

Super-scavengers: Vertebrates outperform invertebrates and microbes at removing carrion from a tropical forest

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Abstract

Scavenging by vertebrates is an important ecosystem service as they are known to remove carrion more efficiently than other taxa. How long would carrion persist bereft of vertebrate scavengers? Our study addresses this question in a forested landscape, by comparing carrion utilization by vertebrate scavengers, invertebrates, and microbes (decomposers). To understand carrion removal, we used experimental placement of chicken carcasses in a dry deciduous forest near Panna Tiger Reserve, Madhya Pradesh, India. Carcasses were placed under different treatment conditions (vertebrate scavenging, invertebrate scavenging, microbial decomposition and control to account for moisture loss), by experimentally excluding other scavengers. The daily rate of carcass utilization and proportion of carrion biomass remaining differed between treatments. Vertebrates consumed carcasses at the highest rates, removing 83% of carcass biomass in one day (CI 95%), followed by invertebrates (7.3%) and microbes (3.9%). Additionally, desiccation accounted for another 3.6% weight loss per day. The study showed drastic differences in carrion removal rates between taxa, indicating the irreplaceable role of vertebrates in the scavenging community of tropical forests, without whom carcasses would persist over prolonged periods. Our results support earlier studies that found overwhelming influence of vertebrate scavengers on carrion removal compared to other scavenging guilds.

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Keywords

Carcass, mesopredators, vultures, central India, Panna, decomposers

Introduction

Vertebrate scavengers consume an estimated 75% of carrion around the world (Devault *et al.* , 2003). Yet, scavenging by vertebrates, as a process had gained recognition only recently. Vertebrate scavengers play important ecosystem functions such as nutrient cycling (Cederholm *et al.* , 1999; Danell, Berteaux and Bråthen, 2002) sanitation and disease moderation (Markandya *et al.* , 2008), and competitive interactions (Kaczensky, Hayes and Promberger, 2005; Materassi *et al.* , 2017). Scavenging retains nutrients from carrion and recycles them in the biotic component of the ecosystem that would otherwise get released into the physical environment through decomposition, thereby playing a regulatory role in biogeochemical cycles (Danell, Berteaux and Bråthen, 2002). Instead of allowing carcasses to decompose completely at a site, leading to a large ‘island’ of nutrients which may persist over years (Danell, Berteaux and Bråthen, 2002; Benninger, Carter and Forbes, 2008; Parmenter and Macmahon, 2009) vertebrate scavengers, in particular, assist in dispersing these nutrients over a larger landscape. This reduces the excessive concentration of nutrients such as Phosphorus, Sodium and Potassium around carrion (Benninger, Carter and Forbes, 2008; Parmenter and Macmahon, 2009) which would inhibit vegetation growth (Towne, 2000). Obligate vertebrate scavengers remove carrion more efficiently and rapidly than facultative scavengers or decomposers (Ogada *et al.* , 2012). The highly acidic digestive tract and gut microbiome of specialized scavengers such as vultures reduces the transmission of pathogens and consequently the risk of disease spread from decomposing carcass (Houston and Cooper, 1975; Roggenbuck *et al.* , 2014; Graves, 2017; Zepeda Mendoza *et al.* , 2018). In the absence of obligate vertebrate scavengers, accumulation of carrion over longer durations, competitive release of facultative scavengers, and disease transmission through facultative scavengers can have serious ecological ramifications that are poorly understood. In light of the global declines of vertebrate populations, understanding these aspects of carrion ecology becomes vital. Such insights can bolster the scientific rationale and global efforts for conservation of vertebrate populations.

Quantifying the relative contribution of vertebrate scavengers to carrion removal in comparison with invertebrate scavengers and microbial decomposition allows us to better understand the role of different scavenging communities, which in turn can inform conservation policy. Conserving the diversity of scavenger assemblages is important in the light of biodiversity loss (Cardinale *et al.* , 2012), as this enhances functional redundancy, thereby stabilizing scavenging systems.

Previous studies have shown that manipulative reduction of a dominant scavenger (raccoons *Procyon lotor*) in an agricultural landscape reduced system efficiency and left more carcasses un-scavenged (Olson *et al.* , 2012). Exclusion of vultures from carcasses did not increase carcass visitation or utilization by facultative scavengers and resulted in 10-fold greater un-scavenged carcasses, indicating that facultative scavengers cannot replace obligate vertebrate scavengers completely (Hill *et al.* , 2018). Yet, in other ecoregions, the decline of top predator and scavenger (Tasmanian devil *Sarcophilus harrisii*) or exclusion of dominant scavengers resulted in higher detection and utilization of carcasses by meso-predators, notwithstanding increased persistence time and availability of carrion to decomposers (Cunningham *et al.* , 2018; Tobajas *et al.* , 2021). Thus, the loss of apex vertebrate scavengers may elicit differential responses in scavenging communities and

carrion persistence between eco-regions. Although rapid removal of carrion by vertebrates was a consistent finding of the above studies, they became less efficient in handling carrion at high carrion densities mimicking Mass Mortality Event ($>350\text{kg}/20\text{ m}^2$) that led to reduced nutrient cycling, die-offs of vegetation and trees due to nutrient overload, and subsequent introduction of new plants in the area (Tomberlin *et al.*, 2017). As scavengers and decomposers compete for carcasses, Devault *et al.* (2004) found that contribution of vertebrates in removing carrion reduced and that of decomposers increased with increasing ambient temperature, indicating an environment-dependent outcome of such competition. However, studies that compare carrion removal rates between scavenger types and decomposers are lacking.

Our experimental study attempts to understand carrion removal in a forested landscape of Central India, by estimating the utilization of carrion by vertebrate scavengers compared to invertebrates, microbes (decomposers), and moisture loss (control). We addressed this question by placing chicken carcasses under uniform environmental conditions in four experimental set-ups that excluded either or all of the scavenging guilds (i.e. vertebrates, invertebrates, microbes and control). We measured daily carcass biomass to compare removal rates between scavenging guilds using linear mixed effect models. Our study showed that vertebrate scavengers contributed to maximum carrion removal per day, followed by invertebrate scavengers, and microbial decomposition.

Methods

Study Area

We carried out this study in the buffer area of Panna Tiger Reserve, Madhya Pradesh, India in April 2019. The dominant vegetation is dry deciduous forests interspersed with grassy meadows. The region has a tropical climate with mean summer temperatures between 24-40 °C. Summers are dry with mean rainfall of 6 mm in April. The rugged land features of the Park – plateaus and gorges – along with tall large trees provide suitable nesting and roosting sites for several vulture species (Red-Headed Vulture *Sarcogyps calvus*, White-rumped Vulture *Gyps bengalensis*, Long-billed Vulture *Gyps indicus*, Egyptian Vulture *Neophron percnopterus*, Griffon Vulture *Gyps fulvus*, Himalayan Griffon *Gyps himalayensis*, and Cinereous Vulture *Aegypius monachus*) that along with the striped hyena (*Hyaena hyaena*) are the obligate scavengers of this system. The study area supports other meat-eating animals such as the tiger (*Panthera tigris tigris*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), jungle cat (*Felis chaus*), golden jackal (*Canis aureus*), wild pig (*Sus scrofa*) and several smaller mammals which also often scavenge. Herbivores which constitute natural prey and carrion in the Park include spotted deer (*Axis axis*), Sambar (*Rusa unicolor*), Nilgai (*Boselaphus tragocamelus*) Indian gazelle (*Gazella bennettii*) and four-horned antelope (*Tetracerus quadricornis*), in addition to domestic cattle (*Bos taurus*).

Experimental Method

To observe the effects of different scavenging guilds (microbial, invertebrate, and vertebrate) on carcass consumption and decay, we conducted an experiment using fresh chicken carcasses (1-2 kg) (Figure 1). To control for other confounding factors that can influence carcass persistence rates, we placed all carcasses in similar conditions – under shade of dry deciduous vegetation with similar canopy cover and horizontal cover (scrub/herbaceous layer density). The above conditions ensured consistency in scavenger composition and similarity in carrion discovery rates. The experimental control and treatments were as follows:

1. Control (for estimating moisture loss): Carcasses with guts removed to prevent decay due to gut bacteria (n=3) were treated with 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 weighed daily to record moisture loss in the absence of microbial decomposition.
2. Microbial decomposition: Whole carcasses (n=3) were placed in cloth sacks to exclude invertebrate scavengers, and placed in a wire cage to exclude vertebrate scavengers. These were weighed daily to record loss of biomass due to microbial decomposition as well as by desiccation.

3. Invertebrate scavenging: Carcasses were placed inside wire mesh cage on the ground with no cloth covering, to allow invertebrate scavengers but to exclude vertebrate scavengers (n=6). These were weighed daily to record invertebrate scavenging, microbe decomposition, as well as moisture loss.
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. All carcasses were weighed at the time of placement and then daily, to measure biomass loss due to scavenging by vertebrates, invertebrates, microbes and by desiccation (figure 2).

Analytical Methods

Proportion of biomass remaining was calculated daily for each carcass. To observe the effects of each ‘treatment’ (control, microbe, invertebrate, vertebrate) on biomass removal, Linear Mixed Effect Models (LMEs) were used to account for the correlated nature of the data, arising from observing the same carcass over time. We modelled logit-transformed (log-odds of) proportional biomass remaining over days against treatment types as fixed effects, and the carcass replicate as random effect. We modelled both additive (time + treatment) and multiplicative (time x treatment) models to find the best fit. An additive model implies that both time and treatment types have independent effects on the loss of carrion biomass, and the resulting graph would have parallel lines for each treatment type. However, a multiplicative model points to an interactive effect between time and treatment on the loss of carrion biomass, which would more closely approach a natural system.

Logit-transformation allowed biomass persistence to be modelled as a logistic function and constrained the predicted values between 0 and 1. Proportion of carcass remaining on day 0 was considered as 0.9999, to avoid the transformed value from becoming infinity. All analysis was carried out in R (R Core Team, 2021). Inferences were based on the least Akaike Information Criterion (AIC) model, which was used to predict carcass persistence over time for different treatments.

We examined the effects (slopes) of each treatment on the decay rate of carcass over time using ‘lrends’ and ‘pairs’ functions in ‘emmeans’ package of R (Lenth, 2021). However, the effects thus estimated were *recompounded effects* as the treatments were nested. Vertebrate scavenging included some carcass weight loss due to invertebrate scavenging, microbial decomposition, and water loss; whereas, invertebrate scavenging included some microbial decomposition and water loss. Hence, to tease apart the individual effects of scavenger guilds on carrion removal rates, we subtracted a) the daily mean carcass weight loss due to evaporation (estimated from control experiment) from the daily proportional carcass weight in the microbes treatment, b) the daily mean weight loss due to microbial decomposition from the daily proportional carcass weight in the invertebrate treatment, and c) daily mean carcass weight loss in invertebrate treatment from the daily proportional carcass weight in vertebrate treatments. The above modelling exercise was repeated on these adjusted measurements, to estimate *individual effects* of each treatment. Graphs were generated using ‘ggplot2’ package in R (Wickham, 2009).

Results

A total of 17 chicken carcasses were used for carrion removal experiments. Control carcasses persisted and were monitored up to 15 days), microbe treatment carcasses up to 14 days, and invertebrate treatment carcasses up to 12 days. Carcasses placed for vertebrate consumption were removed by scavengers within one day of carcass placement. The proportion of carrion biomass remaining over time differed between treatments (figure 2). Comparison of hypothesis found maximum support for the interactive effect of time and treatment on carrion removal rate. Model parameter estimates indicated fastest removal of carcass under vertebrate scavenging followed by invertebrate scavenging, and negligible difference in carrion loss rates between decomposition and evaporation.

The parameter estimates of the best model showing individual effects of treatments on logit-transformed proportional loss of carrion biomass (Table 1) represent the logit-transformed proportional loss of carrion biomass each day under the different treatments. The inverse logit-transformations of these estimates gives us the change in proportion of carrion biomass each day, while the negative sign connotes a loss in biomass. For example, with each passing day, proportion of carrion biomass reduces by 0.99 due to vertebrate scavenging (Time x vertebrate scavenging) (Table 1). For invertebrate scavenging, proportion of carrion lost each day is 0.5, and it is 0.51 for microbial decomposition. Daily loss of carrion biomass due to evaporative moisture loss alone (Control) was estimated at 3.6%. Besides this, microbial decomposition *per se* resulted in 3.8% loss of carrion biomass and invertebrate scavengers *per se* resulted in 7.3% loss of carrion biomass daily. In contrast, vertebrate scavengers *per se* resulted in 83% loss of carrion biomass per day. The compounded effect of vertebrate scavenging along with invertebrate scavenging and microbial decomposition caused 99.9% carrion removal in a day (Table 2).

Discussion

There is little information on carrion removal rates by various carrion feeders in tropical forests. Although limited by sample size, our experiments allowed direct comparison of carrion removal rates between vertebrates, invertebrates, and microbes. After adjusting for carrion losses to other treatments, vertebrate scavengers removed carrion much faster than did invertebrates and microbes (figure 4). However, the daily removal of 83% of biomass by vertebrates was for carcass less than 2 kg, and removal rates would likely decrease with larger carcasses, as scavengers could potentially reach satiation. Nonetheless, the study showed drastic differences in carrion removal rates between taxa, and indicated the irreplaceable role of vertebrates in the scavenging community of tropical forests, without whom carcasses persisted over prolonged time periods. Thus, our results support earlier studies that found overwhelming influence of vertebrate scavengers on carrion removal compared to other scavenging / decomposing guilds (Devault, Brisbin and Rhodes, 2004; Cunningham *et al.* , 2018).

With vertebrates removing a majority of carcass biomass in a short time, most of the nutrients were retained and recycled in the biosphere. Vertebrate scavengers consumed 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. Vertebrate consumption ensures that these minerals – particularly calcium from bones – is at least partly retained in the biotic sphere, instead of its slow loss into abiotic environment, thereby playing an important ecosystem function. Quantitative studies on nutrient cycling through scavenging are rare (Barton *et al.* , 2013; Macdonald *et al.* , 2014), and little is known about the proportions of nutrients absorbed into scavengers from carrion and thereby retained within the biosphere. We can assume that nutrient retention from carrion to scavengers would follow Lindeman’s ‘Ten Percent Law’ of energy transfer between trophic levels (Lindeman, 1942; Brown and Gillooly, 2003). This would likely differ between tropical and temperate regions, with nutrient cycling likely much faster in tropical regions than in temperate regions where cold climate may inhibit microbial action. Very few studies have examined the bioenergetics of carrion so far, with some exceptions (Putman, 1978).

Although invertebrates remove carrion at a slower rate than vertebrates, they do play an important role in decomposition of carcasses and nutrient cycling (Coleman and Hendrix, 2000). Exclusion of invertebrates from a carcass for the initial days decelerated carcass decomposition by several days (Pechal *et al.* , 2013). Thus, even in the paucity of vertebrate scavengers, nutrient recycling will be continued by invertebrate scavengers, but at a slower rate in a tropical dry deciduous forest system. Little is known about invertebrate scavenging, as a process. Future studies are required on succession in invertebrate community as the carrion decomposes, interactions with microbes during carrion decomposition, and if carrion removal rates are influenced by the diversity of invertebrate scavengers. Putman (1978) found that most of the carrion in the form of mouse carcasses was removed by blowfly larvae, among invertebrates. Another study found that carcass size and

type of carrion influenced the dipteran community (Kneidel, 1984). Only two dipteran species which were more specialised with respect to season were found on mouse carrion, while a greater number of dipteran species which were less season-specific consumed other types of carrion.

Besides the quantification of carrion removal rate by different groups, our study yielded many qualitative observations which can contribute to the understanding of carrion natural history. When invertebrates were not excluded from carcasses, flies discovered carrion within a few hours and laid eggs. Maggots hatched after two to three days and consumed most of the carrion over a period of several days if vertebrates were excluded. Some beetles were also observed on/around carcasses but in less numbers than flies and their larvae. Feathers and skin slowed down their consumption; most of the consumption took place where the skin or flesh was exposed to invertebrates. When vertebrates were not excluded, several species visited carcasses such as the Red-Headed Vulture, Egyptian Vulture, Striped Hyena, and Leopard (Figure 3). These species were amongst the first to discover and consume carcasses. Other species which visited the carcass, but subsequently, were Wild Pigs, Ruddy Mongoose, Golden Jackal and Indian Fox. Most scavenging by mammals took place after sunset, while scavenging by vultures was entirely during the day.

Among obligate scavengers, the critically endangered Red-headed Vultures were the most photocaptured at the experimental carcasses followed by Egyptian Vultures. Considering their size, chickens might be predicted to be too small for these vultures. However, as many as five red-headed vultures – normally found in pairs or solitarily – were captured feeding on a single chicken carcass (Figure 3). Three of these appeared to be juveniles. 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 vulture than a dark-coloured goat. An experiment to control for these factors with respect to detection of carcasses may reveal more. Among the species that were not captured at carcasses in the experiment, but were present at other carcasses or sighted in the area include Tiger, Cinereous Vulture, Jungle Cat, and Common Palm Civet.

Our findings, especially the estimates of carrion removal rates, could have been influenced by several ecological factors that were beyond the control of this experiment. Relative abundance of vertebrate scavenger species would influence carrion removal rates; e.g., carrion removal rates might differ between the study area and a different forest with fewer vultures but higher numbers of top and meso- mammalian predators. Carcass size is another important factor. Removal rates would have slowed down if larger carcasses such as goats or cattle were used, as individual scavengers that discovered the carcass became satiated. Further, invertebrate scavengers might take advantage of such larger resources and respond numerically due to their shorter generation times and thereby contribute more to carcass removal than currently estimated. We account for moisture loss by desiccation under natural conditions, and as seen in Fig. 2, moisture loss was a function of ambient humidity and temperature, on day five of the treatment there was mild rain and the carcasses gained weight. Whilst there was a non-significant difference in removal rates between microbes and control (evaporative moisture loss) (Table 2), this could imply that either microbes contributed negligibly to the removal of carrion, or the anti-microbial treatment in our control samples was not effective in reducing microbial activity and our estimates of moisture loss was compounded by some microbial losses. However, this issue does not affect the comparison of carrion removal rates between vertebrates and invertebrates. Our experiment spanned a single season (early summer) and did not capture seasonal variations in environmental conditions that could influence relative contribution of scavenger groups, and the absolute removal rates. Our sample size was also small that might have resulted in large variability in proportional weight of carcasses over time (Figure 2).

Whilst our field experiment provided some insights, many questions remain to be answered to further our understanding of carrion ecology in tropical forests. a) Effects of relative abundance of different species in the scavenging assemblage on carrion utilization (Huijbers *et al.* , 2016; Morales-Reyes *et al.* , 2017; Naves-Alegre *et al.* , 2021), b) succession of scavenging groups on carrion, c) influence of carrion size on the richness, abundance, composition and succession of scavenger community are some of these questions.

Our experimental approach and inferences can form the foundation on which studies investigating the above questions can be developed.

Figure Legends

Figure 1: Experimental setup for observing carrion biomass loss due to different treatments (Clockwise from Top Left): 1. A chicken carcass being weighed after exposure to invertebrate scavenging; 2. vertebrate scavenging – carcasses were placed in the open and monitored through infrared camera traps; 3. invertebrate scavenging – carcasses were placed in a wire cage to exclude vertebrate scavenger; 4. microbial activity – carcasses were placed in cloth bags and hung in a wire cage to exclude invertebrates and vertebrate scavengers. Control carcasses were also placed similarly after treatment with an antimicrobial agent.

Figure 2: Boxplot showing distribution of proportional carcass biomass remaining over days for each treatment.

Figure 3: Some vertebrate scavenger species captured at experimental carcasses. Clockwise from top left - Red-headed Vulture (*Sarcogyps calvus*), Egyptian Vulture (*Neophron percnopterus*), Golden Jackal (*Canis aureus*), Leopard (*Panthera pardus*), Indian Fox (*Vulpes bengalensis*), Striped Hyena (*Hyaena hyanea*). Bottom: A group of Red-Headed Vulture and an Egyptian Vulture feeding on an experimental chicken carcass.

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Author Contributions

BI – Study design, funding acquisition, data collection, analysis, Writing—Original Draft. YVJ – Study design, methodology, review and editing, supervision, funding acquisition. SD - Study design, methodology, review and editing, supervision. QQ - Study design, methodology, supervision.

Data Accessibility

The authors confirm that the data supporting the findings of this study are available in the appendix and on FigShare.

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Competing Interests

The authors declare no competing interests.

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Table 1. Parameter estimates of the best model showing individual effects of treatments on logit-transformed proportional loss of carrion biomass.

Variables	Estimate	SE
Time	-0.19	0.03
Microbial decomposition	0.41	0.45
Invertebrate scavenging	1.64	0.44
Vertebrate	2.98	0.53
Time x microbial decomposition	-0.05	0.06
Time x invertebrate scavenging	-0.02	0.06
Time x vertebrate scavenging	-5.88	0.65

Table 2: Mean (SE) carrion removal rates, estimated as daily proportional weight loss of carcass under

different treatments, with 95% CI.

Treatment	Mean Carrion Removal Rate (SE)	Upper Confidence Interval	Lower Confidence Interval
Control (evaporative water loss)	0.036 (0.0024)	0.041	0.031
Microbial decomposition	0.039 (0.003)	0.08	0.066
Invertebrate scavenging	0.073 (0.004)	0.045	0.033
Vertebrate scavenging	0.833 (0.043)	0.919	0.749





