

IMPACT OF SELECTIVE PREFERENCES OF VERTEBRATE SCAVENGING
ON ARTHROPOD COMMUNITIES ASSOCIATED WITH CARRION OF
VARYING BIOMASS ACROSS SEASONS

A Dissertation

by

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ABSTRACT

Historically, vertebrate and invertebrate scavengers have been studied independent of one another (such as carrion being placed in carrion exclusion cages), or direct consequences of their interaction ignored (vertebrate focused research overlooking arthropod data). This investigation explored the influence of vertebrate scavengers on arthropod community composition (abundance, family richness/diversity, and functional richness/diversity). It also explored how abiotic (season, and habitat) and biotic (carrion type) factors influenced carrion fate (colonized by blow flies or consumed by vertebrate scavengers).

Vertebrate scavenger access to 181 kg carrion biomasses had the greatest increase in arthropod production. Family richness was influenced by a combination of factors, though vertebrate scavenger access to carrion increased arthropod family richness 1.1x and family diversity using the Shannon Diversity Index was only influenced by time. Functional richness remained unchanged through the study sight where diversity was 1.3x greater at the lowest carrion biomass, suggesting that larger carrion biomasses are being oversaturated with few functional groups (i.e. necrophagous arthropods).

In the perspective of relatively smaller remains (< 200 g), both season and habitat played a role in what scavenger taxon consumed or colonized which carcass type had no effect. 75% of the documented species on trail cameras were mesocarnivores and obligate scavengers which consumed 100% of carrion during the winter and 62% of carrion during summer despite having low species richness (2-5 species). Of the remaining carcasses available for arthropod activity during summer, the invasive red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) monopolized 34%, and blow flies (e.g., *Lucilia eximia* and *Chrysomya rufifacies* (Diptera:

Calliphoridae)) were only able to colonize 25%. Approximately 90% of carrion that was utilized by blow flies was co-colonized by fire ants, and subsequent production of adult blow flies experienced up to a nine-fold reduction in production compared to carcasses that were not scavenged by vertebrates or fire ants. Future research should investigate population dynamics of blow flies in systems where small carrion are being largely monopolized by vertebrates, as well as blow fly dynamics in ecosystems following large influxes of carrion, such as with Mass Mortality Events.

DEDICATION

First, I would like to dedicate this dissertation to my husband, who's unconditional love and support over the past ten years has made me the woman, mother, and researcher I am today. This would not be possible without you.

I also dedicate this work to my daughter, who has taught me patience and perseverance. With a lot of work and a little luck, you can do anything you put your mind to.

Finally, I would also like to dedicate this to my family. There is a long list of people who have sacrificed time with myself, my daughter, and my husband for me to complete this work. Your sacrifice, love, and support has made this journey more meaningful.

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Lauren Gagner, David Sohn, and Sophia Imeroni assisted in data collection in College Station, TX.

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TABLE OF CONTENTS

	Page
ABSTRACT	ii
DEDICATION	iv
ACKNOWLEDGEMENTS	v
CONTRIBUTORS AND FUNDING SOURCES	vii
TABLE OF CONTENTS	viii
LIST OF FIGURES	ix
LIST OF TABLES.....	x
CHAPTER I INTRODUCTION.....	1
Brief History of Carrion Ecology	1
Carrion- An Overview	2
Mass Mortality	4
Animals Function in Carrion Decomposition	7
CHAPTER II IMPACTS OF VARYING CARRION BIOMASS AND VERTEBRATE SCAVENGER	
ACCESS ON ARTHROPOD COMMUNITY COMPOSITION AND FUNCTION	14
Introduction	14
Methods	17
Results.....	19
Discussion.....	27
CHAPTER III VERTEBRATE AND INVASIVE INVERTEBRATE COMPETITION WITH BLOW FLIES FOR CARRION IN HUMAN IMPACTED ENVIRONMENTS DEPENDS ON SYNERGISTIC EFFECTS OF ABIOTIC FACTORS.....	35
Introduction	35
Methods	39
Results.....	43
Discussion	47
CHAPTER IV CONCLUSION	55
REFERENCES	62

LIST OF FIGURES

FIGURE	Page
2.1 Average abundance of arthropods collected on sticky traps (\pm standard error) across increasing biomass and scavenger access/exclusion near Starkville, MS	20
2.2 A) Family Richness access biomass and fencing type (\pm standard error), and B) Family Diversity over time (\pm standard error) of arthropods collected on sticky traps near Starkville, MS. (B) Time point 7/5/2016 represents the arthropod community prior to pig placement.	22
2.3 Arthropod A) Functional Richness over time across all treatments (\pm standard error), and B) Functional Richness across carrion biomass (\pm standard error) (A) Time point 7/5/2016 represents the arthropod community prior to pig placement.....	24
2.4 Arthropod A) Functional Diversity of over time (\pm standard error), and B) Functional Diversity across carrion biomass (\pm standard error). (A) Time point 7/5/2016 represents the arthropod community prior to pig placement.	26
3.1 Percent of carrion successfully utilized by (A) Vertebrate animals (B) Blow Flies (Diptera: Calliphoridae), and (C) Fire ants (<i>Solenopsis invicta</i>). Vertebrate animals (\pm standard error) across open and wooded habitats during summer and winter near College Station, TX.	45
3.2 Mean number of blow fly (Diptera: Calliphoridae) emerging per carcass with and without <i>Solenopsis invicta</i> presence (\pm standard error) near College Station, TX.	47

LIST OF TABLES

TABLE	Page
2.1 List of families of identified arthropods grouped with assigned functional groups for this study. Families were categorized by association with vertebrate carrion, if families are not associated with vertebrate carrion, they are categorized by the most common feeding guild associated with the family.	31
2.2 Summary tables of General Linear Models (GLMs) testing how biomass, scavenger access (fencing), and time influenced: abundance, family richness, family diversity, functional richness, and functional diversity. Both family and functional diversity using the normal distribution, and all other metrics utilized the poisson distribution. A Bonferroni correction of multiple comparisons was made and determined to be $\alpha = 0.01$. All significant p-values are bolded, and approached significance italicized.	34
3.1 Species of vertebrates observed on trail cameras consuming carrion in Snook and Bryan, TX. Asterisk indicates that the species was the most documented species. If two species are indicated, both were dominant scavengers of the indicated habitat and season	44
3.2 Maximum, minimum, and average temperatures recorded through data loggers during winter of 2018 and 2019 near College Station, TX with average calculated Accumulated Degree Hours and raw hours to compare insect development	53
3.3 Maximum, minimum, and average temperatures recorded through data loggers during summer of 2018 and 2019 near College Station, TX with average calculated Accumulated Degree Hours and raw hours to compare insect	54

CHAPTER I INTRODUCTION

A Brief History of Community Ecology

A community is a collective of organisms co-occurring spatially and temporally (Begon et. al. 2006). Understanding community dynamics provides a platform for assessing the Earth's biodiversity regarding maintenance and distribution (Mittlebach 2012). Initially, communities were defined as multiple species acting as a "superorganism" where succession over time led to a stable climax within the environment (Clements 1916). Not long after these initial hypotheses were presented, ecological definitions of communities shifted, and suggested individuals are independent, reacting to environmental gradients rather than collectively (Gleason 1926).

Charles Elton was the first to observe animal communities, diversifying community ecology from what was previously reserved for plant communities (Mittlebach 2012). Elton was the frontrunner for the concepts of food webs, ecological niche, and community diversity (Elton 1927) to name a few. These theories matched well with mathematical models created by Alfred Lotka and Vito Volterra which described predator-prey interactions and competition, showing two competing species cannot coexist (Lotka 1925, Voltera 1926). This intersection of concepts gave way to the discovery of the competitive exclusion principle, which stated two species sharing a limited resource cannot coexist, where the more competitive species will lead the other to local extinction (Gause 1934). Elton (1927) defined the ecological niche as the role species play within their given environment, Gause (1934) took this idea a step further, distinguishing niche overlap and how that creates competition.

G.E. Hutchinson (1957) built upon these initial concepts by describing how species can coexist utilizing what he termed the fundamental and realized niche. Where the fundamental niche is the space organisms would occupy without competition, and the realized niche is a subset of the fundamental niche the organisms retreat to in the presence of competing organisms (Hutchinson 1957). These founders of community ecology paved the way for many ecological theories that allow an understanding of the intricate relationships between insects, carrion, and their environment (Benbow et al. 2019).

Carrion- An Overview

Carrion has been described as nutrient islands supporting metapopulations (Hanski 1987), resource pulses (Yang et al. 2008), or ephemeral resource patches (Barton et al. 2013). Carrion typically are non-replenishing and readily exploited by organisms utilizing the patch until it is diminished (Elton and Miller 1954). Few consumers species rely solely on these patches because they are typically stochastic; spatially and temporally unpredictable in habitat patches (Lacy 1984). Resources that do not persist for long periods are expected to attract in large part, trophic generalists (Ostfeld and Keesing 2000). This is likely why many vertebrate scavengers only utilize carrion opportunistically due to high-energy costs (to forage for carrion) (Devault et al. 2003); leaving only obligate vertebrate carrion consumers to be vulture species with some exceptions (Ruxton and Houston 2004). There are also invertebrate species that are obligate carrion scavengers. Well-known species include species of sexton beetles (Coleoptera: Silphidae) who utilize carrion for food and a site for reproduction (Charabidze et al. 2016).

Both vertebrate and invertebrate animals contribute to the carrion cycle by consuming carrion, preying on individuals that do, or at the end of their own life, making carrion integral to food webs (Barton 2016). Carrion nutrients are directly integrated into food webs by both vertebrate and invertebrate animals (Payne et al. 1968, Putman 1978a, Devault et al. 2003). It is estimated that over 72% of food webs contain detritus and primary producer pathways that are connected by a consumer, 20% of which originating with detritus and almost all pathways involving detritus indirectly (Moore and Hunt 1988). Finally, vertebrate scavengers (any organism feeding on carrion) maintaining the structure and stability of food webs in ecosystems by predators that facultatively scavenge, integrating carrion nutrients directly into upper levels of the food web (Wilson and Wilkovich 2011).

Organisms such as plants, arthropods, and soil microbes in terrestrial habitats rely on nutrients from decomposing organic matter. In temperate forests, this is primarily from leaf matter (Elser et al. 2007). On average, fungi represent up to 96% of the micro fauna responsible for the breakdown and recycling of leaf litter (Baldy et al. 1995) Leaf litter has lower concentrations of macronutrients in comparison to carrion, including nitrogen, which is a limiting nutrient in plants, (Elser et al. 2007) and introduces up to five times the concentration of nitrogen into the soil that leaf litter does (Swift et al. 1979, Moore et al. 2004). Generally, concentrations of nutrients made available from the carrion such as nitrogen and phosphorous increase in the soil as decomposition progresses (Petersen and Luxton 1982, Dent et al. 2004, Carter et al. 2010). The increase in carrion nutrients of vertebrate carrion has been linked to an increase in plant performance (Bump et al. 2009)

and an increase in the diversity and species richness of non-necrophagous arthropods (Sawyer and Bloch 2020).

Unlike detritus, carrion supports vertebrate scavengers in addition to insects. Many studies have come to the same conclusion; insects are the major players in the decomposition of carrion (Campobasso et al. 2001, Payne 1965, Bornemissza 1952). This is in large part studied by caging carrion in studies, while the effect of scavenger presence is largely unknown. In the one study that looked at vertebrate and invertebrate animals role in decomposition, it was found that vertebrate animals accelerate decomposition more so than it progresses with insect access alone (Parmenter and MacMahon 2009). Though many scavenger ecologists acknowledge that insects impact the behavior and carrion selection of vertebrate scavengers (Sincerbox and DiGangi 2018, Beasley et al. 2015, Turner et al. 2017), no one has empirically studied this to date.

Mass Mortality

Mass mortality events (MMEs) are defined as a large number of individuals dying within a short space and time and are often considered infrequent in nature (Scheffer et al. 2001, Gutschick and BassiriRad 2003, Hastings 2004, Haney et al. 2015). MMEs are often naturally occurring; caused by disease, viral, bacterial, or fungal infections, biotoxins, climate change, and direct anthropogenic factors such as perturbation, and pollution (Fey et al. 2015). These large mortality events remove a significant percentage of a population in a short period of time (Juarez et al. 2012) and do not always discriminate life stages of the species effected (Lande 1993), though some events such as in the case of over 200,000

adult female and juvenile Saiga antelope (*Saiga tatarica*, (G.)) dying in Kazakhstan, some demographics can be disproportionately affected (Kock et al. 2018).

When these mortalities are onset by naturally occurring events, such as extreme weather, they are considered natural population die-offs and occur when there is at least a 25% decrease in a population within a year (Juarez et al. 2012). With increased climate change, these events will likely occur more often and potentially lead to microbes being overabundant (Wilmers et al. 2003), reducing the biodiversity of terrestrial animals dependent on carrion for nutrients (Wilmers et al. 2003, Ruxton and Houston 2004) and reproduction (Rozen et al. 2008). If this occurs, coupled with reductions of the number of macrofauna consuming carrion, there may be an increased risk to humans, livestock, and wildlife health due to the potential spread of disease (Pain et al. 2003, Markandya et al. 2008). Necrophagous insects can act as a vector of these potential pathogens. A single blow fly can pick up 9,696 *E. coli* cells on average within 30 seconds of contact with a surface (Pace et al. 2017). With the potential increase in microbial communities following large multiple or mass mortality events, there is a concern that necrophagous blow flies can be a mechanical vector of pathogens causing subsequent mortality. Additionally, an increase in competition among necrophagous flies, such as blow flies, has been suggested to be a concern for an increase in myiasis, a parasitic behavior where colonization of living organisms occurs (Hall and Wall 1995). Myiasis is performed facultatively by many necrophagous blow flies, with some populations having a higher propensity to act parasitically than others. The act of myiasis leaves individuals at an increased risk of

secondary infection and death (French et al. 1994), and therefore is a concern for wildlife, domestic animals, and human health.

Like other disturbance events, broad ecosystem impacts of MMEs can be determined by looking at ecosystem resilience and resistance. Resilience is the ability for an ecosystem to regain the same approximate function, structure, feedback, and identity following a disturbance event (Walker et al. 2004). Resistance refers to the degree to which the ecosystem has changed, with highly resistant ecosystems remaining largely unchanged after a disturbance (Pimm 1984). Functional group diversity within the ecosystem is critical for the resistance and resilience of a given ecosystem (Chapin et al. 1997, Luck et al. 2003). To elaborate, resistance of an ecosystem is more likely to occur when a food web has high diversity or a magnitude of omnivores within the system to suppress the effects of trophic cascades (Pace et al. 1999). Alternatively, in the event of trophic downgrading, the deprivation of apex predators or top consumers, effects on the functionality of a given ecosystem will result due to release of predation on lower trophic levels (Chapin et al. 1997, Duffy 2002, Jackson et al. 2001). However, the addition of a species can also change the structure of ecosystems when a specific functional group is absent (Chapin et al. 2000). For the reasons outlined above, there is a need for high diversity to enable an ecosystem to reorganize after a disturbance event (i.e., carrion) (Chapin et al. 1997, Elmqvist et al. 2003). Since carrion has direct and indirect effects on an ecological community (Hocking and Reynolds 2011, Beasley et al. 2012), it is important to study how these effects can alter the state of the ecosystem, leading to various studies in carrion ecology.

Animals Function in Carrion Decomposition

As previously mentioned, terrestrial carrion decomposition attracts several different arthropod orders that can be seen in a predictable fashion and will change based on spatial and temporal constraints. However, the typical carrion community is comprised mostly of Diptera, Coleoptera, Hymenoptera, and Acari (Merritt and De Jong 2016). Payne (1965) found 522 species across taxa utilizing carrion, out of those, the majority (approximately 81%) were arthropods, 78% of fauna representing Coleoptera, Diptera, Hymenoptera, and Araneida.

Dipterans make up the majority of arthropod biomass during carrion decomposition (Putman 1978b, Greenberg 1991, De Jong and Hoback 2006, De Jong et al. 2011) and are primarily of the families Calliphoridae, Sarcophagidae, and Muscidae (Merritt and De Jong 2016) which are largely saprophagous as larvae (Ferrar 1987). Coleoptera will be on the carrion to either consume carrion tissues, other insects (primarily larvae) or consume both resources. The most abundant families of coleopterans are Silphidae, Dermestidae, Trogidae, Histeridae, and Staphylinidae (Payne and King 1970). Hymanopterans encompass Formicidae, Vespidae, which are omnivorous, and parasitoid Hymanopterans such as *Nasonia vitripennis* (W.) (Merritt and De Jong 2016). Acari, specifically phoretic mites, will ride the backs of coleopterans and can be seen frequenting carrion (Perotti 2009).

Understanding carrion insect biology and behavior is vital to understanding the decomposition process. Ecology is useful to help understand these processes and can help applied sciences such as forensics (Tomberlin et. al. 2011). Traditionally, when studying

carrion and its impacts on arthropod communities, community structure is often considered (Bornemisza 1957, Shahid et al. 2003, Hamer et al. 2006, Huntsman et al. 2011, Horenstein et al. 2012, Caballero and Leon-Cortes 2014, Sawyer and Bloch 2020). Community composition is often demonstrated using data (such as species abundance, diversity, and richness), which is useful in observing changes of biodiversity within a community (Legendre et al. 2005). This is very useful when observing complex interactions and behavioral changes of species within a given community; however, in focusing on structure, function is often ignored, leaving gaps in knowledge of big picture ecological phenomenon.

Function in an ecological context has three definitions, where the first explains a process between two species, the second explains how organisms interact with each other and the environment, and the third describes what role an individual plays in an ecosystem (Jax 2005). Ecological functions are ubiquitous across all taxa and are thought to contribute to ecological resistance, the ability for an ecosystem to regain stability in the event of a disturbance (Peterson et al. 1998, Wardwell et al. 2008). Functional groups that are maintained by multiple species, allow the ecosystem in which they reside, to withstand intense environmental changes despite the loss of an abundant species due to the less abundance species filling that niche (Walker et al. 1999, Chillo et al. 2011). Ecosystems that have one or few species filling functional niches, risks losing that niche in a disturbance event (Chapin et al. 1997). However, omnivores can suppress the effects of lost species from herbivorous, or predacious functional guilds by filling those niches in their absence (Pace et al. 1999). The use of functional groups can give insight to how

ecosystems interact and how they respond to internal disturbances (e.g., the introduction of carrion within a forest) (Moore 2001).

For the purpose of this study, function will be described as Jax's (2005) third definition, where ecological roles are the focus. To further this definition, functional groups will be defined as the role an organism plays in an ecosystem in regards to carrion decomposition. Species that do not interact with carrion will be placed in functional groups in regards to their role in the local environment.

Herbivores and Omnivores. Herbivorous insects consume solely plant material and other autotrophs (Abraham 2006), while omnivorous species consume plants and other animals (Reece et al. 2014). Herbivorous and omnivorous species will not directly interact with carrion, and appear stochastically (Merrit and De Jong 2016, Baz et al. 2010). Hundreds of incidental arthropods have been observed at carrion sites but do not play a role in decomposition (Reed 1958, Braack 1986, Goff et al. 1986, Pechal et al. 2011). However, observations have been made of noctuid caterpillars consuming human cadavers (Lindgren et al. 2015).

Necrophages. These insects are those, as adults or larvae, feeding directly on carrion (Campobasso et al. 2001) and are largely responsible for the decomposition of vertebrate animals (Payne 1965). These include many commonly known flies (Diptera) and beetles (Coleoptera), which are the most predominant insect orders responsible for the breakdown of carrion (Byrd and Castner 2010). The earliest colonizing dipterans are blow flies (Diptera: Calliphoridae) and can often be used to determine a portion of the postmortem interval of vertebrate remains (Mohr and Tomberlin 2014). Other dipterans colonizing

carrion include filth flies (Diptera: Muscidae) and flesh flies (Diptera: Sarcophagidae) (Hanski 1987). Scuttle flies, *Megaselia scalaris* (L.) (Diptera: Phoridae) are also common necrophagous dipterans arriving at carrion after blow flies have pupated (Smith 1986). Other notable flies include cheese skippers (Diptera: Piophilidae) and soldier flies (Diptera: Stratiomyidae), which also lay eggs in or around decomposing plant and animal matter (Hall and Gerhardt 2009). Coleopterans, such as skin beetles (Coleoptera: Dermestidae) are often late colonizers, consuming the leathery flesh and cartilage that has been left by the flies (Rivers and Dalhem 2014).

Predators. Predatory insects that are commonly found at carrion sites are referred to as necrophilous: attracted to vertebrate decomposition, but not feeding on the carrion (Rivers and Dahlem 2014). They include rove beetles (Coleoptera: Staphilinidae), which are non-specific predators, feeding on soil arthropods and small insects (Bohac 1999). Examples associated with carrion include, but are not limited to, the hairy rove beetle, *Creophilus maxillosus* (L.), (Coleoptera: Staphilinidae), which consume fly larvae when present (Fichter 1949, Kramer 1955, Byrd and Castner 2010). There are however, other arthropods that will exploit the increase of prey items, such as spiders (Araneae) (Wise et al. 1999, Polis and McCormick 1986, Bornemisza 1957).

Parasites/Parasitoids. Some well-known parasitoids are of *Nasonia* spp. (Hymenoptera: Pteromalidae) parasitize, and eventually completely consume sarcophagid, calliphorid, and muscid flies when they are pupae (Saunders 1966, Whiting 1967). Acari are often found in leaf litter and around carrion (Bornemisza 1957). While most are live within the given environment naturally, some will also be carried to carrion by coleopterans, which

share a commensal relationship with them, and feed on dipteran larvae and eggs (Gibbs and Stanton 2001).

Saprophagous Omnivores. While traditionally omnivorous species are considered to consume plant and animal material, for the purpose of this study, saprophagous omnivorous species will be defined as those that opportunistically consume both carrion and other arthropod species that reside near carrion (Merritt and De Jong 2016). Carrion beetles are the most abundant of this group and are members of the family Silphidae, which include the endangered American burying beetle (*Nicrophorus americanus* (O.) (Coleoptera: Silphidae)). Like others of the genus, *N. americanus* specializes on vertebrate carrion as food and shelter for larvae. Males and females make a crypt of a small vertebrate, such as a rodent, in which to raise offspring, displaying a biparental lifestyle (Ratcliffe 1996). *Necrophila americana* (L.) (Coleoptera: Silphidae), the American carrion beetle, and closely related *Oiceptoma novaboracense* (F.) (Coleoptera: Silphidae), do not show parental care; however, they are present on larger carrion, often in high abundance (Benbow et al. 2013, Ratcliffe 1996). Another notable order in decomposition is Hymenoptera, which includes bees, wasps, and ants. Ant colonies are established rapidly near carrion, due to the rich resources it provides (Goff & Win 1997). Yellow jackets (Hymenoptera: Vespidae) and fly larvae have been observed to use corpses for shelter and food (Moretti et al. 2011). Additionally, some necrophagous flies are predatory, for example *Chrysomya albiceps* (W.) and *Chrysomya rufifacies* (M.) (Coleoptera: Calliphoridae) are predaceous in second and third instar (Del Bianco Faria et

al. 1999, Baumgartner 1993) making them omnivorous intraguild predators; obtaining nutrients from the carrion and other fly larvae (Ullyette 1950).

Detritivores. Detritivores will use carrion advantageously for shelter and nutrients during the decomposition process (Lane 2007). This group often encompasses saprophagous insects living in the soil such as Collembola (Folsom 1902, Tantawi et al. 1996).

Vertebrate Scavengers. Vertebrate scavengers play an important ecological function in recycling carrion (Wilson and Wolkovich 2011). There are two types of scavengers, obligate and facultative (Devault et al. 2013). In terrestrial ecosystems, as previously mentioned, some vulture species are the only known obligate scavengers of carrion (Ruxton and Houston 2004). They have evolved to seek out (via olfaction and visual cues (Wilmers et al. 2003, Ruxton and Houston 2004)) and consume carrion, a resource potentially contaminated with various pathogens (Houston and Cooper 1975).

Facultative scavengers make up a vast majority of vertebrate species consuming carrion (Devault et al. 2003) and can be comprised of three groups, predators, mesopredators, and miscellaneous (Sincerbox and DiGangi 2018). Predators often represent the apex species, such as cougars (*Puma concolor*), bears (Ursidae), and wolves (*Canis lupus*). Since carrion incurs low energy cost to consume, in comparison to hunting, and is a quality energy source, predators will advantageously utilize carrion (Selva and Fortuna 2007). Mesopredators are viewed as “traditional” scavengers, such as coyotes (*Canis latrans*), foxes (*Vulpes*), racoons (*Procyon lotor*), and opossums (Didelphidae). Mesopredators are efficient scavengers often relying on olfaction (Green et al. 2012). Since mesopredators thrive off anthropogenic activity, carrion located in urban landscapes

are more readily scavenged than when located in rural landscapes (Houston 1986). Additionally, urban landscapes often suffer from trophic downgrading as apex predators are removed or excluded from an area (Estes et al. 2005). This shift allows for mesopredators to become overabundant, accelerating scavenging of carrion (Devault et al. 2011), which limits food resource for insect colonizers. In fact, beetle taxon richness was significantly lower in fragmented, urban environments than in rural habitats (Gibbs and Stanton 2001).

Miscellaneous scavengers are represented by those species not thought to commonly consume carrion, such as deer (Cervidae), which consume bones for calcium deposits (Caceres et al. 2011, Kierdorf 1994). Rodents (Rodentia) also degrade bones by using them as a substrate for filing their teeth (Haglund 1992). Whether a carcass is scavenged (and by what) is dependent on many abiotic and biotic factors (e.g., season, location, presence of invertebrates) surrounding carrion availability and decomposition. For example, carrion colonized by insects is not expected to be scavenged by vertebrates (Sincerbox and DiGangi 2018, Beasley et al. 2015). Furthermore, scavenging is dependent on the vertebrate species present in a given area. The same species may implement different strategies depending on the on carrion species; for example, Steadman et al. (2018) observed racoons (*Procyon lotor*) feeding strategically on human limbs while readily tearing other species (Pigs (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) apart with very little feeding. Variation of feeding could secondarily create postmortem oviposition sites for arthropods that could lead to colonization after a vertebrate scavenger feeding event, so long as all the remains were not consumed.

CHAPTER II

IMPACTS OF VARYING CARRION BIOMASS AND VERTEBRATE SCAVENGER ACCESS ON ARTHROPOD COMMUNITY COMPOSITION AND FUNCTION

Introduction

Many vertebrate and invertebrate species compete for carrion in terrestrial ecosystems (Elton and Miller 1954, DeVault et al. 2003) due to its high nutritive value. Carrion nutrients can go directly into upper levels of food-webs if predatory vertebrates opportunistically scavenge remains (Wilson and Wilkovich 2011). Alternatively, necrophagous invertebrate enzymatic and mechanical breakdown of tissues allows for microbial use which releases nutrients for plant use (Barton et al. 2013). With nutrients directly impacting food web dynamics, the decomposition process is vital for overall ecosystem function (Benbow et al. 2019, Barton et al. 2019) and therefore can provide effective ways to determine ecosystem health (Newsome et al. 2021).

Carrion biomass plays a major role in its decomposition rate (Parmenter and MacMahon 2009). Individuals of larger biomass (60-90 kg) tend to decompose slower per gram of body mass than individuals of smaller biomass (<35 kg) (Sutherland et al. 2013). This variation is largely due to a greater surface area to volume ratio of the individual (Parmenter and MacMahon 2009), which can allow for relatively more access to tissues by insects. Vertebrate scavengers can also consume smaller carrion (0.004-0.100 kg) in a single foraging event (DeVault et al. 2003). Vertebrate consumption in single foraging events accelerates the rate at which carrion nutrients enter the food web (Wilson and Wilkovich 2011). In contrast, carrion with larger biomass (>100 kg) maintain higher

diversity of vertebrate (Moleón et al. 2015) and invertebrate (Schoenly and Reid 1983) scavengers feeding on these resources. Biomass can be related to a single individual as well as cumulatively (i.e., multiple animals dying in the same location within a given temporal window). With increasing biomass, the abundance of necrophagous arthropods tends to increase (Schoenly and Reid 1983), where necrophagous arthropod abundance will peak shortly after carrion placement and decrease over time (Sawyer and Bloch 2020). While research has been conducted on carrion in non-necrophagous species (as in Sawyer and Bloch 2020), functional responses have not been studied previously and little research has been conducted on biomasses larger than one or few pig carrion (*Sus scofra*) (Perez et al. 2016). Additionally, it is unknown how vertebrate scavenger consumption of carrion impacts arthropod communities since most studies conducted use vertebrate exclusion cages to cover animal remains. While smaller carrion can expect to have little to no production due to vertebrate consumption, larger carrion that can persist in the environment longer may allow for one or more generations of necrophagous arthropods to proliferate.

Events where multiple deaths occur at the same time are referred to as Mass Mortality Events (MMEs) (Hoffmann and Parsons 1991, Scheffer et al. 2001, Gutschick and BassiriRad 2003, Hastings 2004, Siepielski and Benkman 2007, Haney et al. 2015, Fey et al. 2019). MMEs have been increasing in magnitude and frequency across multiple animal taxa (Fey et al. 2015) and are caused by various agents, from abiotic (e.g., hurricanes and lightning strikes) (Newton 2007) to biotic (disease outbreaks) factors (Rachowicz et al. 2006). As these events are becoming more apparent, a greater

understanding of the ecological impacts of these events becomes necessary (Fey et al. 2015, Fey et al. 2019). Furthermore, the amount of biomass introduced into an ecosystem by a MME can vary depending on the magnitude of the event. For example, a mortality event of 300 reindeer, *Rangifer tarandus* (L.) dying due to a lightning strike, (introducing approximately 25,033kg of carrion biomass (Greshko 2016)) and over 200,000 Saiga antelopes, *Saiga tatarica*, (G.) succumbing to a pathogen, (introducing over 4 million kg of carrion biomass (Kock et al. 2018)) are both categorized as MMEs. However, the differing ecosystem effects of MMEs that vary in size have not yet been determined.

Ecosystem responses to a MME are not frequently studied due to the stochastic nature of these events (Fey et al. 2019). However, some research has been successfully conducted following such events, showing profound changes in local predator-prey dynamics after a MME where prey species left the surrounding area, potentially due to increased presence of predators scavenging on remains (Frank et al. 2020). Other research using artificial MMEs has shown shifts in food-web dynamics (Baruzzi et al. 2018), such as mass dispersal of dipteran larvae at large mortalities (>325 kg), increasing disturbance intensity by insectivorous wildlife along dispersal paths (Lashley et al. 2018). Currently, how such events influence community function and composition is uncertain. For example, an introduction of large carrion biomass has had negligible effects on microbial community dynamics (Harrison et al. 2020). Ecological metrics of other taxa, such as arthropod community composition and function, have not yet been explored.

The purpose of this study is to determine the impact of varying carrion biomass on arthropod populations at decomposition sites. To do this, five field sites were chosen to have pig carrion of increasing biomass (25 kg to 725 kg). Sites consisted of vertebrate included and excluded treatments, and arthropod activity was sampled with sticky traps. We hypothesize that with increasing biomass, there will be a greater saturation of necrophagous arthropods and thus decrease in the overall species diversity and functional groups of arthropods at mortality sites. In addition, we hypothesize that vertebrate scavenger access will have lower arthropod diversity in comparison to alternative vertebrate excluded biomasses.

Methods

Field Set-up

Using the methods based on Harrison et al. (2020), the effects of MMEs were investigated by studying five sites with mortality events of varying biomass (25kg, 60 kg, 181 kg, 363 kg, 725kg) of donated feral swine (*Sus scrofa*) carrion in a managed loblolly pine (*Pinus taeda*) forest, John Starr Forest, Starkville, MS (33.353911°N, 88.890261°W), starting July 5th, 2016. Approximately half of the feral hogs were frozen prior to placement due to variability in carrion availability. Frozen and unfrozen hogs were haphazardly dispersed across all treatments to limit effects of freezing prior to placement. Since swine were culled for reasons other than this research, IACUC approval was not needed for this study. Each site was at least 1 km from each other and had two plots with two levels of scavenger access (fenced or open), each treatment having the same carrion biomass

designated for the site as described above (For example: Site 1 had 25 kg with scavenger access and 25 kg of carrion with scavenger exclusion fencing). All plots were 5 m in diameter (area of 20 m²) and at least 100 m from the next plot to prevent insect communities from traveling between events (Perez et al. 2016). Fencing consisted of 1.2 meter tall Red Brand[®] (Peoria, IL, USA) 4 x 10 m steel welding wire around the respective plot's circumference and held up by t-posts, overlaid with polypropylene Sta-Green[®] (Rowlett, TX, USA) bird netting secured by plastic zip ties as described by Harrison et al. (2020).

Sample Collection

Trapper Max Free sticky traps (Bell Laboratories, INC (Madison, WI, U.S.)) were stapled to a wooden post placed approximately 30 cm from the ground at each plot facing the center most location within the designated plot. All sticky traps were replaced as needed (when full of arthropods) from each site, or after a two-week period. Collection of sticky traps began two weeks prior to the placement of carrion (June 27 to July 5th, 2016), continued through the duration of the study and ceased September 29th, 2016. Sticky traps were stored at room temperature in cardboard boxes and sent to the Texas A&M Forensic Laboratory for Investigative Entomological Sciences (F.L.I.E.S.) Facility. Arthropods were identified to the taxonomic level of family using Triplehorn and Johnston (2005), and were tabulated in Microsoft[®] Excel[®] (Redmond, Washington, U.S.).

Categorizing Taxa

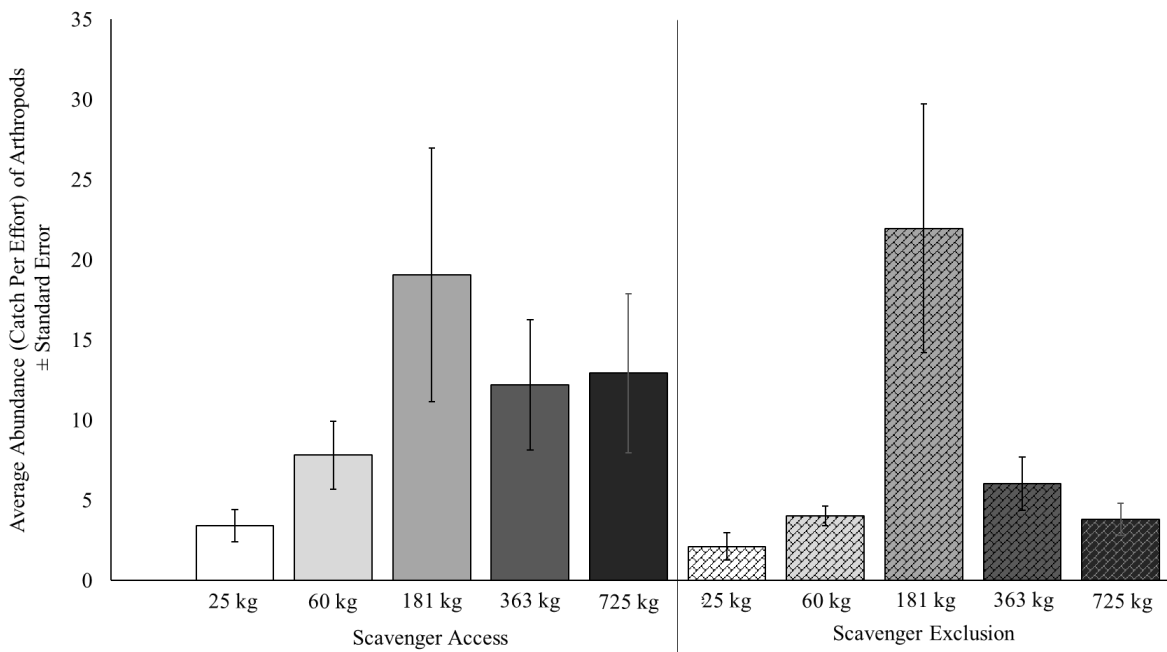
Seven different feeding guilds were distinguished from the families collected. Groups included detritivores, herbivores, necrophages, omnivores, parasites, parasitoids, and predators (see Table 2.1). Detritivores and necrophagous arthropods were differentiated (as opposed to having a “Saprophages” category) to parse out carrion consumers and potentially opportunistic feeders. Parasites and parasitoids were separated due to the impact on different hosts, where the families that were considered parasites have vertebrate hosts and families categorized as parasitoids in this study rely on arthropod hosts that they inevitably kill. Omnivores included predatory arthropods that were also documented eating plant material or vertebrate carrion.

Statistical Analyses

Statistical analyses were performed in R version 3.5.1 “Feather Spray” (R Core Team 2018) using the package “lme4” (Bates et al. 2015). Due to zero replication in treatments, General Linear Models (GLMs) were used (Garrett et al. 2002) to determine if biomass, scavenger access (fencing), and/or time was driving differences in abundance, family richness (number of families), functional richness (number of functional groups) and functional diversity of the arthropod community. Due to preliminary review of the data, abundance, family richness, and functional richness was tested using the Poisson distribution. Family and functional diversity was determined using the Shannon Diversity Index, and a normal distribution was used in statistical analyses. A Bonferroni correction of multiple comparisons was made, and alpha values determined to be 0.01.

Results

Overall arthropod abundance was significantly ($p = 0.006$) impacted by an interaction of biomass and scavenger access (fencing), and time. This interactive effect was driven primarily by all biomasses having significantly more arthropods in open plots, in comparison to scavenger excluded plots of the same biomass, where abundance was greatest after carrion placement. The 181 kg plots had the greatest abundance, where the 181kg fenced plot had 1.15x more arthropods than the open plot of the same biomass, and



up to 10.41x more arthropods than all other treatments (Fig. 2.1). Unexpectedly, abundance for all treatments was greatest after carrion placement and declined over time.

Fig. 2.1: Average abundance of arthropods collected on sticky traps (\pm standard error) across increasing biomass and scavenger access/exclusion near Starkville, MS.

Arthropod family richness was influenced by a significant interaction with biomass and fencing type ($p < 0.001$) in addition to an interaction between biomass and time ($p = 0.001$). Similar to abundance, 181 kg biomass had the greatest richness when

scavengers had access to the resources, however functional richness was 1.1x greater than when scavengers were excluded at the same biomass having the opposite effect than seen with arthropod abundance. When scavengers were excluded, both the 25 and 60 kg biomasses had up to 1.76 x more richness than other biomasses (Fig. 2.2A). A biomass by time interaction was likely influenced to all biomasses having a different family richness prior to carrion placement and followed similar trends through decomposition.

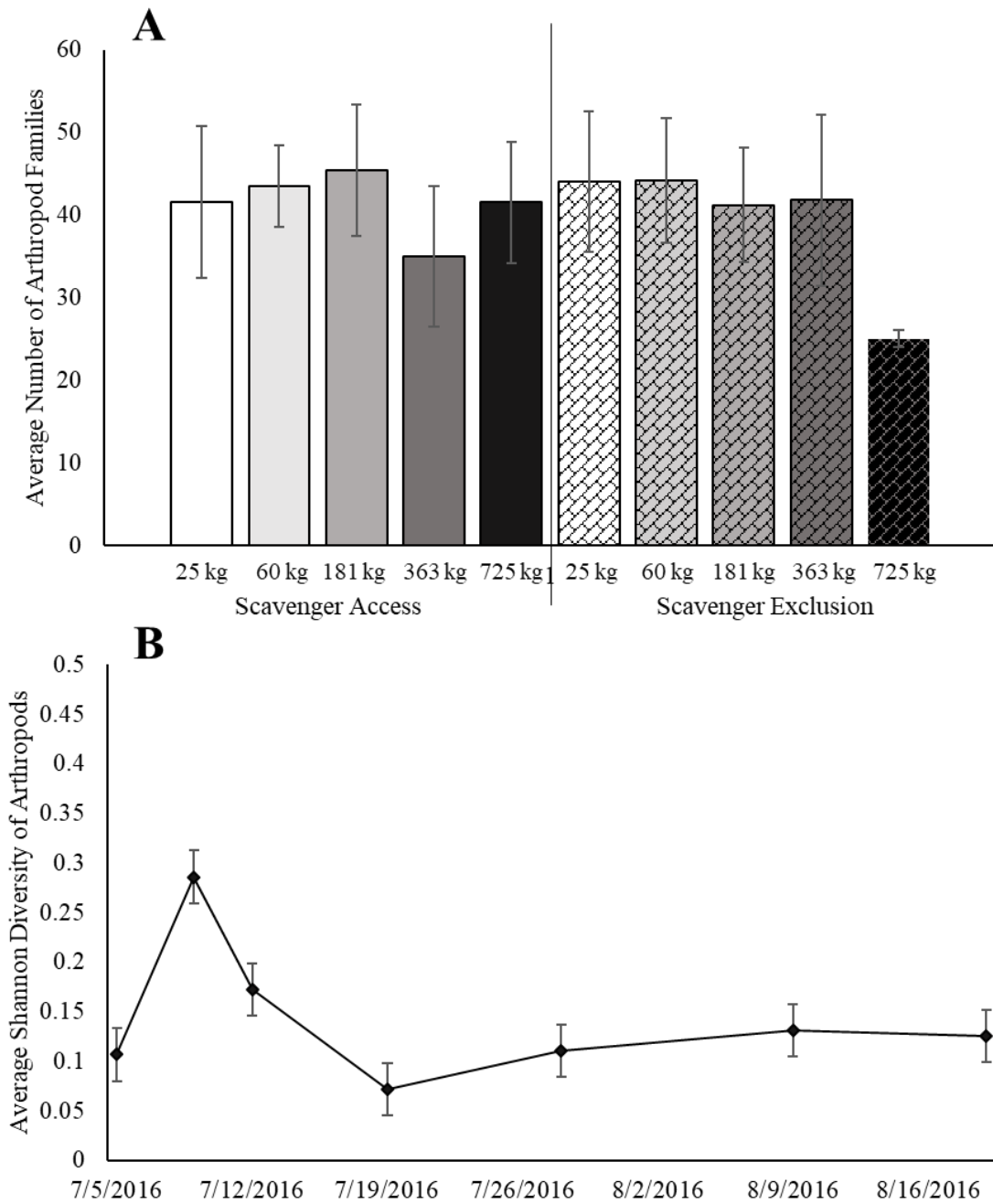


Fig. 2.2: A) Family Richness access biomass and fencing type (\pm standard error), and B) Family Diversity over time (\pm standard error) of arthropods collected on sticky traps near Starkville, MS. (B) Time point 7/5/2016 represents the arthropod community prior to pig placement.

Unlike abundance and family richness, arthropod diversity was significantly impacted by time ($p = 0.021$) (Fig. 2.2 B), where diversity lifted briefly after carrion placement and returned to approximate pre-pig placement levels. Unlike abundance and family richness, there was no biomass by fencing interaction ($p = 0.073$) (Fig. 2.2A), and biomass was approaching significance ($p = 0.021$) where 725 kg biomasses saw up to 1.83x more diversity than other biomasses (Fig. 2.2A).

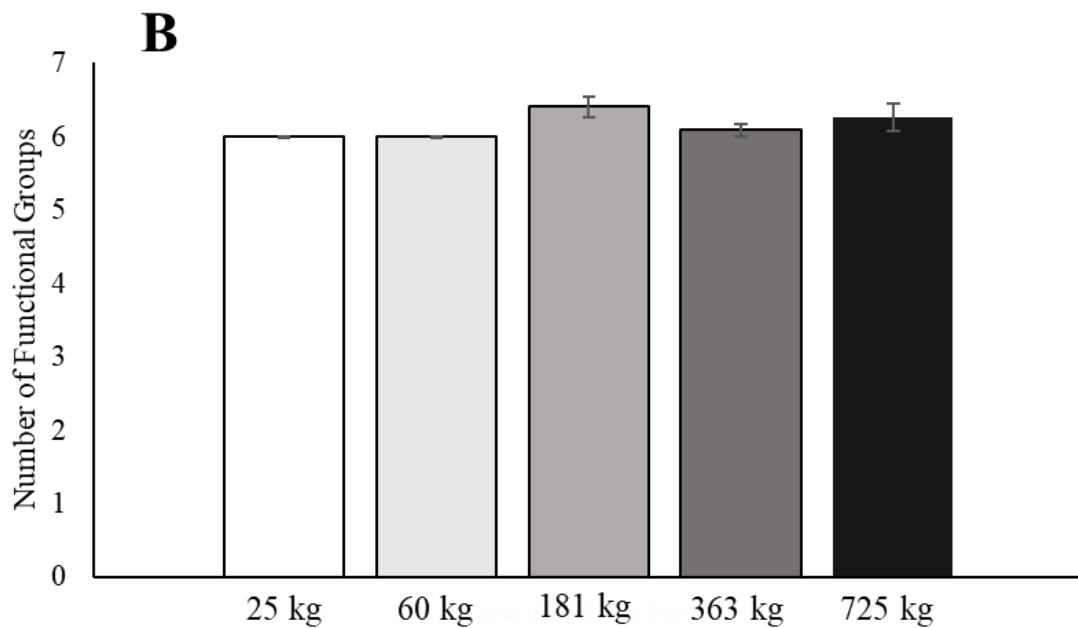
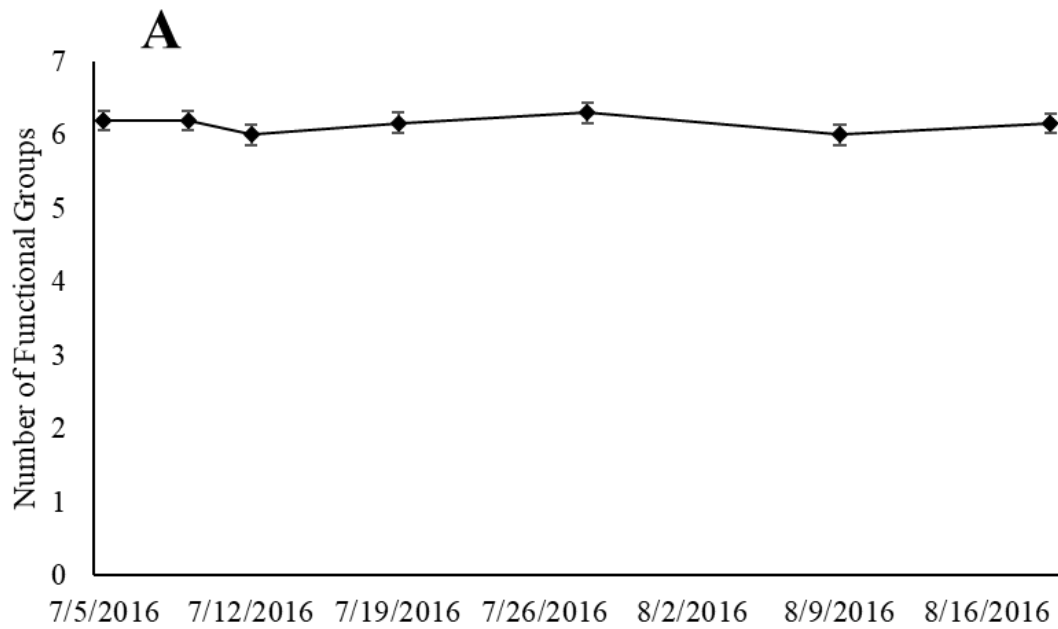


Fig. 2.3: Arthropod A) Functional Richness over time across all treatments (\pm standard error), and B) Functional Richness across carrion biomass (\pm standard error) (A) Time point 7/5/2016 represents the arthropod community prior to pig placement.

Functional richness had zero significant interactions over time, with all functional groups being maintained across biomass ($p = 0.938$), scavenger access ($p = 0.949$), time ($p = 0.966$), and any interaction between these factors (Fig. 2.3) (Supplemental Table (2.2)). However, regarding functional diversity, biomass ($p = 0.009$) and time ($p < 0.001$) were independently significant factors. Generally, the 25 kg biomasses had up to 1.3x more diversity than all other plots (Fig. 2.4). Inversely from family diversity, functional richness saw a temporary decline in functional diversity before approaching approximate pre-pig levels. Due to functional richness being unaffected by biomass and time, the functional diversity of arthropods is likely reflective of functional evenness as this along with functional richness is accounted for using the Shannon Diversity Index. Therefore, plots with lower diversity indices reflect low functional evenness with one or few families maintaining any given functional group and limiting functional redundancy at pig placement.

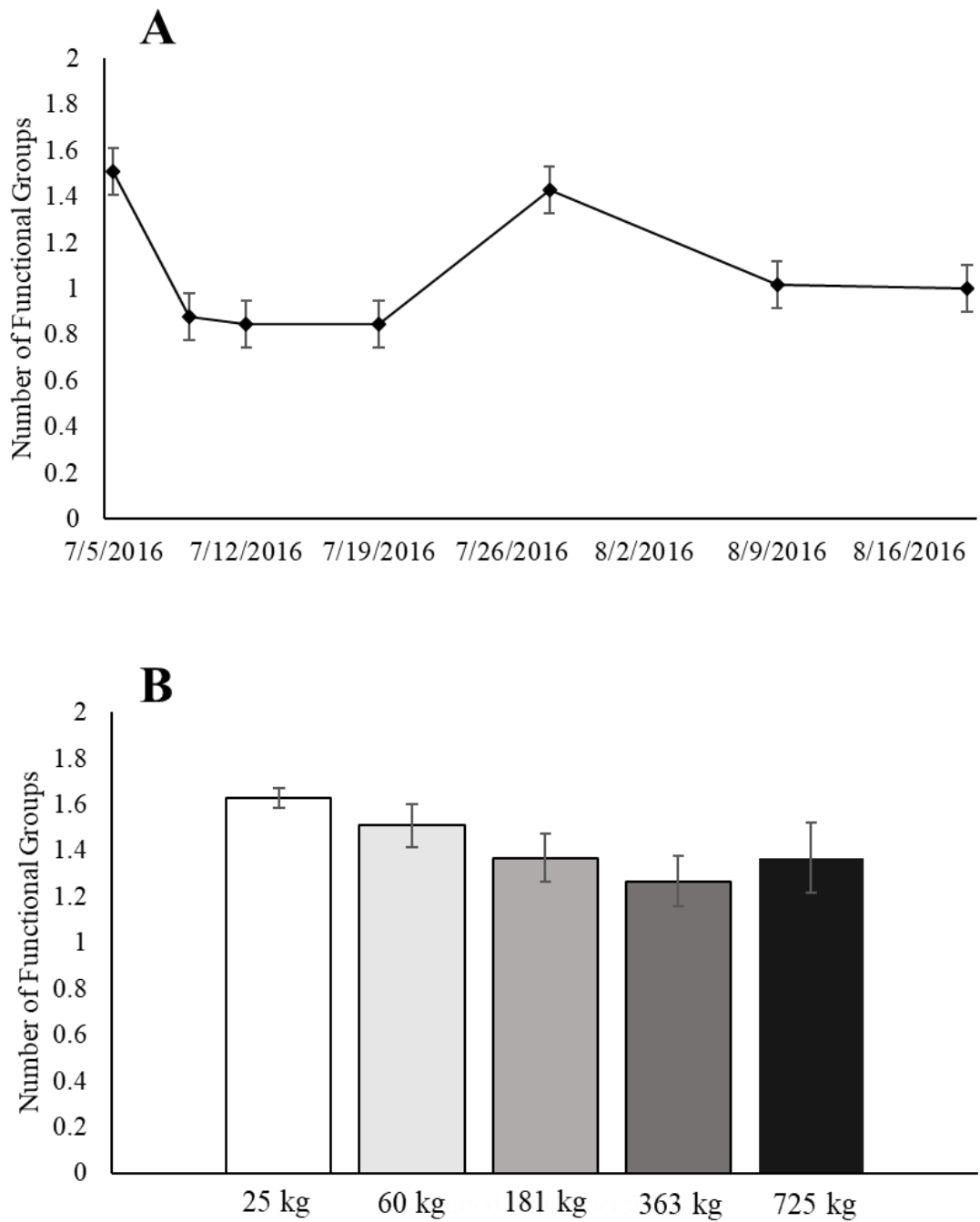


Fig. 2.4: Arthropod A) Functional Diversity of over time (\pm standard error), and B) Functional Diversity across carrion biomass (\pm standard error). (A) Time point 7/5/2016 represents the arthropod community prior to pig placement.

Discussion

Production of necrophagous arthropods on carrion has long thought to increase with increasing biomass (Baruzzi et al. 2018, Barton et al. 2019). For example, a single jackrabbit (*Lepus californicus*) (2000-2500 g) carrion can produce over 1,400 blow flies, nearly 10x more than woodrat (*Neotoma albigula*) (89-290 g) carrion (Schoenly and Reid 1983). The current research shows that abundance (from production at the remains or from recruitment of arthropods in the surrounding environment) increases with biomass but decreases in the largest biomasses (363 and 725 kg). The decrease in large biomasses may be due to similar mechanisms thought to drive the Intermediate Disturbance Hypothesis (IDH). The IDH states that moderate disturbances generate the largest diversity of organisms, and levels of disturbances that are relatively extreme (either no disturbance or constant disturbance) will have little to no diversity (Roxburgh et al. 2004). In the instance of carrion, the carrion serves as the habitat for carrion reproducing arthropods and individuals moving remains (such as scavengers) disrupt microbial populations (Beasley et al. 2015), which would otherwise create toxic byproducts and limit the bioavailability of carrion for animals (Janzen 1977). At biomasses too great to have sufficient disturbance that would lower the abundance of strongly competitive microorganisms, they may be limiting the bioavailability of carrion for animals at these large biomasses. A similar phenomenon has been seen with non-necrophagous animals and coined the “landscape of disgust”; a term used in relation to carrion when nutrients from carrion in the soil allow for significant proliferation of microbes, preventing

herbivores from feeding on surrounding vegetation without risk of exposure to pathogens (Newsome et al. 2021, Weinstein et al. 2018).

In single carrion studies, vertebrate and invertebrate animals are thought to be in severe competition with each other and microbial communities (Barton et al. 2013, Benbow et al. 2019). In this study however, the presence of both taxa may serve mutualistically when competing against microorganisms, where satiation is not met in either taxon. This apparent mutualism is unexpected, as vertebrates can hinder necrophagous arthropod production by up to 100% (DeVault et al. 2003). At larger carrion biomasses, there may be enough soft tissues to allow for consumption by both vertebrate and invertebrate animals without reaching satiation. This is suggested by mummification of remains at 725 kg biomasses, where vertebrates and invertebrates could not consume remains fast enough to prevent toxic microbes from proliferating (Tomberlin et al. 2017). This is likely why at these larger biomasses, even with scavenger access, abundance, richness, and diversity was lower at 725 kg than at 181 and 323 kg biomasses with vertebrate access, as vertebrates can generate new wounds on the remains, allowing for more oviposition sites for necrophagous arthropods (Charabidze et al. 2014, Meyer et al. 2020). The results from this study suggest that in the event of multiple mortalities occurring simultaneously (as seen in mass mortality events), carrion biomass alone may not be a sufficient indicator of abundance, rather, surface area to volume ratios (as proposed in Parmenter and MacMahon (2009) in relation to decomposition rates), may serve as a covariate when it comes to necrophagous arthropod production and should be investigated further.

Understanding carrion biomass' role in ecosystem function has been one of the most understudied topics in carrion ecology and is needed to understand the role carrion plays in food webs (Barton et al. 2019). In fact, carrion is known to be an indicator of healthy ecosystems based on carrion turnover rates (Newsome et al. 2020). In this study, increasing biomass lowered the functional diversity while leaving functional richness unchanged. This provides insight to how carrion may challenge ecosystem resistance at the carrion site. While ecosystem function is maintained through the duration of the research, declines in functional diversity leave ecosystems at risk of losing an entire functional group if the one family or species maintaining it is removed from the system (e.g., through disturbance events, competition, etc.) (Tilman 2001). It is important to consider that samples were only taken at the carrion site, therefore, function in the immediate vicinity can be regained from the surrounding environment through rescue effects (Hanski 1994). How long it would take till the functional diversity is restored in this location, however, is not yet known. Future research should investigate how fast carrion turnover is in the event of large carrion biomasses, such as mass mortality events, through mathematical modeling (Barton et al. 2019).

While community composition and function are exclusive to the carrion site, the proliferation of necrophagous arthropods such as blow flies can have broad ecosystem consequences. In this study, the most abundant consumers of carrion were dipteran families such as blow flies (Diptera: Calliphoridae), flesh flies (Diptera: Sarcophagidae), house flies (Diptera: Muscidae), fanniid flies (Diptera: Fanniidae), sepsid flies (Diptera: Sepsidae), scuttle flies (Diptera: Phoridae), and fruit flies (Diptera: Drosophilae). Many

dipteran species have many ecological services in common, such as pollination (Kearns 2001, Cusser et al. 2021). In areas that carrion is added, pollination services increase exponentially, with 80% of pollinators being carrion Diptera (Cusser et al. 2021). Additionally, flies serve as a food resource for many predatory species, such as spiders and birds. The increased abundance of insects is expected to have a bottom-up effect on the surrounding environment, which can temporarily increase the predator abundance relying on these species (Barton et al. 2013). Inversely, the proliferation of filth flies has potential negative impacts on ecosystems as these flies have been shown to spread pathogens throughout an environment (Pace et al. 2017) and increase the likelihood of myiasis occurring in wild and domestic animals in the area (Wardhaugh and Morton 1990). Additionally, some mortality events are caused by disease agents, such as die offs of white-tailed deer (*Odocoileus virginianus*) due to *Bacillus anthracis* poisoning (anthrax), where blow flies are mechanical vectors of this pathogen (Blackburn et al. 2014); therefore, understanding how carrion placement aids in the proliferation of blow flies and potentially other filth flies is important for understanding the disease ecology of this system.

With the increased frequency and magnitude of MMEs over recent years (Fey et al. 2015), identifying the ecological consequences of large carrion biomasses in ecosystems is integral. This study is the first of its kind to investigate the impacts of large carrion biomasses on arthropod communities. It has shown that in large mortality events, vertebrates play a pivotal role in arthropod communities and may provide insight on to

how to manage carrion remains in future mortalities to limit the proliferation of potentially harmful pathogen vectors.

Table 2.1: List of families of identified arthropods grouped with assigned functional groups for this study. Families were categorized by association with vertebrate carrion, if families are not associated with vertebrate carrion, they are categorized by the most common feeding guild associated with the family.

Functional Group	Families					
Detritivore	Chironomidae	Onychiuridae				
	Chrysomelidae	Scarabaeidae				
	Clusiidae	Stratiomyidae				
	Drosophilidae	Tipulidae				
	Ectobiidae	Tricoptera				
	Entomobryidae	Ulidiidae				
	Erotylidae	Zorotypidae				
	Gastropoda					
	Isotomidae					
	Lauxaniidae					
Herbivore	Acrididae	Cecidomyiidae	Ectopsocidae	Lepismatidae	Nitidulidae	Tetrigidae
	Aeolothripidae	Cerambycidae	Elateridae	Liposcelididae	Peripsocidae	Tettigoniidae
	Aleyrodidae	Ceratocombidae	Euchemidae	Lycidae	Phleothripidae	Thripidae
	Amphipsocidae	Cercopidae	Eucinetidae	Lygaeidae	Philotarsidae	Throscidae
	Anobiidae	Chloropidae	Geometridae	Merothripidae	Pseudo-phasmatidae	Tineidae
	Anthocoridae	Cicadellidae	Halictidae	Miridae	Psocidae	Tingidae
	Aphididae	Cimbicidae	Heteronemiidae	Mordellidae	Ptiliidae	
	Apidae	Cixiidae	Hydropsychidae	Mycetophilidae	Rhyparochromidae	
	Berytidae	Curculionidae	Lachesillidae		Sciaridae	
	Caeciliusidae	Delphacidae	Lampyridae			

Necrophage	Agromyzidae	Syrphidae		
	Anthomyiidae			
	Calliphoridae			
	Fanniidae			
	Muscidae			
	Phoridae			
	Piophilidae			
	Sarcophagidae			
	Sepsidae			
	Sphaeroceridae			
Omnivore	Formicidae			
	Gryllidae			
	Gryllotalpidae			
	Latridiidae			
	Nymphalidae			
	Ptilodactylidae			
	Rhaphidophoridae			
	Vespidae			
Parasite	Ceratopogonidae			
	Ixodidae			
Parasitoid	Aphelinidae	Eulophidae	Perilampidae	Tiphiidae
	Bethylidae	Evaniidae	Platygastridae	Torymidae
	Braconidae	Hippoboscidae	Pompilidae	Trichogrammatidae
	Ceraphronidae	Ichneumonidae	Psychodidae	
	Chalcididae	Megaspillidae	Pteromalidae	
	Crabronidae	Milichiidae	Pulicidae	

	Cynipidae	Mutillidae	Scelionidae	
	Diapriidae	Mymaridae	Signiphoridae	
	Embolemidae	Myrmelliontoda	Sphecidae	
	Encyrtidae		Tachinidae	
	Eulophidae			
Predator	Aeshnidae	Coniopterygidae	Lycosidae	Staphylinidae
	Agelenidae	Corydiidae	Meropeidae	Tabanidae
	Araneidae	Deinoponidae	Sclerosomatidae	Tenebrionidae
	Asilidae	Diguetaeidae	Philodromidae	Tetragnathidae
	Cantheridae	Dolichopodidae	Pholcidae	Thomisidae
	Carabidae	Dysderidae	Pisauridae	Trogossitidae
	Cleridae	Hebridae	Reduviidae	
	Clubionidae	Histeridae	Salticidae	
	Coccinellidae	Hybotidae	Segestriidae	
	Coenagrionidae	Linyphiidae	Sparassidae	

Table 2.2 Summary tables of General Linear Models (GLMs) testing how biomass, scavenger access (fencing), and time influenced: abundance, family richness, family diversity, functional richness, and functional diversity. Both family and functional diversity using the normal distribution, and all other metrics utilized the poison distribution. A Bonferroni correction of multiple comparisons was made and determined to be $\alpha = 0.01$. All significant p-values are bolded, and approached significance italicized.

General Linear Models (GLM)		Abundance			Richness			Diversity			
Taxonomic Grouping	Factor	DF	Deviance	P	DF	Deviance	P	DF	Deviance	P	
Family	Biomass	4	75.993	< 0.001	4	17.380	0.002	4	1029.400	<i>0.021</i>	
	Fencing	1	1.717	0.190	1	0.907	0.341	1	49.500	0.456	
	Time	5	145.154	< 0.001	5	30.773	< 0.001	5	3483.900	< 0.001	
	Biomass x Fencing	4	32.348	< 0.001	4	34.094	< 0.001	4	763.700	0.073	
	Biomass x Time	12	26.569	0.009	12	32.016	0.001	12	866.500	0.640	
	Fencing x Time	4	1.579	0.813	4	1.599	0.809	4	7.400	0.999	
	Biomass x Fencing x Time	6	18.289	0.006	6	8.498	0.204	6	677.200	0.269	
	AIC										328
	Function	Biomass	4			4	0.800	0.938	4	1601.800	0.009
		Fencing	1			1	0.004	0.949	1	61.700	0.471
Time		5			5	0.357	0.996	5	3493.600	< 0.001	
Biomass x Fencing		4			4	0.307	0.989	4	796.100	0.153	
Biomass x Time		12			12	0.491	1.000	12	440.600	0.988	
Fencing x Time		4			4	0.803	0.938	4	109.200	0.923	
Biomass x Fencing x Time		6			6	0.589	0.997	6	135.400	0.980	
AIC											341.02

CHAPTER III

VERTEBRATE AND INVASIVE INVERTEBRATE COMPETITION WITH BLOW FLIES FOR CARRION IN HUMAN IMPACTED ENVIRONMENTS DEPENDS ON SYNERGISTIC EFFECTS OF ABIOTIC FACTORS

Introduction

Ecological interactions within human-impacted landscapes (i.e., highly fragmented with human infrastructure) are historically relatively understudied (Soulsbury and White 2016) but important given continued transformation of wild landscapes to space for human use (such as agriculture and recreation) with accelerating human population growth. Although ecological interactions within human landscapes are being studied more now than in recent past, decomposition and the role of necrophagous arthropods, vertebrate scavengers, and their interactions within these environments continue to be largely neglected. Several studies (e.g., Cusser et al. 2020, Wolf et al. 2004) have examined human mediated landscape effects on target insect communities associated with carrion, while others (e.g., Shwartz et al. 2018, DeVault et al. 2011) focused on vertebrate species; however, no studies to our knowledge have explored these groups in tandem. This manuscript will be the first attempt to look directly at carrion fate between vertebrate and invertebrate scavengers and lay the groundwork for future research.

Necrophagous arthropods and their associated ecosystem services are particularly sensitive to human disturbances. Species composition changes and resulting populations within these communities select different dietary preferences due to resource shifts (Langer et al. 2019), which impact a host of ecological interactions with other species (e.g., competition, mutualisms (Gibbs and Stanton 2001)), and plant-herbivore

interactions (Miles et al. 2019). Vertebrate populations are also impacted by human disturbance in a similar fashion (Lambertucci et al. 2009). Thus, understanding how human land use influences scavenging behavior is paramount to determining ecosystem interactions and their resulting ecosystem services, with potential downstream consequences on human and wildlife health (Bradley and Altizer 2007).

Carrion serves as a resource for numerous vertebrate and invertebrate species in both human and non-human-impacted environments (Benbow et al. 2019, Barton et al. 2013). In fact, carrion is a recognized contributor to the maintenance of ecosystem health (i.e., facilitation of trophic interactions) (Newsome et al. 2021). However, due to the short-lived nature of these resources, competition can be intense, sometimes resulting in its complete consumption shortly after animal death (Barton et al. 2013). Depending on the scavengers that utilize these remains, nutrient flow of carrion within a food web can vary. For example, vertebrate scavengers on higher trophic levels can introduce carrion nutrients into upper levels of the food chain (Wilson and Wolkovitch 2011), while necrophagous arthropods that are prey to many species assimilate carrion nutrients into relatively lower trophic levels (Beasley et al. 2015, Benbow et al. 2019).

Further, dependence on carrion by vertebrates or invertebrates is expected to vary by season. Vertebrate foraging of carrion tends to increase during cooler seasons (DeVault et al. 2011, Beasley et al. 2015) due to several factors, including overwintering by raptors and vultures (Maransky et al. 1997) or decreased prevalence of primary food sources leading to consuming less optimal resources (Sidorovich et al. 2006, Needham et al. 2014, Contesse et al. 2004). Meanwhile, necrophagous invertebrates rely on carrion resources

from wild populations year-round if abiotic factors, such as temperature, are adequate for activity to take place (Tomberlin and Adler 1998). Carrion taxa can also influence the vertebrate (Turner et al. 2017) or invertebrate (Kneidel 1984) community consuming it. For example, carrion of top predators will not be consumed by other carnivores that commonly scavenge ungulate carrion opportunistically (Moleón et al. 2017). Although differences in rates of scavenging among species have been noted, few studies have investigated how certain aspects of the individual animal, drive variability in rates of use. More specifically, it has been postulated that coat color may influence the persistence of remains within the environment (Turner et al. 2017), or influence decomposition rate (Brown and Peckmann 2013), however no study has empirically studied coat colors impact on carrion fate to date. Further, the habitat in which carrion is located plays a major role in the scavenger community available to consume carrion, where fields and grasslands are predominantly comprised of avian scavengers and mammals are the predominant scavengers in forests (DeVault et al. 2003, Turner et al. 2017, Beasley et al. 2015). How the combination of these factors impact scavenging rates by vertebrates, invertebrates, or their interactions remains unknown.

An additional factor not taken into consideration with regards to interactions between native vertebrates or invertebrates competing for carrion is potential interference from invasive species, such as the red imported fire ant [*Solenopsis invicta* (Buren) (Hymenoptera: Formicidae)] that also consumes a variety of resources, including carrion and carrion colonizers (Vinson 1991). Fire ants are a well-documented globally invasive species, with established invasive populations in eight countries, including the United

States. These ants perform well in highly disturbed habitats, such as human mediated landscapes (Linksvayer and Janssen 2009, Tschinkel 2006). Fire ants can reduce ant species diversity by up to 70% in these environments (Porter and Savignano 1990) and can have similarly strong effects on the diversity of other arthropod species via competition and predation (Porter and Savignano 1990, Vinson 1991). While there has been some research addressing the impact of fire ants on arthropods at carrion, there are many gaps in knowledge. In fact, fire ant presence influence on scavenging of carrion by other taxa, such as vertebrates has not yet been quantified (Wells and Greenberg 1994, Eubanks et al. 2019).

We hypothesize that the hyperabundance of several vertebrate scavengers (such as mesocarnivores (i.e. racoons, and opossums)) in human mediated landscapes will outcompete key necrophagous arthropods (i.e., blow flies) for carrion resources and impact their fecundity. Secondly, we investigated the impact of fire ants on blow fly reproduction on carrion remains not consumed by vertebrates. To date, there are no known studies that investigated the impact of vertebrate scavenging on primary invertebrate colonizer reproductive output (such as blow flies (Joseph et al. 2011)), and little research done on interactions between blow flies and fire ants at these resources (De Jong et al. 2021, Sawyer et al. 2020, Eubanks et al. 2019). To test this hypothesis, we measured carrion consumption of vertebrates and blow fly production across habitats within human mediated landscapes (old grass fields and wooded landscapes), season, carrion species, and carrion color. Secondly, data collected allowed for *a posteriori* examination of the impact of fire ants on blow fly populations.

Methods

Study Area

Two human-impacted study sites were used: Texas A&M University Field Laboratory (30.552278°N, 96.424519°W) and Coulter Airfield in Bryan, TX (30.7161°N, 96.3330°W). Both sites are in the East Central Texas Plains (Post Oak Savannah) Ecoregion (ArcGIS.com, Audubon Texas). The Texas A&M Field Laboratory is an agricultural landscape with several grassy and wooded habitats interspersed with agricultural fields. The old grass field was regularly mowed between trials as part of typical maintenance not related to this study. Trials did not take place during harvests (of corn) or lawn treatment periods to prevent direct human activity from impacting scavenging. Vertebrate animal sightings and animal tracks verified that vertebrate animals were located within this landscape.

Coulter Airfield is a public airfield with one air strip. It is flanked by US Highway 190 and comprises largely clear-cut grassy areas, with two wooded habitat patches on the property. Grassy habitat used was a maintained old grass field and was regularly mowed between trials. Wooded habitats comprised largely of floodplain hardwood forest. The property was verified to have vertebrate animal activity within the property prior to the study via Infrared Trail Cameras (Moultrie® M-990i; Birmingham, Alabama) collecting imagery of wildlife the several months preceding the experiment.

Field Set-Up

Carrion type consisted of either a white rat (*Rattus norvegicus*) (175-275 g), brown/black rat (*Rattus norvegicus*) (175-275 g), or yellow chick (*Gullus gullus*

domesticus) (45 g) carrion, all frozen prior to use. Carrion was allowed to thaw indoors at 22°C for two hours prior to deployment in the field. White rats were purchased from RodentPro.com® (Inglefield, Indiana), brown/black rats were purchased from Big Apple Pet Supply Inc. (Delray Beach, Florida), and chicks were donated by the Texas A&M Poultry Science Department (College Station, Texas). All live animals were euthanized via CO₂ fixation for purposes other than this study (such as food for raptors and reptiles); thus, no Institutional Animal Care and Use Committee approval was required. We placed four technical replicates of each carrion type (white rat, brown rat, and yellow chick) in each habitat (old grass field and wooded habitat) for a total of 12 carrion per habitat, and 24 carrion per human-impacted site. Since each habitat had limitations to where carrion could be placed due to land use by the property owners, each site was scouted prior to the study to determine where carrion could be placed to avoid direct vicinity of human activity within each habitat and site (i.e. walking or driving paths). Carcasses were at minimum 50 m apart as done in Perez et al. (2016) to limit the possibility of a singular foraging event by invertebrate scavengers and to maintain distinct replicates, and consistent with vertebrate research such as Turner et al. (2017). However, carrion in this study were placed simultaneously, unlike Turner et al. (2017). Carcass type was randomly assigned at each predetermined location. Twelve Infrared Trail Cameras (Moultrie® M-990i; Birmingham, Alabama) set to motion detection were randomly assigned to one of each carcass type per habitat to identify vertebrate scavengers that may be removing the carrion at a subset of

locations, similarly done in DeVault et al. (2004). We paired a Thermochron DS1922T-F5 iButton® (Sydney, Australia) data logger alongside one camera per habitat to measure and record abiotic conditions during trials. Data loggers were shaded and recorded temperature and relative humidity hourly. We conducted two trials (defined as when carrion is placed to when they were removed from the environment) during summer (July and August) and one trial in the winter (December) in 2018. Trials were replicated again in 2019 for a total of six trials (four in the summer, two in the winter).

Observation and Data Collection

We recorded carrion presence and insect colonization at dawn and dusk at each study site. We also noted if there was movement or partial scavenging of carrion. Accumulated Degree Days were calculated utilizing the National Oceanic and Atmospheric Administration (NOAA) database (via the Easterwood Airport (KCLL) station, College Station, Texas) through the duration of the experiment, to ensure carrion were collected from the field at the onset of the wandering third instar (taking place during active decay (Payne 1965)). The secondary screwworm (*Cochliomyia macellaria*) (Fabricius) (Diptera: Calliphoridae) development data (Boatright and Tomberlin 2010) were used to determine the onset of the feeding third instar in the summer months, and the black blow fly (*Phormia regina*) (Meigen) (Diptera: Calliphoridae) development data (Nunez-Vazquez et al. 2013) in the winter. Using these datasets, carrion was collected on the third day in the summer months, and 63 days in the winter, however carrion did not persist in the environment during winter months past eight days after placement. Data

loggers were placed in the field and utilized at the conclusion of the study to verify estimated Accumulated Degree Hours (Michaud and Moreau 2010) via NOAA weather data. At the conclusion of the field study, carrion remnants were placed in 35.6 cm x 20.3 cm x 12.4 cm plastic Sterilite® (Townsend, Massachusetts) containers and brought back to the lab. Container contents consisted of 4 cm vermiculite on the bottom and two windows (12.5 cm x 5 cm each) on each long side of the container that was covered with Kimberly-Clark Wypall® (Irving, Texas) cloth for ventilation and covered with Glad® (Oakland, California) Press N' Seal® to ensure no insects could get in or out. Containers were placed in an incubator at 25°C and 70% humidity to rear out flies that colonized each carcass. Once all flies completed their life cycle and died, flies were identified to the lowest taxonomic resolution possible using the Whitworth (2006) dichotomous key. During the first summer trial, it was clear that red imported fire ants, altered the ability for blow flies to colonize carrion within our study system. For this reason, fire ants were recorded as present/absent, as well as if there was zero colonization or scavenging by blow flies or vertebrate scavengers every trial.

Vertebrate scavengers were identified via images from field cameras. Carcasses were determined to be removed by a vertebrate if they were not located within ~50 m of their deployment location, regardless of if an animal was captured on camera. If the carcass was removed, and the vertebrate was not detected or not identifiable in the photo to be removing the carcass, the species was deemed “Unknown” but the carcass was still documented to be scavenged by a vertebrate animal.

Statistical Analysis

General Linear Models (GLMs) were utilized to determine which factors contributed most to carrion fate (consumption by vertebrate or invertebrate animals). The set of predictors included the number of carcasses removed by the end of the study as a dependent variable, with season (Summer and Winter), carcass type (white rat, brown rat, and yellow chick), and carcass fate (consumption by vertebrate scavengers, blow flies, or fire ants) as independent factors. Preliminary statistical analyses determined that site, and month (July and August) were not significant factors ($P > 0.05$) and therefore not included in the final model described above. We then created two additional GLMs to determine if the independent factors: habitat, carcass type, and fire ant presence (binomial) or their interactions influenced the abundance of blow flies on carrion. Preliminary review of the data's distribution led us to use a Gaussian distribution for all GLMs tested. Alpha for all statistical tests was set to 0.05 for significance. R version 3.5.1, "Feather Spray" (R Team 2018) was used for all statistical analyses using the "lme4" package (Bates et al. 2015).

Results

General Linear Model (GLM) results indicate carrion fate (average number of carcasses consumed by vertebrates, flies, or fire ants exclusively) was significantly influenced by an interaction between habitat and season ($P = 0.002$), with no significant results for other factors or interactions described in the methods above. Vertebrate scavengers consumed 100% of carrion in the winter across both habitats (Fig. 3.1A), consuming a higher percentage of carrion than in summer ($P < 0.001$). In the summer, vertebrate scavengers consumed 1.8x more carrion in wooded areas than grass fields ($P = 0.001$) (Fig. 3.1A). Of carcasses that were scavenged and had trail cameras, 68%

successfully captured the vertebrate that consumed the remains. Vertebrate scavengers encompassed seven species. The most notable scavengers included turkey vulture (*Cathartes aura*) and red-tailed hawk (*Buteo jamaicensis*) in grass fields (50% and 30% of observed scavenging, respectively) and Virginia opossum (*Didelphis virginiana*) in wooded habitats (50% of observed) in the winter months. However, this differed during the summer where the turkey vulture was the dominant scavenger (83%) in grass fields, while the opossum and raccoon (*Procyon lotor*) were the prominent scavengers (55% and 27%, respectively) in wooded habitats (Table 3.1).

Table 3.1: Species of vertebrates observed on trail cameras consuming carrion in Snook and Bryan, TX. Asterisk indicates that the species was the most documented species. If two species are indicated, both were dominant scavengers of the indicated habitat and season.

Season	Open Habitat	Wooded Habitat
Summer	Turkey Vulture (<i>Cathartes aura</i>)* Skunk (<i>Mephitis mephitis</i>)	Opossum (<i>Didelphis virginiana</i>)* Raccoon (<i>Procyon lotor</i>)* Coyote (<i>Canis latrans</i>) Turkey Vulture (<i>Cathartes aura</i>) Timber Rattle Snake (<i>Crotalus horridus</i>) [†]
Winter	Turkey Vulture (<i>Cathartes aura</i>)* Red Tailed Hawk (<i>Buteo jamaicensis</i>)* Grey Fox (<i>Urocyon cinereoargenteus</i>) Opossum (<i>Didelphis virginiana</i>)	Opossum (<i>Didelphis virginiana</i>)* Grey Fox (<i>Urocyon cinereoargenteus</i>) Skunk (<i>Mephitis mephitis</i>) Coyote (<i>Canis latrans</i>) Raccoon (<i>Procyon lotor</i>)

[†] Seen scavenging in person and documented using an Apple Inc. (Cupertino, California) iPhone® camera.

Flies colonized significantly more carrion in summer than they did in winter in wooded ($P < 0.001$) and open ($P = 0.018$) habitats, as zero flies colonizing remains in the winter in either habitat (Fig. 3.1 B). Additionally, in the summer months, there was

no significant difference in fly colonization of carrion in open or wooded habitats ($P = 0.868$) (Fig. 3.1B). While carcass type was not a significant factor for any scavenger group in this study, blow flies were only found in rodent remains in field habitats and approached significance ($P = 0.057$).

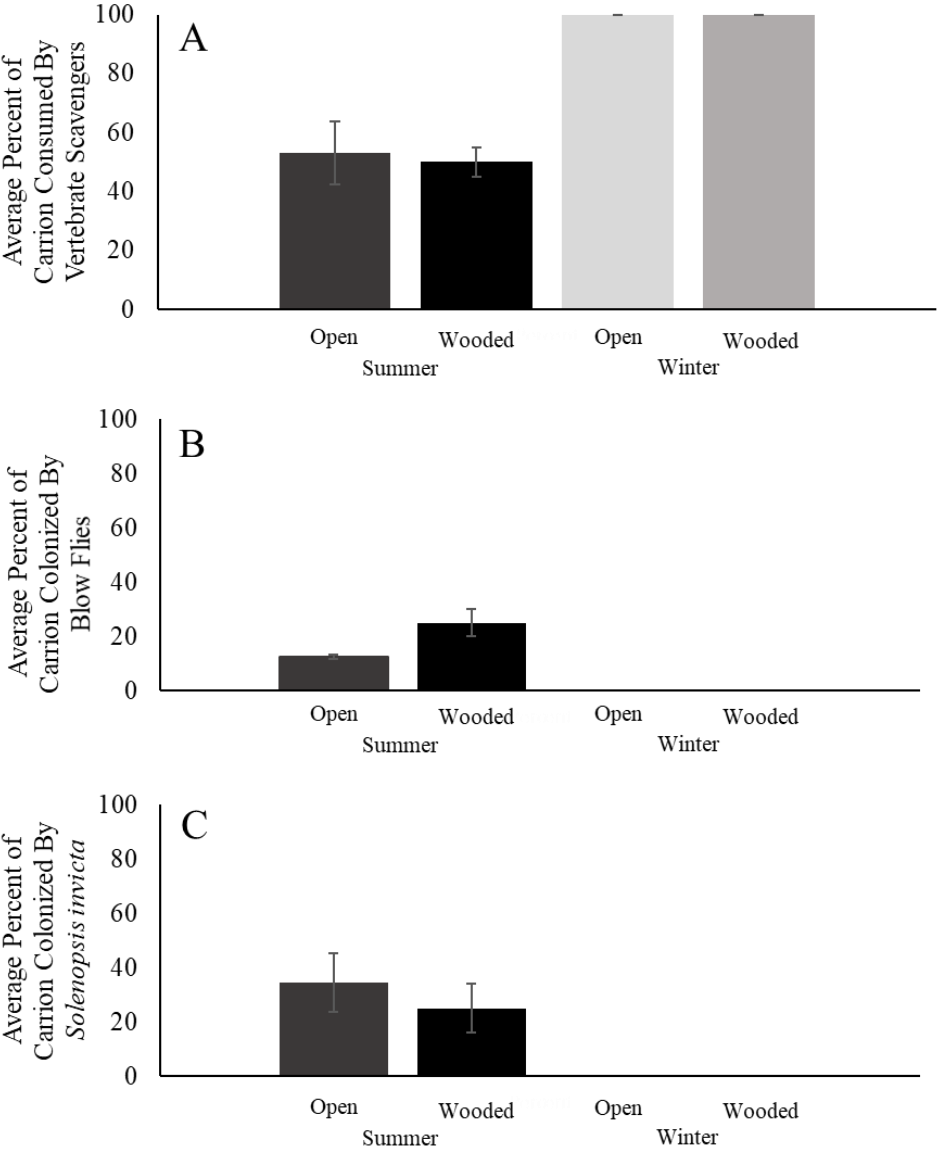


Fig. 3.1 Percent of carrion successfully utilized by (A) Vertebrate animals (B) Blow Flies (Diptera: Calliphoridae), and (C) Fire ants (*Solenopsis invicta*). Vertebrate animals (\pm standard error) across open and wooded habitats during summer and winter near College Station, TX.

Blow fly species present in the current study that successfully reached adulthood were *Lucilia eximia* (Wiedemann) and *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae), with *L. eximia* being the predominant blow fly on all carrion with blow fly activity. Fire ant presence was the only significant factor in determining blow fly production on carrion ($P = 0.005$), whereas habitat ($P = 0.171$) and carcass type ($P = 0.502$), and interactions between these factors had no significant impact ($P > 0.05$). Carrion scavenged by vertebrates (100% during winter, 62% during summer) produced no blow flies. For the carrion not scavenged by vertebrates, and in the absence of fire ants, 1,059 blow fly adults were produced per carcass on average (Fig. 3.2). When fire ants colonized carrion, an average of 278 blow flies, which represents a 71% reduction in blow fly production. It should be noted that carcasses where fire ants successfully excluded blow flies were not included in this model. However, up to 40% of all carrion in grass fields and 9-25% in wooded habitats during the summer (Fig. 3.1C) and no carrion in the winter were colonized by fire ants. Additionally, field observations revealed that 25-45% of carrion consumed by vertebrates had fire ant presence prior to consumption. Due to the experimental design, it is not possible to discern if fire ants are influencing consumption by vertebrates or not.

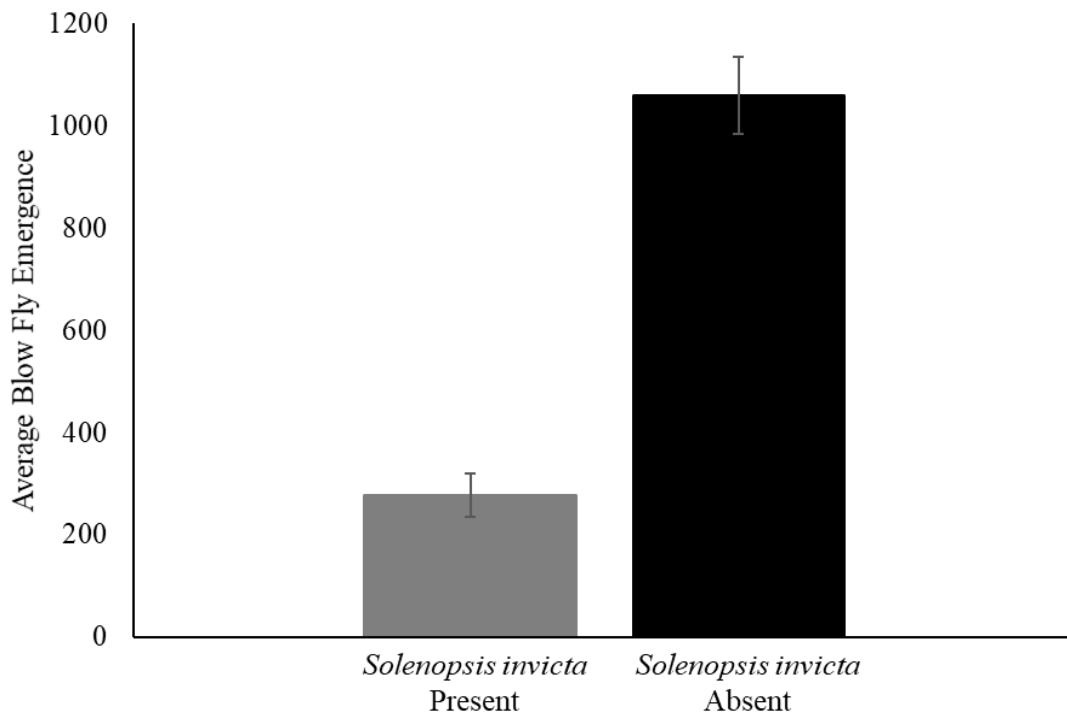


Fig. 3.2 Mean number of blow fly (Diptera: Calliphoridae) emerging per carcass with and without *Solenopsis invicta* presence (\pm standard error) near College Station, TX.

Discussion

Vertebrate scavengers outcompeted arthropods for carrion resources in both summer and winter of this study, significantly reducing the fecundity of female blow flies utilizing small carrion in human mediated areas regardless of habitat type. It is well established that species richness of wildlife decreases, and abundance of only a few species increases with human land use (Shochat et al. 2010). Vertebrate scavengers are not immune to human influence on population dynamics as urbanization is a major predictor of scavenger community composition, though slight seasonal variation in species richness and scavenging rate has been documented in previous studies (Sebastián-

González et al. 2019). The hyperabundance of scavengers limited overall production of blow flies in this study, overwintering of scavengers acted synergistically, leaving no carrion for insect colonization.

Decreased species richness does not necessarily reflect a corresponding reduction in scavenging rates of carrion by vertebrate animals. In fact, vertebrate scavengers were highly efficient in our study system, potentially reflecting the hyperabundance of these select species (DeVault et al. 2011). All carrion was consumed by vertebrates within eight days during the winter, contributing to the lack of blow fly production during any winter trial. During the summer, 62% of the carrion was scavenged by vertebrates before blow fly larvae fully developed. This increased prevalence of scavenging is likely the cause of the predation paradox, where despite hyperabundance of predators in human mediated landscapes, levels of predation are low due to animals relying on subsidiaries including carrion (Shochat et al. 2004. Shochat et al. 2010). For this reason, species richness may not be a good predictor of carrion fate in human-impacted landscapes, but the degree to which humans are altering the landscape may provide useful information for animal foraging behavior and their ecological role within these human-impacted systems (as seen in eusocial animals such as ants (Dáttilo et al. 2021)).

Landscape perturbations can lead to spatial niche partitioning resulting in coexistence of highly abundant species consuming similar resources (e.g., carrion) that would otherwise see local population declines due to competition pressures (Schochat et al. 2010), much like what was observed in this study. In wooded patches and open fields in this study, there was distinct niche partitioning based on habitat. For example, mammals

were the dominant scavengers in wooded habitats and avian scavengers in the open fields (with only one occurrence of vulture scavenging documented in wooded habitats) permitting co-existence. This impact has been observed in other studies, which despite having high dietary overlap, fragmented landscapes allowed for species coexistence to occur between native peccaries (Tayassuidae), and invasive wild pigs (*Sus scofra*) (Desbiez et al. 2009). Similar habitat specific differences in scavenging seen in this study were also documented in Turner et al. (2017), suggesting niche partitioning may be facilitated by differences in foraging behavior among avian and mammalian scavengers. In the current study, the turkey vulture was the dominant scavenger in grass fields. Turkey vultures are obligate scavengers that can seek out small carrion resources with high efficiency, even in forested habitats (Byrne et al. 2019). The lack of mammal scavenging in grass fields as observed in the current study could be due to relatively greater risk from predation (Fahrig 2007) or competition with more efficient, obligate scavengers (such as the turkey vulture). Inversely, mesocarnivores, such as the raccoon and opossum, were the primary scavengers in wooded habitats. This result is not surprising given these species are abundant and highly efficient scavengers along forest-agriculture interfaces (DeVault et al. 2011, Beasley et al. 2011). Thus, a variety of avian and mammalian scavengers can coexist within heterogeneous anthropogenic landscapes supporting differences in foraging behaviors among these groups of vertebrate scavengers, causing more competition pressures on blow flies.

Carrion species and associated coat color were not significant factors in the current study. Carrion type has been suggested by some studies to have an influence on scavenging

vertebrate rate of consumption, albeit these studies attribute this impact to be due to the carrion biomass, not the difference in species (Olson et al. 2016, Muñoz-Lozano et al. 2019, Turner et al. 2017, Abernethy et al. 2016). Other studies have demonstrated that different carrion species of similar size class (>0.5 kg) (i.e., chickens and quails) impact the rate of scavenging where different carrion species were removed faster than others (Smith et al. 2017). In addition, particular carrion species were consumed by scavengers that were highly associated (through predator-prey relationships) with the species used as carrion (Smith et al. 2017). In the current study, carrion species used are not from wild populations, potentially hindering the statistical relevance of carrion species and color. Despite the potential for scavengers not consuming carrion due to neophobia (Stöwe et al. 2006), scavenging rates were similar to those found in other studies other studies in human-impacted landscapes (Such as DeVault et al. 2011).

Overall scavenging was greater during the winter across habitats despite only grass fields experiencing an increase of species richness of vertebrate scavengers, as seen in other studies (DeVault et al. 2011, Pereira et al. 2014). While cooler temperatures reduce competition with microbial communities (DeVault et al 2004, DeVault et al. 2011, Farwig et al. 2014, Ray et al. 2014), increased species richness and scavenging rates may also be due to overwintering vultures and hawks, and depletion of primary food sources leading to increased reliance on carrion (DeVault et al. 2011, Pereira et al. 2013). Winter months tend to have an increased species richness of scavengers, despite impacts of urbanization (Sebastián-González et al. 2019), suggesting that foraging behavior of scavengers differ between seasons and include larger foraging ranges during winter. The opossum for

example was only documented scavenging in wooded habitats during the summer but in both wooded and grass fields during winter in this study. Opossum scavenging in grass fields is unusual, as they are documented to favor wooded areas and grassland-forest interfaces (Allen et al. 1985, Dijak and Thompson 2000, Magle et al. 2016). Shifts in habitat preference may be due to seasonal declines in preferred food sources, such as agricultural crops (Lay 1942, Borchert et al. 2008), and decreased competition with microbes and invertebrates due to lower temperatures (Beasley et al. 2015), consequently increasing frequency of facultative scavenging (Pereira et al. 2013). It may also be that since these habitats are highly fragmented as characteristic of many agricultural and human utilized landscapes, grass fields are relatively smaller, allowing for foraging by animals like the Virginia opossum to persist across these landscapes (Beatty et al. 2014). Seasonal reliance on carrion has been shown to occur for other species, such as the red fox (*Vulpes vulpes*) (Needham et al. 2014). Seasonal facultative scavenging was documented with the grey fox (*Urocyon cinereoargenteus*) and was only seen scavenging in the winter across both habitats of this study.

Seasonality can impact species richness of communities as well. Bird species richness is expected to increase during the winter in human landscapes (Caula et al. 2008), this was evident in the current study, but driven primarily by migration patterns of raptors such as hawks and vultures (Kerlinger and Gauthreaux 1985) where in grass fields the red-tailed hawk (*Buteo jamaicensis*), a documented scavenger (Slabe et al. 2020) was prominent in addition to the turkey vulture. A decrease in nutritional quality in the landscape during the winter season (naturally, or artificially via agriculture), increased

competition among vertebrates and decreased competition with microbes and invertebrates for the resources that are present (Pereira et al. 2013), and may be causing ephemeral resources such as carrion to be more appealing to facultative scavengers at the time of discovery (DeVault et al. 2011).

One could argue that a combination of the factors related to habitat fragmentation above subsequently impacted the ability for blow flies to utilize carrion resources, and ultimately inhibited the productivity of blow flies from small carrion resources. With increased vertebrate scavenger rates across seasons, blow flies had fewer carrion resources to utilize for reproduction in human-impacted areas. Introduction of the red imported fire ant has increased competition and predation pressures on other arthropods reliant on carrion resources (Eubanks et al. 2019) causing significant declines in diversity of arthropods on carrion (Vinson 1991) and up to 70% decrease in arthropod diversity within environments (Porter and Savignano 1990). Low arthropod diversity was also seen in the current study, and the survivorship of blow flies to adulthood at these small resources decreased nine-fold with fire ant presence. The reduction in blow fly prevalence could have profound impacts on ecosystem function and could drive fundamental differences between human-impacted and natural landscapes.

Conclusions

Our findings reveal that vertebrate scavenging was high in human-impacted landscapes, leaving little carrion for necrophagous arthropods. Increased scavenging in these systems is driven by a hyperabundance of scavenging species and facilitated by mosaic landscapes that foster both avian and mammalian scavengers that seasonally

increase consumption of carrion resources. Furthermore, invasive species such as the red imported fire ant reduce blow fly ability to utilize resources not consumed by vertebrates. This fundamental shift in carrion consumption can have profound ecosystem impacts that have not yet been investigated. Future research should investigate necrophagous arthropods (such as blow flies) population dynamics and resource preferences in human-impacted areas, in addition to the potential consequences to nutrient recycling of carrion.

Table 3.2. Maximum, minimum, and average temperatures recorded through data loggers during winter of 2018 and 2019 near College Station, TX with average calculated Accumulated Degree Hours and raw hours to compare insect development.

Winter Trial 1	2018			Trial 2			2019		Overall	Avg	Raw
Day	Max Temp °C	Min Temp °C	Avg Temp °C	Max Temp °C	Min Temp °C	Avg Temp °C	Max Temp °C	Avg Temp °C	Accumulated Degree Hours	Hours	
1	16.67	1.11	8.89	22.78	8.89	15.83		12.36	56.67	24	
2	18.89	10.00	14.45	24.44	11.67	18.05		16.25	206.67	48	
3	22.78	6.67	14.72	17.78	8.89	13.33		14.027	303.33	72	
4	9.44	4.44	6.94	18.89	9.44	14.16		10.55	316.67	96	
5	15.56	8.33	11.94	24.44	16.67	20.55		16.25	466.67	120	
6	17.78	7.22	12.5	-	-	-		12.50	526.67	144	
7	17.22	5.56	11.38	-	-	-		11.38	560.00	168	
8	18.89	10.56	14.72	-	-	-		14.72	673.33	192	
		Average	11.94		Average	16.38		13.51			

Table 3.3. Maximum, minimum, and average temperatures recorded through data loggers during summer of 2018 and 2019 near College Station, TX with average calculated Accumulated Degree Hours and raw hours to compare insect

Day	Trial 1 2018			Trial 2 2018			Trial 3 2019			Trial 4 2019			Overall		Raw Hours
	Max Temp °C	Min Temp °C	Avg Temp °C	Max Temp °C	Min Temp °C	Avg Temp °C	Max Temp °C	Min Temp °C	Avg Temp °C	Max Temp °C	Min Temp °C	Avg Temp °C	Avg Temp °C	Avg Degree Hours	
1	36.11	23.89	30.00	36.11	23.33	29.72	35.56	24.44	30.00	37.78	26.67	32.22	30.47	491.67	24
2	36.67	24.44	30.56	37.22	24.44	30.83	35.56	25.00	30.28	37.78	26.67	32.22	30.97	995.00	48
3	37.78	24.44	31.11	38.33	24.44	31.39	35.56	23.89	29.72	36.67	25.56	31.11	30.83	1495.00	72
	Average 30.55			Average 30.65			Average 30			Average 31.85			30.76		

CHAPTER IV

CONCLUSION

The purpose of my dissertation was to investigate the role vertebrate scavengers play in the ecological structure, function, and productivity of arthropods at carrion of varying biomass. Furthermore, investigation into how abiotic factors such as season and habitat influence this competition was conducted. With this purpose in mind, two major studies were conducted and were successful in addressing this largely understudied area of research.

In chapter two, pig carrion (*Sus scofra*) was used to generate five mortality events with increasing biomass, each biomass was replicated with that second biomass having vertebrate exclusion netting. In sampling the arthropods, it was discovered that both biomass and fencing had interactive effects on the abundance of arthropods, family richness, and the diversity of arthropods using the Shannon Diversity Index. Abundance of arthropods was greatest at 181 kg of pig biomass, where scavenger access decreased this abundance when compared to exclusion sites. When biomasses were greater than 181 kg, there was decreased arthropod abundance, but also a large disparity between abundances in scavenger accessible and exclusion sites, where vertebrate access increased the abundance of arthropods significantly. Family richness across all sites were initially different, however they became insignificant during pig decomposition and differed later in the study. Specifically, the 181 kg biomass with scavenger access was insignificantly different than that of 363 kg biomass without scavenger access, both of which had the greatest species richness when compared to the other sites. Both 363 kg and 725 kg biomasses with scavenger access saw one of the lowest species richness scores, with only the 25 kg biomass (regardless of access) and the 60 kg biomass with scavenger access being lower. The only plots that had lower species richness than prior to pig placement was the 25 kg biomasses, regardless of scavenger access and 60 kg biomass with scavenger access, suggesting carrion in this system is supporting a

variety of arthropods in this location. Family diversity increased after pig placement regardless of fencing or biomass. Additionally, while functional richness was the same over time across all treatments, functional diversity was influenced by time and biomass independently. Since Shannon Diversity accounts for both richness and evenness, it is clear that the decline in diversity after pig placement is due to functional unevenness where larger biomasses saw the greatest declines in diversity before approaching pre-pig levels. This is not surprising, as necrophagous arthropods are expected to be in the highest abundance around the carrion, saturating the community temporarily, before dispersing back to the surrounding environment.

Increased carrion biomasses can have profound effects on ecosystem functioning. Necrophagous flies such as blow flies (Diptera: Calliphoridae), are a food source for many predators, such as spiders. With an increase of blow flies from large carrion biomasses, an expected increase in predatory populations is likely to follow. With a large increase in insects, the largest being necrophagous flies, there is a likelihood that ecosystem services such as pollination will increase temporarily as well. One study found that 80% of pollinators collected were necrophagous flies (Cusser et al. 2020), and increases in pollinator populations can increase pollination events, leading to greater crop yields (Faulkner 1962). The large increase in insect abundance is not limited to the carrion location, as some species of necrophagous flies can fly upwards of 3,500 m/day (Tsuda et al. 2009), thus can have large impacts on the immediately surrounding ecosystem.

There are some notable limitations in the study described in Chapter 2. Primarily, there is limitation on the number of carrion available, therefore treatments were not replicated. This was resolved through choosing a General Linear Model (GLM) and having time as a random factor. In addition, there were sticky traps that were lost or damaged in transit (via being crushed, or heat causing glue to mix across sticky traps). The resolution to this was to use a “per effort” method,

where the number of sticky traps in each treatment were accounted for. This adjustment prevents metrics such as abundance to be greater at one site simply because there were more sticky traps for example. Finally, arthropods were only collected directly at the carrion site, leaving overall ecosystem effects to be largely speculative. Future research should consider modifying storage and shipping methods of sticky traps to lessen the risk of trap loss. Additionally, future researchers should collect arthropods from areas further away from the carrion site to better understand larger ecosystem effects, as done in Cusser et al. (2021).

Scavengers have been shown to have influences on arthropod communities as described above, though the direct competition between these groups was alleviated with biomass, thus research in to small carrion was warranted. To investigate the competition between necrophagous insects and vertebrate scavengers of small carrion biomasses, a study was conducted using rat (*Rattus norvegicus*) and chick (*Gallus gallus domesticus*) carrion in grass field and wooded habitats across summer and winter. The most notable findings of this research were that in the winter, there was 100% scavenging by vertebrates in all habitats and in the multiple trials of this study. In the summer, there was a large amount of scavenging by vertebrates (69%) however, of the carrion that was left, the majority had fire ant activity, where only 25% of carrion had blow fly activity. In the instances with both fire ants and blow flies, blow fly production was decreased 9x that of the remains with blow flies alone. These findings show that blow flies are under a lot of competitive pressures for small carrion resources and unable to access many of them. Since this study was done in human impacted environments it warrants further investigation into blow fly dynamics in human landscapes.

Increased competition between vertebrate and invasive animals for carrion resources in human impacted landscapes can potentially have secondary effects on the ecosystem services of

blow flies. When carrion resources are removed faster than can be colonized by blow flies, there is a risk for population declines. Population declines can negatively impact the pollination services blow flies provide as explained above. Alternatively, blow fly populations are seeking sub-optimal food resources, such as living organisms through myiasis, or food waste and animal excrement. In fact, the dominant blow fly in this study (*Lucilia eximia*) is well known for colonizing such resources (Guimarães et al. 1982, Madeira et al. 1989). Elimination of carrion oviposition sites via competition can lead to high concentrations of blow flies in urban landscapes where alternative resources are abundant, increasing human-blow fly interactions. These human-blow fly interactions can lead to human myiasis when open wounds are neglected (Hall and Wall 1995), or pathogen transmission (Pace et al. 2016). Because the objective of this study does not directly look at blow fly population dynamics in human landscapes, but rather, focuses on carrion oviposition; it cannot be determined if blow flies are in fact seeking out alternative oviposition resources, and/or if populations have declined. Therefore, future research should increase focus on the population dynamics within these human landscapes as done in Patitucci et al. (2011), and Dufek et al. (2021).

While this research has significant findings that increase our knowledge in competition between vertebrate and invertebrate animals, limitations in this research should be addressed to fill further gaps in our knowledge. Most importantly, while much of the wildlife research in human impacted areas are done in urbanized landscapes, this study was conducted exclusively in non-urban highly disturbed human areas (agricultural and airfield). To know conclusively if increasing human activity (i.e., urban infrastructure) increases vertebrate abundance and subsequently intensifies competition, this research should be done in untouched human landscapes to compare to human mediated (i.e., agricultural) and urbanized landscapes. Further improvements can include sampling of scavenger populations prior to placement of remains to better understand the local

wildlife who could utilize these resources. Finally, since invasive species were not included in the original design of this research, there is a limitation in replication on how fire ants impact blow fly production. While this data did show statistically significant findings, more robust datasets can make the conclusion that fire ant presence disrupts blow fly productivity. This is a fertile ground for research as many have posed questions surrounding antipredator defenses in blow flies (Sawyer et al. 2021) and coexistence on large animal remains facilitated by fire ants feeding on carrion (Meyer et al. 2020). Future research should look at competition and resources partitioning between blow flies and fire ants similar to the work done in Denno and Cathran (1975).

As this work pertains to carrion systems, there are clear implications on how this research helps us better understand forensic entomology, in both the medicolegal and urban subfields. Naturally, chapter two provides insight in what to expect during mass casualties as far as proliferation of forensically important insects and their expected diversity. Secondarily, in both chapters two and three, we have a better understanding on the production of blow flies in these two scenarios. In cases where a secondary mortality occurs near a mass mortality, the elapsed time between when an individual dies and is colonized by blow flies is smaller than may be anticipated with a lower density of necrophagous flies in the area. In cases where blow fly populations are expected to be lower due to environmental conditions or competition, the pre-colonization interval is expected to be longer (Tomberlin et al. 2011), decreasing the accuracy of colonization estimations conducted by Forensic Entomologists (Morh and Tomberlin 2014). From the urban entomology perspective, this research can provide insight to how livestock owners manage carcasses to prevent blow flies from surpassing a threshold generally accepted by the Right to Farm Act (Centner 2006), it may also pave the way to adjusting guidelines for farmers to continue to follow best practices without unnecessary nuisance to surrounding residence.

Carrion management has large implications on ecosystem health and is important in mitigating disease spread (Vicente and VerCauteren 2019). Globally, government regulations of carcass management have been established for this purpose as it pertains to livestock (Donazar et al. 2009, Lagos and Barcena 2015, Vincente and VerCauteren 2019), where in some locations remains are not allowed to decompose openly due to fears of scavengers (vertebrate and invertebrate alike) from spreading diseases and increasing risk of zoonotic transfer (Carrasco-Garcia et al. 2018, Moleon et al. 2014). In cases where mass die offs require the use of “boneyards” where remains are allowed to decompose in relatively close proximity, there is a need for understanding the risks to the surrounding environment (Wilson et al. 2006). For example, in Pine Key Florida, the use of bone yards for key deer (*Odocoileus virginianus clavium*) allowed for the new world screw worm (*Cochliomyia hominivorax* (Corquerel) (Diptera: Calliphoridae)) (a blow fly species that colonizes living animals in a phenomenon called myiasis (Hall and Wall 1995)) to finish development on these remains, mate and spread to the surrounding environment to reproduce (Skoda et al. 2018). There is also concern for necrophagous flies to transmit pathogens to surrounding vegetation, contaminating human and domestic animal food products (Pace et al. 2017). Anthrax for example is caused by the bacterial agent *Bacillus anthracis* and is readily spread mechanically by blow flies (Blackburn et al. 2014). With the increase in large mortality events in both frequency and magnitude (Fey et al. 2015), this research helps piece together the ecological impacts that follow in these systems.

The research done in this dissertation is the first of its kind to directly study the interaction between vertebrates and invertebrates for carrion, however, more questions have arisen from this research. There are many new paths for this research to take before we can fully understand this complex relationship. To truly understand the processes surrounding decomposition, we must look

at this process holistically, where historically these taxa have been looked at in a vacuum (Benbow et al. 2019). Hopefully, this research will lay the foundation for new interdisciplinary research where microbes, vertebrate, and invertebrate interactions are looked at in unison.

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