Ecological Aspects of Vertebrate Scavenging in Central Indian Forests

A DISSERTATION SUBMITTED TO SAURASHTRA UNIVERSITY, RAJKOT, IN PARTIAL FULFILMENT OF THE MASTERS DEGREE IN WILDLIFE SCIENCE

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By

Bhavya Iyer

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

But the eyes met straight-on—
whether coyote yellow or sizzling bird-
bead of black metal, whether the tilted
study of gleaming lizard grain,
or the clear gray marble of seal,
or the dark unflickering candle
of fox—the eyes, nailhead-tenacious,
star-steady, searing as salt, unrelenting,
fierce pinions from far foreign realms,
surely no one can ignore being thus
so found and fixed, so disassembled,
so immediately redefined.

~ Pattiann Rogers

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that **Ms. Bhavya Iyer** has carried out original research from the Wildlife Institute of India, titled **"Ecological Aspects of Vertebrate Scavenging in Central Indian Forests"**, in partial fulfilment of a Master's Degree in Wildlife Science from Saurashtra University, Rajkot, India. The study was carried out under our supervision from December 2018 to June 2019. We hereby certify that this work has not been submitted for any other degree to any University.

Jhala

Yadvendradev Jhala, PhD
Scientist G

Prof. Qamar Qureshi
Scientist G

Sutirtha Dutta, PhD
Scientist D

Date: 30th June 2019

Place: Dehradun

पत्रपेटी सं0 18, चन्द्रबनी, देहरादून – 248001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun – 248001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100; **Fax :** 0135-2640117;
ई–मेल / **E-mail:** wii@wii.gov.in, वेब / **website:** www.wii.gov.in

DECLARATION

I, **Bhavya Iyer**, hereby declare that the research work entitled **“Ecological Aspects of Vertebrate Scavenging in Central Indian Forests”**, carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Dr. Y. V. Jhala**, at the Wildlife Institute of India from December 2018 to June 2019. I hereby declare that this work has not been submitted for any other degree of any university.

Date: June 10, 2019
Place: Dehra Dun

Ms. Bhavya Iyer
(XVI M.Sc. Course)

TABLE OF CONTENTS

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- Bhavya
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Executive Summary

Scavengers assist in the cycling of nutrients in the ecosystem. However, few studies have examined the relative importance of microbes, invertebrate and vertebrate scavengers on the decomposition of carrion. Biotic and abiotic factors have both been known to affect scavenger communities. Environmental factors such as region, climate, season, habitat type, along with resource-specific factors such as carcass size influence the species which feed on a carcass as well as the time to detection of the carcass and carcass persistence time. Size in particular plays an important role in the species feeding on a carcass, with larger vertebrate scavengers more prevalent at larger carcasses.

Vultures are the only vertebrates which are obligate scavengers, relying on carrion alone as a food source. Other than vultures, all vertebrate scavengers are facultative scavengers. This includes most mammalian carnivores, which hunt for prey but also make use of carcass availability. This increases the interaction routes linking the processes of scavenging and predation, increasing stability of the food web. Vultures in particular, as the only obligate vertebrate scavengers, seem to play a special role in scavenger communities. Exclusion of vultures from carcasses has been linked with longer decomposition time, more intra-species contacts at carcasses (potentially leading to increased disease spread), and increased number of species feeding at the carcass.

I carried out this study to better understand the interactions between scavengers and carrion, and to observe, if any, the effect vultures and carcass size have on scavenger communities. The study was carried out in two protected areas in Madhya Pradesh – Kanha Tiger Reserve and Panna Tiger Reserve – from December 2018 to April 2019. Carcasses of animals – cattle, chital, and sambar – killed by wild predators, as well as fresh carcasses (goats and chickens) were monitored using infrared camera traps. I also carried out an experiment to observe the comparative rate at which vertebrate,

invertebrates and microbes consume carrion biomass using chicken carcasses and different treatments.

Vertebrate scavengers were found to remove carrion at the highest rate, at 99% biomass per day, followed by invertebrates (4.9% per day), and microbes (2.9% biomass removed per day).

Despite greater vulture presence in Panna Tiger Reserve, and a relatively low vulture population in Kanha, Analysis of Similarity could not find a significant difference in the vertebrate scavenger species assemblage (the number of species and the relative abundances of those species) that visited monitored carcasses between the two study sites. Carcass size also did not significantly affect which species visiting the carcasses.

I carried out occupancy modelling to estimate the probability of detecting a carcass by individual species of the carcass. Covariates which were found to affect detection probability were canopy cover, initial age of carcass, initial weight of carcass, horizontal cover, and vulture presence at the carcass. The use of occupancy modelling for estimating detection probability of carrion for different vertebrate scavengers is a unique approach, and with more data can be highly informative of the patterns and processes that govern the relationship between species and carrion. Detection corrected, model inferred occupancy gave significant improvement over the naïve occupancy estimate for all species, suggesting that carcass detection by scavengers or low abundance of scavengers was a limiting factor for visits of carcasses by vertebrate scavengers.

LIST OF FIGURES

LIST OF PLATES

LIST OF TABLES

Introduction

Vertebrate scavengers consume an estimated 75% of carrion around the world (DeVault et al, 2003), yet scavenging by vertebrates, as a process, has only gained recognition in the last few decades as being a more important part of the food web than previously believed.

Vultures are among the most well-known scavengers. Once ubiquitous, and found in such large numbers as to be considered a serious threat for aircraft (Pain *et al*, 2003), around 73% of vultures around the world are now extinction prone, with Old World Vultures particularly at risk (Buechley *et al*, 2016). Long-billed (*Gyps indicus*) and Indian white-backed (*Gyps bengalensis*) vultures were found to have declined across India by 92% since 1990 (Prakash *et al*, 2003). The decline in vulture populations has been staggering, and the effects of this on the environment are still being studied.

Vultures are the only vertebrates which are obligate scavengers, relying on carrion alone as a food source (Ruxton *et al*, 2014). Other than vultures, all vertebrate scavengers are facultative scavengers. This includes most mammalian carnivores, which hunt for prey but also make use of carcass availability, sometimes going so far as to engage in what is termed kleptoparasitism -- stealing kills from other predators (Durant *et al*, 2000, Materassi et al. 2017). This increases the interaction routes linking the processes of scavenging and predation. Scavenging by crows has been known to increase predation rates by wolves (Kaczensky *et al*, 2005), as so much of the prey biomass was removed by crows that wolves were forced to increase regularity of kills to compensate for the meat lost to scavenging. These are only a few of the ways in which vertebrate scavengers influence the environment they live in.

Scavengers are often perceived to be a threat to human health, as they may feed on the carcasses of diseased animals, posing a risk to other animals, humans, and livestock, through either mechanical transfer or via urine, faeces, or blood. However, scavengers also perform several cultural and ecosystem services which benefit humans. Humans have often relied on scavengers (vertebrate scavengers, unless specified otherwise) to consume the carcasses of dead livestock, saving farmers in the European Union €0.97–1.60 million annually (Margalida and Colomer, 2012) in carcass disposal costs. By feeding on carrion, scavengers reduce the biomass available to decay and putrefy due to microbial action. Some scavenger species are believed to be resistant to pathogens and toxins they are exposed to through carcasses. Thus scavengers play a critical role in 'cleaning up' the ecosystem by reducing or preventing the spread of diseases from putrefying flesh. The recent massive decline in vulture populations in India was believed to lead to a subsequent increase in facultative scavengers like free-ranging dogs and rats, which substantially increased transmission of diseases like Rabies (Markandya *et al*. 2008).

Scavengers perform several beneficial roles for humanity. However, what constitutes a healthy scavenger community? A community with higher species diversity or abundance, one with more obligate scavengers (vultures), or both? Absence of vultures at carcasses has been shown to increase the carcass decomposition time (Ogada *et al*, 2012), as well as increase the number of contacts between mammals – a factor which has implications in disease ecology. With vulture populations on the decline, it is important to understand whether the functional roles played by vultures can be filled by facultative scavengers.

Studying the role of vertebrate scavenger species in the environment, their interactions with the resource (carrion) and each other will help us better understand scavenging as a system. Vultures and larger carnivores like wolves sometimes play the role of facilitators to other scavengers, assisting them in locating a carcass, or enabling feeding by opening up the tough hide. Decline in such facilitator species could thus set off a trophic cascade affecting other links in the food chain. It may make way for other species which are otherwise kept in check by competitive exclusion, which may in turn monopolise a resource and prevent other species from accessing it (Mesopredator release; Morales-Reyes *et al*, 2017).

Keeping these points in mind, along with the dearth of studies on vertebrate scavenger communities in India, I conducted this study to better understand the interactions between vultures, other vertebrate scavenger species and carrion in my study area in Central India, which is host to a diverse assembly of carnivores that utilize carrion.

Specifically, in this study, I ask how much vertebrate scavengers contribute to carrion consumption compared to invertebrates and microbes. I ask what factors contribute to detection of carcasses by scavengers, and whether vulture presence plays a role. I also examine the difference in the scavenger community between the two study areas – a vulture-rich site and vulture-poor site - using carcasses in an experimental setup and monitored through remote camera-traps.

Literature Review

The last few decades have seen an increase in studies on scavenging as a part of the food web (DeVault *et al., 2*003) and not just individual natural history observations of species scavenging habits. These studies have been mostly carried out in North America, Europe, Africa, and Australia. Here, I refer to consumption of the carrion of vertebrate carcasses as 'scavenging', unless specified otherwise.

Role of Scavengers in the Environment

Scavengers assist in the cycling of nutrients in the ecosystem. Instead of allowing carcasses to decompose completely in one place, leading to a large 'island' of nutrients which may be present even years later (Danell *et al., 20*03), vertebrate scavengers in particular assist in the dispersal of the nutrients across a larger landscape area. For example, studies in North America have demonstrated how various carrion-feeding species disperse nutrients and energy throughout aquatic and terrestrial systems, as derived from feeding on carcasses of anadromous salmonid fishes (Cederholm et al. 1999). Carrion decomposition can alter soil chemistry, by increasing pH as well as the concentration of various nutrients like P, Na, and K (Benninger *et al.* 2008, Parmenter and MacMohan 2009). This can affect vegetation in an area, causing mortality of plant life (Towne, 2000). Carrion decomposition thus allows release of nutrients in inorganic form into the environment, while consumption of carrion by scavengers retains these nutrients in higher trophic levels.

Few studies have examined the relative importance of microbe, invertebrate and vertebrate scavengers on the decomposition of carrion. Tomberlin *et al.* (2017) examined the relative contributions of microbe, vertebrate and invertebrate scavengers to carrion decomposition, particularly at very high concentrations of carrion biomass. Their study mimicked a Mass Mortality Event, by placing varying amounts of carrion biomass (25-725 kg/20 m^2). At carrion densities of >350kg/20 m^2, the system seemed less capable to handle the carrion, leading to reduced nutrient cycling, die-offs of vegetation and trees due to an overload of nutrients, and a subsequent introduction of new plants in the area. Interestingly, in plots where vertebrates were not excluded, the decomposition stage was slightly advanced (by about one day) than those where vertebrate scavengers were excluded (Lashley *et al., 2*018).

Factors Affecting Scavenger Communities

When studying scavenging as a system, we may look at the scavenging community as made up of two components: the scavenger community made up of different scavenger species, and the carrion. Different factors may influence these components, causing a change in the scavenger community, the interactions between them, the rate of carrion removal, and interactions between scavengers and the carrion.

Biotic and abiotic factors have both been known to affect scavenger communities (Turner *et al., 2*017). Environmental factors such as region, climate, season, habitat type, along with resource-specific factors such as carcass size influence the species which feed on a carcass as well as the time to detection of the carcass and carcass persistence time. Carcass size in particular plays an important role in the species feeding on a carcass, with larger vertebrate scavengers more prevalent at larger carcasses.

The carrion itself also influences the scavenger community. Nestedness of scavenger communities has been linked with carcass size (Ulrich *et al*. 2009, Moleon *et al*. 2015, Sebastián-González *et al*. 2016). This may facilitate coexistence between scavenger species. Smaller species may be at risk of predation or aggression at larger carcasses, where there are larger scavengers, and therefore they may prefer smaller carcasses. On the other hand, more species may feed on larger carcasses as they are larger, provide more meat, and last longer than smaller carcasses. Thus, the community of scavengers at a small carcass would likely be a subset of that at a large carcass. Certain scavenger assemblages would then be likely to be a subset of the more species rich assemblage. This may also be explained by simple allometric scaling - a large scavenger of over 100 kilograms would not benefit much by scavenging on a carcass of less than 1 kilogram, but smaller animals might find it easier to scavenge on a smaller carcass than compete with larger species at a large carcass.

Role of Carrion

Carrion is an integral part of any food web, a constant but unpredictable resource utilised by many species. Scavengers take advantage of this resource, which involves lower cost than capturing and handling live prey. When carrion resources are low, facultative scavengers may swing between predating on vulnerable sections of prey populations, steal or scavenge on kills from other predators, or rely on small animals or non-animal food sources. Vultures are the only obligate scavengers. Likely, vultures can rely only on carrion as a source of food due to the evolution of flight, without which they would not be able to search large areas as quickly. Terrestrial vertebrate scavengers cannot rely solely on carrion as a food source for this reason (Ruxton *et al*, 2004).

Carrion acts as a ‘pulsed’ resource, promoting species diversity in a community. Where carrion resources are predictable, as in feeding stations for vultures, species diversity is lower than that when carcasses placed at unpredictable places (Cortés-Avizanda *et al*, 2012). Where carrion resources were predictable, the local dominant scavenger species (The Griffon Vulture, *Gyps fulvus*) would arrive first in much larger numbers and monopolise the resource. Smaller, endangered scavengers profited more at unpredictable feeding stations, and were facilitated by the Griffon vultures, which tore open the carcass, allowing the smaller scavengers access to the resource.

Carrion decomposition influences not only nutrient cycling, but also microclimate, soil physical properties, and fauna (Parmenter and MacMohan 2009). This in turn may affect the surrounding vegetation. Nutrient cycles and decomposition are a crucial part of environmental functioning. Vertebrate scavengers in particular thus provide critical ecosystem services which also place them at undue risk. Biomagnification of toxins through the food chain makes scavengers more likely to die of toxic compounds present in the biomass of a dead animal.

Where carrion is available as a pulsed resource, vertebrate scavengers play an important role in dispersing nutrients such as carbon, nitrogen, and phosphorus. Vertebrate scavengers slow the release of such nutrients from an organic matter state to the biogeochemical cycle by consuming carrion and assimilating the nutrients and often excreting them elsewhere.

Very high concentrations of carrion can overwhelm even vertebrate scavengers, however, as in the case of mass die-offs. Such events may have long-lasting effects on the landscape due to the high concentrations of nutrients released into the landscape from the decomposition of the carrion (Tomberlin et al., 2017). In this we can observe the effects of such an ‘island’ of nutrients. High nutrient levels may throw off the natural soil properties and cause changes in vegetation species and growth rates, even affecting succession and microhabitat (Parmenter & MacMahon, 2009).

Interactions Between Species

The relationship between scavenging by vertebrates and other pathways of the food web is more complicated and multifaceted than once believed. Scavenging, particularly by vultures, has been shown to lead to an increase or decrease in predation rates (Moleon *et al*, 2014, Cortes-Avizanda *et al.* 2009a), and can even regulate mesopredator densities by modifying their access to carrion (Morales-Reyes *et al., 20*17). Predation, particularly by large carnivores, provides a source of food to mesocarnivores like coyotes, and avian scavengers like ravens and crows (Wilmers *et al*, 2003a). A mesopredator release is also believed to have occurred after the decline of vultures in India – with the decline in vultures, feral dog numbers have increased (Markandya *et al., 2*008), though whether this can be attributed to the decline of vultures is still uncertain. However, assuming the decline of vultures and subsequent increased resource availability is at least partly responsible for the increased in feral dog populations, a similar relationship may also exist between vultures and facultative scavengers in a forest ecosystem.

The interactions between predation and scavenging also may provide stability to an ecological assemblage, or at least resistance to disturbance, by increasing the number of interactions in the food web (McCann *et al*, 1998). Functional redundancy, for example, helps in continued ecological functioning even when some species are lost, providing resilience to the ecosystem (Rosenfeld 2002).

Scavenger species composition will change across different habitat types or landscapes due to biogeographical differences. Whether this alters the ecological functioning or not was tested in a study by Huijbers *et al* (2016) by measuring carrion detection and removal on tropical and temperate beaches in Australia. The study found that taxonomically different scavenger species assemblages carried out a similar functional role – in this case, detection and removal of carrion. Changes in species composition in different habitat types could lead to empty niches if a certain species is absent in an area. Conversely, there could be continued ecological functioning due to functional redundancy (multiple species fulfilling the same role) or replacement (another species plays the same role as that of a species present in a different habitat).

Facilitation or competition may exist between the same vertebrate scavenger species. A group of ravens may consume enough of an elk carcass killed by a wolf pack that the wolves are forced to kill another to obtain enough nutrition (competition; Wilmers *et al*, 2003a), while the raven may be unable to feed on the elk until the wolves have torn the tough hide of the carcass open (facilitation). Vultures have been known to circle over hunting carnivores, awaiting a kill, while Hyenas may watch for descending vultures and follow them to a carcass (Kruuk, 1972).

Vultures in particular, as the only obligate vertebrate scavengers, seem to play a special role in scavenger communities. Exclusion of vultures from carcasses has been linked with longer decomposition time, more intra-species contacts at carcasses (potentially leading to increased disease spread), and increased number of species feeding at the carcass (Ogada *et al., 2*012).

Scavenging in India

Few studies have been carried out in India on scavengers, those mostly on vulture species. While several studies have looked into vultures in India, particularly after the population decline post 1990 (Prakash et al., 2003), there are few studies on vertebrate scavenger communities or carrion ecology in India. Some studies have assessed vulture populations in different parts of India (Pain et al., 2003), and the potential implications of this decline, particularly with regards to human health (Markandya et al., 2008). Grubh (1978a) studied the ecology of *Gyps* vultures in Gir National Park, Gujarat, and their interactions with a large predator, the Asiatic Lion (*Panthera leo persica*).

Another aspect of scavenging which is important to keep in mind is the relationship between humans and scavengers. With carrion as a low-cost resource, most carnivores will consume carcasses when available. This may lead to complications, as in the case of a large carnivore, feeding on human carcasses, which may then find humans an easy prey and become a man-eater, like the famed ‘Man-eater of Rudraprayag’. As narrated by Jim Corbett, the man-eater was a leopard which likely fed on unburied human carcasses after an epidemic tore through the Rudraprayag region of Uttarakhand, and ‘acquired a taste’ for human flesh. (Corbett, 1948).

On the other hand are the ecosystem services provided by scavengers. After the vulture populations of India were decimated, feral dog and rodent populations shot up, taking the place of the obligate scavengers, feeding off of carrion. This lead to an increase in diseases like rabies (Markandya *et al*, 2008). Additionally, obligate scavengers consume carcasses much faster than carnivores; thus the slower rate of consumption allows for a greater risk of spreading of disease due to putrefaction.

To understand scavenging communities, most studies monitor carcasses either through direct observation or remotely through camera traps. The carcass is either the kill of a wild animal found by chance or radio-telemetry, or killed by some other means (roadkill, game hunting, etc.) placed for the purpose of the study. From this data, conclusions can be drawn on the species visiting the carcasses, the order they arrive in, the consumption rate of carcasses, and even interactions between species.

Objectives

Vertebrates are a major group that consume more carrion than do non-vertebrate species including arthropods and microbes. Vertebrate scavengers are capable of removing large amounts of carrion in shorter periods of time and thus should contribute disproportionately to carrion biomass removal compared to invertebrate microbial scavengers. Carrion consumption retains important nutrients within the biosphere, whereas decomposition releases these nutrients into the abiotic environment – air, soil, and water – as part of the biogeochemical cycles of elements like carbon, nitrogen, phosphorus, etc. To understand the importance of vertebrates in relation to invertebrates and microbes in their role as scavengers, I formulated the following objective:

1. To compare carrion removal rates between vertebrate scavengers, invertebrate scavengers, and microbes.

Vultures have been known to influence scavenger communities. We examined the scavenger communities of two areas – Kanha and Panna – with differing vulture abundance to see if the presence of vultures affected the scavenger assemblage. In addition, carrion as a resource is likely to influence the scavenger community that feeds upon it. Size of the carcass is likely to be an important covariate that affects this community. Small carcasses are likely to attract smaller scavengers while larger carcasses should be fed upon by scavengers of all sizes. To better understand how vulture presence and carcass size determines the scavenger community in an area (diversity and relative abundance of various scavengers) I formulated the objective:

2. To assess how scavenger communities are affected by carcass size and vulture presence.

Research Questions

Objective 1: To compare carrion removal rates between vertebrate scavengers, invertebrate scavengers, and microbes.

1. Do vertebrate scavengers remove carrion at a higher rate than invertebrates and microbes?

Objective 2: To assess how scavenger communities are affected by carcass size and vulture presence.

2. What is the difference between scavenger communities in two areas of differing vulture density?
3. What are the covariates that determine scavenger visitation of carcasses?

Study Area

General Description

The study was carried out in two different protected areas of Madhya Pradesh – Kanha Tiger Reserve (KTR) and Panna Tiger Reserve (PTR).

Kanha was notified as a tiger reserve in 1973, though legal protection of the area began in 1935 when some parts of the Halon and Banjar valleys were declared as absolute Sanctuaries. KTR forms part of the Deccan Peninsula of India. It is composed of a Core Zone of 940 sq. km and a buffer area of 1134 sq. km. The reserve is broadly composed of Sal and Mixed Deciduous (both Moist and Dry) forests. Twenty-seven percent of the park is composed of grassland areas, with 7.56% being grassland with shrubs. The park is home to several charismatic and unique species including the tiger (*Panthera tigris tigris*) and the famed Barasingha (*Rucervus duvauceli branderi*) (Schaller, 1967).

Panna Tiger Reserve, in the Panna district of Madhya Pradesh, was first established in 1981 as a National park, and declared India's 22nd Tiger Reserve in 1994. It has a core zone of 576.13 Sq Km and a buffer of 1021.97 Sq Km. The dominant vegetation is Dry Deciduous forests with grasslands. The Ken river, a tributary of the Yamuna, flows through the park. The rugged land features of the park – plateaus and gorges – provide suitable nesting sites for several vulture species.

Flora and Fauna

Kanha Tiger Reserve harbours several species of conservation importance including the Tiger, *Panthera tigris tigris*. The reserve has a diverse assemblage of flora and fauna, including several species of mammalian carnivores such as the leopard (*Panthera pardus*), dhole (*Cuon alpinus*), sloth Bear (*Melursus ursinus*), jungle cat

(*Felis chaus*), golden jackal (*Canis aureus*), and several smaller mammals which make up its potential scavenger assemblage. Herbivores which are often predated upon include spotted deer (*Axis axis*), Sambar (*Rusa unicolor*), Gaur (*Bos gaurus*), Barasingha (*Rucervis duvauceli branderi*), and four-horned antelope (*Tetracerus* quadricornis). Vulture species found in the park include Egyptian Vulture (*Neophron percnopterus*), White-rumped Vulture (*Gyps bengalensis*), and the Red-headed Vulture (*Sarcogyps calvus*). Other potential scavenging birds include the Large-billed Crow (*Corvus macrorhynchos*), and Rufous treepie (*Dendrocitta vagabonda*). Common trees are *Shorea robusta*, *Madhuca indica*, *Terminalia tomentosa*, *Ougeinia oojenensis*, *Schleichera oleosa, Diospyros melanoxylo,* and *Anogeissus latifolia*

Panna Tiger Reserve shares many species of wild fauna with Kanha such as the tiger, sloth bear, golden jackal, leopard, spotted deer, four-horned antelope, and sambar, in addition to other species such as the Indian gazelle (*Gazella bennettii*) and the striped hyena (*Hyaena hyaena*). Panna is also home to several vulture species – Egyptian, White-Rumped, Red-Headed, Long-Billed Vulture (*Gyps indicus*), as well as Cinereous Vulture (*Aegypius monachus*), and visiting Himalayan Griffons (*Gyps himalayaensis*) in the winter. Common tree species including *Tectona grandis*, *Terminalia tomentosa*, *Acacia catechu*, *Madhuca indica*, *Buchnania latifolia*, *Anogeissus latifolia*, and *Diospyros melanoxylon*.

The composition of flora and fauna is overlapping between KTR and PTR. Notably, PTR has more Dry Deciduous Forests than KTR, which has extensive sal forests (absent in Panna). The faunal composition is mostly the same, though there are differences in the abundance of species. Panna has a much larger population of vulture species than Kanha, particularly Long-Billed Vultures.

Methodology

Field Methods

Ungulate kills made by wild carnivores were located through active search for carnivore kills, and monitored using infrared-flash camera traps in KTR (n= 32 carcasses) and PTR (n=9). Fresh goat carcasses were weighed and placed in similar habitat types in both study sites in areas adjoining the National Park as well (n= 5 goat carcasses in both sites). One carcass of a Ruddy mongoose (roadkill) was also monitored with a camera trap. Five chicken carcasses also were placed for vertebrate consumption as part of the experiment in Objective 1.

Figure 1: An experimental setup of a chicken carcass with two infrared camera traps placed nearby to monitor scavengers.

Proportion of carcass already consumed was visually estimated (viscera consumed, torso, torso and legs, etc) as well as carcass species, approximate carcass weight or size class, stage of decomposition (fresh, beginning to rot, rotting) and the species which made the kill, wherever possible (to distinguish between predators and scavengers). Two camera traps were placed at most carcasses at different angles to reduce chances of failure to detect scavenger visits and feeding events.

Site covariates noted were latitude and longitude coordinates using a handheld GPS, canopy cover, and horizontal ground vegetation cover (measured with a marked checkerboard). Canopy cover was measured using the Android OS-based application CanopyApp (University of New Hampshire, 2018). Horizontal cover was measured using a 30cmx40cm checkerboard of forty 6cmx8cm rectangles (Mysterud, 1996). Horizontal cover readings were measured by the observer standing 10 metres away from the carcass, in each of the four cardinal directions. The average of these four values was taken for analysis. Canopy cover was also measured at each of these points as well as directly above the carcass, and the average of these five readings was used in analysis. Horizontal and canopy cover may influence detection of carcasses by scavengers depending on density of the foliage and thus was estimated as a site covariate.

Objective 1: To compare carrion removal rates between vertebrate scavengers, invertebrate scavengers and microbes.

Question 1: By what magnitude do vertebrate scavengers remove carrion compared to invertebrates and microbes?

Experimental Method

To observe the differential effects of different scavenger communities (microbial, invertebrate and vertebrate) on carcass consumption and decay, an experiment was carried out using fresh chicken carcasses (1.1-2 kg, n=18) in the buffer of Panna Tiger Reserve from 9th April 2019 to 23rd April 2019. All experiment carcasses were placed under similar vegetation types – dry deciduous forests – nearby one another (<1 km distance, excluding 2 samples in vertebrate treatment) to ensure consistency in scavenger community availability. Carcasses placed in cages for the control, microbe and invertebrate treatments were all placed under indirect shade. Canopy cover and horizontal cover were similar for all experiment sites, and were also noted as for all other carcasses.

1. Control – Moisture Loss

Control carcasses (with guts removed to prevent decay due to gut bacteria; n=3) were weighed and treated with an antimicrobial agent (Neosporin) in powder form on the outside and inside of the body cavity, placed in a cloth sack and hung in a cage to exclude invertebrate and vertebrate scavengers. These were then weighed daily to observe moisture loss in the absence of microbial decomposition.

2. Microbial Decomposition

To observe microbial decomposition, whole chicken carcasses (n=3) were placed in cloth sacks to exclude invertebrate scavengers, and placed in a wire cage (to exclude vertebrate scavengers) and weighed daily. The carcasses were originally placed on the ground of the cage to allow soil microbes to access the carcasses, however, as this made the cloth sacks more vulnerable to being breached by invertebrates, they were hung up.

Figure 2: Experimental setup for observing carrion biomass loss due to microbial activity - carcasses were placed in cloth bags and hung in a wire cage to exclude invertebrates and vertebrate scavengers.

3. Invertebrate Scavenging

Carcasses were placed inside a wire mesh cage on the ground with no cloth covering to observe invertebrate scavenging (n=6). Each carcass was weighed before placement in the cage and again after a period of a few days.

Figure 3: A chicken carcass being weighed after some exposure to invertebrate scavenging.

4. Vertebrate Scavenging

Carcasses were weighed and staked in the open and monitored with camera traps to observe scavenging by vertebrate scavengers (n=5). All carcasses were placed in the day time, before noon, to give equal opportunity to avian and mammalian scavengers (as mammals may also be active at night but avian scavengers were active only in the day time).

Analytical Methods

Biomass remaining was calculated for each carcass for each day. This was converted to proportion remaining of original weight to make all carcass biomass losses comparable. To observe the effects of each 'treatment' (control, microbe, invertebrate, vertebrate) on biomass removal, I used Linear Mixed Effect Models (LMEs) to account for the grouped nature of the data arising from observing a carcass over time. We modelled the log-odds of proportional biomass remaining on the experimental treatment and time since the experiment began as fixed effects, and the carcass replicate as random effect. Log-odds was calculated as

$$= \log(P/(1-P))$$

where P = Proportion of weight of carcass still remaining. This transformation was done to model biomass persistence as a logistic function and to constrain the predicted proportions within the limits of 1 and 0. Carcass weight proportion was taken as 0.9999 at day 0, as otherwise the log-odds would be infinity ($\log(1/1-1) = \infty$).

All analysis was carried out in R (R Core Team, 2019). Model selection was on the basis of lowest Akaike Information Criterion (AIC). From the best fitting model, I predicted new values of proportional weight of the carcasses over time for different treatments based on the resulting, best-fitting and most parsimonious model.

I then compared the contribution of each treatment to the decay of the carcasses with time using the 'lstrends' function, and whether there was a significant difference between slope comparisons of treatments using the 'pairs' function in 'emmeans' package in R (Length, 2019). This gives us the magnitude in difference between treatments as pairs, and the significance of the difference.

The effect of each treatment was a subset of the other – vertebrate scavenging also involved scavenging by invertebrates, microbes, and water loss. Loss of biomass due to invertebrate scavenging was compounded by microbial decomposition and water loss, etc. To subtract these effects and get the slopes of each treatment alone, I subtracted the mean proportional loss of weight due to water loss, for each day of the control experiment from the proportional weights for each day of the microbes experiment, and similarly subtracted the daily mean proportional weight loss due to microbial decomposition from the invertebrate proportional weights, and of invertebrate treatment from the vertebrate treatments. Graphs were made with R's 'ggplot2' package (Wickham, 2016)

Objective 2: To assess how scavenger communities are affected by carcass size and vulture presence

<u>Question 2: What is the difference between scavenger communities in two areas having different vulture density?</u>

To calculate the diversity and richness of scavenger species, I first had to calculate the relative abundance index of species visiting each carcass (explained below), and the number of independent captures at each site per trap night. To remove bias arising from an animal feeding on a carcass right in front of the camera trap and inflating the number of photo-captures during a single feeding bout, I counted a species as having visited a carcass once, for every half hour it spends at a carcass. If a species triggers multiple photographs in one half hour segment, it is counted as a single visit. Half an hour was selected as a suitable time period to calculate visits consistently across species in keeping with published literature (O'Brien *et al., 2*003).

The sum of individuals at each of these visits for each species at each carcass was then divided by the number of trap nights, or the number of days a particular carcass was monitored. From this data, I obtained a matrix of the Relative Abundance Index, or RAI, of each species for each carcass, where

$$RAI = frequency\ of\ independent\ visits/Number\ of\ camera\ trap\ days$$

Using this matrix, I calculated the Shannon's H' Index of Diversity for each carcass using the 'diversity' function from the 'vegan' package in R (Oksanen *et al., 2*019). From this I obtained the mean diversity at both sites – Kanha and Panna – and for each carcass size. Shannon's H' Index of Diversity is calculated as

$$H' = \Sigma p_i ln(p_i)$$

Where p_i is the proportion of individuals of each species out of the whole.

I also calculated the species richness for both Kanha and Panna and for carcasses of different sizes using the 'specpool' function. Richness was the total number of scavenger species at a particular carcass site.

To compare the species assemblage between the two study sites, one vulture-abundant (Panna) and one with lower vulture numbers (Kanha), and between different carcass sizes at each site, I used the 'anosim' function to perform an Analysis of Similarity between matrices of relative abundance index of species at different carcasses.

The RAI of each species was also plotted against the carcass size to obtain boxplots of relative use of carcasses of different sizes for each scavenger species. Species accumulation curves were also generated using the 'specaccum' function in 'vegan', to account for missing species due to variable sampling effort.

Question 3: What are the covariates that determine scavenger visitation of carcasses?

Visitation of a carcass by a scavenger is likely to depend on a) carcass size, b) habitat covariates, and c) detection of the carcass by the scavenger. I used an Occupancy approach to model this process in the program Presence (MacKenzie, 2003). Each carcass was taken as a site, and every 24-hour period as a survey. Occupancy models were run for each scavenger species separately.

In traditional Occupancy Modelling, two variables are modelled – ψ (psi), the probability of occupancy of a species at a site given a particular detection history, and ρ (phi), the probability of detecting a species given that it is present. In this case, ψ would signify that a carcass was visited by a species, and ρ would signify the detection of the carcass by the scavenger and its frequency of visits to the carcass, instead of the detection of the scavenger by the detector (in this case, a camera trap).

Keeping the occupancy parameter as a constant, I modelled different site covariates to find which model best explained the detection of the carcass by different species. This was because by the use of heat and movement-detecting remote cameras, I was unlikely to miss detecting scavenger visits. The variability in the capture history of scavengers to an individual carcass was likely due to scavenger's inability to detect a carcass or alternatively by the abundance of a particular scavenger in the area. The site covariates modelled as detection covariates were initial weight of the carcass, initial age of the carcass, presence of vultures, average canopy cover over the carcass, and average horizontal cover around the carcass. Best fitting model was selected using AIC. C-hat was estimated by 10000 bootstraps of the best-fitting models in Presence, to check for over-dispersion.

Results

Objective 1: To compare carrion removal rates between vertebrate scavengers, invertebrate scavengers, and microbes:

<u>Question 1: By what magnitude do vertebrate scavengers remove carrion compared to invertebrates and microbes?</u>

A total of seventeen chicken carcasses were used for the experiment for the four different treatments. Control carcasses were monitored for a maximum of 15 days (n=3 carcasses), microbe treatment carcasses for a maximum of 14 days (n=3), and invertebrate treatment carcasses for a maximum of 12 days (n=6). Carcasses placed for vertebrate consumption were all removed within one day of placing the carcass and were completely consumed (n=5).

A boxplot of the proportion of weight of each carcass remaining for each treatment illustrates the rate at which carrion biomass is removed in each of the treatments. The carcasses consumed by vertebrates are all removed the fastest (and thus have the steepest slope), followed by carcasses consumed by invertebrates, then microbes and control. It is more difficult to discern the difference in rate of removal of carrion between the control treatment (where weight loss per day is essentially water loss due to evaporation) and microbial decomposition.

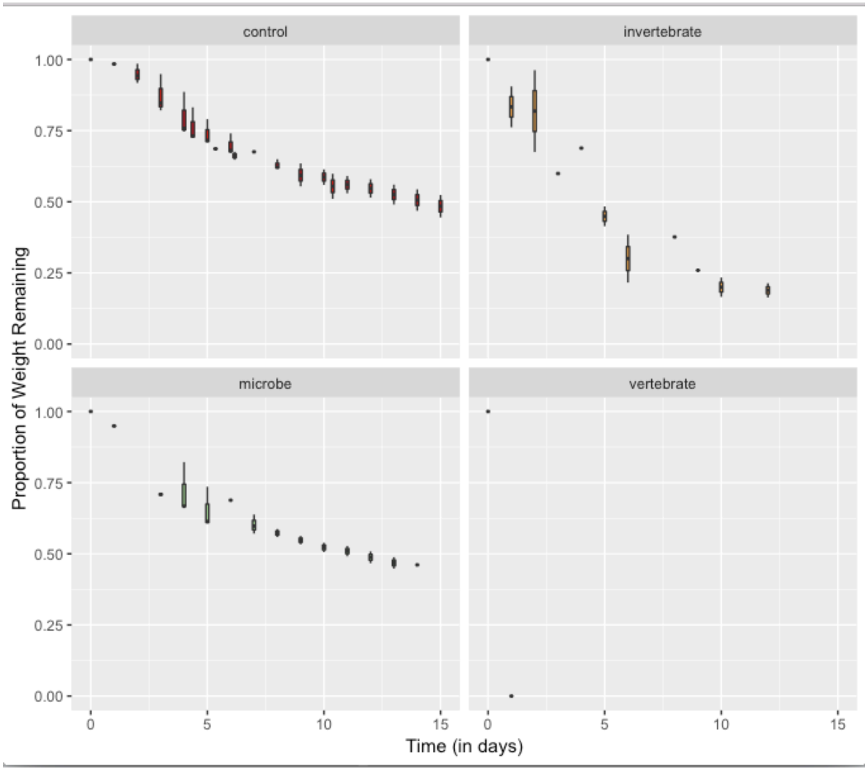

Figure 4: Boxplot of proportion of remaining weight of carcasses for each treatment over time

Linear Mixed Effect Models

Table 1: Summary of results of Linear Mixed Effect Models to determine effect of time and treatment on the log odds of proportional loss of biomass from carcass.

Model	**Fixed Effect Variables**	**Mixed Effect Variables**	**AIC**	**ΔAIC**
lm4	Time+Treatment + Time*Treatment	Replicate	106.1	0
lm3	Time+Treatment	Replicate	318.68	212.58
lm2	Time	Replicate	352.3	246.2
lm1	1	Replicate	361.11	255.01

The model with the interaction between effects of time and treatment on the log-odds – Ln(P/1-P) (where P is proportion of weight remaining) – of the proportional weight of carcasses was the best fitting model based on AIC. The untransformed coefficients for the covariates are as below:

Table 2: Untransformed coefficients of best-fitting model for log-odds of proportional weight loss of carcass

Fixed Effects	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.34	0.10	13.125	<0.01
time	-0.12	0.01	-9.217	<0.01
treatmentinvertebrate	0.16	0.15	1.009	0.31517
treatmentmicrobe	-0.10	0.16	-0.637	0.52572
treatmentvertebrate	0.65	0.19	3.35	<0.01
time:treatmentinvertebrate	-0.10	0.02	-4.522	<0.01
time:treatmentmicrobe	-0.003	0.02	-0.172	0.86345
time:treatmentvertebrate	-5.88	0.23	-24.97	< 0.01

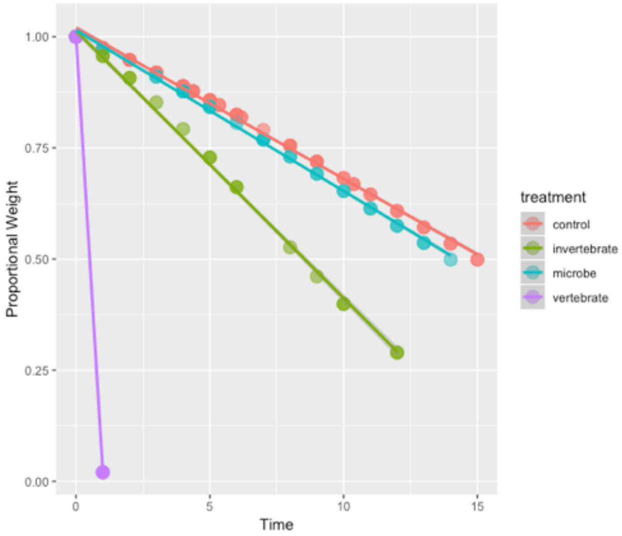

Figure 5: Comparative slopes of the four different treatments based on predicted data from the best-fitting LME model – Proportion of weight vs. Time (in days).

Vertebrate removal of carcasses creates the sharpest decline in proportional weight of a carcass, reaching zero in one day. Control treatment carcasses showed the slowest proportional weight loss over time, followed by microbe treatment and invertebrate treatment.

Comparison of Decay Rates

Carcass decay rates were assessed by comparing slopes (emmeans package), given in Table 3.

Table 3: Rate of decay over time, calculated with lsmeans function in emmeans package

Treatment	time.trend	SE	lower.CL	upper.CL
Control	-0.036	0.0025	-0.041	-0.031
Microbe	-0.038	0.003	-0.044	-0.031
Invertebrate	-0.074	0.004	-0.081	-0.066
Vertebrate	-0.999	0.046	-1.091	-0.909

Results illustrate the comparative effect of each treatment on the loss of biomass over time. The loss of biomass from a carcass due to moisture loss, denoted by the ‘Control’ experiment, is 3.56 per unit time (in this case, one day). For microbes it is marginally higher, 3.8% biomass loss per day. The biomass loss per day is 7.4% and 99.9% due to invertebrate and vertebrate treatments, respectively.

The estimates in Table 3 denote the difference in trend over time (Table 2) between different treatments. We can see that the control treatment had a significantly (signified by the P values <0.05) lower trend slope compared to the other treatment types except the microbe treatment. The microbe treatment has a lower trend slope than both invertebrate and vertebrate treatments, whereas invertebrate treatment showed a greater trend slope than control and microbe treatments but a lower trend slope than the vertebrate treatment.

Table 4: Comparison of effect (slope) of treatments on proportional weight loss of carcasses

Contrast	Estimate	SE	P Value
control-invertebrate	0.038	0.004	<.0001
control-microbe	**0.002**	**0.004**	**0.9662**
control-vertebrate	0.964	0.046	<.0001
microbe-invertebrate	**0.036**	**0.005**	**<.0001**
invertebrate-vertebrate	**0.926**	**0.046**	**<.0001**
microbe-vertebrate	0.962	0.046	<.0001

The difference between the control and microbial treatments is small and statistically insignificant.

Individual Treatment Effects

To better understand the effect of each separate taxa on the carrion removal rates, the analysis was repeated after subtracting the relative contributions of the lower taxa from the data.

The model with the interaction between effects of Time and Treatment continued to be the best fitting model for this data.

Table 5: Summary of results of Linear Mixed Effect Models to determine effect of time and each individual treatment on the log odds of proportional loss of biomass from carcass.

Model	Fixed Effect Variables	Mixed Effect Variables	AIC
lm4	Time+Treatment + Time*Treatment	Replicate	320.73
lm3	Time+Treatment	Replicate	382.66
lm2	Time	Replicate	377.56
lm1	1	Replicate	435.47

The untransformed coefficients for the covariates are as below:

Table 6: Untransformed coefficients of best-fitting model for log-odds of proportional weight loss of carcass, for each individual treatment

Fixed Effects	**Estimate**	**Std. Error**	**Pr(>|t|)**	**Fixed Effects**
Intercept	2.02	0.28	17.625	<.0001
time	-0.19	0.03	-12.378	<.0001
treatmentinvertebrate	1.64	0.44	-5.196	<.0001
treatmentmicrobe	0.41	0.45	-4.689	<.0001
treatmentvertebrate	2.98	0.53	4.499	<.0001
time:treatmentinvertebrate	-0.02	0.06	0.594	<0.001
time:treatmentmicrobe	-0.05	0.06	3.061	0.34
time:treatmentvertebrate	-5.88	0.65	-33.532	<.0001

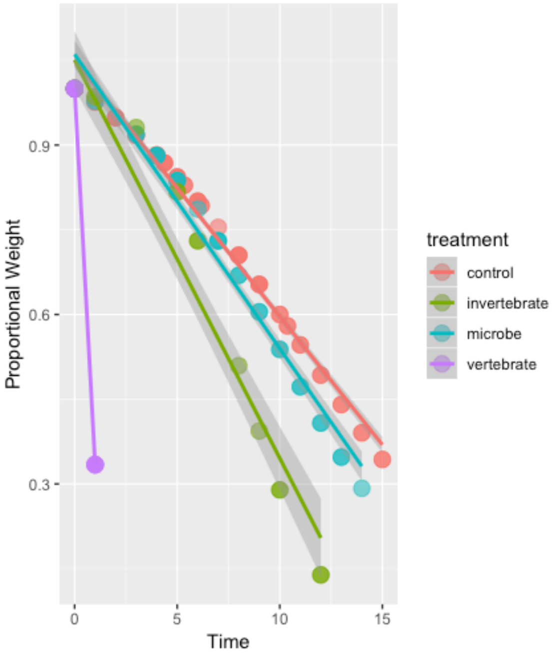

Figure 6: Comparative slopes of the four different treatments based on predicted data from the best-fitting LME model – Proportion of weight vs. Time (in days), for each independent treatment

Vertebrate removal of carcasses continues to create the sharpest decline in proportional weight of a carcass, followed by the invertebrate treatment. However, the control treatment – representing moisture loss – now shows a faster decline than the microbial treatment. That is, the rate of proportional weight lost due to water loss is greater than that due to microbial decay alone. However, when the two are clubbed together as in a natural system, the microbial decay rate adds slightly to the weight lost due to moisture loss from the carcass.

A comparison of treatment trend with time gives us the degree of this rate change. Moisture loss contributes to 3.6% biomass loss per unit time, while microbial decomposition contributes to 7.3%. Biomass loss due to invertebrates alone is 3.9% per day, and is 83.3% due to vertebrates.

Table 7: Trend in proportion over time for each individual treatment

Treatment	time.trend	SE	lower.CL	upper.CL
Control	-0.036	0.00235	-0.0405	-0.0312
Microbe	-0.039	0.003	-0.045	-0.033
Invertebrate	-0.073	0.004	-0.080	-0.066
Vertebrate	-0.833	0.043	-0.918	-0.75

Objective 2: To assess how scavenger communities are affected by carcass size and vulture presence.

Question 2: What is the difference between scavenger communities in two areas having different vulture density?

A total of 19 species were observed scavenging on monitored carcasses in Kanha Tiger Reserve, and 20 species were observed in Panna Tiger Reserve. Of these, 14 species were common to the two areas (Appendix 1).

The species with the highest relative camera-trap captures were Large-Billed Crow, followed by Wild Pig and Jackal in Kanha, and Wild Pig, Crow and Red-Headed Vulture in Panna. Other species which scavenged on monitored carcasses include Tiger, Leopard, Ruddy Mongoose, Common Palm Civet, Jungle Cat, Porcupine, Hyena, and Indian Fox. Other vulture species observed were White-Rumped Vulture and Griffon Vulture in Kanha and Long-Billed Vulture, Egyptian Vulture and Cinereous Vulture in Panna.

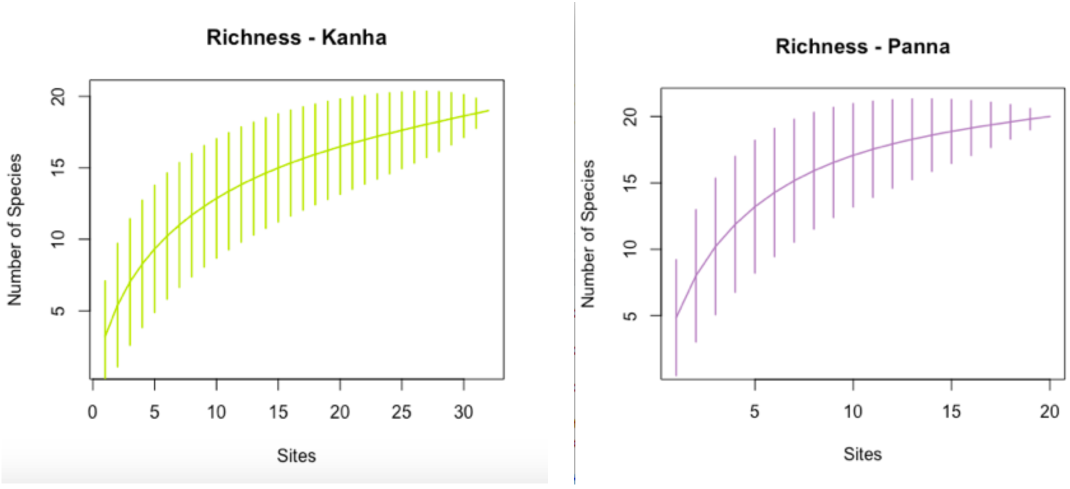

Figure 7: Species accumulation curves for Kanha (left) and Panna (right) - carcass sites against number of species

Species accumulation curves for the two study sites show that an asymptote was reached with respect to number of species in the two sites (Figure 7). Species accumulation curves for the three carcass sizes show that while large and medium carcasses have reached an asymptote with respect to species, and thus it is plausible that all scavenger species were detected at those carcass sizes. However, some scavenger species likely remain undiscovered at small carcasses as suggested by those curves not apparently reaching an asymptote (Figure 8).

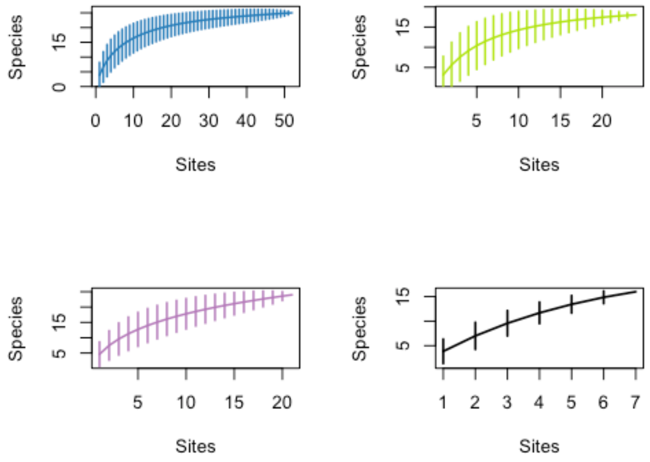

Figure 8: Species accumulation curve for different carcass sizes (Large Carcasses in top left, Medium Carcasses in bottom left, Small Carcasses in bottom right)

Diversity of Species in Kanha and Panna

PTR had a slightly higher scavenger species diversity than did Kanha (Figure 9). The mean diversity of species at Kanha was H' = 0.72 (SD = 0.51), and that in Panna was H' = 1.18 (SD = 0.32). This difference is significant based on Wilcoxon Sign Rank Test (p=0.012)

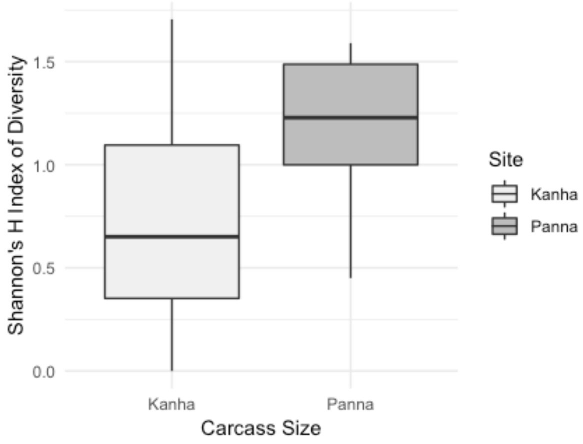

Figure 9: Scavenger Species Diversity (Boxplots) for Kanha and Panna

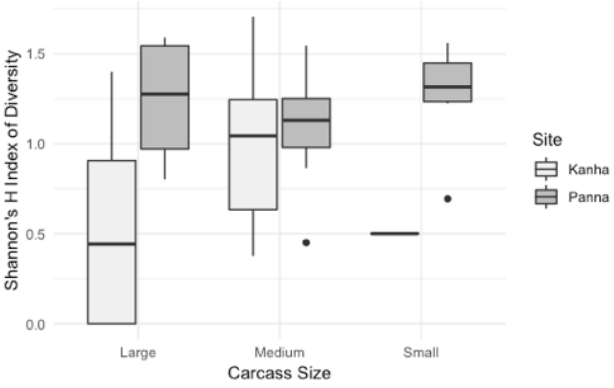

Figure 10: Scavenger Species Diversity (Boxplots) for Different Carcass Sizes in Kanha and Panna

Comparing the diversity across carcass sizes (Figure 10), medium sized carcasses seem to attract a more diverse scavenger community than do large or small carcasses in Kanha, although the confidence intervals are overlapping, and small carcasses slightly more diverse in Panna (Table 8).

Table 8: Scavenger Diversity for different carcass sizes in Kanha and Panna - Mean (Standard Deviation)

Carcass Size	Shannon's H – Kanha	Shannon's H - Panna
Large	0.51 (0.48)	1.24 (0.35)
Medium	1.03 (0.40)	1.08 (0.33)
Small	0.50	1.26 (0.31)

Richness of Species in Kanha and Panna

Species richness calculated for the two study areas is given in Table 9.

Table 9: Species richness (bootstrap method) and standard errors calculated for both study areas

Site	Number of Species	Richness	Standard Error	Samples (n)
Kanha	19	21.44	1.66	32
Panna	20	21.82	1.46	20

Richness of species visiting different carcass sizes in the two study areas is given in Table 10-11.

Table 10: Species richness (bootstrap method) and standard errors for different carcass sizes calculated for Panna

Carcass Size	Number of Species	Richness	Standard Error	Samples (n)
Large	15	17.39	2.57	6
Medium	17	20.61	2.59	8
Small	15	18.14	1.95	6

Table 11: Species richness (bootstrap method) and standard errors for different carcass sizes calculated for Kanha

Carcass Size	Number of Species	Richness	Standard Error	Samples (n)
Large	13	14.88	1.204304	18
Medium	17	19.89	1.98047	13
Small	2	2	0	1

Relative Use of Different Size Carcasses by Scavengers

Boxplots of the Relative Abundance Index for different carcass sizes were made for some species where there was sufficient data. These give an idea of whether there is a pattern to carcass usage with respect to size (Fig. 11-16).

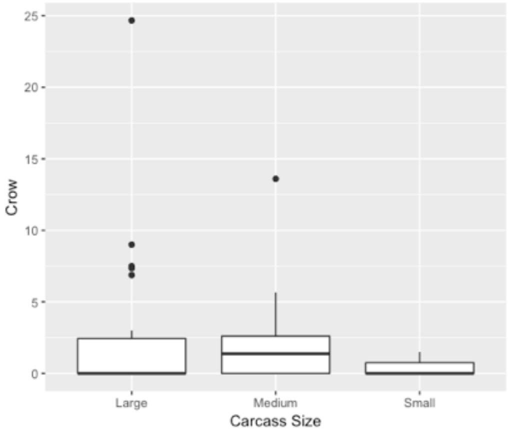

Figure 11: RAI of crow for different carcass sizes.

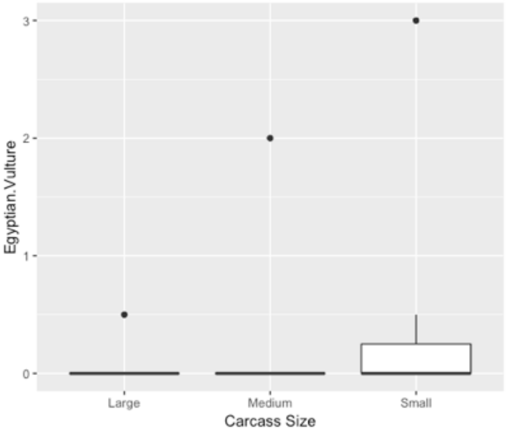

Figure 12: RAI of Egyptian Vulture for different carcass sizes.

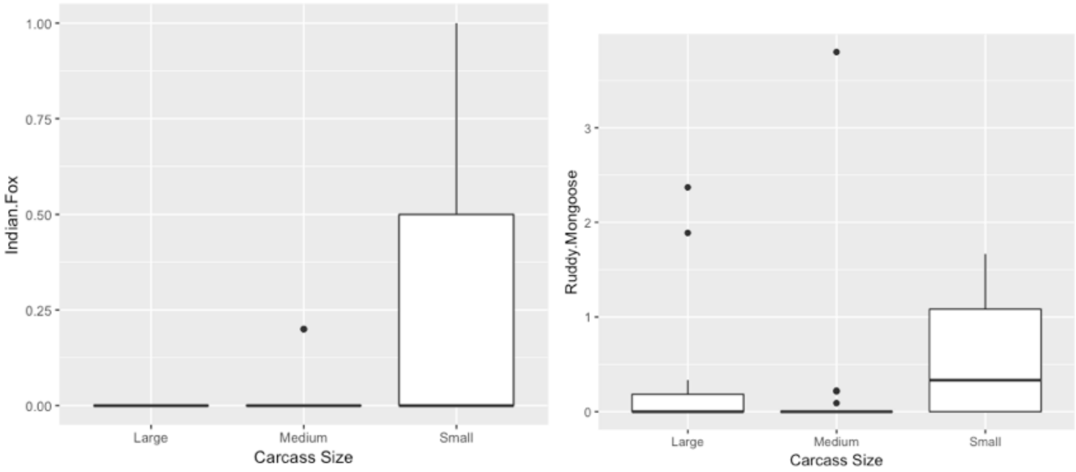

Figure 13: RAI of Indian Fox (left) and Ruddy Mongoose (right) for different carcass sizes.

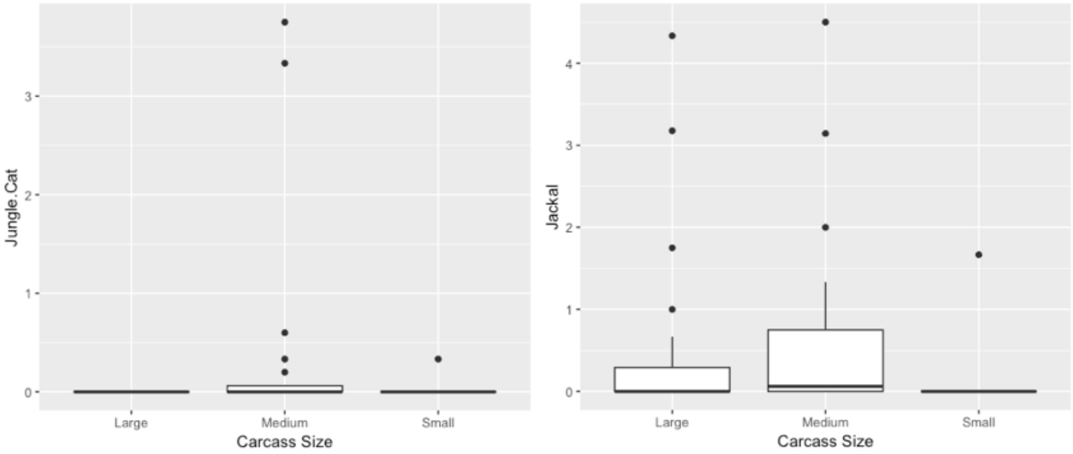

Figure 14: RAI of Jungle Cat (left) and Jackal (right) for different carcass sizes.

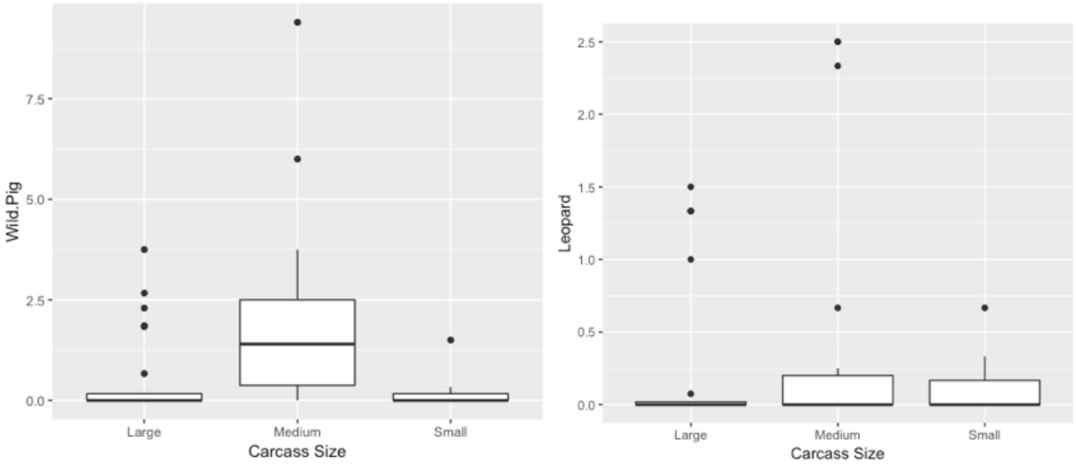

Figure 15: RAI of Wild Pig (left) and Leopard (right) for different carcass sizes.

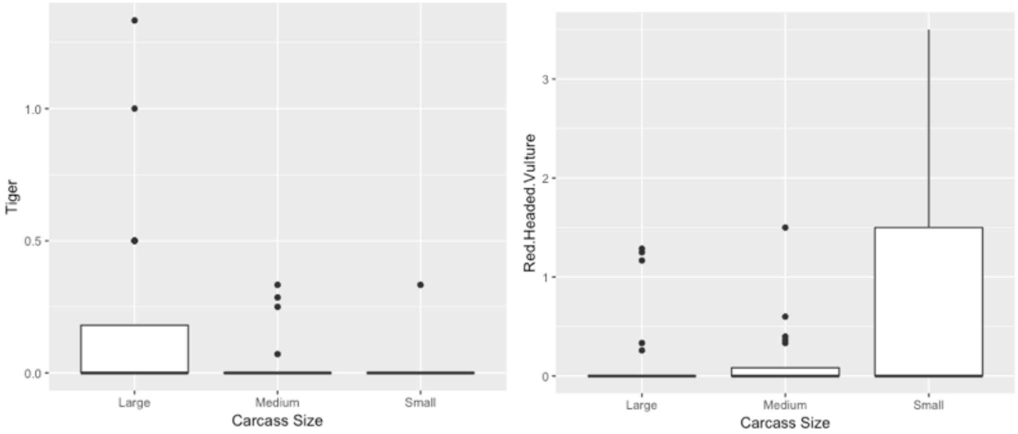

Figure 16: RAI of Tiger (left) and Red-Headed Vulture (right) for different carcass sizes.

Similarity between Study Areas – High Vulture and Low Vulture Abundance

Performing an Analysis of Similarity between the two study sites gave an ANOSIM statistic (dissimilarity) of 0.1808 (p-value <0.05). This implies that there is a significant but small difference between the species assemblage in Kanha and Panna.

Similarly, for Kanha and Panna, the similarity between species community for different carcass sizes is given in Table 12.

Table 12: ANOSIM statistic and p-value for comparison between three carcass sizes within each study area

Area	ANOSIM Statistic	p-value
Kanha	0.075	0.01
Panna	0.116	0.069

Again, there appears to be no significant difference in the scavenger species found at carcasses of different sizes.

We also compared the Relative Abundance Index vultures (pooled together) and three facultative scavengers – feral dogs, jackal, and wild pigs – which may potentially numerically respond to vulture densities, due to the high amount of scavenging in their diets. I found higher visitation to carcasses by jackal and feral dogs in the Kanha landscape (poor vulture abundance) compared to Panna landscape (higher vulture abundance) Fig 16.

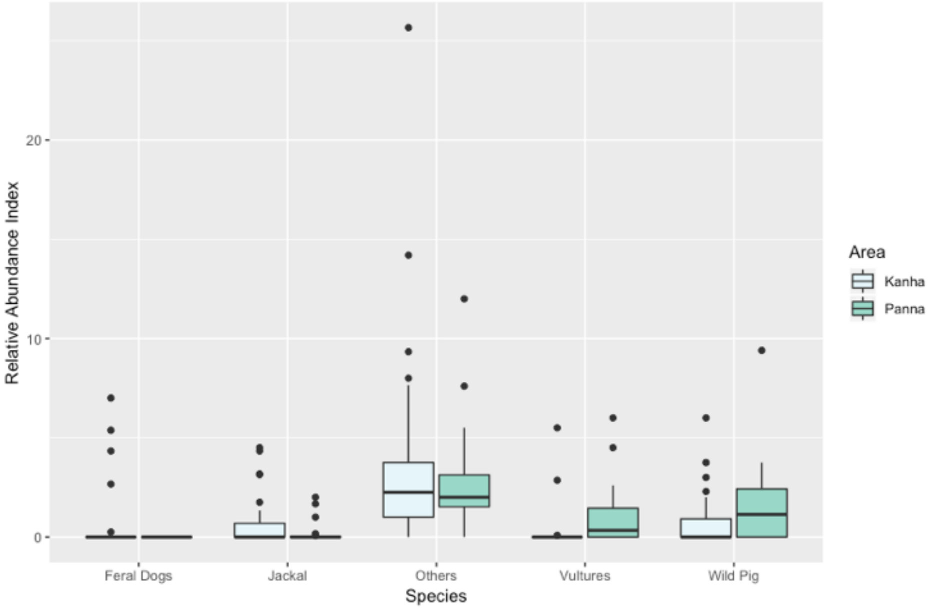

Figure 17: RAI for different species(Feral dog, jackal, wild pig, vultures, other scavengers) in low and high vulture abundance areas

Question 3: What are the covariates that determine scavenger visitation of carcasses?

Detection of carcasses was modelled for 8 species (out of a total of 22) which were present at sufficient sites to obtain convergence of models – Red-Headed Vulture, Crow, Jackal, Leopard, Ruddy Mongoose, Porcupine, Tiger, and Wild Pig. C-hat values for these models ranged from 0.6 to 1.06.

Table 13: Summary of best-fit model covariates and untransformed coefficients for covariates of detection probability, c-hat, Naïve Occupancy and Conditional Occupancy estimates.

Species	**Covariates**	**Estimate**	**Std. Error**	**Naïve ψ**	**Conditional ψ**
Red-Headed Vulture	*Intercept*	-0.06	0.83	0.23	0.58
	Canopy Cover	-0.11	0.04		
	Initial Weight	0.009	0.01		
	Initial Age	-0.61	0.28		
Crow	*Intercept*	-0.44	0.28	0.52	0.58
	Canopy Cover	0.02	0.01		
Jackal	*Intercept*	-0.91	0.32	0.38	0.50
	Horizontal Cover	-0.30	0.45		
	Vulture Presence	0.83	0.45		
	Initial Weight	0.005	0.002		
Leopard	*Intercept*	-0.80	0.52	0.31	0.59
	Canopy Cover	-0.03	0.02		
	Initial Weight	0.01	0.01		
	Initial Age	-0.82	0.27		
Mongoose	*Intercept*	-0.63	0.27	0.29	0.45
	Canopy Cover	-0.01	0.01		
Porcupine	Intercept	-1.26	0.41	0.15	0.22
	Initial Age	-0.71	0.26		

	Canopy Cover	3.68	1.18		
	Horizontal Cover	-0.50	0.30		
Tiger	*Intercept*	1.13	1.24	0.25	0.76
	Initial Age	-0.46	0.31		
	Initial Weight	0.01	0.004		
Wild Pig	*Intercept*	0.01	0.21	0.48	0.75
	Initial Weight	-0.01	0.003		

Discussion

Objective 1: To compare carrion removal rates between vertebrate scavengers, invertebrate scavengers, and microbes.

Question 1: By what magnitude do vertebrate scavengers remove carrion compared to invertebrates and microbes?

The experiment I conducted yielded not only quantitative data, but also many qualitative observations. Within the first few hours of placing the carcasses for invertebrate consumption, flies were observed sitting on the carcasses, likely laying their eggs. Maggots hatched after two to three days and consumed most of the carrion. Some beetles were also observed on and around the carcasses but not in as great abundance as flies and their larvae. Feathers and skin slightly slowed down the consumption – most of the consumption took place where the skin or flesh was exposed to the invertebrates while the skin and feathers remained in place. Invertebrates were also attracted to the carcasses in cloth bags, placed for the microbial decomposition and control treatments. These bags had to be hung within cages to reduce the exposure to invertebrates and subsequent risk of the cloth bags being compromised. A few of the bags failed as barriers after a few days and invertebrates – mostly flies - were able to gain access to the carcasses. These carcasses were then removed from the original experiment and placed instead in the sample category of invertebrate consumption after weighing.

The wire mesh cage was also not an entirely vertebrate-proof barrier. A ruddy mongoose was able to dig under the cage and chew part of two of the chicken carcasses placed to observe invertebrate scavenging, through the wire. These carcasses were excluded from the final experiment and replaced with fresh replicates. Interestingly, the mongoose had targeted two freshly-placed chicken carcasses in the cage and ignored two more decayed ones.

Several species of vertebrates visited and fed on the experimental carcasses for vertebrate scavenging. These include Red-Headed Vultures, Egyptian Vulture, Long-Billed Vulture, Hyena, Leopard, and Wild Pigs. These species were amongst the first to detect and consume the carcasses. Other species which also visited the carcass site, but after most of the carcasses had already been consumed, were Wild Pigs, Ruddy Mongoose, and Indian Fox. Most scavenging by mammals took place after sunset, while scavenging by vultures was entirely during the day.

There is little information on removal rates by various detritus feeders in tropical forests. My experiment on removal rates by vertebrates, arthropods, and microbes, though simple and limited in its sample size, provides insights into the drastic differences in these removal rates by the various taxa.

Microbial decomposition of carrion releases several nutrients in compound form, such as carbon as CO_2, nitrogen as NH_4^+, $NO2^-$, and $NO3^-$, and sulphur as H_2S and SO_4^{2-} (Parmenter and MacMohan 2009). In the absence of scavenging, decomposition of a carcass can lead to a large 'island' of nutrients which may be present even years later, in the case of large carcasses (Danell *et al., 20*03). By consuming a large part of the carrion biomass before it is completely decomposed by microbes, vertebrate scavengers retain a major component of the nutrients at higher trophic levels and assist in dispersion of the nutrients across a larger landscape area. The nutrients in the biomass are either assimilated by the cells of the scavenger (and later broken down again by microbes on the death of the animal) or excreted soon after, thus allowing only a part of the nutrients to re-enter the biogeochemical cycle in the abiotic realm (air, water and soil). As most vertebrate scavengers move over large distances – vultures are particularly wide-ranging (Houston, 1974) – they help retain nutrients in the biotic realm, and within that, disperse the nutrients they consume over the larger landscape.

Quantitative studies on nutrient cycling with respect to carrion and scavenging are rare (Barton *et al., 2*012), and little is known, if at all, how much of each nutrient is absorbed into a scavenger from the amount it consumes from carrion, that is, how much of the nutrients consumed from carrion are retained within the biosphere, and how much returns to the abiotic environment? We can estimate that the underlying principle of such a proportion would be similar to Lindeman's 'Ten Percent Law' of energy transfer between trophic levels. This would likely differ between tropical and temperate regions, with cycling likely much faster in tropical regions than in temperate regions where cold climate may inhibit microbial action. Some studies, however, have looked at the bioenergetics of carrion, calculating the calorific values of the carrion and the amount of carbon dioxide released per gram of carrion over the decomposition of the carcass (Putnam, 1978b), in the presence and absence of invertebrate scavengers (Putnam, 1978a). Carbon dioxide evolved was higher when fly larvae were present – this due to the addition of respiratory carbon dioxide by the larvae.

Carrion is a nutrient-rich and low-cost food source for many mammalian carnivores, which feed opportunistically on carrion when it is available. It must be taken into consideration that the treatments in our experiment are subsets of one another. That is, the removal of carrion by vertebrates also involves the removal of biomass by invertebrates and decomposition by microbes, as well as moisture loss. Similarly, the loss of weight in carcasses fed on by invertebrates was also contributed to by decomposition by microbes, and moisture loss.

Therefore, for taxon-specific rates of carrion removal, I subtracted the effect of invertebrates, microbes, and evaporation from the carcass removal rate of vertebrates, and microbial removal rate and evaporation from that of invertebrates. After these corrections, from our experiment, it is clear that vertebrate scavengers remove carrion biomass at a much higher rate (83% of biomass removed per day) than do invertebrates (7.3% biomass loss per day) and microbes (3.9% biomass loss per day). However, 83% of biomass was removed by vertebrates when the weight of the carcass was less than 2 kilograms. The proportional rate of removal of biomass likely decreases with heavier carcasses and as scavengers reach satiation.

Different taxa, at least among the species pools available at the two study sites in this study, thus have a different rate of removal of carrion. With vertebrates removing a majority of the carcass biomass, most of the nutrients from this carrion is retained in the biotic sphere. In my experiment, vertebrate scavengers removed the chicken carcasses completely, down to the bones and skin. Invertebrates removed only the soft tissue, leaving the bones, skin, and feathers behind. This would need to be mineralised by microbes or consumed by vertebrates to re-enter the biotic sphere, but vertebrate consumption ensures that these minerals – particularly calcium from the bones – is at least partly retained and utilised by fauna in the biotic ecosystem, instead of a slow loss into the abiotic environment.

A landscape with a different assemblage of vertebrate scavengers, or different diversity and abundance of the same scavengers, may also influence the outcome of such an experiment, particularly the rate of carrion removal by vertebrates. If we could carry out the same experiment in Kanha, where there are fewer vultures, higher numbers of meso-predators like jackals and fewer small carnivores, we might have a better overall idea of the contribution of different scavengers to the removal rates. Use of larger carcasses, like that of goats or cattle, would require a longer time period but would give a better understanding of how removal rates change with larger carrion biomass. It would also tell us if removal rates remain constant, increase with carrion biomass, or reach an asymptote as the scavengers become satiated over time. While vertebrate scavengers may get satiated over time, invertebrate scavengers could potentially take advantage of the abundant resources and respond numerically, due to their shorter lifecycles, so that they are able to increase consumption with time because of an increase in abundance.

While it is clear from the data that there is a significant difference between the removal rate of carrion by microbes, invertebrates and vertebrates, the difference in slopes between microbes and the control treatment was small, and not significant. This could imply (1) that either the microbes do not contribute much to the removal of carrion more than water loss does, or (2) that the anti-microbial treatment in our control experiment was not sufficient to reduce microbial activity drastically and my estimates of moisture loss were compounded by some microbial losses as well, or (3) simply that the sample size was too small.

A repetition of this experiment in a controlled setting, with temperature and humidity controlled for and the ‘control’, non-microbial treatment carried out under more sanitised conditions to completely preclude microbes, may be able to better reveal the contribution of microbes to carrion decay.

In our experiment, we have not looked into invertebrate scavengers in detail. Little is known about the invertebrates which scavenge upon carcasses. A future study on these may reveal the succession in invertebrate community over time as the carrion decomposes, interactions with microbes during the decomposition of the body, and whether richness or diversity of the invertebrate scavengers has an affect on the removal rate of carrion. Putnam (1978) found that little carrion from mouse carcasses was removed by visiting arthropods – most of the carrion removed by an invertebrate was that consumed by blowfly larvae. A study by Kneidel (1984) found that carcass size (from arthropods to small rodents) and, interestingly, *type* of carrion, influenced the dipteran community that were reared. Just two dipteran species which were more specialised with respect to season were found on the mouse carrion, while a greater number of dipteran species which were less season-specific were found consuming other types of carrion.

Although invertebrates remove carrion at a slower rate than do vertebrates, as we observed in our experiment, they do play an important role in the decomposition of carcasses and cycling of their nutrients (Coleman and Hendrix 2000). Pechal *et al., 2*014), found that excluding invertebrates from carcass decomposition for the first few days after placement decelerated the decomposition by several days, compared to carcasses where invertebrates were not excluded. Thus even in the absence, or paucity, of vertebrate scavengers nutrient recycling will continue, if at a slower pace.

Our experiment was carried out over a single season in early summer, and with a small sample size. This sample size may be the cause for the large variability in proportional weight of carcasses at different times as show in Figure . A multi-season study may reveal if carrion removal rates of scavengers, particularly invertebrates and microbes, change with the season. While the experiment was illuminating, many more questions remain to be answered which may be addressed in the future to better our understanding of carrion removal in a tropical system.

Objective 2: To assess how scavenger communities are affected by carcass size and vulture presence

Question 2: What is the difference between scavenger communities in two areas having different vulture density?

Although both study sites are tiger reserves situated in Central India, with similar climate, forest types, and animal species, Panna had a slightly higher diversity of scavenger species than did Kanha. While mammalian species like wild pig, jackal, tiger, leopard and others were shared between the two sites, more vultures were captured in Panna than in Kanha, as well as small carnivores like ruddy mongoose and common palm civet.

To observe if there is a difference in the scavenger communities of the two study areas, which could potentially be due to the higher presence of vultures in much higher numbers at Panna, I compared the similarity of the scavenger species composition between the two study areas. Statistically, from the ANOSIM results, there is no significant difference in the scavenger species composition that visited carcasses between the two study areas. There were far fewer captures of small carnivores in Kanha than Panna, which can be observed in the table of RAI for both sites for all species (Annexure 1). Whereas ruddy mongoose was rarely captured in Kanha, it was one of the most common species in Panna. Conversely, one of the most common species in Kanha, the jackal, was only captured in Panna at a few sites. Wild pigs were captured at similar rates in both study areas. This supports our original hypothesis that vultures play the role of keystone species. In their absence, or when vulture abundance is low, a meso-predator release takes place, allowing species such as jackals and wild pigs to proliferate and in turn depress the population (or activity) or smaller carnivores like mongoose, porcupines and civets. This could potentially explain the greater number of smaller carnivores observed in Panna than Kanha. While we cannot clearly make this inference from our data, further study may reveal if this is the case.

To understand if carcass size influences the scavenger community that feeds upon it, I assessed the similarity of scavenger species composition (ANOSIM analysis on the species matrix) of each site on the basis of carcass size. Despite a slight difference in richness, there was a small difference in the specific species visiting carcasses of different sizes. Although it has been documented in published literature (Moleon *et al., 2*015), which shows that different species show preference for carcasses of different sizes, my results show that scavengers do not seem to show any preference or avoidance of a carcass size. However, as the R value was not significant ($p>0.05$), this may be an artefact of sample size, as the samples for small carcasses in particular are low, and have not reached an asymptote for species richness.

The species accumulation curves give an idea of whether I observed all the scavengers in the study sites. Looking at the curves for the two study areas, both seem to have reached an asymptote, implying most of the scavenger species have been sampled. This is reflected in the richness measure – the estimate of species richness by the bootstrap method is not very different from the number of species in the data. However, when we observe the richness of species feeding on different carcass sizes at each site, we can see that there is some difference in the number of species observed and the predicted estimate of species. The species accumulation curve for the different carcass sizes points to a sufficient sample size for large and medium samples, but more samples are required of small carcasses to observe all the available scavenger species that may feed on small carcasses. This is reflected in the richness estimates – the estimates are slightly higher than the observed number of species, though by a small degree. Due to the smaller sample size, I used the bootstrap estimates for species richness.

Interestingly, here again medium sized carcasses appear to be slightly more rich in species than large and small carcasses. This was unexpected as I expected large carcasses, having greater biomass and more easily detectable, to be the most species rich as they would be sufficiently large to attract large scavengers as well as smaller scavengers. However, this may be due to the sample size. Further study may better reveal the relationship between scavenger species size and carcass size.

No clear pattern can be observed in the boxplots of carcass use for different species. However, it is interesting that red-headed vultures had a much higher RAI at small carcasses – domestic chickens placed for the experiment on carrion removal by vertebrate scavengers. Considering their size, chickens might be predicted to be too small for these vultures. However, up to six red-headed vultures – normally found in pairs or solitarily – were photocaptured feeding on a single chicken carcass. Interestingly, a goat carcass placed nearby – although not at the same time – was not visited by any vultures at all. This could be due to random chance, or because of some difference in detectability. For example, the bright white feathers of the chicken might be more noticeable for a gliding vultures than a dark-coloured goat. An experiment to control for these factors with respect to detection of carcasses may reveal more.

Plate 1: A group of Red-Headed Vulture Sarcogyps calvus *and an Egyptian Vulture* Neophron percnopterus *feeding on an experimental chicken carcass*

Although I had expected scavenger communities to differ significantly between the two study sites, and across carcass sizes, the results of my data do not support this. This may in part be due to issues of sample size, as there are relatively fewer whole carcasses monitored compared to predator kills, where initial scavenging data may be missed due to later discovery of the carcass. Supplementing this sample size with more experimental carcasses, including some of large sizes, could solve some of these issues.

When we compared the relative abundance index for jackal, wild pig, feral dogs, and vultures, in the two areas – low vulture abundance (Kanha) and high vulture abundance (Panna), what is striking is the low relative abundance of jackals in Panna compared to Kanha. Jackals in Kanha have attained high densities, and occasionally form small packs of up to four individuals and hunting prey as large as adult chital (*Axis axis*). In the absence of vultures, more carrion is available for facultative scavengers to feed on. Jackals in Kanha may have potentially made use of this extra resource, leading to an increase in population. With an abundance of vultures in Panna, jackals may not have been able to obtain the necessary energy to increase numerically. This may also be the case with feral dogs in Kanha, where they were observed scavenging on several carcasses, but were mostly absent in Panna. Wild pigs would be expected to follow the same pattern, however their relative abundance appears to be similar in the two study areas.

<u>Question 3: What are the covariates that determine scavenger visitation of carcasses?</u>

The site covariates used in the occupancy models were selected for their potential effect on the detection of a carcass by different scavenger species. Initial carcass age (when monitoring began for that particular carcass) may influence detection, as a carcass at a later stage of consumption may have already been detected before, thus increasing chances of a species revisiting the carcass during monitoring or acting as a signal to trigger visitation by other scavenger species. Additionally, carcasses at a later stage of decay tend to have a strong smell which can attract more scavengers. However, some species may prefer fresh carrion and thus the relationship will be positive – higher detection probability when the initial carcass age is younger.

Initial weight of the carcass tells us how much of the carcass is available to be consumed. If the remaining biomass is very little, then larger scavengers may fail to detect it or may not find the small amount of biomass worth the potential costs of competition with other scavengers.

Habitat variables like canopy cover and horizontal cover may influence visibility of the carcass – high canopy and horizontal cover make a carcass harder to detect. Vulture species are less likely to detect carcasses where there is high canopy cover, as they rely on sight while flying to locate carcasses.

Increasing canopy cover seemed to reduce detection probability of all species by all scavengers, including red-headed vultures, except for crows (Table 13). Increased age of the carcass also resulted in decreased detection probability for most species. Vulture presence was a significant factor for detection probability only for jackals and also porcupines.

Vulture presence at a carcass was included as the presence of vultures – particularly when in large numbers – can signal to other species that carrion is available, attracting other scavengers to feed on the carcass as well. Vultures can locate a carcass much faster than terrestrial scavengers, even when a predator is still feeding on it, and this can also act as a signal to other scavengers of the existence of carrion biomass for consumption. Conversely, vulture presence can also decrease the carrion biomass available for other species to feed on, resulting in a negative relationship.

The covariates in the best fitting model for detection of carcasses by Red-Headed Vulture were canopy cover, initial carcass weight, and initial carcass age. A negative coefficient for canopy cover implies that the higher the canopy cover, the lower the detection probability of a carcass by Red-Headed Vulture. This is logical as most vultures rely on sight to locate carcasses, which would be impeded by dense canopy cover. A dense canopy would also limit manoeuvrability for the vultures to land, thus vultures are unlikely to detect or feed at carcasses in dense bushes. Although Red-Headed Vultures were observed in forested patches, unlike other vulture species which remained mostly in grassland areas, they were absent from carcasses in dense bushes. The coefficient for initial carcass age was negative, implying that the older the carcass the lower the probability of detection by vultures. This could be because much older carcasses have little to no biomass available for vultures to eat and thus the vultures are no longer attracted to the carcass. The coefficient for initial carcass age was positive, implying that fresher carcasses are more likely to be detected by the vultures than older carcasses. This fits with the negative relationship with initial weight – carcasses which are fresher and have more biomass remaining are more likely to be detected by red-headed vultures than older carcasses with less biomass.

Other species show different factors affecting detection probability. Crows and mongoose both have best fitting models with canopy cover as the only covariate, but with opposite effects. Crows were the only species for whom detection probability increased with canopy cover, likely because crows were found more in forested areas with trees than in grasslands with no cover, or could use a carcass in the absence of vultures. Mongoose detection of carcasses was negatively impacted by canopy cover, implying mongoose are less likely to detect a carcass with a high canopy cover.

Jackals appear to be less likely to detect carcasses when horizontal cover is higher. Dense horizontal cover likely makes it difficult to find a carcass, particularly if it has been hidden in dense bushes by a predator such as a tiger or leopard, making a jackal unlikely to venture into dense cover to feed on a carcass. Higher initial carcass weight increases likelihood of jackals detecting carcasses, likely as larger carcasses persist longer and are more easy to detect than small carcasses. Interestingly, jackals are also more likely to locate carcasses at which vultures have also fed. This may be because of an interactive relationship between the jackals and vultures, where jackals locate carcasses by watching for descending vultures, as has been observed in hyenas in Africa (Kruuk, 1967), or vultures locate kills made by jackals. The exact nature of this relationship is likely more complicated and likely changes in nature with the abundances of these species in different areas. At higher vulture densities, removal of carrion is higher and this may limit carrion resources for facultative scavengers like jackals. In areas with low densities of vultures, jackals may be able to increase numerically in response to higher availability of carrion as a food resource, over time. At high densities, jackals may form packs and hunt larger prey or hunt more frequently, as can be observed in Kanha Tiger Reserve – possibly an example of meso-predator release due to the low vulture numbers. Further study of the interactions between these species in areas of differing abundances will shed more light on the nature of the relationship.

The coefficients of the covariates of the best fitting model for detection probability of carcasses by leopards reveals that leopards may be less likely to detect carcasses under dense canopy cover. Detection probability s higher, however, when initial weight is higher and initial age is lower. Fresh carcasses with more remaining biomass are more likely to be detected by leopards. The fit of this model may be partly explained by the fact that several of the carcasses were kills made by leopards and were visited and fed on by the leopards in early stages of consumption. However, as some of the fresh chicken and goat carcasses placed in the study area were also located and consumed by leopards, it is likely that leopards are quick to detect fresh carcasses and prefer to scavenge on fresh over decayed carrion.

Tigers were similarly more likely to detect carcasses with higher initial weight and a lower initial age. As with leopards, this is likely because many of the carcasses monitored were tiger kills. Most kills in Kanha were kills of domestic cattle by tigers. As only one individual tiger could be identified in the camera trap photographs, it was assumed to be the predator. Cases where a tiger was confirmed to be scavenging were few – in one kill, a collared tigress in Panna was learned to have ‘stolen’ a kill – a large sambar – from a leopard. Tigers were also observed feeding on two of the fresh goat kills placed in Kanha, but in both cases, the tigers attempted to drag the carcasses away and were unsuccessful because the carcasses had been firmly tied to prevent scavengers from moving them out of site of the camera. The tiger then left the carcasses where they were, after eating a little of the meat – this is in contrast to leopards, who either persisted in dragging a carcass away or sat in front of the camera and consumed the carrion almost entirely.

Detection of carcasses by porcupines was negatively associated with initial age of the carcass and positively with vulture presence. Porcupines may be able to detect carcasses more when the carcass is fresh and vultures may be present at these carcasses. However, it seems unlikely that the presence of vultures is attracting porcupines, considering that vultures are entirely diurnal and porcupines are entirely nocturnal, hence some other factor may be causing this association. Further study may reveal more intricacies that have so far escaped notice due to low sample size and the selection of specific site covariates in the present study.

Detection of carcasses by wild pigs appears to be negatively associated with the initial weight of the carcass – the lower the initial weight, the higher the probability of detecting the carcass. This could imply that wild pigs are more likely to detect smaller carcasses. However, this seems counterintuitive. Instead, it is possible that carcasses at a later stage of consumption and thus with less biomass remaining may be more easily detected by wild pigs because a) there were previous detections of the carcass before monitoring began or b) the strong smell of rotting carrion emitted by older carcasses may draw wild pigs to undetected carcasses. A larger sample size may reveal if initial age also plays a significant role in the detection probability of carcasses by wild pigs along with initial weight.

Vultures did not appear to play a significant role in the detection of carcasses by any species other than jackals. However, we cannot rule out facilitative or competitive interactions between these species, as they are likely too complex to be detected by presence data alone.

A caveat to these results is that changes in the detection probability due to increased age or decreased carcass weight remain unmodelled. These may help us obtain better fitting models in the future, with a larger sample size that allows for more parameters to be modelled.

All ψ values after correction for detection bias were substantially larger than the naïve occupancy. This suggests that the detection of carrion by vertebrate scavengers was a major limiting factor in forested ecosystems. Crows had the least difference between naïve and conditional ψ (0.52 and 0.58, respectively). Red-headed Vultures had the highest difference between naïve and conditional ψ, 0.23 and 0.58 respectively, followed by wild pigs (0.48 and 0.75). With falling detection probability, more carcasses are likely to go entirely undetected, or less consumed than if they were better detected by scavengers. The disparity in detection probability, leading to carcasses being underutilized, suggests that there may be a paucity of scavengers, or that the detection of carrion by the scavengers is not efficient. Alternatively, facultative scavengers may be relying less on carrion and more on predation or other sources for their food. Occupancy modelling can thus be used in a novel way to answer questions on the detection of carrion by scavengers under different circumstances.

Way Forward

In this study, I have attempted to look at different facets of scavenging ecology with a particular focus on vertebrate scavengers. This is a relatively nascent, vast topic, on which there is much to study, particularly in tropical systems, of importance to understanding the basis for trophic systems, nutrient cycling, and ecosystem health. There are several interesting ways to continue with this work, including testing if avian scavengers, and vultures in particular, are more likely to locate carcasses first, and if carcasses located by avian scavengers are consumed more quickly than other carcasses. Studying the sequence of species arrival or ‘colonization’ at a carcass may reveal more on the inter-species interactions, particularly facilitation of locating and feeding on carcasses. Further, understanding the different and specific behavioural roles of each scavenger species could aid better understanding their functional diversity in, and contributions to, ecosystem nutrient cycles.

Examining the number of ‘contacts’ between individuals and species which feed at a carcass has implications for disease spread, particularly in a landscape where feral dogs are becoming ubiquitous and compete with wildlife for live prey as well as carrion. Increasing feral dog populations could be a threat to wild predators and scavengers, as reservoirs and vectors of disease. They may have a compounding effect on vulture population loss, as feral dogs have been shown to outcompete vultures at carcasses due to the dogs' habits of being both nocturnal and diurnal, and their great tolerance of human disturbance, higher densities, and sheer physical dominance (Butler et al, 2006). Feral dogs may outcompete vultures and curtail the recovery of vulture populations. Since dogs are less efficient at removing carrion from the ecosystem than obligate scavengers, the risk of spreading diseases from remaining carcasses increases, particularly as free-ranging dogs frequently move between human habitats and wild areas.

The use of occupancy modelling for estimating detection probability of carrion for different scavengers is a unique approach, and with more data can be highly informative of the patterns and processes that govern the relationship between species and carrion.

Scavenging has been less studied in tropical systems. This study adds to the growing body of work on the topic in India. It is hoped that the work gives a perspective on scavenging in a tropical forest system, and provides a stepping stone for future work in this area.

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Appendices

Appendix 1: Mean Relative Abundance Index for each species for both sites combines (Mean) and for each site separately (Mean (Kanha) and Mean (Panna), along with Standard Deviations

Species	MEAN	SD	Mean (Kanha)	SD	Mean (Panna)	SD
Crow	2.09	4.23	2.80	5.03	0.97	2.12
Wild Pig	1.08	1.77	0.75	1.39	1.61	2.19
Jackal	0.53	1.08	0.71	1.28	0.25	0.59
Feral Dog	0.38	1.38	0.61	1.72	0.00	0.00
Leopard	0.31	0.67	0.25	0.57	0.41	0.80
Ruddy Mongoose	0.27	0.71	0.02	0.08	0.67	1.04
Red-Headed Vulture	0.27	0.70	0.00	0.01	0.70	1.01
Jungle Cat	0.17	0.69	0.25	0.87	0.03	0.08
Porcupine	0.14	0.45	0.14	0.49	0.15	0.38
Egyptian Vulture	0.12	0.50	0.00	0.00	0.30	0.78
Tiger	0.11	0.26	0.18	0.32	0.00	0.02
Treepie	0.11	0.30	0.04	0.12	0.22	0.45
White-Rumped Vulture	0.11	0.76	0.17	0.97	0.00	0.00
Rodent	0.08	0.26	0.10	0.31	0.03	0.15
Hyena	0.06	0.19	0.00	0.00	0.16	0.28
Griffon Vulture	0.05	0.40	0.09	0.51	0.00	0.00
Indian Fox	0.04	0.17	0.00	0.00	0.11	0.26
Small Indian Civet	0.04	0.16	0.01	0.06	0.08	0.24
Long-Billed Vulture	0.03	0.13	0.00	0.00	0.08	0.20
Common Palm Civet	0.03	0.09	0.02	0.09	0.03	0.09
Dhole	0.02	0.07	0.02	0.09	0.00	0.00

Mynah	0.01	0.06	0.01	0.04	0.02	0.09
Crested Hawk Eagle	0.01	0.04	0.01	0.05	0.00	0.00
Cinereous Vulture	0.00	0.02	0.00	0.00	0.01	0.03
Sloth Bear	0.00	0.02	0.00	0.00	0.01	0.02

Appendix 2: Top three models for detection probability modelling for each species ranked by AIC

Species	**Detection Probability Covariates**	**AIC**
Red-Headed Vulture	Canopy Cover, Initial Weight, Initial Age	**118.36**
	Canopy Cover, Initial Age	118.81
	Canopy Cover, Horizontal Cover, Initial Age	120.22
Tiger	Initial Weight, Initial Age	**105.78**
	Initial Weight, Vulture Presence	105.99
	Initial Weight	106.29
Leopard	Canopy Cover, Initial Weight, Initial Age	**136.43**
	Canopy Cover, Initial Weight, Initial Age, Horizontal Cover	137.99
	Initial Weight, Initial Age, Horizontal Cover	138.7
Mongoose	Canopy Cover	**206.62**
	NULL	207.44
	Horizontal Cover	208.07
	Canopy Cover, Horizontal Cover	208.23
Crow	Canopy Cover	**267.9**
	Canopy Cover, Initial Age	268.21
	Canopy Cover, Vulture Presence	268.5
Jackal	Initial Weight, Vulture Presence, Horizontal Cover	**240.83**
	Horizontal Cover	241.45
	Horizontal Cover, Vulture Presence	241.46
Porcupine	Initial Age, Canopy Cover, Horizontal Cover	**125.4**
	Initial Age, Canopy Cover	126.64
	Initial Age, Canopy Cover, Initial Weight	128.14
Wild Pig	Initial Weight	**279.96**
	Horizontal Cover, Initial Weight	280.7
	Vulture Presence, Initial Weight	281.39

Appendix 3: Map of Study Areas within Madhya Pradesh, India

Appendix 4: Snapshots from the field

Plate 2: Measurement of horizontal cover using checkerboard in Panna TR

Plate 3: White-rumped vultures attempting to scavenge on a chital kill made by a group of four jackal, in Kanha. This carcass was later monitored.

Plate 4: Four wild dogs feeding on a female chital kill, Kanha. The kill was consumed in under one hour and the carcass was then monitored for several days afterwards.

Plate 5: A ruddy mongoose attempting to gain access to experimental chicken carcasses, placed for invertebrate scavenging experiment, from camera trap.

Plate 6: A Red-Headed Vulture and a Cinereous Vulture feed at a sambar carcass, from camera trap.

Plate 7: A female dhole scavenging on a cattle kill, from camera trap