IMPACTS OF INVASIVE SPECIES ON ECOSYSTEM ENERGY TRANSFER ON THE BIG ISLAND OF HAWAI'I: ARE YOU REALLY GOING TO EAT THAT?

by

ERIN F. ABERNETHY

(Under the Direction of Olin E. Rhodes, Jr.)

ABSTRACT

Invasive species have negative ecological, economic, and health impacts globally, especially on island ecosystems, but their impacts on ecosystem processes, like scavenging, remain largely unknown. Determining the scavenging efficiency of invasives on the carcasses of invasives will reveal how this altered ecosystem process contributes to invasional meltdowns and/or food web stability and whether scavenging on and by invasive species exacerbates or alleviates the negative impacts of invasives. I quantified the use of invasive species carcasses, specifically reptiles, amphibians, mammals, and birds, by vertebrate scavengers on a highly invaded island ecosystem, the Big Island of Hawai'i. Invasive vertebrate species scavenged 16.0-82.5% of these carcasses, and the percentage of carcasses scavenged by vertebrates compared to other scavenger guilds differed relative to habitat and carcass type. My results provide insight on basic scavenging ecology and suggest that carcasses provide a valuable resource to invasive species that may contribute to invasional meltdown and/or stability.

INDEX WORDS: Amphibians, Birds, Camera trap, Carcass, Invasional meltdown, Invasive species, Mongoose, Rat, Reptiles, Scavenging, Stability

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DEDICATION

My thesis is dedicated to Mom, Dad, and Garrett. Throughout the entire process y’all have provided unwavering encouragement and patience. I am truly grateful to have such a wonderful and powerful support network. Thank you so much for your love and help. I can’t wait to see where we take the coming years! Y’all are the best!

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TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Scavenging is an important ecosystem service spanning several organismal kingdoms and involving various scavenger guilds, populated primarily by vertebrates, invertebrates, or decomposers. The proportion of nutrients acquired by each of these guilds and their relative importance to ecosystem functioning is highly variable. Recently the importance of the vertebrate scavenger guild and the prevalence of scavenging among vertebrate species have been recognized. When the percentage of carcasses scavenged by vertebrates is taken from the growing body of scavenging research and averaged, it reveals that 75% of experimentally placed carcasses are consumed by vertebrate scavengers (DeVault, Rhodes & Shivik 2003). Factors that influence this efficiency are thought to be temperature, moisture, habitat heterogeneity, scavenger density, and carcass size (DeVault & Rhodes 2002; DeVault, Brisbin & Rhodes 2004; Parmenter & MacMahon 2009; DeVault *et al.* 2011).

Recent camera trapping technology allows scientists to delve beyond scavenging efficiency into scavenger behavior, specifically preference. Photographs of scavengers at the carcass site allow us to make inferences about the choice that a scavenger makes once it finds carcasses. The choice to scavenge is thought to be influenced by the nutritional state, toxicity, and size of the carcass and the threat of predation at the carcass site (McKillup & McKillup 1994). This choice to scavenge an available carcass or not adds complexity to our understanding of vertebrate scavenging efficiency and preference.

Researchers are just now starting to realize the complicated decisions and strategies that are involved in vertebrate scavenging.

The degree to which scavenging strategies influence the energy budgets and population dynamics of scavengers likely depends on the availability of carcasses on the landscape. In the review by DeVault, Rhodes & Shivik (2003), it is suggested that in many environments mortality may result more frequently from causes other than predation, such as malnutrition, disease, exposure, parasites, and accidents, providing a significant number of animals to be scavenged by vertebrates. Also, in environments that lack large numbers of predators, prey species are more likely to die of natural causes (Tyler & Øritsland 1999; Oksanen & Oksanen 2000). Thus in environments with few predators there should theoretically be more carcasses to scavenge and a lower threat of predation to scavengers searching for and consuming carcasses. Scavenging efficiency could be higher in these environments and a scavenger could choose to consume carcasses more often, depending on the environmental and carcass conditions as well as on scavenger density.

The majority of scavenging studies have been conducted in intact, relatively natural landscapes within temperate regions (see DeVault, Rhodes & Shivik 2003 for a review). Exceptions to this are several studies in landscapes that have been heavily altered by agricultural practices (DeVault *et al.* 2011; Olson *et al.* 2012). Such altered landscapes are now representative of the vast majority of environments available worldwide. Understanding how carcass resources are utilized by scavengers in human-altered landscapes is crucial for understanding the ecosystem-wide implications of altered scavenging behavior and for mediating the negative ecological impacts of ecosystem modification, a task of global relevance. In addition to ecosystems that are physically altered by the presence of humans, invasive species represent a significant ecosystem perturbation introduced by humans. However, the impacts that invasive species have on ecosystem processes are largely unknown, and how communities of invasive species engage in scavenging behaviors has rarely been investigated (Wilson & Wolkovich 2011). Nonetheless, the potential for negative impacts on native ecosystems via scavenging of energetic resources by invasive species could be great given the recognized importance of scavengers in natural ecosystems and the general lack of predators in invaded ecosystems.

What is an invasive species exactly? In the scientific literature invasive species are defined through their movements, but in the policy context the definition is narrower. For a species to be considered invasive, humans must assist its movement to an area in which it is not native. The species must then establish a population and spread, establishing populations away from the area of initial introduction (Simberloff 2013). For policy makers and federal agencies the term invasive species applies only to those newly introduced species that cause or are likely to cause economic harm, harm to the health of humans, plants, or animals, or harm to the environment, as set forth in President Bill Clinton’s 1999 Executive Order 13112 (Beck *et al.* 2008). This narrows the definition of an invasive species to only those that cause harm, drawing attention to the human values infused in this term and consequently what has directed much of the scientific research. While there are many understudied groups, such as reptiles and amphibians, that have the potential to cause great harm, there are several groups, particularly mammals and birds, which are recognized as successful and highly detrimental invasive species.

The global economic, health, and ecological impacts of numerous invasive mammal and bird species have long been recognized (Pimentel, Zuniga & Morrison 2005). The impacts of these groups in Europe have recently been reviewed and categorized to identify those species with the most significant impacts and to call for preventive and control measures, including eradication, for such species (Kumschick and Nentwig 2010; Nentwig, Kuhnel & Bacher 2010). The following ecological and economic impacts of invasive mammals and birds were described: competition, predation, hybridization, transmission of disease, herbivory, agriculture, livestock, forestry, human health, and infrastructure. While the negative impacts of invasive mammals and birds are generally accepted to be globally widespread, with significant amounts of economic resource devoted to their control efforts, some scientists are concerned that calls for eradication of certain invasive species, particularly invasive birds in Europe, are unfounded due to the lack of empirical evidence quantifying their negative ecological and economic impacts (Strubbe, Shwartz & Chiron 2011). Clearly more experimental evidence is needed that explicitly quantifies the impacts of invasive mammal and bird species, especially their ecological impacts in imperiled ecosystems.

Negative impacts of reptiles and amphibians have been quantified for only a few invasive herpetofauna species, although many certainly have the potential to cause harm (Pimentel, Zuniga & Morrison 2005; Kraus 2008). Understanding these impacts is imperative for choosing invasive species to target for preventive and control measures to effectively conserve imperiled ecosystems, such as tropical islands (Glen *et al.* 2013). While estimates of the economic costs of invasive herpetofauna are not widely available, three species have become so destructive that many millions have been spent on their control: the brown tree snake (*Boiga irregularis*), coqui frog (*Eleutherodactylus coqui*), and cane toad (*Rhinella marina*). On Guam costs for brown tree snakes exceed $12 million/year in damages and control, coqui frogs on Hawai'i incurred >$4.2 million in control costs in 2007 alone, and in Australia more than $9.5 million is estimated to have been spent on controlling cane toads as of 2006 (Pimentel, Zuniga & Morrison 2005; Shine *et al.* 2006; Kraus 2008). With respect to health, there is evidence to suggest that some herpetofauna species can spread novel fungi, viruses, and parasites, as well as cause harm through the direct or indirect contact with toxins, to both wildlife and humans (Weldon *et al.* 2004; Jancovich *et al.* 2005; Fisher & Garner 2007; Skerratt *et al.* 2007; Kraus 2008). While the health risks associated with herpetofauna are poorly studied, current evidence suggests they have the potential to greatly impact human and animal health and may already be doing so unnoticed. As for ecological impacts, the following have been attributed to invasive herpetofauna: disruption of food webs through predation, poisoning of predators, resource competition, genetic contamination, and changes in inherited traits in native species (see Kraus 2008 for review). One of the most drastic examples of ecological harm by invasive herpetofauna has been on the island food web dynamics of Guam.

Brown tree snakes (*Boiga irregularis*) completely removed most native vertebrate species (i.e. birds, bats, and lizards) from forested areas within a matter of decades of being introduced to Guam (Rodda & Savidge 2007). This fundamentally changed the structure of food webs from native vertebrates that fed on plants and invertebrates to a food web in which all major components were invasive species that preyed on invasive species (Fritts & Rodda 1998). The synergistic effect of invasive species inadvertently assisting the success of other invasive species illustrates the invasional meltdown theory (Simberloff & Holle 1999).

The invasional meltdown theory posits that some invasive species may have a positive impact on other invasive species, accelerating the impacts of one or both parties through an increased probability of survival and/or increased population size (Simberloff & Holle 1999). Since the inception of this theory, studies have shown examples of one invasive species facilitating another, but few have been able to clearly demonstrate population and ecosystem-level impacts (Simberloff 2006, Simberloff 2011). Invasion ecology is starting to embrace scavenging ecology with a few studies examining the ability of invasive species to scavenge, the successful use of invasive carcasses by native species, and competition between native and invasive species for carcass resources (Gangoso *et al.* 2006; McNatty, Abbott & Lester 2009; Beckmann & Shine 2011). By examining scavenging both on and by invasive species, scientists combine theoretical invasion and scavenging ecology to explore the importance of carcass resources in creating invasional meltdowns and/or stability within invasive species populations and invaded ecosystems.

It would be most valuable to conservationists and ecologists to conduct research exploring scavenging on and by invasive species in ecosystems widely considered imperiled as a result of invasive species. Globally, islands are considered to be one of the ecosystems at greatest risk from invasive species, and many islands already have large numbers of established invasive species, thus providing an optimal ecosystem type in which to examine these topics. Invasive species on the islands of Hawai’i, which include herpetofauna, mammals, and birds, are considered the top threat to native species, with

Hawai’i leading the USA in number of extinctions and federally endangered species (Dodson *et al.* 1997; Cox 1999). The island also largely lacks native predators for invasive species, likely leaving an abundance of invasive carcasses to be scavenged by invasive species.

My study seeks to develop an understanding of the utilization of invasive reptile, amphibian, mammal, and bird carcasses within the food webs of imperiled tropical island ecosystems, so that further conclusions can be drawn about the role that carcasses and scavenging play in the invasional meltdown process and/or stability. In Chapter 2, I present data on how efficiently invasive herpetofauna (coqui frogs, geckos, and cane toads) were utilized within and among the scavenger guilds on the Big Island of Hawai’i and vertebrate preference for each carcass type. In Chapter 3, I present data quantifying the efficiency and preference of scavenger guilds that utilize invasive mice, rats, birds, and mongoose carcasses on the Big Island of Hawai’i. To accomplish this research, I experimentally placed camera traps baited with carcasses in three distinct habitats on the Big Island of Hawai’i and recorded the vertebrate species that interacted with each carcass, each type of interaction (removed, partially consumed, touched, investigated but not touched, investigated area after carcasses removed, or passed without interaction with carcass or area), and the time that it occurred. My objectives were to:

1) Describe the vertebrate scavenger community on the Big Island of Hawai’i and quantify the number and percentage of each carcass type each vertebrate scavenger species removed from each site,

2) Quantify the efficiency of the vertebrate scavenger community, as a whole, compared to other scavenger guilds (invertebrates and decomposers) and quantify the efficiency of

the dominant vertebrate scavenger (based on frequency of scavenging events) compared to the other vertebrate scavengers and determine whether differences in these efficiencies occurred as a function of site or carcass type,

3) Evaluate the ability of the dominant scavenger to find carcasses at each site as a function of time, and

4) Evaluate carcass preference of vertebrate scavengers between site and carcass type.

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CHAPTER 2

EMPIRICAL EVIDENCE FOR AN EXPANSION OF THE INVASIONAL MELTDOWN THEORY: HOW INVASIVE REPTILE AND AMPHIBIAN CARCASSES ARE INCORPORATED INTO ECOSYSTEM ENERGY FLOW ON THE BIG ISLAND OF HAWAI’I[1]

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[1] Abernethy, E., K. Turner, J. Beasley, T. DeVault, W. Pitt and O. Rhodes. To be submitted to *Journal of Applied Ecology*.

ABSTRACT

1. Invasive species have had increasing ecological impacts throughout the Anthropocene. Reptiles and amphibians (herpetofauna) have demonstrated the ability to be successful invasive species worldwide, but the impacts of these species upon ecosystem function are not widely studied.

2. One way that invasive herpetofauna could significantly influence invaded ecosystems, such as islands, is through energy flow dynamics, particularly by contributing to ecosystem energy resources as carcasses. Carcasses could promote positive feedbacks and/or stability within other invasive species populations contributing to an invasional meltdown.

3. We quantified how experimentally placed invasive herpetofauna carcasses were incorporated into energy flow on the Big Island of Hawai'i in three island habitats, a coastal lava field (Site 1), mid-elevation shrub/woodland (Site 2), and alpine rainforest (Site 3). We used remote camera traps to record vertebrate species, type of interaction, and elapsed time to detection for each carcass visit.

4. These data were analyzed to evaluate differences in scavenging efficiency and preference in different habitats and for herpetofauna carcass types between the vertebrate scavenger community and other scavenger guilds as well as within the vertebrate scavenger community, which was comprised solely of invasive species. Our data indicate that a large percentage (37.3%) of the invasive species carcasses experimentally placed in the field was consumed by invasive vertebrate species.

5. *Synthesis and Applications*. Our data provide empirical support at the ecosystem-level for our call to expand the invasional meltdown theory to include scavenging. We show

the potentially large contributions of invasive herpetofauna to the energy budgets of other invasive species, which may be a critical component of island invasions and subsequent impacts.

INDEX WORDS: Camera traps, Cane toad, Carrion, Coqui frog, Food web, Gecko, Mongoose, Positive feedback, Scavenging, Stability

INTRODUCTION

What is an invasive species?

An invasive species is a species that through the assistance of humans, intentionally or not, is brought to a region in which it is not native, establishes itself, and spreads well beyond the arrival area (Simberloff 2013). During the Anthropocene, the era of significant human influence on the Earth (ecologically, geologically, chemically, etc.), invasive species have become prevalent worldwide and continue to spread at an increasing rate (Hulme 2009). While the impacts of some invasive taxa, such as mammals and birds, have been well documented, those of herpetofauna, i.e. reptiles and amphibians, are largely unknown, and most importantly, experimental research examining their impacts is lacking.

Invasive herpetofauna are globally widespread but have received relatively little attention until recently. Of the 322 established, and perhaps invasive, herpetofauna species documented across the globe, the extent of their spread and impacts has only been characterized for 14 species, only three of which are considered moderately well-studied (Kraus 2008). While predicting invasiveness through biotic traits has proven elusive across taxa, other factors, including taxonomic classification, propagule pressure, climate matching, and establishment success elsewhere, could be useful in predicting herpetofauna invasion success and their potential for impacts (Hayes & Barry 2008; Bomford *et al*. 2009). Given the global invasion success of some herpetofauna, ecosystems with favorable climates and many introduction pathways, such as tropical islands, should be considered at high risk from invasion and the concomitant negative impacts from certain herpetofauna (Reaser *et al.* 2007; Kraus 2008). When compared to mainland ecosystems, invasive species cause greater ecological harm and are considered to be one of the greatest drivers of environmental change within islands (D'Antonio & Dudley 1995; Clout & Veitch 2002). Thus there is a clear need for additional research on the mechanisms through which invasive herpetofauna negatively impact island ecosystems and the role that these species may play in an invasional meltdown.

The impacts of invasive herpetofauna

The ecological, economic, and health impacts of numerous invasive species have been widely recognized (Pimentel, Zuniga & Morrison 2005). Invasive species are considered the primary risk to 42% of threatened or endangered species globally and the greatest threat to island ecosystems, which hold almost half of the world's endangered biodiversity (Wilcove *et al.* 1998; Glen *et al.* 2013). While the impacts of only a few invasive herpetofauna species have been described, many certainly have the potential to cause ecological and economic harm and harm to human and wildlife health. With respect to ecological impacts, the following have been attributed to invasive herpetofauna: disruption of food webs through predation, poisoning of predators, resource competition, genetic contamination, and changes in inherited traits in native species (see Kraus 2008 for review). One of the most drastic examples of ecological harm by invasive herpetofauna has been on food web dynamics on the island of Guam.

Brown tree snakes (*Boiga irregularis*) completely removed most native vertebrate species (i.e. birds, bats, and lizards) from forested areas within a matter of decades of being introduced to Guam (Rodda & Savidge 2007). With the extirpation of so many native species, brown tree snakes altered their hunting patterns to focus on invasive species, changing their activity patterns from nocturnal to diurnal and arboreal to ground-dwelling (Fritts & Rodda 1998). This fundamentally changed the structure of food webs from native vertebrates that fed on plants and invertebrates to food webs in which all major components were invasive species that preyed on other invasive species (Fritts & Rodda 1998). The synergistic effect of invasive species inadvertently assisting the success of other invasive species illustrates the invasional meltdown theory.

Expanding the invasional meltdown theory to include scavenging

The invasional meltdown theory posits that some invasive species may have a positive impact on other invasive species, accelerating the impacts of one or both parties through an increased probability of survival and/or increased population size (Simberloff & Holle 1999). Since the inception of this theory, studies have shown examples of one invasive species facilitating another, but few have been able to clearly demonstrate ecosystem-level impacts (Simberloff 2006; Simberloff 2011). In addition, there has been a call for researchers to examine positive feedback loops that invasive species may create, thus destabilizing native ecosystems through “snowballing” impacts (Gurevitch 2006). Scavenging ecology is a promising area of research that is beginning to examine such positive feedback loops (Hobbs 1996; Wipfli *et al.* 1999; Towne 2000; Chaloner *et al.* 2002; Bump, Peterson & Vucetich 2009). Conversely, it has been theorized that carcass resources may lend stability to certain populations and food webs (Wilson & Wolkovich

2011). Invasion ecology is starting to embrace scavenging ecology with a few studies examining the ability of invasive species to scavenge, the successful use of invasive carcasses by native species, and competition between native and invasive species for carcass resources (Gangoso *et al.* 2006; McNatty, Abbott & Lester 2009; Beckmann & Shine 2011). By examining scavenging both on and by invasive species, scientists can combine invasion and scavenging ecology to explore the theoretical importance of carcass resources in creating positive feedback loops and/or stability within invasive species populations and invaded ecosystems.

Only recently has the importance of the scavenging pathway, particularly the value of carcass resources to vertebrates, within food web ecology been recognized. Research indicates that many vertebrate species utilize facultative scavenging, and the efficiency of vertebrate scavengers at removing carcasses, as compared to removal by other scavenger guilds (invertebrates and decomposers), is surprisingly high, 75% on average depending on various environmental factors and scavenger densities (DeVault, Rhodes & Shivik 2003; DeVault *et al.* 2011; Wilson & Wolkovich 2011). Given that vertebrate scavengers are efficient at finding carcasses, the importance of the vertebrate scavenging pathway within food webs depends on how many carcasses are available to be scavenged. In the review by DeVault, Rhodes & Shivik (2003), it is suggested that in many environments mortality may result more frequently from causes other than predation, such as malnutrition, disease, exposure, parasites, and accidents, providing a significant number of animals to be scavenged by vertebrates. Also, in environments that lack large numbers of predators, prey species are more likely to die of natural causes (Tyler & Øritsland 1999; Oksanen & Oksanen 2000). Thus it is reasonable to suggest that in areas with invasive species and few natural predators there could be a high number of available carcasses (Leader-Williams 1988). This highlights the likely importance of invasive species carcasses in assisting invasive species scavenger populations within invaded ecosystems, and the relevance of understanding this relationship for predicting the potential for invasional meltdowns and negative impacts on native species and ecosystems.

What carcasses and ecosystems should be used to explore these topics?

Invasive herpetofauna are globally prevalent, often attain high densities throughout their non-native range, and generally have few predators in invaded ecosystems. Thus, we propose that they may be a widely abundant carcass resource and represent a unique opportunity to examine how scavenging on and by invasive species relates to invasional meltdowns, positive feedbacks, and/or stability in highly invaded ecosystems. Except for Cornaby (1974) who examined invertebrate scavenging on 4 cane toad (*Rhinella marina*) carcasses, the few previous studies on scavenging of herpetofauna carcasses have focused primarily on the use and persistence of roadkilled carcasses (Antworth, Pike & Stevens 2005; Beckmann & Shine 2011; Degregorio *et al.* 2011; Santos, Carvalho & Mira 2011). The lack of experimental research on scavenging of herpetofauna carcasses makes it difficult to estimate how often these relatively small carcasses are scavenged in the natural environment, where they are perhaps not as visible as on roads. Scavenging research on invasive herpetofauna carcasses experimentally placed away from roads is needed to elucidate the importance of these carcasses to food web dynamics in island ecosystems and the potential role of scavenging in facilitating invasional meltdowns.

It would be most valuable to conservationists and ecologists to conduct this research exploring scavenging on and by invasive species in ecosystem types widely considered imperiled as a result of invasive species. Globally, islands are considered to be one of the ecosystems at greatest risk from invasive species, and many islands already have large numbers of established invasive species, thus providing an optimal ecosystem type in which to examine these topics. On the Hawaiian Islands, invasive species, including herpetofauna, are considered the top threat to native species, with Hawai’i leading the USA in number of extinctions and federally endangered species (Dodson *et al.* 1997; Cox 1999). The Hawaiian Islands also largely lack native predators for invasive species, likely leaving an abundance of invasive carcasses to be scavenged by invasive species.

What questions should be addressed?

How invasive species act as carcasses and scavengers to influence food webs, potentially creating an invasional meltdown through positive-feedback loops and/or stabilizing invasive species populations, awaits the results of theoretical and experimental research. Nonetheless, the first step to evaluating these scenarios is to quantify the scavenger guilds in a highly invaded ecosystem and to determine the amount of carcass resources being utilized by different scavenger guilds, vertebrates as opposed to invertebrates and decomposers, and the species composition of each, particularly whether species are invasive or native. Given the ubiquitous occurrence of vertebrate scavenging, the stability that scavenging may lend to an ecosystem, and the immense energy resources represented by invasive species carcasses, the combination of scavenging and invasion ecology presents a unique opportunity to experimentally assess the invasional meltdown theory and contribute greatly to our understanding of how invasive species are able to initially invade, persist, facilitate future invasions, and impact native ecosystems.

Our study seeks to develop understanding of the utilization of invasive reptiles and amphibians within the food webs of imperiled island ecosystems, so that further conclusions can be drawn about the role that carcasses and scavenging play in the invasional meltdown process, creating positive feedback loops, and/or food web stability. To achieve this goal, we investigated how three invasive herpetofauna taxa, coqui frogs (*Eleutherodactylus coqui*), geckos (various species), and cane toads, were utilized within the scavenging pathway of the Big Island of Hawai'i. We experimentally placed camera traps baited with carcasses in three distinct habitats on the Big Island of Hawai'i and recorded the vertebrate species that interacted with each carcass, each type of interaction (removed, partially consumed, touched, investigated but not touched, investigated area after carcasses removed, or passed without interaction with carcass or area), and the time that it occurred. Our objectives were to use these data to:

1) Describe the vertebrate scavenger community on the Big Island of Hawai'i and quantify the number and percentage of each carcass type each vertebrate scavenger species removed from each site,

2) Quantify the efficiency of the vertebrate scavenger community, as a whole, compared to other scavenger guilds (invertebrates and decomposers), as well as the efficiency of the dominant vertebrate scavenger compared to the other vertebrate scavengers, and to evaluate whether differences in efficiencies occurred as a function of site or carcass type,

3) Evaluate the ability of the dominant scavenger to find carcasses at each site as a function of time, and

4) Evaluate carcass preference of vertebrate scavengers between site and carcass type.

MATERIALS AND METHODS

Study Species

There are approximately 30 species of non-native herpetofauna present on Hawai'i, some of which are considered invasive (Kraus 2005). We choose to utilize the following common, invasive herpetofauna in our experiments: coqui frogs (carcasses used were approximately 2-5 grams), geckos (1-10 g), and cane toads (25-150 g). Geckos arrived to Hawai'i first, brought over in the canoes of Polynesian settlers sometime before Western contact occurred in 1778 (Kraus 2005). The Polynesian introduced species used in this study were the Indo-Pacific Gecko (*Hemidactylus garnotii*), Mourning Gecko (*Lepidodactylus lugubris*), Stump-Toed Gecko (*Gehyra mutilata*), and Tree Gecko (*Hemiphyllodactylus typus*). The European introduced gecko species used in this study were the Common House Gecko (*Hemidactylus frenatus*), accidently introduced in the 1940s through the importation of exotic plants, and the Gold-dust Day Gecko (*Phelsuma laticauda*), intentionally introduced in the 1970s for aesthetic purposes (McKeown 1996). Cane toads were intentionally introduced in the 1930s as a biological control agent for the sugar cane beetle (*Tomarus subtropicus*, Lever 2003). Coqui frogs were unintentionally introduced in the 1980s through the importation of exotic plants (Kraus *et al.* 1999). While island-wide population estimates have not been calculated for these three taxa, geckos are considered common island-wide, and cane toads and coqui frogs are common in some areas with coqui frogs able to reach densities of >2,000 adults per acre (Lever 2003; Kraus 2005; Woolbright *et al.* 2006).

Study Area

Two protected areas, Hawai’i Volcanoes National Park (HAVO) and Pu’u Maka’ala Natural Area Reserve, on the Big Island of Hawai’i were chosen to assess the utilization of invasive herpetofauna carcasses within the island ecosystem of Hawai’i. These parks represented ideal areas to conduct experimental research due to their security, accessibility, and relatively low human impact, aside from the large numbers of vertebrate invasive species present. Three sites, representing the range of soil and habitat types that occur on the island, were chosen from these two protected areas. Site 1 was a coastal lava field, characterized by relatively intact lava with few trees and shrubs and sparse grasses (Figure 2.1). Refuges on this site were small and consisted of caves under layers of buckled lava. Carcasses were placed approximately 500 m to 2 km from the coastline at this site. Site 2 was further inland, approximately 10 km, and had soil varying from intact lava to small pebble-like substrate. The vegetation consisted of trees, shrubs, and grasses that were thick in some areas but short in height. Wide, deep cracks were interspersed throughout this site. Site 3, also inland (16-25 km), had moist soil that gave rise to an abundance of thick vegetation, mostly shrubs and relatively tall trees, that provided a multitude of refuges. All sites experienced similar levels of rainfall and temperature that were consistent year-round, but due to differences in lava flow history and subsequent substrate and vegetation development, the sites exhibited very different structural and vegetative characteristics. An inventory of the reptiles and amphibians in HAVO conducted by Kraus (2005) revealed that only geckos have established populations at all three sites. Cane toads and coqui frogs were found occasionally near Site 3, and the threat of establishment by coqui frogs in HAVO is considered high (Kraus

2005). While cane toads and coqui frogs are not established in the park, these three sites represent the diversity of habitats on the Big Island of Hawai'i and the potential vertebrate scavenger communities that are likely to utilize these carcass resources that are available throughout the island.

Experimental Design

To study the vertebrate scavenger communities at these three sites on the Big Island of Hawai'i, camera traps baited with invasive herpetofauna carcasses were experimentally placed in the field from June-August 2013. At each of the sites, approximately 96 carcasses, comprising 32 each of three herpetofauna taxa, coqui frogs, geckos, and cane toads, were used in experimental trials. Animals were collected from the Big Island of Hawai'i and euthanized following the Institutional Animal Care and Use Committee protocol approved through the University of Georgia (A2013 04-007-Y1-A0). Carcasses were placed on an external triggering device approximately 1/3-1 m in front of cameras (Reconyx HyperFire PC900, Wisconsin, USA) that were attached to trees or rocks a few centimeters to 1/2 m above the ground (DeVault, Brisbin & Rhodes 2004). To maintain independence among trials, cameras were placed approximately 100 m from other camera traps at each site along transects and 50 m away from major roads (Pitt, Sugihara, & Berentsen 2015). Cameras were programmed to record 5 photos when triggered by movement or the external trigger. After each 5-6 day long trial, any remaining carcass material was collected, described, and evidence of invertebrate scavenging noted. The camera traps were then moved 50-100 m and set-up with fresh carcasses. Once approximately 32 successful trials had been run for each carcass type at each site, all camera traps and carcasses were removed from the field. A trial was considered successful if the fate of the carcass could be determined through photo analysis, i.e. scavenging event recorded, or through observation in the field, i.e. carcass remained.

To verify consumption of cane toad carcasses, we placed three additional cane toad carcasses fitted with small (2 g) internally secured radio transmitters (Advanced Telemetry Systems, Minnesota, USA) at each site in August-September 2014. The carcasses were tracked after approximately 5 days and the location and evidence of scavenging was noted.

Data Analysis

All photos were examined and each independent vertebrate visit to a carcass was recorded. A visit was considered independent if it occurred more than 2 minutes from the previous visit by the same vertebrate species. Sequential visits by different vertebrate species were all recorded, regardless of time between visits. For each visit by vertebrates, the species, time of observation, and type of interaction with the carcass (removed, partially consumed, touched, investigated but not touched, investigated area after carcasses removed, or passed without interaction with carcass or area) was recorded. An interaction was characterized as “removed” if the scavenger removed the carcass from the view of the camera or was photographed fully consuming the carcass. “Partially consumed” was recorded if the scavenger consumed or removed only part of the carcass. Invertebrates that were visible on photographs or present when the carcass was retrieved at the end of the trial were noted. When carcasses were removed wholly or primarily by invertebrates or decomposers, the carcass was recorded as having been scavenged by other scavenger guilds.

After photos were examined, we compiled a list of the vertebrate scavenger species that removed carcasses, and for each site, we quantified the numbers of each carcass type that were acquired by each vertebrate species (expect for rodent species which were grouped together) and the percentages that were acquired by the dominant vertebrate, all other vertebrate species, and other scavenger guilds. To address Objective 2 (comparing scavenging efficiencies between guilds and across sites and carcass types), we used log-linear models to examine two data sets 1) the vertebrate scavenger guild's efficiency (percentage of carcasses removed) at acquiring different herpetofauna carcass types at the three sites compared to other scavenger guilds and 2) the efficiency of the dominant scavenger at each site at acquiring carcasses compared to all other vertebrate scavengers observed at each site. Initially we evaluated the three-way interaction between site, carcass type, and scavenger for both data sets; based on those results, we evaluated two-way interactions and main effects as needed by sorting data sets by site and by carcass type. We conducted log-linear models using the CATMOD procedure in SAS software, Version 9.3 (SAS Institute Inc., Cary, NC, USA).

To address Objective 3, which was to evaluate the time (dependent variable) that it took for the dominant vertebrate scavenger across all sites to find and to remove each of the carcass types at each of the sites, we used a 2-way factorial ANOVA. This was only done for the dominant vertebrate scavenger because of low scavenging rates by other vertebrates. Site and carcass type were incorporated as independent variables, and the 2-way factorial ANOVA accounted for variation between and within both independent variables. We conducted this analysis to determine if there were differences in the relative swiftness of the dominant vertebrate scavenger to find and remove carcasses across site and/or carcass type. If this test was significant, we performed a Tukey HSD test to determine which components of the 2-way ANOVA were different.

To address Objective 4, which was to evaluate carcass preference of vertebrate scavengers, we adapted methods for describing bait preference from Berentsen, Johnson & VerCauteren (2014). Five different carcass interactions were assigned classifications of carcass preference. The highest class (4) was assigned to the interaction that showed the greatest preference for a carcass, removed completely on the first visit. If the carcass was removed on a subsequent visit, partially consumed, or found but not removed by a vertebrate, it was classified as 3, 2, or 1 respectively. If a carcass was never found by vertebrates, it was classified as 0. When carcasses were visited multiple times, the highest class of interaction recorded was assigned to that carcass. Each carcass was thus given one score, 0 through 4, and scores from all three sites were summed for each carcass type to get a separate rank sum for each carcass type across all sites. This was done separately for carcasses found by the dominant vertebrate scavenger, all other vertebrate scavengers, and all vertebrate scavengers combined. These rank sums were used to give each of the carcass types a preference rank. Ranks were compared among carcass types using a Kruskal-Wallis test adjusted for ties and pairwise differences in mean ranks of carcass types were compared using the Mann-Whitney test. To help relate scavenging efficiency to preference within our analysis, we also reported the average elapsed time and average number of visits that it took for the dominant vertebrate scavenger, all other vertebrate scavengers, and all vertebrates combined to remove carcasses.

Lastly, we summed all the times that an individual vertebrate scavenger species was recorded by our camera traps at each site, regardless of the carcass type or carcass presence or absence. We did this to provide an index of relative occurrence for each vertebrate scavenger species at each site, which was used to interpret differences in scavenging efficiency data between sites.

RESULTS

Vertebrate scavenger species and scavenging efficiencies on Hawai'i – Obj. 1

The following vertebrate species, all invasive, were found to scavenge our experimentally placed herpetofauna carcasses: mongoose (*Herpestes javanicus*), rodents (*Rattus sp.* and *Mus musculus*), cats (*Felis catus*), pigs (*Sus scrofa*), and myna birds (*Acridotheres tristis*) (Figure 2.2). Of the 287 herpetofauna carcasses experimentally placed in the field, 107 carcasses were scavenged by vertebrates (37.3%, Table 2.1). Vertebrate scavengers removed 16.0%, 45.3%, and 52.2% of all carcasses experimentally placed at Sites 1, 2, and 3 respectively. Mongoose were the dominant vertebrate scavenger at all sites and removed 13.0%, 34.7%, and 30.4% of all carcasses placed at Sites 1, 2, and 3 respectively (Table 2.2). Rodents, a cat, pigs, and a myna bird all scavenged at Site 2, but never scavenged a cane toad. Other than mongoose, cats were the only scavenger to remove carcasses (a coqui frog and geckos) at Site 1, and rodents were the only additional scavenger to remove carcasses (all types) at Site 3.

Scavenger guild efficiencies analyzed by site and by carcass type – Obj. 2.1

For the analysis of the efficiency of all scavenger guilds, the three-way interaction was significant (p-value = 0.0450), justifying our examination of the two-way interactions and main effects sorted by the remaining variable (i.e. site or carcass type, Table 2.3). When the data were sorted by site, there was a significant main effect of scavenger, classified as vertebrate and other scavenger guilds, at Site 1 (p-value =

<0.0001) where other scavenger guilds removed more of all carcass types. At Site 2, there was a significant interaction between scavenger and carcass type; other scavenger guilds removed more coqui frog and gecko carcasses and vertebrates removed more cane toads (p-value = <0.0001). At Site 3 there was no significant difference between the efficiency of scavenger guilds for any of the carcass types. When these data were sorted by carcass type, there was a significant interaction between scavenger and site for each of the three carcass types. Coqui frogs, geckos, and cane toads were each scavenged by vertebrates and other scavenger guilds at efficiencies that varied by site (p-value = 0.0070, 0.0012, and <0.0001 respectively). While coqui frogs were removed more by other scavenger guilds at all sites, vertebrates were able to remove more coqui frog carcasses at Sites 2 and 3 than at Site 1. Gecko carcasses were removed more often by other scavenger guilds at Sites 1 and 2 and more by vertebrates at Site 3. Cane toads were removed more by vertebrates at Sites 2 and 3 and more by other scavenger guilds at Site 1.

Vertebrate scavenging efficiencies as a function of site and carcass type – Obj. 2.2

For the analysis of differences in scavenging efficiency within the vertebrate scavenger guild (mongoose compared to other vertebrate scavengers) as a function of site and carcass type, there was insufficient data to analyze the three-way interaction. Almost half of the counts for the 18 observational categories fell below the 5% threshold of the total counts (107), i.e. less than 5 observations in each category. Given this limitation, we chose to examine the model for all two-way interactions and main effects only. Using this approach, we detected a significant interaction only between scavenger and carcass indicating that when pooled across sites, carcass type influenced which vertebrate scavenger removed the carcasses (p = 0.0001, Table 2.3). Mongoose removed more coqui frogs and cane toads, but other vertebrates removed more gecko carcasses.

Dominant vertebrate scavenger time to find and remove carcasses – Obj. 3

There was no difference in the amount of time that elapsed before a mongoose, the dominant vertebrate scavenger, made an initial visit to any of the carcass types among the three sites, regardless of what ultimately scavenged the carcass. However, mongoose removed 74 out the 91 carcasses that they found (81.3%), and there was a significant main effect of carcass type in the analyses of elapsed time to carcass removal (not always on the initial visit), that revealed that the amount of time that elapsed before mongoose removed different carcass types did significantly differ, regardless of site (p-value = 0.0077). A Tukey HSD test revealed that significantly more time elapsed before cane toad carcasses were removed compared to gecko carcasses (p-value = 0.0106). Elapsed times to carcass removal for other pairwise carcass comparisons were not significantly different. The average time until removal and average number of visits to a coqui frog, gecko, and cane toad by a mongoose was 45.97 (1.0), 31.98 (1.0), and 59.12 (1.4) hours (visits) respectively (Table 2.4). Table 2.4 also provides the average time until removal and average number of visits to a coqui frog, gecko, and cane toad carcass by other vertebrate scavengers and all vertebrate scavengers combined.

Vertebrate scavenger preference – Obj. 4

Vertebrate scavenger preference was analyzed for the following three groups: mongoose, all other vertebrate scavengers, and all vertebrate scavengers combined. When the carcass preference of vertebrate scavengers was analyzed separately, i.e. mongoose and all other vertebrates, there were three carcasses with which both mongoose and rodents had the same type of interaction. Thus those three carcasses were counted in the analysis for both groups. One coqui frog was partially removed (Class 2), and two cane toads were investigated (Class 1) by both mongoose and rodents. Other carcasses had interactions from both groups but not at the highest classification level, so those carcasses were only counted in the analysis for the group with the highest class interaction. The carcasses not found by vertebrate scavengers (N=130) received scores of zero in the analysis for mongoose, other vertebrates, and all vertebrates. For the carcass preference of all vertebrate scavengers pooled together, the highest class interaction of each carcass was only counted once.

With respect to mongoose preference, there was a significant treatment effect of carcass type (p-value = <0.0001) with cane toads ranked the highest (rank sum = 154), then geckos (57), and coqui frogs last (53, Table 2.4). Cane toads ranked significantly higher than coqui frogs (p-value = <0.0001) and geckos (p-value = 0.0002), but there was no significant difference between the ranks of coqui frogs and geckos. For other vertebrate scavengers, there was not a significant effect of carcass type, although geckos ranked highest (rank sum = 92), coqui frogs second (54), and cane toads last (22). When all vertebrate scavengers were pooled together, there was a significant effect of carcass type (p-value = 0.0017) with cane toads ranked highest (174), then geckos (149), and last coqui frogs (99). There was a significant difference between the ranks of cane toads and coqui frogs (p-value = 0.0002) but not between geckos and cane toads or coqui frogs.

Relative occurrence data

The relative occurrence data from camera traps indicated that mongoose, rodents, and cats were present at all 3 sites, and that pigs were present only at Site 2 (Table 2.5).

Camera trap data and observational data from the field showed that myna birds were present at Sites 1 and 2. The two scavengers recorded most frequently by our camera traps were mongoose and rats. Mongoose appeared most at Site 2, followed by Sites 3 and 1 respectively. Rodents were recorded 12 times more frequently at Site 3 than at the next most visited site, Site 2, and were recorded least at Site 1. Total vertebrate scavenger relative occurrence as measured by photographic evidence was highest at Site 3 (688), followed by Sites 2 (200) and 1 (85) respectively (Table 2.5).

Confirmation of carcass consumption

Of the cane toad carcasses outfitted with radio transmitters, it was determined from photographic evidence that 8 out of 9 were removed by mongoose, and the other carcass was not removed by a vertebrate. One carcass was consumed in front of the camera and the others were carried 3-18 m away. Of those carcasses that were carried away, transmitters were recovered in areas of heavy grass (1), under shrubs (4), or in shallow lava caves (2). Only one partially scavenged carcass was recovered with a transmitter, and in that case, only the head of the cane toad remained. From this evidence, we concluded that the cane toads were generally carried a short distance away from camera traps to a refuge and consumed wholly, leaving the transmitter.

The invertebrate scavenger guild

While we were not able to quantify the carcass biomass acquired by other scavenger guilds (invertebrates vs decomposers) for this study, we did gather some evidence concerning the activity level of invertebrate communities at each site. We noted that at the end of experimental trials at Sites 1 and 2 all remaining carcasses had been completely stripped of flesh, whereas some carcasses that remained at Site 3 still had unconsumed flesh available. Anecdotally, we recorded the following large invertebrates dragging carcasses outside the view of the camera and/or consuming large portions of carcasses in view of the cameras at Sites 1 and 2: centipedes (Class: Chilopoda), yellow jackets (Family: Vespidae), cockroaches (Order: Blattodea), ants (Family: Formicidae), flies (Order: Diptera), grasshoppers (Order: Orthoptera), and slugs (Class: Gastropoda). Our observational and photographic evidence suggest that invertebrate communities at Sites 1 and 2 were able to consume carcasses more quickly, leaving less time for vertebrates to find and acquire the carcasses.

DISCUSSION

Our study clearly demonstrates that invasive species take advantage of the novel resources provided by other invasive species, i.e. their carcasses, in one of the ecosystems most devastated by the spread of invasive species in the Anthropocene, islands. This suggests that invasive species are evolutionarily equipped and behaviorally willing to find and take advantage of carcass resources, even if they have not been seen before within that environment, such as the coqui frog and cane toad carcasses used in this experiment. This willingness to consume a novel carcass resource could be critical to the success of these species as they invade and sustain themselves in new ecosystems. Invasive species that are able to utilize carrion from a variety of species have an advantage while invading a new ecosystem, since the available food resources may be unfamiliar. With the worldwide distribution of herpetofauna and their ability to reach high densities, these invasive taxa represent a potentially important source of carcass resources for other invasive species. With the information from our research, we were able to draw conclusions about the species composition, efficiency, and behavior of the scavenger community on the Big Island of Hawai'i. These data can be used to expand theories relating carcass resources to invasional meltdowns, positive feedbacks, and stability.

Invasive vertebrate scavengers of Hawai'i and invasional meltdown

Our results revealed that invasive herpetofauna carcasses were efficiently scavenged by invasive vertebrates on the Big Island of Hawai'i, showing the efficiency of invasive vertebrates at acquiring resources compared to other scavenger guilds, i.e. invertebrates and decomposers. These results support an expansion of the invasional meltdown theory to include the role that scavenging on and by invasive species may have for accelerating the impacts of invasive species establishment. To the knowledge of the authors, our study is the first of its kind to quantify the utilization of vertebrate carcass resources within an ecosystem that is highly impacted by invasive species. Our study is also the first to look at vertebrate scavenging efficiencies on herpetofauna in a setting away from a road. We showed that invasive vertebrates on Hawai'i are able to scavenge at rates comparable to vertebrate scavenging rates within native ecosystems but at rates generally lower than those shown by scavenging studies of herpetofauna carcasses placed on roads (DeVault, Rhodes & Shivik 2003; Antworth, Pike & Stevens 2005; DeGregorio *et al.* 2011). Of all carcass types across sites, 37.3% were acquired by invasive vertebrate scavengers. Interestingly, some vertebrate species were able to find and scavenge extremely small carcasses (a few grams) before other scavenger guilds could consume them completely. Given the high rates of observed vertebrate scavenging efficiency and the potentially large, but unknown, number of available carcasses, it is likely that invasive vertebrates are assimilating a large amount of nutritive resources through scavenging. The utilization of this potentially large resource could contribute to the invasion success of some invasive species and potentially to an invasional meltdown. With the expansion of the invasional meltdown theory, future experimental and theoretical research should examine how other invasive species carcasses are being utilized, how many carcasses are available, what portion of a facultative scavenger’s diet are carcass resources, and how the populations of established and invading invasive species change as new species invade.

Patterns of variable vertebrate scavenging efficiencies

In addition to describing the vertebrate scavenger community and quantifying scavenging efficiencies on the Big Island of Hawai’i, our research indicated that patterns of vertebrate scavenging efficiency vary among habitats and carcass types as a function of relative vertebrate scavenger occurrence and invertebrate activity, but the ability of the vertebrate scavenger to find carcasses does not vary. Elucidation of the influence of habitat and carcass type on vertebrate scavenging efficiency across a landscape is critical for predicting the relative importance of specific carcass resources to vertebrate scavenger populations. In terms of habitat types, we found that at sites characterized by soil and vegetation typical of more recent lava flows (Sites 1 and 2) vertebrate scavenger species were significantly less efficient at acquiring carcasses than were other scavenger guilds. Although our experiment was not designed to identify what caused this spatial pattern, we suspect that it may be due to the lower relative occurrences of vertebrate scavengers and more active invertebrate scavengers at these two sites and/or a higher availability of other resources at Site 3.

With respect to a vertebrate scavenger's ability to find these relatively small carcasses in different habitats, we found that the time it takes for the dominant vertebrate scavenger, mongoose, to initially find these carcasses did not vary as a function of site or carcass type. In other words, if a mongoose was in the vicinity, with the chances of that depending on relative occurrence, it would find all herpetofauna carcass types at approximately the same time in any of the sampled environments. We also observed that if invertebrates are very active (Sites 1 & 2), then a mongoose would be less likely to find a smaller carcass type, which could simply be because those carcasses are available for less time. While we can only apply this analysis to mongoose, as they were the only vertebrate to scavenge all carcass types at all sites, it is important to entertain the idea that environmental factors and differences in carcass type may have a lesser influence on the efficiency of certain vertebrate scavengers in this invaded environment than vertebrate and invertebrate scavenger community composition and abundance.

In addition to the above evidence, the efficiency data sorted by carcass type also suggested that there are carcass attributes that influence a vertebrate's chance of finding a carcass. For example, coqui frogs, generally the smallest carcass type used in this study, were less likely to be removed by vertebrates than by invertebrates at any of the three sites. Geckos, which were generally larger than coqui frogs but much smaller than cane toads, were removed at a higher percentage by vertebrates than by invertebrates only at Site 3 where vertebrate scavenger numbers were highest and invertebrate communities were least efficient. On the other hand, cane toads, having comparatively large carcasses, were removed by vertebrates at a higher percentage than by other scavenger guilds at both Sites 2 and 3, suggesting that when vertebrate numbers are high enough and carcasses are of large enough size, vertebrates can out-compete invertebrates to acquire carcass resources. This evidence reinforces our conclusions that smaller carcasses are more readily consumed by invertebrates and are thus not as available to vertebrates, regardless of how fast they can find them (also see DeVault, Brisbin & Rhodes 2004).

Moreover, the analysis of the amount of time mongoose took to remove different carcass types suggests an influence of carcass type on preference. Mongoose took significantly more time to remove a cane toad (less preferred) carcass than a gecko carcass (the most swiftly removed carcass on average, although not significantly different from coqui frogs). This suggests there is an influence of carcass type on preference, as well as on vertebrate scavenging efficiency.

Scavenging efficiencies within the vertebrate community on Hawai'i

While examining the efficiency of scavenger guilds in total is valuable for the purpose of understanding competition between and the amount of resources acquired by each guild, it is especially valuable for conservation and management efforts to understand the distribution of carcasses utilized within the vertebrate scavenger guild itself. This reveals how the amount of resources acquired by individual vertebrate species differs and whether this efficiency varies by site or carcass type. Vertebrate scavengers were grouped by the dominant vertebrate scavenger, mongoose, and all other vertebrates, due to low scavenging rates by other vertebrates. The non-significant interaction of scavenger and site revealed that site was not an important factor in determining the proportion of carcasses acquired by mongoose vs other vertebrates. Regardless of site, the significant interaction of scavenger and carcass revealed that carcass type did have an effect on whether it was scavenged by a mongoose or another vertebrate. This effect of carcass type could be driven by the ability of mongoose to consume cane toad carcasses, of which they removed vastly more (45 compared to 3 removed by rats). Although mongoose and rats will readily consume cane toads, the bufotoxin located in their parotoid glands has been shown to negatively affect cats and pigs and can remain potent several days after death (Nellis & Everard 1983; Shine 2010). Also the larger size of the cane toads may have made them more difficult for smaller scavengers, like rats, to consume completely. We had photographic evidence of mongoose and rats eating cane toad carcasses at the camera trap, as well as evidence from our transmitter trials showing that when mongoose carried off cane toads they likely consumed them, entirely or at least in large part, in a refuge away from the camera trap.

Vertebrate scavenger preference influences patterns of scavenging efficiency

Our preference analysis is novel and unique in that it takes into account the efficiencies of scavengers at finding certain carcass types, the choice to consume the carcass or not, and whether multiple visits were made by a particular species before the carcass was removed. This is fundamentally different from traditional preference tests, such as the presentation of 3 different baits simultaneously for vertebrates to choose from. Our test is more ecologically relevant in that it essentially describes both a vertebrate scavenger’s ability to find a carcass before it is completely consumed by other scavenger guilds and its willingness to take it, reflecting overall vertebrate scavenging efficiency and preference for taking certain carcasses. The preference analysis of mongoose and all vertebrates combined indicated that vertebrates more easily acquired larger carcasses (i.e. cane toads), followed by smaller gecko carcasses, and then the smallest carcasses, coqui frogs. While the vertebrates may not “prefer” a cane toad carcass, as evidenced by the increased time and number of visits that mongoose required taking them, a cane toad is able to provide the largest number of carcasses to the vertebrate community. The carcasses are ranked differently for the other vertebrate scavengers (gecko-1st, coqui frog-2nd, cane toad-3rd), reflecting their decreased utilization of (and lack of preference for) cane toad carcasses. Our preference analysis results also reinforce our analysis of vertebrate scavenger carcass efficiency by demonstrating that certain carcass types, particularly cane toads, were removed more efficiently by certain scavengers (i.e. mongoose). These efficiency and preference patterns across sites and carcass types can be used to understand the relative importance of certain carcasses to different vertebrate scavengers in particular environments.

Conclusions

Our study is the first research to characterize the vertebrate scavenger community on the Big Island of Hawai’i, the efficiency and preference of those vertebrate scavengers, and the patterns that exist for different sites and carcass types. It is also the first research to characterize these metrics within a highly invaded ecosystem and the first to examine scavenging on herpetofauna carcasses. The next step in this research is to develop the theoretical framework for how the utilization of a novel carcass resource influences invasive species communities and could possibly contribute to an invasional meltdown. The invasional meltdown theory needs to be expanded to include scavenging, primarily exploring whether carcasses create positive feedback loops or act as a stabilizing force within food webs dominated by invasive species. Positive feedback loops associated with scavenging would involve increased invasive species population growth as a result of an ability to utilize readily available invasive species carcasses, exacerbating negative impacts on native species and ecosystems. In contrast to this idea of positive feedback, carcasses may simply provide a stabilizing resource to populations of invasive species. While not providing enough resources to allow the populations to grow exponentially and intensifying their impacts on native species, carcasses could allow invasive species to maintain an existence in an inhospitable or novel habitat and may even relieve some of the pressure on native species. Once this theory is developed, models and experiments can be used to determine the influence of carcass resources on invasive species population dynamics, specifically by determining scavenging efficiency rates on other carcasses, estimating the number of available carcasses, and the proportion of a scavenger's diet that is carcasses and of what type. Ultimately this information could be used to predict how invasive species populations will respond to carcass availability and help to mitigate the subsequent negative impacts on native species and ecosystems.

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Table 2.1 The number of carcasses scavenged by all scavengers (vertebrates and other scavenger guilds) shown separately for each herpetofauna carcass type and site. The percentages show the number of carcasses scavenged by vertebrates compared to other scavenger guilds at each site (combining all carcass types) and total for all sites (in the far right column).

All Scavengers		**Site 1**		**Site 2**		**Site 3**		**Total Removed sorted by:**		
	Carcass	**Count**	**%**	**Count**	**%**	**Count**	**%**	**Carcass**	**Scavenger**	**%**
Vertebrates	Coqui	2		8		11		21		
	Gecko	7		11		20		38		
	Toad	7		24		17		48		
Total removed		16	16%	43	45.3%	48	52.2%		107	37.3%
Other	Coqui	32		23		20		75		
	Gecko	26		22		11		59		
	Toad	26		7		13		46		
Total removed		84	84.0%	52	54.7%	44	47.8%		180	62.7%
Total set out		100		95		92			287	

Table 2.2 The number of carcasses scavenged by all vertebrate scavenger species shown separately for each herpetofauna carcass type and site. The percentages show the number of carcasses scavenged by mongoose compared to other vertebrates at each site (combining all carcass types) and total for all sites (in the far right column).

Vertebrate		**Site 1**		**Site 2**		**Site 3**		**Total Removed sorted by:**		
Scavengers	**Carcass**	**Count**	**%**	**Count**	**%**	**Count**	**%**	**Carcass**	**Scavenger**	**%**
Mongoose	Coqui	1		5		6		12		
	Gecko	5		4		8		17		
	Toad	7		24		14		45		
Total removed		13	13.0%	33	34.7%	28	30.4%		74	25.8%
Rodent	Coqui	-		2		5		7		
	Gecko	-		4		12		16	26	
	Toad	-		-		3		3		
Cat	Coqui	1		-		-		1		
	Gecko	2		1		-		3	4	
	Toad	-		-		-		-		
Pig	Coqui	-		-		-		-		
	Gecko	-		2		-		2	2	
	Toad	-		-		-		-		
Myna bird	Coqui	-		1		-		1		
	Gecko	-		-		-		-	1	
	Toad	-		-		-		-		
Total removed		3	3.0%	10	10.5%	20	21.7%		33	11.5%
Total set out		100		95		92			287	

Table 2.3 Factors and associated p-values that significantly influenced the percentage of herpetofauna carcasses removed by vertebrates when compared to other scavenger guilds and by mongoose compared to other vertebrate scavengers. This is shown for 2-way log-linear models used to analyze these data sorted by site and then by carcass type and for full 2 and 3-way log-linear models. NS shows tests that were non-significant.

Sorted by		**Removed by Vertebrate/ Other Scavenger**	**Significant p-values**	**Removed by Mongoose/ Other Vertebrate**	**Significant p-values**
Site	1	scavenger	<0.0001	-	-
	2	scavenger*carcass	<0.0001	-	-
	3	NS	-	-	-
Carcass type	Coqui frog	scavenger*site	0.0070	-	-
	Gecko	scavenger*site	0.0012	-	-
	Cane Toad	scavenger*site	<0.0001	-	-
Not sorted		scavenger* carcass*site	0.0450	scavenger*carcass	0.0001

Table 2.4 Vertebrate scavenger interaction with and preference for herpetofauna carcasses. Shows the descriptions for carcass interaction classifications; the rank for mongoose, other vertebrate, and all vertebrate preference; the sum of the interactions of each class multiplied by that class; the average time it took for each scavenger to remove the carcass; and the average number of visits that each scavenger made before the carcass was ultimately scavenged by a vertebrate.

Description	Class
Carcass removed completely on first visit	4
Carcass removed completely on subsequent visits	3
Carcass partially consumed	2
Carcass investigated only	1
Carcass not found by vertebrate scavengers	0

Scavenger	Coqui Frog	Gecko	Cane Toad
Rank – Mongoose	3	2	1
Rank sum	53	57	154
Average time until removal (hours)	45.97	31.98	59.12
Average # of visits	1.0	1.0	1.3
Rank – Other Vertebrate	2	1	3
Rank sum	54	92	22
Average time until removal (hours)	20.80	22.72	15.19
Average # of visits	2.2	1.7	3.0
Rank – All Vertebrates	3	2	1
Rank sum	99	149	174
Average time until removal (hours)	35.18	26.86	56.37
Average # of visits	2.0	1.5	2.4

Table 2.5 Relative occurrence of the vertebrate scavengers recorded by our camera traps in Hawai'i Volcanoes National Park and Pu'u Maka'ala Natural Reserve Area on the Big Island of Hawai'i in 2013. All the independent visits that a vertebrate scavenger made to the camera traps in each site were summed regardless of whether the carcass had already been scavenged.

Scavenger	Site 1	Site 2	Site 3
Mongoose	46	127	95
Rodent	35	51	586
Cat	4	5	7
Pig	0	12	0
Myna Bird	0	5	0
Total	85	200	688

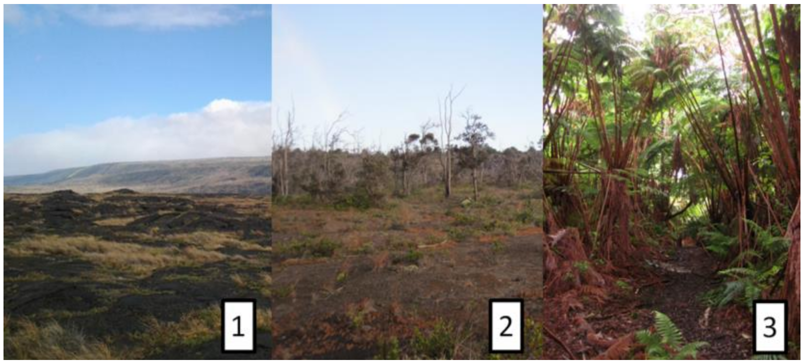

Figure 2.1 The three sites used for scavenging research on invasive herpetofauna carcasses in Hawai’i Volcanoes National Park and Pu’u Maka’ala Natural Area Reserve during June-August 2013. Pictures (from left to right) showing Site 1, an area characterized by lava fields with little vegetation; Site 2, characterized by weathered lava fields and vegetation of short trees, shrubs, and grasses; and Site 3, a rainforest like area with lush, thick vegetation.

Figure 2.2 Images from our scavenging research on the Big Island of Hawai’i showing a mongoose, the dominant vertebrate scavenger, taking a cane toad at Site 2 (top left), a rat taking a gecko at Site 3 (top right), a cat taking a gecko at Site 1 (bottom left), and a pig taking a coqui frog at Site 2 (bottom right). In the bottom right image the pig has partially uncovered the external trigger in the process of consuming the coqui frog.

CHAPTER 3

THE ECOLOGY OF SCAVENGING IN A HIGHLY INVADED ISLAND ECOSYSTEM: QUANTIFYING VERTEBRATE SCAVENGING EFFICIENCIES AND PREFERENCE FOR INVASIVE MAMMAL AND BIRD CARCASSES ON HAWAI'I[2]

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[2] Abernethy, E., K. Turner, J. Beasley, T. DeVault, W. Pitt and O. Rhodes.
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ABSTRACT

1. The scavenger community provides the influential ecosystem function of quickly removing carcasses from the landscape and recycling carcass nutrients. Vertebrate scavengers are an underappreciated and understudied scavenger guild.
2. The ability to scavenge may be most advantageous in habitats altered by human activity. Tropical islands are now heavily altered by invasive species, especially mammals and birds. Understanding scavenging on and by these animals may provide insight into whether carcasses are acting as a stabilizing resource for invasive species populations and/or contributing to invasional meltdowns.
3. This study sought to elucidate the influence of invasive mammal and bird carcasses on island ecosystem food webs by experimentally placing carcasses in several different habitats with trail cameras to quantify vertebrate scavenging efficiency and preference. We documented the following vertebrates scavenging on the Big Island of Hawai'i: mongoose, rodents, cats, and pigs, all invasive mammals. The following experimentally placed carcass types: mouse, rat, bird, and mongoose, were scavenged by vertebrates at 76.4%, 80.0%, 80.2%, and 36.7% efficiency, respectively.
4. We elucidated the potential importance of energy derived from these invasive species carcasses to invasive species scavengers, as well as the factors that influence a scavenger's decision to utilize specific carcass resources in certain habitats. Furthermore, this information can be used to model the importance and impact of carcass resources on invasive species populations and as a result help to predict their impact on native species and ecosystems with the influx of future invasive species.

INDEX WORDS: Birds, Camera traps, Food web, Invasional meltdown, Mammals, Mongoose, Pacific, Rats, Scavenging ecology

INTRODUCTION

Indisputably, the breakdown of carcass resources is a vital ecosystem service provided by organisms across biological kingdoms, and quantifying the amount of resources processed by the various scavenger guilds (i.e. vertebrates, invertebrates, decomposers) is critical to our understanding of how carcass resources sustain these groups and influence their impacts on other ecosystem processes (Putman 1978). It is likely that the redistribution of energy by the vertebrate scavenger guild, as opposed to other guilds, could be far more influential in ecosystem-wide trophic interactions and processes than is currently understood (DeVault, Rhodes & Shivik 2003). Scavengers, such as vertebrates, invertebrates, and decomposers, such as bacteria and fungi, convert a carcass into useable energy in fundamentally different ways, each with cascading influences on how that resource is incorporated back into the ecosystem (Putman 1978; Brussaard *et al.* 1997; Wilkinson, Hocking & Reimchen 2005; Bump, Peterson, & Vucetich 2009). While decomposers convert carcass protein into its elemental components that are further broken down into minerals and taken up by plants, scavengers assimilate carcass protein directly into their own bodies. Through this process, scavengers are more able to rapidly transfer carcass resources to higher trophic levels than decomposers (Putman 1983). Until recently, invertebrate scavengers and decomposers were thought to acquire the vast majority of carcass resources, but recognition of the prevalence of facultative scavenging (scavenging by organisms not reliant solely on carcasses for survival and reproduction) within the vertebrate predator community and the magnitude of resources it processes is increasing (Swift & Anderson 1994; Jedrzejewska & Jedrzejewski 1998; DeVault *et al.* 2003; Roth 2003; Selva *et al.* 2003; Wilmers *et al.* 2003a; Wilmers *et al.* 2003b; Selva *et al.* 2004; Selva *et al.* 2005). A review of this research revealed that on average vertebrates consume 75% of available carcasses, pointing to the relative importance of vertebrates for carcass removal, as well as the importance of carcass resources to a wide range of vertebrates (DeVault *et al.* 2003). While environmental factors (such as temperature, moisture, predation risk, and population densities) are thought to influence vertebrate scavenging efficiency, a theory synthesizing how and why efficiencies differ across different environments is lacking (McKillup & McKillup 1994; DeVault & Rhodes 2002; Parmenter 2005; DeVault *et al.* 2011).

Recent, experimental scavenging research has greatly expanded our understanding of vertebrate scavenger diversity and efficiency, but the majority of such studies have been conducted in intact, relatively natural landscapes within temperate regions using native species (DeVault *et al.* 2003). Exceptions to this are several studies conducted in landscapes heavily altered by agriculture and human development that suggest vertebrate scavenging efficiencies may be higher here than in comparable forest habitats (DeVault *et al.* 2003; DeVault, Brisbin & Rhodes 2004; DeVault *et al.* 2011; Olson *et al.* 2012; Huijbers *et al.* 2013). Human-altered landscapes are now prevalent worldwide and this type of habitat disturbance significantly impacts native species and ecosystem function through a variety of processes (Lindenmayer & Fischer 2013). Thus, understanding changes in the critical ecosystem process of scavenging and specifically the distribution of carcasses between scavenger guilds in human-altered landscapes is a topic of global relevance (Sekercioglu 2006; Kibblewhite, Ritz & Swift 2008; DeVault *et al.* 2011).

In addition to habitat alteration, the introduction of invasive species represents one of the most significant human-mediated changes to ecosystem function at a global scale (Crowl *et al.* 2008; Pejchar & Mooney 2009; Pimentel 2011). Where invasive species invade an ecosystem, native biodiversity tends to be degraded, especially on islands, but concomitant impacts upon ecosystem processes are poorly understood (James 1995; Sax, Gaines & Brown 2002; Blackburn *et al.* 2004; Clavero & Garcia-Berthou 2005; Steadman 2006). Unfortunately, determining which vertebrate invasive species scavenge and their efficiency in highly invaded ecosystems has never been investigated, but the potential for negative impacts on invaded ecosystems could be great considering how influential scavengers are in their native ecosystems.

Invasive species now have a worldwide distribution and negatively influence health, economics, and the environment at a cost of $120 billion per year in the USA alone (Pimentel, Zuniga & Morrison 2005). Many mammal and bird species, especially, are considered to be very successful, harmful invaders, but while much research has been conducted on their negative impacts, there is still controversy in quantifying the magnitude of their impacts on native species and ecosystem processes (Nentwig, Kuhnel & Bacher 2010; Kumschick & Nentwig 2010; Strubbe, Shwartz & Chiron 2011). Of those ecosystem types most vulnerable to invasions, tropical islands have suffered greatly from the negative impacts of invasive species, especially invasive mammals and birds, which can achieve extremely high densities within such environments (D’Antonio & Dudley 1995; Crooks & Soule 2001; Clout & Veitch 2002; Borroto-Paez 2009; Glen *et* *al.* 2013). Additionally, it is likely that the lack of predators in tropical, insular habitats helped many mammal and bird species invade and has led to a high availability of carcasses via other mechanisms, such as starvation, exposure, and disease (Schoener & Spiller 1995; Tyler & Øritsland 1999; Oksanen & Oksanen 2000; Reaser *et al.* 2007). Only a handful of studies have examined how carcass resources are utilized in island ecosystems, but results have shown the potential for carcasses to have dramatic impacts, potentially contributing to invasional meltdowns (Howald *et al.* 1999; McNatty, Abbott & Lester 2009; Wilson & Wolkovich 2011; Beasley, Olson & DeVault 2012; Schlacher, Strydom & Connolly 2013). Invasional meltdowns occur when invasive species have a positive impact on other invasive species and accelerate the negative impacts of one or both groups through an increased probability of survival and/or increased population size (Simberloff & Holle 1999). By examining scavenging efficiency both on and by invasive species in island ecosystems, scientists can combine both invasion and scavenging ecology to explore whether invasive species carcasses contribute to invasional meltdowns or, conversely, act as a stabilizing force within food webs (O'Dowd, Green & Lake 2003; Wilson & Wolkovich 2011).

Quantifying vertebrate scavenging efficiency within invaded, tropical, island ecosystems is critical research that will provide insights into the abilities of invasive species to utilize carcass resources, which may have assisted their initial invasion and/or persistence. This will also help to evaluate and mitigate the realized and potential impacts of invasive species on native species and ecosystems. Our study quantifies the use of mouse (*Mus musculus*), rat (*Rattus rattus* and *exulans*), bird (various species), and mongoose (*Herpestes javanicus*) carcasses within the highly invaded tropical island ecosystem of the Big Island of Hawai'i. We experimentally placed camera traps baited with carcasses in three distinct habitats on the Big Island of Hawai'i and recorded the vertebrate species that interacted with each carcass, each type of interaction (removed, partially consumed, touched, investigated but not touched, investigated area after carcasses removed, or passed without interaction with carcass or area), and the time that it occurred. Our objective was to use these data to:

1) Describe the vertebrate scavenger community on the Big Island of Hawai'i and quantify the number and percentage of each carcass type each vertebrate scavenger species removed from each site,

2) Quantify the efficiency of the vertebrate scavenger community, as a whole, compared to other scavenger guilds (invertebrates and decomposers) and quantify the efficiency of the dominant vertebrate scavenger compared to the other vertebrate scavengers and determine whether differences in these efficiencies occurred as a function of site or carcass type,

3) Evaluate the ability of the dominant scavenger to find carcasses at each site as a function of time, and

4) Evaluate carcass preference of vertebrate scavengers relative to site and carcass type.

MATERIALS AND METHODS

Study Species

The invasive species carcasses used in this study were Polynesian and roof rats (carcasses used were approximately 40-175 grams), mice (10-25 g), mongoose (300-900 g), and birds (12-130 g). Rodent species were accidentally brought to Hawai'i on ships. Polynesian rats were brought to Hawai'i by the Polynesians in the 5th century (Kirch

1982). Roof rats were brought over in the 1870s, and the house mouse arrived in 1816 (Atkinson 1977). Rodents, mainly the roof rat, are common throughout Hawai'i and are thought to have contributed to the decline of native bird species through nest predation, as well as damage to agricultural crops (Atkinson 1977; Tobin *et al.* 1993). Mongoose were brought to Hawai'i intentionally by Europeans in 1883 as a biological control agent for rats that had proliferated on the islands (Baldwin, Schwartz & Schwartz 1952). While the success of mongoose at decreasing rodent populations is debated, this species is thought to have contributed to the decline of native bird species through nest predation, although this is supported by limited evidence (Hays & Conant 2007). Mongoose have large, well-established populations on the Big Island of Hawai'i. The invasive bird species used in this study were zebra (*Geopelia striata*) and spotted-necked (*Spilopelia chinensis*) doves, nutmeg mannikins (*Lonchura punctulata),* and common mynas (*Acridotheres tristis*). All species were intentionally introduced to Hawai'i for aesthetic purposes. Zebra doves were introduced in 1922 (Williams & Fleischer 1989), spotted-necked doves in the late 1800s (Marshall & Kozar 2008), and nutmeg mannikins and common mynas in 1866 (Meier 2005). These species are common in some, mostly urban, areas and are believed to act as reservoirs for avian malaria, contributing to the decline of native bird populations (van Riper, III, van Riper & Hansen 2002). All of the invasive species used in this study are considered common and widespread through the Big Island of Hawai'i.

Study Site

Two protected areas, Hawai'i Volcanoes National Park and Pu'u Maka'ala Natural Area Reserve, on the Big Island of Hawai'i were chosen to assess the utilization of invasive mammalian and bird carcasses within the island ecosystem of Hawai’i. Three sites, representing a range of soil and habitat types which occur on the island, were chosen from these two protected areas. Site 1 was a coastal lava field, characterized by mostly intact lava with relatively few trees and shrubs and sparse grasses (Figure 3.1). Refuges on this site were small and consisted of caves under layers of buckled lava. Carcasses were placed approximately 500 m to 2 km from the coastline. Site 2 was further inland, approximately 10 km, and had soil varying from intact lava flows to small pebble-like substrate. The vegetation consisted of trees, shrubs, and grasses that were thick in some areas but short in height. Wide, deep cracks were interspersed throughout this site. Site 3, also inland (16-25 km), was rainforest-like in nature with moist soil that gave rise to an abundance of thick vegetation, mostly shrubs and relatively tall trees, that provided a multitude of refuges. All sites experience similar levels of rainfall and temperature that are consistent year-round, but due to differences in lava flow history and subsequent substrate and vegetation development, the sites exemplify very different habitats. These three sites were chosen to represent the diversity of habitats on the Big Island of Hawai’i, as well as potential vertebrate scavenger communities.

Experimental Design

To study the vertebrate scavenger communities at these three sites on the Big Island of Hawai’i, camera traps baited with invasive mammal and bird carcasses were experimentally placed in the field from July-September 2014. At each of the three sites, approximately 120 carcasses, including 30 from each of the four taxa, mice, rats, birds, and mongoose, were used in experimental trials. Carcasses were acquired from the UDSA, Wildlife Services Field Office in Hilo. Carcasses were placed on an external triggering device approximately 1/3-1 m in front of cameras (Reconyx HyperFire PC900, Wisconsin, USA) that were attached to trees or rocks a few centimeters to 1/2 m above the ground. To maintain independence among trails, cameras were placed approximately 200 m from other camera traps at the site along transects and 50 m from major roads (Pitt, Sugihara, & Berentsen 2015). Cameras were programmed to record 3 photos every 15 minutes, whenever triggered by movement, or when prompted by the external trigger. After approximately 6 days, the camera traps were moved 50-100 m and set-up with fresh carcasses. After each trial, any remaining carcass material was described and removed from the field and evidence of invertebrate scavenging was noted. Once approximately 30 successful trials had been run for each carcass type at each site, all camera traps and carcasses were removed from the field. A trial was considered successful if the fate of the carcass could be determined through photo analysis, i.e. scavenging event recorded, or observation in the field, i.e. carcass remained.

Data Analysis

All photos were examined and each independent vertebrate visit to a carcass was recorded. A visit was considered independent if it occurred more than 2 minutes from the previous visit by the same vertebrate species. Visits by different vertebrate species that occurred within 2 minutes of each other were recorded. For each visit, the vertebrate species was recorded, the time of observance, and the type of interaction with the carcass (removed, partially consumed, touched, investigated but not touched, investigated area after carcasses removed, or passed without interaction with carcass or area). An interaction was characterized as “removed” if the scavenger was photographed fully consuming the carcass or removing the carcass from the view of the camera. “Partially consumed" was recorded if the scavenger consumed or removed only part of the carcass. Invertebrates that were visible on photographs or present when the carcass was retrieved at the end of the trial were noted. When carcasses were removed wholly or primarily by invertebrates, the carcass was recorded as having been scavenged by other scavenger guilds.

To determine the vertebrate scavengers on the Big Island of Hawai'i and their scavenging efficiency (Objective 1), we compiled a list of the vertebrate scavenger species that removed carcasses, and for each site, quantified the numbers of each carcass type that were acquired by all vertebrate species combined, other scavenger guilds, and then each vertebrate species separately (expect for rodent species which were grouped together). The percentages that were acquired by all vertebrate species combined and other scavenger guilds were calculated, as well as for the carcasses removed by the dominant vertebrate and all other vertebrate species within the vertebrate scavenger community.

To address Objective 2 which sought to compare scavenging efficiencies between guilds and across sites and carcass types, we first used log-linear models to examine the vertebrate scavenger community's efficiency (percentage of carcasses removed) at acquiring different carcass types at the three sites, as compared to the other scavenger guilds. We then ran this same analysis to examine scavenging efficiency solely within the vertebrate community, comparing the dominant scavenger to all other vertebrate scavengers. Initially three-way interactions between scavenger, site, and carcass were analyzed for both data sets; if appropriate based on those results, we evaluated two-way interactions and main effects by sorting data sets by site and by carcass type. We used the

CATMOD procedure in SAS software, Version 9.3 to construct log-linear models (SAS Institute Inc., Cary, NC, USA).

To identify differences in time to scavenge and time to find carcasses across sites (Objective 3), we used a 2-way factorial ANOVA to compare the time (dependent) that it took for the dominant vertebrate scavenger to find and then to remove each of the carcass types (independent) at each of the sites (independent). We did this to evaluate differences in the relative swiftness of vertebrate scavengers at finding and removing different carcass types among the 3 sites. If the ANOVA was significant, we performed a Tukey HSD test to evaluate differences among mean times to find or to remove different carcass types within and between sites.

To quantify carcass preference (Objective 4), we modified methods for describing bait preference from Berentsen, Johnson & VerCauteren (2014). Five different carcass interactions were assigned classifications for carcass preference. The highest class was assigned to the interaction that showed the greatest preference for a carcass, removed completely on the first visit. If the carcass was removed on a subsequent visit, partially consumed, or just investigated it was classified as 3, 2, or 1 respectively. If a carcass was never found by vertebrates, then it was classified as 0. When carcasses were visited multiple times, the highest class of interaction recorded was assigned to that carcass. Each carcass was thus given one score, 0 through 4, and all the scores for each carcass type were summed to get the rank sum for mice, rats, birds, and mongoose carcasses separately. Ranks sums were calculated using the highest classification observed at each carcass and were evaluated in three groups, 1) carcasses for which the highest classification was associated with the dominant vertebrate scavenger, 2) carcasses for which the highest classification was associated with vertebrates other than the dominant vertebrate scavenger, and 3) the entire pooled set of vertebrate scavengers. Carcasses that were not found by vertebrate scavengers (score of zero) were included in analyses of all three groups. These rank sums were used to give each of the carcass types a preference rank for each of the three groups. Ranks were compared using a Kruskal-Wallis test adjusted for ties and carcass types were compared using the Mann-Whitney test. We also reported the average elapsed time and average number of visits that it took for the dominant vertebrate scavenger, other vertebrate scavengers, and all vertebrates combined to remove carcasses.

Lastly, we summed all the times that an individual vertebrate scavenger species was recorded by our camera traps at each site, regardless of the carcass type or its presence or absence. We did this to provide an index of relative occurrence for each vertebrate scavenger species at each site, which was used to interpret differences in scavenging efficiency data between sites.

To verify carcass consumption, we outfitted a rat, bird, and mongoose carcass at both Sites 1 and 2 and a mouse and bird carcass at Site 3 with small (2g) internally secured radio transmitters (Advanced Telemetry Systems, Minnesota, USA) in August-September 2014. The carcasses were tracked after approximately 5 days, and the location and evidence of scavenging was noted.

RESULTS

Vertebrate scavenger species and efficiencies on Hawai'i – Obj. 1

The following vertebrate species, all invasive, were found to scavenge our experimentally placed mammal and bird carcasses: mongoose (*Herpestes javanicus*), rodents (*Rattus sp.*), cats (*Felis catus*), and pigs (*Sus scrofa*, Figure 3.2). Of the 360 mammal and bird carcasses experimentally placed in the field, a total of 246 carcasses were scavenged by vertebrates (68.3%, Table 3.1). Vertebrate scavengers together removed 57.5%, 82.5%, and 65.0% of all carcasses experimentally placed at Sites 1, 2, and 3 respectively. Mongoose were the dominant vertebrate scavenger at all sites, removing 49.2%, 60.8%, and 33.3% of all carcasses placed at Sites 1, 2, and 3 respectively (Table 3.2). Rodents and cats also scavenged at all sites. Pigs scavenged at Site 2. Mongoose and pigs were the only scavengers to remove mongoose carcasses.

Scavenger guild efficiencies analyzed by site and by carcass type – Obj. 2.1

For the analysis of scavenging efficiency between the scavenger guilds, the initial three-way interaction for scavenger, carcass type, and site was significant (p-value = 0.0010), so the data were sorted, first by site and then by carcass, and analyzed for two-way interactions and main effects (Table 3.3). When the data were sorted by site, the log-linear models used to evaluate scavenging efficiency between vertebrates and other scavenger guilds revealed significant interactions between scavenger and carcass type at Sites 2 and 3 (p-value = 0.0036 and <0.0001 respectively). At these sites vertebrates removed a significantly higher percentage of all carcass types than those completely or partially consumed by invertebrates, except for mongoose carcasses at Site 3, of which none were removed by vertebrates. When the data were sorted by carcass type, log-linear models revealed significant interactions between scavenger and site for mice, rat, and mongoose carcass types. Mouse carcasses were removed by vertebrates at a higher percentage than by other scavenger guilds at Sites 2 and 3 and at a slightly lower percentage at Site 1 (p-value = <0.0001). Rat carcasses were removed at a higher percentage by vertebrates than by other scavenger guilds at all 3 sites, but only slightly higher at Site 1 (p-value = 0.0010). Mongoose carcasses were removed by vertebrates more so than by other scavenger guilds at Site 2, slightly less at Site 1, and not at all at Site 3 (p-value = <0.0001). For bird carcass there was a main effect of scavenger (p-value = <0.0001) with the majority of bird carcasses at all 3 sites being removed by vertebrates.

Scavenging efficiencies within the vertebrate community as a function of site and carcass type – Obj. 2.2

For the analysis of scavenging efficiency between the dominant vertebrate scavenger and all other vertebrate scavengers combined, the three-way interaction was not significant, but both the interactions of scavenger and carcass, as well as scavenger and site, were significant in the full model (p = 0.0183, 0.0165 respectively, Table 3.3). This indicated that carcass type influenced what scavenger (mongoose vs other vertebrate) would remove carcasses when data were pooled across sites; and when pooled across carcass type, the site influenced what scavenger would remove carcasses. When the data were pooled across site, mongoose removed more of all carcass types (rat – 57 vs 15, bird – 47 vs 26, mongoose – 31 vs 2), although only slightly more mouse carcasses (37 vs 31). When the data were pooled across carcass type, mongoose removed vastly more carcasses than other vertebrates at Sites 1 (59 vs 10) and 2 (73 vs 26) but only slightly more at Site 3 (40 vs 38).

Dominant vertebrate scavenger time to find and remove carcasses – Obj. 3

The amount of time that elapsed before a mongoose, the dominant vertebrate scavenger at all three sites, found a carcass was significantly influenced by the main effect of site, but not carcass type (p-value = 0.0347). The Tukey HSD test revealed that mongoose found carcasses at Site 2 significantly faster than at Site 3 (p-value = 0.0259). Mongoose removed 172 out the 225 carcasses that they found (76.4%). The ANOVA also revealed significant differences in the amount of time that elapsed before a mongoose removed (but not found) different carcass types, regardless of site (p-value = 0.0065). Significantly more time elapsed before mongoose carcasses were removed when compared to mouse and rat carcasses (p-value = 0.0059 and 0.0412 respectively). The average time until removal and average number of visits to a mouse, rat, bird, and mongoose carcass by a mongoose was 42.43(1.0), 50.00(1.0), 59.80(1.1), and 70.34(6.1) hours (number of visits) respectively (Table 3.4). The average time until removal and average number of visits to carcasses by other vertebrate scavengers and all vertebrates together is provided in Table 3.4.

Vertebrate scavenger carcass preference analysis – Obj. 4

Vertebrate scavenger preference was analyzed for the following three groups: mongoose, all other vertebrate scavengers, and all vertebrate scavengers combined. When the carcass preference of vertebrate scavengers was analyzed separately, i.e. mongoose and all other vertebrates, there were 65 carcasses with which both mongoose and rodents had the highest class interaction. Thus those 65 carcasses were counted in the analysis for both groups. None of the other carcasses (N = 295) had interactions from both groups concomitantly at the highest classification level. A total of 41 carcasses were not found by vertebrate scavengers (11.4%) and a classification of 0 was counted for these carcasses in the analysis of mongoose, other vertebrates, and all vertebrates together. When all vertebrate scavengers were analyzed as one group, the highest class interaction for each carcass was only counted once.

For carcasses scavenged by mongoose, there was a significant treatment effect of carcass type (p-value = <0.0001) with rats ranked the highest (most preferred, rank sum = 208), then birds (165), mongoose (144), and mice (133, Table 3.4). Mongoose carcasses had significantly different ranks than mouse, bird, and rat carcasses (p-value = 0.0051, <0.0001, and <0.0001), but there was no significant difference between the ranks of the other carcass types. For carcasses scavenged by other vertebrate scavengers, there was a significant effect of carcass type (p-value = 0.0217) with mice ranked highest (most preferred, rank sum = 115), birds second (101), rats third (57), and mongoose last (44). There was a significant difference between the ranks of mongoose carcasses and those of mouse and bird carcasses (p-value = 0.0102 and 0.0036). When all vertebrate scavengers were analyzed together, there was a significant effect of carcass type (p-value= <0.0001) with birds ranked highest (266), then rats (265), mice (248), and lastly mongoose (163). There was a significant difference between the ranks of mongoose carcasses and mouse, bird, and rat carcasses (p-value= <0.0001 for all).

Relative occurrence data, invertebrate scavengers, and carcass consumption

The relative occurrence data indicated that mongoose, rodents, and cats were present at all 3 sites, and that pigs were present at Site 1 and Site 2 (Figure 3.5). Pigs were never recorded at Site 3, where feral swine removal efforts are most intense. The two scavengers recorded most by our camera traps were mongoose and rats. Figure 3.5 shows the relative occurrence of each scavenger at each site during our trials.

Unexpectedly, we were also able to record large invertebrates dragging away carcasses and consuming large portions of carcasses in view of the cameras. Invertebrates were identified to the lowest possible classification from photographs. The following invertebrates were recorded scavenging: centipedes (Class: Chilopoda), yellow jackets (Family: Vespidae), cockroaches (Order: Blattodea), ants (Family: Formicidae), flies (Order: Diptera), beetles (Order: Coleoptera), grasshoppers (Order: Orthoptera), and slugs (Class: Gastropoda), many of which are invasive.

Of the carcasses outfitted with radio transmitters, we determined from photographs that 6 out of 8 were scavenged by mongoose, one was scavenged by a rodent, and the other carcass was not removed by a vertebrate. Transmitters were recovered 0.3-23m away under shrubs (3), in burrows (1), or in lava caves or cracks (2). With three of the recovered transmitters, a small part of the carcass was left un-scavenged. For the one mongoose and two bird carcasses found, only the head and spine of the mongoose and feathers of the birds remained. This evidence suggested to us that when vertebrate scavengers did not eat carcasses in full view of the camera trap, they took carcasses a short distance away to a refuge where they then consumed the majority of the carcass.

DISCUSSION

Our study indicates that invasive mammal and bird carcasses are scavenged in very high percentages by mammalian vertebrate scavengers in the highly invaded ecosystem of Hawai’i. This evidence adds to a growing body of research that suggests some invasive species could be assisting the invasions of other invasive species and in doing so accelerating the impacts of one or all parties on native species and ecosystems, a process referred to as invasional meltdown. Our data provide insights into the composition and efficiencies of the vertebrate scavenger community relative to habitat and carcass types in a highly invaded tropical island ecosystem. Our research also explores the decision by vertebrates to scavenge or not. While it may seem advantageous to always scavenge a carcass, some carcasses are associated with higher consumption and searching costs, including costs associated with toxins, predation, or carcass longevity. Our preference analysis is the first of its kind to combine the complicated set of choices made by scavengers with scavenging efficiency. From these data, we start to get an idea of how different types of scavengers utilize different carcass types in different habitats that vary by a multitude of factors, such as invertebrate scavenger communities, other available nutrient resources, refuges, temperature, and retained moisture.

With respect to patterns observed between vertebrate and other scavenger guilds across sites, we found that vertebrates were able to remove carcasses at percentages higher than other guilds in Sites 2 and 3 and were able to scavenge at efficiency rates comparable to other guilds at Site 1. We believe that this pattern was influenced by the relative occurrence of vertebrate scavengers at the sites. Relative vertebrate occurrence was highest at Sites 2 and 3 and least at Site 1. Although the amount of time mongoose required to remove and consume carcasses did not differ among the sites, the time to find carcasses of any type was least at Site 2. This is likely due to the high occurrence of mongoose at Site 2 and possibly environmental characteristics that increase mongoose searching efficiency and the amount of effort devoted to searching for carrion. The efficiency of vertebrates was also influenced by carcass type, which we interpret as being related to the size of and preference for particular carcass types. The smallest carcass, mouse, was removed at a higher percentage by vertebrates than by other scavenger guilds at Sites 2 and 3, but vertebrates removed lower percentages of mice at Site 1. Rat and bird carcasses, which were slightly larger than mice, were removed more often by vertebrates at all three sites, although rats were removed only slightly more often at Site 1, reflected in the significant interaction between scavenger and site. We suggest that this pattern is due to the persistence of the carcasses in the environment. The longer persistence time of the larger rat and bird carcasses, compared to mouse, made them available to vertebrates for longer amounts of time.

Alternatively, mongoose carcasses are large and persist the longest in the environment, but it may be that their consumption by vertebrates is more reflective of scavenger preference. For example, while there was no difference in the amount of time to detection of various carcass types by mongoose, the amount of time that elapsed before mongoose scavengers removed mongoose carcasses was significantly higher than the amount of time used to remove mouse or rat carcasses. Also, the average number of visitations to mongoose carcasses by mongoose prior to carcass consumption trips was greater than that for mice and rat carcasses (6.1 compared to 1.0). Mongoose carcasses were removed more often by vertebrates than by other guilds only at Site 2 and were removed by vertebrates slightly less than the percentage consumed by other guilds at Site 1. No mongoose carcasses were taken by vertebrates at Site 3. The trend at Site 1 could reflect the low number of vertebrate scavengers seen at Site 1 relative to Sites 2 and 3. The fact that no mongoose carcasses were removed by vertebrates at Site 3 could be due the higher available resources at that site, suggesting that mongoose carcasses are only utilized in resource limited habitats. This trend could also be due to the large size of the mongoose which makes them difficult to move and a potentially riskier resource to be consuming in areas with a higher threat of predation. Regardless, mongoose carcasses were generally less utilized by vertebrates than the other experimentally placed carcasses.

Our data on scavenging efficiency rates for vertebrate and non-vertebrates provides insights into the relative amount of carcass resources entering the food web through each scavenger guild. However, the resolution of our data for vertebrates as individual species was limited, thus scavenging data for cats and pigs were combined with rodents for our intraguild analysis of the vertebrate scavenger community, where we compared data for the dominant scavenger, mongoose, to that for the remainder of the vertebrate species we detected scavenging. With respect to the influence of site and carcass type on scavenging efficiencies within the vertebrate scavenger guild, mongoose acquired vastly more rat, bird, and mongoose carcasses, but the strength of their dominance varied by site. We revealed that mongoose removed more carcasses than all other vertebrates combined at Sites 1 and 2, while the data for Site 3 indicated no difference in the number of carcasses acquired by mongoose compared to other vertebrate scavengers, mainly due to the increased number of carcasses removed by rodents at Site 3 compared to the other sites. We interpret this finding as a consequence of the higher relative occurrence of rodents at Site 3, compared to Sites 1 and 2, as well as scavenger preference for certain carcasses.

When data were pooled across sites, mongoose removed vastly more carcasses, except for mouse carcasses which were scavenged by both mongoose and other vertebrates at similar rates, with mouse carcasses least preferred by mongoose and most preferred by other vertebrates. We believe that these contrasting patterns of scavenging efficiency and preference for mouse carcasses reflect the ease with which other vertebrates can scavenge this small carcass as well as the limited ability of mongoose to find a small mouse carcass before it is entirely degraded.

While our data reveal the seemingly critical importance of facultative scavenging to invasive vertebrates on the Big Island of Hawai'i, we are not able to further quantify the role of invertebrates below the level of the scavenger guild. The next phase of this research is to classify the invertebrate scavenging community, specifically describing those that are invasive. The available data indicate that on average 20 alien invertebrate species become established on Hawai'i each year, compared to historic rates of 1 every 50-100,000 years (Holt 1999). These invasive invertebrates could potentially be as influential on ecosystem processes as invasive vertebrates, but as is the case with scavenging, their impacts could go unnoticed. Ultimately, the competition between the vertebrate and invertebrate communities for carcass resources may dictate the value of carcass resources to the success of establishment for invasive species.

In conclusion, there is still much we don't understand about the ecology of scavenging and the influence that this behavior has on invasive species establishment and success within ecosystems. However, our data reveal evidence that invasive species consume the carcasses of invasive vertebrates at very high rates, some even cannibalistically, leading us to conclude that scavenging may contribute to invasive species establishment via the process of invasional meltdown. Despite this conclusion, we still do not know how carcass resources influence the growth of invasive vertebrate populations (increased growth vs stabilization) or contribute to the impacts of invasive vertebrates on native species and ecosystems (alleviating or exacerbating pressure). Our data provide insight into the potentially complex interaction between scavenging efficiency and scavenger preference, which likely varies as a function of habitat type, carcass type, and scavenger abundance. More experimentation is needed to dissect the interactions among these factors, hopefully leading to a more synthesized theoretical framework by which to evaluate the process of island invasion. The combination of scavenging and invasion ecology presents an exciting new avenue for research that should ultimately lead to an understanding of the population-level impacts of invasive species and possibly provide substantive empirical support for the invasional meltdown theory. Research that can provide concrete data on the impacts of invasive species is in critical need for conservation initiatives to help mitigate the impacts of detrimental invasive species on highly imperiled species and ecosystems, especially tropical islands.

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Table 3.1 The number of mammal and bird carcasses scavenged by all scavengers (vertebrates and other scavenger guilds) shown separately for each carcass type and site. The percentages show the number of carcasses scavenged by vertebrates compared to other scavenger guilds at each site (combining all carcass types) and total for all sites (in the far right column).

All Scavengers		**Site 1**		**Site 2**		**Site 3**		**Total Removed sorted by:**		
		Count	**%**	**Count**	**%**	**Count**	**%**	**Carcass**	**Scavenger**	**%**
Vertebrates	Mouse	14		27		27		68		
	Rat	18		29		25		72		
	Bird	23		24		26		73		
	Mongoose	14		19		-		33		
Total removed		69	57.5%	99	82.5%	78	65.0%		246	68.3%
Other	Mouse	16		3		2		21		
	Rat	12		1		5		18		
	Bird	7		6		5		18		
	Mongoose	16		11		30		57		
Total removed		51	42.5%	21	17.5%	42	35.0%		114	31.7%
Total set out		120		120		120			360	

Table 3.2 The number of mammal and bird carcasses scavenged by all vertebrate scavenger species shown separately for each carcass type and site. The percentages show the number of carcasses scavenged by mongoose compared to other vertebrates (combining all carcass types) and total for all sites (in the far right column).

Vertebrate		**Site 1**		**Site 2**		**Site 3**		**Total Removed sorted by:**		
Scavengers	**Carcass**	**Count**	**%**	**Count**	**%**	**Count**	**%**	**Carcass**	**Scavenger**	**%**
Mongoose	Mouse	10		16		11		37		
	Rat	17		26		14		57		
	Bird	18		14		15		47		
	Mongoose	14		17		-		31		
Total removed		59	49.2%	73	60.8%	40	33.3%		172	47.8%
Rodent	Mouse	1		8		14		23		
	Rat	-		2		10		12	54	
	Bird	1		7		11		19		
	Mongoose	-		-		-		-		
Cat	Mouse	3		-		2		5		
	Rat	1		1		1		3	13	
	Bird	4		1		-		5		
	Mongoose	-		-		-		-		
Pig	Mouse	-		3		-		3		
	Rat	-		-		-		-	7	
	Bird	-		2		-		2		
	Mongoose	-		2		-		2		
Total removed		10	8.3%	26	21.7%	38	31.7%		74	20.6%
Total set out		120		120		120			360	

Table 3.3 Factors and associated p-values that significantly influenced the percentage of mammal and bird carcasses removed by vertebrates when compared to other scavenger guilds and by mongoose compared to other vertebrate scavengers. Shown for 2-way log-linear models used to analyze these data when sorted by site and by carcass type and for full 2 and 3-way models. NS shows the tests that were non-significant.

Sorted by		**Removed by Vertebrate/ Other Scavenger**	**Significant p-values**	**Removed by Mongoose/ Other Vertebrate**	**Significant p-values**
Site	1	NS	-	-	-
	2	scavenger*carcass	0.0036	-	-
	3	scavenger*carcass	<0.0001	-	-
Carcass type	Mouse	scavenger*site	<0.0001	-	-
	Rat	scavenger*site	0.0010	-	-
	Bird	scavenger	<0.0001	-	-
	Mongoose	scavenger*site	<0.0001	-	-
Not sorted		scavenger*carcass*site	0.0010	scavenger*carcass	0.0183
				scavenger*site	0.0165

Table 3.4 Vertebrate scavenger interaction with and preference for mammal and bird carcasses. Shows the descriptions for carcass interaction classifications; the rank for mongoose, other vertebrate, and all vertebrate preference; the sum of the interactions of each class multiplied by that class; the average time it took for each scavenger to remove the carcass; and the average number of visits that each scavenger made before the carcass was ultimately scavenged by a vertebrate.

Description	Class
Carcass removed completely on first visit	4
Carcass removed completely on subsequent visits	3
Carcass partially consumed	2
Carcass investigated only	1
Carcass not found by vertebrate scavengers	0

Scavenger	Mouse	Rat	Bird	Mongoose
Rank – Mongoose	4	1	2	3
Rank sum	133	208	165	144
Average time until removal (hours)	42.43	50.00	59.80	70.34
Average # of visits	1.0	1.0	1.1	6.1
Rank – Other Vertebrate	1	3	2	4
Rank sum	115	57	101	44
Average time until removal (hours)	41.56	31.06	28.66	47.75
Average # of visits	2.3	2.8	5.1	1.8
Rank – All Vertebrates	3	2	1	4
Rank sum	248	265	266	163
Average time until removal (hours)	42.03	46.06	48.71	68.98
Average # of visits	2.0	2.3	3.9	6.3

Table 3.5 Relative occurrence of the vertebrate scavengers recorded by our camera traps in Hawai’i Volcanoes National Park and Pu’u Maka’ala Natural Reserve Area on the Big Island of Hawai’i in 2014. All the independent visits that a vertebrate scavenger made to the camera traps in each site were summed regardless of whether the carcass had already been scavenged.

Scavenger	Site 1	Site 2	Site 3
Mongoose	284	546	347
Rodent	32	393	952
Cat	19	8	11
Pig	2	38	0
Total	337	985	1310

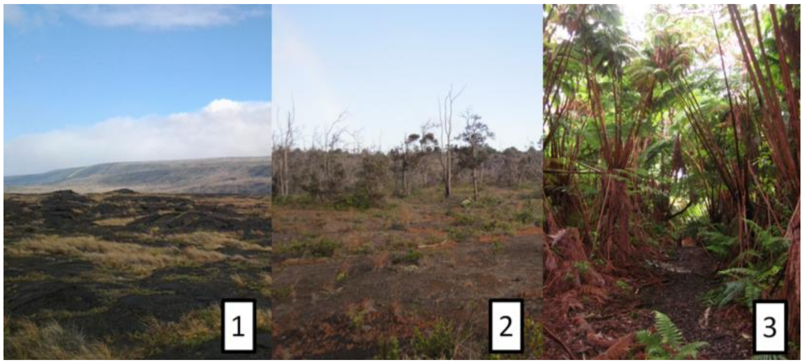

Figure 3.1 The three sites used for scavenging research on invasive mammal and bird carcasses in Hawai'i Volcanoes National Park and Pu'u Maka'ala Natural Area Reserve during July-September 2014. Pictures (from left to right) showing Site 1, an area characterized by lava fields with little vegetation; Site 2, characterized by weathered lava fields and vegetation of short trees, shrubs, and grasses; and Site 3, a rainforest like area with lush, thick vegetation.

Figure 3.2 Images from our scavenging research on the Big Island of Hawai'i showing a mongoose, the dominant vertebrate scavenger, taking a rat and mongoose at Site 2 (top left and right), a rat taking a mouse at Site 3 (middle left), a cat taking a mouse at Site 3 (middle right), and a pig taking a myna bird and mongoose at Site 2 (bottom left and right).

CHAPTER 4

CONCLUSIONS

The main objective of my master's research was to identify the vertebrate scavengers on the Big Island of Hawai'i and to quantify patterns associated with vertebrate scavenging efficiency in habitats characteristic of the island and for a wide variety of readily available carcass types. I was able to identify the vertebrate species that composed the scavenging community relatively easily with the recent advancements in camera trapping technology. My camera traps were programmed to take photographs when triggered by a timer, motion, or a pressure sensitive external trigger. This made my camera traps extremely accurate at capturing scavengers removing carcasses, as well as any action that was performed in the view of the camera. This allowed me to classify interactions between potential scavengers and carcasses in more detail than has ever been accomplished for invasive vertebrate species. With this interaction information and by experimentally placing different types of carcasses at different sites, I was able to evaluate patterns in scavenger behavior associated with scavenging efficiency. This research expands our understanding of basic scavenging ecology by determining what factors influence a vertebrate's ability to find and choice to consume a carcass.

In chapter 2, I experimentally placed carcasses of herpetofauna, coqui frogs, geckos, and cane toads, in three distinct habitats on the Big Island of Hawai'i. I found that invasive vertebrate scavengers, mongoose, rodents, cats, pigs, and myna birds, were willing and able to scavenge at high rates, 37.3% for all carcass types at all sites. In addition to characterizing the vertebrate scavenging community and efficiency rates on the Big Island of Hawai'i, our research showed that patterns of vertebrate scavenging efficiency and preference vary across different habitats and for different carcass types on this highly invaded island. Smaller carcasses were less often removed by vertebrates in habitats with fewer vertebrate scavengers and a more active invertebrate scavenger guild. Larger carcasses were more often removed by vertebrate scavengers, especially in habitats with higher relative abundances of vertebrate scavengers. Toxicity of cane toad carcasses made them apparently unavailable to all scavengers but two, mongoose and rats. Carcass size and type and the numbers and composition of the scavenger community determined the efficiency of the vertebrate scavengers, but I found that previously identified factors, such as temperature and moisture, probably play less of a role in determining scavenging efficiency in this highly invaded, climatically stable tropical island ecosystem.

In chapter 3, I experimentally placed mice, rats, birds, and mongoose carcasses at the same sites wherein the herpetofauna experiments were conducted the previous summer. Using these carcass types, I detected the same vertebrate scavenger community, with the exception of myna birds. However, when using mammalian and avian carcasses, vertebrates scavenged at much higher rates, 68.3% for all carcass types at all sites, than were observed for herpetofauna carcasses. The analysis of the scavenging efficiencies compared across and within scavenger guilds by site and carcass type revealed that the mammal and bird carcasses followed the same patterns as the herpetofauna carcasses. Larger carcasses were more likely to be consumed by vertebrates at all sites, with the exception of the mongoose carcasses that were likely difficult to move. Smaller carcasses were consumed evenly by vertebrates and invertebrates at sites with fewer vertebrate scavengers and more active invertebrate scavenger guilds.

Ultimately, the conclusions from the two studies I performed strongly reinforce some common themes. First, invasive vertebrate scavengers on Hawai'i scavenge invasive species carcasses at relatively high rates. Second, the probability that carcasses will be scavenged by vertebrates increases with the size of the carcass and the number of vertebrate scavengers in the area. Third, the probability that a carcass will be scavenged by vertebrates can be negatively affected by the carcass type (e.g. potentially toxic or difficult to handle) as well as the characteristics of the invertebrate scavenger guilds in each particular habitat. Understanding the interactions among these factors should lead to the enhancement of our ability to quantify the importance of scavenging as a strategy for invasive species and ultimately allow predictions to be made for how invasive species utilize carrion resources in the invasion process and potentially contribute to invasional meltdowns.