

DEMOGRAPHY OF FERAL PIG POPULATIONS
AT FORT BENNING, GEORGIA

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DEMOGRAPHY OF FERAL PIG POPULATIONS
AT FORT BENNING, GEORGIA

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THESIS ABSTRACT
DEMOGRAPHY OF FERAL PIG POPULATIONS
AT FORT BENNING, GEORGIA

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Feral pigs are an ecologically harmful invasive species that wildlife managers have been unsuccessful at controlling. Understanding the demography and population dynamics of a species is necessary to create successful management strategies because the most effective way to reduce population growth is to target the vital rate which has the largest potential to influence the population growth rate (λ). I estimated survival, recruitment, λ , and the sensitivity of λ to changes in vital rates for a control population and a treatment population, where a lethal removal management strategy was implemented. I also created novel density estimation methods to address known biases in closed capture-mark-recapture methods.

Reducing total survival via lethal removal was successful in reducing feral pig population growth; however the most effective management strategy to reduce λ would be to target juvenile survival. Density was difficult to estimate because feral pigs have low and heterogeneous capture probabilities.

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INTRODUCTION

This thesis describes the demography and population dynamics of feral pigs (*Sus scrofa*) at Fort Benning, Georgia. This research was conducted to determine the population size, survival rates, recruitment rates, population growth rates (λ), and the sensitivity of λ to changes in age-specific vital rates of feral pigs at Fort Benning, Georgia in order to determine the most effective method to reduce feral pig population growth rates.

Feral pigs are an ecologically harmful invasive species with expanding distributions in many parts of the world. Within the southeastern United States, Fort Benning personnel are concerned about the effects of feral pigs on threatened and endangered species and ecosystem functions. Because of their range expansion, habitat use, and potential for spreading disease, many wildlife managers, including those at Fort Benning, are interested in reducing feral pig population sizes and λ .

In order to develop an effective management plan, feral pig demography, including density, survival, recruitment, and λ , must be understood because the most effective way to reduce λ is to target the vital rate, which has the largest potential to influence λ . Density can be used to determine the intensity of management required to reduce the population size and to monitor the effects of a management strategy over time. I developed novel density estimation methods to address biases associated with

estimating population sizes for wildlife species, such as feral pigs, with low or heterogeneous probabilities of being captured.

Creating effective management plans requires not only understanding the demography of a species, but also how a particular management strategy affects various aspects of the demography. To understand how a lethal removal management strategy affects the vital rates and the influence of those vital rates on λ , I compared demography and vital rate sensitivity of a non-manipulated control population to that of a manipulated treatment population, where I conducted lethal removal of feral pigs via trapping and shooting. I conducted an experimental manipulation to more fully understand how lethal removal affects the population dynamics of feral pigs and to create an effective feral pig population reduction strategy. I also used the experimental manipulation to examine the possibility of a density dependent response in feral pig recruitment rates.

EFFECT OF EXPERIMENTAL MANIPULATION ON DYNAMICS OF FERAL PIG POPULATIONS

Abstract

1. Invasive species, such as feral pigs (*Sus scrofa*) are often ecologically harmful and have expanding distributions. Effectively reducing feral pig populations, which is becoming an increasingly common objective of wildlife managers, requires determining how reduction efforts affect vital rates and which vital rate potentially has the largest effect on the population growth rate (λ).
2. We implemented a manipulative experiment of feral pig populations at Fort Benning, Georgia to assess the demographic effects of a lethal reduction. We compared demography of a non-manipulated control population with a treatment population, where feral pigs were experimentally removed. Using mark-recapture data from trapping, re-sight with cameras, telemetry of radio-collared pigs, and hunter-returned tags, we estimated survival, recruitment, and population growth rates of treatment and control populations for 2004-2005. Matrix model analytical and simulation sensitivity analyses were used to determine which seasonal vital rate could potentially contribute most to changes in the population growth rate.

3. The top ranked model for survival included a treatment effect; survival was lower for the treatment population compared to that for the control. Recruitment estimates did not differ between treatment and control populations, but the population growth rate was lower for the treatment population compared to that for the control.
4. Both analytical and simulation sensitivity analyses indicated that the population growth rate was potentially most sensitive to changes in juvenile survival, especially during fall/winter and summer. Simulation sensitivity analysis revealed that the sensitivity of λ to juvenile survival increased as survival decreased in the treatment population.
5. Based on our lethal removal efforts, reducing survival can be used in management to lower population growth rates of feral pigs. However, management actions lowering juvenile survival or juvenile recruitment will most effectively lower the growth rate of feral pig populations and ultimately reduce the adverse effects of feral pigs on native species.

Key-words: elasticity, mark-recapture, matrix model, population growth rate, recruitment, sensitivity analysis, survival, *Sus scrofa*

Introduction

Management of invasive species is becoming increasingly important for protecting native species and ecosystem functions (Townsend 2003, Batten et al. 2006). Modeling population dynamics with the use of demographic data aids in understanding

what drives persistence and expansion of invasive species populations in their introduced range. Population matrix models are often used to develop management strategies for controlling invasive species (Citta and Mills 1999, McEvoy and Coombs 1999, Shea and Kelly 1998).

Feral pigs (*Sus scrofa*) are an invasive species with expanding populations in North America, Australia, and New Zealand (Clarke and Dzieciolowski 1991, Hone 2002, Mayer and Brisbin 1991). Feral pigs are considered economic and environmental pests due to their effect on ecological processes by competing with native wildlife for food resources (Dickson 2001), disturbing soil and vegetation while rooting for food (Hone 2002), reducing species richness in plant communities (Kotanen 1995), and occupying areas with sensitive animal species (MacFarland et al. 1974).

Lethal removal efforts are commonly used to attain short-term reductions in population density to reduce detrimental effects of feral pigs (Hone and Pedersen 1980, Engeman et al. 2001), but rarely have long-term density reductions or eradications been achieved (Singer 1981, Izac and O'Brien 1991, but see Katahira et al. 1993). A model constructed from demographic data on a feral pig population in New Zealand predicted that a population reduced by 95% would recover to its original size in less than five years (Dzieciolowski et al. 1992), demonstrating the potential difficulty in controlling feral pig populations. While lethal removal is frequently used in feral pig management, little is known about its effects on population growth rates (λ) and other vital rates (e.g., survival, recruitment, etc.).

Development of an effective management approach for invasive species requires accurate estimates of population vital rates and an evaluation of how removal affects

them. Vital rates of feral pig populations need to be understood because the most effective way to reduce λ is to target the vital rate that has the greatest potential to influence λ . Currently, the effect of management on the potential influence of each vital rate is unknown. Species with long life spans and low reproductive rates often have population growth rates which are most influenced by changes in adult survival (Heppell et al. 2000). However, feral pigs are unlike most large mammals in that they have an early age of maturity and high reproductive rates indicating that λ could be most influenced by changes in recruitment.

The objectives of my research were to examine the demography of feral pig populations and determine the demographic effects of an experimental population manipulation using lethal removal methods. To accomplish these goals, I first estimated survival and recruitment rates of treatment (lethal removal) and un-manipulated control populations using maximum likelihood mark-recapture methods (Williams et al. 2002). I used the vital rate estimates and population matrices to calculate λ and to evaluate the effectiveness of the lethal removal efforts. To determine the potentially most influential vital rate on λ , which is necessary for developing effective management strategies to reduce λ , I conducted analytical and simulation sensitivity analyses (Caswell 2001, Wisdom et al. 2000). To understand how each vital rate actually contributed to λ , I conducted life table response experiments (LTRE) and examined seniority parameters. Finally, to assess possible demographic density dependence, I compared vital rates and λ from both control and treatment populations.

Survival and recruitment rates can be accurately estimated using mark-recapture methods, which incorporate detection probabilities (Williams et al. 2002). The few

studies that have estimated survival rates for feral pigs used only age structure data or radio-telemetry of a few individuals (Gabor et al. 1999, Saunders 1993). The Barker mark-recapture model produces relatively robust estimates of apparent survival because it provides a way to incorporate mark-recapture data, live re-sight, and dead recovery data, which greatly increases the precision of the parameter estimates (Barker 1997).

No studies have been published documenting recruitment (i.e., the rate at which individuals are added to the population through births and immigration) of feral pigs, but data on fecundity (i.e., litter size or number of young produced per female per year) is abundant. Female feral pigs can become sexually mature by five months old, an early age compared to mammals with similar body mass (Read and Harvey 1989, Dzieciolowski et al. 1992). Adult females often breed seasonally two times a year, but can breed up to three times in a 14 month period (Coblentz and Baber 1987, Dzieciolowski et al. 1992). Females produce approximately 5-7 piglets per litter (Taylor et al. 1998), but can produce as many as 11 (McIlroy 1990). Although much is known about feral pig fecundity, these data do not include estimates of immigration, which can also affect λ . The Pradel reverse-time model uses mark-recapture data to estimate recruitment rates by inverting capture histories to estimate seniority, the probability an individual caught at time t was present in the population at time $t-1$ (Pradel 1996).

Population matrix models incorporate survival and recruitment rates to estimate λ . I used matrix models to calculate the sensitivity of λ to changes in vital rates and the relative contribution of each vital rate to λ (Caswell 2001). The use of recruitment rates in matrix models instead of the traditionally used fecundity estimates should more accurately estimate λ and vital rate sensitivity by including the potential contribution of

immigration to λ . Analytical sensitivity analysis is a useful tool to examine how relative changes in mean vital rates potentially affect λ . Life-stage simulation analysis (LSA) takes into account variation and uncertainty in vital rates in order to address the influence of large, simultaneous, and disproportionate changes in vital rates on the variation in λ (Wisdom et al. 2000). In contrast, LTRE is an extension of analytical sensitivity analysis that takes into account observed changes in vital rates and vital rate sensitivity to determine which vital rate actually contributed most to λ over a period of observation. The seniority parameter, estimated to derive recruitment in the Pradel mark-recapture model, can also be used to calculate the contributions of survival and recruitment to λ (Nichols et al. 2000). Using multiple techniques to answer the same question strengthens support for conclusions when the results are similar and highlights uncertainty when results differ. The comparison of vital rate sensitivity analyses to actual vital rate contributions can elucidate which vital rate is most important to population growth as well as the demographic mechanisms for population change (Wisdom et al. 2000).

For environments with seasonal variation in food resources or hunting pressure, the use of seasonal matrix models is valuable for examining differences in vital rate sensitivity by season. Recruitment rates of feral pigs may vary seasonally with differences in the availability of food resources. Seasonal mast crops, such as acorns, are known to be important for body condition (Matschke 1967a), which is positively correlated with reproductive performance (Gaillard et al. 1993). Survival may vary seasonally as hunting pressure changes throughout the year. Sensitivity analyses of seasonal matrix models will provide insights into how survival, recruitment, and the effectiveness of different management techniques might vary by season.

Demographic density dependence has been shown in many wildlife populations with survival and recruitment rates varying at different population densities (Rotella et al. 1996, Portier et al. 1998). In general, λ increases as population density decreases for most animal populations (Tanner 1966), but the exact relationship between density and λ is rarely known. Although understanding how vital rates change at different densities has strong management implications, Sibly and Hone (2002) identified only 25 studies in the literature that plotted λ against population density. In the case of invasive species, wildlife managers are concerned about density dependence acting to limit the effectiveness of management efforts as animals compensate by increasing survival or recruitment at lower densities. Examination of vital rates and population growth rates within a species can lead to increased knowledge of how and when density dependence operates.

I studied feral pig populations at Fort Benning, Georgia, to examine four alternative hypotheses describing the sensitivity of λ to changes in vital rates. I hypothesized that λ was potentially most sensitive to changes in juvenile recruitment, adult recruitment, juvenile survival, or adult survival. I examined the effect of experimental manipulation on the sensitivity of each vital rate.

I also evaluated two hypotheses regarding density dependence. I hypothesized that if the feral pig population at Fort Benning demonstrated density dependence such that experimental removal did not reduce λ because the population exhibited demographic density dependence, then I predicted A) recruitment rates would be greater in the treatment population than the control population as the remaining females in the treatment area increased their reproductive output or as pigs immigrated into the

treatment area and B) juvenile survival would be greater in the treatment population than the control population. If either of the predictions were supported, the population would be considered density dependent, but if both predictions were shown to be false, it would be considered density independent.

Methods

STUDY AREA

My research was conducted between spring 2004 and fall 2005 at the Fort Benning Military Reservation in west-central Georgia (32°21'N, 84°58'W). The 737 km² military base is located on the Coastal Plain-Piedmont Fall Line with elevations ranging from approximately 50 to 230 m. The climate is semi-tropical with an average annual rainfall of 132 cm (Dilustro et al. 2002). The average maximum temperatures in July and January are 33.2° C and 13.8° C, respectively. Fort Benning is primarily dominated by stands of longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), shortleaf pine (*P. echinata*), and scrub oak species (*Quercus* spp.) in the uplands. The understory is generally open with some shrubs and grasses. The riparian bottomlands consist of yellow poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and oak species (King et al. 1998).

EXPERIMENTAL DESIGN

To determine the effects of experimental removal on population demography, I compared a non-manipulated control population with a treatment population. I

considered the 50 km² control and treatment areas, located approximately 8 km apart and separated by a large creek, independent study sites (Fig. 1). I caught, tagged, and released feral pigs in both the control and treatment populations during summer 2004 (May –July), before I began the experimental removal. The experimental removal consisted of killing feral pigs via lethal trapping and shooting in the treatment study area from August 2004 through May 2005. Lethal trapping involved shooting pigs captured in spring-loaded cage traps baited with corn. I estimated survival, recruitment, and λ from summer 2004 to summer 2005 of feral pigs in both control and treatment populations. During the summer of 2005, I repeated the mark-recapture of pigs in both control and treatment areas. Hunting by off-duty military personnel occurred year-round in both study areas.

TRAPPING AND HANDLING

I conducted capture-mark-recapture sessions during each summer, 2004 and 2005. I spaced 20 trap locations 1-2 km apart across each study area. I pre-baited traps with shelled corn and corn mash for two weeks prior to each trapping session. I trapped feral pigs in cage traps capable of catching multiple pigs. I checked traps each morning of the 18 day trapping sessions.

I tagged all captured feral pigs with uniquely numbered ear tags in both ears using yellow and white tags to indicate study area (National Band and Tag, Newport, KY). I measured head and body length in order to estimate age (Boreham 1981). I recorded sex and estimated weight prior to release. I used Telazol (1 cc/ 30 kg), administered with a jab stick, to sedate adult females and attach ear tags and a GPS collar (Advanced

Telemetry Systems, Isanti, MN). I recorded body measurements of each sedated female and aged them based on tooth eruption patterns (Matschke 1967b). I monitored GPS-collared feral pigs via radio-telemetry weekly to determine potential mortality. Handling and removal of all pigs was conducted in accordance with institutional animal care and use guidelines of Auburn University (# 2003-0531).

CAMERAS

I used digital game cameras (infrared Digital-Scout 3.2 megapixel; Penn's Woods, Export, Pennsylvania, USA) to re-sight ear tagged and other individually identifiable feral pigs passively in both study areas between August 2004 – May 2005. I baited 16 cameras with fermented corn and moved them every 2 to 3 weeks in order to fully sample the study area several times. I set cameras with a 2 minute delay between photographs being taken to acquire multiple photographs of the same feral pig group to assist with identification. I photographed each feral pig before its initial release to aid in identifying tagged feral pigs re-sighted with the game cameras. I identified untagged feral pigs by unique pelage markings.

SURVIVAL

To estimate survival using a maximum likelihood method, I used the capture-mark-recapture Barker model in program MARK (White and Burnham 1999, Barker 1997). I included data on live trapping, “re-sight” of GPS collared feral pigs via radio-telemetry, camera re-sight, and hunter returns of ear tags to estimate apparent survival and a reporting parameter (r), the probability of a tag being reported given that the

individual was found dead. This model also estimates capture probability (p), re-sight probability (R), probability the animal is re-sighted and then dies within the interval (R'), probability of fidelity to study area (F), and probability of temporary emigration from study area (F'), all of which I considered nuisance parameters, i.e., parameters that must be estimated in order to estimate survival. I simplified models by holding nuisance parameters constant over time and space because survival was the primary parameter of interest and I had limited data. I modeled the reporting parameter by study area because I reported most (93%) of the dead ear tagged feral pigs in the treatment area, whereas only hunters reported dead feral pigs in the control area. Because the size of my dataset prevented me from estimating movement parameters, I assumed random emigration by constraining $F = F' = 1$. I modeled survival using individual covariates including treatment effect, sex, age, estimated weight, and presence of a GPS-collar.

I based model selection on the information-theoretic approach (Burnham and Anderson 2002). I used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to rank models (Akaike 1973).

Before running my *a priori* candidate model set, I constructed the most highly parameterized, biologically relevant model for which all parameters could be estimated. I used this global model to run a goodness-of-fit test to evaluate overdispersion in my data. I assessed goodness-of-fit using a median \hat{c} test available in program MARK (White and Cooch 2005). If data are not overdispersed, $\hat{c} = 1$. Any values of $\hat{c} > 1$ indicate lack of fit. I incorporated the estimated \hat{c} value into the AIC calculation. I calculated odds ratios by exponentiating the slope estimate from the logit link of the survival models.

Program MARK uses capture histories created for each individual feral pig to estimate survival. I considered pigs less than 8 months old to be juveniles based on the youngest age of first reproduction (Dzieciolowski et al. 1992, B. Jolley unpublished data). Because feral pigs less than one month old were too small to be caught in traps, estimates of juvenile survival included only feral pigs between 1-8 months old. I estimated both annual and seasonal survival rates. I divided the year into three equal 4 month long seasons: summer (June – September), fall/winter (October – January), and spring (February – May). Summer months are associated with lower food availability compared to fall/winter with mast crops and spring with new vegetative growth. Fall/winter months also correspond with deer hunting season. I estimated annual variance using total variance because process variance could not be isolated (Seber 1982).

I estimated the mean lifespan of feral pigs at Fort Benning using the average survival rate for all age and sex classes as well as for all females from the non-manipulated control population. Mean lifespan = $-1/\ln(\text{survival rate})$ (Brownie et al. 1985).

RECRUITMENT

I modeled recruitment using the maximum likelihood capture-mark-recapture approach by Pradel in Program MARK (Pradel 1996). The Pradel model directly estimates 3 parameters: survival probability, capture probability, and seniority probability. The Pradel parameterization uses the seniority probability (γ), the probability that an individual was present in the population at the previous time step and

is the equivalent of reverse-time survival, to estimate a per capita recruitment rate, which includes reproduction, immigration, emigration, and juvenile survival. The seniority parameter can also be used to examine contributions of survival and recruitment to λ (Nichols et al. 2000).

I created capture histories for ear tagged and uniquely identifiable individuals using only camera sight and re-sight data to reduce heterogeneity that can be caused by including other capture methods. I modeled recruitment solely by treatment and season because I lacked measurable covariates from un-tagged individuals. I estimated seasonal recruitment rates for both control and treatment populations, but lack of data prevented estimation of summer recruitment rates. To approximate summer recruitment, I created a range of probable recruitment rates by using the rates from other seasons to get low, average, and high summer rates.

I estimated fecundity by calculating average litter size in reproductive tracts collected from harvested feral pigs. I divided pregnant sows into two groups, first time breeders (≤ 1 year) and non-first time breeders (> 1 year old), to examine a potential litter size difference between juveniles and adults.

To examine possible density dependence in recruitment, I compared λ estimates for the control and treatment populations to recruitment estimates.

POPULATION MODELS AND SENSITIVITY ANALYSES

To examine λ , sensitivity, and elasticity in both annual and seasonal contexts, I created 3 different types of post-birth pulse age-based population matrices modeling only the female portion of the population based on the life-cycle of feral pigs (Fig. 2). I

created matrices populated with recruitment estimates and fecundity estimates to compare λ estimates and vital rate sensitivity. First, I created matrices using annual survival rates and Pradel recruitment rates. Second, I created two types of matrices populated with annual survival rates and two different assumptions of annual fecundity. Finally, I created seasonal matrices using seasonal survival rates and seasonal Pradel recruitment rates to examine vital rate sensitivity by season.

I structured the first set of matrices using annual survival and Pradel recruitment as

$$M = \begin{bmatrix} S_j * F & S_a * F \\ S_j & S_a \end{bmatrix}$$

where F is the annual per capita recruitment rate for all individuals in the population. I assumed equal recruitment for juveniles and adults. S_j represents the annual survival rate of juveniles less than 8 months old while S_a represents annual adult survival. I created matrices using low, average, and high probable summer recruitment rates to address summer recruitment uncertainty.

I structured the second set of matrices using annual survival and fecundity as

$$M = \begin{bmatrix} S_j * R_j & S_a * R_a \\ S_j & S_a \end{bmatrix}$$

where R_j is the fecundity of juveniles using litter size of first time breeders*0.5 and R_a is adult fecundity using litter size of non-first time breeders*0.5, assuming a litter sex ratio

of 0.5 for both age classes. S_j represents the annual survival rate of juveniles less than 8 months old while S_a represents annual adult survival. I created matrices with the conservative assumption that all juveniles and adults breed only once a year. I also created matrices with the alternative assumption that 0.75 of juveniles breed once and 0.75 of adults breed twice a year based on fecundity data from wild boar which breed once a year. In an average year, 0.74 of adult wild boar breed once per year and 0.4 of juvenile breed once per year (Bieber and Ruf 2005). I assumed that feral pigs with high food resource availability would have approximately twice the fecundity of wild boar.

Finally, I created seasonal matrices using seasonal survival and recruitment rates structured as

$$M = \begin{bmatrix} S_j * (F_s / 3) & S_a * F_s \\ S_j & S_a \end{bmatrix}$$

where F_s is the seasonal per capita recruitment rate for all individuals in the population. I divided juvenile recruitment by three because I assumed that an equal number of young were born each season and if all juveniles reproduced once per year, only 1/3 of juveniles reached the age of reproduction during each season. S_j represents the seasonal survival rate of juveniles younger than 8 months old and S_a represents seasonal adult survival. I constructed one seasonal matrix for each season except summer where I created three matrices using the range of probable summer recruitment rates.

Analytical sensitivity analysis is used to determine how absolute changes in a mean vital rate potentially influence λ , while elasticities provide information on how proportional changes are expected to affect λ . As scaled, dimensionless values,

elasticities are comparable among vital rates and populations. Both sensitivity and elasticity are calculated using left and right eigenvectors and the dominant eigenvalue (λ) of the matrix assuming the population is at stable age distribution (Caswell 2001). For a given matrix element a_{ij} , sensitivity is defined as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

and elasticity is defined as

$$e_{ij} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

When matrix elements are composed of more than one vital rate, analytical sensitivity and elasticity can be calculated separately for each vital rate as well as for the matrix elements themselves.

For annual population matrices, I calculated λ and elasticities of λ to vital rates. Sampling variance exceeded total variance, thus I used sampling variance to calculate confidence intervals for λ . I examined sensitivities of λ to vital rates for the three seasonal matrices.

In order to address variation and uncertainty in vital rate estimates, I used LSA, a simulation based approach, to examine the influence of each vital rate on variation in λ (Wisdom et al. 2000). Vital rates were chosen randomly from a uniform distribution bounded by low and high vital rate estimates to create 1000 matrices (Table 1). I chose a uniform distribution to investigate a full range of possibilities in vital rate combinations. I used the 95% confidence intervals as the high and low estimates for survival rates. Because of uncertainty in summer recruitment values, I used the lower 95% confidence estimate from the low summer recruitment estimate and the upper 95% confidence

estimate from the high summer recruitment estimate. I calculated elasticities and their 95% confidence intervals for each vital rate. In addition, regression analyses based on the simulated matrices produced r^2 values that indicated the relative influence of each vital rate on the variation in λ .

I used the seasonal matrix models to conduct life table response experiments (LTRE) to determine the actual influences of each vital rate on λ during the year. LTRE, an extension of analytical elasticity analysis, takes into account observed changes in vital rates over time. I compared the results of the analytical and simulation elasticity analyses to the LTREs for both the control and treatment populations.

Results

EXPERIMENT

During the summer of 2004, I caught 55 feral pigs 134 times in the control area and 35 feral pigs 73 times in the treatment area. During the following summer of 2005, I caught 51 pigs 117 times in the control area and 39 pigs 53 times in the treatment area. Capture probabilities did not differ between the two study areas.

Over a 10-month period, 108 feral pigs were killed in the treatment area. Approximately 1300 lethal trap nights occurred, primarily during November – March. Of the 108 killed, 49% were male, 51% females, 64% juvenile (< 1 year), and 36% adult.

No feral pigs from the treatment area were ever re-captured, re-sighted in cameras or by radio-telemetry, or reported dead in the control area, or vice versa, thus supporting my assumed independence of the control population and the treatment population.

SURVIVAL

During the summer of 2004, 90 feral pigs were ear tagged. Between August 2004 and May 2005, 39% were re-sighted in digital game camera photographs, 13% were re-sighted via radio telemetry, and 31% were reported dead by hunters. The goodness of fit test indicated little overdispersion in the data with a $\hat{c} = 1.15$.

Based on AIC model selection, the top ranked model included a treatment effect; total survival was lower for the treatment population compared to that for the control population, however the null model, which lacked a treatment effect, also ranked high ($\Delta\text{AIC}_c = 0.69$; Table 2). I averaged these top two models (Burnham and Anderson 2002) to acquire annual survival rates of 0.25 (95% CI: 0.19, 0.31) and 0.17 (95% CI: 0.10, 0.24) in the control and treatment populations, respectively (Table 3). Models including covariates such as sex, age, and weight did not rank as high, but all top models had $\Delta\text{AIC}_c < 2$ indicating that these covariates may influence survival (Table 2). Seasonal survival models indicated equal survival during spring and summer with lower survival during fall/winter (Fig. 3).

Using models with $\Delta\text{AIC}_c < 2$, the odds ratio indicated that the likelihood of surviving in the treatment area was 0.56 times less than in the control area. The odds of a male surviving were 0.45 times less than a female (Table 3). A likelihood ratio test of the model with treatment effect versus the null model showed support for a treatment effect ($\chi^2 = 3.23$, d.f. = 1, $p = 0.072$).

The mean lifespan of any feral pig in the control population was 8.8 months (95% CI: 7.3, 10.3). The mean lifespan for females in the control population was 10.4 months (95% CI: 8.1, 13.2).

RECRUITMENT

Pradel models produced similar estimates of recruitment for the control and treatment populations (Table 4), but differences were present among seasons in both populations (Fig. 3). Recruitment, the number of individuals added to the population per capita, during the fall/winter was greater (recruitment = 2.228, S.E. = 0.329 and recruitment = 2.698, S.E. = 0.384) than during the spring (recruitment = 0.130, S.E. = 0.066 and recruitment = 0.157, S.E. = 0.081), in the control and treatment populations, respectively (Fig. 3). I assumed that summer recruitment rate ranged from as low as the spring recruitment rate to as high as the fall recruitment rate. With no differences in estimated recruitment between the control and treatment populations, I assumed that the summer recruitment rates also did not differ between study areas (summer recruitment range in treatment population: 0.133 - 2.698; summer recruitment range in control population: 0.130 – 2.228). In the control population, the annual recruitment rate was 2.48, 3.54, and 4.58 for low, average, and high summer recruitment values, respectively. In the treatment population, the annual recruitment rate was 3.01, 4.28, and 5.55 for low, average, and high summer recruitment values, respectively.

Of 61 reproductive tracts collected from females, 29 had visible fetuses. Average litter size for first time breeders (≤ 1 year old) of 5.0 (95% CI: 4.45, 5.55) was lower than for adults (> 1 year old) with litter sizes of 6.87 (95% CI: 5.68, 8.05).

POPULATION MODELS AND ELASTICITY

Population growth rates from the annual survival and Pradel recruitment rate matrices were 1.42 (95% CI: 1.30, 1.54) and 1.14 (95% CI: 1.02, 1.26) for the control and

treatment populations, respectively (Fig. 4). Using the low and high summer recruitment values, λ was 1.10 and 1.75 for the control population and 0.87 and 1.40 for the treatment population, respectively. These estimates reveal a consistently lower λ in the treatment population compared to the control.

The traditional annual matrices using fecundity and assuming that juveniles and adults breed once a year generated a λ of 1.17 (95% CI: 1.00, 1.35) and 0.81 (95% CI: 0.59, 1.04) for the control and treatment populations, respectively (Fig. 4). Population growth rates were slightly higher with the assumption that 3/4 of juveniles breed once and 3/4 of adults breed twice a year: 1.23 (95% CI: 1.03, 1.44) and 0.86 (95% CI: 0.65, 1.07) for the control and treatment populations, respectively (Fig. 4).

The analytical elasticity analyses for all annual matrices populated with mean vital rates revealed that λ is potentially more influenced by survival than recruitment. Results from elasticity analyses did not differ between control and treatment populations. Elasticity analysis of vital rates showed that juvenile survival has the highest elasticity and adult survival has the lowest elasticity in all matrices (Table 5 and Fig. 5). Juvenile recruitment had a higher elasticity than adult recruitment in all matrices except the traditional matrices that assumed that adults could breed more than once a year (Table 5).

LSA resulted in similar elasticity values for the simulated matrices compared to the mean matrices (Fig. 5 and 6). The r^2 values for the control population closely matched predictions from elasticity analyses regarding the potential influence of each vital rate on λ . However, r^2 values for the treatment population showed that juvenile survival accounted for more (control $r^2 = 0.511$, treatment $r^2 = 0.720$) and juvenile recruitment accounted for less (control $r^2 = 0.430$, treatment $r^2 = 0.187$) of the variation

in λ compared to the control population and results from elasticity analyses (Fig. 6 and 7). Juvenile survival explained 51% and 72% of the variation in λ while adult survival explained only 2% and 4% of the variation in the control and treatment populations, respectively. Regardless of these differences, the rankings of vital rate sensitivity based on r^2 values did not differ from the rankings using elasticity values for either population.

Using LTREs, I discovered that adult recruitment contributed at least 2.5 times more to λ than did juvenile recruitment for all possible summer recruitment rates (Table 6). Both juvenile and adult survival made small contributions to λ (Table 6), except at the highest possible summer recruitment value. LTRE contributions did not differ between control and treatment populations.

Pradel's reverse-time modeling approach resulted in seniority estimates of $\gamma_{i+1} = 0.22$ and $\gamma_{i+1} = 0.19$ for the control and treatment populations, respectively. A seniority estimate of 0.22 indicates that an individual from the population during 2005 was 3.5 times as likely to be a new recruit than a survivor from 2004 (Nichols et al. 2000). The seniority approach indicates that total recruitment, the number of individuals added to the population per capita through births and immigration, was more than 3 times as important to λ as survival in the control population and more than 4 times as important in the treatment population between 2004 and 2005.

Sensitivity analysis of seasonal matrix models incorporating a range of summer recruitment values for both control and treatment populations revealed that the highest juvenile recruitment and juvenile survival elasticity occurred during the fall/winter (Fig. 8).

DENSITY DEPENDENCE

The population growth rate in the treatment population was less than that in the control population (Fig. 4). Lower λ in the treatment population indicates that density differed between populations at least at some point during the year. Based on the total number of pigs caught in each study area and the similar capture probabilities between each population, it appears that the density was greater in the control population both before and after lethal control, but low sample sizes for density estimates prevented detection of a statistical difference. A difference existed in λ , yet per capita recruitment rates did not vary between populations. With a lower λ and equivalent recruitment rate in the treatment population compared to the control, survival in the remaining pigs could not have increased to compensate for experimental removal.

Discussion

My objectives were to determine the population dynamics of an invasive feral pig population and to use that information to determine the most effective way to reduce λ . I used survival estimates and recruitment or fecundity estimates to determine differences in λ between control and treatment populations. I examined the sensitivity of vital rates in both annual and seasonal contexts to determine which vital rate was potentially most influential to λ and how the sensitivity of each vital rate was affected by experimental removal. This is the first study to examine effects of an experimental manipulation on vital rates of feral pig populations. My results lend strong support to the conclusion that experimental removal had an effect on λ .

VITAL RATES

My study represents the first time robust mark-recapture methods have been used to estimate survival and recruitment in feral pig populations. The top ranked survival model showed that feral pig survival was reduced by the experimental removal; however, other highly ranked models showed that survival rates might have varied by sex and age (Table 2). A single year of survival data may not be sufficient to determine how each covariate affects survival. Experimental removal reduced survival by over 30% for both age classes and sexes, even though hunting occurred year round in both study areas. Although adults had slightly higher survival rates than did juveniles in both populations, the more striking difference was between males and females. Males had a survival rate half that of females in these heavily hunted populations perhaps because they have larger body sizes and larger home ranges (Saunders and McLeod 1999) making males more likely to be encountered by a hunter. Low male survival, however, does little to reduce the per capita growth rate in polygamous species, such as feral pigs, because only a few males are needed to fertilize all the females.

Seasonal models revealed interesting trends in both survival and recruitment. Survival was constant during spring and summer months, but notably lower from October to January, which corresponds directly with the deer season and an increase in the numbers of hunters on Fort Benning. Recruitment showed an opposite trend with significantly higher recruitment rates during the fall/winter than the spring. A heavy mast crop of acorns became available during October providing a food resource full of fat and protein (Matschke 1967a), which likely improved female body condition and, subsequently, increased reproductive output.

MATRIX MODELING AND POPULATION GROWTH

The three matrix model structures I used had different assumptions, each with potential biases. For the first set of matrices using Pradel recruitment, I assumed that juvenile and adult recruitment were equal although it is likely that juveniles produce fewer young per year than adults because they do not produce their first litter until at least 8 months old, whereas adults potentially have an entire year to reproduce multiple times. However, recruitment estimates are likely more accurate than litter size estimates because they include immigration and multiple reproductive events per year. The second set of matrices using fecundity, where juveniles produce fewer young per litter than adults addressed some of the bias in differential reproduction, but ignored possible immigration and multiple litters per year. The assumption of 3/4 of juveniles breeding once and 3/4 of adults breeding twice a year, although still biased in the assumption of no immigration, is more biologically likely, especially for a good mast year when reproduction was probably higher than usual.

Comparison of λ from the Pradel recruitment matrices to the traditional fecundity matrices revealed the potential biases in using fecundity estimates with apparent survival rates, which includes both survival and emigration. The population growth rate for the treatment population was lower in both traditional matrices compared to all matrices using recruitment estimates, including the matrix assuming the lowest possible summer recruitment rate. The use of litter size in matrix modeling can bias λ low because it ignores immigration and the possibility of multiple litters per year. Interestingly, the matrices incorporating the assumption that 3/4 of adults had two litters per year instead of one increased the λ estimate by only 5%. Because of the assumptions required and the

biases of using fecundity estimates along with apparent survival in matrix modeling, the use of recruitment estimates are more apt to accurately portray population dynamics.

The Pradel recruitment matrices revealed a strong effect of the experimental removal on λ in the treatment population. The population growth rate was reduced 20% in the treatment population compared to the control population through a reduction in survival. The matrices using fecundity showed a 30% reduction in λ , but had overlapping confidence intervals because small sample sizes for fecundity estimates led to higher standard errors (Fig. 4). All matrices estimated, with 95% confidence, λ equal to or greater than 0.99 for the control population lending strong support for the conclusion that the non-manipulated population was increasing in size. The traditional matrices estimated $\lambda < 1$ for the treatment population, while the Pradel recruitment matrices using low, average, and high summer recruitment values estimated growth rates from 0.87 to 1.40, creating uncertainty about whether the control efforts reduced the population size in addition to reducing λ .

ANALYTICAL SENSITIVITY ANALYSES AND LSA

The hypothesis that λ was potentially most sensitive to changes in juvenile survival was supported by both analytical and simulation sensitivity analyses (Fig. 5 and Fig. 7). Both analyses also supported the hypothesis that λ was potentially most sensitive to changes in juvenile recruitment in the control population (Fig. 6 and Fig. 7), however, LSA regression results provided little support that juvenile recruitment has high potential to influence λ in the treatment population (Fig. 7). Conversely, I rejected the hypotheses that λ was most sensitive to adult recruitment and adult survival (Fig. 5 and Fig. 7).

Surprisingly for a feral pig population with early age at maturity and high reproduction, survival had a higher potential to influence λ than recruitment. Typically, recruitment has the highest elasticity in species with short life spans because adults have high fecundity and most individuals in the population are pre-reproductive juveniles (Caswell 2001, Heppell et al. 2000). Most hunted populations of feral pigs are unique in that their populations are composed primarily of juveniles who are able to reproduce, which increases the influence of juveniles on λ . The mean lifespan for female feral pigs at Fort Benning was 10.4 months old, so that if a female managed to survive to become a first-time breeder that may have been the only reproductive event in her life. Thus, surviving until the first reproductive event has the most potential to affect λ .

Results from analytical sensitivity analysis of mean matrices, however, can be misleading when two or more vital rates change simultaneously and by proportionately different amounts (Mills et al. 1999) leading more researchers to conduct elasticity analyses that include variation in vital rates (Crooks et al. 1998, Wisdom and Mills 1997). The absence of summer recruitment estimates in my study highlights another key reason to use LSA in order to incorporate uncertainty in vital rates. While LSA did not produce mean elasticity rankings that differed from analytical elasticity analysis, the confidence intervals for each elasticity value emphasize the lack of a clear answer as to the most potentially influential vital rate when variation is included (Fig. 6). Although I cannot say with confidence whether λ is most sensitive to juvenile survival or juvenile recruitment, results from sensitivity analyses indicate that the juvenile age class has much more potential to influence λ compared to the adult age class. The lack of influence of the adult age class was even more pronounced by the regression results which indicated

that less than 3% of the variation in the control λ was explained by either adult survival or adult recruitment (Fig. 7). In this study, LSA demonstrated the robustness of the analytical elasticity rankings, however outcomes could differ if process variance as well as possible correlations between vital rates had been known and used in these analyses (Wisdom et al. 2000).

Although elasticity rankings were comparable using analytical sensitivity analyses and LSA, I discovered differing outcomes in these two analyses using control and treatment populations. Analytical sensitivity analysis predicts that juvenile and adult survival will have a decreasing influence on λ as survival rates are reduced. Interestingly, LSA showed that the reduction in both juvenile and adult survival in the treatment population led to an increase in the influence of both of these vital rates on the variation in λ . The differences in r^2 values for yearling survival and recruitment are caused because the variation in juvenile survival is higher in the treatment population in relation to the variation in recruitment compared to the control population. While these differences exist, I cannot say whether this indicates that lethal removal caused the change in potential influence of vital rates or if it is an artifact of the sampling variance, which was included in the analyses. Bieber and Ruf (2005) found that juvenile survival of wild boars had the highest elasticity during good environmental conditions while during environmentally poor years, adult survival had the highest elasticity. The increase in the influence of juvenile survival as λ declined may have been caused by an improvement in environmental conditions as availability of food resources increased for the remaining individuals (Bieber and Ruf 2005). Additional years of survival and

recruitment rate estimates will allow process variance and co-variation between vital rates to be determined for the Fort Benning population.

CONTRIBUTIONS TO λ

In contrast to results from analytical and simulation elasticity analyses, both LTRE and the seniority approach showed that recruitment contributed most to λ . However, all analyses revealed that adult survival had and potentially has the least influence on λ . LTRE and the seniority approach are considered retrospective analyses that are used to examine population dynamics at a particular point in the past (Caswell 2000, Nichols and Hines 2002). Given the high λ estimated for feral pig populations with such low survival rates, it is not surprising that recruitment contributed most to population growth. While these analyses are useful in understanding what vital rates are driving population growth, they may not be valuable for guiding future management decisions because λ is not necessarily easily influenced by changes in the rate with the largest contribution to λ .

Few researchers estimate both the contributions of vital rates to variation in λ as well as the sensitivity of λ to different vital rates (but see Kiviniemi 2002, Oli and Armitage 2004). Of those studies that report results for both types of analyses, there is not a consistent correlation between the rankings of vital rate elasticities and the rankings of vital rate contributions to λ (Cooch et al. 2001). This lack of a relationship indicates that the results from elasticity analysis cannot be used to infer which vital rate was contributing most to λ or vice versa and highlights the importance of examining both in order to more fully understand the population dynamics.

DENSITY DEPENDENCE

The hypothesis that density dependence would be observed in the treatment population following experimental manipulation was not supported. As λ was lowered in the treatment population, recruitment rates remained the same and juvenile survival decreased, compared to the control population. Both predictions supporting density dependence were falsified leading to the conclusion that the present population did not exhibit demographic density dependence.

The relationship between λ and density is often assumed to be linear indicating that density dependence should be detected at any density, however this is rarely observed in actual wildlife populations (Sibly and Hone 2002, Sibly et al. 2005). In an analysis of 3,269 time series from 674 species of mammals, birds, fish, and insects, Sibly et al. (2005) found a concave relationship between λ and density for most species. This trend of a high, but decreasing λ at low densities quickly asymptoting to a constant rate as density increased was seen in 79% of mammal species. Additionally, the relationship between λ and density for mammal species is increasingly concave as body weight increases (Sibly et al. 2005). In an experimental manipulation of feral pig density, Choquenot (1998) did not detect higher λ in populations at lower densities. Considering that feral pigs have a large body size compared to the majority of mammal species, density dependence may only be detectable at very low population densities, which the current Fort Benning populations do not likely exhibit.

MANAGEMENT IMPLICATIONS

Analyses of annual population matrices can have strong implications for future management plans of invasive species. In the case of feral pigs, although recruitment had been contributing most to population growth, λ is most likely sensitive to changes in survival. Specifically, managers should focus efforts on reducing survival rates of juvenile females to most effectively lower λ . However, managers are unlikely to be able to create management schemes with current tools that target specific feral pig age classes, instead overall survival will likely be the focus of management.

A caution that managers must exercise when using results from analytical elasticity analysis or LSA to guide management decisions is that the most influential vital rate may not be capable of responding to major management manipulations (Heppell et al. 2000, Mills et al. 1999). LSA may provide more realistic results by incorporating vital rate process variance (Wisdom et al. 2000); however, process variation in the most influential vital rate may not be extensive enough to match the management manipulations needed to sufficiently reduce invasive species populations. I showed through experimental manipulation that juvenile survival, the most influential vital rate based on both analytical elasticity analysis and LSA, could be effectively manipulated in order to reduce feral pig population growth rates.

With financial or logistical constraints that prevent year-round management, sensitivity analysis of seasonal matrix models can be used to examine changes in the potential effectiveness of management techniques at different times of the year. For hunted populations of feral pigs that respond strongly to availability of fall mast-crop resources, targeting survival during the summer or fall/winter should be the most

effective time of year to reduce λ . However, targeting survival during the summer is recommended because it is difficult to catch and kill feral pigs during periods of high food availability. However, the most effective management would occur during years of mast crop failure because λ is increasingly sensitive to changes in survival as reproduction decreases.

While controlling invasive species populations is a major challenge, my research uncovered promising characteristics of feral pig population dynamics that may benefit management efforts. First, the LSA regression results revealed an increase in the influence of survival on the variation in λ as survival was reduced. Typically, catch per unit effort declines as populations become smaller (Seber 1982), but if the influence of survival increases at lower survival rates, perhaps this will offset the reduced ability to remove individuals. Second, the lack of density dependence and the probable concave relationship between λ and density indicate that managers will not see compensation in reproduction or survival until population densities are quite low. Thus, initial removal efforts will be more effective than if density dependence were occurring.

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Tables and Figures:

Table 1. Mean, low, and high annual survival and recruitment rates, based on 95% confidence intervals, used to construct life-stage simulation analysis matrices for feral pigs in control and treatment populations at Fort Benning, Georgia, 2004-2005.

Population	Vital Rate	Mean	Low	High
Control	Juvenile recruitment	3.540	2.236	4.838
	Adult recruitment	3.540	2.236	4.838
	Juvenile survival	0.3108	0.2156	0.4061
	Adult survival	0.3193	0.2376	0.4010
Treatment	Juvenile recruitment	4.280	2.698	5.865
	Adult recruitment	4.280	2.698	5.865
	Juvenile survival	0.2147	0.0966	0.3327
	Adult survival	0.2211	0.1255	0.3207

Table 2. Model selection results for survival of feral pigs at Fort Benning, Georgia, 2004-2005. Models are ranked in ascending order by Akaike's Information Criterion, adjusted for overdispersion and small sample size (QAIC_c). Survival was modeled by a treatment effect (trmt), sex, juvenile vs. adult (age), estimated weight at capture (weight), and the presence of a GPS collar (collar).

Model	QAIC _c ¹	ΔQAIC _c	QAIC _c Weight	K ²	Deviance	Evidence ³ Ratio
trmt	640.627	0.00	0.113	8	622.756	
null	641.314	0.69	0.080	7	625.562	1.41
trmt + sex	641.529	0.90	0.072	9	621.524	1.57
trmt + sex + age + sex * age	641.616	0.99	0.069	11	617.301	1.64
sex + age + sex * age	641.733	1.11	0.065	10	619.581	1.74
sex	641.999	1.37	0.057	8	624.127	1.98
trmt + weight	642.203	1.58	0.051	9	622.198	2.22
trmt + collar	642.342	1.71	0.048	9	622.337	2.35

¹ Akaike's Information Criterion corrected for overdispersion and small sample size

² Number of parameters

³ Likelihood of the top ranked model versus the competing model (e.g., the top model is 1.41 times more likely to be the model that best approximates truth than the second ranked model)

Table 3. Annual survival rates (S.E.) of juvenile male, juvenile female, adult male, and adult female feral pigs at Fort Benning, Georgia, 2004-2005. Survival rates were estimated for the control and treatment populations using averaging of models with and without treatment effect.

	Treatment	Control
Juvenile female	0.215 (0.058)	0.311 (0.047)
Adult female	0.223 (0.046)	0.319 (0.040)
Juvenile male	0.126 (0.056)	0.200 (0.049)
Adult male	0.132 (0.044)	0.207 (0.042)

Table 4. Model selection results for recruitment of feral pigs at Fort Benning, Georgia, 2004-2005. Models are ranked in ascending order by Akaike's Information Criterion, adjusted for small sample size (AIC_c). Recruitment was modeled by a treatment effect (trmt) and season.

Model	AIC_c ¹	ΔAIC_c	AIC_c Weight	K^2	Deviance	Evidence ³ Ratio
trmt + season (spring = summer)	1114.312	0.00	0.427	6	100.665	
season	1115.646	1.33	0.219	7	99.911	1.95
trmt + season	1116.399	2.09	0.151	7	100.664	2.84
trmt	1130.265	15.95	0.000	9	110.316	2848.53
null	1172.058	57.75	0.000	3	164.597	>100,000

¹ Akaike's Information Criterion corrected for overdispersion and small sample size

² Number of parameters

³ Likelihood of the top ranked model versus the competing model (e.g., the top model is 1.95 times more likely to be the model that best approximates truth than the second ranked model)

Table 5. Elasticity values calculated using analytical sensitivity analyses of mean survival and recruitment rates. Analyses were conducted for both the control and treatment feral pig populations at Fort Benning, Georgia, 2004-2005, using 3 matrix model forms: Matrix 1, annual survival and Pradel recruitment using the average summer value; Matrix 2, annual survival and fecundity with the assumption that all juveniles and adults breed once a year; Matrix 3, annual survival and fecundity with the assumption that 3/4 of juveniles breed once and 3/4 of adults breed twice a year. F_j , juvenile recruitment; F_a , adult recruitment; S_j , juvenile survival; S_a , adult survival.

Population	Vital Rate	Matrix 1	Matrix 2	Matrix 3
Control	F_j	0.6007	0.4516	0.2758
	F_a	0.1743	0.2311	0.3083
	S_j	0.7751	0.6826	0.5840
	S_a	0.2249	0.3174	0.4158
Treatment	F_j	0.6497	0.4484	0.2737
	F_a	0.1563	0.2320	0.3087
	S_j	0.8061	0.6804	0.5824
	S_a	0.1939	0.3196	0.4175

Table 6. Comparison of relative vital rate elasticities to relative LTRE contributions using average summer recruitment rates for control and treatment populations of feral pigs at Fort Benning, Georgia, 2004-2005. F_j , juvenile recruitment; F_a , adult recruitment; S_j , juvenile survival; S_a , adult survival.

	Control		Treatment	
	Elasticity	LTRE Contribution	Elasticity	LTRE Contribution
F_j	0.34	0.21	0.36	0.23
F_a	0.10	0.69	0.09	0.65
S_j	0.44	0.04	0.45	0.05
S_a	0.13	0.06	0.11	0.07

Figure captions:

Figure 1. Map of the 737 km² Fort Benning Military Reservation in west-central Georgia, site of the experimental feral pig study, showing the control and treatment study areas.

Figure 2. Basic life cycle for feral pigs with juvenile and adult age classes. F represents fecundity or recruitment and S represents survival corresponding to the population matrix models.

Figure 3. Seasonal survival and recruitment rates estimated for female feral pigs in control and treatment populations for each 4 month season (summer, fall/winter, and spring) at Fort Benning, Georgia, 2004-2005. Squares, survival rate; triangles, recruitment rate; closed symbols, control population; open symbols, treatment population.

Figure 4. Annual population growth rates and 95% confidence intervals for feral pigs in control and treatment populations at Fort Benning, Georgia, 2004-2005, calculated using the following matrix model forms: Matrix 1, annual survival and Pradel recruitment; Matrix 2, annual survival and fecundity with the assumption that all juveniles and adults breed once a year; Matrix 3, annual survival and fecundity with the assumption that 3/4 of juveniles breed once and 3/4 of adults breed twice a year. Closed symbols, control; open symbols, treatment; circles, matrix using recruitment; squares, matrix using fecundity.

Figure 5. Analytical elasticities of juvenile recruitment, juvenile survival, adult recruitment, and adult survival for control and treatment feral pig population at Fort Benning, Georgia, 2004-2005, calculated using the matrix incorporating annual female survival rates and annual Pradel recruitment rates.

Figure 6. Life-stage simulation analysis elasticity values and 95% confidence intervals of juvenile recruitment, adult recruitment, juvenile survival, and adult survival for feral pigs in control and treatment populations at Fort Benning, Georgia, 2004-2005.

Figure 7. Life-stage simulation analysis r^2 values, indicating the relative influence of each vital rate on the variation in λ , based on 1000 random matrices of juvenile recruitment, adult recruitment, juvenile survival, and adult survival for feral pigs in control and treatment populations at Fort Benning, Georgia, 2004-2005.

Figure 8. Analytical elasticity values of juvenile survival and juvenile recruitment rates during each 4 month season (summer, fall/winter, and spring) of the control population of feral pigs at Fort Benning, Georgia, 2004-2005. The un-estimated summer recruitment rate was calculated by averaging known fall/winter and spring recruitment rates. Squares, survival rate; triangles, recruitment rate.

Fig. 1

Fort Benning

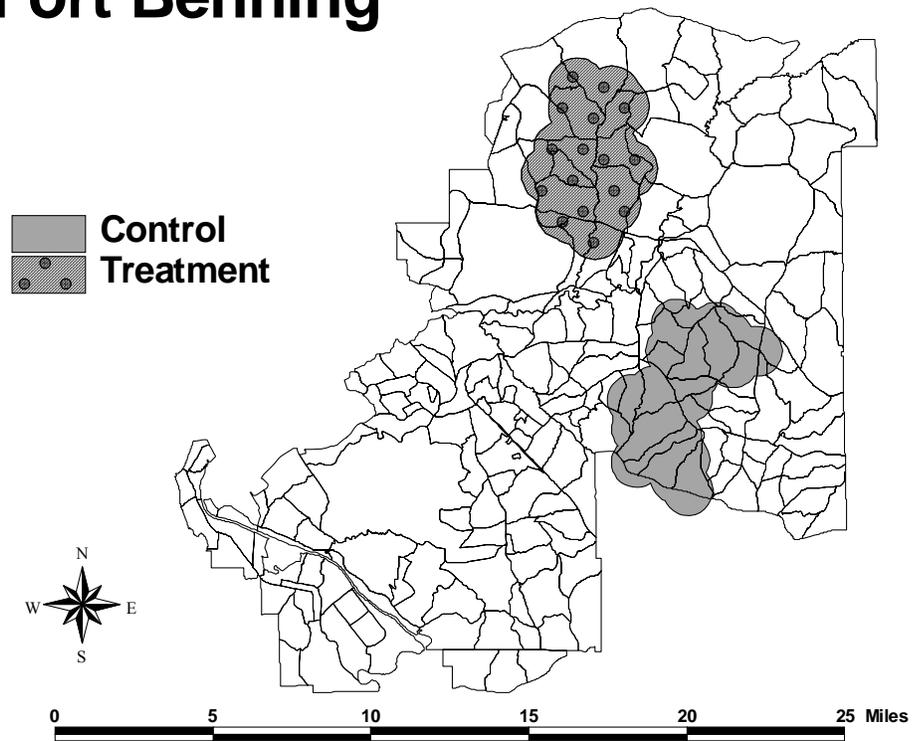


Fig. 2:

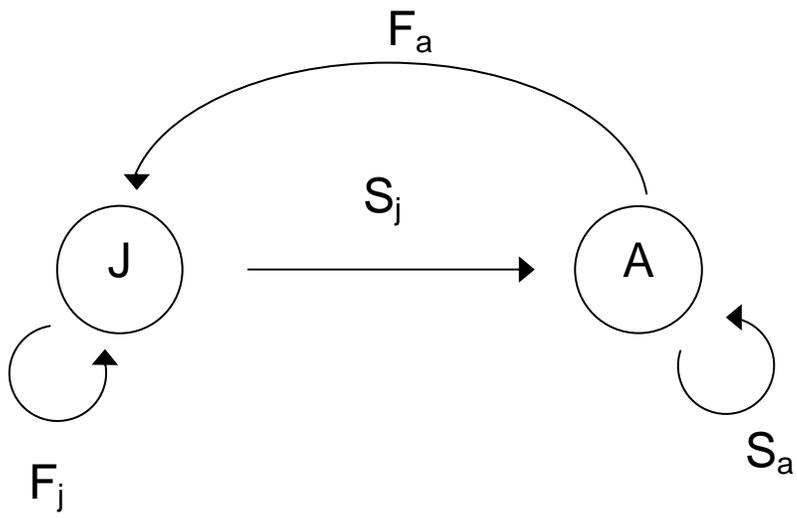


Fig. 3.

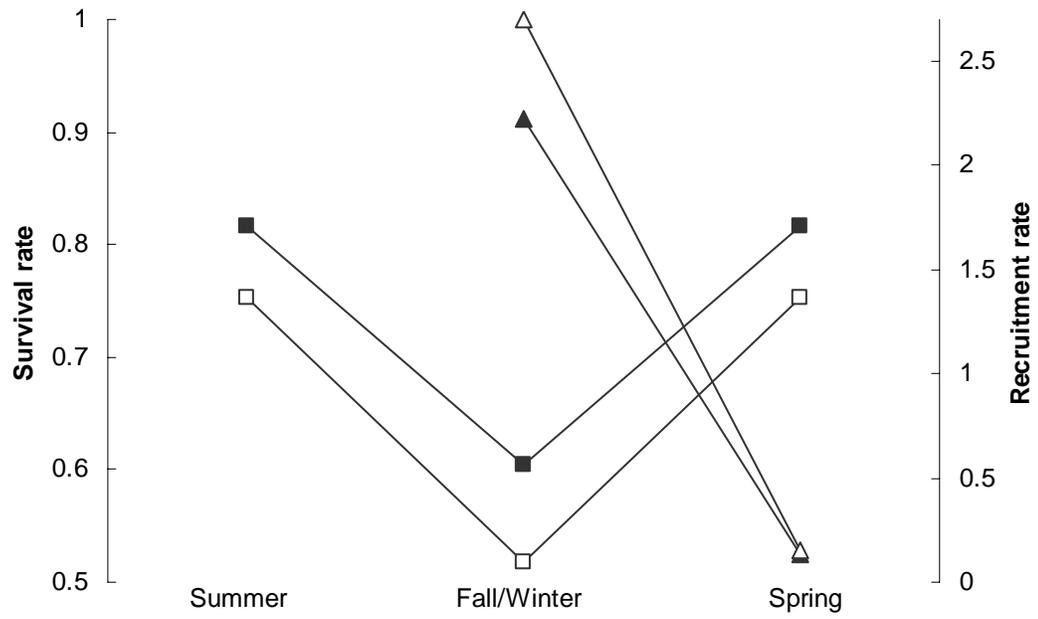


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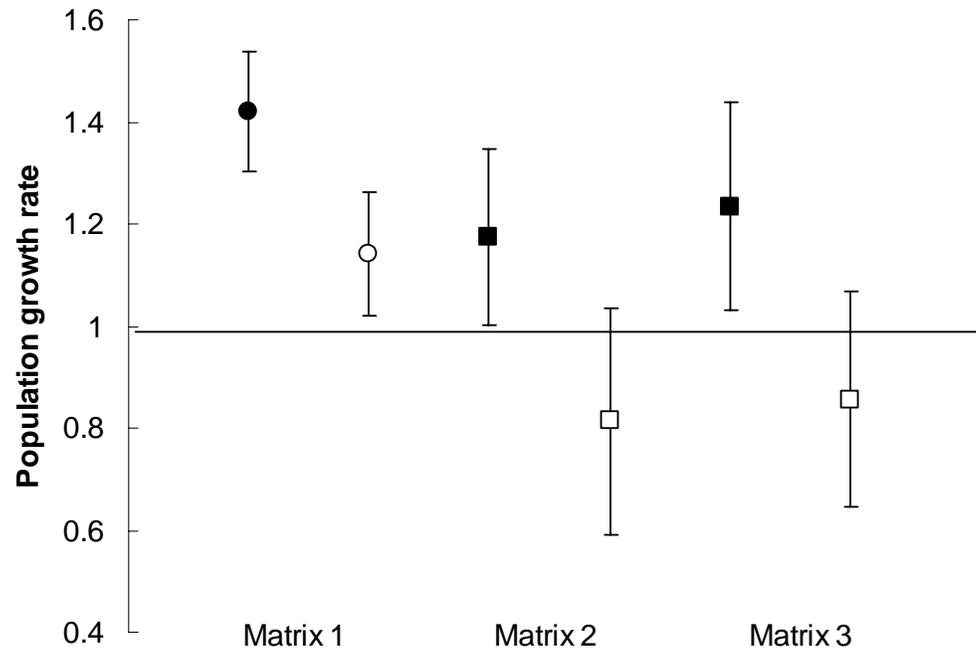


Fig. 5:

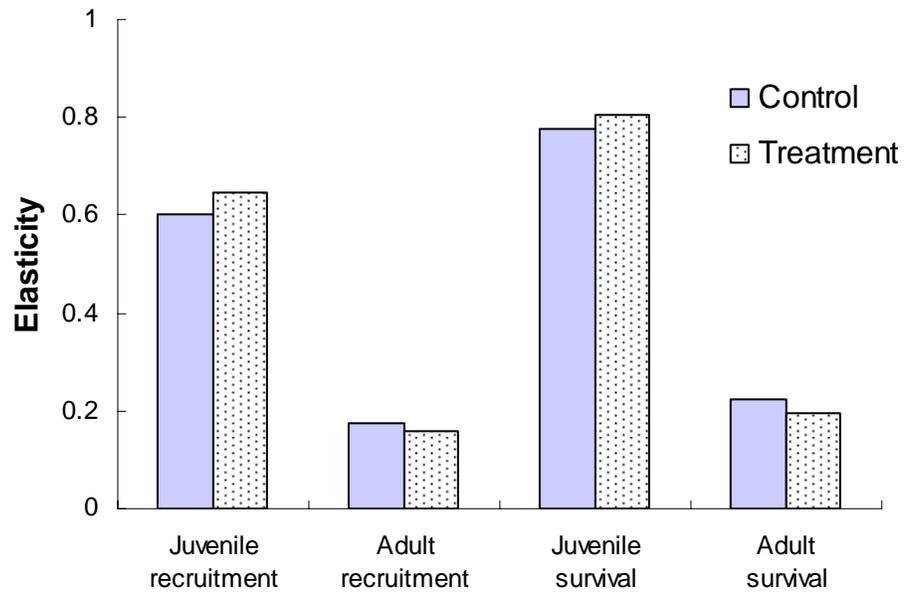


Fig. 6:

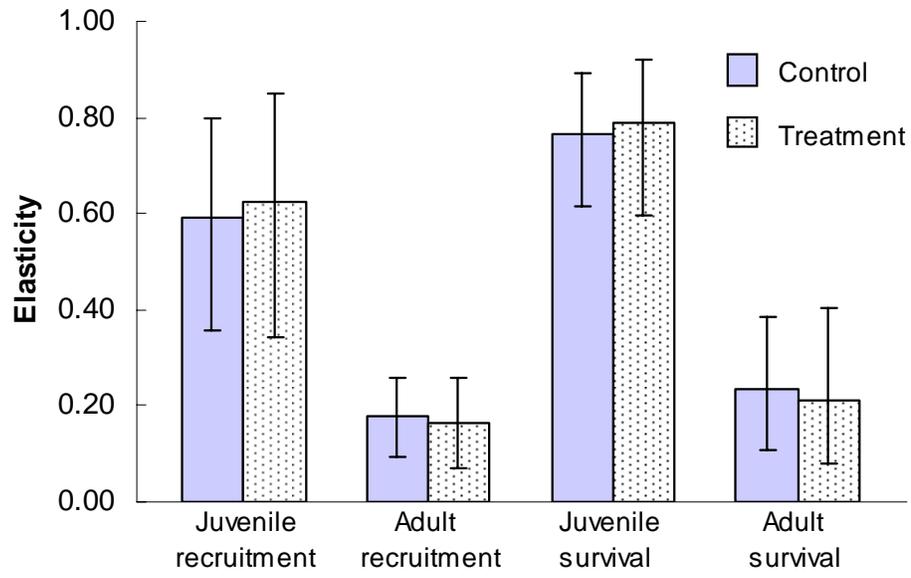


Fig. 7:

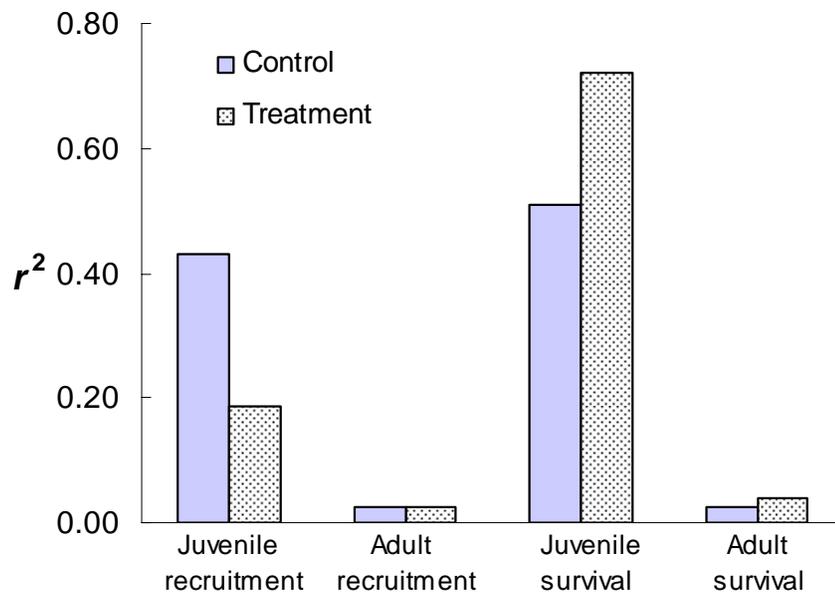
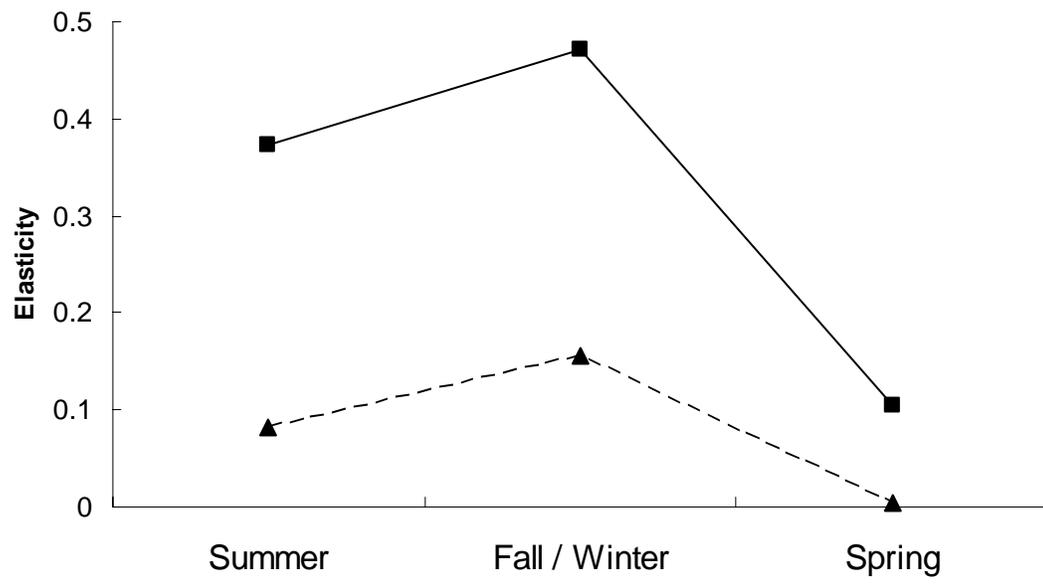


Fig. 8:



NOVEL DENSITY ESTIMATION METHODS USING OPEN MARK-RECAPTURE MODELS

Abstract: Density estimation is commonly used to help managers understand wildlife population dynamics. Closed capture-mark-recapture (CMR) methods produce negative biases in density estimates for species with low or heterogeneous detection probabilities. I developed 2 novel density estimation methods that incorporate detection probabilities, the survival/reporting rate method and the group size/home range size method, to address biases associated with CMR methods. The survival/reporting rate method, which addresses the heterogeneous detection probability bias, can be used for game species when hunters report their kills and survival rates are known. The group size/home range size method, which addresses the low detection probability bias, can be used for any wildlife species when average group size and home range size (with potential overlap) is estimated. Comparison of density estimates from a feral pig population revealed that the 2 novel methods produced density estimates that were almost equivalent to each other, lower than a change-in-ratio method, and higher than a count of the minimum number known alive and estimates from closed CMR methods. Both novel methods may provide less biased density estimates than closed CMR methods for species with low or heterogeneous detection probabilities, however these methods estimate density over longer periods of time and may incur additional costs.

Key words: change-in-ratio, density estimation, detection probability, effective sampling area, feral pig, home range size, index, individual heterogeneity, mark-recapture, survival

Density, a derivation of abundance, is equal to the number of individuals per unit area. A primary goal of many wildlife researchers and managers is to estimate population density accurately. Density is commonly used to understand how a wildlife population relates to an area of concern or how the population changes over time.

Acquiring accurate estimates of density requires the estimation of detection probabilities (Anderson 2001, Williams et al. 2002); however, many researchers use indices of abundance or density, which do not incorporate detection probabilities (Woodall 1983, Saunders 1995, Engeman 2005). The use of some indices to estimate density require the unrealistic assumption of a constant detection probability across observers, habitat types, weather conditions, time of year, and individuals in the population (Anderson 2001). Such indices of density are not necessarily comparable over time or related to true abundance. While indices may be less expensive and easier to implement than density estimation methods that include detection probabilities, they may not produce useful estimates of density when they fail to account for heterogeneity (Anderson 2001, White 2005).

Capture-mark-recapture (CMR) methods are often employed to estimate abundance or the size of a population by incorporating detection probabilities (Williams et al. 2002). Although closed CMR models incorporate detection probabilities,

heterogeneity in detection probabilities caused by time, behavior, or differences between individuals and low detection probabilities can lead to negative biases in abundance estimates (Williams et al. 2002, Link 2003). Each additional source of heterogeneity adds bias to the abundance estimator (Chen and Lloyd 2000). The use of individual covariates, information specific to the individual animal, can alleviate problems associated with individual heterogeneity, but only if the measured covariates relate to differences in detection probabilities between individuals (Huggins 1989, Alho 1990).

The area over which a population of animals is distributed must be determined in order to calculate density. For studies that use field observations to estimate density, another potential bias is the need to estimate the effective sampling area. An edge effect exists because the sampling grid covers only a portion of the area occupied by the population of interest (Bondrup-Nielsen 1983, Efford et al. 2005). Estimating the average distance moved by individuals in the population through their recapture locations or home range size has been used to calculate an appropriate buffer around the sampling grid (Smith et al. 1971, Hagen et al. 1973, Van Horne 1982, Bondrup-Nielsen 1983). The density estimates are potentially biased by the spacing or distance between traps and the likelihood an individual covers the diameter of their home range during a closed sampling period.

Density estimation methods other than closed CMR should be investigated for species that are difficult to capture or have unmeasured or unmeasurable traits that affect detection probability. Feral pigs represent a species with a low probability of being captured in traps and heterogeneous detection probabilities. In attempts to estimate the density of a feral pig population at Fort Benning, Georgia, I calculated density using 5

methods that incorporate detection probabilities and compared each to a count-based density of the minimum number known alive (MNKA). MNKA can be used to determine the minimum population size; however, this is not necessarily proportional to the actual population size (White 2005). I compared density estimates from program MARK (D_M), which can incorporate individual covariates into the estimation of detection probabilities, to density estimates from program CAPTURE (D_C), which cannot incorporate covariates, but can incorporate unmeasured heterogeneity. I developed 2 novel density estimation methods and used a change-in-ratio method (D_{CIR}) that reduce biases associated with closed capture models and compared density estimates from these methods to those of closed CMR methods. The D_{CIR} method and the first novel method, the survival/reporting rate (D_{S-RR}) method, both employ an open CMR model, which in contrast to closed CMR models, is robust to heterogeneity in detection probabilities. The second novel method, the group size/home range size (D_{GS-HR}) method, addresses biases associated with both low and heterogeneous capture probabilities and does not require estimation of the effective sampling area.

Feral pig density is of interest to researchers and land managers because, as an invasive species, they are considered economic and environmental pests because they compete with native wildlife for food resources (Dickson 2001), disturb soil and vegetation while rooting for food (Hone 2002), reduce species richness in plant communities (Kotanen 1995), and occupy areas with sensitive animal species (MacFarland et al. 1974). Density has been the population metric of choice to determine the extent of a feral pig problem and the success of feral pig population reduction efforts (Coblentz and Baber 1987, Choquenot et al. 1997, Hone 2002). The majority of feral pig

studies have used an index to estimate density (Woodall 1983, Saunders 1995, Choquenot et al. 1997, Hone 2002); however, the few studies that used closed CMR methods found that feral pigs generally have low and heterogeneous detection probabilities (Baber and Coblentz 1986, Coblentz and Baber 1987, Caley 1993). While there are numerous estimates of density for feral pig populations around the world, few were calculated using robust methods that include detection probabilities.

I examined density based on MNKA, 2 closed CMR methods, a change-in-ratio method, and 2 novel density estimation methods using a variety of data collected from a population of feral pigs. This feral pig research employed an experimental study design to examine population dynamics, home range size, habitat use, food habits, and body condition in order to determine how to most effectively reduce the pig densities.

STUDY AREA

My research was conducted between spring 2004 and fall 2005 at the Fort Benning Military Reservation in west-central Georgia (32°21'N, 84°58'W) (Fig. 1). The 737 km² military base is located on the Coastal Plain-Piedmont Fall Line with elevations ranging from approximately 50 to 230 m. The climate was semi-tropical with an average annual rainfall of 132 cm (Dilustro et al. 2002). The average maximum temperatures in July and January were 33.2° C and 13.8° C, respectively. Fort Benning was primarily dominated by stands of longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), shortleaf pine (*P. echinata*), and scrub oak species (*Quercus* spp.) in the uplands. The understory was generally open with some shrubs and grasses. The riparian bottomlands consisted of yellow poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), red maple

(*Acer rubrum*), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and oak species (King et al. 1998).

METHODS

Study Design.-- I estimated density for a control population at Fort Benning, however I used data collected from a lethally manipulated treatment population to assist with some density estimation methods. I considered the 50 km² control and treatment areas, located approximately 8 km apart and separated by a large creek, independent study sites (Fig. 1). I caught, tagged, and released feral pigs in both the control and treatment populations during summer 2004 (May –July), before I began the experimental removal. The experimental removal consisted of killing feral pigs via lethal trapping and shooting in the treatment study area from August 2004 through May 2005. Lethal trapping involved catching and shooting pigs in spring-loaded cage traps baited with corn. I estimated survival from summer 2004 to summer 2005 of feral pigs in both control and treatment populations. Hunting by off-duty military personnel occurred year-round in both study areas.

Capture-Mark-Recapture

Trapping and Handling.--I split the control area into 2 equal sections and conducted 2 18-day closed CMR sessions during each summer, 2004 and 2005 to sample an approximately 50 km² area. I had 20 trap locations spaced 1-2 km apart in the study area. I pre-baited traps with shelled corn and corn mash for 2 weeks prior to each trapping session. I trapped feral pigs using spring-loaded cage traps capable of catching multiple pigs. I checked traps each morning of the 18 day trapping sessions.

I tagged all captured feral pigs with uniquely numbered ear tags in both ears (National Band and Tag, Newport, KY). I measured head and body length in order to estimate age (Boreham 1981). I recorded sex and estimated weight prior to release. I used Telazol (1 cc/ 30 kg), administered with a jab stick, to sedate adult females and attach ear tags and a GPS collar (Advanced Telemetry Systems, Isanti, MN). I recorded body measurements, including chest girth and neck circumference, of each sedated female and aged them based on tooth eruption patterns (Matschke 1967). I monitored GPS-collared feral pigs via radio-telemetry weekly to determine potential mortality. Handling of all pigs was conducted in accordance with institutional animal care and use guidelines of Auburn University (PRN# 2003-0531).

Cameras.--I used digital game cameras (infrared Digital-Scout 3.2 mega pixel; Penn's Woods, Export, Pennsylvania, USA) to recapture ear tagged feral pigs passively between August 2004 – May 2005. I photographed each feral pig before its initial release to aid in identifying feral pigs recaptured with the game cameras.

I placed cameras at and between trap locations. I baited 8 cameras with fermented corn and moved them every 2 to 3 weeks in order to fully sample the study area several times. I set cameras with a 2-minute delay between photographs being taken to acquire multiple photographs of the same feral pig group to assist with identification and group size estimation. I recorded sightings of all feral pig group sizes and composition. A sighting included all photographs taken of a feral pig group over a 12-hour period beginning when the group was first sighted.

Effective Sampling Area

To calculate density (pigs/km²) from the MNKA, the closed CMR abundance estimates, and the change-in-ratio method, I estimated the effective sampling area of the control area with 95% confidence intervals by creating buffers around each trap. Buffer distance equaled half the longest straight-line distance feral pigs moved during the length of a trapping session (18 days). I restricted analysis to the summer months (May-August), corresponding to trapping dates, to remove potential bias in seasonal movements. I acquired movement data from GPS locations of collared sows and assessed the data using the Animal Movement extension in ArcView 3.2 (Hooge and Eichenlaub 1997). I also used ArcView to create buffers around GPS recorded trap locations and determine total effective sampling area.

Density Estimation

Minimum number known alive, D_{MNKA} --I conducted a count of feral pigs to estimate MNKA. MNKA equaled the total number of feral pigs caught in traps added to the total number of identifiable individuals seen by cameras during late summer and early fall in the control area. Feral pigs seen in cameras by early fall were likely in the population during the summer because newly born juveniles were not seen in cameras until late fall. I calculated D_{MNKA} by dividing the MNKA by the effective sampling area.

CMR Program MARK, D_{M} --I used the Huggins closed capture model within program MARK to estimate abundance during each summer trapping session in the control area (Huggins 1989). Program MARK uses a maximum likelihood method to derive abundance estimates from estimated detection and re-capture probabilities. I modeled detection probabilities using individual covariates including sex, age, estimated weight,

and observed weather conditions, which I hypothesized affected the probability of catching pigs. I created a capture history for each feral pig caught in a trap at least once. I used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to rank models (Akaike 1973). I divided abundance estimates by the effective sampling area to estimate density. In order to compare the D_M estimate to the 3 continuous density estimation methods, I averaged density over the 2 years.

CMR-Program CAPTURE, D_C --I also used program CAPTURE to estimate the abundance of the closed control population for each summer trapping session. Program CAPTURE uses estimated detection probabilities, but cannot incorporate individual covariates to generate abundance estimates. I attempted to control for individual heterogeneity in my dataset by estimating abundance separately for each of 4 groups: juvenile males, juvenile females, adult males, and adult females, to simulate using the covariates of sex and age. I divided abundance estimates by the effective sampling area to estimate density. In order to compare the D_C estimate to the 3 continuous density estimation methods, I averaged density over the 2 years.

Change-in-Ratio Density Estimation, D_{CIR} --To estimate density in the control area using a change in ratio method (Williams et al. 2002), I used information on control and treatment population survival rates and the number of pigs experimentally removed from the treatment area.

To estimate survival using a maximum likelihood method, I used the capture-mark-recapture Barker model in program MARK, which incorporates live captures, live re-sights, and dead recoveries (White and Burnham 1999, Barker 1997). I included my data on live trapping, "re-sight" of GPS collared feral pigs via radio-telemetry, camera

re-sight, and hunter returns of ear tags to estimate apparent survival and a reporting parameter (r), the probability of a tag being reported given that the individual was found dead. This model also estimates detection probability, re-sight probability, probability the animal is re-sighted and then dies within the interval, probability of fidelity to study area (F), and probability of temporary emigration from study area (F'), all of which I considered nuisance parameters, i.e., parameters that must be estimated in order to estimate survival and reporting rate. I simplified models by holding nuisance parameters constant over time and space because survival was the primary parameter of interest and I had limited data. Because the size of my dataset prevented me from estimating movement parameters, I constrained $F = F' = 1$, which assumes random emigration is occurring. I modeled survival using individual covariates collected upon original capture, including study area, sex, age, estimated weight, and presence of a GPS-collar.

I based model selection on the information-theoretic approach (Burnham and Anderson 2002). I used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to rank models (Akaike 1973).

Before running my *a priori* candidate model set, I constructed the most highly parameterized, biologically relevant model that could estimate all the parameters using my dataset. I used this global model to run a goodness-of-fit test to evaluate overdispersion in my data. I assessed goodness-of-fit using a median \hat{c} test, which provides more robust \hat{c} estimates than the bootstrapping approach, both available in program MARK (White and Cooch 2005). If $\hat{c} = 1$, data are not overdispersed. Values of $\hat{c} > 1$ indicate lack of fit. I incorporated the estimated \hat{c} value into the AIC calculation.

Program MARK uses capture histories created for each captured individual to estimate survival. Because feral pigs less than 1 month old were too small to be caught in traps, estimates of survival only include feral pigs older than 1 month. I used 3 evenly spaced re-sighting and tag recovery intervals over the course of the year, which resulted in a survival rate for each interval. I raised the interval survival rate to the 3rd power to calculate annual survival. I estimated annual variance by incorporating interval sampling and process variance using the Delta method (Seber 1982).

Abundance was estimated by dividing the total number of pigs experimentally removed from the treatment area by the percent survival was reduced in the treatment population compared to the control population. The D_{CIR} method requires the assumption that survival rates were equal in the control and treatment populations prior to the experimental removal efforts. I divided abundance estimates by the effective sampling area to estimate density.

Survival and Reporting Rate, D_{S-RR} .--This novel density estimation method requires estimating survival, the rate hunters report killed tagged individuals, and the total hunting area. I estimated survival rates and the reporting rate using the Barker model method described in the previous section.

Hunters at Fort Benning turned in hunter kill cards, which listed the number of feral pigs they killed during the hunting season. To estimate the total number of feral pigs killed at Fort Benning from summer 2004 through spring 2005, I divided the total number of feral pigs reported killed during the hunting season (K) by the estimated reporting rate (r) from the Barker model.

Humans are the only known predator to regularly kill feral pigs at Fort Benning, therefore I assumed *a priori* that all but 10% of the annual mortality rate was hunter-related. Other sources of mortality may include starvation, disease, and predation from non-human sources. I divided the total number of feral pigs killed on Fort Benning by the mortality rate caused by hunters (M) to obtain a total population size. I estimated D_{S-RR} density by dividing the total population size by the total area of training and hunting compartments on Fort Benning (A), excluding highly developed areas with numerous buildings.

$$D_{S-RR} = \frac{K}{r(M - 0.10)A}$$

where K = number of pigs reported killed by hunters, r = reporting rate, M = total mortality rate (or 1-survival rate), and A = area of hunting and training compartments (km²).

Group Size and Home Range Size, D_{GS-HR} . Using data from camera sightings, I separated feral pig groups into solo adult males, solo adult females, females with juveniles (sounders), and a group representing all other combinations. I calculated the number of juveniles sighted per sounder and the number of females sighted per sounder. Based on equal sex ratio, I considered the number of adult males equal to the number of adult females across Fort Benning. To account for errors in detecting all members of a group, I used the detection probability (p) estimated using the open CMR Pradel model in program MARK. The model used data consisting of sightings of ear tagged or individually identifiable pigs exclusively from camera data. I estimated average home range size for sounders using Kernel home range analysis of GPS-collar location data in

the Animal Movement extension of ArcView 3.2 (Hooge and Eichenlaub 1997). I calculated home range area based on a 95% utilization distribution, which is the probability an individual is found at a given location based on the data collected (Seaman and Powell 1996). Animal Movement uses the least squares cross-validation technique for bandwidth and auto calculates grid extent. Because sounder home ranges do not overlap at Fort Benning (B. Sparklin, unpublished data), I divided the number of feral pigs sighted in a home range by the home range size (H) and then by detection probability (p) to estimate density.

$$D_{GS-HR} = \frac{2F + J}{p * H}$$

where F = number of females, J = number of juveniles, p = detection probability, and H = home range size (km²)

RESULTS

Capture-Mark-Recapture

During the 2 18-day trapping sessions in 2004, I caught 64 feral pigs and recaptured 53.1% in the control area. In 2005, I caught 62 feral pigs with a recapture rate of 40.3%.

Digital game cameras produced over 4200 total photographs over the course of the 10-month period. Feral pigs were captured in 35% of the photographs. I recorded 275 sightings of pigs groups with an average of 5.6 photographs of feral pigs per sighting. I documented 116 sightings of sow groups (sounders). The mean number of feral pigs sighted was 3.11 (S.E. = 0.28) piglets per sounder and 1.19 (S.E. = 0.09)

females per sounder. This estimate is the lowest possible average group size because not all group members were necessarily photographed.

Effective Sampling Area

I used the location data from 12 collared sows to determine appropriate buffer distance and home range size. The maximum distance moved by collared feral pigs between two points was 2.56 km over any 18-day period. Half the distance moved equaled 1.28 km, thus I added a 1.28 km (95% CI: 1.08, 1.48) buffer around each trap. Buffers placed around the 20 traps created an effective sampling area of 51.8 km² (95% CI: 44.1, 58.6) in 2004 and 49.1 km² (95% CI: 41.6, 56.1) in 2005. I took into account the area of overlap between the 2 sections of the control area, when estimating effective sampling area, to prevent overestimation of the total sampling area.

Density Estimation

Minimum number known alive, D_{MKNA} --The number of feral pigs caught in traps plus the number of identifiable individuals seen by cameras divided by the estimated effective sampling area produced a minimum known density of 1.92 feral pigs/km² (95% CI: 1.70, 2.26) (Fig. 2).

CMR Program MARK, D_M --The highest ranked Program MARK model included detection ($p = 0.12$) and re-capture probabilities ($c = 0.06$) that were affected by sex, age, and rainfall (Table 1). All candidate models, including the top model, produced population size estimates that varied little from the actual number of individuals caught during the trapping sessions.

Estimates of population size divided by the estimates of effective sampling area resulted in D_M equal to 1.16 pigs/km² (95% CI: 0.95, 1.67) in 2004. During 2005, the

estimated D_M was 1.23 pigs/km² (95% CI: 1.01, 1.77). Average D_M between both years equaled 1.20 pigs/km² (95% CI: 0.98, 1.72) (Fig. 2).

CMR-Program CAPTURE, D_C --The model selection procedure within program CAPTURE selected M_{tbh} as the best model for the entire dataset, where detection probability varies over time, between individuals, and with behavior, such as trap-happiness. When the dataset was divided into 4 groups (juvenile males, juvenile females, adult males, and adult females), the top model chosen was either M_{tbh} or M_h indicating that there was additional heterogeneity in the data beyond age and sex. M_{tbh} lacks a density estimator, thus I used the second ranked model, M_h , and estimated abundance using Chao's moment estimator, which is the best abundance estimator for species with low detection probabilities and high individual heterogeneity (Chao 1988, Davis et al. 2003). Chao's moment estimator for M_h estimated a low average detection probability of 0.055, with a range from 0.04 to 0.10.

Estimates of population size divided by the estimates of effective sampling area resulted in D_C equal to 1.79 pigs/km² (95% CI: 1.13, 4.06) in 2004. During 2005, the estimated D_C was 2.45 pigs/km² (95% CI: 1.33, 6.71). Average D_C between both years equaled 2.12 pigs/km² (95% CI: 1.23, 5.38) (Fig. 2).

Change-in-Ratio Density Estimation, D_{CIR} --During the summer of 2004, 90 feral pigs were ear tagged from the control and treatment areas. Between August 2004 and May 2005, 39% were re-sighted in digital game camera photographs, 13% were re-sighted via radio telemetry, and 31% were known dead because of hunter reported ear tags.

The goodness of fit test using my global model indicated little overdispersion in the data with a $\hat{c} = 1.15$. The Barker model estimated apparent annual survival for all

feral pigs older than 1 month to be 0.25 (95% CI: 0.19, 0.31) and 0.17 (95% CI: 0.10, 0.24) in the control and treatment populations, respectively. Between August 2004 and May 2005, 108 feral pigs were experimentally removed from the treatment area. Lethal manipulation resulted in 34.0% (95% CI: 24.4, 49.5) lower survival rates in the treatment population compared to the control population. Estimates of abundance based on the change-in-ratio of survival and the number of pigs lethally removed divided by the estimates of the control effective sampling area resulted in D_{CIR} equal to 6.13 pigs/km² (95% CI: 3.72, 10.04) (Fig. 2).

Survival and Reporting Rate Density Estimation, D_{S-RR} .--The Barker model estimated the reporting rate (r) to be 0.29 (95% CI: 0.17, 0.45) and the apparent annual survival rate for all feral pigs in the control area older than 1 month to be 0.25 (95% CI: 0.19, 0.31). Hunters reported killing 538 pigs (K) on Fort Benning during the 2004-2005 hunting season. Using the reporting rate (r) of 0.29 (95% CI: 0.17, 0.45), the estimated number of total feral pigs killed was 1857 (95% CI: 1201, 3163). An annual survival rate of 0.25 is equal to a mortality rate (M) of 0.75. If all but 10% of mortality was hunter-related, then hunters cause 67.5% of the annual mortality. I estimated the total Fort Benning feral pig population to be 2868 (95% CI: 1702, 5367). The total area (A) of the training and hunting compartments at Fort Benning was 694.3 km². The D_{S-RR} estimate was 4.13 pigs/km² (95% CI: 2.45, 7.73) (Fig. 2).

Group Size and Home Range Size Density Estimation, D_{GS-HR} .--The average home range size (H) was 3.03 km² (95% CI: 2.15, 3.92). The group size sighted in photographs was 3.11 juveniles per sounder (J) and 1.19 females per sounder (F). I assumed that there were an equal number of males and females at Fort Benning because I observed an equal

sex ratio in camera sightings and trap captures. This resulted in a total estimate of 5.49 feral pigs per 3.03 km² home range. The detection probability (p) for photographed feral pigs from the Pradel model was 0.46 (95% CI: 0.35, 0.57) making the estimated number of feral pigs per home range equal to 12.06 (95% CI: 9.63, 15.90). The D_{GS-HR} estimate was 3.98 pigs/km² (95% CI: 2.46, 7.40, Fig. 2).

DISCUSSION

Density is a useful metric to understand how a wildlife population relates to a given area. While density estimation methods which include detection probabilities are less biased than indices (Anderson 2001, White 2005), density estimates can be negatively biased for populations with low or heterogeneous detection probabilities when using closed CMR methods (Williams et al. 2002). Biases in density estimation can also occur when the area in which a population resides is estimated incorrectly (Bondrup-Nielsen 1983, Efford et al. 2005). I developed and evaluated novel density estimation methods to reduce biases associated with closed CMR density estimation methods.

Feral pigs have a very low probability of being captured in traps and detection probabilities that differ between individuals for unknown reasons. These characteristics create negative biases in density estimates from closed CMR models (Williams et al. 2002). The wide variety of data collected during my study allowed me to develop novel density estimation methods and compare these novel methods to traditional closed CMR methods. I compared a count-based MNKA density to the 5 density estimation methods that incorporated detection probabilities. This comparison of the 6 density estimation methods revealed some striking differences in density estimates for the same population.

The closed CMR models in program MARK and program CAPTURE produced relatively low density estimates. The analysis in program MARK produced an abundance estimate, including the confidence interval, less than the MNKA (Fig. 2). Although detection probabilities were modeled by time, behavior, and all collected individual covariates in program MARK, abundance estimates did not differ between the null model and models using these covariates (Table 1). This indicates that heterogeneity I did not measure was affecting detection probabilities and may have been more important to estimating abundance than the measured covariates (Williams et al. 2002). Program CAPTURE is able to incorporate unmeasured individual heterogeneity and thus, produced higher abundance estimates compared to program MARK, however, the point estimate was only slightly higher than the MNKA (Fig. 2). Within program CAPTURE, Chao's moment estimator M_h , is the least biased estimator when faced with low detection probabilities and high individual heterogeneity, yet may still produce some negative bias in abundance (Chao 1988).

Additionally, CMR abundance estimates can be biased low because of temporary emigration, which occurs when individuals in the population leave the study area during the trapping session or otherwise become unavailable for capture because they do not encounter the traps. It is likely that feral pigs with home ranges on the edge of the sampling grid became temporarily unavailable for capture. My trap placement and spacing may have also caused temporary emigration as individuals may have been located between traps and therefore, temporarily unavailable for capture.

The D_{CIR} method addresses closed CMR biases associated with heterogeneous detection probabilities by using the open CMR Barker model, which is robust to

heterogeneity in detection probabilities (Williams et al. 2002), to estimate survival. Open CMR models do not have the same biases associated with heterogeneous detection probabilities as closed CMR models. The D_{CIR} method requires sampling at least 2 populations, one population from which individuals are removed, to examine the change-in-ratio. The primary assumption for this method was that survival rates were equal across Fort Benning prior to the experimental removal. The D_{CIR} method also requires the estimation of an effective sampling area in order to calculate density.

I developed the D_{S-RR} method to address the closed CMR biases associated with heterogeneous detection probabilities. This novel method also uses the open CMR Barker model to estimate both the annual survival rate and the reporting rate. While open CMR models are robust to heterogeneous detection probabilities, low detection probabilities in open CMR models may cause a positive bias in D_{S-RR} density estimates because the lower the detection probability, the higher the survival estimates (Williams et al. 2002). Although, in the case of this feral pig population, detection probabilities were low, survival rates were also low meaning that an increase in the detection probability would only slightly decrease survival estimates and produce little bias to density results. Another potential bias using the D_{S-RR} method for this feral pig population included the required assumption of the percentage of mortality caused by hunters. However, this bias can be eliminated if hunter-related mortality is estimated separately from total mortality. Finally, the D_{S-RR} method requires estimating the total sampling area used by hunters.

The D_{GS-HR} method addresses closed CMR biases associated with both low and heterogeneous detection probabilities. I used data collected solely from one source, game cameras, and used an open CMR model to estimate group size, which minimized

potential heterogeneity in detection probabilities by eliminating captures through other techniques, such as trapping. The use of cameras to capture pigs also resulted in higher detection probabilities than closed CMR technique of trapping. The detection probability using cameras was 4 times higher than the probability of catching pigs in traps indicating that it is easier to sample a larger portion of the population using this passive sampling technique. Additionally, the D_{GS-HR} method does not require estimating the size of the sampling area.

Comparison of all 6 density estimation methods revealed an interesting trend. The fact that both program MARK and program CAPTURE produced density point estimates similar to or less than the MNKA provides little support for using closed CMR methods to estimate density of wildlife populations, such as feral pigs, that exhibit low or heterogeneous detection probabilities. The D_{CIR} method used an open CMR model to produce the highest density estimate, with 95% confidence intervals that largely overlapped with the density estimates and confidence intervals from the novel methods (Fig. 2). The novel D_{S-RR} and D_{GS-HR} methods used entirely different datasets to generate density estimates and confidence intervals that were greater than the MNKA. Both novel methods produced similar density estimates ranging from 2 to 3.5 times larger than the index and the closed CMR methods (Fig. 2). Given the known biases in closed CMR analyses involving heterogeneity in low detection probabilities, the D_{CIR} , D_{S-RR} and D_{GS-HR} methods could be promising techniques in density estimation.

MANAGEMENT IMPLICATIONS

The D_{CIR} method and the novel D_{S-RR} and D_{GS-HR} methods can be applied to a variety of wildlife populations. The D_{CIR} method can be used in experimental studies, where individuals are removed from at least 1 population, and survival rates are known for populations of interest. The D_{S-RR} method can be used to estimate density of any game species population for which hunters report their harvest, survival can be estimated, and hunter-related mortality can be differentiated from natural mortality. This is a practical density estimation method because many game species are of high management importance with intensive monitoring studies, which often include survival estimation (Krementz et al. 1997, Unsworth et al. 1999). The D_{GS-HR} method can be used to estimate density of any wildlife population with known home range sizes and potential home range overlap, coupled with group size estimates. This method is most accurate if individuals can be uniquely identified through tags or pelage markings in order to estimate a detection probability.

Although my 2 novel density estimation methods and the D_{CIR} method improve upon traditional CMR methods, they can involve additional time and monetary costs. Closed CMR data collection requires intense, short-term investments, whereas the D_{CIR} , D_{S-RR} and D_{GS-HR} methods require less intensive effort over longer periods of time. A downfall to this extended sampling period is that density estimates are averages over a longer period of time where the population may be fluctuating in size, thus making it difficult to compare density estimates between months or years. The D_{GS-HR} method may also be more expensive to implement than a short-term trapping session because it involves additional equipment, such as radio-collars and game cameras.

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Table 1. Model selection results for abundance of feral pigs at Fort Benning, Georgia, 2004-2005 using program MARK. Models are ranked in ascending order by Akaike's Information Criterion, adjusted for small sample size (AIC_c). Capture (p) and re-capture (c) probabilities were modeled by year, sex, age, estimated weight, and rainfall presence on the day of capture (rain).

Model	AIC_c ¹	ΔAIC_c	AIC_c Weight	K^2	Deviance	Density estimate ³
{p. c (year)}+ rain + sex + age	2216.49	0.00	0.38	6	2204.5	1.20
{p. c (year)}+ rain + sex	2216.92	0.42	0.31	5	2206.9	1.20
{p. c (year)}+ rain + sex + weight	2218.78	2.29	0.12	6	2206.8	1.20
{p. c (year)}+ sex + age	2219.58	3.09	0.08	5	2209.6	1.20
{p. c (year)}	2223.36	6.87	0.01	3	2217.4	1.18
{p. c.} + sex	2224.14	7.65	0.01	3	2215.7	1.20
{p. c.} + rain	2226.03	9.53	0.00	3	2217.6	1.18
Null {p. c.}	2227.99	11.50	0.00	2	2221.6	1.18

¹ Akaike's Information Criterion corrected for overdispersion and small sample size

² Number of parameters

³ Abundance estimate divided by average effective sampling area = pigs/km².

Figures

Figure 1: Map of the 737 km² Fort Benning Military Reservation in west-central Georgia showing the control and treatment feral pig study areas, in context of the United States.

Figure 2: Density of feral pigs at Fort Benning, Georgia with 95% confidence intervals estimated using a count of the minimum number known alive (D_{MNKA}) from 2004, Program MARK (D_M), Program CAPTURE (D_C), the change-in-ratio method (D_{CIR}), the survival/reporting rate density estimation method (D_{S-RR}), and the group size/home range size density estimation method (D_{GS-HR}) averaged between 2004-2005.

Fig. 1:

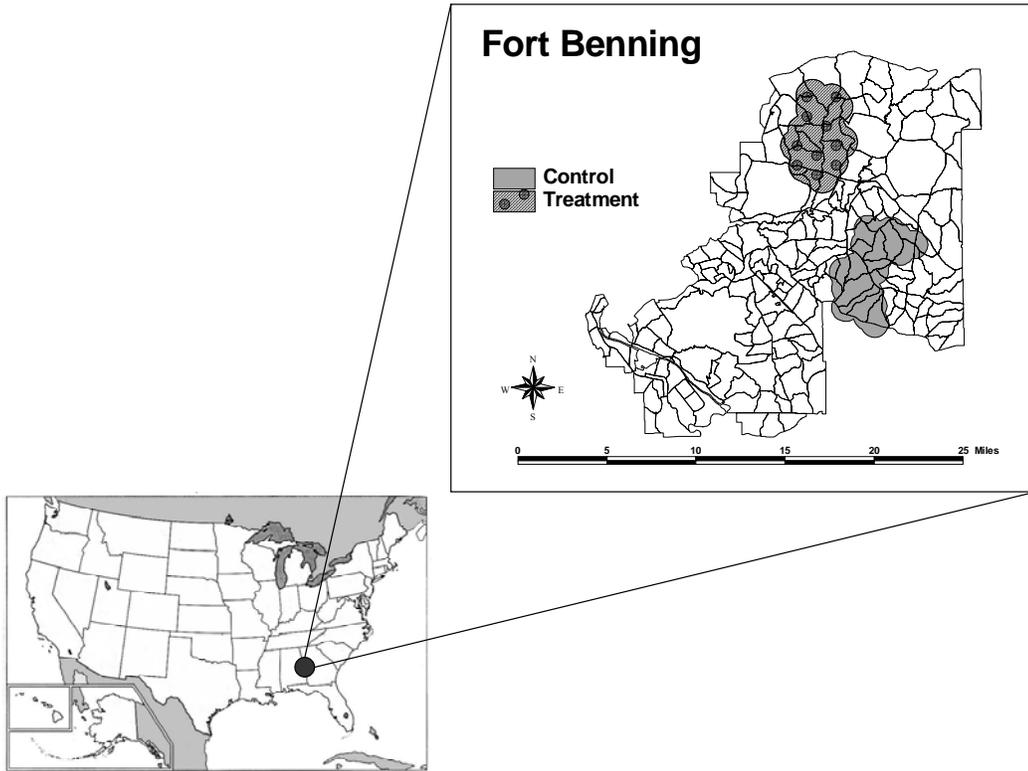
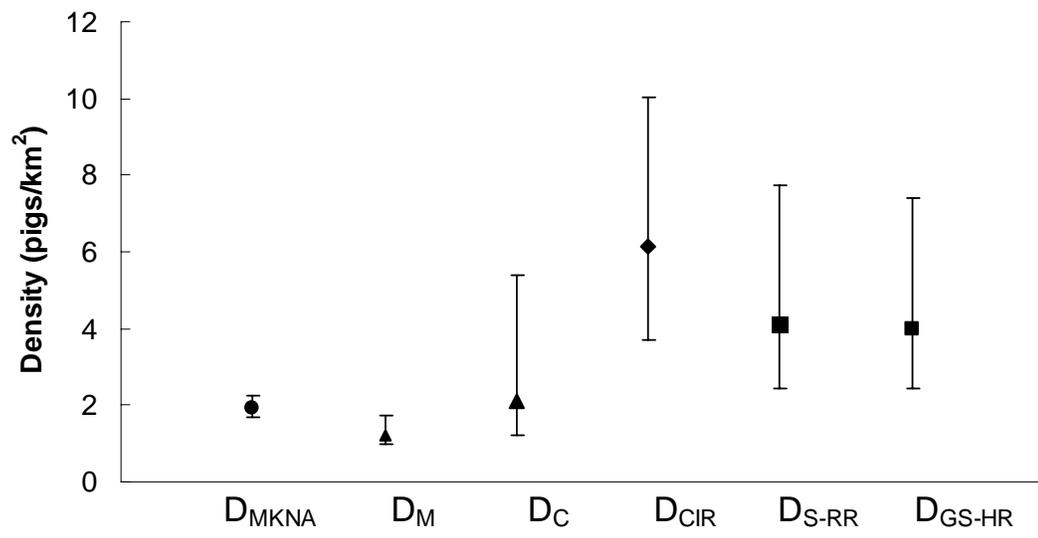


Fig. 2:



CONCLUSION

My experimental research on the demography of feral pigs led to interesting insights regarding the ecology, population dynamics, and management of the hunted feral pig populations at Fort Benning, Georgia. Experimental manipulation led to a reduction in survival for the treatment population compared to the control population, but no change in recruitment rates. While survival rates were quite low even in the control population, recruitment was high enough to result in a growing population size indicating that recruitment contributed most to λ throughout the year. Lethal removal successfully reduced population growth in the treatment population compared to the control population. Demographic density dependence did not occur because recruitment rates remained equal between control and treatment populations while population growth rates differed. Both survival rates and recruitment rates differed by season; survival was lowest during the deer hunting season from October through January and recruitment was highest during that same period.

Sensitivity analyses revealed that the population growth rate (λ), for both treatment and control populations, is potentially most influenced by changes in juvenile survival, especially from June to January. The treatment λ may even be more sensitive to changes in juvenile survival than the control λ . Thus, management strategies that target juvenile survival, specifically during summer and fall, should be the most effective way to reduce feral pig population growth rates.

While my research provides useful information about feral pig population dynamics, the data was collected over the course of only one year. Additional years of demographic data would provide stronger support that my vital rate estimates and sensitivity are close to the truth for feral pigs at Fort Benning. Multiple estimates of survival and recruitment rates over time would also allow temporal variance in vital rates to be calculated and used to more accurately inform management decisions based on sensitivity analyses.

Density proved to be difficult to estimate using closed capture-mark-recapture methods (CMR) because feral pigs have low and heterogeneous capture probabilities, which negatively bias density estimates. I developed two novel density estimation methods to address biases associated with closed CMR methods. Both novel methods produced estimates of feral pig density which were higher than closed CMR methods, however, further research should be conducted using a population of a known size to determine the accuracy and potential biases of these novel density estimation methods.

Regardless of their density, feral pigs are a challenging invasive species to manage because of their high population growth rates. While my research showed that population growth can be reduced by lowering survival rates through lethal removal, long-term population reduction and eradication will likely be costly and time consuming. However, my research provides wildlife managers with important information to understand the population dynamics of feral pigs in order to effectively reduce population growth.

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APPENDIX 1

Appendix 1. Group structure data collected from digital game cameras (infrared Digital-Scout 3.2 megapixel; Penn's Woods, Export, Pennsylvania, USA) placed throughout both the control and treatment study areas to passively capture feral pigs at Fort Benning, Georgia, August 2004 – May 2005. I baited 16 cameras with fermented corn and moved them every 2 to 3 weeks in order to fully sample each study area several times. I set cameras with a 2 minute delay between photographs being taken to acquire multiple photographs of the same feral pig group to assist with identification. I considered a sighting to include all photographs taken of a feral pig group over a 12 hour period beginning when the group was first sighted. I listed adults by sex unless sex could not be determined. I could not determine the sex of juveniles in photographs. I considered pigs to be juvenile based on size and the presence of adult females. I recorded over 8200 photographs including 511 different sightings of feral pigs groups.

Group structure	% of sightings
Male solo	41.68
Females and juveniles	16.24
Adults - unknown sex	11.55
Female solo	11.35
Juveniles	7.83
Females – multiple	4.11
Males and females	2.93
Males – multiple	2.15
Males, females, and juveniles	1.57
Males and juveniles	0.59

APPENDIX 2

Appendix 2. Daily activity time data collected from digital game cameras (infrared Digital-Scout 3.2 megapixel; Penn's Woods, Export, Pennsylvania, USA) placed throughout both the control and treatment study areas to passively capture feral pigs at Fort Benning, Georgia, August 2004 – May 2005. I baited 16 cameras with fermented corn and moved them every 2 to 3 weeks in order to fully sample each study area several times. I recorded activity time as the time the first sighting of each feral pig group occurred during a 12 hour period. I recorded over 8200 photographs including 508 different activity time photographs for feral pigs groups.

Fig. 1

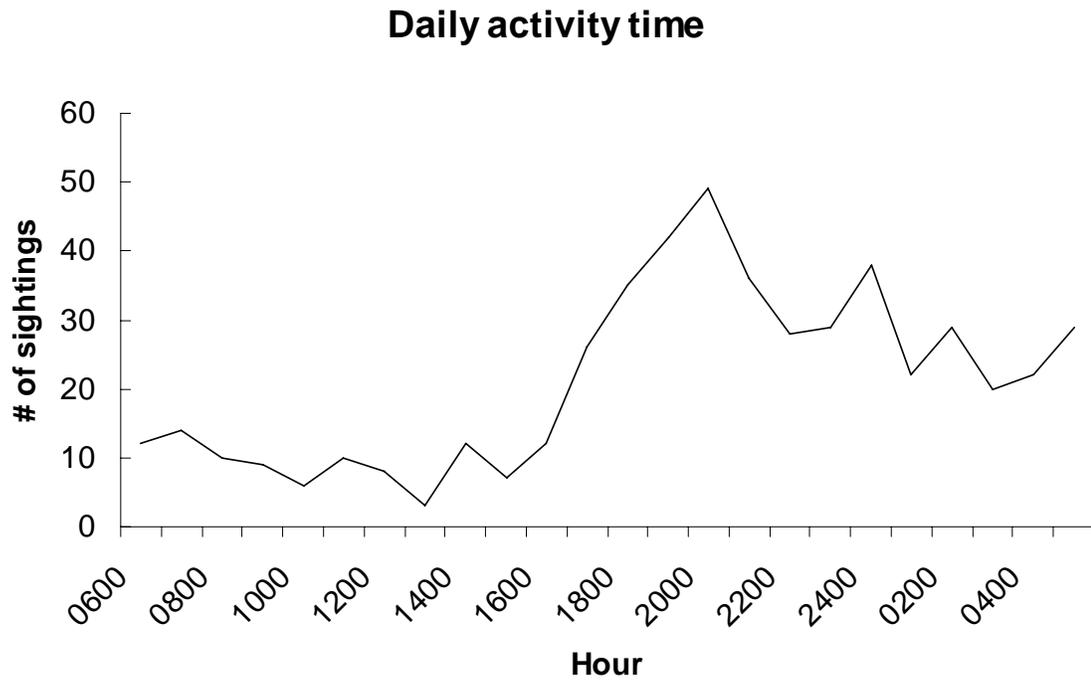


Figure 1. Daily activity time of feral pigs at Fort Benning, Georgia, mid-August 2004 – May 2005.

Fig. 2

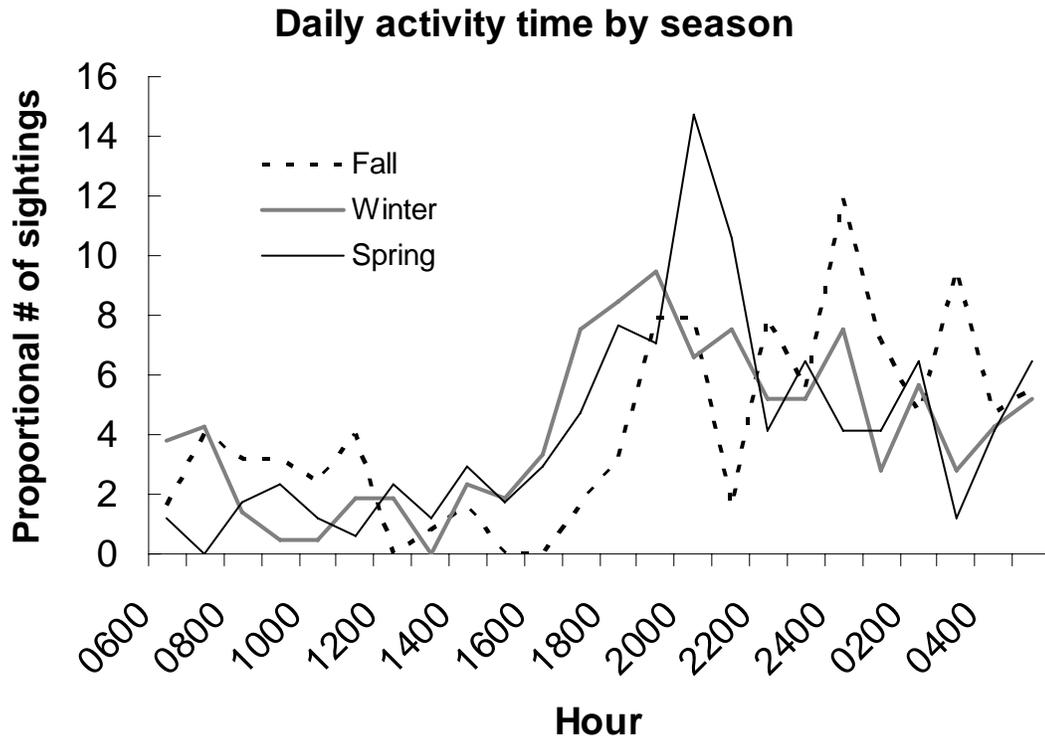


Figure 2. Activity time of feral pigs at Fort Benning, Georgia, 2004-2005 by season: fall = mid August – mid November, winter = mid November – mid February, spring = mid-February – May. To compare the number of sightings in each season, I computed a proportional number of sightings for each hour by dividing the number of sightings during that hour by the total number of sightings during that season.