

1-1-2018

Estimating Feral Swine Abundance and their Effects on Native Wildlife in the Mississippi Alluvial Valley

Matthew Ryan Ivey

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Estimating feral swine abundance and their effects on native wildlife in the
Mississippi Alluvial Valley

By

Matthew Ryan Ivey

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries, and Aquaculture
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

May 2018

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2018

Estimating feral swine abundance and their effects on native wildlife in the
Mississippi Alluvial Valley

By

Matthew Ryan Ivey

Approved:

Marcus Lashley
(Major Professor)

Bronson K. Strickland
(Committee Member)

Michael E. Colvin
(Committee Member)

Kevin M. Hunt
(Graduate Coordinator)

George Hopper
Dean
College of Forest Resources

Name: Matthew Ryan Ivey

Date of Degree: May 4, 2018

Institution: Mississippi State University

Major Field: Wildlife, Fisheries, and Aquaculture

Major Professor: Marcus Lashley

Title of Study: Estimating feral swine abundance and their effects on native wildlife in the Mississippi Alluvial Valley

Pages in Study 41

Candidate for Degree of Master of Science

Feral swine (*Sus scrofa*) are an invasive species in the Mississippi Alluvial Valley (MAV). They cause millions in damage annually to agriculture, and likely negatively affect native wildlife species. Using camera traps, I monitored 36 forest patches within the MAV to assess the effects of swine invasions on native wildlife species richness. I also modified the double-observer point count technique into a new method for estimating swine abundance with camera traps. Feral swine suppressed native vertebrate richness by 26% when compared to uninvaded patches. I validated the new double-observer technique by determining if it could detect an abundance-area relationship in wildlife populations and estimate a known decrease in abundance following swine removal. This technique was sensitive enough to detect the increase and decrease in abundance and estimated the number of individuals removed from the population relatively accurately. This technique may be useful in the future to manage feral swine populations.

DEDICATION

I dedicate this thesis to my loving parents who have always supported my endeavors. Also, to my wonderful fiancé Victoria who has and always will be my greatest cheerleader and favorite field assistant. Finally, I want to dedicate this thesis to my brother Taylor, who has always been an inspiration to me. You have always persevered and never looked back, accomplishing everything you have dreamed of.

ACKNOWLEDGEMENTS

I thank the Mississippi Agricultural and Forestry Experiment Station (MAFES) for funding this project through their Special Research Initiative. I would like to thank Kevin Nelms for his help in arranging all landowner contacts throughout the project. None of this would have been possible without the help of my dedicated technicians D.J. Steakley, Rainer Nichols, and Bonner Powell. I would like to thank my major advisor Dr. Marcus Lashley and my committee members Dr. Bronson Strickland and Dr. Michael Colvin. Thank you for putting up with my endless questions and constant office visits. Without your help and guidance this would have never come to fruition. I am thankful to have had such brilliant minds to collaborate with throughout my time at Mississippi State. Ultimately, I would like to acknowledge God's unwavering faithfulness through this project and in my life.

TABLE OF CONTENTS

DEDICATION	ii
ACKNOWLEDGEMENTS	iii
LIST OF FIGURES	v
CHAPTER	
I. INTRODUCTION	1
Literature Cited.....	3
II. EFFECTS OF VERTEBRATE INVASIONS ON SPECIES RICHNESS ARE NOT SCALE-DEPENDENT	4
Abstract.....	4
Introduction	5
Methods	8
Results	10
Discussion.....	10
Literature Cited.....	18
III. MODIFIED DOUBLE-OBSERVER TECHNIQUE TO ESTIMATE ANIMAL ABUNDANCE WITH CAMERA TRAPS	23
Abstract.....	23
Introduction	24
Methods	27
Results	29
Discussion.....	29
Literature Cited.....	37
IV. SYNTHESIS AND CONCLUSIONS	41

LIST OF FIGURES

- 2.1 The spatial distribution of forest fragments sampled between February and October of 2016 and 2017 to determine the effects of feral swine invasion on species richness. Located in the Mississippi Alluvial Valley.....14
- 2.2 Species accumulation over time for 36 forest fragments sampled to determine the effects of feral swine (*Sus scrofa*) on species richness. Most species were detected within 14 days in most fragments indicating our 30-day sampling period was sufficient to estimate species richness. The lines depict species accumulation and the grey margins represent the number of possible species to detect (derived from 1000 random permutations within Program R).....15
- 2.3 Log-Log relationship between species richness and area for forest fragments in the Mississippi Alluvial Valley invaded and absent of feral swine. Lines indicate that area has a positive effect on species richness, species richness was 26% lower when invaded by swine, and a lack of scale-dependence (i.e. increased slope when invaded) in the effects of the invasion. In this analysis, naturalized non-native nine-banded armadillos were not included in the species richness.16
- 3.1 This figure depicts overlapping camera trap detection ranges when using paired opposing camera technique. Also displayed are the 5 capture states associated with the double-observer camera trapping technique. Capture states: 1) captured by camera A, but behind camera B, 2) within range overlap, but only captured by camera A, 3) within range overlap, but only captured by camera B, 4) captured by both cameras within range overlap, and 5) captured by camera B, but behind camera A.....34
- 3.2 This figure depicts the detection range of a Bushnell[®] Trophy Cam HD, as determined by an experiment using captive feral swine to trigger the cameras sensors (units = meters).....35

3.3 This plot depicts the positive relationship ($P < 0.001$) between feral swine abundance and patch size of sampled forest patches invaded by swine. Located within the Mississippi Alluvial Valley. This analysis included a large patch (4000 ha) that far exceeded the areal extent of the next largest patch.....36

CHAPTER I

INTRODUCTION

Feral swine (*Sus scrofa*) are an invasive species that are expanding their range across the United States. This invasion is concerning because swine are destructive to the environment, agriculture, and cause other human wildlife conflicts (e.g. vehicle accidents, disease transmission). With natural behaviors like rooting and wallowing, they can cause extensive damage to fields, streams, and crops (Barrios-Garcia and Ballari 2012) and account for an estimated \$1.5 billion in damages each year in the U.S. (Pimental 2007).

With populations on the rise, swine have devastated agriculture production in the Mississippi Alluvial Valley (hereafter MAV) and other areas of the state, accounting for almost \$19 million in damages in 2014 (Anderson et al. 2016). Swine root up freshly planted seed, and force farmers to replant their crops. If crops make it to maturity, swine can damage standing crops. Some of the targeted crops are corn (*Zea mays*), soybeans (*Glycine max*), and rice (*Oryza sativa*). Soil damages by swine may also lead to damaged equipment and injured operators (MSU-ES 2014).

The MAV has a patchy landscape of agriculture and cover, creating a heterogeneous matrix of food resources and cover for swine. With cover ranging from bottomland hardwood forests to Conservation Reserve Program (CRP) lands, most patches are susceptible to feral swine invasion. Swine can thrive in these differing cover

types due to their omnivorous diet and utilization of various food sources (Seward et al. 2004). When inhabiting these patches, swine may affect native wildlife and plant communities in addition to neighboring agriculture fields. Competition for resources with native wildlife species occurs and has the potential to increase with growing swine densities. During foraging, rooting and digging behavior disturbs soil and causes erosion, the set back of plant succession, and acceleration of exotic plant invasion (Mungall 2001). Swine herbivory, predation, competition and habitat effects may have negative effects on many of the native flora and fauna (Gurevitch and Padilla 2004). However, not only is there little empirical evidence on how swine affect native wildlife, those effects are also most likely relative to density, and there are currently no good techniques to robustly estimate swine density. Thus, in this study, I examined the effects of swine on native wildlife species, and developed a new technique to robustly estimate swine abundance to improve swine management efforts.

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CHAPTER II
EFFECTS OF VERTEBRATE INVASIONS ON SPECIES RICHNESS ARE NOT
SCALE-DEPENDENT

Abstract

Biological invasions often have contrasting consequences with reports of invasions decreasing diversity of native species in some cases and facilitating diversity in others. Several authors have suggested these contrasting results in plant and invertebrate communities are an artifact of a fundamental scale-dependent relationship of the effects of invasions on species richness. That is, diversity is suppressed at small scales but facilitated at large scales when invaded. Thus, the scale-dependent relationship is assumed to be universally applicable to all biological invasions but has not been tested in a vertebrate invasion. Whether the scale-dependent effects of biological invasions apply to vertebrate invaders is questionable because invasion ecology studies consistently report that vertebrate invasions in island systems produce different outcomes than plant or invertebrate invasions. Namely, vertebrate invasions generally have a larger effect size on species richness and vertebrate invaders commonly cause extinction whereas extinctions are rare following invertebrate or plant invasions. In an agro-ecosystem invaded by a nonnative ungulate, we monitored species richness of native vertebrates detectable by camera trapping in forest fragments ranging across four orders of magnitude in area. We tested three predictions of the scale-dependence hypothesis

following this vertebrate invasion: 1) vertebrate species richness would positively increase with area, 2) the species richness y-intercept would be lower when invaded, and 3) the rate of native species accumulation with area would be steeper when invaded. Native species richness increased with area and the species-area relationship was indeed suppressed by the invasive ungulate. In fact, feral swine invasion suppressed native vertebrate species richness by 26%. However, we found no evidence that the effects of the invader on species richness were scale dependent. Coupled with the previously observed disparity in the effects of invasions across taxa, our data indicate the scale-dependent effect of biological invasions may not apply to vertebrate invasions.

Introduction

Biological invasions can have contrasting effects on native biodiversity. Most studies report negative effects of biological invasions on native species richness (Mollot et al. 2017). For example, introduced fire ants (*Solenopsis invicta*) reduced native ant diversity by 70% (Porter and Savignano 1990), feral cats (*Felis catus*) are responsible for at least 14% of vertebrate extinctions on islands worldwide (Medina et al. 2011), and most plant invasions in Mediterranean regions negatively impact native plant diversity (Gaertner et al. 2009). However, meta-analyses of biological invasions also report that facilitation of species richness by invaders is common (Rodriguez 2006, Gaertner et al. 2009). For example, zebra mussels (*Dreissena polymorpha*) decrease native bivalve richness substantially, but facilitate invertebrate biodiversity when present (Bially and Macisaac 2000). Invasive European green crabs (*Carcinus maenas*) preyed upon a dominant clam species, which resulted in greater diversity of benthic invertebrates (Grosholz et al. 2000, Grosholz 2005). An introduced toad (*Bufo marinus*) facilitated

native anuran prey through the reduction of native predatory anuran populations (Crossland 2000). Thus, the consequences of biological invasions to biodiversity are variable, and sometimes are context dependent even within a species of invader.

Scale-dependent effects of biological invasions have been proposed as a universal explanation of contrasting effects of biological invasions on biodiversity (Powell et al. 2013). For example, Powell et al., (2013) reported plant invasions negatively affected plant diversity at small scales but had no effect at large scales. Similarly, Altieri et al. (2010) reported a positive relationship only at the large-scale between invasibility and biodiversity of an invertebrate invasion. This positive relationship was explained by facilitation cascades resulting from small-scale positive interactions across trophic levels. However, dissimilarities between the effects of non-vertebrate and vertebrate biological invasions on islands brings into question whether the scale-dependent pattern reported by Powell et al. (2013), Altieri et al. (2010), and many others also applies to vertebrate biological invasions. That is, on islands, vertebrate invasions generally have a larger effect size than non-vertebrate invaders (Mollot et al. 2017), and plant invasions rarely cause extinctions of plant species (Sax and Gaines 2008), but vertebrate invaders are the leading cause of vertebrate extinctions (Clavero and Garcia-Berthou 2005, Bellard et al. 2016, Doherty et al. 2016). More importantly from the perspective of the scale-dependence hypothesis, biodiversity facilitation is most commonly reported in non-vertebrate invasions (Rodriguez, 2006), which may indicate facilitation at large scales occurs less often following vertebrate invasions (Sax and Gaines 2008).

The species-area relationship is fundamental in ecology (May 1975, Connor and McCoy 1979, Rosenzweig 1995) and is a widely used tool to predict declining diversity

(Primack 2006). Because species richness has a predictable positive relationship with area, this tool could be useful to evaluate how biological invasions affect native species richness (Sax and Gaines 2008). Agricultural ecosystems create islands through forest fragmentation in which plant species-area relationships have been documented (Giladi et al. 2011). Thus, because forest fragments may vary substantially in size, they may also serve as a good model system to evaluate how invasive vertebrate species affect native vertebrate species-area relationships. Moreover, feral swine (*Sus scrofa*) are one of the most invasive vertebrate species in the world with one of the widest geographic ranges of any large mammal (Lowe et al. 2000, Barrios-Garcia and Ballari 2012) and have become a nuisance in many agricultural ecosystems (Anderson et al. 2016). Also, feral swine commonly have a strong negative influence on native species via exploitative competition and predation (Graves 1984, Gurevitch and Padilla 2004, Yang et al. 2008, Bevins et al. 2014, Doherty et al. 2016, Mollot et al. 2017). Thus, forest fragments invaded by feral swine in agricultural ecosystems should allow a rigorous test of the scale-dependence hypothesis following vertebrate biological invasions.

In forest fragments recently invaded by feral swine within agro-ecosystems of the Mississippi Alluvial Valley and utilizing the fundamental species-area relationship, we tested three predictions to evaluate the hypothesis that vertebrate biological invasions have a scale-dependent effect on vertebrate species richness. We predicted the number of native species detected would increase with increasing area (i.e., follow predictions of the species-area relationship), that we would detect less native vertebrates than expected in small-scale forest fragments that were invaded by feral swine, and that invaded forest fragments would have a steeper slope of accumulation with increasing area (i.e., scale-

dependent effect on species richness, Powell et al. 2013). To test these predictions, we monitored species richness of vertebrate communities detectable via camera trapping in forest fragments ranging across four orders of magnitude in area with and without feral swine.

Methods

We monitored vertebrate species richness within forest fragments in agroecosystems of the Mississippi River Alluvial Valley in Mississippi, USA (33°40'18.0"N 90°29'57.8"W, Figure 2.1). Nearly 75% of the historic bottomland hardwood forests found in the Mississippi Alluvial Valley have been converted into agriculture, with the remaining forest fragmented into over 38,000 fragments larger than 2 ha (Twedt and Loesch 1999). Forest fragment plant communities were dominated by bottomland hardwood forests. We established systematically random grids of sample points across each forest fragment *a priori* using a 20-hectare grid overlay in ArcMap 10.3.1 (ESRI 2015). We used paired opposing camera traps (Rovero and Marshall 2009) approximately 0.75 meters above the ground and approximately 6 meters apart at a density of 1 pair per 20 hectares in 36 forest fragments ranging from 3-4000 hectares in size. We used the trail-targeting method to strategically place camera traps near animal activity to maximize detection without the use of attractants (Tobler et al. 2008, Kays et al. 2009, Rovero and Marshall 2009, Kolowski and Forrester 2017). Area of fragments was calculated within ArcMap 10.3.1 (ESRI 2015). Any fragment with at least one feral swine detection was considered invaded. Similarly, all species detected on at least one occasion were included in the estimate of species richness for the respective fragment.

We acknowledge that only counting species detectable by camera traps does not represent

all species within a fragment. However, using a subset of true species richness has been determined sufficient and statistically sound for ecological studies on biodiversity (Vellend et al. 2008). Between February and October 2016 and 2017, we sampled each forest fragment for 30 days. To ensure sampling events were long enough in duration to detect the majority of species present based on species accumulation rates, species accumulation curves for each fragment were created within R Studio version 1.0.136 using the *vegan* package and “*specaccum*” function set to random with 1000 permutations. Results from that analysis confirmed that species accumulation satiated at around 10 days on average (Figure 2.2). Thus, the 30 day period should detect the majority if not all species detectable via camera trapping within a forest fragment. We analyzed the data both with and without nine-banded armadillo (*Dasypus novemcinctus*) in species richness due to their human facilitated expansion into the United States (Humphrey 1974, Taulman and Robbins 1996). While the armadillos are non-native, they are also a naturalized species. So, it could be argued that they should or should not be included in our analysis based on their status. Thus, in the interest of transparency, we modeled species richness with and without the inclusion of armadillos. Two linear models were fit within Program R (1: $\ln(\text{SpeciesRichness}) \sim \ln(\text{Area})$, 2: $\ln(\text{SpeciesRichness}) \sim \ln(\text{Area}) + \text{Swine Occurrence}$) to test the predictions that 1) species richness would increase with increasing area, 2) species richness would be suppressed within invaded fragments. A third model was fit ($\ln(\text{SpeciesRichness}) \sim \ln(\text{Area}) + \text{Swine Occurrence} + \ln(\text{Area}) * \text{Swine Occurrence}$), testing our prediction that invaded fragments would have a higher species accumulation rate (increased slope) than non-invaded (i.e., significant interaction term). We evaluated which of these 3 competing

nested models best supported the data using a likelihood ratio test (Hilborn and Mangel 1997).

Results

We detected 41 unique species with species richness ranging from 4 to 26 species in a single forest fragment. We detected feral swine in 11 out of 36 fragments ranging from 28 to 4000 hectares in size. Based on the likelihood ratio test, $\ln(\text{SpeciesRichness}) \sim \ln(\text{Area}) + \text{Swine Occurrence}$ was the top model ($P=0.028$). This model revealed a strong positive effect of area on richness ($R^2 = 0.83$; $P<0.001$, Figure 2.3). Species richness per area of feral swine-invaded forest fragments was 26% lower ($P = 0.026$) than uninvaded forest fragments (17% lower when including the naturalized armadillos in the species richness; $P=0.029$; Figure 2.4). The effect of feral swine was not scale-dependent as indicated by the lack of interaction between area and invasion (Model 3: $\ln(\text{SpeciesRichness}) \sim \ln(\text{Area}) + \text{Swine Occurrence} + \ln(\text{Area}) * \text{Swine Occurrence}$; $P=0.43$).

Discussion

Feral swine invasions suppressed native vertebrate species richness by almost 30%. Although our study was not designed to determine the mechanism by which species richness suppression occurred, our observations are consistent with the average declines observed in other biological invasions (i.e., 21-27%; Mollot et al. 2017). Feral swine have a wide dietary breadth and disturb habitat structure through rooting and wallowing (Graves 1984, Barrios-Garcia and Ballari 2012). Thus, predation, habitat degradation, or exploitative competition could be responsible for the observed decrease. Because the

effect size of predator invasions on richness are generally on the larger end of the scale as is the case with our observations (Mollot et al. 2017), we believe direct and indirect effects of predation risk are the more likely drivers of declines reported herein though habitat disturbance and competition are probably contributing factors.

The lack of scale-dependent effects of feral swine on species richness brings into question whether scale-dependent hypothesis is a universal consequence of biological invasions. In fact, we were unable to find any examples of vertebrate invasions having scale-dependent effects on native species richness even though this relationship commonly has been demonstrated when the invader is a plant (e.g., Fridley et al. 2004, Davies et al. 2005, Powell et al. 2013) or invertebrate (e.g., Mayer et al. 2002, Altieri et al. 2010, Pintor and Sih 2011). Those scale-dependent effects were likely a function of facilitation (Rodriguez 2006). Thus, we may not have detected scale dependence because feral swine may not facilitate native large vertebrates at any scale. However, a scale-dependent effect could be present if feral swine facilitated species richness of taxa not detectable via camera trapping, as they have been documented to facilitate some plant and animal species as a result of biopedurbation (Barrios-Garcia and Ballari 2012, Baruzzi and Krofel 2017).

More than 70% of the world's forests are within 1 km of forest edge, which is within range of being influenced by human activity (Haddad et al. 2015). With increased human influence, habitat fragmentation will likely become more common (Tilman et al. 2001). This increase in fragmented landscapes affects species differently. Generalists are less sensitive habitat fragmentation (Keinath et al. 2017), and fragmentation may even favor invasion by habitat generalists (Marvier et al. 2004). Because habitat fragmentation

is likely to increase with land use change (Sala et al. 2000), vertebrate invaders are not as vulnerable to fragmentation (Keinath et al. 2017), and vertebrate invasions may substantially decrease species richness per area (Blackburn et al. 2004), biological invasions coupled with habitat fragmentation may be nonlinearly increasing threat to biodiversity (Haddad et al. 2015).

Eradication of invasive species may be a necessary step to maintain biodiversity (Courchamp et al. 2003, Glen et al. 2013). Several examples exist where eradication of invasive species resulted in an increase in native species richness or endangered species recovery. For example, eradication of red (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) from Alaskan islands resulted in recovery of endangered Aleutian Canada geese (*Branta hutchinsii leucopareia*; Byrd 1998). In a meta-analysis of invasive mammal eradications, Jones et al. (2016), documented 123 recolonizations of formerly extirpated native species following invader eradication. However, there has been little success in large-scale eradication efforts with exception of the eradication of Norway rats (*Rattus norvegicus*) in New Zealand from large islands (Clout and Veitch 2004). However, most case studies have demonstrated eradication success on small islands and local scales (Zavaleta et al. 2001). In fact, 78% of successful rodent eradications were on islands < 100 ha in area (Howald et al. 2007). Interestingly, populations on small islands that are more isolated have a higher probability of extinction – a fundamental of the equilibrium theory (MacArthur and Wilson 1967). Thus, this fundamental concept may be useful to predict the probability of success in invasive species eradication efforts. If the island area relationships with extinction probability hold true in fragmented terrestrial landscapes, eradication efforts focused on small fragments with the most vulnerable populations may

be most effective. With isolation as a secondary contributing factor, increasing isolation of larger islands by eradicating small island populations first may also be an effective strategy for eradication.

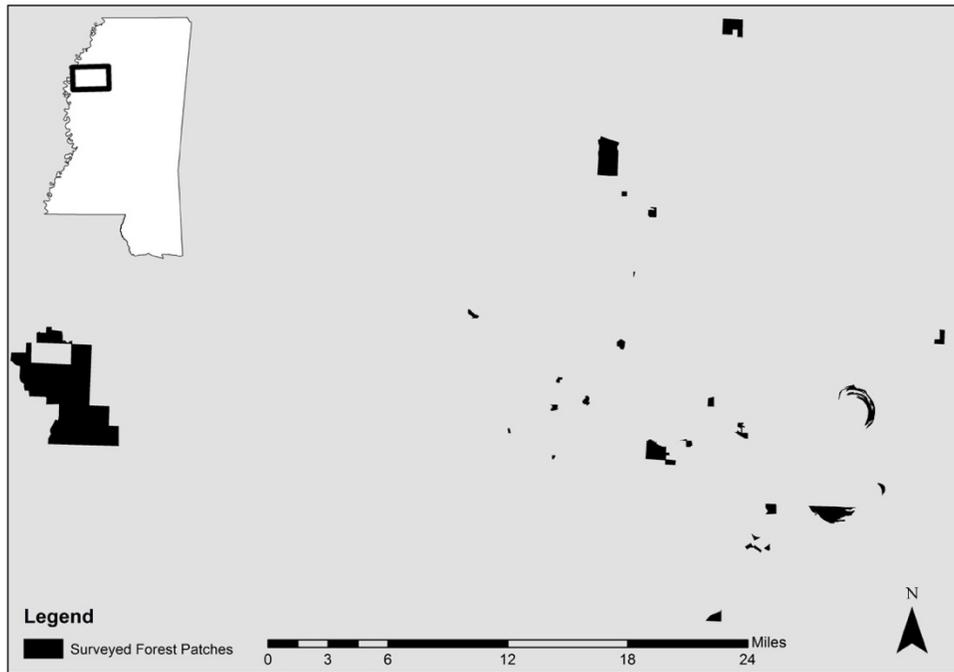


Figure 2.1 The spatial distribution of forest fragments sampled between February and October of 2016 and 2017 to determine the effects of feral swine invasion on species richness. Located in the Mississippi Alluvial Valley.

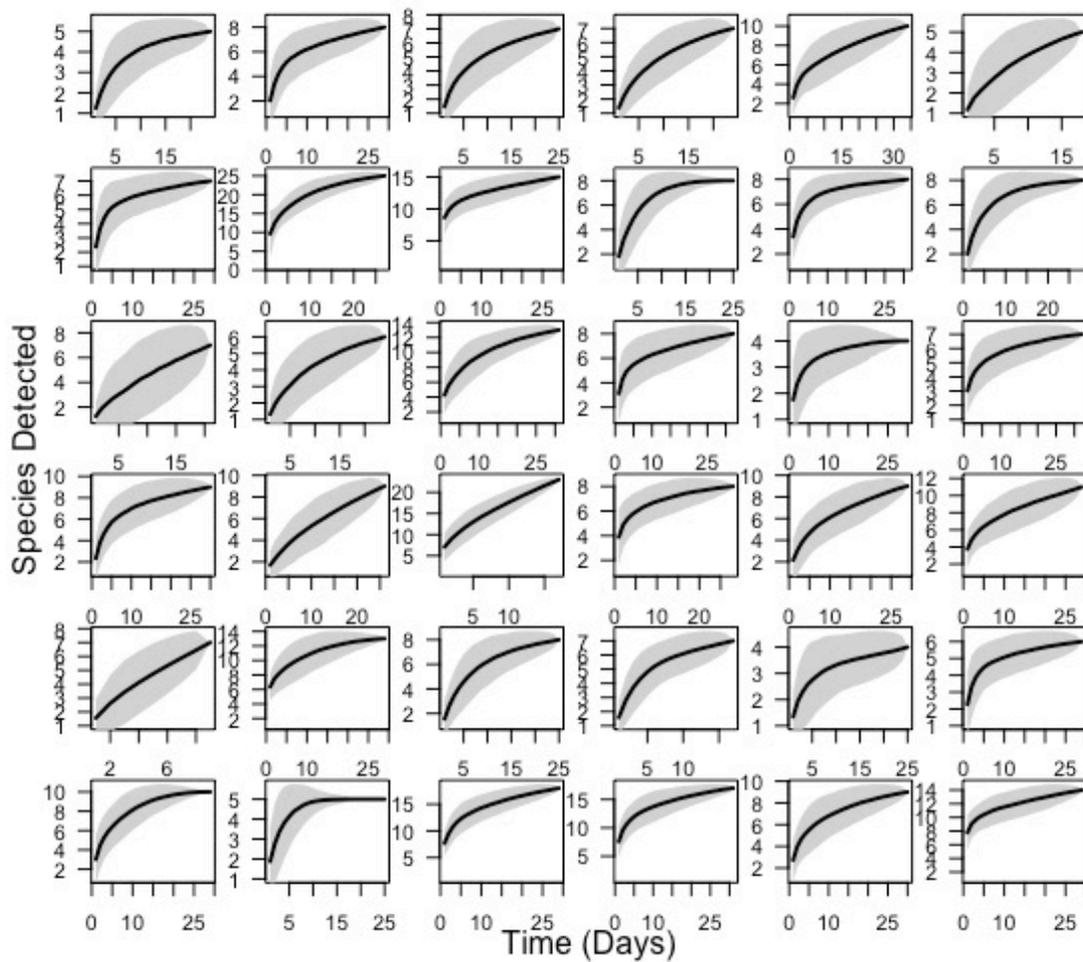


Figure 2.2 Species accumulation over time for 36 forest fragments sampled to determine the effects of feral swine (*Sus scrofa*) on species richness. Most species were detected within 14 days in most fragments indicating our 30-day sampling period was sufficient to estimate species richness. The lines depict species accumulation and the grey margins represent the number of possible species to detect (derived from 1000 random permutations within Program R).

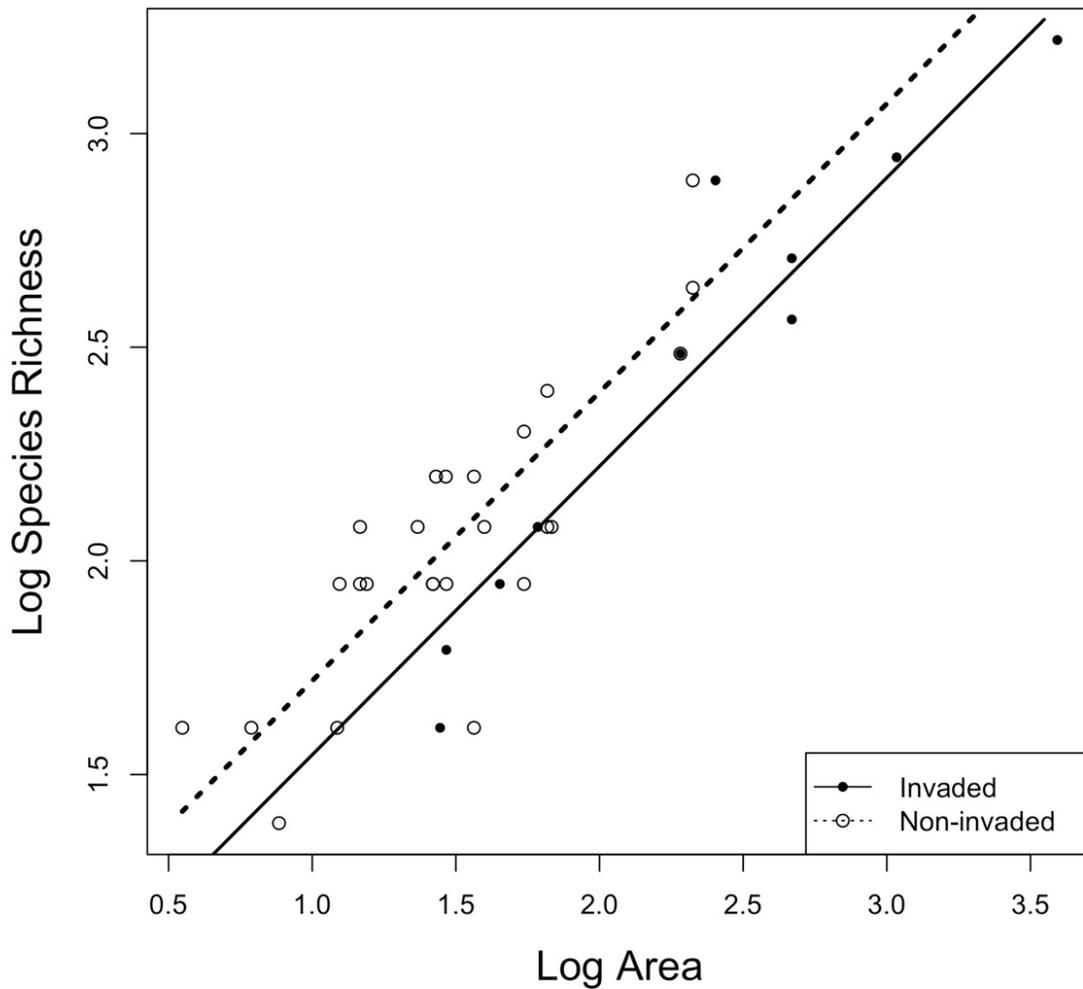


Figure 2.3 Log-Log relationship between species richness and area for forest fragments in the Mississippi Alluvial Valley invaded and absent of feral swine. Lines indicate that area has a positive effect on species richness, species richness was 26% lower when invaded by swine, and a lack of scale-dependence (i.e. increased slope when invaded) in the effects of the invasion. In this analysis, naturalized non-native nine-banded armadillos were not included in the species richness.

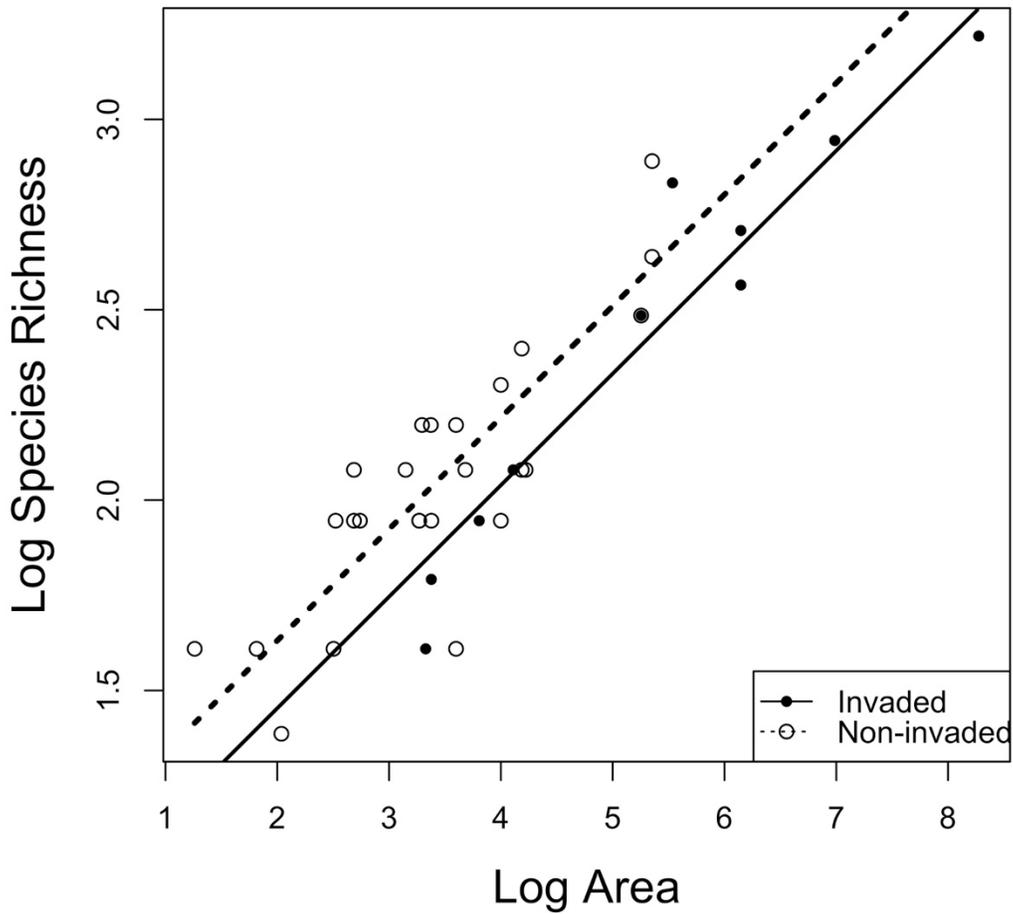


Figure 2.4 Log-Log relationship between species richness and area for forest fragments in the Mississippi Alluvial Valley invaded and absent of feral swine. Lines indicate that area has a positive effect on species richness, species richness was 17% lower when invaded by swine, and a lack of scale-dependence (i.e. increased slope when invaded) in the effects of the invasion. In this analysis, naturalized non-native nine-banded armadillos were included in species richness.

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CHAPTER III
MODIFIED DOUBLE-OBSERVER TECHNIQUE TO ESTIMATE ANIMAL
ABUNDANCE WITH CAMERA TRAPS

Abstract

Use of camera traps in ecology is rapidly increasing because they provide the versatility to economically collect data on a wide range of community-level ecological processes. One of the most common applications for camera trapping is to estimate animal abundance. Moreover, pairing opposing cameras is becoming common in sampling designs because it allows calculation of detection bias. The paired-opposing camera trapping design potentially allows a new application of the double-observer point count technique to estimate animal abundance. This technique has the advantages of not requiring attractants or marked individuals, which are common limitations to other techniques. To validate this application of the double-observer technique, over two years, we monitored vertebrate communities in 36 forest patches and detected feral swine (*Sus scrofa*), an invasive species in North America, in 11 of those patches. Feral swine are a good model species because they are easily detectable, unmarked, and eradication efforts allow the opportunity to collect data before and after known changes in abundance to validate estimates. Moreover, the invaded forest patches in which we estimated swine abundance ranged across three orders of magnitude in area. Because abundance of animals generally increases with patch size, we were able to use this general pattern as

additional validation of the sensitivity of our estimator to changes in abundance. The estimator was sensitive enough to detect increasing abundance with patch size and to detect the change in abundance following swine removal. However, the technique overestimated the number of individuals removed from the population by 53%, indicating additional parameters to inform the model were needed, or changes in behavior or dispersal decreased detection of the remaining animals. Our data indicate that the double-observer technique may be useful for estimating animal abundance with camera traps but future validation with known animal abundances are needed.

Introduction

With advances in technology, camera trapping has become a widespread survey method to estimate wildlife abundance, behavior, and occupancy (Burton et al. 2015). The use of modern camera traps is popular for cryptic or elusive species that range over large areas (Noss et al. 2012). This non-invasive versatile technology can sample continuously, simultaneously monitor many species, and sample for extended periods of time without frequent researcher disturbance (O'Connell et al. 2010). Several density and abundance estimators have been developed in concert with increasing popularity of camera trapping. Spatial capture-re-capture modeling (hereafter SCR) has been the most popular method because viable information about density and animal movement can be obtained with smaller trap arrays allowing applicability to wide-ranging mammals (Sollmann et al. 2012). The main advantage of using SCR is the ability to relate encounters of unique individuals to where they spend time during the camera trapping (Royle et al. 2011).

Many estimation methods require uniquely marked individuals, and are extensively used to monitor large felid carnivores (Borah et al. 2014; Rich et al. 2014; Karki et al. 2015; Weingarth et al. 2015). More recently, models to estimate animal abundance with unmarked individuals have been developed (Chandler and Royle 2013). However, these models rely heavily on underlying parametric assumptions and are sensitive to spatial study design (Sollmann et al. 2013). Another camera trapping method determines relative abundance indices (RAI) or number of records per trap effort (Liu et al. 2013). The RAI method has been scrutinized due to inflation and bias of indices based on species specific parameters (i.e. home range and detectability; Sollmann et al. 2013). The method was shown to have misleading abundance estimates compared to more robust SCR estimates (Mann et al. 2015). Density and abundance estimation for unmarked species is an ongoing research focus, and all approaches have limitations and assumptions (Sollmann et al. 2013).

Point counts are the most widely used method of counting bird populations (Ralph et al. 1995; Rosenstock et al. 2002). The double-observer point count method uses multiple observers to adjust counts for individuals that are present but not detected. A primary observer relays all individuals they detect at a point to a secondary observer, who records those individuals and any additional birds that the primary observer missed (Nichols et al. 2000; Thompson 2002). The locations of the birds are mapped at each survey point, and compared to generate an estimate using the “mark-recapture” approach. The first observer’s detections act as the “mark”, and “recaptures” are denoted by the common detections between both observers (Nichols et al. 2000). This method also determines the detection probability from points and has been successfully used to

estimate bird abundance and perceptibility of different species (Forcey et al. 2006; Leston et al. 2015; Golding and Dreitz 2016). Using paired opposing camera traps has become a common technique for camera trapping studies (Rovero and Marshall 2009). With this trapping technique, the double-observer method could be applicable to other species and systems. The camera pair would act as the double-observers at sample points within a study area. Within this study a double-observer based camera trapping technique was developed and tested.

Fragmented landscapes create relatively isolated populations that may be a good model system to validate the double-observer technique in camera trapping because most species increase in abundance as patch size increases (Bender et al. 1998; Dooley and Bowers 1998; Chiarello 2000; Michalski and Peres 2007). Because of this positive association with large animals and patch size, the Mississippi Alluvial Valley (MAV) is a good model system because agriculture has fragmented bottomland hardwood forests (Twedt and Loesch 1999) which have also been invaded by a large non-native (i.e., feral swine, *Sus scrofa*). Feral swine may be a good model species because removal efforts are underway in many of the remnant forest patches to mitigate economic losses associated with feral swine-human conflicts (Anderson et al. 2016). Thus, this model system and species allows two forms of validation to the sensitivity of the double-observer technique: 1) validate that the technique estimates increasing feral swine abundance as patch size increases, and 2) determine if the double-observer technique can detect, and how accurately it can estimate, a known change in feral swine abundance following a removal event.

Methods

We monitored feral swine within fragmented forest patches (Figure 2.1) in agroecosystems of the Mississippi River Alluvial Valley in Mississippi, USA (33°40'18.0"N 90°29'57.8"W). Forest patches included: bottomland hardwood forests, wetlands, and previous agricultural lands actively being restored to hardwood forests. Camera trapping was conducted without the use of attractants between February and October 2016 and 2017. We systematically established a 20-hectare grid overlay of each forest patch *a priori* within ArcMap (ESRI 2015). We used paired opposing camera traps which were placed near each grid intersection (Rovero and Marshall 2009) ~0.75 meters above the ground and 6 meters apart. We sampled 36 forest patches ranging from 3-4000 hectares in size (Figure 2.1). We used the trail-targeting method to strategically place camera traps near animal activity to maximize detection without the use of attractants (Tobler et al. 2008; Kays et al. 2009; Rovero and Marshall 2009; Kolowski and Forrester 2017). The delay between pictures was set to 1 minute. Each forest patch was monitored for 30 days. Area of patches was calculated within ArcMap (ESRI 2015). We analyzed the data both with and without our largest property (4000 ha) because it was more than triple the size of the next largest patch.

To estimate feral swine abundance, we applied the double-observer point count data to the camera trap data (Nichols et al. 2000). In this application, paired cameras acted as the paired observers with an overlap in observed area (Figure 3.1). Traditionally, the double observer estimator assumes observers capture animals in the same area, but we modified the technique so that the overlap between observer capture areas was a subset of the potential capture area for either observer (Figure 3.1). Therefore, detections of swine

at a site can be in 5 possible states: 1) captured by camera A but outside the capture area of camera B, 2) captured by camera A but not camera B while inside the capture area overlap, 3) captured by camera B but not camera A while inside the shared capture overlap, 4) captured by both cameras A and B within the shared capture zone, and 5) captured by camera B but outside the capture area of camera A (Figure 3.1). The varying capture states of animals allows the estimation of camera-specific capture probability and abundance by modifying the approach described by Nichols et al. (2000). Since, the area of overlap was not 100% of the total area, and capture states varied in the proportion of the total capture area, we weighted capture probability by weighting the state specific capture probability by the proportional detection area that each state could occur in.

To calculate detection area, we set up a camera trap overlooking a flagged grid within a captive swine facility. Distance from the front of the camera was marked at 5 m increments, with a row of flags intersecting horizontally at 10 m in 0.5 m increments. This Cartesian coordinate system allowed us to determine the position of each animal detected. After 14 days, we recorded the position of the first animal within a group to trigger the camera. The coordinates of each capture were plotted within Program R to calculate the area of detection specific to our camera traps and species.

The double observer estimator was developed within JAGS (Just Another Gibbs Sampler; Plummer 2012), a program analyzing Bayesian graphical models using Gibbs sampling (Hornik et al. 2003). We input swine counts within the previously described capture states, and the estimator operated under the following assumptions. Swine density of a patch was constant over the sampling period. Feral swine were assumed to remain

active during sampling. Third, swine were assumed to be randomly distributed within the patch. Finally, swine capture probability was equal across all camera sites and properties.

Results

Feral swine were detected in 11 out of 36 fragments sampled during the study with a total of 1288 feral swine detections. The percentage of capture states in 1, 2, 3, 4, and 5 were 43%, 5%, 5%, 11%, and 36%, respectively. Our effective detection area based on the captive feral swine study was 67.5 m² (Figure 3.2). When using our paired cameras, this increased the detection area of each camera site to 126 m² with 8% overlap. Feral swine were removed from one property during the sampling period. We estimated 529 swine before removal and 194 after the event. Our estimator was sensitive enough to detect the removal of an estimated 335 feral swine. However, the actual number of animals removed was 179, revealing an overestimation of 53%. Our estimator was able to detect the expected positive relationship between swine abundance and patch area ($P < 0.001$; $R^2 = 0.99$; Figure 3.3). Excluding our largest property from the analysis, the relationship between abundance and area was still positive ($P < 0.01$; $R^2 = 0.71$).

Discussion

The double-observer technique with paired opposing camera traps was able to detect an increase in abundance with area, and a decrease in abundance following swine removal. The model overestimated how many swine were removed by 53% indicating the need for additional parameters to refine estimate accuracy or if estimates were accurate, swine removals efforts may have changed swine behavior to make remaining individuals less detectable or may have caused swine emigration from the patch. However, it should

be noted that all estimators that require encounter data to derive estimates have the assumption that the relationship between the estimate and true abundance is linear and constant. This may not have been true in our case and thus, without being verified, would be a weakness in any approach relying on encounter data (Pollock et al. 2002). In either case, the density estimates were comparable to those determined with other methods, and did not require unique identification of individuals (Karki et al. 2015; Sirén et al. 2016) or the use of attractants (Tobler et al. 2008; Kays et al. 2009; Rovero and Marshall 2009; Kolowski and Forrester 2017), two major advantages over other current techniques (but see Rowcliffe et al. 2008). Moreover, a common application of population estimators is to monitor trends in populations and not necessarily accurate abundance (Pollock et al. 2002), which our estimator was able to detect. Thus, this method may be useful in the future for estimating population demographics with unmarked individuals.

The double-observer technique (Magnusson et al. 1978) is widely used in ecology to estimate population demographics in various systems. One of the most common uses for this technique in terrestrial systems is to estimate bird population demographics (Nichols et al. 2000). Interestingly and despite the common use of paired opposing camera trap designs, we were unable to find a single application of the double-observer technique to camera traps. Paired camera traps improve on one major flaw inherent to other double-observer methods in that the paired observers have identical detection ranges which allows for more precise estimates of abundance (Nichols et al. 2000). Thus, applying the age-old double observer method with camera trap-observers may have widespread usefulness in estimating population demographics more accurately than other double observer methods.

Most camera trap estimators fall under some variation of the capture-recapture modelling approach which requires marked individuals in the population (Foster and Harmsen 2012). Obviously, this approach is limited in application because many wildlife species do not have unique markings and marking individuals is often not feasible. Rowcliffe et al. (2008) made a notable advancement in camera trap density estimation, relaxing the requirement of marked individuals by modelling the underlying animal detection process. Our model has similar assumptions to the Rowcliffe approach: 1) animals move randomly and independent of each other, 2) animal movement is not affected by camera triggers or placement, 3) closed populations that do not vary over the sample period. We dealt with the first two assumptions in the way recommended by Rowcliffe et al. (2008) by establishing a systematically random grid of cameras and by using demographic information in the photo-captures to inform priors on the independence of individuals. Further, their model may have performed well in their study in part because they were estimating closed populations and thus, the third assumption was met. While our method still makes the assumption that the population is closed, our approach provides two opportunities to relax that assumption in open populations. First, our estimates were means of animal abundance across many time slices. Thus, an empirical distribution in the error associated with fluctuations in populations could be derived from the distribution of estimates across time slices. Second, because we used a Bayesian approach that is flexible to adjust priors to accommodate parameter estimates, the empirical distribution of error caused by emigration and immigration in the open population can be used to inform the site-specific openness of the population to site-specifically relax the closed-population assumption. Moreover, the paired opposing

camera traps allowed us to develop a site- and species-specific empirical estimate of detection probability, a significant contribution to the approach presented in Rowcliffe et al. (2008).

Our double-observer camera trapping design was not without flaw. First, using pairs of camera traps at each location obviously doubles the cost of camera trapping equipment and technician support for sorting data. Recent advances in technology may provide opportunity to decrease the burden on the technician support side (Norouzzadeh et al. 2017) and camera traps are already relatively cheap compared to other monitoring equipment (Rowcliffe 2017). Also, our opposing cameras were 6m apart in this study yielding an 8% overlap of detection ranges. Increasing the distance between cameras so the shared detection range was closer to 50% would have been helpful because it would have increased sample size for estimating detection probability. Also, our modelling approach had the assumption that animals were equally detectable throughout the day which may have influenced our abundance estimates. The Bayesian modelling approach that we performed would allow site-specific information on activity patterns which are commonly generated via camera trapping (Frey et al. 2017) but may extend the trapping period so that adequate sample sizes can be obtained for the activity pattern estimates (Lashley et al. 2018).

Swine abundance increased with patch area. This area-abundance relationship was expected because it is common in nature (Chiarello 2000; Michalski and Peres 2007). This relationship was likely a result of niche space increasing with the heterogeneity and biodiversity that come with increasing patch size (Currie 1991; Tews et al. 2004). Because feral swine are generalist omnivores that thrive on a variety of food resources

(Graves 1984; Seward et al. 2004) the larger the patch the greater the chance to expand the dietary breadth to support more animals. Given that swine are a nuisance species in agricultural landscapes (Anderson et al. 2016), which create highly fragmented forest cover (Saunders et al. 1991), understanding basic swine abundance-area relationships in these landscapes could be essential to swine management efforts and conservation.

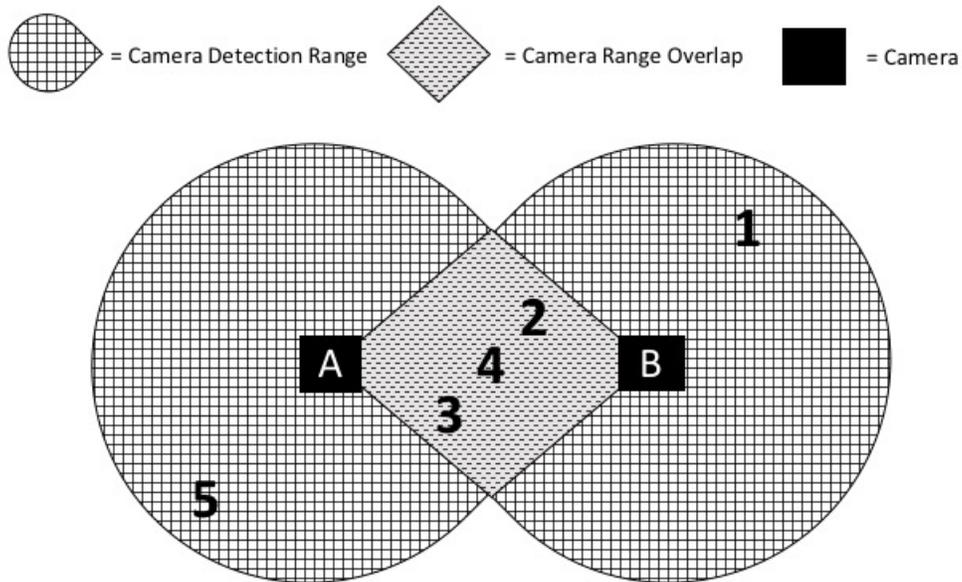


Figure 3.1 This figure depicts overlapping camera trap detection ranges when using paired opposing camera technique. Also displayed are the 5 capture states associated with the double-observer camera trapping technique. Capture states: 1) captured by camera A, but behind camera B, 2) within range overlap, but only captured by camera A, 3) within range overlap, but only captured by camera B, 4) captured by both cameras within range overlap, and 5) captured by camera B, but behind camera A.

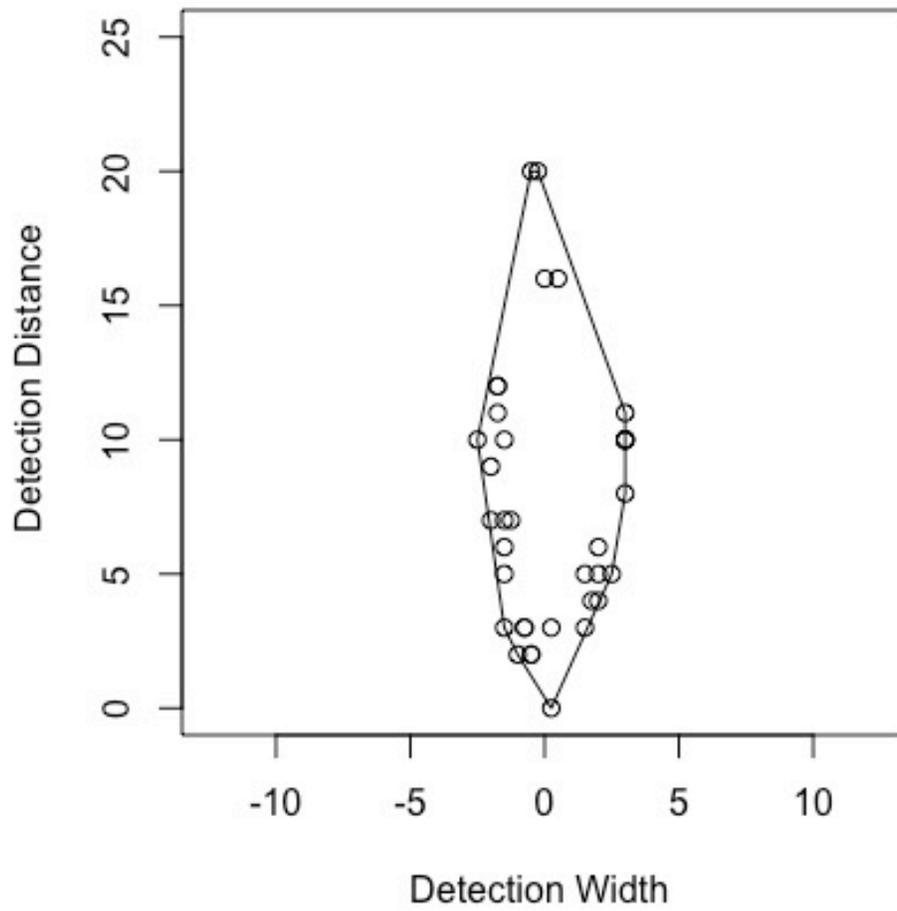


Figure 3.2 This figure depicts the detection range of a Bushnell Trophy Cam HD, as determined by an experiment using captive feral swine to trigger the camera's sensors (units = meters).

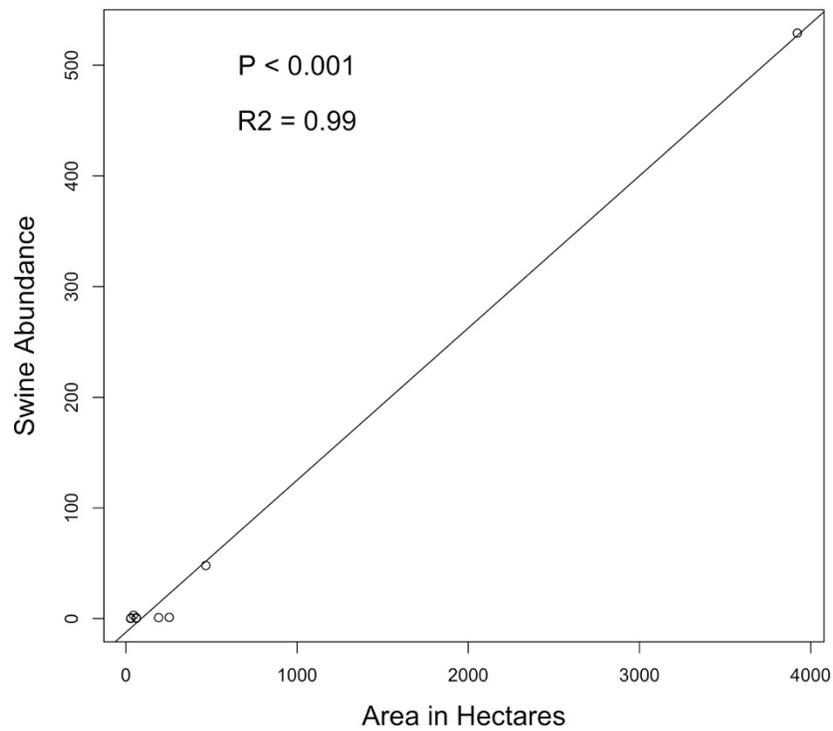


Figure 3.3 This plot depicts the positive relationship ($P < 0.001$) between feral swine abundance and patch size of sampled forest patches invaded by swine. Located within the Mississippi Alluvial Valley. This analysis included a large patch (4000 ha) that far exceeded the areal extent of the next largest patch.

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CHAPTER IV

SYNTHESIS AND CONCLUSIONS

While swine damage to agriculture in the MAV is well reported, my research also reported negative effects of swine on native wildlife. The 26% decrease in species richness following swine invasions is among the greatest impact reported from any biological invasion. Thus, successful eradication of swine is necessary for conservation of wildlife, but eradication efforts require robust abundance estimators to monitor success of removal efforts. My modified double-observer technique using camera traps provided a cost efficient way to robustly monitor swine populations without requiring the use of attractants or marked individuals. This is a huge advancement in the ability to monitor success of removal efforts and provides a direction into the future of battling swine invasions with robust removal and monitoring methods.