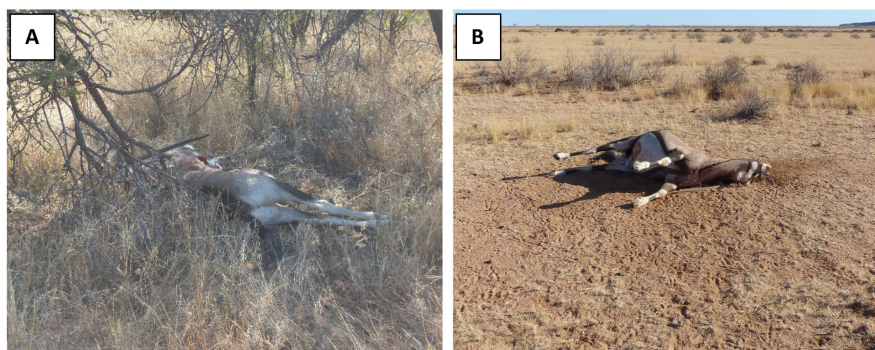
FIGURE 2 | Examples of oryx (*Oryx gazella*) carcass visibility to vultures located in dense vegetation with almost complete canopy cover (A), and carcass visibility located in open and sparse vegetation (B).

During wildlife prey counts, care was taken to minimise 'double counting' by recording group size and species, taking note of the animals' direction of travel, and foregoing recording a future sighting if any doubt was present of it being a re-sighting. Also checking the periphery of the cluster for their direction of movement so that further dispersed group members were not recorded separately. The sighting angle to individuals or groups detected was determined using a standardised protractor sheet, demarcating 5° increments from 0° (straight ahead on transect) to 90° (perpendicular to transect travel) on either side of the 0° direction of travel. This same method was used for sightings detected past the 90° increment, covering a full 360° radius at 0°–90° increments. Thus, a 40° sighting recorded in front of or behind the 90° angle was still recorded as 40°. Detection distances to individuals and clusters were measured using a laser rangefinder with 6×25 magnification and a 15–600 m range accuracy of ±1 m (Lite Optec LR1). When the distance to the sighting could not be accurately measured, then the distance to the closest vegetation or structure (e.g., large rock) to the sighting was used. All measurements were recorded from the location of the initial sighting.

2.4 | Density Estimation

To explore the effect of spotted-hyaena presence on carcass density and size, we first estimated wildlife prey and carcass densities using Distance 7.5 software (Thomas et al. 2010). This assured an estimated density for each of the variables based on detectability and sampling effort. Because transects were sampled multiple times during the sampling at each site, the effort data were pooled from all visits for individual transects, and the survey effort was entered as the line lengths multiplied by the effort (Buckland et al. 2015). The covariates included in the Distance analyses included species, cluster size, time of day, terrain ruggedness index (TRI) and vegetation density index (VDI) (mean site TRI and VDI shown in Table S1). The key function and series expansion model best fitting the data was chosen by the engine for analysis (Marques et al. 2007). Due to the distance accuracy limitation of the laser rangefinder, models were truncated to exclude sightings with a perpendicular distance beyond 600 m before running analyses.

2.5 | Statistical Analyses

Two-sample, two-tailed t-tests were used to compare carcass density (adjusted for detectability by unit per km per transect) between sites with spotted-hyaenas present and absent. We also used t-tests to compare total wildlife prey density and large prey density between site types, to explore whether wildlife prey availability was confounded with spotted-hyaena presence. Large wildlife was defined as having a body weight ≥ 100 kg (Table S2) based on Moleón et al. (2015). To examine the effect of site type (spotted- hyaena present vs. absent) on the estimated live weight of large carcasses (large live weight) at sites ($n = 34$), we first checked the estimated large live weight data for normality using a Shapiro–Wilk test and for homogeneity of variance using a Bartlett test. As the data fulfilled both assumptions, to test the effect of spotted-hyaena presence on large carcass density, we used a linear mixed effects model. Site was included as a random effect and spotted-hyaena presence, lion presence (as the only other large predator regularly targeting prey above 100 kg; Clements et al. 2014; Owen-Smith and Mills 2008), and large wildlife prey density were fixed effects (to account for the availability of large prey). The model was fitted by maximum likelihood estimation. The resulting model was tested and found to be within acceptable limits of outcome and predictor linearity, variance of residuals and normality of residuals assumptions. All analyses were done in R 4.4.2 (R Core Team 2020).

Finally, we compared carcass distance to the nearest cover between sites with and without spotted-hyaenas. The carcass distance to the nearest cover did not have a normal distribution, so the data were divided into two categories between 'covered' (0–1.0 m) and 'further away' (> 1.0 m) distances to create a 2×2 table with spotted-hyaena presence and absence. A chi-square test of independence was used to compare whether carcasses were further away from cover at sites with spotted-hyaena presence than at sites without.
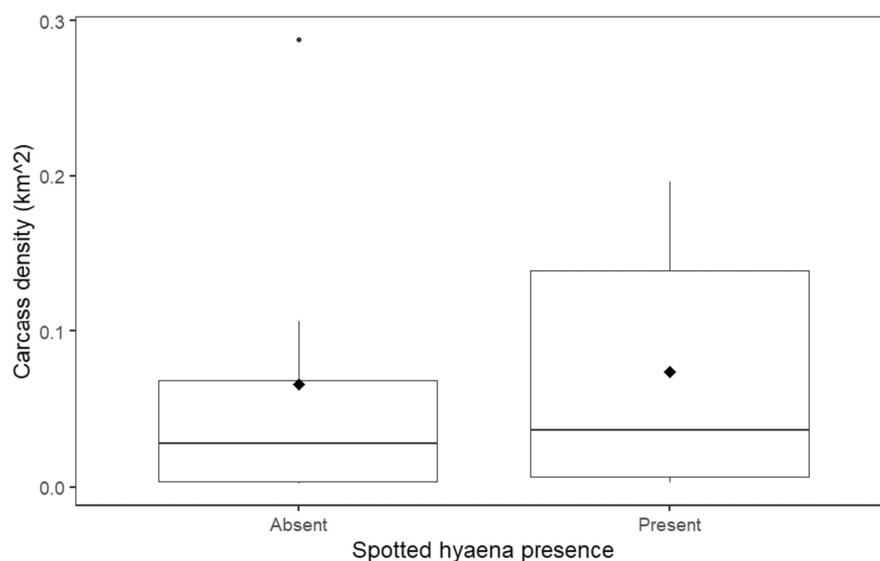

FIGURE 3 | Carcass density per km^2 at the six sites with and seven sites without spotted-hyenas.

3 | Results

3.1 | Carcass Density

A total of fifty-four carcasses were recorded across all sites, with twenty-four at sites with spotted-hyaenas and thirty at sites without spotted-hyaenas. There were no significant differences in carcass density between sites with and without spotted-hyaenas (present: 0.074 ± 0.035 per km²; absent: 0.066 ± 0.040; $t = -0.145$, $d.f. = 10.993$, $p = 0.887$; Figure 3) nor for wildlife prey density (present: 0.853 ± 0.192; absent: 0.893 ± 0.233; $t = -0.134$, $d.f. = 10.894$, $p = 0.896$).

3.2 | Carcass Size

The linear mixed effects model suggested that large carcass density did not differ significantly between sites with and without spotted-hyaenas (Table 2). Similarly, large carcasses (≥ 100 kg) were present at 75% (18/24) and 53% (16/30) at sites with and without spotted-hyaenas, respectively, but this difference was not significant ($t = 0.580$, $d.f. = 7.704$, $p = 0.579$). The presence of lions also did not significantly affect carcass size nor did the density of large prey (Table 2).

3.3 | Carcass Visibility

Carcass distance to cover (as a proxy for visibility) did not differ significantly (X^2 [1, $N = 54$] $= 0.117$, $p = 0.732$) between sites with and without spotted-hyaenas.

4 | Discussion

We found no differences in carcass availability, size and visibility between sites with and without spotted-hyaena presence. Our first question was to determine whether carcass density and size differed between sites with and without spotted hyaena presence. Our results suggest that in our study system, spotted-hyaena presence neither positively, through additional predation, nor negatively, through competitive scavenging, affect carcass availability in relation to other large predator presence. However, this study was conducted in areas of relatively low spotted-hyaena densities, with estimates of 0.008–0.09 spotted- hyaenas/km² (Hanssen et al. 2022; Trinkel 2009a), where such effects may be less pronounced. A replicate study carried out in areas of higher spotted-hyaena densities, such as in east African regions, with estimates of 0.12–0.94 spotted-hyaenas/km² (Holekamp et al. 1997; Kruuk 1972; Mwampeta et al. 2021) could yield differing results.

Increases in spotted-hyaena hunting group size have been directly correlated to increase in targeted wildlife prey size (Trinkel 2009b). Studies directly tracking spotted-hyaenas on hunting or foraging excursions generally recorded smaller group sizes in Namibia (Gasaway, Mossestad, and Standers 1991; Trinkel 2009b). In the case of our study, Namibia's low spotted-hyaena density (Fouche et al. 2020; Hanssen et al. 2022) and thus smaller clan sizes may mean that spotted-hyaenas at the sites were less likely to consistently target larger prey (Gasaway, Mossestad, and Standers 1991; Kruuk 1972), and therefore did not affect the density of larger carcasses in this study. It is worth noting that the preferred wildlife prey size ranges of 91–139+ kg estimated for spotted-hyaenas (Clements et al. 2014; Owen-Smith and Mills 2008) were observed in this study. A slightly higher, but not significant, proportion of carcasses above 100 kg estimated live weight were encountered at sites with spotted hyaenas (75%) than at sites without (53%).

Our second question was to examine and compare carcass visibility from above. Using carcass distance to cover as a proxy, our results show that carcass distance to cover was not influenced by the presence or absence of spotted hyaenas. At only one of the sites was caching of carcasses observed, and this was at a site with high densities of predators (which tends to increase carcass caching; Edwards et al. 2019; Noack et al. 2019). However, we recognise that the line transect sampling method likely biased our detections, with more concealed carcasses less likely to be detected. An aerial search method using low-flying aircraft (Chase et al. 2018; Jachmann 2002), or drones (Rietz et al. 2023), could have yielded higher carcass detections.

Our results did not provide evidence for either greater facilitation of carcasses suitable for vultures by spotted-hyaenas or, indeed, large predators in general, but equally did not support the idea that spotted-hyaenas reduce carcass availability for vultures through competition. Thus, when managing for natural carcass availability to threatened vultures in Namibia, and throughout southern Africa, spotted-hyaenas should not be considered negatively as a threat to resource availability. This topic has had surprisingly little attention considering both vultures and large predators continued global declines. Further investigations into carcass use by the larger vertebrate scavenger guild between areas of spotted-hyaena presence or absence could reveal a greater understanding of interspecific relationships, similar to work by Wirsing and Newsome (2021) on large canid impacts on scavenging dynamics. Interspecific cues (Jackson et al. 2020) and nutrient resource facilitation (Abraham et al. 2021; Richardson, Mundy, and Plug 1986) involving spotted-hyaenas and scavengers have been previously documented, and their relationship with threatened vultures

TABLE 2 | Linear mixed effects model output for the effect of predator and prey on the density of large carcasses (≥ 100 kg, $d.f. = 33$).

Predictor variables	Estimate	SE	t-value	p
Intercept	192.609	19.412	9.922	< 0.001
Spotted-hyaena presence	14.444	22.693	0.636	0.540
Lion presence	−10.371	29.638	−0.350	0.731
Large prey density (≥ 100 kg)	−3.413	9.589	−0.356	0.725

should be further investigated. Our results are informative and representative of a natural-state observational study without introducing carrion influx biases inherent in anthropogenic carcass provisioning.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available at: https://doi.org/10.48610/a7bd235.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.