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Factors influencing the discovery and use of carrion by vertebrate scavengers from human-induced mass-mortality events

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Abstract: Scavengers play critical roles in ecosystem health and stability, and both biotic and abiotic factors can influence scavenger guild dynamics. Carrion is often limited both temporally and spatially on the landscape, but mass mortality events (MMEs)—in which there is an influx of carrion biomass on the landscape—may result in different scavenger community dynamics compared to when carrion is scarcely distributed. In this study, we investigated factors affecting the discovery and use of carrion by a natural, unharrassed scavenger guild during wild pig (*Sus scrofa*) MMEs conducted at East Foundation's San Antonio Viejo Ranch in South Texas, USA. We placed trail cameras on wild pig carcasses that were dispatched by Wildlife Services during 4 aerial gunning events between November 2020 and June 2022. Black vultures (*Coragyps atratus*), coyotes (*Canis latrans*), crested caracaras (*Caracara cheriway*), and turkey vultures (*Cathartes aura*) were documented scavengers at carrion sites. Carcasses were found and consumed more quickly during the summer and when wild pigs were dispatched earlier in the day. Time to carcass discovery increased as canopy cover increased and as distance to nearest water source decreased. Coyotes were more likely to be the species that discovered carcasses in the fall, and their discovery was facilitated by their use of linear features on the landscape. Coyotes started carcass consumption less quickly than avian scavengers and spent a greater proportion of time scavenging at fall over summer sites, whereas vultures spent a greater proportion of time scavenging at summer over fall sites. There was some overlap of site use by all scavenger species, and overlap of activity was greater in the summer than in the fall. Our results suggest that, should land managers wish to utilize their local scavenger guilds for carcass disposal, eradication efforts should be conducted during mornings in summer.

Key words: carrion, coyotes, mass-mortality, scavengers, vultures, wild pigs

Species that consume carrion are an important but often overlooked guild across the globe. Through scavenging behavior, vertebrate and invertebrate scavengers play critical roles in ecosystem health and stability by removing waste from the environment (Ćirović et al. 2016, DeVault et al. 2016, Mateo-Tomás et al. 2017, Grilli et al. 2019), promoting the flow of energy throughout food webs (DeVault et al. 2003, Wilson and Wolkovich 2011), and mitigating the spread of disease (O'Bryan et al. 2018, Le Sage et al. 2019, Szcodronski and Cross 2021). Understanding the role of scavengers in food webs is of critical importance, as the consumption of carcasses resulting from predation and other natural causes offers a rich source of nutrients that are then maintained within higher trophic levels of food webs (Turner et al. 2017).

Despite their importance, research on scavengers is underrepresented in the literature, and there is still much to learn about factors influencing the behavior of scavengers on the landscape. In more recent years, researchers have begun to investigate the influence of both biotic and abiotic factors on scavenger community composition and dynamics with arguments that carrion use by scavengers is not random but is instead determined by extrinsic factors and behavioral adaptations (Selva et al. 2005). However, research into the effects of other factors that may influence scavenger composition and dynamics—such as carcass characteristics and habitat—is still in its infancy. Nevertheless, there is a growing body of evidence that factors such as carcass mass, season, habitat, spatial complexity, and weather can influence species richness and diversity, the fate of carcasses, and time to carrion discovery and consumption (DeVault et al. 2004, Selva et al. 2005, DeVault et al. 2011, Moleón et al. 2015, Smith et al. 2017, Turner et al. 2017, Arrondo et al. 2019).

As a resource, carrion tends to occur sporadically in the landscape and is often ephemeral in nature. The unpredictability of this resource often generates competition between organisms and selection for rapid detection and utilization of carrion (Tomberlin et al. 2017), and most research on scavenger ecology has therefore focused on factors that influence use of carrion that is limited both temporally and spatially. However, in the case of mass mortality events (MMEs), the quantity of carcasses on the landscape increases the availability of carrion, which may in turn influence scavenger community dynamics. MMEs are a special case of carrion deposition in which there is an influx of carrion biomass on the landscape, providing an abundant source of nutrients for scavengers for longer periods of time than scarcely distributed individual carcasses. MMEs can be the result of disease epidemics (Jones et al. 2017, Kock et al. 2018, Gizzi et al. 2020, Hamilton et al. 2021), annual migrations (Bleich 2018, Handler et al. 2021), or inclement weather or natural disasters (e.g., heatwaves and wildfires; Newton 2007, Garrabou et al. 2009, Diehl et al. 2014, Piatt et al. 2020). They can also be human-induced through human–wildlife conflict and recreation (King 2012, O'Shea et al. 2016, Davies and Brillant 2019), human–human conflict (Stalmans et al. 2019), and culling and management efforts as either target species, or as non-target by-kill (e.g., poisoning or prescribed fires; Goldstein et al. 1999, Russell et al. 1999, Buchanan et al. 2021). Evidence suggests that MMEs are increasing in both frequency and magnitude (Fey et al. 2015) and are expected to become more common due to warming global temperatures (Coma et al. 2009, Fey et al. 2015, Sanderson and Alexander 2020), and thus understanding scavenger guild responses to such events may be informative in understanding disease dynamics and the effects of MMEs on food web dynamics and ecosystem health.

Despite MMEs seemingly becoming more frequent, little is known about how scavengers respond to MMEs. Recent research by Handler et al. (2021) investigated the use of carrion by avian scavengers as a result of mass mortality during annual wildebeest (*Connochaetes taurinus*) migrations in the Serengeti-Mara Ecosystem (East Africa). Approximately 200,000 wildebeest die each year, mostly due to several drowning events in the Mara River, resulting in an influx of carrion on the landscape that acts as an important source of nutrients for both avian and terrestrial scavengers. There was distinct temporal partitioning of resources as well as variation in diel patterns of scavenging behavior between avian scavengers, as well as a lower density of scavengers per carcass during MMEs when compared to single carcass scavenging. Such observations speak to the importance of investigating scavenger behavior during MMEs to further understand scavenger guild dynamics during these increasingly common events and how this may influence disease dynamics.

One avenue through which MMEs can be created is via anthropogenic management of game or pest species. Wild pigs (*Sus scrofa*) are a prominent invasive species in many parts of the world, including the Americas (Lowe et al. 2000, Mayer and Brisbin 2008). The significant ecological and environmental damages that are attributed to wild pigs (Seward et al. 2004, Pimental 2007, Barrios-Garcia and Ballari 2012, Bevins et al. 2014, Anderson et al. 2016) have resulted in rigorous management efforts to control or eradicate the species, which at times results in an influx of carrion on the landscape. Wild pigs act as reservoirs of diseases that affect humans, domesticated livestock, and wildlife, and thus an influx of wild pig carrion can be of significant concern for public health (Miller et al. 2017, Anderson et al. 2019). A simulated MME using wild pig carcasses in Mississippi, USA, showed that heavy loads of carrion can have adverse effects on environmental and soil health (Tomberlin et al. 2017, Lashley et al. 2018, Limon 2020), but that vertebrate scavengers can reduce the indirect effects of carrion in the surrounding community and hasten carcass decomposition. Research suggests that vultures—the only extant obligate vertebrate scavenger—provide vital ecosystem services by reducing greenhouse gas emissions. If vultures are not present, carcasses tend to remain longer in the environment and continue to produce greenhouse gases as they decompose (Sakata et al. 1980, Dalva et al. 2015, Zeng 2015). It is estimated that global vulture populations (~134–140 million individuals) may reduce emissions of 3.03–60.70 Tg of CO_2 equivalent per year, depending on the carcass disposal method implemented (e.g., composted, buried, left in the environment), and North American vulture species are responsible for 96% of all vulture-related emissions mitigation worldwide (Plaza and Lambertucci 2022). Utilizing vultures instead of relying on vehicular movement of carcasses to waste removal centers can further reduce greenhouse gas emissions (Morales-Reyes et al. 2015). By creating an influx of carrion in the environment through MMEs, land managers must consider both the increase in greenhouse gas emission and disease transmission threat being created. A greater understanding of factors affecting the use and depletion of carrion derived from MMEs has important management implications by providing land managers with recommendations on how best to utilize local scavenger guilds to quickly dispose of carcasses on the landscape, particularly in situations where access to large-scale carcass disposal options (e.g., incinerators) are logistically infeasible.

In this study, we investigated the influence of biotic and abiotic factors on the discovery and use of carrion by a natural, unharrassed scavenger guild during a human-induced MME in South Texas, USA. Previous research at this study site has shown that carcasses are quickly utilized and depleted regardless of season (Leivers et al. 2023), but the factors influencing the use of these carcasses are unknown. Using trail cameras placed at carrion sites, we investigated what factors influence (1) the time to discovery and consumption of carrion, (2) the scavenger species to first discover and consume carrion, and (3) the proportion of time spent utilizing carrion by each scavenger species. Finally, we examined the temporal partitioning of carrion by scavenger species.

Study area

This study was conducted on the East Foundation's 61,000-ha San Antonio Viejo Ranch (SAVR) in Jim Hogg and Starr counties in South Texas. The East Foundation's ranches are managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The area is dominated by shrub savannas, primarily composed of blackbrush (*Acacia rigidula*), cat-claw acacia (*Acacia greggii*), granjeño (*Celtis palida*), honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), and whitebrush (*Alloysia gratissima*), and with early to mid-successional grasses, including little bluestem (*Schizachyrium scoparium*), three-awns (*Aristida* spp.), and windmill grasses (*Chloris* spp.). The 30-year normal mean temperature for the region was 22.2–23.9° C (max temperature 31.1–33.3° C) with an annual mean precipitation of 50.8–61.0 cm (PRISM Group 2022).

The SAVR is home to many scavenging species, including both obligate scavengers, such as black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*), and facultative scavengers, such as bobcats (*Lynx rufus*), crested caracaras (*Caracara cheriway*), crows and ravens (*Corvus* spp.), and coyotes (*Canis latrans*). Lethal harvest and harassment of native animals have not occurred on SAVR since the East Foundation's inception in 2007, providing the opportunity to examine the ecology of a natural, unaltered scavenger guild on this landscape.

Methods

Data collection and processing

We collected wild pig carcasses opportunistically during biannual wild pig control efforts undertaken by the U.S. Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS), Wildlife Services (WS) during the course of routine operations to reduce wild pig damage on SAVR. Aerial gunning events took place during fall (November 17–19, 2020, and November 8–11, 2021) and summer (May 24–26, 2021, and June 6–9, 2022). The WS aerial teams located wild pigs from a helicopter and euthanized animals using a shotgun and nontoxic #2 (6.86-mm diameter) buckshot ammunition in accordance with routine WS aerial operations procedures. Once a wild pig, or a sounder of wild pigs, had been euthanized, the helicopter crew provided 2 ground crews with Global Positioning System (GPS) coordinates to the site of the carcass(es) to count the number of wild pigs euthanized. The date and time of each euthanasia event was also recorded. Wild pig control efforts were only undertaken during daylight hours, with no wild pigs dispatched after sunset. No ethical approval was required, as we were passively monitoring visitation to carrion on private lands after sched-

Table 1. Number of carrion sites with trail cameras, carrion sites with no trail cameras, and total number of carrion sites for each aerial wild pig (*Sus scrofa*) gunning event, and the dates and season of each event. The numbers in parentheses indicate the number of cameras from which we were able to analyze data.

Dates	Season	Camera sites	No camera sites	Total sites
November 17–19, 2020	Fall	26 (22)	60	86
May 24–26, 2021	Summer	26 (26)	38	64
November 8–11, 2021	Fall	37 (28)	32	69
June 6–9, 2022	Summer	29 (29)	34	63

uled and approved operations conducted by USDA-APHIS-WS.

The 2 ground crews split carrion site visits to maximize the number of sites that could be visited. Upon arrival at a carrion site, the ground crew assigned a site identification (ID; e.g., FH-01), and a pig ID (e.g., FH-01-01) to each euthanized pig at the site. Ground crews confirmed the number of pigs at the site, the age, sex, and color/markings of all pigs at the site, and weighed each pig. Ground crews moved carcasses located in thick vegetation (e.g., under a shrub) to an area that allowed for data collection but were kept as close to the original carcass location as possible. Carcasses were also moved from locations that would impede normal ranch operations (i.e., directly in front of a gate). If >1 wild pig was present at the site, carcasses were laid next to each other. We collected exact site GPS coordinates of the carcass(es), recorded the date and time of the site visit, and took a photograph of the carcass(es).

We randomly designated which carrion site would be assigned a trail camera, no trail camera, or a dummy trail camera (due to an additional study being conducted concurrently). We categorize sites with working trail cameras as "camera sites" and sites with dummy trail cameras, no trail cameras, and sites that were not visited (either due to time constraints or dense vegetation that could not be penetrated by an all-terrain vehicle) as "no camera sites" (Table 1). For camera sites, carcasses were positioned with the ventral side facing the trail camera, at a distance of ~5 m from the camera. This distance increased as the number of carcasses at the site increased to fit all carcasses in the camera frame. Trail cameras were attached to existing vegetation or fenceposts or, where this was not possible, they were attached to T-posts. Loose vegetation was removed from in front of the camera to prevent false triggers and provide a clear view of the carcass(es). We used both HyperFire 2 Professional HP2X and PC900 HyperFire Professional IR trail cameras with external data cards. Trail cameras were set to high sensitivity and were programmed to take a burst of 3 photographs, 3 seconds apart when triggered, with a quiet period of 1 minute between subsequent triggers. Cameras were active throughout the full 24-hour period to capture both day and night visitations by scavengers. Trail cameras were left in the field for a minimum of 5 days and were only removed once the carcass(es) had been depleted or otherwise removed from the site (e.g., dragged elsewhere by human or animal). Sites were not visited during the data collection period in order to minimize the effects of human disturbance on scavenger activity. For this reason, cameras could not be repositioned to show the carcass(es) within the frame if they were moved out of frame during this 5-day period.

We downloaded photographs from the external data cards and uploaded to an online file sharing platform for processing. We examined photographs for the presence of wildlife at each carrion site from the time of the first trigger until the carcass(es) was/were depleted (i.e., no bones, viscera, or other remains being consumed by scavenger species) or was/were removed from the camera's frame by humans or animals and did not return to the frame. We recorded data in a relational database created using FileMaker Pro. For each photograph in which 1 or more wildlife species (other than the wild pig carrion) was present, we recorded: site ID, time and date of observation, species observed, weather (sunny, cloudy, foggy, unknown), and decomposition score of the carcass(es).

Habitat characteristics

We collected data on several habitat characteristics that we believed might influence discovery and use of carrion by scavenger species, and species-specific use of carrion. Predators are known to utilize linear features in the landscape for terrestrial movement (Dodge and Kashian 2013, Gese et al. 2013, Zimmerman et al. 2014, Hinton et al. 2015), and thus we used shapefiles in ArcGIS to calculate the distance in meters to the nearest ranch road and the nearest fence line for each carrion site. As our study site was hot and semiarid, we theorized that water sources may also play a role in the use of the landscape by wildlife; thus, we also calculated distance in meters to the nearest permanent water source for each carrion site. Mammalian scavengers such as coyotes are terrestrial, whereas many avian scavengers, including vultures and caracaras, often perch on vegetation or human-made structures such at utility poles. For this reason, we also used shapefiles to assign a vegetation category (mesquite, sand grassland or savanna) and a canopy cover value for each site (0–100%).

Data analysis

We conducted data analyses in R Studio version 4.0.3 (R Development Core Team 2023*b*, using packages "car" (Fox and Weisberg 2019), "DHARMa" (Hartig 2022), "regclass" (Petrie 2020), "dplyr" (Wickham et al. 2023), "ggplot2" (Wickham 2016), "jtools" (Long 2024), "foreign" (R Development Core Team 2023*a*), "nnet" (Venables and Ripley 2002), "knitr" (Xie 2024), "overlap" (Meredith et al. 2024), "betareg" (Cribari-Neto and Zeileis 2010), and "reshape2" (Wickham 2007). Dependent variables in our analyses included: the time in hours from carrion euthanasia to carrion discovery by a scavenger species (time to discovery), the time from carrion euthanasia to the first consumption event by a scavenger species (time to consumption), the first scavenger species to discover the carrion site (species to discover), the first scavenger species to consume the carrion (species to consume), and proportion scavenged. To calculate proportion scavenged, we first calculated the total number of minutes where the carcass(es) had each scavenger species present between the time of euthanasia and the time of depletion/carcass removal. As there was a 1-minute quiet period between triggered photograph bursts, we assigned a value of 1 minute of scavenging per photo in which each scavenger species was present. We then divided this species-specific presence value by the total number of minutes that a scavenger of any species had been present to determine the proportion of time each species spent scavenging on a carcass(es).

We ran multiple linear regressions for continuous dependent variables (time to discovery, time to consumption), multinomial logistic regressions for categorical dependent variables (species to discover, species to consume), and we created beta regressions for proportion scavenged for each scavenger species. Predictors in our models included: vegetation type (mesquite, sand-grassland, or savanna), canopy cover (0–100%), distance to nearest ranch road (m), distance to nearest water source (m), distance to nearest fence line (m), carrion mass (kg), time of day carrion was euthanized (morning: first light to 1159 hours; afternoon: 1200 hours until last light), and season (fall or summer). We ran a global model with all predicator variables because these were determined as important *a priori*. We checked Variance Inflation Factors (VIF) and removed any predictors from the model where VIF >5. For linear and logistic regressions, we assessed goodness of fit using the DHARMa package. For the purpose of detecting outliers or influential data points in our multinomial logistic regression, we created separate logistic models for each species comparison and assessed goodness of fit using the DHARMa package. To determine if our multinomial and beta regression models fit significantly better than the intercept-only model, we calculated the likelihood ratio tests. For all regression models, we removed outliers with a Cook's distance greater than 4 times the mean Cook's distance if they were found to have a significant influence on the main effects of our models. Predictor coefficients with $P < 0.05$ were considered significant predicators. We report adjusted R^2 for linear regressions, and pseudo R^2 for multinomial logistic regressions and beta regression models. For pseudo R^2, we interpreted values >0.2 as a large effect (Louviere et al. 2000).

To examine temporal partitioning of carrion by scavengers, we created a data file with date and time of all observations of scavengers at all sites and dummy coded our species variable. Us-

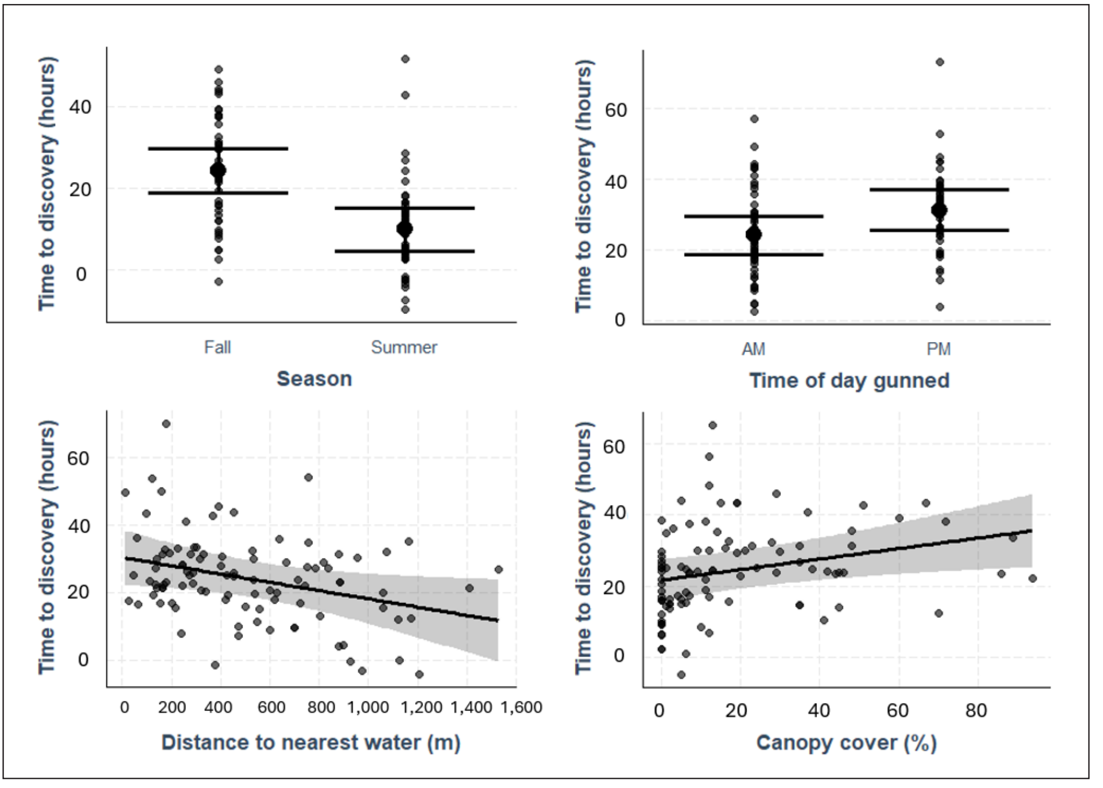

Figure 1. Partial residuals plots showing the significant main effects of season, time of day the carrion was dispatched, distance to nearest water source, and canopy cover on the length of time it took for a scavenger species (black vulture [*Coragyps atratus*], coyote [*Canis latrans*], crested caracara [*Caracara cheriway*], and turkey vulture [*Cathartes aura*]) to discover a carrion site from time of dispatch.

ing the "overlap" package, nonparametric kernel density functions were fitted to examine the temporal overlap in activity within and between species across seasons (Ridout and Linkie 2009). The "overlap" package can generate 2 estimates of overlap referred to as d-hat (Δ): Δ1 for <75 observations and Δ4 for >75 observations (Ridout and Linkie 2009, Meredith et al. 2024). Overlap values range from 0 (no overlap, complete separation in activity) to 1 (complete overlap, no separation in activity). We calculated overlap coefficients for all pairwise comparisons for scavenger species for fall and summer data.

Results

Carrion sites and scavenger species

Over the course of the study, we placed trail cameras on a total of 118 carrion sites (fall = 63, summer = 55). Due to technical failures with cameras, camera placement after scavenging had begun and placement errors (camera either initially placed incorrectly or moved by wildlife or livestock), we were able to collect data for at least 1 of our dependent variables from 105 camera sites (fall = 50, summer = 55). The median number of wild pig carcasses at both summer and fall sites was 1 (summer: total carcasses = 81, range = 1–5; fall: total carcasses = 66, range = 1–4). The mean mass of carrion at each site was 70.90 kg (SD = 36.89 kg) for summer, and 73.34 kg (SD = 47.60 kg) for fall, and this difference was not significant (Mann-Whitney U = 1,346, P = 0.857). We observed 3 mammalian scavenger species—bobcats, coyotes, and wild pigs—but only coyotes were observed scavenging on carcasses, and bobcats and wild pigs were less common at carrion sites (a bobcat was observed only once) and were not seen consuming carrion, so we did not class bobcats and wild pigs as scavenger species in this study. We observed 5 avian scavenger species actively scavenging on carrion: black vultures, crested caracaras, unknown *Corvus* species, Harris hawks (*Parabuteo unicinctus*), and turkey vultures.

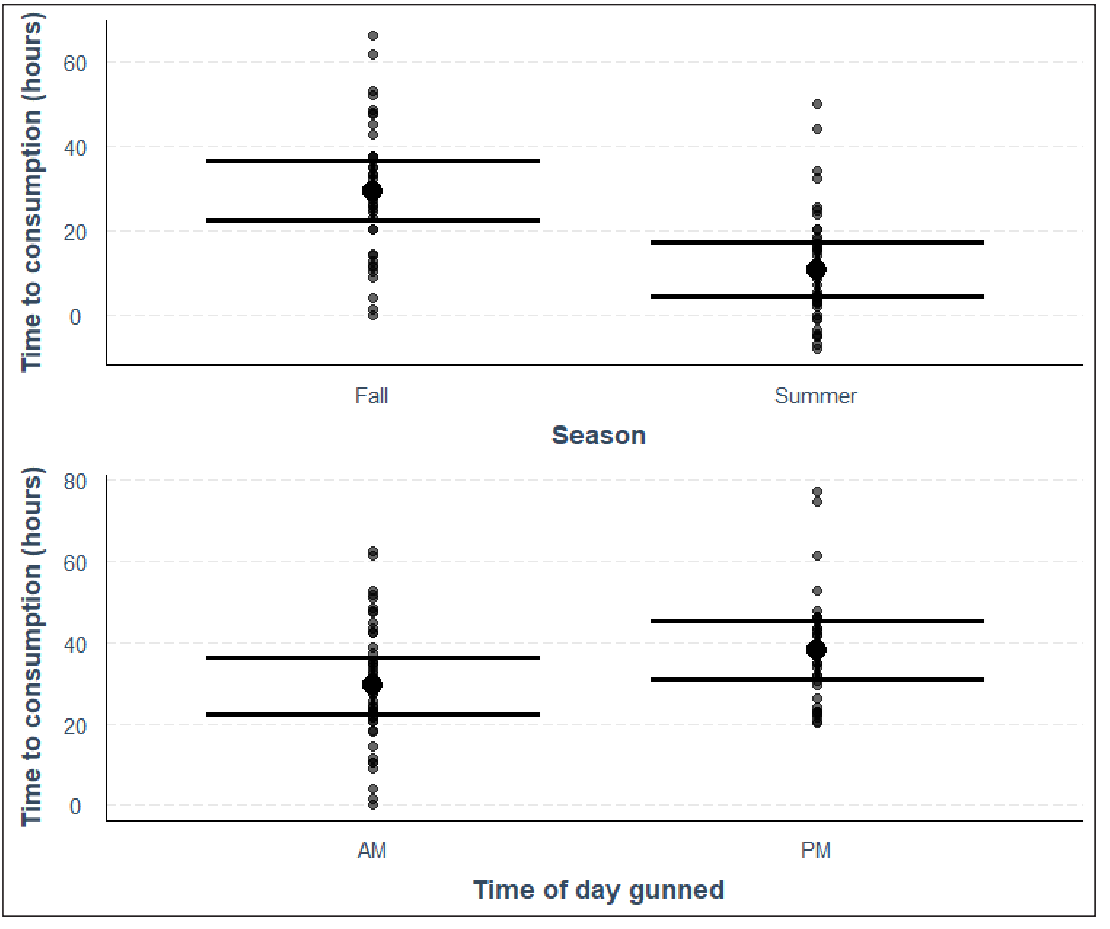

Figure 2. Partial residuals plots showing the significant main effects of season and time of day the carrion was dispatched on the length of time it took for a scavenger species (black vulture [*Coragyps atratus*], coyote [*Canis latrans*], crested caracara [*Caracara cheriway*], and turkey vulture [*Cathartes aura*]) to begin consumption of carrion from time of dispatch.

Time to discovery and time to consumption

We found a significant relationship for time to discovery ($F_{9,88}$ = 5.75, P <0.001, Adj R^2 = 0.31, n = 98). Carrion sites were discovered more quickly in summer than in fall (β = 14.44, P <0.001; summer: $\bar{x}$ = 12.80 hours, SD = 11.12; fall: $\bar{x}$ = 26.90 hours, SD = 115.73) and when the wild pigs were dispatched in the morning rather than the afternoon (β = 7.07, P = 0.011; morning: $\bar{x}$ = 17.17 hours, SD = 14.34; afternoon: $\bar{x}$ = 21.74 hours, SD = 15.78). Time to discovery increased as canopy cover increased (β = 0.15, P = 0.024) and as distance to water decreased (β = -0.01, P = 0.032; Figure 1).

At 12 sites, carrion was removed prior to the first consumption so that was not included in analysis for time to consumption. We detected a significant relationship for time to consumption ($F_{8,78}$ = 5.79, P <0.001, Adj R^2 = 0.31, n = 87). Carrion were consumed more quickly in summer than in fall (β = 18.60, P < 0.001; summer: $\bar{x}$ = 16.17 hours, SD = 13.24; fall: $\bar{x}$ = 34.60 hours, SD = 17.80) and when the wild pigs were dispatched in the morning rather than the afternoon (β = 8.78, P = 0.011; morning: $\bar{x}$ = 21.61 hours, SD = 17.98; afternoon: $\bar{x}$ = 27.58 hours, SD = 17.35; Figure 2).

Species to discover and species to consume

We recorded black vultures, coyotes, crested caracaras, and turkey vultures as the first species to either discover or consume carrion. However, due to the few occurrences of black vultures discovering (n = 3) or consuming car-

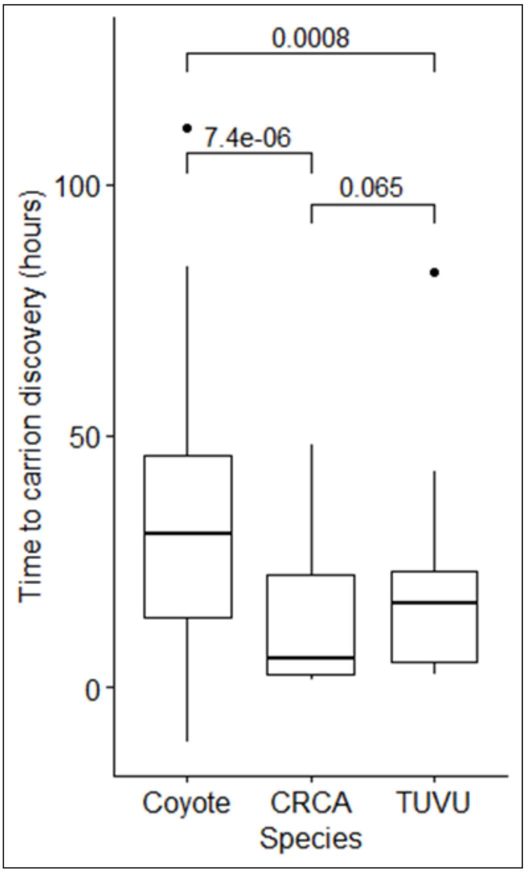

Figure 3. Wilcoxon signed-rank tests comparing time to carrion discovery from time of carrion dispatch for coyotes (*Canis latrans*), crested caracaras (*Caracara cheriway*; CRCA), and turkey vultures (*Cathartes aura*; TUVU) during 4 aerial gunning events on East Foundation's San Antonio Viejo Ranch in South Texas, USA, between November 2020 and June 2022.

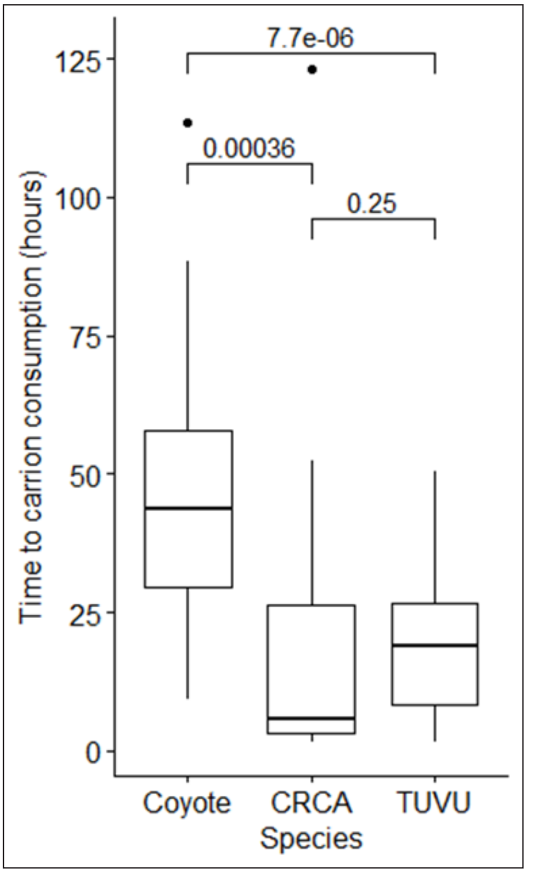

Figure 4. Wilcoxon signed-rank tests comparing time to carrion consumption from time of carrion dispatch for coyotes (*Canis latrans*), crested caracaras (*Caracara cheriway*; CRCA), and turkey vultures (*Cathartes aura*; TUVU) during 4 aerial gunning events on East Foundation's San Antonio Viejo Ranch in South Texas, USA, between November 2020 and June 2022.

rion first ($n = 10$), we dropped these occurrences from our analyses.

Our model predicting the species to first discover carrion sites was significantly better than the intercept-only model LR: $\chi^2_{16} = 39.10$, $P < 0.001$, McFadden $R^2 = 0.18$). The log odds of a coyote or crested caracara being the first to discover a carrion site before a turkey vulture increased by 4.06 ($P < 0.001$) and 3.64 ($P < 0.001$), respectively, for fall over summer carrion sites. The log odds of a coyote being the first to discover a carrion site over a turkey vulture increased by 1.70 for each unit decrease in distance to nearest road, but this did not quite reach statistical significance ($P = 0.09$). Both crested caracaras and turkey vultures discovered carrion more quickly than coyotes (Kruskal Wallis: $\chi^2_2 = 23.75$, $P < 0.001$; Figure 3).

Our model predicting the species to first consume carrion sites was significantly better than the intercept-only model (LR: $\chi^2_{16} = 55.71$, $P < 0.001$, McFadden $R^2 = 0.33$). The log odds of a coyote or crested caracara being the first to consume at a carrion site before a turkey vulture increased by 4.56 ($P < 0.001$) and 3.34 ($P < 0.001$), respectively, for fall over summer carrion sites. The log odds of a coyote being the first to consume at carrion sites before a turkey vulture increased by 12.53 ($P < 0.001$) and 13.98 ($P < 0.001$) respectively for sites in mesquite and sand grassland, over sites in savanna vegetation. The log odds of a coyote being the first to consume at

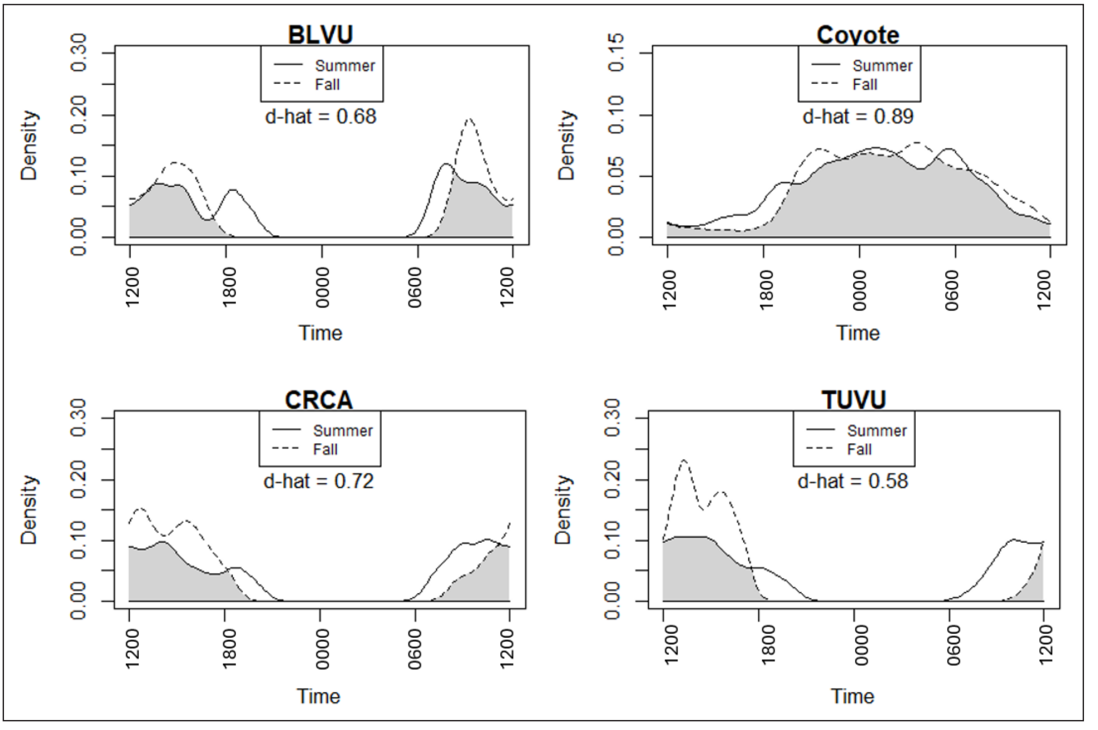

Figure 5. Overlap plots activity curves of black vultures (*Coragyps atratus*; BLVU), coyotes (*Canis latrans*), crested caracaras (*Caracara cheriway*; CRCA), and turkey vultures (*Cathartes aura*; TUVU) at wild pig (*Sus scrofa*) carrion sites (created via aerial gunning efforts by Wildlife Services) at East Foundation's San Antonio Viejo Ranch in South Texas, USA, between November 2020 and June 2022 for each season (Δ4 = 1, perfect overlap; Δ4 = 0, no overlap).

carrion sites before a crested caracara increased by 10.71 (P <0.001) and 12.81 (P <0.001), respectively, for sites in mesquite and sand grassland, over sites in savanna vegetation. The log odds of a turkey vulture being the first to consume at carrion sites over a crested caracara increased by 3.34 (P <0.001) for summer sites over fall sites. Both crested caracaras and turkey vultures began consumption of carrion sooner than coyotes (Kruskal Wallis: χ^2_2 = 22.27, P <0.001; Figure 4).

Proportion scavenged

After removing sites where there were technical failures with cameras and placement errors, we analyzed 91 carrion sites. However, carcasses were removed from the trail camera frame (almost exclusively by coyotes) prior to being fully depleted at 77 sites. As this reduced the total amount of time that we were able to observe scavenging behavior, we only analyzed sites where we recorded at least 60 minutes of scavenging behavior (all species combined) for a total of 59 carrion sites. Our models predicting the proportion of time coyotes, turkey vultures, black vultures, and crested caracaras spent scavenging carrion were better than their intercept-only models (coyotes: χ^2_2 = 44.94, P <0.001, pseudo R^2 = 0.40; turkey vultures: χ^2_2 = 73.16, P <0.001, pseudo R^2 = 0.55; black vultures: χ^2_2 = 65.59, P <0.001, pseudo R^2 = 0.59; crested caracaras: χ^2_2 = 22.97, P = 0.002, pseudo R^2 = 0.23). Coyotes spent a greater proportion of time scavenging at fall over summer carrion sites (β = 2.76, P <0.001, summer: $\bar{x}$ = 0.16, SD = 0.18; fall: $\bar{x}$ = 0.70, SD = 0.30), whereas turkey vultures spent a greater proportion of time scavenging at summer over fall carrion sites (β = 4.000, P <0.001, summer: $\bar{x}$ = 0.780, SD = 0.211; fall: $\bar{x}$ = 0.098, SD = 0.149). Black vultures spent a greater proportion of time scavenging at summer over fall carrion sites (β = 2.64, P <0.001; summer: $\bar{x}$ = 0.18, SD = 0.12; fall: $\bar{x}$ = 0.02, SD = 0.03) and as distance to water decreased (β = -0.01, P = 0.024). The proportion of time crested caracaras spent scavenging increased as canopy cover decreased (β = -0.02, P = 0.005), and they spent a greater proportion of time scavenging at carrion sites located on savanna ($\bar{x}$ = 0.36, SD

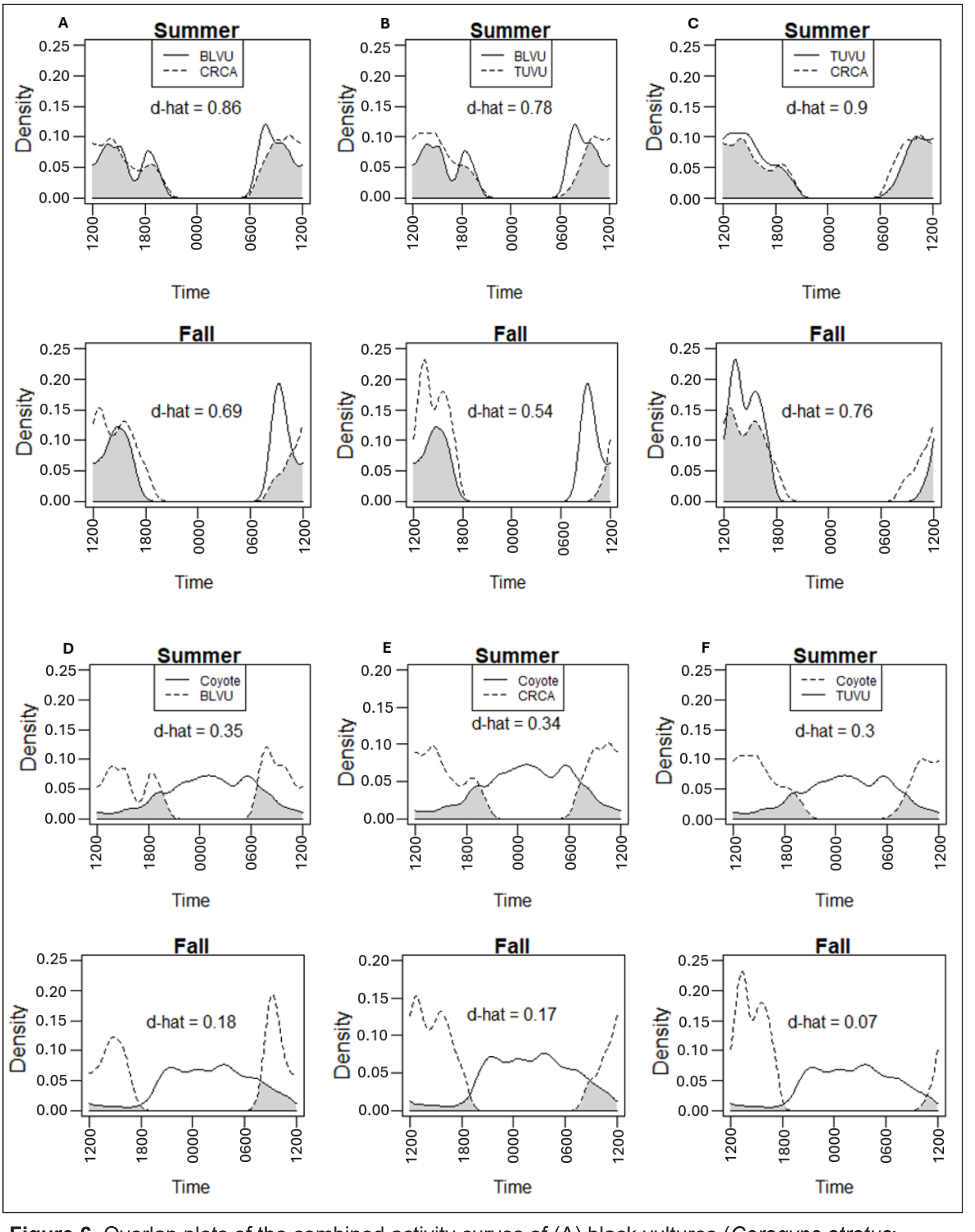

Figure 6. Overlap plots of the combined activity curves of (A) black vultures (*Coragyps atratus*; BLVU) and crested caracaras (*Caracara cheriway*; CRCA), (B) BLVU and turkey vultures (*Cathartes aura*; TUVU), (C) TUVU and CRCA, (D) coyotes (*Canis latrans*) and BLVU, (E) coyotes and CRCA, and (F) coyotes and TUVU at wild pig (*Sus scrofa*) carrion sites at East Foundation's San Antonio Viejo Ranch in South Texas, USA, between November 2020 and June 2022 for each season ($\Delta 4$ = 1, perfect overlap; $\Delta 4$ = 0, no overlap).

= 0.28, β = 1.39, P = 0.008) and mesquite vegetation ($\bar{x}$ = 0.23, SD = 0.21, β = 0.08, P = 0.019) compared to sites on sand grassland ($\bar{x}$ = 0.13, SD = 0.17).

Temporal partitioning of carrion

There were 7,914 records of coyotes (summer = 2,733, fall = 5,181), 4,357 records of black vultures (summer = 3,956, fall = 401), 5,334 records of caracaras (summer = 3,494, fall = 1,840), and 13,917 records of turkey vultures (summer = 12,848, fall = 1,069) used in the analysis. Due to large sample sizes, we used the Δ4 overlap coefficient. Avian scavengers were active diurnally between dawn and dusk, whereas coyotes exhibited both diurnal and nocturnal activity at carrion sites, with the greatest activity between the hours of dusk and dawn (Figure 5). Each species showed variation in activity based on season, with coyotes showing the most overlap and turkey vultures showing the least overlap. The Δ4 values for avian scavengers ranged between 0.78 and 0.90 for summer, and 0.54 and 0.76 for fall (Figure 6). The greatest activity overlap between species was for crested caracaras and turkey vultures. Coyotes and avian scavengers showed activity overlap around dawn and dusk in both summer and fall, with the greatest overlap in summer. The Δ4 values for coyotes and all avian scavengers were similar in summer (0.30–0.35) but differed during fall, with a Δ4 value of only 0.07 for coyotes and turkey vultures.

Discussion

We investigated the processes of carrion discovery and consumption during an anthropogenic MME on wild pigs in South Texas. The scavenging guild at the site included both mammalian and avian species, but due to limitations in numbers of observations for some species, we analyzed site use by black vultures, coyotes, crested caracaras, and turkey vultures.

It is unsurprising that carcasses tend to be found sooner during warmer times of the year and when wild pigs were dispatched earlier in the day. Similarly unsurprising was that increasing canopy cover slowed the speed of carcass location, as canopy in this ecosystem most frequently was composed of densely growing midstory woody species that may act as screening cover, both overhead and at ground-level. Nevertheless, it was somewhat surprising that carcasses that were located farther from water sources were found sooner than carcasses closer to water sources. Some scavengers do not require free water, as they are adapted to rely on dietary water, so perhaps these locations were not necessarily important sites to visit frequently. Conversely, because these water sources were primarily designed for livestock watering, it is possible that scavengers in our study area avoided them due to frequent human presence.

Although all species were documented at times to find carcasses first, coyotes discover carcasses more quickly in the cooler months, and their early discovery also seems to be facilitated by the species' conspicuous and well-documented use of roads, trails, and paths (Dodge and Kashian 2013, Gese et al. 2013, Hinton et al. 2015). Regardless of environmental conditions, however, coyotes started carcass consumption less quickly than avian scavengers, which readily begin consuming quickly after carcass discovery. By treating scavengers at the species level, as opposed to taxa, we detected several differences in activity, consumption, and time to detection of carcasses between vultures and caracaras. Black vultures rarely discover or initiate carcass consumption, perhaps due to their functional ecology as predatory birds and facultative scavengers, compared to turkey vultures and crested caracaras, which are considered to be obligate scavengers. Potentially, the cooperative association between the 2 vulture species at our study site lends itself to improved foraging efficiency for both species. Scavenger use of sites showed some overlap among all species, greatest in the summer, but lowest in the fall. Interestingly, turkey vultures and crested caracaras displayed great degrees of overlap, further highlighting the potential for similar foraging ecology for these species. Another consideration is interspecific dominance at our carrion sites and how this could alter carcass utilization. Because we used still photographs and not video to collect data, it was not possible for us to accurately record interspecific interactions at our sites beyond those caught at the time the camera was triggered. Nevertheless, other research undertaken on vulture species has shown a despotic dominance gradient from the larger species to smaller ones (Moreno-Opo et al. 2020). Of the 3 main avian scavengers at our study site, turkey vultures were the largest. Although interactions captured with photographs provide only a small portion of the full story, we anecdotally observed more instances of aggression (that sometimes resulted in displacement) toward other avian scavengers performed by turkey vultures than black vultures, as one might expect based on the literature. How these interactions may influence the utilization of carcasses on the landscape is unknown at this study site. For example, if a dominant species arrives first, does this cause subordinate species to avoid a site? Additional research will further elucidate the behavioral organization and the relationship of hierarchies according to the feeding behavior of this scavenger guild.

We could not determine how quickly our experimental carcasses (i.e., with trail cameras) were depleted due to carcasses being moved from the frame of the camera in a vast majority of cases. However, direct visual inspection of carcasses with no cameras on them at this study site showed quick depletion with clear evidence of scavenging and active invertebrate communities utilizing the carcass (Leivers et al. 2023). We believe it would be informative to exclude vertebrate scavengers, to determine the time needed for carcasses to decompose at this site because the invertebrate community may well play an active role in carcass removal on this landscape. Carrion flies such as blow flies (Diptera: Calliphoridae) and flesh flies (Diptera: Sarcophagidae) are widespread and can locate a carcass within minutes (Mondor et al. 2012). Although higher temperatures are generally associated with higher insect activity, the extreme heat waves of South Texas may be beyond the upper thermal limits of blow flies, resulting in reduced activity and thus rates of decomposition (Mohr and Tomberlin 2015, Tarone et al. 2021). Further investigation into the effects of temperature and scavenger activity for both invertebrate and vertebrate scavengers may provide additional insight into the most effective time to best utilize scavenger guilds to dispose of carrion on the landscape.

An additional difficulty that arises due to our inability to observe most of the carcasses for the full duration of their utilization is that it also prevents us from determining any temporal variation in species use of the carcasses (e.g., avian scavengers utilizing carcasses at more advanced stages of decomposition than coyotes). One could potentially tether carcasses in place, which would likely not perturb the behavior of avian scavengers, but would likely alter the scavenging behavior of coyotes, as they so regularly dragged carcasses from their original position. Given that coyotes were particularly important for carcass consumption in fall, this would significantly alter the results of our study.

Quantifying the ecological benefit of vultures has garnered interest in the literature in the past few years, but the positive ecological benefits provided by other scavenger species is still understudied. Our research shows that coyotes were very active at carrion sites, particularly in fall when they were more likely to be the first species to find and consume carrion. In Europe, golden jackals (*Canis aureus*) occupy largely the same ecological niche as coyotes in North America, and research in Serbia suggest that golden jackals provide a $500,000 USD value in waste removal each year (Ćirović et al. 2016). At the continental scale, these results suggest that golden jackals remove 13,000 tons of discarded animal waste across human-dominated landscapes in Europe as well as 13.2 million crop pest rodents. Increasingly, there is consideration that they may assist in the mitigation of transmission of African Swine Fever (ASF; Kemenszky et al. 2021), a spreading viral pathogen of global concern that results in death in 95–100% of infected suids (Costard et al. 2013). As ASF is predicted as likely to enter the contiguous United States (USDA-APHIS 2019) and could potentially result in significant economic loss (Carriquiry et al. 2020), coyotes and other scavengers may play an important role in removing infected tissue from the environment. Little is known about the rate at which carcasses leave the landscape, which may inform the level of intensity of lethal removal and/or removal of carcasses to limit the spread of ASF. Research in the Greater Yellowstone Ecosystem, USA, has shown that coyote scavenging reduces the risk of brucellosis transmission (Szcodronski and Cross 2021), and there is preliminary evidence to suggest that ASF fomites do not seem to survive well in digestive systems of vertebrates (Szewczyk et al. 2021). Thus, as new disease challenges present themselves, we find new value for the ecosystem services provided by scavengers. There are many future avenues of research for quantifying the ecosystem benefits of coyotes and other mesocarnivores through their scavenging behavior.

Although the concept of MMEs has gained interest in recent years, great variability can be observed in the literature on what constitutes an MME—from a few dozen individuals to many thousands (Handler et al. 2021). Naturally, widespread deaths of a critically endangered species (e.g., Florida Key deer [*Odocoileus virginianus clavium*]) are ecologically important, but often not classified as an MME. It seems that variation in the mass of the animal, typical abundance in the ecosystem, and the spatial scale of the mortality event drive science to classify mortality events as MMEs (Lashley et al. 2018). Regardless, no rigorous standard by which to assign this status to a mortality event has yet emerged. Not only is studying MMEs with wild pigs important as significant efforts are made to eradicate them, but pigs are a long-studied model system for carrion, and thus these findings could be applicable to the MMEs involving other terrestrial vertebrates (Tomberlin et al. 2017).

This research took place in a hot and semiarid study site, and thus the results may not be applicable to MMEs that take place in colder or wetter climates. Carcasses decompose more quickly on the landscape in hot climates (Archer 2004, Woollen 2019), potentially providing fewer opportunities for scavengers to interact with them prior to colonization by insects. Indeed, Cukor et al. (2020) noted that carcasses in their study examining wild pig decomposition in the Czech Republic decomposed extremely slowly due to the cold climate and were not colonized by insects, thus increasing the temporal availability of the carcasses on the landscapes. Repeating our study in different climates may reveal variation in species-specific use and discovery of carrion, even when similar scavenger guilds are present. Indeed, the range of coyotes extends into Alaska, USA (Hody and Kays 2018), and resident vulture populations continue to expand northward (Marneweck et al. 2023), providing the opportunity for a large proportion of this South Texas scavenger guild to be studied in a more temperate climate.

Management implications

Our results provide land managers with information on how to best utilize the services of their local scavenger community in terms of carcass placement and the time of year in which eradication efforts are undertaken and how best to use this knowledge to help with other management issues. For example, a livestock rancher in this region who does not want to encourage coyotes onto his property may do best to dispose of animal remains in the morning, during summer, on sites with savanna vegetation, as coyotes are less likely than avian scavengers to utilize carrion during the day, when it is summer, and when carrion is located on site with savanna vegetation. In addition, carrion disposed of in the morning is discovered more quickly than carrion disposed of in the afternoon.

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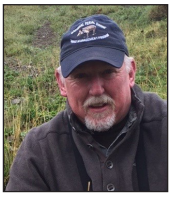

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