EVALUATING PERFORMANCE OF DENSITY ESTIMATORS AND COMMON TRAP TYPES FOR INVASIVE WILD PIGS (*SUS SCROFA*)

by

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(Under the Direction of James C. Beasley)

ABSTRACT

Wild pigs (*Sus scrofa*) are a globally distributed invasive species whose populations have expanded rapidly in recent decades. While population management for wild pigs is paramount, there are knowledge gaps surrounding density estimation methods and the most effective management practices to control growing wild pig populations. In this thesis, I quantified wild pig densities using removal and spatial mark-resight models from data collected across private properties in South Carolina, USA, and assessed which model-specific and environmental variables influenced the precision of each model type (Chapter 2). In addition, I evaluated the performance of three common trap types used to capture wild pigs across three distinct forage seasons using data collected across four southeastern US states over a three-year period (Chapter 3). This research advances our understanding of the performance of density estimators under varying conditions and provides critical information to aid in the continued implementation of wild pig population management.

INDEX WORDS: Invasive species, removal models, spatial mark-resight, trapping, wild pig management

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DEDICATION

I dedicate this thesis to my loving and supportive wife Karley, who I know will not read a single word beyond this point (just kidding!). You are my rock, and I could not have completed this journey and all the preceding steps without your endless belief in me and my abilities, especially when I lacked belief in myself. I also dedicate this work to my parents, who from a young age fostered my love for animals and the natural world and constantly encouraged me to pursue a career in doing what I love. I will forever be grateful for all your love and support over the years, I love you both so much.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Invasive species are an ecological issue worldwide, and their management is one of the biggest challenges natural resource managers and livestock producers face today. The term invasive refers specifically to a species whose introduction does or is likely to cause harm to either anthropogenic or environmental resources such as agriculture, waterways, and native flora and fauna (Beck et al. 2008). Although invasive species have always been a concern, we have seen a substantial increase in the distribution and abundance of invasive alien species in recent decades; this is attributed to increased globalization through both the anthropogenic movement of species and natural range expansions of certain species due to climate change (Hulme 2009; Tabak et al. 2017).

Today, invasive species are responsible for billions of dollars in damages and management costs annually, as well as population declines in numerous native species worldwide (Gurevitch & Padilla 2004; Pimentel 2007; Bradshaw et al. 2021). Wild pigs (*Sus scrofa*) are among the most ecologically damaging invasive vertebrate species on Earth, inhabiting every continent except Antarctica, making their range one of the most widespread of any mammal (Massei & Genov 2004; Barrios-Garcia & Ballari 2012). In North America, many consider wild pigs to be one of the greatest invasive threats to native species, natural resources, and economic interests (Lowe et al. 2000; McClure et al. 2018).

The first known self-sustaining population of free-ranging pigs in North America was established following Christopher Columbus' second expedition in 1493 (Mayer & Beasley 2018). Early explorers brought domestic pigs with them to provide a stable food source, and in many cases these pigs were released by settlers and allowed to forage for themselves (Mayer & Brisbin 2009). Eventually, this led to the establishment of numerous small populations of feral pigs in the eastern and southwestern United States (US), and by the late 1800s as introductions continued, pigs were widespread throughout much of the country (Mayer & Beasley 2018). In the late 19th and early 20th century, wealthy sport hunters began bringing Eurasian wild boar to North America to release into fenced hunting preserves (Hoehne 1994; Kreith 2007). Over time, wild boar escaped from many of these facilities and interbred with feral pigs already present on the landscape (Mayer & Brisbin 2009; Wilcox 2015).

In addition to accidental releases, wild pigs were intentionally moved by hunters to establish new populations in previously unoccupied areas (Gipson et al. 1998). By moving wild pigs into new areas, hunters were rewarded with a novel big game species they could hunt year-round for meat and sport. The anthropogenic movement of wild pigs across the US, along with their reproductive capabilities and high birth rates caused a population spike starting in the late 20th century, with wild pig abundance increasing from an estimated 2.4 million in 1982 to approximately 6.9 million in 2016 (Waithman et al. 1999; Mayer 2014; Lewis et al. 2019). Although an important factor in the population increase is believed to be human-led movement (Tabak et al. 2017), wild pigs also exhibit many characteristics that help them flourish in the areas where they are introduced.

Once present on a landscape, wild pigs have numerous attributes that allow them to thrive and expand in novel environments. Wild pigs are an extremely fecund species, and their potential

reproductive rate is the highest of any ungulate in North America (Taylor et al. 1998). Sows usually produce one or two litters per year but have been observed having as many as three litters over 14–16 months (Dzięciołowski et al. 1992; Chinn et al. 2022). Each litter produces between four and six piglets on average (Taylor et al. 1998; Koen 2018; Chinn et al. 2022) but can produce as many as 14 (Mayer & Brisbin 2009). Wild pigs also have few natural predators to suppress their population growth. Although larger predators such as black bears (*Ursus americanus*) and cougars (*Puma concolor*) do coexist with wild pigs in some areas and could pose a predation threat to wild pigs, the extent of this predation has not been thoroughly studied in the US (Waithman et al. 1999). Throughout most of their range in North America, the greatest natural predation threats wild pigs face are coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), both of which typically only prey on juvenile or weakened individuals (Tolleson et al. 1995). Furthermore, studies have shown both neonate (44%; Chinn et al. 2021) and adult (41–81% depending on season; Hayes et al. 2009) survival to be relatively high despite any predation risk.

In addition to their reproductive capacity and lack of natural predators, wild pigs are highly adaptable generalists which allows them to thrive in a variety of habitats and climates (VerCauteren et al. 2020). Diets of wild pigs largely consist of plant matter (~80–90%; Massei & Genov 2004), varying seasonally between hard and soft mast such as acorns and berries (Schlichting et al. 2015; Froehly et al. 2020). Wild pigs also consume vertebrate and invertebrate material to a lesser degree (~10% of diet; Mayer & Brisbin 2009; Mayer & Beasley 2018; VerCauteren et al. 2020) through scavenging (DeVault & Rhodes 2002; Turner et al. 2017) as well as active predation of various native and sensitive species such as reptiles, amphibians, birds, and mammals (Seward et al. 2004; Wilcox & Van Vuren 2009; Jolley et al. 2010; Wilcox 2015; Sanders et al. 2020; McDonough et al. 2022). In addition, studies have shown that wild

pigs occasionally predate livestock, mainly through the killing and consuming of newborn lambs and calves (Choquenot et al. 1996; Frederick 1998; Seward et al. 2004).

Wild pigs present a multitude of problems for both native flora and fauna, as well as anthropogenic interests such as agriculture, recreation, and livestock (Tisdell 1982; Massei & Genov 2004; Seward et al. 2004; Bevins et al. 2014; McDonough et al. 2022), although the biggest economic impact of wild pigs is damage to agriculture. Invasive wild pigs cause an average of $1.5 billion in damages and control costs every year in the US alone (Pimentel 2007), with crop and agricultural damage making up about $800 million of that cost (Pimentel et al. 2005). This damage is mainly due to wild pig foraging habits which include overturning soil (e.g., rooting) while accessing roots, bulbs, and tubers (Baubet et al. 2004). Rooting behavior can be especially devastating in agricultural fields, where farmers often have to re-till or re-plow the soil following wild pig damage before they are able to replant. Furthermore, private property in urban and suburban landscapes such as golf courses, lawns, and cemeteries are also at risk of rooting damage (Frederick 1998; McKee et al. 2022), and although not considered common, wild pigs have also caused human injury and casualties through attacks (Chauhan et al. 2009).

Wild pigs also act as a reservoir for several viruses and pathogens that can be transmitted to livestock, humans, and wildlife and cause disease (Tisdell 1982; Corn & Yabsley 2020). The most common examples found in livestock and wildlife include classical swine fever, swine brucellosis, pseudorabies, and African swine fever (Meng et al. 2009; Bevins et al. 2014; Miller et al. 2017). Most of these diseases are transmitted through direct contact with wild pigs or their bodily fluids (i.e., saliva, urine, blood). In humans, bacterium such as *Mycobacterium bovis*, which causes tuberculosis, or parasites such as *Trichinella* spp. can be contracted by consuming undercooked or contaminated wild pig meat (Meng et al. 2009; Barrios-Garcia & Ballari 2012).

Moreover, wild pigs outcompete native species for resources and degrade both terrestrial and aquatic habitats and communities. In oak woodlands, rooting behavior reduces above-ground plant biomass, which results in local herbivores such as white-tailed deer (*Odocoileus virginianus*) having limited access to high value foods (e.g., acorns; Sweitzer & Van Vuren 2002; Keiter & Beasley 2017). Due to the large dietary overlap between wild pigs and many native species, wild pigs likely compete directly with native wildlife for food resources (Wood & Barrett 1979; Garabedian et al. 2023), however more research is needed to elucidate the level of impact. Rooting behavior has been shown to impact species richness and abundance of native vegetation (Singer et al. 1984; Tierney & Cushman 2006) and can increase the prevalence of non-native or invasive plant species (Stone 1985; Cushman et al. 2004). The act of rooting itself is thought to alter soil structures and processes, although studies have shown contrasting results on the effects of rooting to soil communities (Singer et al. 1984; Barrios-Garcia & Ballari 2012; Barrios-Garcia et al. 2023).

In wet soil, another activity frequently carried out by wild pigs is wallowing. Wild pigs lack sweat glands, and therefore regularly use water sources for thermoregulation (Baber & Coblentz 1986; Campbell & Long 2009). Wallowing in saturated soil coats wild pig skin and hair with fresh mud which provides cooling relief as well as protection against insect pests such as mosquitoes and other parasites (Graves 1984). This concentrated use of water sources by wild pigs for wallowing leads to structural damage to stream beds as well as defecation in waterways, causing increases in waterborne bacteria, degraded water quality, and negative impacts on several invertebrate species across wild pigs' introduced range (Kaller & Kelso 2006; Kaller et al. 2007; Brown et al. 2012; Keiter & Beasley 2017; Bradley & Lockaby 2021). Wallows are another potential source for disease transmission between wild pigs and wildlife (Eckert et al.

2019), although the extent to which wallows may serve as point sources for disease transfer has not been thoroughly investigated.

Nationwide management of wild pigs is a relatively new priority in North America. As hunting for wild pigs became more popular in the 20th century and anthropogenic translocations of wild pigs increased, wild pig populations increased in size, distribution, and impact, and management plans became necessary to reduce damages caused by wild pigs. Non-lethal methods for reducing wild pig damage include exclusion fencing (Doupé et al. 2010), sterilants (Pepin et al. 2017), and repellants (Snow et al. 2021a), among others. Although these methods are more humane and tolerable to certain stakeholders and members of the general public than lethal methods, they are also either expensive, short-term, or uncertainties remain regarding their efficacy (Massei et al. 2011).

Lethal methods offer a more permanent solution to wild pig management but come with their own share of drawbacks. Some of the most common lethal methods for wild pig control include ground shooting, recreational hunting, aerial shooting, trapping, snares, and poisoning through toxicants, although each of these methods come with issues pertaining to either their expense or their effectiveness. For example, studies looking at poisoning through toxicants have shown mixed results regarding the efficacy of the bait delivery systems, the potential impacts of possible exposure to non-target species, as well as the palatability of the toxic bait itself (Snow et al. 2018; Poché et al. 2019; Beasley et al. 2021; Snow et al. 2021b). Recreational hunting and snares have been shown to have little effect on overall abundance and are time and effort intensive (Barrett & Stone 1983; Anderson & Stone 1993). In contrast, aerial gunning can be extremely efficient at dispatching wild pigs (Hone 1983) but comes with high aircraft operating expenses and decreasing removal efficiency as wild pig densities are reduced (Choquenot et al.

1999). However, in areas with high wild pig densities and open landscapes with high visibility, aerial gunning has been shown to be the most cost-effective method of removal (West et al. 2009; Bodenchuk 2014; Davis et al. 2018).

Trapping is one of the most popular and widespread methods of removing wild pigs (Barrett & Birmingham 1994; West et al. 2009), and intense trapping has been shown to be effective at reducing wild pig populations and related damages (Choquenot et al. 1993; Gaskamp et al. 2018; Kilgo et al. 2023; Treichler et al. 2023). However, trapping may be more effective as a control measure when used in conjunction with other methods due to drawbacks such as trap shyness of some individuals and the varying effectiveness of baiting that comes with seasonal shifts in natural food availability on the landscape (Barrett & Birmingham 1994; Massei et al. 2011). With the increased interest in wild pig control, there has been extensive progress in the development of new trap features and styles such as remote triggers and passive net traps. Traps can vary in attributes such as price, ease of mobility, trigger method, and overall size, all with the goal of maximizing wild pig captures while minimizing the cost associated with trapping. Although recent studies have started to look at the effectiveness of different trap designs (Williams et al. 2011; Metcalf et al. 2014; Smith et al. 2014; Gaskamp et al. 2021), this is an important question to the future of wild pig management that demands more research and attention (West et al. 2009; Mayer & Beasley 2018; Beasley et al. 2018). Through understanding and implementing the most effective and efficient methods of wild pig removal, management objectives can be more easily and quickly achieved which will help to conserve agricultural and natural resources, as well as native floral and faunal species.

Alongside implementing effective removal techniques, managers need to estimate density effectively and efficiently over time to assess progress in removal efforts. In recent decades,

there have been numerous advances in statistical models and monitoring techniques that facilitate abundance estimation (Engeman et al. 2013). However, more research is needed to determine how these models perform as animal densities, specifically wild pig densities, decrease over time (Beasley et al. 2018). Although comparisons between multiple types of models using differing monitoring data (i.e., camera traps, GPS collars, aerial surveys) have been made (Keiter et al. 2017; Moeller et al. 2018), further examination is needed to fully understand the pitfalls and advantages of each method and the amount of data needed to achieve accurate estimates. For wild pigs, accurate density estimates are essential to allow management agencies to make decisions regarding the amount of effort, type of removal techniques, and the timeline needed to achieve management objectives.

My thesis aims to address two critical gaps in wild pig research that are needed to improve the management of this destructive invasive species: 1) improve the efficiency and efficacy of estimating wild pig density and 2) evaluating the effectiveness and efficiency of common trap types used for capturing wild pigs. To address my first objective, in chapter two I use a combination of wild pig removal data collected from the United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS) and baited camera trap surveys to estimate wild pig density on privately owned properties in South Carolina, USA. Using a combination of removal models (Davis et al. 2022), and partial ID spatial mark-resight (SMR) models developed using these data, I compared density estimates derived from these models for all surveyed properties to determine the overlap in performance as well as to ascertain variables that influence the precision of densities estimated by these methods. These results will help to improve estimations of wild pig density in the future by providing information on the factors that impact the precision and dissimilarity between model type density

estimates. This will allow agencies to better evaluate and adjust ongoing management efforts and objectives.

In chapter three, I focus on three different types of traps used to capture wild pigs and evaluate each based upon several metrics including effectiveness, efficiency, and effort. The data for these metrics are derived from >850 trap events across several southeastern states. This represents the most extensive comparison of wild pig trap performance to date. Thus, the information from this study will be vital to help facilitate ongoing improvement of management programs for effective population control of this highly destructive invasive species. Through my results, I hope to give stakeholders, land managers, and managing agencies information that will prove useful in the successful population control of wild pigs.

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CHAPTER 2

EVALUATION OF REMOVAL AND SPATIAL MARK-RESIGHT MODELS FOR ESTIMATING WILD PIG (*SUS SCROFA*) DENSITY

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Abstract

Density estimation is critical to effectively manage invasive species and elucidate areas of highest concern. For wild pigs (*Sus scrofa*), the ability to estimate density is complicated due to their expansive home ranges, and common methods for estimating density are often unsuitable due to conflicting priorities relative to management goals. Specifically, density estimation methods that call for the release of captured individuals (i.e., standard capture-recapture) are often considered inappropriate for wild pigs due to their invasive nature. Previous studies have estimated nationwide or statewide densities of wild pigs and compared commonly used population estimation methods such as removal models and spatial mark-resight (SMR) models. However, property-level density estimations have not been characterized across a wide range of environments and wild pig populations. In addition, variables that influence density estimations and their precision have not been thoroughly examined. To address these issues, we gathered wild pig camera trap and removal data from 25 private properties ranging in size from 0.5 km^2 to 95 km^2 in South Carolina, USA between 2020-2023 to compare property-level density estimates between removal and SMR models. Furthermore, we investigated instances where density estimates between model types differed from each other and determined which variables influenced those differences. Overall, removal models were found to be more precise, with lower coefficients of variation on average (0.82 for removal, 1.22 for SMR) and a smaller range of density estimates than SMR models (0.22–43.39 wild pigs/km^2 for removal, 0.16–94.90 wild pigs/km^2 for SMR). We found that the precision of removal models was impacted by both the number of wild pigs dispatched in the removal period (3 months) and the area over which they were removed. However, none of the variables evaluated influenced either the SMR model density estimates or their precision. At the individual property level, density estimates produced

by our two estimators had non-overlapping confidence intervals in over 45% of instances, suggesting the choice of estimator can greatly influence derived estimates of density. Despite the extensive variability in density estimates between removal and SMR models, none of the variables included in our models were found to influence the dissimilarity observed between estimators. Our results provide support for the future use of removal models in wild pig density estimation and can be used as a reference for wild pig densities found throughout different regions of South Carolina, USA.

Introduction

Estimating animal density and the habitat attributes that contribute to spatio-temporal patterns of animal occurrence is paramount for the effective management and ecological understanding of wildlife species. Furthermore, the ability to obtain accurate density estimates over time provides insight into population fluctuations and how populations change in response to management activities. However, accurate density estimates of wildlife are often difficult to achieve due to the movement behavior and elusiveness of many species, particularly in areas of low species population density (Southwell et al. 2008; Gilbert et al. 2021; Hinton et al. 2022). Thus, development and refinement of analytical methods for estimating density continues to remain an active area of ecological research (Buckland et al. 2000; Thompson et al. 2010; Iijima 2020). For invasive species, development of methods to estimate density accurately and efficiently are critical to optimize control efforts and quantify the success of ongoing management efforts. However, invasive species present unique challenges to estimating density through popular methods such as standard mark-recapture, as it is often undesirable to release individuals back onto the landscape after capture (Engeman et al. 2013). Population control or

elimination is often a goal in invasive species management, and thus density estimators must be able to yield robust estimates using data collected during ongoing management activities.

Wild pigs (*Sus scrofa*) have become one of the most widespread and harmful invasive vertebrate species globally, with negative impacts that include damage to agriculture, disease transmission, and competition and predation of native species, among others (Meng et al. 2009; Barrios-Garcia & Ballari 2012; Bevins et al. 2014; VerCauteren et al. 2020; McDonough et al. 2022). Due largely to high birth rates, anthropogenic movements of wild pigs to previously unoccupied areas (Mccann et al. 2014; Tabak et al. 2017; Clontz et al. 2023), and the ability to adapt to new environments (Waithman et al. 1999; Mayer & Beasley 2018), wild pigs have expanded in range and abundance over the last few decades. Once established in new areas, wild pigs have numerous attributes that allow them to thrive, including high fecundity and survival, a generalist diet, and an ability to live in a variety of climates and habitats (VerCauteren et al. 2020). Due to recent rapid increases in wild pig populations and the invasive nature of wild pigs in introduced areas, management of the species has emerged as a priority for afflicted regions.

Despite the importance of accurate density estimates in wild pig management programs, there are several challenges associated with density estimation in wild pigs. In particular, removal efforts often take precedence over density estimation, popular methods of density estimation are often inappropriate or inefficient for wild pigs, and most methods of estimating density require extra cost or effort (Bengsen et al. 2014; Beasley et al. 2018). Nonetheless, the ability to accurately estimate density is critical to quantify the effectiveness of population control efforts and elucidate areas of highest concern. Several methods of density estimation for wild pigs have been explored in recent years including aerial surveys, tracking plots, road surveys, DNA sampling, camera surveys, removal models and distance sampling, among others

(Engeman et al. 2013; Keiter et al. 2017; Consortium et al. 2018; Davis et al. 2020). However, because population control is a priority, density estimation for wild pigs often must operate within the framework of management and removal efforts. This limitation has made most of these methods impractical, and therefore research has shifted to more appropriate means of estimating density.

Removal models are popular abundance estimators for wild pigs that utilize take data to estimate population size over time (Davis et al. 2016; Davis et al. 2022). Removal models can be efficient in estimating animal abundance because they use data that is already being collected by most management agencies. Not only are these data often readily available or easy to obtain, but removal models also do not require additional materials or effort on top of current management activities. Removal models utilizing take data are also advantageous over other methods that require releasing marked animals back onto the landscape after capture (e.g., standard capture-recapture), as many land managers are reluctant to release a species as destructive as wild pigs back into the environment (Engeman et al. 2013). Alternatively, spatial mark-resight (SMR) models are a data-intensive method of density estimation that utilize camera trap data and incorporate both marked and unmarked species detections to estimate density (Chandler & Royle 2013; McClintock et al. 2019). SMR models are a popular method of estimating animal densities because camera traps are a relatively inexpensive and commonly used tool within wildlife management. However, SMR models that involve individually identifying a portion of a population based on natural pelage and features from camera trap images can be time-consuming and have specific and intensive data requirements to run effectively (Keiter et al. 2017; Davis et al. 2020).

Although studies have demonstrated advantages in both removal and SMR models for estimating abundance of wild pig populations (Davis et al. 2016; Jimenez et al. 2017, Keiter et al. 2017; Teton et al. 2020; Davis et al. 2022), the attributes impacting the precision and variability of those estimates under varying densities and environmental conditions have not been fully examined. Furthermore, although broad-scale estimations of abundance have been achieved for wild pigs (Mayer 2014; Lewis et al. 2019), comparison of SMR and removal model estimators at the property-level have not been performed concomitantly across a suite of different environments and landscapes.

Therefore, our objectives in this study were three-fold: 1) quantify wild pig density across a broad range of study sites using two different methods of population estimation (removal models and SMR models), 2) elucidate factors influencing both removal and SMR density estimates and their precision, and 3) determine variables that influence instances of dissimilarity between density estimates produced from each model type. We predicted that both estimators would be density dependent and would have greater variance at lower densities. We also predicted removal model density estimates would become more precise as the number of removals in the primary period, and subsequently the amount of removal data, increased. Additionally, we predicted SMR model density estimates would become more precise as the number of total detections and the proportion of cameras with detections increased. Finally, in instances where density estimates from each model type were dissimilar from each other (i.e., non-overlapping 95% confidence intervals), we expected both estimators to perform poorer in ecoregions with lower wild pig densities where wild pig presence within our study sites was more variable.

Study Area

We conducted this research on 25 privately owned properties located across three ecoregions of South Carolina, USA, including the Coastal Plain (n=15), Southeastern Plains (n=8), and Piedmont (n=8), and within the counties of Hampton, Newberry, Jasper, Darlington, Marlboro, Chester, Fairfield, Dillon, Marion, and Barnwell (Figure 2.1). Properties ranged in size from ~0.5 to ~95 km^2 with a median size of ~3.38 km^2. The Coastal Plain region of southeastern South Carolina is low-elevation (<200m) and comprised of mainly swampland, with pine (*Pinus* spp.) stands, oak and hickory hardwood forests (*Quercus* spp., *Carya* spp.), and scattered cropland (Griffith et al. 2002). Many riparian habitats within the coastal plain region are partially saturated for most of the year with marshes and wetlands throughout (Drummond 2016).

The Southeastern Plains region contains a mixture of pine and hardwood forest, cropland, and ranchland pasture (Griffith et al. 2002). Elevations are greater than the Coastal Plain region but lower than in the Piedmont region, and with less water and saturated soil than the Coastal Plain region. The Piedmont region of South Carolina includes higher elevations than the other two ecoregions (~200–500m). While the Coastal and Southeastern plains are primarily sandy, soils in the Piedmont region contain more clay (Griffith et al. 2002). Over the past 200 years, the Piedmont region has shifted from primarily hardwood and pine forest to large-scale cropland, and now back to hardwood and pine forestland (Griffith et al. 2002; Napton 2016).

Wild pigs have occurred throughout South Carolina for centuries, dating back to initial mainland introductions by the Spanish in the 16th century (Wood & Barrett 1979; Mayer et al. 2020). Today, wild pigs occur in every county in South Carolina, with an estimated population of ~160,000 based on statewide harvest counts (Mayer 2014). While wild pigs occur throughout

South Carolina, the Coastal and Southeastern Plains regions generally experience higher densities than the Piedmont region primarily due to the prevalence of agriculture and wetter environments. Thus, our 25 study sites included both a wide range of habitats, as well as variable levels of wild pig densities.

Methods

Camera Surveys

For spatial mark-resight density estimates, we conducted two-week baited camera surveys on the 25 study properties every six months (winter and summer) over the course of four years (2020-2023). However, because properties were signed up and enrolled in the study at different times, anywhere between one and seven camera surveys were conducted on any individual property. We used ArcGIS Pro (Version 3.1.0, Esri, Redlands, CA, USA) to generate random points across each property for camera locations. We placed one camera for every 0.25 km^2 of suitable habitat on each property and maintained a minimum spacing of ~500m between cameras (Treichler et al. 2023). We defined suitable habitat for wild pigs as forested areas which we determined using the imagery basemap from ArcGIS Pro (Gaston et al. 2008). Water bodies, agricultural fields, and developed land were excluded from camera placement. There were two properties that were too large to sample in this manner. For these two properties, we subdivided each property into 2 km^2 grids of suitable habitat that were spaced ~2 km apart to minimize the possibility of wild pigs moving between grids within a survey session. Each of these grids included the same camera density and spacing as the rest of the properties, resulting in one property including three grids and the other including four.

At each camera site, we placed a single Reconyx white-flash camera (Reconyx HP2W; Reconyx, Holmen, WI, USA) ~1m high on a tree ~3m from a bait pile (Schlichting et al. 2020; Treichler et al. 2023). We set cameras to take a three-photo burst with one second between each photo and a one-minute quiet period between bursts. We baited cameras with 22.7 kg of whole corn when first set and checked bait levels, SD cards, and batteries on day seven. We replenished sites with 11.3 kg of whole corn as needed on day seven and pulled cameras on day 15 (Treichler et al. 2023).

Once cameras were collected, we manually reviewed camera images, and all pictures including wild pigs were compiled and delineated into detection events within the Colorado Parks and Wildlife Photo Warehouse program (CPW; Ivan & Newkirk 2016). We classified detection events as a group of pictures where at least one wild pig was in frame; new detection events were distinguished whenever there was at least a 15-minute gap in between photos of wild pigs (Jimenez et al. 2017). We then classified wild pigs into unique individuals within detection events based on a myriad of markings including pelage patterns, scarring, and unique features. Within our study area, wild pigs exhibited a wide range of coat colorations which allowed a subset of individuals to be identified across all surveys (Keiter et al. 2017; Davis et al. 2020; Figure 2.2). Individuals were eligible to be marked (identified) throughout the entire two weeks of each individual survey, and individual IDs were not carried over in subsequent surveys. For every detection event, each wild pig that was unable to be identified was classified as “unknown” in CPW. For each property, each sighting of a known individual and the total number of unmarked detections for every camera was organized for input into R (R Core Team 2023). For the two larger properties, camera data from the grids for each property were grouped and

analyzed together so that one density estimate was achieved for each property during each survey period.

Wild Pig Removals

All properties involved in this study were enrolled in a federal wild pig population management program managed by the United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS). Removals of wild pigs on these properties were ongoing until ~1 month leading up to the start of each camera survey and resumed immediately after the conclusion of each camera survey. Removal methods were carried out by professionals and consisted of trapping, aerial take with helicopters, and targeted ground/night shooting, although the majority of wild pigs were removed via trapping (~70% of all removal events). Traps used by USDA-APHIS-WS included corral, drop, and passive net style traps (Wight et al. 2022). Traps were baited with whole corn and trapping took place year-round wherever applicable outside of our camera trap survey periods. All captured pigs were euthanized by USDA-APHIS-WS trappers, and no wild pigs were specifically captured or euthanized for this study. Aerial dispatch events took place primarily in the winter and on properties with enough open space to ensure efficient removal. Targeted shooting events were conducted year-round where applicable outside our camera trap survey periods. USDA employees recorded all removal events in ArcGIS Collector (Esri, Redlands, CA, USA), and information logged included number of wild pigs removed, age class and sex of removed individuals, removal method, GPS coordinates of event, and date and time.

SMR Model Density Estimates

We used the secr package in R to generate SMR population estimates and densities for each camera survey (Efford 2023; R Core Team 2023). We used the sf package in R to read in and transform shapefiles of each property to the proper coordinate reference system to create habitat masks for each site (Pebesma 2018). We included a two-kilometer buffer around each property to match the area used for the removal models to estimate density (see below in Removal Model Estimates). We ran a series of SMR models using the function secr.fit that allowed density and the detection parameters (g0: magnitude of detection function; sigma: spatial scale of detection function) to vary in relation to variables built into the package (e.g., site response, time, coordinates). For models that only included covariate effects on density, we included possible east-west and north-south trends within properties as well as their interaction. We also included models that allowed detection parameters (g0 and sigma) to vary with respect to animal behavior, a site response, and the interaction of these parameters, and models that allowed detection parameters to be uniquely estimated within each occasion (day). Finally, we included models that influenced both density and the detection parameters using combinations of all explanatory variables.

We calculated density estimates for every survey that was conducted, ranging from one to seven per site depending on when properties were enrolled in the program. We then used Akaike Information Criterion (AIC; Akaike 1973) to rank models for each survey to determine which model(s) best fit the data. We considered all models within two AIC units of the top model to be similar and estimates from these models were evaluated further (Burnham & Anderson 2002). Finally, we ran absolute goodness of fit tests on all supported AIC models using the function secr.test and ran each test for 1000 simulations to determine how well the observed dataset was

represented by the best-fit model(s). All analyses were performed in R (Version 4.1.0; R Core Team 2023).

Removal Model Density Estimates

We fit a Bayesian dynamic removal model to the wild pig removal data following methods outlined by Davis et al. (2022). The Davis et al. (2022) methodology estimates site-level abundance and capture probabilities using a multinomial distribution to allow for the incorporation of multiple methods of removal with a different capture rate for each method. Because the model allows for multiple capture types and rates, an area of influence for each removal method also must be included to avoid violating the assumption that all animals are equally catchable throughout the site. The model included information on each removal event (number of wild pigs removed, date/time, name of property, method of removal, effort in hours, and GPS coordinates), and the size of the property with a two-kilometer buffer to account for removals near the border of the properties and the average maximum daily movement patterns of wild pigs (Kay et al. 2017; Clontz et al. 2022; Davis et al. 2022). Abundance estimates from the removal model were divided by the area of the property plus the two-kilometer buffer to obtain final density estimates.

We modeled capture rates by method with logit-transformed normal distributions, abundance with a Poisson distribution, and growth rate with a log-normal distribution (Davis et al. 2022). Abundance was estimated within three-month primary periods, and removals were modeled as occurring during daily secondary periods. To adjust tuning parameters within the removal model, we ran a custom Markov Chain Monte Carlo simulation (MCMC; Davis et al. 2022) for 1,000 iterations across four chains and examined posterior results and trace plots with a 500-iteration burn-in for convergence. We determined convergence by observing proper mixing

within trace plots in which each chain was able to explore the entire parameter space of each trace plot (Kass et al. 1998). Once we tuned priors for the model parameters of interest (capture rates by method, abundance, growth rate) we ran the MCMC for 20,000 iterations across four chains with a 10,000-iteration burn-in to obtain abundance estimates. We then averaged the abundance estimates produced from the four different chains and divided them by the property size plus a two-kilometer buffer to yield final density estimates. The estimated density for each property during the three-month primary period immediately following each camera survey was used for comparison with the SMR estimates. All analyses were performed in R (R Core Team 2023).

Evaluation of SMR and Removal Model Density Estimates

We defined a replicate as a single survey period (i.e., 3-month primary period and 2-week camera survey) in which we were able to obtain both a removal model and SMR model density estimate for a specific property. For each replicate, we derived a suite of general (i.e., ecoregion, years of management, season) and method-specific (e.g., total detections, number of wild pigs removed in the primary period) attributes we anticipated could influence variance within and between density estimators (Table 2.1). For the SMR models, we investigated variables including the number and distribution of detections due to their correlation with relative abundance estimated in previous research (Treichler et al. 2023). For the removal models, we examined variables including both recent and cumulative removals to investigate the effect of the number of removals and the removals per area across two temporal scales (See Table 2.1 for the list of variables used). Specifically, we divided both the number of wild pigs removed in the final 30 days of the primary period and the cumulative number of wild pigs removed on that property by USDA at the time of sampling by an estimated area of impact to get a unique removals/area

impacted metric for each estimate. We calculated the estimated area of impact used in these variables using minimum convex polygons (MCPs) in ArcGIS Pro around removal events for each property and adding a 6.7km buffer around the MCP, in accordance with a prior study conducted in a similar region to account for the area of influence for our removal methods (i.e., the area of a circle with the daily movement distance for wild pigs used as the radius; McRae et al. 2020). We also calculated the coefficient of variation (CV; Brown 1998) for each density estimate to use as a scale-free indicator of precision. We then tested density estimates and CV values from both model types (SMR and removal) for normality using a Shapiro-Wilk test. Due to the non-normality of both model type's density estimates and the SMR estimate CV values, we log transformed the density estimates, and cube-root transformed the SMR CV values.

We then ran four separate series of linear models (LMs) to distinguish the influence of our predictor variables on removal and SMR model density estimates, as well as their CV values using the variables listed in Table 2.1. Prior to running each series of LMs, we used the cor function in R to test for correlation between our numeric fixed effects. We excluded all variables with correlation values ≥ 0.7 from the same model. After checking for correlation, we used the dredge function in R to compare all possible combinations of the fixed effects for each of our response variables and ranked models based on AIC corrected for small sample size (AICc; Hurvich & Tsai 1989; Table 2.1). However, because the dredge function does not include interactions, we ran additional LMs that included interactions between variables within the most parsimonious models revealed by the dredge function, and a null model was included for comparison in each of the four series of LMs (removal and SMR density estimates, and removal and SMR CV values). We considered all models within $\Delta 2$ AICc of the top model competitive (Burnham & Anderson 2002).

In addition to our assessment of the factors influencing removal and SMR model performance, we also developed an additional suite of models to determine factors contributing to dissimilarity between removal and SMR density estimates. We considered property-specific density estimates to be dissimilar to each other when they exhibited non-overlapping 95% confidence intervals for the same survey period. To investigate attributes influencing dissimilarity between these density estimates, we ran a series of logistic regression models that included season, ecoregion, years of management, and property size as explanatory variables (Table 2.1). We included interactions between variables and added a null model for comparison. All analyses were performed in R (R Core Team 2023).

Results

After removing instances where we had insufficient data to yield density estimates (e.g., no camera detections during survey, no removals in the primary period), we were left with density estimates from 24 replicates across 14 properties (Figure 2.3). These replicates spanned six counties (Hampton, Newberry, Jasper, Fairfield, Darlington, Barnwell) across all three ecoregions (Coastal Plain, Southeastern Plains, Piedmont) and all four years of the study (2020-2023). Throughout the four years of the study, there was a total of 1874 wild pigs removed across our 14 replicate properties, ranging from 16–291 ($\bar{x}$ = 142.69 ±29.51 SE) wild pigs removed per property. Additionally, the number of wild pigs removed ranged from 2–108 ($\bar{x}$ = 25.52 ±5.33 SE) in any 3-month primary period used to obtain a density estimate. The number of cameras deployed per property ranged from 2–60 ($\bar{x}$ = 20.71 ±4.35 SE) for each survey conducted, resulting in between 6–1212 ($\bar{x}$ = 276.25 ±68.08 SE) total wild pig detections, and between 2–75 ($\bar{x}$ = 17.21 ±3.64 SE) unique individuals per replicate.

Estimates of densities across the 24 replicates from removal models ranged from 0.22–43.39 ($\bar{x}$ = 4.41 ±1.74 SE; Figure 2.4) wild pigs/km^2, and CV values ranged from 0.27–1.32 ($\bar{x}$ = 0.82 ±0.06 SE; Figure 2.5). Within the series of models investigating the influence of variables on removal model density estimates, the only supported (<Δ2 AICc) model included 30-day removals/area impacted and the years of management as fixed effects (Table 2.2; multiple R^2=0.46; adjusted R^2=0.35; AICc weight=0.45). This top model revealed that the densities in the second year (β=-1.00 ±0.40 SE, p=0.02), and the third year of management (β=-1.16 ±0.50 SE, p=0.03) were lower compared to the first year of management. Furthermore, there were 2 supported models within the series of models investigating the influence of variables on the removal model CVs. The top model included both the 30-day removals/area impacted and the number of wild pigs removed in the primary period as fixed effects (Table 2.3; multiple R^2=0.29; adjusted R^2=0.22; AICc weight=0.36). This top model revealed the 30-day removals/area impacted (β=2.50 ±1.09 SE, p=0.03) had a positive relationship, and the number of wild pigs removed in the primary period (β=-0.01 ±0.002 SE, p=0.01) had a negative relationship with the CVs of the removal model density estimates. This suggests that removal model CVs increased as the 30-day removals/area impacted increased and decreased as the number of wild pigs removed in the primary period increased. The second supported model included the same variables as the top model, with ecoregion added as a fixed effect (Table 2.3; multiple R^2=0.45; adjusted R^2=0.33; AICc weight=0.26), although ecoregion was determined to be an uninformative parameter with no discernable effect on the removal model CVs.

Within our supported SMR models of the 24 replicates, the density parameter was either constant (n=11) or varied across a north-south trend (n=13). Meanwhile, the detection parameter g0 varied across a site transient response (site effectiveness depends on preceding occasion;

n=17), across time (n=6), or was constant (n=1), and sigma varied across a site transient response (n=9), across time (n=3), or was constant (n=12). Our SMR densities across the 24 replicates ranged from 0.16–94.90 ($\bar{x}$ = 11.38 ±4.05 SE; Figure 2.4) wild pigs/km^2, while their CV values ranged from 0–7.59 ($\bar{x}$ = 1.22 ±0.39 SE; Figure 2.5). Within the series of models investigating the influence of variables on SMR model density estimates, there were eight models that were considered supported which included the number of unmarked detections in the camera survey, the total number of detections, the number of marked individuals, the proportion of cameras with detections, and the density of marked individuals as fixed effects, as well as the null model (Table 2.4). In addition, the R^2 values for these models ranged from 0.10–0.20 and adjusted R^2 values ranged from 0.04–0.12, suggesting none of the variables we considered properly explained variation in the density estimates. Within the series of models investigating the influence of variables on SMR CV values, there were 14 models that were considered supported, including the null model (Table 2.5). Because the null model was within our range of supported models, no variables included in the remaining 13 models were considered to influence SMR model CVs.

We had 11 instances of replicates containing dissimilar density estimates (Figure 2.3), which occurred on eight properties within two ecoregions (Coastal Plain and Piedmont), and in every year of the study period outside of 2022. The density estimates of our dissimilar replicates differed by an average of 21.46 wild pigs/km^2, with the SMR models producing a higher density in 7 of the 11 replicates. After model selection, there were three supported models investigating dissimilarity between model type density estimates, one model including property size as a fixed effect (R^2=0.06; AICc weight = 0.25), another model including season as a fixed effect (R^2=0.06; AICc weight = 0.23), and the null model (AICc weight=0.37; Table 2.6). Because the null model

was considered supported, no variables investigated were determined to influence dissimilarity among density estimates.

Discussion

We evaluated two common population estimators (removal and SMR models) across a broad range of environmental conditions and wild pig densities to elucidate the influence of model-specific and environmental attributes (e.g., ecoregion, season) on model performance and dissimilarity between estimates. Our results revealed that the precision of removal models was impacted by the number of removals made in the primary period and the area over which they occurred. Surprisingly, none of our tested variables influenced either the SMR model density estimates or their precision. We also investigated the comparability of density estimates produced between model types and found that none of our measured variables were influential in explaining differences between estimates. Finally, our data suggests that removal models may provide more precise density estimates than SMR models for wild pigs through lower mean CV values and smaller density estimate ranges. Collectively, our results provide new insights into the underlying factors influencing the performance of SMR and removal models for estimating densities of wild pigs and the efficacy of each method across a broad range of environmental conditions.

Previous density estimates reported for wild pigs in the southeastern US have ranged from 0.4–39 wild pigs/km^2 with an average density of 8 wild pigs/km^2, although some prior studies excluded juveniles from their estimates (Hanson et al. 2009; Keiter et al. 2017; Mayer et al. 2020; Snow et al. 2020). Our density estimates from both model types incorporated both juveniles and adults and produced similar ranges of wild pig density estimates for removal models (0.22–43.39 wild pigs/km^2) and greater ranges for SMR models (0.16–94.90 wild

pigs/km^2) than previous studies, although the mean densities of each model type (4.41 wild pigs/km^2 for removal models; 11.38 wild pigs/km^2 for SMR) were generally comparable to previous estimates. Both the mean density and CV (4.41, 0.82, respectively) of our removal model estimates were lower than values produced by the SMR models (density: 11.38, CV: 1.22). This difference in CVs combined with a lower range in density estimates for the removal models suggests that removal models generally produced more precise estimates than the SMR models, however it is important to note that higher precision does not necessarily reflect the accuracy of these density estimates. Similar studies on wild pigs have found SMR model estimates to have greater variability compared to other forms of density estimation (e.g., removal models, DNA sampling; Keiter et al. 2017; Davis et al. 2020). Thus, future studies should consider alternative experimental designs for increasing the precision of SMR models for estimating wild pig density such as longer sampling periods or a capture-mark-resight modeling approach.

Our results revealed that removal model density estimates were influenced by the number of years that wild pig removal efforts occurred on the properties, with densities decreasing in the first two years of population control. Previous studies have shown federal management programs to be effective in reducing wild pig populations substantially in as little as 12 months (Treichler et al. 2023), which further supports our results. In addition, our finding that removal model density estimates became more precise as the number of removals in the primary period increased supported our prediction and illustrates the importance of concentrated removal efforts when calculating precise density estimates in a removal model framework. Density estimates produced from our removal models were generally below 10 wild pigs/km^2 and were within a similar range of wild pig densities reported in our study region, apart from a single outlier. This

outlier included few total removal events (4) that only occurred in two months throughout the four-year study period, which further suggests the importance of regular removals to obtain useful density estimates from this method. Indeed, the removal model we employed in this study has not been recommended for use in regions where populations are nearing elimination due to poor model performance under low capture probabilities (Davis et al. 2022), and our findings further support this suggestion.

Research has shown SMR model precision benefits from an increasing number of marked individuals and unmarked detections (Chandler & Royle 2013; Bengsen et al. 2022). However, the results of our evaluation of SMR models revealed that none of the model parameters nor environmental attributes measured contributed markedly to performance, including the number of marked and unmarked detections. We suspect this is due to a high level of variability in site-level attributes both across properties and within camera surveys, resulting in variables influencing SMR model estimates on a case-by-case basis. For example, some of our study sites were smaller than a wild pig's home range and thus likely contained transient populations of wild pigs whose core home ranges and movements extended beyond the property boundaries (Clontz et al. 2022). On these smaller properties, wild pigs occasionally occurred on a small subset of cameras at sporadic intervals, including the final day(s) before a survey concluded, which may have contributed to decreased precision in SMR estimates for these sites. Furthermore, our camera surveys were relatively short in duration (14 days), and we implemented sighting-only SMR models that did not include a marking period within our camera surveys and allowed new individuals to be identified throughout the 2-week period. Wild pigs typically locate bait sites within 7-10 days of deployment and typically revisit sites multiple times once located (Beasley et al. 2021). While previous studies have used similar

methodologies to estimate wild pig density (Keiter et al. 2017; Davis et al. 2020), our data suggest future camera based SMR studies in wild pigs could benefit from longer sampling periods as well as separate marking and resighting periods to allow enough time for marked individuals to be captured and recaptured on multiple detectors (Jimenez et al. 2017; Harihar et al. 2020).

Finally, we investigated instances where our two density estimation methods produced dissimilar estimates to determine whether any of our measured environmental attributes, property size, or the years of management contributed to variability between estimates. Surprisingly, none of our measured attributes were important drivers of the variability between estimators, likely reflecting site-specific variability in factors for which we did not have data to explain the variation. For instance, two different camera surveys produced 1212 and 394 total wild pig detections with 75 and 27 marked individuals, respectively, but only 8 and 2 wild pigs were removed and included in the corresponding removal model estimates for each replicate. We also encountered the opposite scenario in which two replicates included 71 total wild pig detections each with 5 and 6 marked individuals respectively, yet there were 30 and 32 wild pigs removed from these sites, respectively and included in the corresponding removal model estimates. In these cases, each model type was given conflicting data regarding the population (e.g., many detections, few removals) during the time of sampling and therefore produced dissimilar results. Thus, site specific factors influencing the movement behavior, detectability, capture success of wild pigs, or other factors appeared to be more influential in driving disparate density estimates between methods than any of our measured variables.

Density estimation is vital to the effective management of invasive species and the evaluation of population control efforts. Recently, studies have compared density estimates

across multiple estimators, resulting in useful recommendations that can be used to improve future population surveys (Rich et al. 2014; Keiter et al. 2017; Davis et al. 2020). In our study we build upon this foundational literature through estimating density across a broad range of environmental conditions and wild pig populations in the southeastern US using two commonly used methods. We believe the outcomes of this research hold critical results that can be used to inform how to maximize the efficacy of removal model and SMR population estimators. Overall, our research illustrated the importance of considering removal intensity, consistency, and available data when choosing the appropriate density estimation method for a given region to maximize precision of estimates and contribute to effective management. Additionally, the results from this study suggest that if adequate data can be achieved (i.e., maximize captures over a broad area), removal models can produce similar wild pig density estimates reported in previous studies alongside more data-intensive methods such as SMR models. Collectively, our results aid in the decision-making process regarding density estimation methods by providing support for the use of removal models in future wild pig density estimation and will enhance the use of density estimators by distinguishing important factors that influence model output.

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Tables and Figures

Table 2.1. Variables and variable descriptions used in linear and logistic regression models to distinguish important factors in density estimates and coefficients of variation for both removal and SMR models using data collected across 14 private properties in South Carolina, USA from 2020-2023.

Variable	Variable Descriptions	Removal Model Density and CV Variable	SMR Model Density and CV Variable	Density Estimate Dissimilarity Variable
Ecoregion	Coastal Plain, Southeastern Plains, Piedmont	X	X	X
Years of management	Number of years that management has been implemented on property (0-3)	X	X	X
Property size	In km^2			X
Season	Winter or summer	X	X	X
Removal events in PP	The number of removal events in the 3-month primary period	X		
Removals in PP	The number of wild pigs removed in the primary period	X		
Density of removals	The number of wild pigs removed in the PP divided by the property size (km^2)	X		
Removals in last 30 days of PP	The number of wild pigs removed in the final 30 days of a primary period	X		

30-Day removals/area impacted	The number of wild pigs removed in the final 30 days of a primary period divided by the area of the minimum convex polygon plus a 6.7km buffer	X		
Cumulative removals at time of sampling	The cumulative number of wild pigs removed at the time of sampling	X		
Cumulative removals/area impacted	The cumulative number of wild pigs removed at the time of sampling divided by the area of the minimum convex polygon plus a 6.7km buffer	X		
Total detections	The number of marked and unmarked detections within camera survey			X
Marked individuals	The number of individually identified wild pigs within the camera survey			X
Unmarked detections	The number of unmarked detections within the camera survey			X
Density of marked individuals	The number of marked individuals in the camera survey divided by the property size (km^2)			X
Cameras with detections	The proportion of cameras with detections within the camera survey			X

Table 2.2. Linear model results including the model variables (β), number of variables (K), Akaike's Information Criterion corrected (AICc), ΔAICc, model weight, cumulative model weight, and log likelihood (LL) evaluating the impact of removal efforts and season on wild pig (*Sus scrofa*) removal model density estimates using data collected across 14 private properties in South Carolina, USA from 2020-2023. All interactions are designated with the symbol (*).

†Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
30-Day area (7.67) + YrsMgmt (Yr1: -1.00, Yr2: -1.16, Yr3: -0.30)	6	69.06	0.00	0.45	0.45	-26.06
30-Day area (7.57) + YrsMgmt (Yr1: -0.89, Yr2: -1.02, Yr3: -0.07) + Se (Winter: -0.40)	7	71.49	2.43	0.13	0.59	-25.24
30-Day area (10.06) + YrsMgmt (Yr1: -1.09, Yr2: -1.36, Yr3: -0.20) + Pigs rem in PP (-0.01)	7	71.63	2.57	0.13	0.71	-25.31
Null model	2	71.66	2.60	0.12	0.84	-33.54
30-Day area (8.66) + YrsMgmt (Yr1: -1.03, Yr2: -1.28, Yr3: -0.33) + Rem events in PP (-0.02)	7	72.73	3.67	0.07	0.91	-25.86
30-Day area (10.20) + YrsMgmt (Yr1: -0.99, Yr2: -1.22, Yr3: 0.06) + Se (Winter: -0.43) + Pigs rem in PP (-0.01)	8	74.14	5.08	0.04	0.94	-24.27
30-Day area (9.12) + YrsMgmt (Yr1: -0.92, Yr2: -1.19, Yr3: -0.08) + Rem events in PP (-0.03) + Se (Winter: -0.47)	8	75.08	6.02	0.02	0.97	-24.74
30-Day area * Se (0.66) + YrsMgmt (Yr1: -0.91, Yr2: -1.04, Yr3: -0.07)	8	76.08	7.02	0.01	0.98	-25.24

30-Day area ***** YrsMgmt (Yr1: -4.24, Yr2: -6.05, Yr3: N/A)	8	77.05	7.99	0.01	0.99	-25.73
30-Day area (11.71) + YrsMgmt (Yr1: -1.13, Yr2: -1.61, Yr3: -0.04) + Se (Winter: -0.51) + Tot.rem (0.002) + Pigs rem in PP (-0.01)	9	78.21	9.15	0.00	0.99	-23.68
30-Day area ***** Se (-1.50) + YrsMgmt (Yr1: -0.96, Yr2: -1.19, Yr3: 0.07) + Pigs rem in PP (-0.01)	9	79.33	10.27	0.00	1.00	-24.24
30-Day area ***** YrsMgmt (Yr1: -6.89, Yr2: -9.18, Yr3: N/A) + Pigs rem in PP (-0.01)	9	79.91	10.85	0.00	1.00	-24.53
30-Day area ***** YrsMgmt (Yr1: 0.26, Yr2: -3.17, Yr3: N/A) + Se (Winter: -0.38)	9	81.11	12.05	0.00	1.00	-25.13
YrsMgmt ***** Se (Yr1: 0.01, Yr2: 0.07, Yr3: N/A) + 30-Day area (7.51)	9	81.34	12.28	0.00	1.00	-25.24
30-Day area ***** YrsMgmt (Yr1: -2.52, Yr2: -6.35, Yr3: N/A) + Pigs rem in PP (-0.01) + Se (Winter: -0.36)	10	84.76	15.70	0.00	1.00	-23.92

†30-day removals/area impacted (30-day area), years of management (YrsMgmt), season (Se), number of wild pigs removed in the primary period (Pigs rem in PP), number of removal events in the primary period (Rem events in PP), cumulative removals at the time of sampling (Tot.rem)

Table 2.3. Linear model results including the model variables (β), number of variables (K), Akaike's Information Criterion corrected (AICc), ΔAICc, model weight, cumulative model weight, and log likelihood (LL) evaluating the impact of removal efforts and ecoregion on wild pig (*Sus scrofa*) removal model density estimate coefficient of variation values using data collected across 14 private properties in South Carolina, USA from 2020-2023. All interactions are designated with the symbol (*).

†Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
30-Day area (2.50) + Pigs rem in PP (-0.01)	4	6.96	0.00	0.36	0.36	1.57
30-Day area (2.73) + Pigs rem in PP (-0.01) + Eco (Piedmont: -0.21, SE Plains: 0.16)	6	7.60	0.64	0.26	0.63	4.67
Null model	2	9.49	2.53	0.10	0.73	-2.46
30-Day area ***** Pigs rem in PP (0.03)	5	9.75	2.79	0.09	0.82	1.79
Pigs rem in PP ***** Eco (Piedmont: 0.01, SE Plains: 0.03) + 30-Day area (3.03)	8	10.04	3.08	0.08	0.90	7.78
30-Day area ***** Eco (Piedmont: 0.11, SE Plains: -63.68) + Pigs rem in PP (-0.01)	8	10.76	3.80	0.05	0.95	7.42
30-Day area ***** Pigs rem in PP (0.02) + Eco (Piedmont: -0.20, SE Plains: 0.18)	7	11.32	4.35	0.04	1.00	4.84
Pigs rem in PP ***** Eco (Piedmont: 0.01, SE Plains: 0.02)	7	15.89	8.93	0.00	1.00	2.56
30-Day area ***** Eco (Piedmont: 2.20, SE Plains: -39.77)	7	20.80	13.84	0.00	1.00	0.10

† 30-day removals/area impacted (30-day area), number of wild pigs removed in the primary period (Pigs rem in PP), ecoregion (Eco)

Table 2.4. Linear model results including the model variables (β), number of variables (K), Akaike's Information Criterion corrected (AICc), ΔAICc, model weight, cumulative model weight, and log likelihood (LL) evaluating the impact of camera trap data on wild pig (*Sus scrofa*) spatial mark-resight model density estimates using data collected across 14 private properties in South Carolina, USA from 2020-2023. All interactions are designated with the symbol (*).

†Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Unmarked.dets (0.002)	3	70.41	0.00	0.17	0.17	-31.60
Marked.den (1.26)	3	70.82	0.41	0.14	0.31	-31.81
Cams.w.dets (1.67)	3	70.87	0.47	0.14	0.45	-31.84
Null model	2	71.66	1.25	0.09	0.54	-33.54
Unmarked.dets (0.001) + Cams.w.dets (1.14)	4	71.81	1.40	0.09	0.63	-30.85
Tot.dets (0.001)	3	71.86	1.45	0.08	0.71	-32.33
Marked.den (0.88) + Cams.w.dets (1.15)	4	72.28	1.87	0.07	0.78	-31.09
Marked.ind (0.02)	3	72.32	1.91	0.07	0.84	-32.56
Cams.w.dets (1.32) + Tot.dets (0.001)	4	72.82	2.41	0.05	0.89	-31.36
Cams.w.dets (1.40) + Marked.ind (0.01)	4	72.90	2.49	0.05	0.94	-31.40

Umarked.dets ***** Cams.w.dets (-0.004)	5	74.64	4.23	0.02	0.97	-30.65
Marked.den ***** Cams.w.dets (0.46)	5	75.50	5.09	0.01	0.98	-31.08
Cams.w.dets ***** Tot.det (-0.002)	5	75.91	5.50	0.01	0.99	-31.29
Cams.w.dets ***** Marked.ind (0.03)	5	76.04	5.63	0.01	0.99	-31.35

† Number of unmarked detections in the camera survey (Unmarked.dets), density of marked individuals (Marked.den), proportion of cameras with detections within camera survey (Cams.w.dets), total number of detections during camera survey (Tot.dets), number of marked individuals within camera survey (Marked.ind)

Table 2.5. Linear model results including the model variables (β), number of variables (K), Akaike's Information Criterion corrected (AICc), ΔAICc, model weight, cumulative model weight, and log likelihood (LL) evaluating the impact of camera trap data and ecoregion on wild pig (*Sus scrofa*) spatial mark-resight model density estimate coefficient of variation values using data collected across 14 private properties in South Carolina, USA from 2020-2023. All interactions are designated with the symbol (*).

†Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Eco (Piedmont: 0.51, SE Plains: -1.36)	4	70.63	0.00	0.10	0.10	-30.26
Eco (Piedmont: 0.51, SE Plains: -1.21) + Tot.dets (-0.001)	5	70.99	0.35	0.09	0.19	-28.83
Cams.w.dets (1.60) + Tot.dets (-0.001)	4	71.01	0.37	0.08	0.27	-30.45
Tot.dets (-0.001)	3	71.13	0.50	0.08	0.35	-31.97
Cams.w.dets (1.45) + Eco (Piedmont: 0.57, SE Plains: -1.02) + Tot.dets (-0.001)	6	71.47	0.83	0.07	0.42	-27.26
Eco (Piedmont: 0.55, SE Plains: -1.16) + Marked.ind (-0.02)	5	71.48	0.84	0.07	0.48	-29.07
Marked.ind (-0.02)	3	71.49	0.85	0.07	0.55	-32.14
Eco (Piedmont: 0.65, SE Plains: -1.30) + Marked.den (-0.94)	5	71.51	0.88	0.07	0.62	-29.09
Eco (Piedmont: 0.80, SE Plains: -1.12) + Cams.w.dets (1.63) + Marked.den (-1.54)	6	71.53	0.90	0.07	0.68	-27.29

Null Model	2	71.66	1.03	0.06	0.74	-33.54
Cams.w.dets (1.35) + Marked.ind (-0.02)	4	72.18	1.55	0.05	0.79	-31.04
Eco (Piedmont: 0.52, SE Plains: -1.26) + Unmarked.dets (-0.001)	5	72.35	1.72	0.04	0.83	-29.51
Cams.w.dets * Eco (Piedmont: 2.13, SE Plains: 15.69) + Tot.dets (-0.001)	8	72.39	1.76	0.04	0.87	-23.40
Unmarked.dets (-0.001)	3	72.52	1.89	0.04	0.91	-32.66
Eco * Tot.dets (Piedmont: -0.001, SE Plains: 0.002)	7	73.95	3.32	0.02	0.93	-26.48
Cams.w.dets * Tot.dets (-0.001)	5	74.19	3.56	0.02	0.95	-30.437
Eco * Cams.w.dets (Piedmont: 3.51, SE Plains: 9.67)	7	74.59	3.96	0.01	0.96	-26.79
Marked.ind * Eco (Piedmont: 0.001, SE Plains: 0.05)	7	74.68	4.04	0.01	0.98	-26.84
Cams.w.dets * Tot.dets (-0.001) + Eco (Piedmont: 0.54, SE Plains: -1.08)	7	75.42	4.79	0.01	0.99	-27.21
Marked.den * Eco (Piedmont: -0.22, SE Plains: 3.46)	7	76.18	5.55	0.01	0.99	-27.59
Marked.den * Eco (Piedmont: 0.30, SE Plains: 3.92) + Cams.w.dets (1.73)	8	76.32	5.68	0.01	1.00	-25.36

† Ecoregion (Eco), proportion of cameras with detections within camera survey (Cams.w.dets), total number of detections during camera survey (Tot.dets), number of marked individuals within camera survey (Marked.ind), density of marked individuals (Marked.den), number of unmarked detections in the camera survey (Unmarked.dets)

Table 2.6. Logistic regression model results including the model variables (β), number of variables (K), Akaike's Information Criterion corrected (AICc), ΔAICc, model weight, cumulative model weight, and log likelihood (LL) evaluating the impact of season, property size, years of management, and ecoregion on the dissimilarity of wild pig (*Sus scrofa*) spatial mark-resight and removal model density estimates using data collected across 14 private properties in South Carolina, USA from 2020-2023. All interactions are designated with the symbol (*).

†Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Null Model	1	35.29	0.00	0.37	0.37	-16.55
Prop.size (0.02)	2	36.12	0.84	0.25	0.62	-15.78
Se (Winter: -0.99)	2	36.28	0.99	0.23	0.85	-15.85
Eco (Piedmont: 0.42, SE Plains: -17.43)	3	37.49	2.20	0.12	0.97	-15.14
YrsMgmt (Yr1: 0.63, Yr2: -0.69, Yr3: 16.97)	4	40.43	5.14	0.03	1.00	-15.16
Eco (Piedmont: 1.55, SE Plains: -19.30) + Se (Winter: -0.93) + YrsMgmt (Yr1: 1.77, Yr2: -0.71, Yr3: 20.53) + Prop.size (0.03)	8	46.71	11.43	0.00	1.00	-10.56
YrsMgmt * Se (Yr1: 20.61, Yr2: 40.00, Yr3: N/A) + Eco (Piedmont: 1.01, SE Plains: -20.46)	9	50.06	14.78	0.00	1.00	-9.60
Eco * Se (Piedmont: 0.03, SE Plains: N/A) + YrsMgmt (Yr1: 1.66, Yr2: -0.31, Yr3: 18.81)	8	50.40	15.11	0.00	1.00	-12.40

Eco * YrsMgmt (Yr1/Pied: 17.71, Yr1/SE Plains: N/A, Yr2/Pied: -20.00, Yr2/SE Plains: N/A, Yr3/Pied: N/A, Yr3/SE Plains: N/A) + Se (Winter: -1.78)	9	52.39	17.10	0.00	1.00	-10.77

† Property size (Prop.size), Ecoregion (Eco), season (Se), years of management (YrsMgmt)

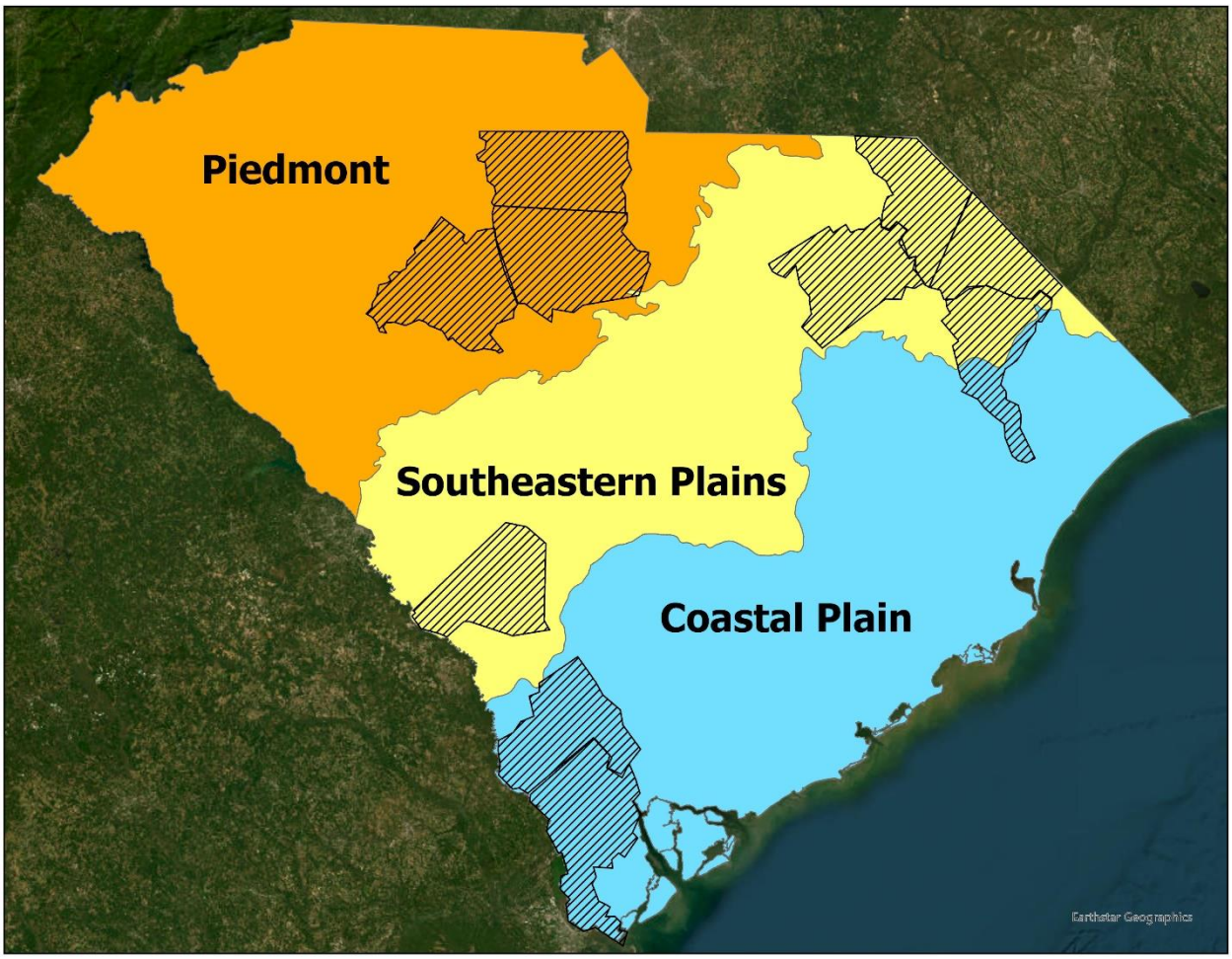

Figure 2.1. Map of South Carolina, USA, showing the three ecoregions including Piedmont (orange), Southeastern Plains (yellow), and Coastal Plain (blue), and the ten counties (shaded in black) where study properties were located.

Figure 2.2. Examples of differing pelages of wild pigs (*Sus scrofa*) in South Carolina, USA.

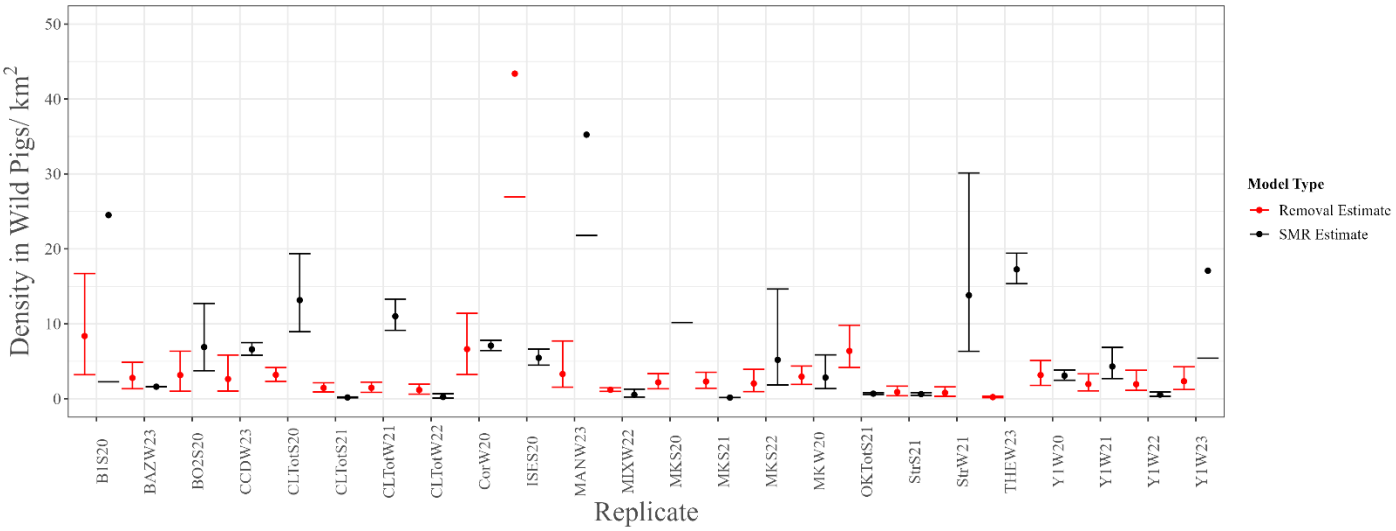

Figure 2.3. Spatial mark-resight and removal model wild pig (*Sus scrofa*) density estimates for all 24 replicates within our study with 95% confidence interval bars using removal and camera trap data collected across 14 privately owned properties in South Carolina, USA from 2020-2023.

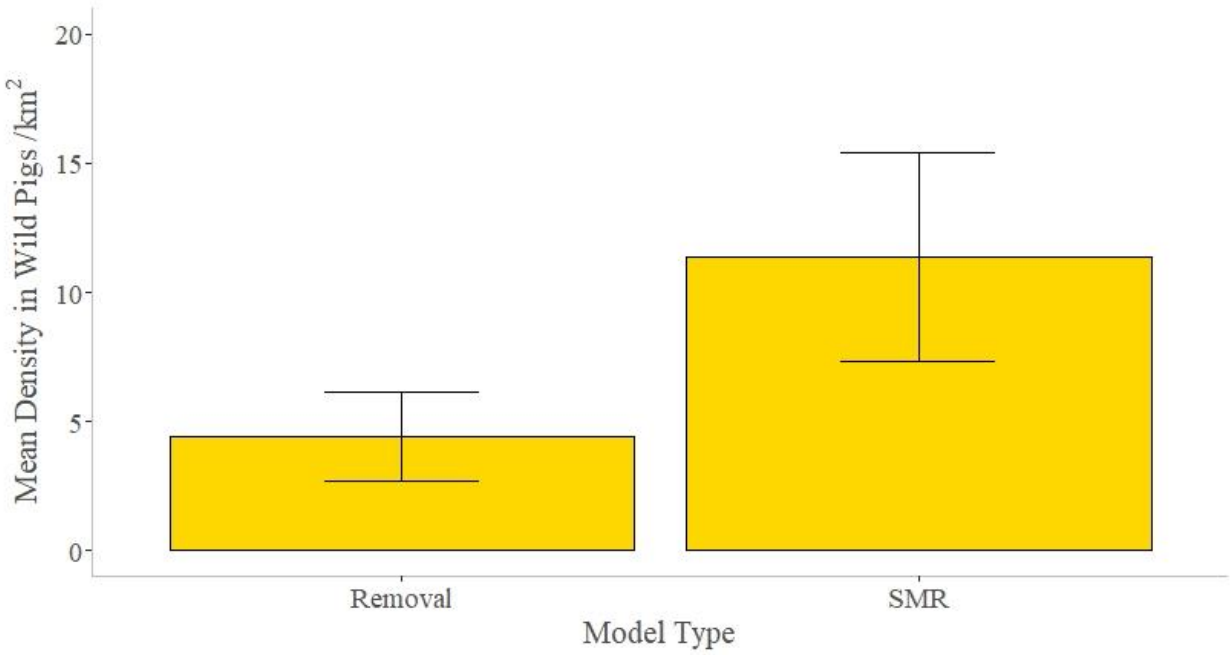

Figure 2.4. Mean estimated densities of wild pigs (*Sus scrofa*) with standard error bars of each model type (removal and SMR) from 24 replicates using data collected across 14 private properties (mean area = 15.34 km^2) in South Carolina, USA from 2020-2023.

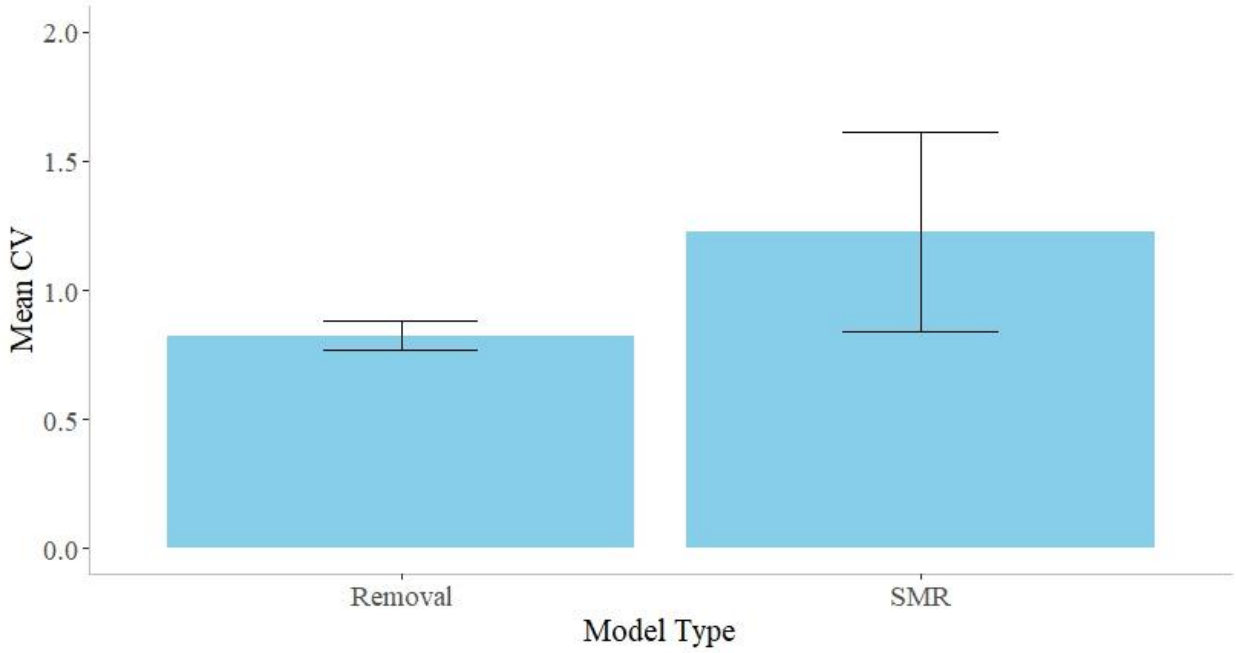

Figure 2.5. Mean coefficients of variation (CV) of estimated wild pig (*Sus scrofa*) densities with standard error bars of each model type (removal and SMR) from 24 replicates using data collected across 14 private properties in South Carolina, USA from 2020-2023.

CHAPTER 3

EVALUATION OF COMMON TRAP TYPES FOR CAPTURING INVASIVE WILD PIGS (*SUS SCROFA*)

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Abstract

Wild pigs (*Sus scrofa*) are one of the most ecologically harmful and economically costly invasive vertebrates in North America. Trapping is an effective tactic in wild pig population management, and there has been considerable effort to develop improved trap designs to maximize capture efficiency. Despite the importance of trapping in wild pig management programs, studies investigating the performance of various trap designs have been limited in duration, location, and trapper personnel. Using data from professional trappers across the southeastern US, our objective in this research was to compare the performance of common wild pig trap types (corral, drop, passive net), as well as the effect of forage season on trapping success. Specifically, we compared trap effectiveness (proportion of wild pigs captured per trap event), number of days to first catch, and the amount of bait and time used per take over the lifetime of each trap location across the three trap types and forage seasons. Across >850 capture events by 31 trappers, we did not observe any differences in time spent per take among trap types. However, we found that forage season impacted performance of corral and drop traps regarding trap effectiveness, and the number of trap nights until first catch. We also observed differences in the amount of bait used per take among trap types, with net traps requiring slightly more bait per catch than drop traps. Our findings reflect how three common wild pig trap types perform across a range of environments, seasons, and professional trappers. Results of this research will provide critical insights into the efficacy of common capture methods, and the time of year when that efficacy is maximized, which can be used to optimize trapping programs for wild pigs.

Introduction

Globally, invasive species pose a severe threat to both ecological and anthropogenic resources and are a primary cause of many native species declines and extinctions across all taxa (Clavero & Garciaberthou 2005; Simberloff 2010; Pitt et al. 2018). The cost of restoring damages and conducting population management practices to control or eradicate invasive species exceeds billions of dollars (US) across afflicted areas (Marbuah et al. 2014; Bradshaw et al. 2021; Haubrock et al. 2021). Additionally, invasive species have continued to expand in range and abundance worldwide due to factors such as changing landscape use, climate change, and human-led translocations (Rahel & Olden 2008; Pitt et al. 2018; Clontz et al. 2023). Research investigating effective and efficient management techniques for invasive species is ongoing and is a primary concern for biologists and land managers (Clout & Williams 2009).

Wild pigs (*Sus scrofa*) are a globally distributed species, inhabiting all continents except Antarctica, making them among the widest ranging invasive vertebrate species on Earth (Barrios-Garcia & Ballari 2012). Across both their native and introduced range, wild pigs are a focal concern for managers and biologists due to their expanding populations and range, numerous deleterious environmental impacts, and damage to anthropogenic resources (e.g., agriculture, property; Tisdell 1982; Barrios-Garcia & Ballari 2012; Bengsen et al. 2014; VerCauteren et al. 2020). In addition, wild pigs carry numerous viruses, parasites, and bacteria that can cause disease in humans, livestock, and other wildlife, particularly cervids (Meng et al. 2009; Bevins et al. 2014; Miller et al. 2017), and wild pigs' feeding habits (e.g., rooting, or digging up of soil), cause damage to both agricultural crops and native flora (Seward et al. 2004; Pimentel et al. 2005; Chavarria et al. 2007; Pimentel 2007). Along with rooting, wild pigs also wallow in wet soil which can cause erosion to natural landscapes and increase runoff volume

(Sierra 2001; Dunkell et al. 2011). The majority of their diet is plant-based (Massei & Genov 2004), however, wild pigs have also been shown to actively predate and scavenge on both native and sensitive animal species, as well as livestock (Choquenot et al. 1997; Jolley et al. 2010; Turner et al. 2017; Sanders et al. 2020), and competition with native animal species such as white-tailed deer (*Odocoileus virginianus*) for food and other resources is also a concern (Taylor & Hellgren 1997; Sweitzer & Van Vuren 2002; Keiter & Beasley 2017; Garabedian et al. 2023).

In addition to the many negative impacts that wild pigs exhibit across their invasive range, they are also a highly fecund generalist species that thrive in most environments (Barrios-Garcia & Ballari 2012; McClure et al. 2015; VerCauteren et al. 2020). Moreover, there has been an increase in human translocations of wild pigs in recent decades due to their popularity as a game species (Spencer & Hampton 2005; Mccann et al. 2014; Tabak et al. 2017; Clontz et al. 2023). This anthropogenic movement of wild pigs, coupled with their innate ability to adapt and survive in novel areas, has caused wild pig populations to rapidly expand globally in recent years (Mayer 2014; Bengsen et al. 2017; Lewis et al. 2019).

Due to the numerous impacts wild pigs have on their environment and their continued expansion in population size and distribution across their invasive range, there has been a surge in management programs at the local, state, and national level to reduce damages from this invasive species. For example, in the US a nationwide effort to control wild pig populations began in 2014 with the formation of the National Feral Swine Damage Management Program headed by the United States Department of Agriculture (USDA; USDA 2013). These programs have proven effective at reducing both population size of wild pigs and related damages as well as slowing the spatial expansion of the species (Pepin et al. 2019; Treichler et al. 2023). While most management has focused on population reduction, management programs have successfully

eliminated wild pigs from multiple US states at the fringe of their range (USDA 2019) and there have been multiple examples of successful elimination on islands (Cruz et al. 2005; Parkes et al. 2010).

Wild pigs are highly adaptable generalists, and thus successful management requires continued innovation and implementation of a multitude of methods employed in an adaptive approach (West et al. 2009; Hamrick et al. 2011; Massei et al. 2011). Non-lethal methods such as exclusion fencing and repellents have been shown to have some success in deterring wild pigs (Doupé et al. 2010; Snow et al. 2021a) but are not a viable long-term solution due to their continuous cost and waning effectiveness over time. Thus, management programs have largely implemented lethal approaches to curb expanding wild pig populations. Recent lethal developments such as toxicants have been used in research trials in both Australia and the US (Cowled & O'Connor 2004; Lapidge et al. 2012; Beasley et al. 2021; Snow et al. 2021b), however concerns over non-target exposure through scavenging and the effectiveness of bait delivery systems to prevent non-target consumption remain. Because of this, agencies and land managers have largely used trapping, strategic ground shooting, and aerial gunning for both efficient and effective management of wild pigs (Sterner & Barrett 1991; Saunders 1993; McCann & Garcelon 2008; West et al. 2009; Bodenchuk 2014).

Trapping, in particular, is one of the most widely used and efficient methods of wild pig population control (West et al. 2009; Hamrick et al. 2011; Wight et al. 2022). Numerous designs and styles of traps such as box traps, drop nets, and silo traps have been developed and used to capture wild pigs (Choquenot et al. 1993; Saunders et al. 1993; Barrett & Birmingham 1994; Caley 1994; Gaskamp et al. 2021), and there has been continued innovation of these trap types to improve their efficacy (Williams et al. 2011; Metcalf et al. 2014; Smith et al. 2014; Wight et al.

2022). Research has shown that both whole sounder (i.e., social group) removal and organized culling across sections of targeted areas are critical for reducing wild pig populations (Pepin et al. 2017; Lewis et al. 2022; Kilgo et al. 2023). Thus, there has been considerable innovation in developing new trap designs and trigger mechanisms (e.g., cellular activated) to reduce the number of wild pigs missed (i.e., outside the trap) or that escape during capture (Beasley et al. 2020; Ditchkoff & Bodenchuk 2020). Nonetheless, further improving trap efficacy remains a top research priority to increase the efficiency and effectiveness of management programs (Mayer & Beasley 2018; Beasley et al. 2018).

Today, the three most common trap types used among managers include corral, drop, and passive net traps (Beasley et al. 2020; Ditchkoff & Bodenchuk 2020; Wight et al. 2022). Corral-style traps have historically been used to capture wild pigs (Choquenot et al. 1993; Barrett & Birmingham 1994; Higginbotham 2012), whereas drop and passive net traps are relatively newer innovations (ShalekBriski et al. 2021; Chen & Dokes-Dumas 2022; Wight et al. 2022). There are several variations of each, but generally corral traps consist of wire panels set on the ground in a circular fashion with one or multiple drop gates at the entrance(s). Drop, or suspended style, traps involve wire panels that connect to create an enclosed circle, which is then raised off the ground as a single unit and drops to the ground when triggered, capturing any wild pigs inside. Both corral and drop style traps can be triggered using a cell phone or remote device, which allows trappers to select when to close a trap in real-time, limiting the number of wild pigs missed at the time of activation (Keiter & Beasley 2017; Ditchkoff & Bodenchuk 2020). Passive-style traps are similar in size and shape as corral and drop traps but are constructed of netting material. Similar to passive traps used for fish and herpetofauna, passive traps for wild pigs do

not require any direct action to enclose or activate the trap; instead, animals are able to enter the trap freely, but cannot readily escape (Willson & Gibbons 2010).

Although studies have investigated the benefits and drawbacks of different styles and variations of traps (Williams et al. 2011; Metcalf et al. 2014; Smith et al. 2014; Lavelle et al. 2019; Gaskamp et al. 2021), the three most-deployed trap types (corral, drop, and passive net) have not been thoroughly investigated concomitantly. Additionally, trapping events used in previous studies have largely been performed by the researchers themselves and involved a relatively small sample size of traps within a limited area and over a limited timeframe. These limitations may introduce biases that hinder the application of study results outside of these regions and seasons, and across a broad range of trappers. Furthermore, while previous studies have investigated the productivity of trapping efforts in relation to forage availability and season (Caley 1994; Yokoyama et al. 2020), none have quantified the success of these efforts relative to the proportion of targeted wild pigs captured in each trap event.

Therefore, our objective in this research was to evaluate the performance of corral, drop, and passive net traps by quantifying effectiveness (proportion of wild pigs captured per trap event), effort (number of trap nights until first catch), and efficiency (bait used and time spent per pig in trap lifetime) using removal data collected from >850 trap events from 31 professional trappers across the southeastern US over a three year period. Additionally, we tested the hypothesis that trap performance would vary seasonally across all trap types relative to the availability of food. Specifically, we predicted the number of trap nights until first catch would be greatest during periods of high forage availability. Furthermore, across all trap types we predicted trap effectiveness to be lowest following periods of peak parturition due to altered movements of sows (Chinn et al. 2023) and increased vigilance in the presence of new young.

Study Area

We collected trapping data across four states within the southeastern US, including Arkansas, Georgia, North Carolina, and South Carolina. These states were chosen due to their variety of habitats across a gradient of wild pig densities, their implementation of multiple styles of traps, and their interest in participating in the study. All states cover a range of physiographic regions from coastal to mountains, with diverse habitats including mixed hardwood and pine (*Pinus* spp.) forest, bottomland swamp (*Nyssa* spp., *Quercus* spp.), small-scale cropland, and various wetlands and floodplains. These states cover multiple mountain ranges including the Appalachian, Ouachita, Boston, and Blue Ridge mountains. Three of the four states (Georgia, North Carolina, and South Carolina) border the Atlantic Coast, with Arkansas being the only completely inland state.

Although all four states have stable or increasing wild pig populations, North Carolina historically has had lower densities than the other three states. Populations of wild pigs have recently been estimated at 130,000 for Arkansas, 1,000,000 for Georgia, 1,500 for North Carolina, and 160,000 for South Carolina (Mayer 2014). Wild pigs occur in every county in both Georgia and South Carolina, and all but one county in Arkansas (Corn & Jordan 2017). In North Carolina, wild pigs occur in 83% of counties. Management for wild pigs has been ongoing in these states to some extent for decades, however organized governmental efforts began within the past decade through federal management programs such as the National Feral Swine Damage Management Program created in 2014 by the USDA.

Methods

Data Collection

We recorded data from trap events carried out over a three-year period (2021–2023) by professional United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS) trappers in each state. Only data from corral, drop, and passive net style traps were recorded and used for analysis. Brands or specific builds (i.e., different materials or styles of gates/panels used) of the different styles of traps were ignored and not considered in the analysis. Data collected for each trap event included total take, number of wild pigs missed, date of capture, trap construction date, county, name of trapper, GPS coordinates of trap (if provided), trap trigger type for corral and drop traps (e.g., remote, trip wire, root stick), and approximate amount of bait (kg) used and time (hours) spent for each trap event. For bait and time estimation, counts began at the initiation of prebaiting and were summed over all trap events made at a trap site (individual trap placed in a specific location). We defined a trap event as an individual capture of a wild pig(s) recorded at a single trap, and all trap events were included in analyses.

Wild pigs change their diet based on seasonality and availability of vegetation and other food resources (Taylor & Hellgren 1997; Froehly et al. 2020; Canright et al. in print). In addition, trapping performance can be seasonal (Mayer & Beasley 2018; Yokoyama et al. 2020), largely related to the feeding habits of wild pigs and resource availability. Because of the impacts seasonality can have on trapping efforts, we also classified each trap event into a forage season based on the date of capture. We partitioned the calendar year into three foraging seasons which we referred to as green-up, masting, and barren. Green-up was defined as March–July and referred to the arrival of the new year's green vegetation. Masting was defined as August–

November and referred to the production and distribution of seeds, such as acorns, by hardwood trees. Finally, the barren period was defined as December–February and referred to the time of year where mast had largely disappeared, and green vegetation had not begun to sprout.

Trap Effectiveness

We quantified trap effectiveness as a metric to convey the proportion of targeted wild pigs that were captured during a trap event (i.e., incidence where wild pigs were captured or a trap was triggered by wild pigs), determined by each trapper based on their knowledge of the number of wild pigs they were pursuing using images from camera traps placed at trap sites. We calculated trap effectiveness for each trap event and distinguished values by trap type for analysis. Our response variable for this metric was the proportion of targeted wild pigs captured per trap event; therefore, we modeled its distribution with a binomial regression using the lme4 package in R (See below; Bates et al. 2009).

Trap Night Effort

We quantified trap night effort as a metric to determine the length of time a new trap site takes to yield a successful catch, which was calculated by tallying the number of trap nights, which were defined as the number of days from trap construction date to date of capture. We defined trap construction date as the date trap building was initiated for a specific trap. In certain instances, a trap might be built and set on the same day if wild pigs immediately enter a trap after building. However, other traps are built in stages, and the time between trap construction and trap setting can be days or even weeks. For this metric, only the first catch for each trap site was considered. We fit a generalized linear mixed model (GLMM) with a Poisson distribution and log link to the count data using the lme4 package in R (See below; Bates et al. 2009).

Bait and Time Efficiency

We derived two different metrics to represent trap efficiency. We summed bait (kg) used and time (hours) spent during the entire tenure of each trap site and divided each by the total number of wild pigs captured at that site to determine bait-per-take and time-per-take efficiencies. All trap events that occurred at a particular trap site were considered to quantify both the number of individuals caught at a particular location and the resources (e.g., bait and time) needed to achieve those results and bait- and time-per-take efficiencies were calculated separately for each trap site. We fit a GLMM specifying a gamma distribution and log link to the above-zero continuous response data using the lme4 package in R (See below; Bates et al. 2009).

Model Fitting

To evaluate the influence of trap type and forage season on our metrics of trap performance, we ran a GLMM for each metric and obtained predictions for each model using the ggpredict function in R. For trap effectiveness and trap night effort we ran the same global model which included both trap type and forage season as fixed effects, an interaction between trap type and forage season, and trapper as a random effect. For the bait- and time-per-take efficiencies, forage season was not included due to the tenure of trap sites often spanning over multiple forage seasons. Instead, we ran a model for each of these metrics that included trap type as a fixed effect and trapper as a random effect. All analyses were performed in R (Version 4.1.0; R Core Team 2023).

Results

Between 2021-2023 we compiled 894 trap events from 31 professional trappers across the four study states, with the majority (74%) of data coming from South Carolina. Of those 894

trap events, 465 (52%) involved corral traps, 179 (20%) involved drop traps, and 251 (28%) involved passive net traps. Moreover, 172 (19%) trap events occurred in the barren season, 573 (64%) occurred in the green-up season, and 149 (17%) occurred in masting season.

Trap Effectiveness

Trap effectiveness (i.e., proportion of wild pigs caught per trap event) values ranged from 0–1 ($\bar{x}$ = 0.92 ±0.01 SE) for corral traps, 0–1 ($\bar{x}$ = 0.97 ±0.01 SE) for drop traps, and 0.05–1 ($\bar{x}$ = 0.88 ±0.01 SE) for passive net traps (Figure 3.1). This resulted in an average number of targeted wild pigs missed for any single trap event being 0.80 (±0.11 SE) for corral traps, 0.35 (±0.11 SE) for drop traps, and 1.10 (±0.15 SE) for passive net traps (Figure 3.2). The global model that included trap type and forage season as fixed effects, an interaction between trap type and forage season, and trapper as a random effect (marginal R^2=0.01, conditional R^2=0.06) predicted drop traps in masting season to capture a significantly higher ($p<0.001$) proportion of wild pigs per trap event than either corral traps in barren or masting season or passive net traps in green-up or masting season (Figure 3.3). However, there was generally little variation observed between trap types and across forage seasons regarding the proportion of wild pigs captured per trap event.

Trap Night Effort

The number of trap nights until the first catch within our trapping data ranged from 1.00–198.00 ($\bar{x}$ = 15.41 ±1.43 SE) for corral traps, 1.00–134.00 ($\bar{x}$ = 11.28 ±1.95 SE) for drop traps, and 2.00–122.00 ($\bar{x}$ = 18.02 ±1.40 SE) for passive net traps (Figure 3.4). The global model that included trap type and forage season as fixed effects, an interaction between trap type and forage season, and trapper as a random effect was used to obtain model predictions (marginal R^2=0.14, conditional R^2=0.80). The model showed considerable variation among forage seasons for both

corral and drop traps, with little variation among forage seasons in passive net traps (Figure 3.5). For example, our model results revealed corral traps in masting season required more trap nights before the first catch ($p<0.001$) than in barren or green-up forage seasons. In addition, drop traps in barren season were shown to require more trap nights before the first catch ($p<0.001$) than in green-up forage season.

Bait and Time Efficiency

The total amount of bait used per trap site within our trapping data ranged from 11.34–2948.35 kg ($\bar{x}$ = 202.34 ±15.41 SE) for corral traps, 9.07–544.31 kg ($\bar{x}$ = 111.42 ±10.68 SE) for drop traps, and 11.34–1814.37 kg ($\bar{x}$ = 146.39 ±14.28 SE) for passive net traps. This translated to mean bait-per-take efficiencies of 19.01 kg/wild pig (±1.34 SE) for corral traps, 12.97 kg/wild pig (±4.30 SE) for drop traps, and 21.37 kg/wild pig (±2.73 SE) for passive net traps (Figure 3.6). For bait-per-take efficiency, a model with trap type as a fixed effect and trapper as a random effect (marginal R^2=0.02, conditional R^2=0.28) was used to obtain model predictions which revealed a significantly higher ($p=0.001$) bait-per-take for passive net traps compared to drop traps, although this was the only difference detected among trap types (Figure 3.7).

The total time spent per trap site by personnel within our trapping data varied from 1.00–161.00 hours ($\bar{x}$ = 11.10 ±0.96 SE) for corral traps, 1.00–90.00 hours ($\bar{x}$ = 9.84 ±1.35 SE) for drop traps, and 1.00–44.00 hours ($\bar{x}$ = 7.51 ±0.53 SE) for passive net traps. This translated to mean time-per-take efficiencies of 1.08 (±0.09 SE) for corral traps, 1.53 (±0.54 SE) for drop traps, and 1.13 (±0.12 SE) for passive net traps (Figure 3.8). For time-per-take efficiency, our model with trap type as a fixed effect and trapper as a random effect (marginal R^2=0.01, conditional R^2=0.32) did not yield any significant differences among trap types in the number of hours spent per wild pig captured (Figure 3.9).

Discussion

Using a robust dataset of trap performance data collected from professional trappers across a broad geographic region, our results demonstrate that modern corral, drop, and passive net traps are highly effective at capturing entire social groups of wild pigs. While we did observe notable interactions between trap types and forage seasons for some of our performance metrics, performance was generally similar among trap types. Specifically, the interaction of trap type and forage season was shown to influence the proportion of wild pigs captured per trap event and the number of trap nights until first catch in some instances, however this influence was only observed in a couple isolated trap type/forage season combinations and could have been a result of limited data for those trap type/forage season combinations. We also observed differences among trap types in the amount of bait used per wild pig caught, although no differences were observed in the amount of time spent per wild pig caught among trap types. Our results indicate that trap type and the interaction of forage season and trap type can be important to consider when implementing management efforts for wild pigs, although all of the trap types utilized in our study are effective in capturing wild pigs.

Within our trapping data, all trap types performed well regarding trap effectiveness, with each trap type on average catching >88% of wild pigs targeted in a single trap event. Whole sounder removal has been demonstrated to be critical to achieve wild pig population reduction goals (Lewis et al. 2022; Kilgo et al. 2023), and thus all three trap types we investigated are effective means of wild pig population control. Although previous studies investigating passive net traps are scarce, our findings support previous research that suggest both corral and drop style traps are effective means of wild pig trapping (Williams et al. 2011; Gaskamp et al. 2021). Furthermore, although all drop traps and ~94% of corral traps in our study used a human

activated trigger mechanism, passive net traps where no trigger mechanism exists captured similar proportions of sounders as both actively triggered traps. Moreover, our data suggests that despite remote trigger systems theoretically maximizing capture potential, the difference between trigger mechanisms might not be substantial, although more research is needed on this subject. Additionally, we did not distinguish between wild pigs remaining outside a trap at the time of activation, and wild pigs that escaped after trap enclosure. Because of this lack of clarification, it is difficult to ascertain the impact trigger mechanisms had on trapping efficacy in our study.

Although our model predictions revealed an interaction of trap type and forage season influenced the proportion of wild pigs captured in any particular trap event, this was only evident for drop traps in masting season, which were estimated to capture a greater proportion of wild pigs compared to other season and trap type combinations. Our findings refute our prediction that the proportion of wild pigs captured during trap events would decrease during our green-up season when a large proportion of wild pigs are caring for natal young in the southeastern US (Chinn et al. 2022). Moreover, the differences observed between green-up and other forage seasons were not consistent across trap types regarding the proportion of wild pigs captured per trap event. Although wild pigs give birth more often in the green-up season, studies have shown wild pigs to be pregnant every month out of the year in the southeastern US (Chinn et al. 2022), which could have contributed to the lack of consistency in the proportion of wild pigs captured among forage seasons and trap types. The significant interaction between forage season and trap type relative to the proportion of wild pigs captured per trap event could also be due to a lack of data for specific trap type/forage season combinations. Despite the large sample size of trapping events recorded for this study, some trap type/forage season combinations were less represented

in our dataset. For example, our data only included 22 trap events for drop traps during masting season, compared to 123 trap events for drop traps during green-up. Given that most trap events captured the majority of wild pigs, it is possible the limited number of drop trap replicates during masting season could have been a contributing factor to drop traps in masting season capturing a greater proportion of wild pigs per trap event in our model predictions.

Due to the extraordinary reproductive potential and rapid expansion capabilities of wild pigs (Read & Harvey 1989; Taylor et al. 1998; Chinn et al. 2022), control efforts in newly introduced areas must occur quickly, and consistent removals are needed to effectively reduce populations. Our data revealed traps were able to yield a first catch on average within 11–18 days from the start of trap construction. Model predictions demonstrated more variability in the number of trap nights until the first catch across forage seasons for both corral and drop traps. In particular we observed a significantly higher number of trap nights until the first catch for corral traps during masting season compared to other seasons. This finding partially supports our prediction that we would expect increased effort capturing wild pigs during periods of high forage availability. Although, this increased effort was not consistent across trap types, as there was little variability in passive net traps across forage seasons and a higher number of trap nights until the first catch found in the barren season for drop traps. This variability across trap types and forage seasons makes direct assumptions about the role that forage season plays in the number of trap nights until the first catch difficult, and most likely means other factors were influencing these results (e.g., outliers in data, limited sample size for certain combinations). Additionally, previous research has shown that factors such as location of initial bait placement influence the rate at which wild pigs find and accept a new trap location (Saunders et al. 1993; Beasley et al. 2021). Although our results point to the interaction of trap type and forage season

being an important factor in the timing of a particular trap's first catch after trap construction begins in some cases, more research is needed to investigate the extent of this impact.

Prebaiting is an important step in the process of wild pig trapping that can influence the effectiveness of a trapping program (West et al. 2009; Higginbotham 2012). Because prebaiting can be an expensive and time intensive process (Saunders et al. 1993), we wanted to quantify how much bait and time each trap type used per wild pig captured. Our model revealed passive net traps to have a higher bait-per-take than drop traps. The slight increase in bait used for passive net traps may reflect that they typically are built in stages, which requires a longer prebaiting period, due to the need for wild pigs to become accustomed to rooting under the net to enter the trap. Apart from this lone difference, the minimal differences found between trap types regarding bait- and time-per-take values suggest these parameters are not heavily influenced by trap type.

Our study results reflecting the performance of three common trap types used for wild pigs are critical to the improvement of tactical trapping efforts and offer a unique perspective due to the scale and timeframe over which our data was collected. Our study was conducted over four states within the southeastern US, encompassing some of the highest wild pig densities in North America. Thus, future research could benefit from additional ecoregions and areas not represented in this study and investigating whether these different environments influence trapping efficacy. Moreover, it is important to note that our trap effectiveness metric considered each trap event as an independent occurrence with no relation to future captures made at that trap site. This lack of relation between captures can be misleading in cases where a partial sounder is caught by a trap in the first trap event, and in subsequent trap events the remainder of the group is captured, as these successional captures are important in understanding a trap's overall

effectiveness. Lastly, up-to-date research on wild pig behavior, movement, and ecology is continually needed to better manage the species across its invasive range (Beasley et al. 2018). For many of these studies, wild pigs need to be captured, handled, and often recaptured to collect various data (e.g., blood/tissue samples) or attach tracking devices (e.g., radio collars). For this reason, it would be valuable to investigate the frequency and ability of a trap type to recapture individual animals in the future, as well as the ability to limit trap related injuries during capture (Lavelle et al. 2019). Indeed, being able to recapture individuals could enhance trapping efforts, while also benefiting future wild pig research.

The continued management of wild pigs is key to the proper conservation of both native flora and fauna, as well as the reduction in anthropogenic damages (e.g., agriculture, property). Accordingly, management strategies for wild pigs are regularly being updated and refined, although more research is needed to optimize the reduction of populations. Research has shown trapping to be one of the most effective and efficient removal techniques used for wild pigs in reducing agricultural and environmental damage (Higginbotham 2012; Gaskamp et al. 2018; Treichler et al. 2023), and our research enhances wild pig trapping by informing managers and agencies of the effect trap type and forage season have on trapping efforts. Overall, our results suggest that factors other than trap type (e.g., forage season, trapper personnel) have a greater impact on trap performance, although there are situations where trap type can improve certain trapping metrics. In addition, all trap types included in this study were effective means of capturing wild pigs, and when used appropriately and during optimal timeframes, can be used to successfully control wild pig populations. We believe this study will aid wild pig trapping efforts in the future and allow for the continued enhancement of wild pig management.

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Figures

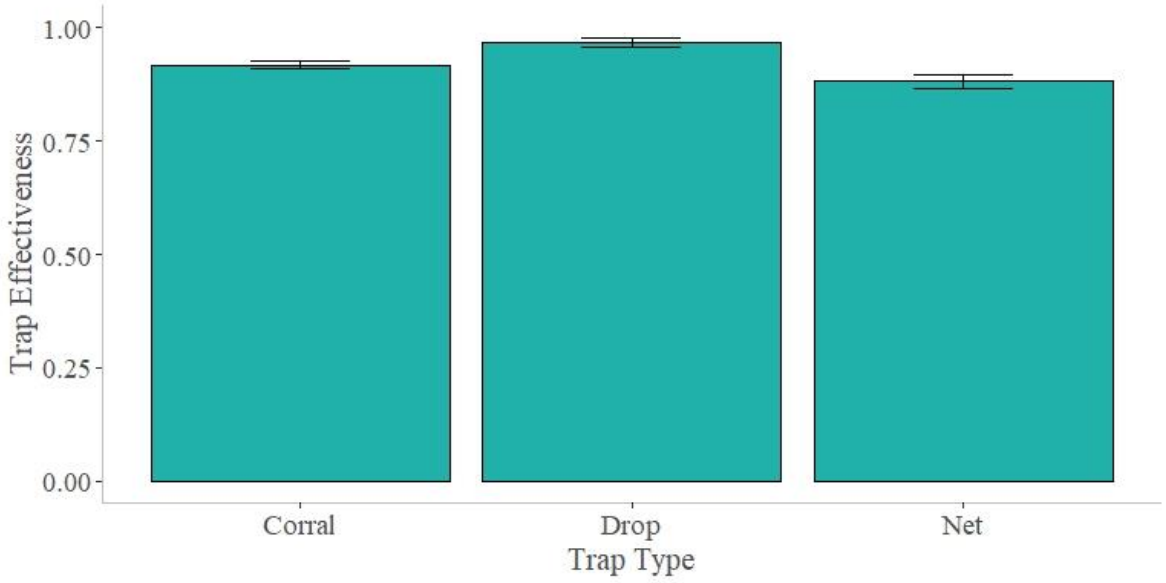

Figure 3.1. Proportion of targeted wild pigs (*Sus scrofa*) captured per trap event (trap effectiveness) with standard error bars for three trap types (corral, drop, passive net) using trap data collected from 31 professional trappers across Arkansas, Georgia, North Carolina and South Carolina, USA from 2021-2023.

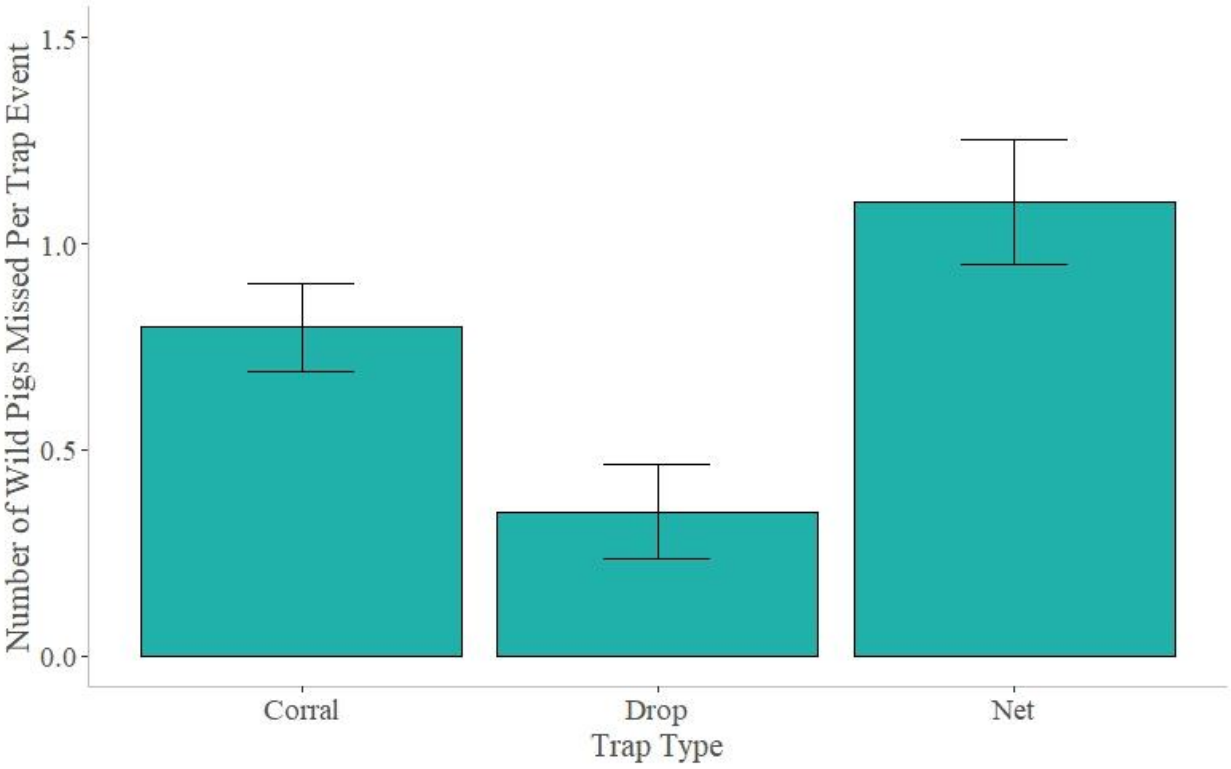

Figure 3.2. Number of targeted wild pigs missed per trap event with standard error bars using trap data collected from 31 professional trappers across Arkansas, Georgia, North Carolina and South Carolina, USA from 2021-2023.

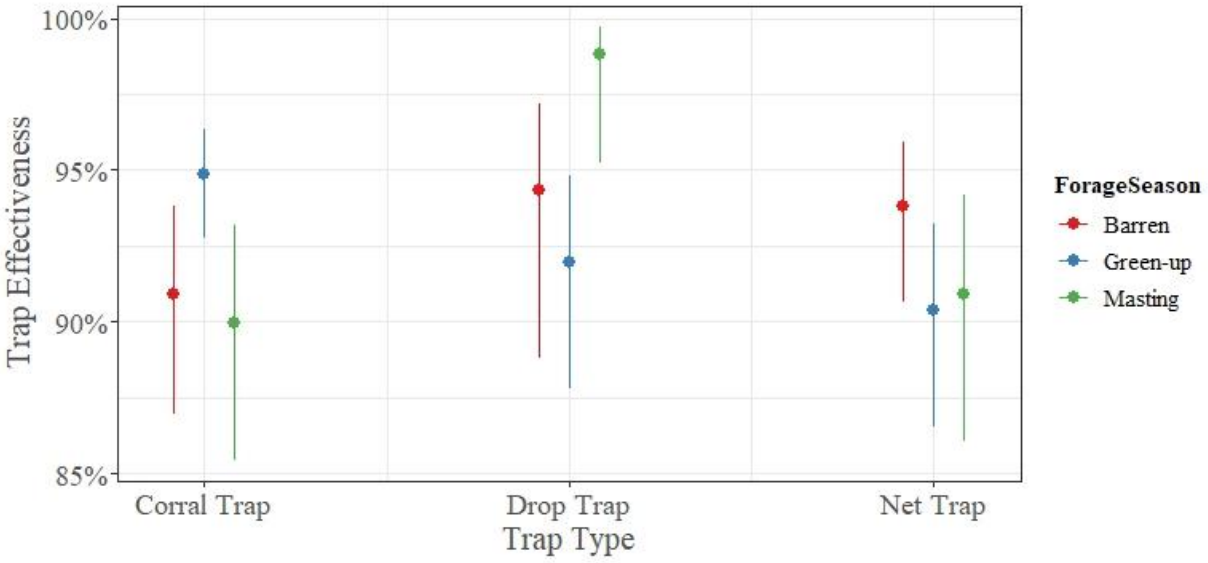

Figure 3.3. Model predictions of the percentage of targeted wild pigs captured per trap event (i.e., trap effectiveness) across three trap types (corral, drop, passive net) and three forage seasons (barren, green-up, masting) with 95% confidence interval lines. Trapping data was collected from 31 professional trappers across Arkansas, Georgia, North Carolina, and South Carolina, USA between 2021-2023.

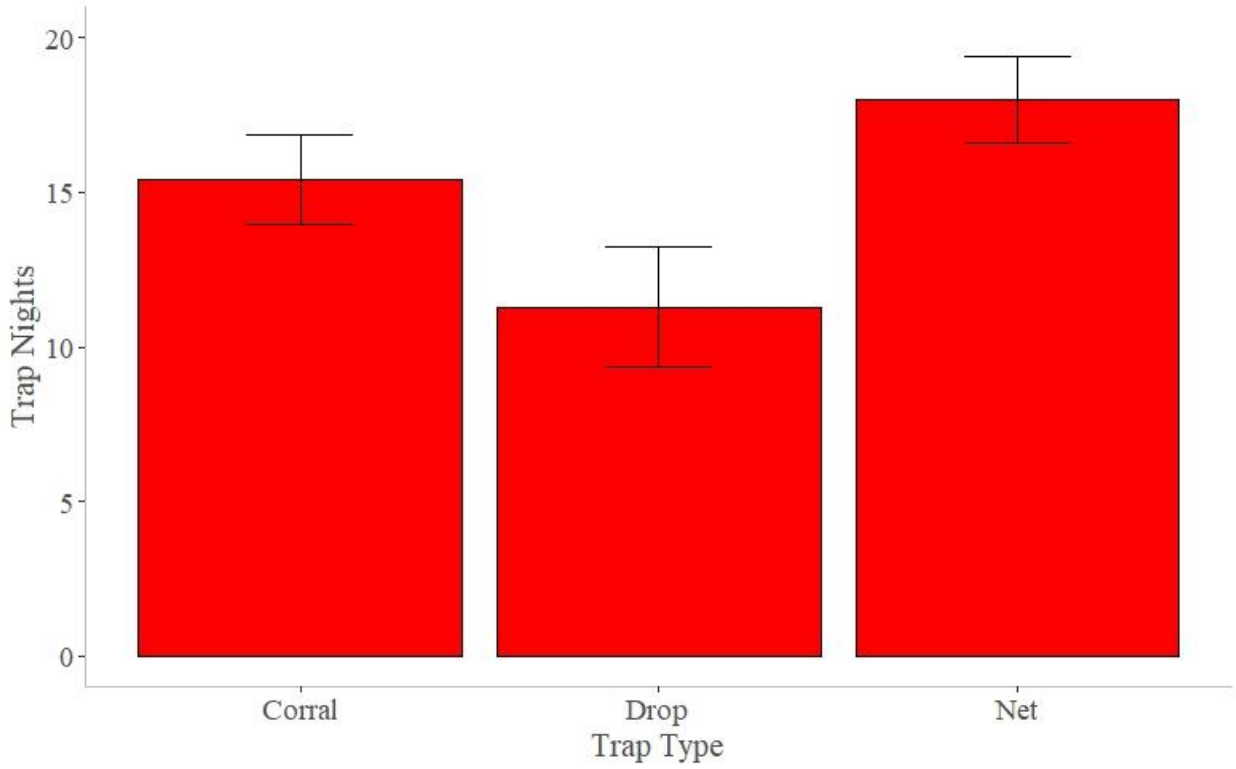

Figure 3.4. Average number of trap nights until first catch with standard error bars for three trap types (corral, drop, passive net) using trap data collected from 31 professional trappers across Arkansas, Georgia, North Carolina and South Carolina, USA from 2021-2023.

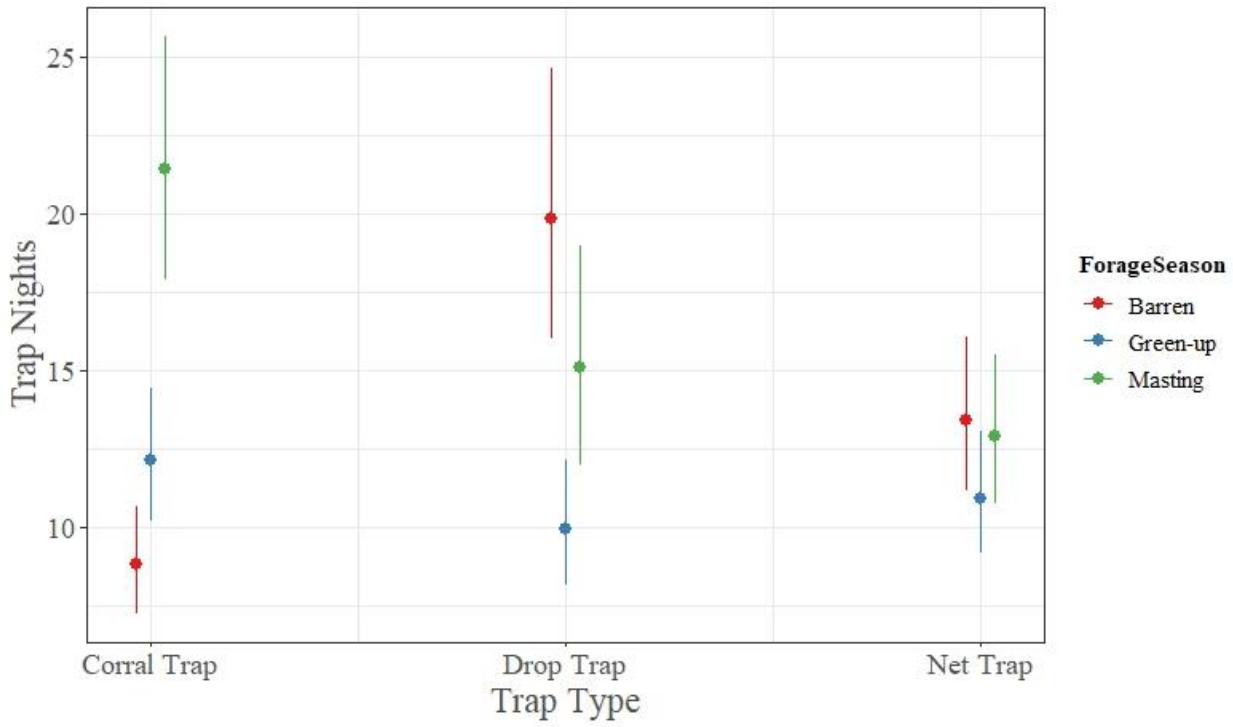

Figure 3.5. Model predictions of the number of trap nights until the first catch across three trap types (corral, drop, passive net) and three forage seasons (barren, green-up, masting) with 95% confidence interval lines. Trapping data was collected from 31 professional trappers across Arkansas, Georgia, North Carolina, and South Carolina, USA between 2021-2023.

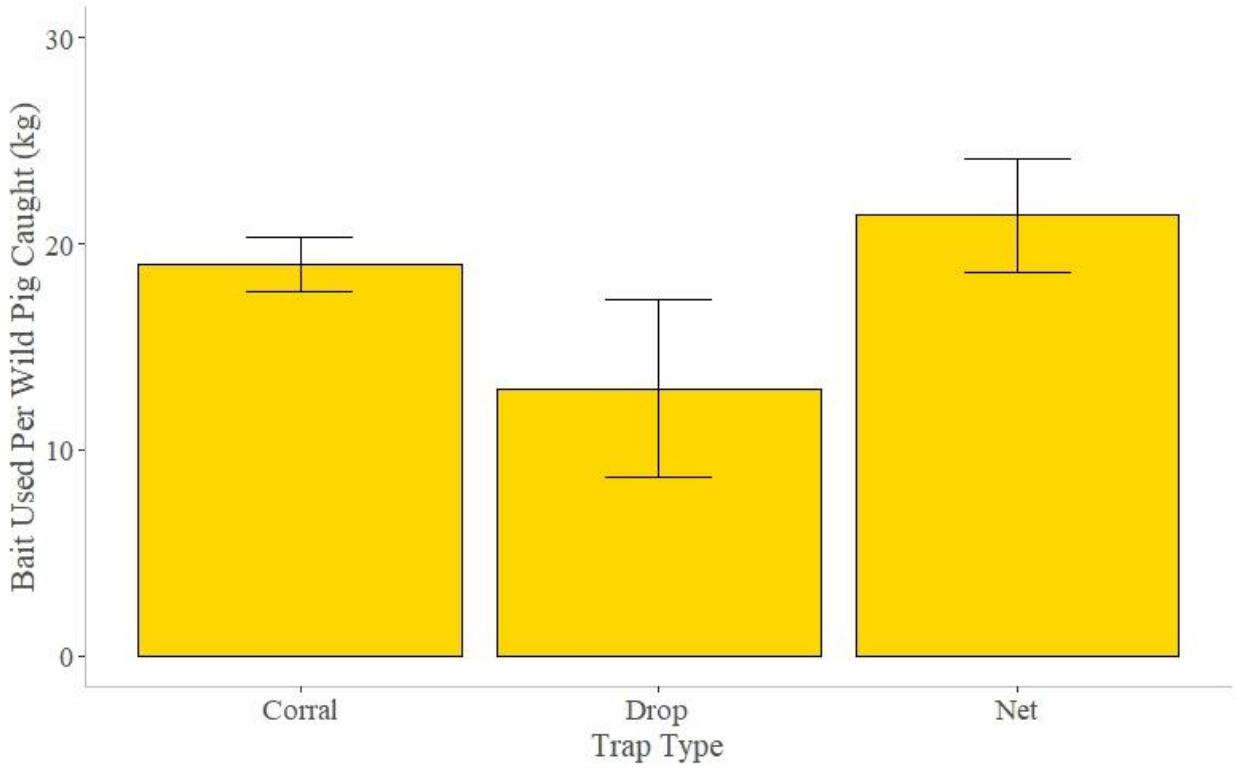

Figure 3.6. Average amount of bait (kg) used per wild pig caught with standard error bars for three trap types (corral, drop, passive net) using trap data collected from 31 professional trappers across Arkansas, Georgia, North Carolina and South Carolina, USA from 2021-2023.

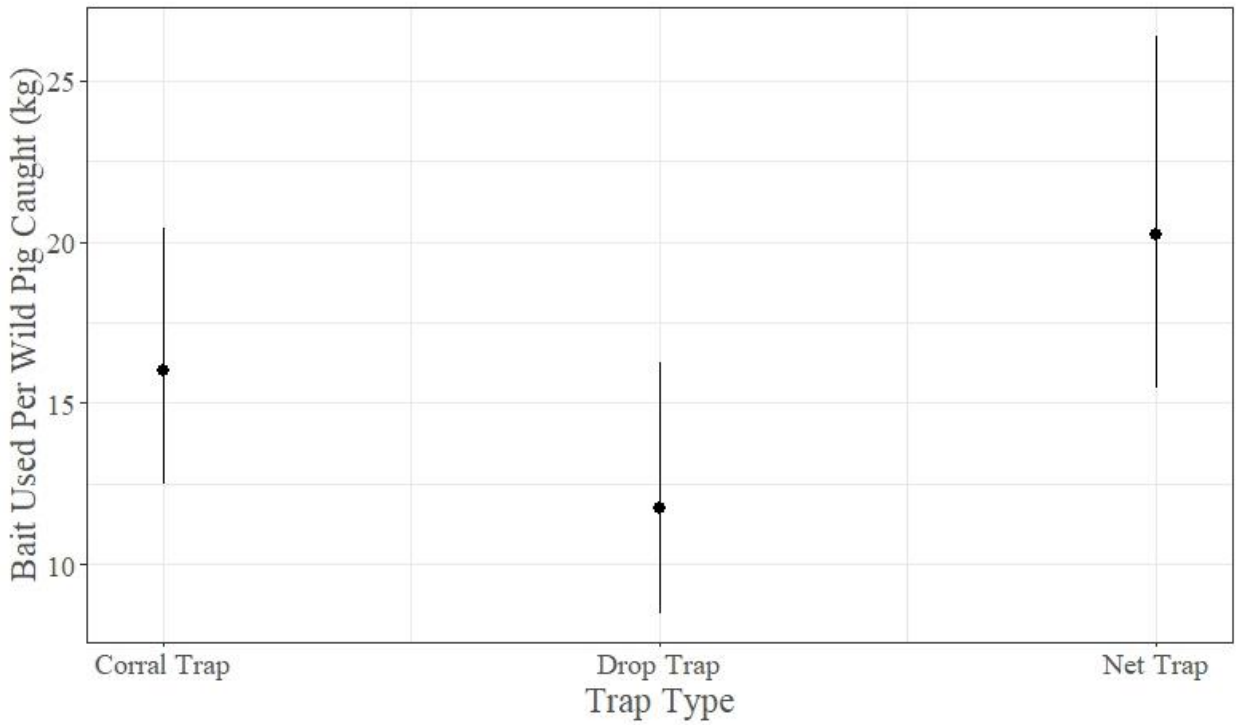

Figure 3.7. Model predictions of the amount of bait (kg) used per wild pig caught across three trap types (corral, drop, passive net) with 95% confidence interval lines. Trapping data was collected from 31 professional trappers across Arkansas, Georgia, North Carolina, and South Carolina, USA between 2021-2023.

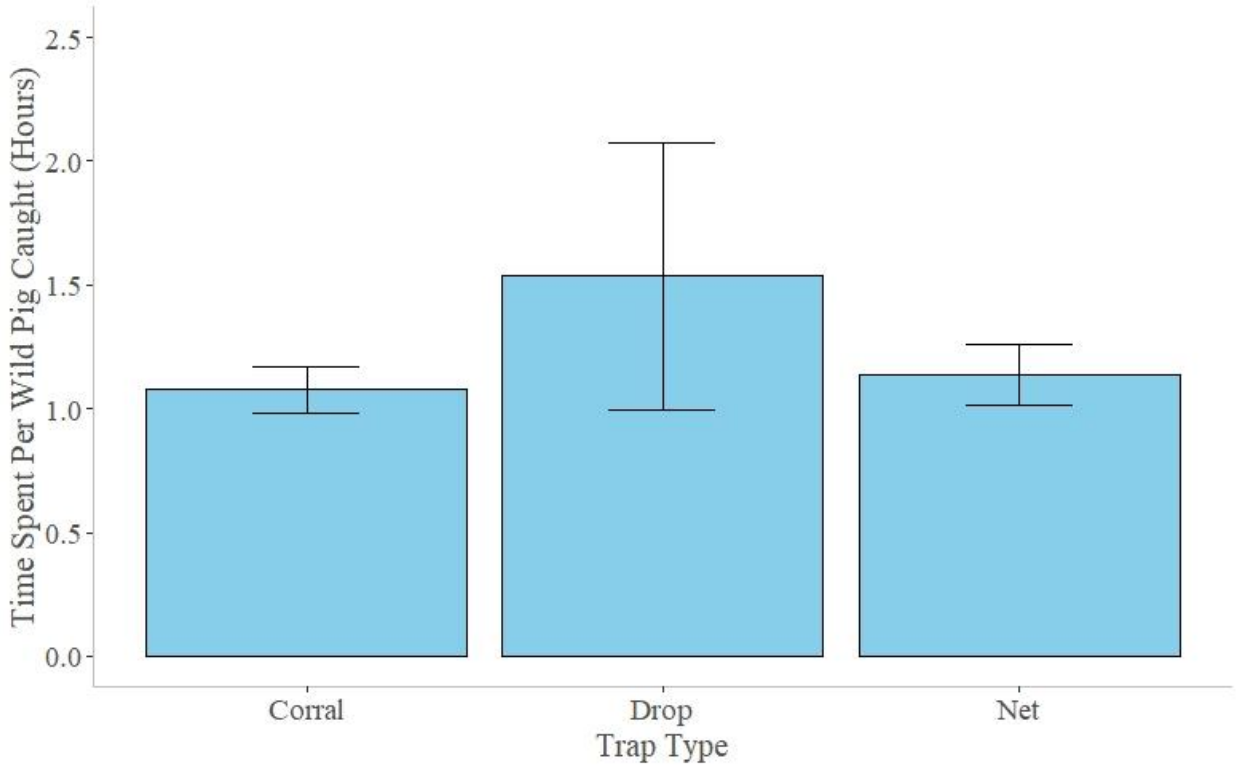

Figure 3.8. Average time (hours) spent per wild pig caught with standard error bars for three trap types (corral, drop, passive net) using trap data collected from 31 professional trappers across Arkansas, Georgia, North Carolina and South Carolina, USA from 2021-2023.

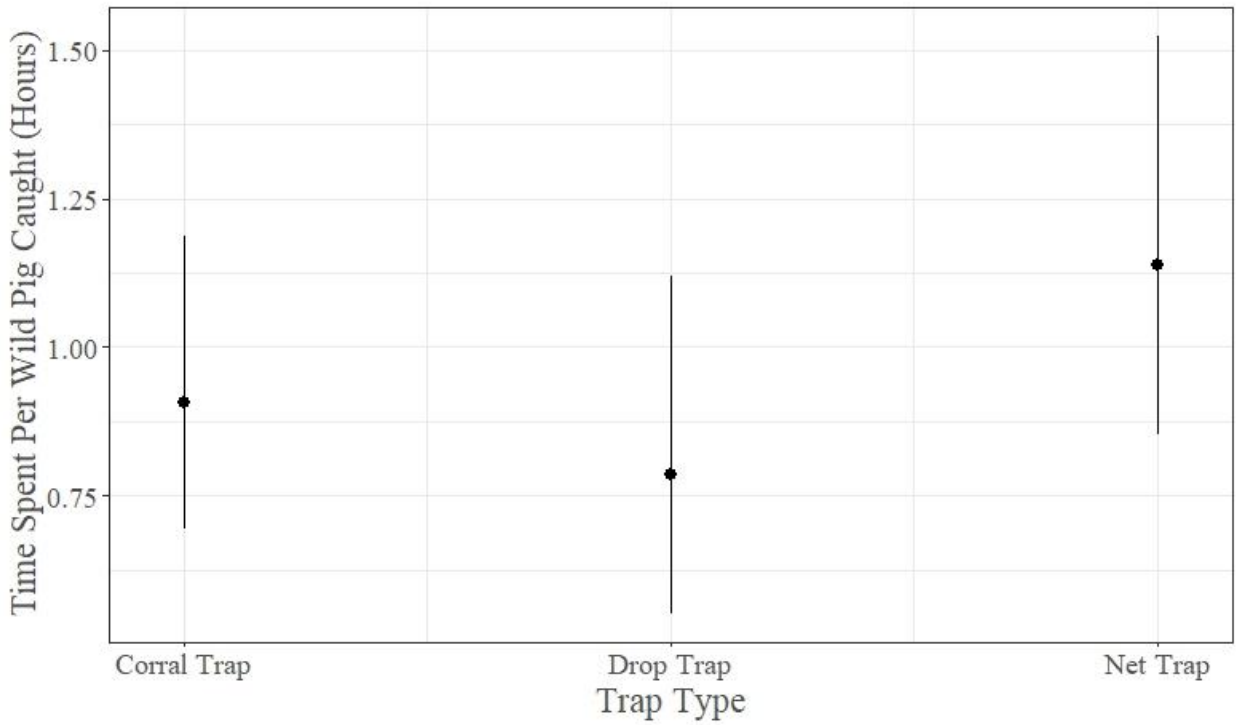

Figure 3.9. Model predictions of the amount of time (hours) spent per wild pig caught across three trap types (corral, drop, passive net) with 95% confidence interval lines. Trapping data was collected from 31 professional trappers across Arkansas, Georgia, North Carolina, and South Carolina, USA between 2021-2023.

CHAPTER 4

CONCLUSIONS

Although management for wild pigs (*Sus scrofa*) is currently ongoing across most regions that they inhabit, there are still many areas for improvement. Specifically, two important knowledge gaps that exist within wild pig management are 1) the development of reliable and robust population estimators, and 2) the improvement upon and evaluation of current management techniques. By estimating density of wild pigs effectively and efficiently, areas of highest concern can be identified, and localized population control efforts can be better quantified. Additionally, there have been numerous innovations in wild pig population control techniques in recent years. However, studies investigating the differences in the productivity of these techniques are rare, and often are limited in scope and scale.

In my thesis, I evaluated two methods of estimating population size of wild pigs including removal models utilizing take data from a professional trapping program and spatial mark-resight (SMR) models incorporating both marked and unmarked detections of individuals in camera trap images. Data from each model type were obtained concomitantly on private properties across South Carolina, USA from 2020-2023. In addition, I evaluated three common trap types used to capture wild pigs using trapping data collected by a federal management agency across four US states (Arkansas, Georgia, North Carolina, South Carolina), and three years (2021-2023). The data and results from this research hold vital information that will improve future wild pig management and research.

In chapter 2, I obtained wild pig density estimates from both removal and SMR models across private properties in South Carolina, USA to characterize wild pig densities across a broad range of environments, and to determine variables that influence each model type's density estimates and precision. I also investigated instances where density estimates from each model type within a replicate were dissimilar from each other to determine factors influencing the dissimilarity among estimates. For the SMR model estimates, two-week baited camera surveys were conducted on private properties in both winter and summer from 2020-2023. All wild pigs in photos were individually identified whenever possible, and both unmarked and marked detection data were used to compute density estimates. To achieve removal model estimates, take data from United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS) was input into a dynamic removal model (Davis et al. 2022). I used linear models (LMs) to reveal which variables influenced differences in density estimates and their coefficients of variation (CV) across replicates. In addition, I used logistic regression models to determine the variables that influenced dissimilarity in density estimates between model types.

I found that removal models were more precise on average in estimating density compared to SMR models, and that the number of wild pigs removed in the primary period, and the number of individuals removed relative to the area sampled in the last 30 days of the removal period influenced removal model precision. I also concluded variability observed in SMR densities and CVs were likely caused by a variety of factors unique to each replicate, as that none of our variables were determined to be important predictors of SMR density or precision. Finally, none of our measured variables (i.e., ecoregion, season, years of management, property size) were found to influence dissimilarity in estimates produced between density estimators. My

results support the use of removal models for density estimation of wild pigs and will increase the efficacy of future population surveys by elucidating factors that influence the precision of common population estimators. In addition, I characterized property-level wild pig densities across a broad range of environments that can be used as a reference in future research.

In chapter 3, I utilized trapping data collected by USDA-APHIS-WS trappers across four southeastern US states over a period of three years to evaluate the performance of three common trap types used to capture wild pigs. Corral, drop, and passive net traps were all evaluated based on metrics (i.e., trap effectiveness, trap night effort, bait- and time-per-take efficiency) we established and in relation to three forage seasons. Predictions obtained from generalized linear mixed models (GLMMs) were used to determine any significant differences in trap performance among trap types and forage seasons. While I did observe notable interactions between trap types and forage seasons for some of my performance metrics, performance was generally similar among trap types. For example, there were a few trap type/forage season combinations that yielded significant differences regarding the average proportion of wild pigs captured per trap event and the number of trap nights until a first catch is made. Additional variability was also observed in both corral and drop traps across forage seasons regarding the number of trap nights until first catch as opposed to passive net traps, which performed similarly across all forage seasons. The only metric where I observed differences among trap types was in the amount of bait-per-take, with passive net traps having higher bait-per-take than drop traps, although no differences were detected among trap types regarding time-per-take values. By comparing the performance of the three most commonly used trap types for capturing wild pigs across three forage seasons and a broad geographic area, I was able to gain detailed insight into how these traps perform under various environmental conditions. Although all trap types included in my

study were proven to be effective at capturing wild pigs, my data suggests that the interaction between trap type and forage season can influence trapping success and how quickly a trap yields a first catch, and that trap type can influence the amount of resources used during trapping efforts.

The results from my thesis contain critical information that can be used to increase effectiveness and efficiency in wild pig population control and research. Accurately estimating the density of wild pigs is paramount to understanding the efficacy of localized control efforts over time, as well as determining specific target areas for management based on wild pig density. My results indicate that removal models can be used alongside more data-intensive methods such as SMR models for wild pig density estimation which will improve the efficiency of such efforts in the future. I also suggested means of improving the precision of removal models, however more research is needed regarding SMR models and the data parameters needed to produce useful density estimates with these models. Furthermore, trapping is one of the most popular methods of wild pig population control, and research investigating how to maximize current trapping techniques and strategies is one of the most important questions remaining regarding the effective management of the species (Beasley et al. 2018). In my thesis I was able to investigate the impact that both trap type and forage season have on overall trapping success and provide insight into how agencies can enhance their trapping efforts. This is critical information that will influence the implementation of wild pig trapping efforts in the future and will improve the overall efficacy of wild pig population control.

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