Title: Animal scavenging on pig cadavers in the Lowveld of South Africa

Authors: Keyes CA[1], Myburgh J[2], Brits D[3]

Affiliations:

[1]Department of Forensic Medicine and Pathology, School of Clinical Medicine, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]Department of Anatomy, School of Medicine, Faculty of Health Sciences, University of Pretoria, South Africa

[3]Human Variation and Identification Research Unit, School of Anatomical Sciences, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

Corresponding author: Craig A. Keyes; email: craig.keyes@wits.ac.za; postal address: Faculty of Health Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

Source of Funding: National Institute of Justice and the Forensic Technology Center of Excellence along with the American Academy of Forensic Sciences Humanitarian and Human Rights Resource Center

Declaration of Interest: None

Presentations: Accepted for presentation at the 48th Annual Conference of the Anatomical Society of Southern Africa in Durban. South Africa.

Acknowledgements: The authors acknowledge the financial assistance of the National Institute of Justice and the Forensic Technology Center of Excellence along with the American Academy of Forensic Sciences Humanitarian and Human Rights Resource Centre. Also acknowledged are GHB Farms and Mr. Dries Du Plessis for providing the pig cadavers; Mr. Richard Keyes and Ms. Allison Gilbert for assistance in the laying out of the pigs and the mapping of the scattering patterns; Wits Rural Facility, Prof. Wayne Twine and Mr. Cameron Watt for providing the research site; Ms. Tracy Reindorp who took the photographs in this article; and Ms. Rethabile for her assistance with the maceration of the bones.

Highlights

- Vultures are dominant scavengers (hooded, white-backed, and lappet-faced vultures)
- Marabou stork, mongoose, genet, civet, warthog and honey badger also scavenged
- Vultures skeletonized pig cadavers rapidly between 5 - 98 minutes
- Remains were scattered over 157.9m^2/1705.5ft^2 with a radius of 7.09m/23.3ft
- Scavenging marks on bone by vultures and warthogs were described

Abstract

Scavenging animals often scatter skeletal remains of forensic interest and leave bite marks. This study aimed to identify scavenging animals in the rural Lowveld of South Africa and to describe their scattering pattern and bite marks on bone. Ten pig cadavers (*Sus scrofa domesticus*) (40-80 kg) were placed at the Wits Rural Facility, Limpopo, South Africa during the summer and winter seasons. Motion activated cameras recorded the scavenging. Scavenger species were identified and their behaviors, scattering pattern, and bite marks were described. Scavenging was primarily by vultures (hooded, white-backed, and lappet-faced). Marabou stork, slender and banded mongoose, genet, civet, warthog and honey badger also actively scavenged. Vultures began to scavenge the pig cadavers after 18hrs in summer and between 26-28 hours in winter and skeletonized pig cadavers rapidly between 5 - 98 minutes. Skeletonization occurred more rapidly and diffusely in summer while winter cases were densely scattered. Overall the scattered remains were within an area of 157.9m^2/1705.5ft^2 with a radius of 7.09m/23.3ft. Vultures cleaned bones thoroughly with very minimal markings - primarily nonspecific scores. The described scattering pattern and bite marks will assist in the recovery and analysis of scavenged remains.

Key words: taphonomy, scavenging, vulture, South Africa, scattering

Introduction

An important part of any forensic investigation is the recovery of remains. The quantity of evidence available to forensic investigators for analysis is determined by the quality of a scene's management. Young *et al.* (1) highlighted that 53% of police specialists (n=90) who participated in a survey on scavenging in a forensic context, in the United Kingdom, indicated that they had been involved in a search for scattered scavenged human remains (1). The scattering of remains by scavenging animals presents an obstacle to the recovery of forensic evidence. Regrettably, there are no international standardized protocols for the search and recovery of scavenged and scattered human remains. A large proportion of the investigators surveyed by Young *et al.* (1) (80.83%) indicated that they were unable to recover the entire set of human skeletal remains even when assisted by a cadaver dog (1). In a subsequent study, Young *et al.* (2) found that investigating officers with an understanding of scavenging behaviors were twice as successful in the recovery of skeletal remains than those without the same knowledge (2). It is therefore pertinent to have an understanding of the scavenging animals which are active in an area of forensic interest, and an understanding of their scavenging behavior and scattering patterns.

Some scavenging animals commonly associated with the post-mortem modification of human remains include dogs, rodents, birds, coyotes, vultures, fish, crabs, turtles, opossum, and raccoons (3, 4). House pets have also been recorded to scavenge on their deceased owner (5). Other less common animals which have opportunistically scavenged on forensic cases include wolves, leopards, and lions (6, 7). The scavenging animals that are active are often geographically isolated or unique. North American scavenging studies of a forensic nature have included wolves, coyotes, rodents, raccoons, foxes, opossums, striped skunks, crows, and turkey vultures (7, 8). European research has described scavenging by deer, buzzard, carrion crow, wood mouse, and gray squirrel (7). In African and Asian countries, large felids such as lions, leopards and tigers have been known to occasionally scavenge on human remains (6). South African research on animal scavenging and scattering behaviors in a forensic context is lacking with only a few studies having been published in South Africa (9-11).

It is of forensic importance to understand the behaviours of these scavenging animals, such as their scattering patterns. The pattern of scattering of elements from their original site of deposition has been shown to be specific to different scavenging animals (12). Bones in particular are often disarticulated by scavengers from a body and moved from the original area of deposition. For example, skulls are often removed and buried elsewhere as a form of food storage by raccoons and coyotes (13). The disarticulation and scattering of skeletal elements has shown to extend over a large area (12). Animal scavenging also often cause some trauma or modification to skeletal elements which is often not related to the feeding of the animal but rather the relocation of the remains. For example, the previously fused sutures of the cranium often split open when a skull is scattered away from its original depositional site by a scavenging animal (13).

The morphology and location of animal bite marks on skeletal remains and the state of the bones can be indicative of the species of the offending scavenger since different species have unique preferences for body regions and decomposition stages (11). Dogs commonly bite the head and neck of decedents (14). Pickering and Carlson (6) found that the skeletal elements most likely to be recovered after leopard feeding, are the C1 and C2 vertebrae, scapulae, os coxae and long bones of the limbs, as they are not consumed in their entirety. A number of other skeletal elements may be recovered in the scat including fragments of thoracic and lumbar vertebrae, clavicles, patellae, and the bones of the hands and feet; including the carpals, tarsals, and phalanges (6). Felids (including lions, leopards, and caracals) prefer to gnaw the greater trochanter of the femur and greater tubercle of the humerus leaving deep, parallel furrows (11). Bite marks caused by the scavenging activities of rodents are common on skeletal remains that are dry and weathered (15) – thus the timing of skeletal trauma can be assessed.

The behavior of scavenging species is variable. Knowledge of how scavengers behave and when they are active can assist in the reconstruction and timing of post-mortem events. The timing of when scavenging trauma occurred might be broadly estimated if the identity of the scavenger can be inferred from the trauma it has inflicted. For example a rudimentary estimated post-mortem interval could be established in cases of vulture scavenging. When environmental and weather conditions are favourable, cadavers can be completely skeletonised by vulture scavenging in less than 12 hours (12).

The sequencing of trauma caused by different scavenger species may be possible as Young *et al*. (7) observed, in their European study, that there was never more than one scavenging species feeding on a cadavers at one time and never more than two individual animals of the same species scavenging a cadaver at one time. A study of these behaviors has the potential for the development of a time-line in a forensic case where understanding the post-mortem sequence of events is crucial.

Literature of a forensic nature identifying scavenging animals, their behaviors, and scattering patterns in South Africa is severely lacking. In rural South Africa, the proximity of humans to wild animals is high. Animal attacks are common and often involve tourists in game reserves and poachers. Human skeletal remains are often recovered in such rural locations (11). Therefore, the aim of this study is to identify the scavenging animals of forensic significance in a rural region of South Africa and to describe the animals' behavior and scattering patterns as well as the bite marks left on the remains. The results from this study will assist in the more thorough collection and analysis of scattered remains.

Methods

Research was conducted at the Wits Rural Facility (WRF) which is a rural campus of the University of the Witwatersrand situated near the border of the Kruger National Park game reserve (Figure 1). The WRF is a 315 hectare estate of savannah woodland in the central Lowveld of the Limpopo Province. The WRF is home to a variety of antelope, large cats (serval and caracal), vervet monkeys, baboons, and giraffes. The WRF is neighbored by private game reserves containing elephant, buffalo, lion, leopard, and hyenas - which occasionally cross the fences into the WRF.

The study sample comprised of 10 domestic pig cadavers (*Sus scrofa domesticus*) weighing between 40-80kg. The pigs were donated by a licensed pig farm and died from natural causes due to hemorrhagic bowel syndrome, commonly called red gut. This is commonly caused by Lawsonia intracellularis or Clostridium perfringens and is a common cause of death experienced in large pig farms. Such pigs are often used in forensic decomposition and taphonomy research (16).

Five pigs were placed at the site in August (winter) and five in October (summer). Five pigs were placed under trees (three in summer; two in winter) and five were exposed in the open (i.e. avian view not obscured by foliage) (two in summer; three in winter). The pigs were placed at least 50m apart from each other (Figure 1).

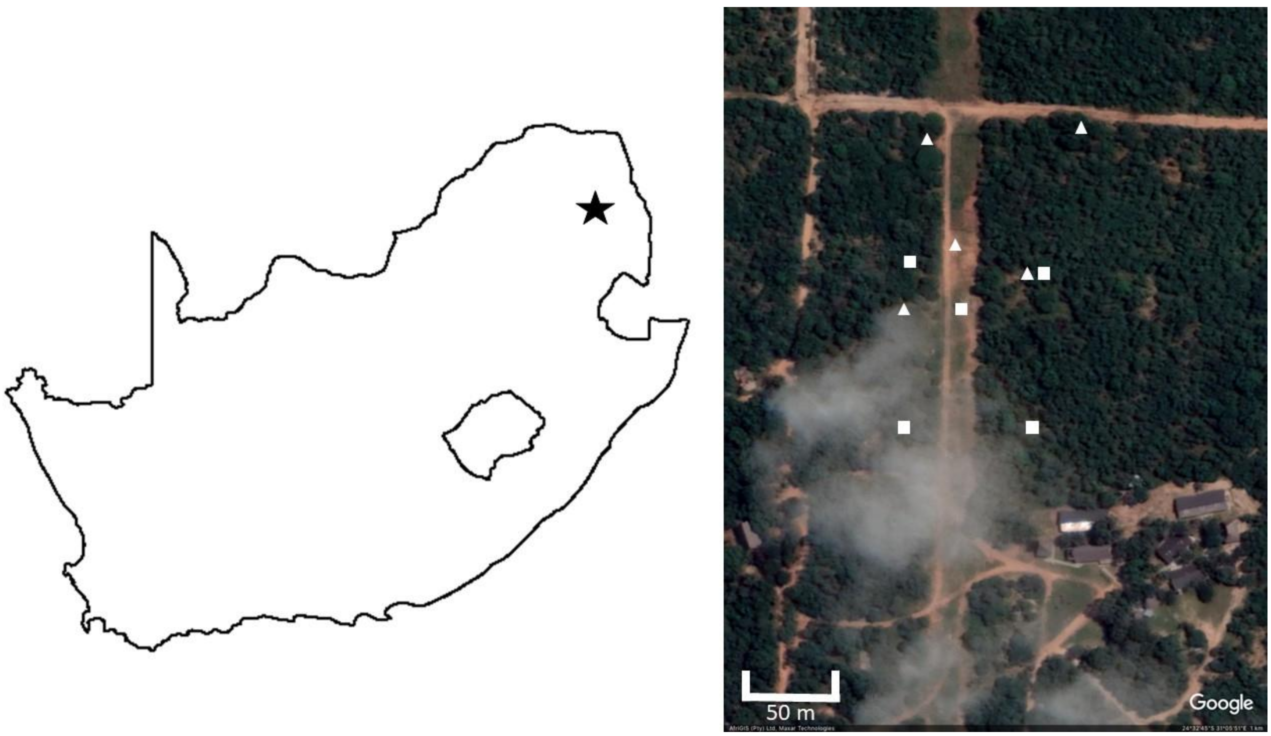

Figure 1: Location of Wits Rural Facility in South Africa (star in the map on left) and the approximate location of where the pigs were placed (winter pigs marked with a triangle and summer pigs marked with a square) on a Google Earth photograph of the Wits Rural Facility

The first five pigs placed at the WRF (in winter) were secured in place by a chain around the torso, secured to a nearby tree or fence to facilitate longer viewing and recording times of the scavenging activity before remains are disarticulated and scattered beyond the view of the cameras. However this was deemed unnecessary after the first five pigs were studied because the scavenging of the remains largely fell within the scope of the camera and were recorded. As such, subsequent pigs placed in summer were not secured by chains. The scavenging and scattering of remains were not influenced by the chains.

Motion activated, infrared Bushnell Trophy Cam HD Essential E2 12MP Trail cameras were used to photograph the scavenging of the cadavers. The cameras were set to the highest sensitivity, took three consecutive photographs when activated by motion, with a five second interval between motion activation.

The photographs captured by the cameras were used to identify the scavenger species, describe the animal behavior including the time of day it is active, the number of scavengers active at a given time, the season it is active, the decomposition stage it is active, and the body region it prefers to feed upon. Due to the rapid rate of scavenging, the decomposition stage was simply recorded as fresh or skeletonized.

After the remains were skeletonized and scattered, the location of each element was located using a spiral search method and remains were flagged. Each surviving element was mapped using a grid pattern method common in archaeological and forensic anthropological practice.

The bones were macerated to remove all remaining soft tissues for bite mark analysis. An external light source in the form of a flashlight with controllable light intensity was used to locate and observe the trauma. The remains were visited daily and the visible bone modifications were recorded *in situ*. If only one species was recorded by the cameras to scavenge on the skeletal element that day, that species recorded as the perpetrating scavenger. The scavenging bone damage, which was observable after maceration, was directly assigned to a scavenger species if the damage event was captured on camera, or indirectly by comparing the patterns described in previous research (11, 17, 18).

Results

A number of animals actively scavenged on the pig cadavers, including the white-backed vulture (*Gyps africanus*), hooded vulture (*Necrosyrtes monachus*), lappet-faced vulture (*Torgos tracheliotos*), marabou stork (Leptoptilos crumenifer), common large-spotted genet (*Genetta tigrina*), African civet (*Civettictis civetta*), slender mongoose (*Galerella sanguinea*), banded mongoose (*Mungos mungo*), common warthog (*Phacochoerus africanus*), and honey badger (*Mellivora capensis*) (Figures 2-4; Table 1). Bush pig (*Potamochoerus larvatus*) and giraffe (*Giraffa*) were attracted to the cadavers, however they were not recorded actively scavenging the remains (Figure 4).

The different vulture species and marabou storks would scavenge together at the same time however all other scavenging species would not scavenge at the same time as another species. These other species would also scavenge in isolation (i.e. only one single animal would scavenge at a time) with the exception of the honey badgers and banded mongooses which both scavenged as a pair (Table 1). Ribs were the most common skeletal element scavenged in this study (Table 1). All of the scavengers were active when the remains were skeletonized, however the white-backed vulture, hooded vulture, and common large-spotted genet were also active in the early stage of decomposition.

The white-backed and hooded vultures, marabou stork, common large-spotted genet and slender mongoose were active and scavenged year-round. The lappet-faced vulture, African civet, and banded mongoose were only observed in winter while the honey badgers and warthogs were only observed in summer (Table 1).

Figure 2: Avian scavengers including white-backed vulture (top left), lappet-faced vulture (top right), hooded vulture (bottom left), and marabou stalk (bottom right)

Figure 3: Smaller mammalian scavengers including slender mongoose (top left), banded mongoose (top right, common large-spotted genet (bottom left), and honey badger (bottom right)

Figure 4: Larger mammalian scavengers including giraffe (top left), African civet (top right), warthog (bottom left), and bush pig (bottom right)

Table 1: The scavenging behaviors of Lowveld scavenging animals

Animal	Maximum number of animals of the same species active at the same time at the same cadaver	Decomposition stage active	Body region preference	Time active	Season active
White-backed vulture	40	Early, skeletonized	No particular preference noted	Diurnal	Summer & winter
Hooded vulture	4	Early, skeletonized	Abdomen, intestines, anus (head inserted)	Diurnal	Summer & winter
Lappet-faced vulture	1	Skeletonized	No particular preference noted	Diurnal	Winter only
Marabou stork	2	Skeletonized	Ribs, scapula and loose skin	Diurnal	Summer & winter
Common Large-spotted Genet	1	Early, skeletonized	Anus (head inserted) and ribs	Nocturnal (late evening)	Summer & winter
Slender mongoose	1	Skeletonized	Skin and ribs	Diurnal (early morning)	Summer & winter
Warthog	1	Skeletonized	Ribs and vertebrae	Diurnal (early morning, late afternoon)	Summer only
African civet	1	Skeletonized	Ribs and pelvis	Nocturnal	Winter only
Banded mongoose	2	Skeletonized	Ribs	Diurnal (late afternoon)	Winter only
Honey badger	2	Skeletonized	Ribs and limbs bones	Nocturnal (early morning)	Summer only

Diurnal scavengers impacted more significantly on the consumption and scattering of the pig cadavers than nocturnal scavengers. Vultures (white-backed, hooded, and lappet-faced) were responsible for the consumption of the soft tissues and accounted for most of the scattering of the skeletonized remains, however the marabou stork and warthog consumed whole skeletal elements which affected the specific skeletal elements recovered after scavenging.

Vultures were the most prolific scavengers in the Lowveld, and as such their scavenging behavior will be highlighted. The pig cadavers were deposited in the late afternoon in both the summer and winter periods. In summer the vultures began to scavenge early the following morning at 09h00 (18 hours after pig deposition). In winter the vultures began to scavenge after two different periods depending on the location of the pig deposition. Vulture scavenging of pig cadavers lying in the open began in the afternoon (13h00-14h00), 26-28 hours after deposition. Pigs that were laid near fences began to be scavenged by vultures in the morning (09h00-10h00), 90 hours after deposition (Figure 5). The exposure of pigs either in the open or beneath trees did not have an impact on when the pigs were scavenged by vultures in both seasons.

A single hooded vulture was typically attracted to the cadavers first and began to scavenge on the abdomen, thorax, head, and often would insert their head into the anus to gain access to the intestines. White-backed vultures would also be attracted to the cadaver during the early decomposition stage and would insert their heads deep into the mouth and throat of the pig cadaver. Once the abdomen was perforated and the intestines were exposed, white-backed vultures would push out the hooded vultures and would congregate in numbers ranging from 20 to 30 vultures (up to 40 vultures in one case) in a feeding frenzy. In winter this behavior would start after 2-72 minutes after the first vulture is attracted; however in summer this would begin after 1-2 minutes.

In winter the pig cadavers were skeletonized by the vultures between 20-98 minutes after first arrival, however, in summer the vultures skeletonized the cadavers between 5-26 minutes (Figure 5) after first arrival. The number of vultures drastically decreased (n<10) once skeletonization was achieved. Marabou stork, lappet-faced vultures, and hooded vultures would join the white-backed vultures after the pig cadavers were skeletonization and disarticulated.

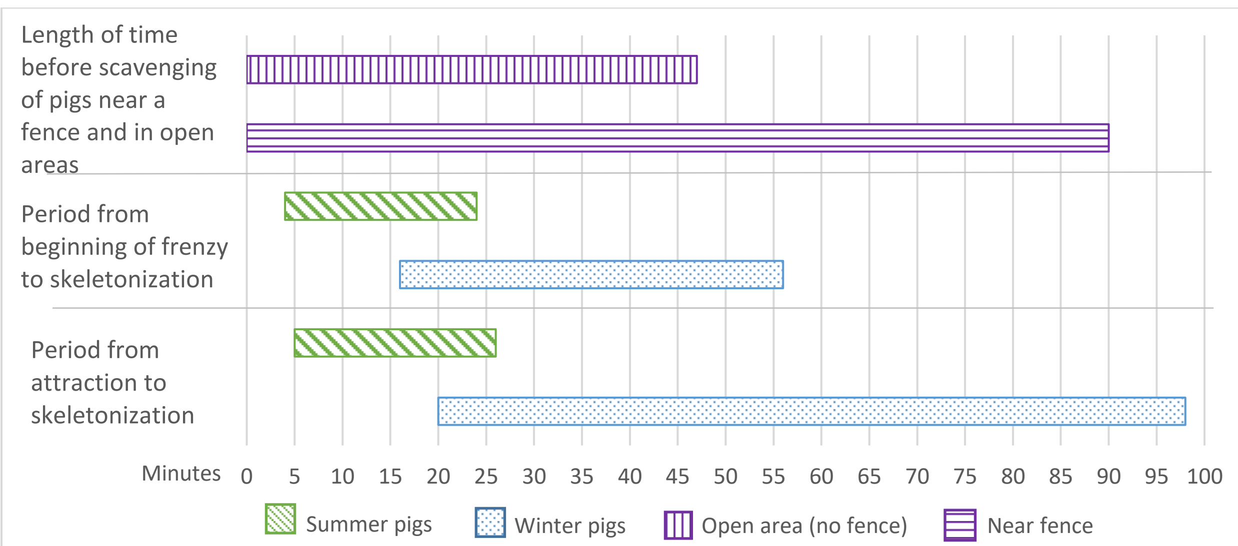

Figure 5: The range of time taken for vultures to begin scavenging and skeletonize pig cadavers in summer and winter

Vultures were very efficient in the skeletonizing of the pig cadavers. The skeletonized vertebral column, rib cage, and pelvis often remained articulated together. The skin was often intact in a single piece with the skull and limbic bones sometimes partially attached. The cranium, mandible, limbs, scapulae, and some ribs were often disarticulated and scattered. The skeletal remains of the winter sample were scattered in a dense pattern within an area of 102.1m^2/1098.6ft^2 with a radius of 5.7m/18.7ft (one outlying element – pelvis - was scattered beyond this radius at 23.9m/78.4ft) (Figure 6). The summer sample was scattered in a more diffuse pattern within an area of 157.9m^2/1705.5ft^2 with a radius of 7.09m/23.3ft (Figure 6).

After skeletal remains were scattered by vultures, other animals (mongoose, civet, banded and slender mongoose, genet, warthog, and honey badger) would further scatter the remains, however within the radius of the vulture scattering.

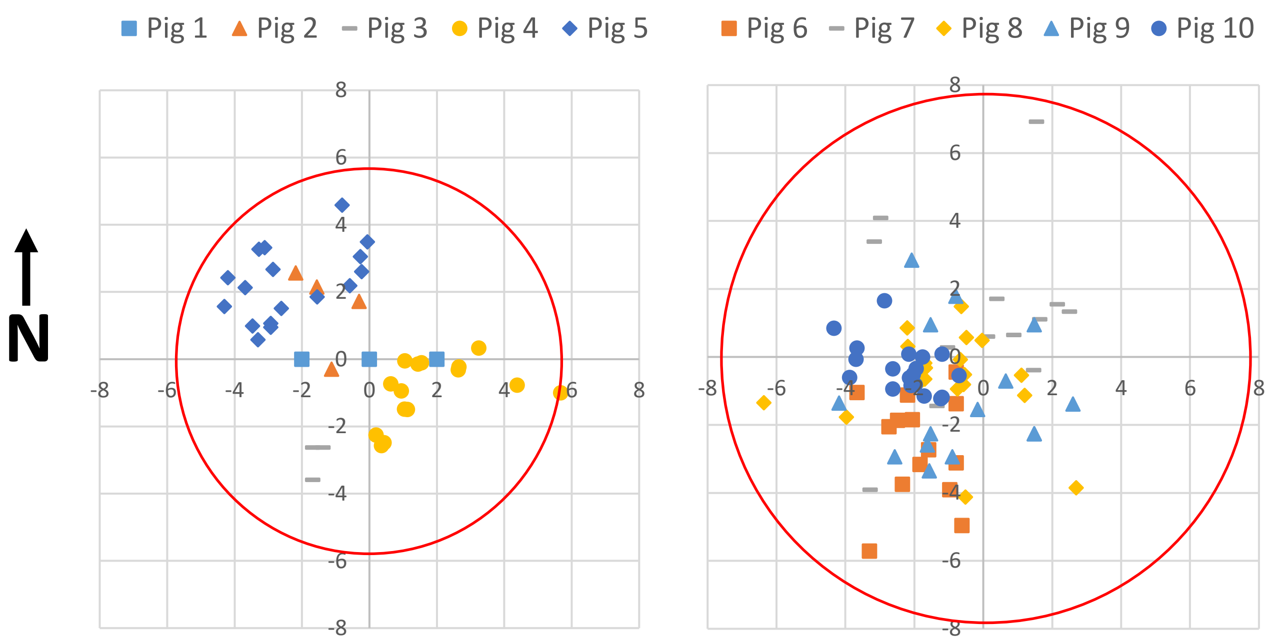

Figure 6: Scatter plot of the skeletal elements of ten pigs, five in winter (left) and five in summer (right), scattered primarily by vultures, showing distance (in meters) and direction of scattering. The origin (0;0) indicates the original position of each pig. The compass arrow indicates the relative scatter direction. Circles indicate the scatter radius (summer radius = 7.09m; winter radius = 5.7m with one outlying element scattered beyond this radius not included in the figure)

Vultures left very few marks on the bones. The few markings that were produced were isolated to superficial scores on the flat surfaces of the cranium, mandible, scapulae, and long bones (Figure 7). The distal ends of the transverse processes of the vertebrae were often broken off (Figure 7) while large superficial pits were noted on the humerus in one case (Figure 7).

Of note is the skeletal trauma caused by warthogs. Warthogs caused considerable damage to bone, mostly consuming all ribs and vertebrae, with only splintered and fragmented vertebrae and ribs surviving (Figure 8).

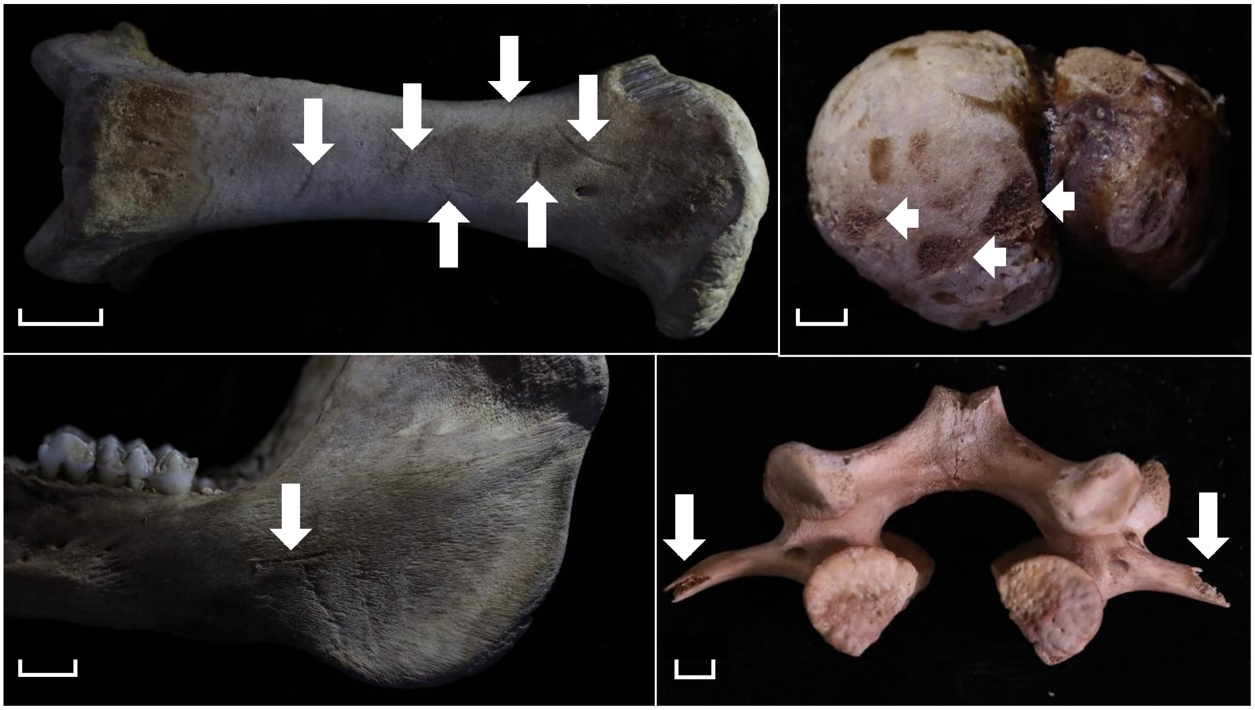

Figure 7: Vulture bite marks pointed out by arrows in the form of scores on the femur (top left) and mandible (bottom left), pits on the head of humerus (top right), and fractured transverse process on vertebrae (bottom right). Scale represents 10mm.

Figure 8: Warthog scavenging resulting in the splintering of the transverse process on vertebrae (left) and fragmentation and splintering of the ribs (right). Scale represents 10mm.

Discussion

The scavenging behaviors of animals is variable and an understanding of their behaviors can assist in the reconstruction and timing of post-mortem events. Vultures were the most prolific scavengers in the South African Lowveld and an understanding of how long it takes for them to be attracted to a body and to skeletonize the body is necessary in the estimation of a postmortem interval.

The white-backed vulture, lappet-faced vulture, and hooded vulture are all common to the Lowveld of South Africa (19). The white-backed vulture is most common and is present year-round (19). Marabou storks also visit the area although they are often observed mostly in the wet season during the warmer months (19). The hooded vulture inhabits a variety of habitats (20). South of the African equator this species is solitary and can be located in deserts, forests, and savanna (21). North of the African equator, the hooded vulture can be found in large groups and can also be located in urban areas near rubbish dumps and slaughterhouses (21).

White-backed vultures, lappet-faced vultures, and hooded vultures rely on their vision to find cadavers to eat (22). Hooded vultures are often the first avian scavengers to locate and feed on a cadaver, followed closely by lappet-faced and white-backed vultures (23). Lappet-faced vultures regularly search for cadavers within a restricted area, as a result they often detect a cadaver before larger groups of white-backed vultures do (24). The white-backed vultures exhibit herd-following behavior whereby they follow other vertebrate and avian scavengers, on an inter- and intraspecific level, to a food source (24, 25). Although lappet-faced vultures often find cadavers before the white-backed vultures, they only feed on the cadaver after the large group of white-backed vultures have already started to feed on a cadaver (23). These behaviours were all observed in the present study.

The vultures in the present South African study began to scavenge the pig cadavers after 18hrs in summer and between 26-28 hours in winter. This is in contrast to the Texan studies by Reeves (12) and Spradley *et al.* (26). Reeves (12) noted that American black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) waited approximately 24 h before they began to scavenged the pig remains in the warmer months compared to the 37 days observed by Spradley *et al.* (26) in colder months on human remains. Comparing the temperatures between the two studies' sites - the South African study site reached a maximum of 40°C (104°F) in summer and a minimum of 16°(60°F) in winter and the Texan studies' site reached a maximum of 32°C (90°F) in summer and a minimum of 4° (39°F) in winter (12, 26). Temperature plays an important role in relation to when New World vultures (those in the Americas) begin to scavenge as they rely on olfaction to locate cadavers (27). Colder temperatures delay decomposition and the release of volatile organic compounds which will result in the delay of vulture attraction and scavenging. The role of temperature on olfaction would not play a role in the onset of scavenging in Old World vultures (those in Africa, Asia and Europe) as they rely on their vision to locate cadavers (27). The delay in winter scavenging compared to summer scavenging in the present South African study could be attributed to the smaller number of vultures that are active in winter. Vultures are relatively less active in winter because the thermal convections they use to fly long distances are weaker and less frequent than in summer (28). It must be highlighted that it is possible that the vultures could have begun scavenging earlier in both seasons if the pig cadavers were laid out earlier. The pig cadavers were laid out in the late afternoon just prior to sunset in both summer and winter. Since the vultures in this study are diurnal and rely on sight to locate cadavers, it is suggested that the vultures might have scavenged earlier if the pig cadavers were laid out sooner. This needs to be explored further in future research.

The number of vultures observed feeding on a single cadaver is a result of two factors: abundance and behavior. The overall number of vultures feeding on a single cadaver may indicate the abundance of nesting sites related to the location of their nests (19). The number of individual vultures per species (white-backed, lappet-faced, and hooded vultures) feeding on a single cadaver is the result of their species-specific behavior. Lappet-faced vultures roost and forage for food in isolation or in pairs (25) whereas white-backed vultures are social breeding and feeding colonies (19, 29). In Africa, a variety of vulture species often feed on the same cadaver with the following approximate percentages: white-backed vultures (85%), hooded vultures (10%), Ruppell's Griffons (2%), lappet-faced vultures (2%), and white-headed vultures (1%) (23). A similar trend, in regards to the number of individuals per vulture species present at a cadaver, was observed in the present study between the white-backed (n=40), hooded (n=4), and lappet-faced (n=1) vultures. These numbers of feeding vultures per species are also consistent with those observed scavenging on cadavers in the nearby Kruger National Park conservation park (19). The diversity and abundance of vulture species is different between Africa and the USA. White-backed, hooded, and lappet-faced vultures and marabou storks all scavenged at the same time in South Africa whereas, in Texas, American black vultures tended to feed in isolation or in conjunction with only turkey vultures (12, 26). This can be attributed to the species-specific behavior of different vulture species in different geographic locations. It is therefore important to note that ecologically diverse areas need to perform their own scavenging research and not solely rely on research that is not applicable to their location.

It is common for multiple vulture species to compete for cadavers which often results in the species fighting or displacing each other from a cadaver – fighting is common between the white-backed and lappet-faced vultures (24, 29-31). To reduce the conflict over food, these different vulture species will often partition the cadaver between themselves and consume different types or sizes of cadavers (22). Lappet-faced vultures have larger skulls and beaks and tend to consume harder parts of a cadaver such as tendons and skin, and smaller cadavers (29, 30); while the white-backed vultures will prefer softer tissues and larger cadavers (24, 25, 30). This was observed in the one case when a lappet-faced vulture was recorded, which scavenged on disarticulated remains on the periphery of the larger group of white-backed vultures feeding on the pig cadaver. Hooded vultures are often pushed aside by the larger white-backed vultures whilst feeding, leaving the hooded vultures to scavenge on remains scattered around the periphery (23). Hooded vultures often are present near a cadaver the longest; they are the first vulture species to arrive and they remain long after the cadaver is skeletonized, picking at skin and scattered bones (22). This too was observed in the present study.

The skeletonization rate of remains by white-backed, hooded, and lappet-faced vultures in South Africa was drastically faster than that by American black vultures and turkey vultures in Texas. Skeletonization of ten 40-80kg pigs in the present South African study ranged from 5-98 minutes (faster in summer, slower in winter) compared to the 4hrs-12 hours in the study by Reeves (12) (three pigs weighing 27-63kg) and the "5 hours of active feeding over a 24 hour period" observed by Spradley *et al.*(26) (a single adult human cadaver of unknown weight). The number of vultures feeding in a single frame caught by cameras was comparable between the present study (20-30 vultures on average) and that by Reeves (12) (25-30 vultures).

White-backed, hooded, and lappet-faced vultures scattered the skeletonized remains over an area of 157.9m2/1705.5ft2 which was much larger than the 83.6m^2/900ft^2 by American black vultures (26). The scattering pattern in the present South African study showed a more diffuse pattern in summer compared to a denser scatter pattern in winter. This could be due to the summer period exhibiting feeding vulture groups that were much larger than in winter, with skeletonization and scattering occurring much more rapidly in summer. In summer cadavers are less numerous and the thermal convections used by vultures to fly longer distances are stronger and more frequent than in winter (28). This could account for the greater numbers of vultures and increased activity in the summer period compared to the winter period. There is little evidence to suggest that white-backed vultures migrate seasonally (32, 33) therefore migration is an unlikely reason for the difference in the seasonal behavior of the vultures.

The vultures left very few marks on the bones. These marks were mainly isolated to superficial scores with the distal ends of the transverse processes of the vertebrae often broken off. These were most likely caused by the vultures' beaks and not their claws. Beak marks on bone surfaces can be differentiated from claw and bite marks. Vulture beak marks have been described as shallow, irregular, linear scratches measuring up to 4cm (12) which is consistent with those seen in this study. The irregular nature of the scores prevents their misinterpretation as sharp force trauma caused by claws. The beak scratches are more similar to root etching than sharp force trauma in their appearance (12). Furthermore, the scratches are assumed to be caused by the beaks of the vultures and not their talons, as their feet are relatively weak and used mostly for leverage and not grasping and manipulation of the cadaver (12). Previous conflicting literature has reported on the trauma caused by vultures on eye orbits. Anecdotal accounts of vultures pecking out the eyes and damaging the orbits has been reported (12) but this was not observed in this study. Pecking out the eyes was observed but no orbit trauma was present.

Apart from the vultures, marabou storks and warthogs caused considerable loss of surviving skeletal elements as the marabou storks would swallow bones whole (such as ribs and scapulae) and warthogs would consume ribs and vertebrae. Osteophagia (consumption of bones) has been recorded in warthogs before (34) however their modification of the bones has not been described previously. The splintered and fractured nature of surviving ribs and vertebral transverse processes described in this needs to be further investigated in more controlled circumstances.

Osteophagia is also common in giraffes and the giraffes observed in the present study were observed to have been attracted to the skeletonized remains however they were not recorded scavenging on them. Herbivorous ungulates such as giraffe and deer, in abnormal situations, have been observed scavenging on dry bones. It is suggested that this occurs when the animal has a phosphorous deficiency caused by a nutritional dysfunction (35). Bones will be consumed in any stage from fleshed and fresh to dried and weathered (36). Antlers, horns, and ivory have also been observed to be consumed by herbivores in order to maintain their nutritional requirements (36). Although the giraffes recorded in this study did not consume the scattered remains during the period of this study, it was reported in the week prior to the study that one giraffe was observed consuming an impala femur.

Other animals scavenged the remains after vultures had skeletonized and scattered the remains. The sequencing of trauma caused by different scavenger species may be possible as Young *et al*. (7) observed, in their European study, that there was never more than one scavenging species feeding on a cadaver at one time and never more than two individual animals of the same species scavenging a cadaver at one time. This was also observed in the present South African study as all other scavengers (slender mongoose, civet, genet and warthog) scavenged in isolation, with the honey badgers and banded mongoose scavenging in pairs. Further studies, such as that by Morton and Lord (8) in the United States, have recorded that scavenging animals are active at different times of the day based on their diurnal or nocturnal behavior. These animals however do not intermingle with other species that have the same diurnal/nocturnal predilection. Rather each species is active at different periods during the diurnal/nocturnal periods. This was also observed in the present study.

This study was limited due to the use of motion-activated cameras, as only what was caught on camera could be reported on. On occasion the cadavers were moved beyond the view of the cameras by scavengers which limited the observation of scavengers and their behaviors. The study also only occurred over the period of one week in summer and one week in winter. As such this study only reported on the short term scavenging and it is suggested that future studies look into scavenging in the long term. Another limitation that was unforeseen was the delay in vulture scavenging in two pigs during the winter season. The delay is attributed to the two pigs being placed near fences. It is assumed that the vultures were weary of the fences as the barrier fences are electrified which might have warded of the vultures and other scavenging animals. Pigs laid out in the summer period were not placed near the fences for this reason and may also be the reason for a more rapid onset of scavenging.

Conclusion

Scavenging behavior has proven to be species-specific and region-specific (7). This understanding is critical in the forensic context as it will assist in the identification of scavengers from their bite marks on bone and discerning between animal bite marks and tool marks, in the search and recovery of scattered remains and evidence, and in the reconstruction of postmortem events and postmortem interval estimation. Vultures proved to be the most prolific scavengers in the Lowveld of South Africa, skeletonizing remains rapidly between 5 - 98 minutes, scattering remains within an area of $157.9m^2/1705.5ft^2$ and cleaned bones thoroughly with very minimal markings.

Reference list

1. Young A, Stillman R, Smith MJ, Korstjens AH. Scavenging in Northwestern Europe: a survey of UK police specialist search officers. Policing: A Journal of Policy and Practice. 2014;8(2):156-64.
2. Young A, Stillman R, Smith MJ, Korstjens AH. Applying Knowledge of Species-Typical Scavenging Behavior to the Search and Recovery of Mammalian Skeletal Remains. Journal of Forensic Sciences. 2016;61(2):458-66.
3. Smith JB, Laatsch LJ, Beasley JC. Spatial complexity of carcass location influences vertebrate scavenger efficiency and species composition. Scientific reports. 2017;7(1):1-8.
4. Steadman DW, Dautartas A, Kenyhercz MW, Jantz LM, Mundorff A, Vidoli GM. Differential scavenging among pig, rabbit, and human subjects. Journal of Forensic Sciences. 2018;63(6):1684-91.
5. Rothschild MA, Schneider V. On the temporal onset of postmortem animal scavenging:"motivation" of the animal. Forensic Science International. 1997;89(1-2):57-64.
6. Pickering TR, Carlson KJ. Baboon taphonomy and its relevance to the investigation of large felid involvement in human forensic cases. Forensic Science International. 2004;144(1):37-44.
7. Young A, Stillman R, Smith MJ, Korstjens AH. An experimental study of vertebrate scavenging behavior in a Northwest European woodland context. Journal of Forensic Sciences. 2014;59(5):1333-42.
8. Morton RJ, Lord WD. Taphonomy of Child-Sized Remains: A Study of Scattering and Scavenging in Virginia, USA. Journal of Forensic Sciences. 2006;51(3):475-9.

9. Spies MJ, Finaughty DA, Gibbon VE. Forensic taphonomy: Scavenger-induced scattering patterns in the temperate southwestern Cape, South Africa—A first look. Forensic Science International. 2018;290:29-35.
10. Spies MJ, Gibbon VE, Finaughty DA. Forensic taphonomy: Vertebrate scavenging in the temperate southwestern Cape, South Africa. Forensic Science International. 2018;290:62-9.
11. Keyes CA, Myburgh J, Brits D. Taphonomic bone trauma caused by Southern African scavengers. International Journal of Legal Medicine. 2019;134(3):1227-38.
12. Reeves NM. Taphonomic effects of vulture scavenging. Journal of Forensic Sciences. 2009;54(3):523-8.
13. Calce SE, Rogers TL. Taphonomic changes to blunt force trauma: a preliminary study. Journal of Forensic Sciences. 2007;52(3):519-27.
14. Chute DJ, Bready RJ. A Case of Postmortem Canine Depredation. The American Journal of Forensic Medicine and Pathology. 2017;38(2):100-2.
15. Toledo VA, Fonseca GM, González PA, Ibarra L, Torres FJ, Sáez PL. A Morphological and Morphometric Study of Bite Marks Caused by Mice (Mus Musculus) on Different Baits for Forensic Purposes. Journal of Forensic Sciences. 2017;62(2):462-7.
16. Matuszewski S, Hall MJ, Moreau G, Schoenly KG, Tarone AM, Villet MH. Pigs vs people: the use of pigs as analogues for humans in forensic entomology and taphonomy research. International Journal of Legal Medicine. 2019:1-18.
17. Haynes G. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology. 1983;9(2):164-72.
18. Andrés M, Gidna AO, Yravedra J, Domínguez-Rodrigo M. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. Archaeological and Anthropological Sciences. 2012;4(3):209-19.
19. Kemp A, Kemp M. Observations on the White-backed Vulture Gyps africanus in the Kruger National Park, with notes on other avian scavengers. Koedoe. 1975;18(1):51-68.
20. Ogada D, Buij R. Large declines of the Hooded Vulture Necrosyrtes monachus across its African range. Ostrich. 2011;82(2):101-13.
21. Anderson M. The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. Johannesburg: Birdlife South Africa; 1990. 71-2 p.
22. Spiegel O, Getz WM, Nathan R. Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? The American Naturalist. 2013;181(5):E102-E15.
23. Petrides GA. Competition for food between five species of East African vultures. The Auk. 1959;76(1):104-6.
24. Kruuk H. Competition for food between vultures in East Africa. Ardea. 1967;55(171):3-4.
25. Pennycuick CJ. Gliding flight of the white-backed vulture Gyps africanus. Journal of Experimental Biology. 1971;55(1):13-38.
26. Spradley MK, Hamilton MD, Giordano A. Spatial patterning of vulture scavenged human remains. Forensic Science International. 2012;219(1-3):57-63.
27. Grigg NP, Krilow JM, Gutierrez-Ibanez C, Wylie DR, Graves GR, Iwaniuk AN. Anatomical evidence for scent guided foraging in the turkey vulture. Scientific Reports. 2017;7(1):1-10.
28. Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? PloS One. 2013;8(1).
29. Mundy PJ, Butchart D, Ledger J, Piper S, editors. On the vultures of Africa. Wings Over Africa—Proceedings of the International Seminar on Bird Migration: Research, Conservation, Education and Flight Safety; 2001.

30. Houston D. Food searching in griffon vultures. African Journal of Ecology. 1974;12(1):63-77.
31. Kendall C, Virani MZ, Kirui P, Thomsett S, Githiru M. Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. The Condor. 2012;114(3):523-31.
32. Kendall CJ, Virani MZ, Hopcraft JGC, Bildstein KL, Rubenstein DI. African vultures don't follow migratory herds: scavenger habitat use is not mediated by prey abundance. PLoS One. 2014;9(1).
33. Howes CG. Power line risk to Cape (Gyps coprotheres) and White-backed (G. africanus) Vultures in southern Africa 2016.
34. Field C. Observations on the food habits of tame warthog and antelope in Uganda. African Journal of Ecology. 1970;8(1):1-17.
35. Cáceres I, Esteban-Nadal M, Bennàsar M, Fernández-Jalvo Y. Was it the deer or the fox? Journal of Archaeological Science. 2011;38(10):2767-74.
36. Hutson JM, Burke CC, Haynes G. Osteophagia and bone modifications by giraffe and other large ungulates. Journal of Archaeological Science. 2013;40(12):4139-49.