

Effect of experimental manipulation on survival and recruitment of feral pigs

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Abstract. Lethal removal is commonly used to reduce the density of invasive-species populations, presuming it reduces population growth rate; the actual effect of lethal removal on the vital rates contributing to population growth, however, is rarely tested. We implemented a manipulative experiment of feral pig (*Sus scrofa*) populations at Fort Benning, Georgia, USA, to assess the demographic effects of harvest intensity. Using mark–recapture data, we estimated annual survival, recruitment, and population growth rates of populations in a moderately harvested area and a heavily harvested area for 2004–06. Population growth rates did not differ between the populations. The top-ranked model for survival included a harvest intensity effect; model-averaged survival was lower for the heavily harvested population than for the moderately harvested population. Increased immigration and reproduction likely compensated for the increased mortality in the heavily harvested population. We conclude that compensatory responses in feral pig recruitment can limit the success of lethal control efforts.

Introduction

Many invasive species displace native wildlife, disrupt ecosystem function and cause economic losses (Huxel 1999; Pimentel *et al.* 2001). To reduce impacts of invasive species, lethal control is often used on the basis of the assumption that it will decrease population growth of the invasive species, and thereby their density and their negative effects. The effects of lethal removal on the vital rates contributing to the growth of invasive populations (i.e. survival and recruitment), however, are rarely tested; thus, the efficacy of lethal removal as a tool for managing invasive species is often uncertain. Feral pigs (*Sus scrofa*) are an invasive species considered an economic and environmental pest because they compete with native wildlife for food resources (Dickson *et al.* 2001), disturb soil and vegetation while rooting for food (Hone 2002), prey on livestock (Choquenot *et al.* 1997), and reduce species richness in plant communities (Kotaniemi 1995). Lethal control is commonly used in attempts to reduce population density and thus detrimental effects of feral pigs (Hone and Pedersen 1980; Katahira *et al.* 1993; Choquenot *et al.* 1999; Cowled *et al.* 2006). The effects of lethal control on populations of feral pigs, however, are poorly understood; little is known about the extent to which increased mortality influences the survival and reproductive rates contributing to population growth (λ). Levels of lethal control that do not substantively lower survival, or for

which feral pigs have the capacity to increase reproduction compensatorily, will ultimately be unsuccessful in reducing population density or the negative effects of feral pigs on native ecosystems.

Survival and recruitment rates can be estimated accurately by mark–recapture methods, which incorporate detection probabilities (Williams *et al.* 2002). The few studies that have estimated annual survival rates for feral pigs used only age-structure data or radio-telemetry of a small number of individuals (Saunders 1993; Gabor *et al.* 1999), resulting in estimates with uncertain accuracy or poor precision. No studies have documented recruitment (i.e. the rate at which individuals are added to the population through births and immigration) of feral pigs; however, data on fecundity (i.e. litter size or number of young produced per female per year) are abundant. The reproductive capacity of feral pigs is prodigious; adult females can breed up to three times in a 14-month period (Dzieciolowski *et al.* 1992), producing ~5–7 piglets per litter (Taylor *et al.* 1998). This reproductive potential makes a compensatory response to increased mortality highly feasible for feral pigs. No studies have estimated emigration or immigration rates for feral pigs, which also affect density and λ .

The objectives of our research were to acquire accurate estimates of vital rates for a population of feral pigs and to determine the demographic effects of an increased level of

mortality. To accomplish these goals, we compared estimates of apparent survival rates (i.e. survival and emigration), recruitment rates (i.e. reproduction and immigration) and λ between populations of feral pigs inhabiting areas with high and moderate intensities of lethal control on Fort Benning, Georgia, USA. We hypothesised that high-intensity lethal control would reduce survival; however, compensation in recruitment would result in comparable λ s between the heavily harvested and moderately harvested populations.

Materials and methods

Study area

This research was conducted between April 2004 and August 2006 at the Fort Benning Military Reservation in west-central Georgia, USA (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 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 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 riparian bottomlands consist of yellow poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), hickory (*Carya* spp.) and oak species (King *et al.* 1998). Hunting of feral pigs by off-duty military personnel occurred year-round across Fort Benning.

Experimental design

We compared annual apparent survival rates, recruitment rates and λ between a moderately harvested population (hunting only) and a heavily harvested population (lethal control plus hunting). The study areas were randomly assigned a treatment. Lethal

control consisted of intensive lethal trapping and shooting, on top of year-round hunting pressure, in the heavily harvested area from August 2004 through May 2006. Hunting pressure was comparable between study areas. These populations occupied separate 50-km² study areas, located ~8 km apart and separated by a large creek (Fig. 1). Study areas were ~15 times larger than the mean home-range size of female pigs on Fort Benning (Sparklin *et al.* in press). We estimated vital rates from summer 2004 to summer 2006 of feral pigs in both populations.

Trapping and handling

We conducted capture–mark–recapture sessions during the same 18-day trapping sessions each summer in 2004, 2005 and 2006. We used box traps made from 1-inch angle iron and cattle panels, with spring-activated doors capable of catching multiple pigs placed at 20 riparian trap locations spaced 1–2 km apart across each of the two study areas. We prebaited traps with corn for 2 weeks before each trapping session. We checked traps each morning of each trapping session.

We tagged all captured pigs with uniquely numbered ear tags in both ears, with different-coloured tags (National Band and Tag, Newport, KY) indicating different study areas. Males and juvenile females were handled in a chute by using a mouth snare. We measured head and body length to estimate age (Boreham 1981). We recorded sex and estimated weight. We used Telazol (Fort Dodge Animal Health, Fort Dodge, IA; 1 cc per 30 kg) to sedate adult females and attach a mortality-sensing G2000 Large Mammal 12-channel Garmin receiver GPS/VHF collar (Advanced Telemetry Systems, Isanti, MN). We monitored GPS-collared feral pigs via ground-based 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).



Fig. 1. Fort Benning military installation, showing trap locations in both the moderately harvested and heavily harvested study areas.

Camera recapture

We used digital game cameras (infrared Digital-Scout 3.2 megapixel; Penn's Woods, Export, PA) to resight ear-tagged feral pigs passively in both study areas between August 2004 and May 2006. We baited 15 cameras with corn and moved them among evenly spaced sampling sites every 3 weeks during three 12-week sampling periods to fully sample the study areas several times. We set cameras with a 2-min delay to acquire multiple photographs of feral pigs to assist with identification.

Survival

We included recaptures from trapping, 'resightings' of collared feral pigs via radio-telemetry, camera sightings and hunter returns of ear tags to estimate apparent survival (ϕ), which includes survival and emigration. We considered pigs less than 12 months old to be juveniles. Because feral pigs less than 1 month old were too small to be caught in our traps, estimates of juvenile survival included only feral pigs 1–12 months old. We used the Barker model in Program MARK to estimate apparent survival (Barker 1997; White and Burnham 1999), which allows a population to be open to changes in births, deaths, emigration and immigration. We simplified models by holding capture probability (p), probability the animal is resighted and then dies within the interval (R'), probability of fidelity to study area (F), and probability of temporary emigration from study area (F') constant across time and space. Because the small size of the dataset prevented us from estimating movement parameters, we assumed random emigration by constraining $F = F' = 1$, where F is the probability an individual remains in the study area. We modelled resight probability (R) by time and presence of a GPS collar. We modelled survival by harvest intensity, season, year and using individual covariates including sex, age, estimated weight and presence of a GPS collar.

We used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to rank models (Akaike 1973; Burnham and Anderson 2002). We used a global model to run a goodness-of-fit test to evaluate overdispersion in our data. We assessed goodness-of-fit by using a median \hat{c} test available in Program MARK, where $\hat{c} = 1$ indicates that data are not overdispersed and $\hat{c} > 1$ indicates a lack of fit between the model and the data; $\hat{c} \leq 3$ generally indicates that the model adequately fits the data (White and Cooch 2005).

Recruitment

We estimated fecundity by calculating average litter size in reproductive tracts collected from experimentally harvested feral pigs and by estimating number of litters per year. Feral pigs were harvested from inside and outside the heavily harvested area (i.e. the remaining area on Fort Benning besides the moderately harvested area). We divided pregnant sows into two groups, juveniles (≤ 1 year old) and adults (> 1 year old), to examine litter size on the basis of age. By the method of Green and Evans (1940), we estimated the proportion of juveniles breeding and the average number of litters per adult female per year. Average number of litters per year equals the sum of the proportion of pregnant females during each season multiplied by the number of days in the season and finally divided by the number of days during the pregnancy that embryos are visible. To

estimate the total number of juveniles and to account for the low probability of catching juveniles < 1 month old, we divided the number of juveniles harvested in older age classes by the average monthly juvenile survival rate to estimate the number of juveniles < 1 month old available, but not harvested.

We estimated annual recruitment, the number of individuals added to the trappable population per capita per year, using population growth rates acquired from density estimates and estimated annual survival rates during the 2-year period. Population growth consists of apparent survival and recruitment, so that the estimates of any two demographic rates can be used to calculate the third. We used matrix models with juvenile and adult female survival rates and known population growth rates for both the moderately and heavily harvested populations to estimate recruitment rates. Specifically, estimated annual survival rates were entered into a 2×2 matrix by using Microsoft Excel then recruitment values were entered into the same matrix until they produced our estimated population growth rates. We assumed that juveniles and adults had equal recruitment rates.

Population growth rate

We used Chao's moment estimator in Program CAPTURE to estimate the abundance, based on detection probabilities, of the moderately and heavily harvested populations for each closed mark-recapture summer trapping session (Chao 1988). We calculated density (pigs km^{-2}) by dividing abundance estimates by the size of the sampling area. We calculated average annual population growth rates from summers 2004–06 by taking the square root of the density from the last year divided by the square root of the density from the first year (Williams *et al.* 2002).

Results

Trapping, camera recaptures and removal

During the three summer mark-recapture sessions, we caught 310 individuals 600 times during 2160 trap-nights. During 18 months of camera trapping and > 5000 photographs of pigs, we resighted 39 and 17 ear-tagged pigs, in the moderately and heavily harvested areas respectively. Between August 2004 and May 2006, 182 feral pigs were killed via lethal trapping and shooting in the heavily harvested area. Of the 182 pigs killed, 51% were male, 49% females, 65% less than 1 year old and 35% adult. Using hunter-returned ear tags, hunting success was found to be slightly higher in the moderately harvested area (26% hunting mortality of ear-tagged pigs) than in the heavily harvested area (19% hunting mortality of ear-tagged pigs). Our lethal manipulation resulted in a total of 46% of ear-tagged pigs being killed by both hunters and lethal control in the heavily harvested area, whereas a total of 26% of ear-tagged pigs was killed in the moderately harvested area.

No feral pigs from the moderately harvested area were ever recaptured, resighted or reported dead in the heavily harvested area, or vice versa, supporting our assumption about independence of the populations.

Survival

During the summers of 2004 and 2005, 90 and 89 feral pigs were ear-tagged respectively. Between August 2004 and May 2006, 30% were resighted in digital game camera photographs, 8%

were resighted via radio-telemetry only and 37% were reported killed by hunters. The goodness-of-fit test indicated slight overdispersion in the data, with a $\hat{c} = 1.72$.

The top-ranked model, which included a harvest intensity effect, produced a lower survival rate for the heavily harvested population than for the moderately harvested population (Table 1). Survival was higher for females than for males and higher for adults than for juveniles on the basis of other high-ranked models (Table 2). We used model averaging (Burnham and Anderson 2002) to estimate annual survival rates of 0.28 (95% CI: 0.22, 0.33) and 0.15 (95% CI: 0.09, 0.22) for the moderately and heavily harvested populations respectively. The covariates of weight and year were found in models, with a $\Delta\text{QAIC}_c < 2$ indicating that these covariates may have influenced survival (Table 1).

Recruitment

Of 63 reproductive tracts collected from females, 35 had visible fetuses. Average litter size for juveniles (≤ 1 year old) of 4.80 (95% CI: 4.25, 5.35) was lower than that of 6.40 (95% CI: 5.60, 7.20) for adults (> 1 year old), whereas there was no difference in litter size between females collected inside and those collected outside of the heavily harvested area. Adult females had an average of 2.28 and 2.90 litters per year in the moderately and heavily harvested areas respectively. On average, 75.0% of juveniles bred. Our sample size of 16 did not allow us to estimate proportion of juveniles reproducing separately in moderately and heavily harvested areas. Juveniles produced 1.8 (95% CI: 1.6, 2.0) female young per year. Adults produced 7.3 (95% CI: 6.4, 8.2) and 9.3 (95% CI: 8.1, 10.4) female young per year in the moderately and heavily harvested areas respectively.

Annual recruitment, the number of individuals added to the trappable population per capita per year, of 3.00 (95% CI: 2.23, 4.26) was lower in the moderately harvested population than was that of 6.38 (95% CI: 3.70, 16.85) in the heavily harvested population.

Population growth rate

We estimated density for the moderately harvested population as 1.79 (95% CI: 1.27, 3.46), 2.45 (95% CI: 1.52, 5.68) and 2.74

(95% CI: 1.85, 4.52) pigs km^{-2} for 2004, 2005 and 2006 respectively. We estimated the density for the heavily harvested population as 1.07 (95% CI: 0.80, 2.34), 1.26 (95% CI: 0.87, 2.69) and 1.61 (95% CI: 1.16, 2.81) pigs km^{-2} for 2004, 2005 and 2006 respectively. Density estimates increased between 2004 and 2006, resulting in mean annual λ of 1.24 and 1.23 in the moderately and heavily harvested populations respectively.

Discussion

Our study is the first to examine effects of an experimental manipulation on annual survival and recruitment of feral pig populations. Assuming our lethal removals were the only substantive difference in mortality between our 50- km^2 study areas, our removals reduced annual survival by $> 40\%$ for both age classes and sexes, almost doubling mortality resulting from hunting alone. The nearly equal population growth rates in the moderately and heavily harvested populations indicate that as annual survival was reduced, recruitment rates (which included both reproduction and immigration) increased in the population with high harvest intensity. Although the density estimates were likely to be biased low because of low capture probabilities and individual heterogeneity (Hanson *et al.* 2008), the estimates of population growth rates should not be biased because the magnitude of bias in density should have been similar each year across the study areas.

Annual survival rates were lower than for other reported feral pig populations, even when only survival rates of pigs in the population with moderate harvest intensity are considered. Gabor *et al.* (1999) reported average annual female survival of 0.56 ± 0.17 for a southern Texas population where most of the mortality was anthropogenic. Hunter harvest reported by Gabor *et al.* (1999), however, was 77% lower than on Fort Benning, which could explain the considerably lower survival rates we observed (28% and 15% for the moderately and heavily harvested areas respectively).

Survival differed by both age and sex; juvenile and adult females had survival rates higher than those of males, and juveniles had lower survival rates than adults. Across sexually dimorphic mammal species, females often have higher survivorship than males (Jeziarski 1977; Gaillard *et al.* 2000), possibly explained by male mortality related to sexual selection

Table 1. Model selection results for survival (ϕ) of feral pigs at Fort Benning, Georgia, 2004–2006

Models are ranked in an ascending order by Akaike's Information Criterion, adjusted for overdispersion and small sample size (QAIC_c). Only models with $\text{QAIC}_c \leq 2$ are shown. Survival was modelled by a harvest intensity, year, season, sex, juvenile v. adult (age), estimated weight at capture (weight), and the presence of a GPS collar (collar)

Model	QAIC_c^A	ΔQAIC_c	QAIC_c weight	K^B	Deviance	Evidence ratio ^C
ϕ harvest intensity + season	599.71	0.00	0.20	10	575.17	1.00
ϕ harvest intensity + season + year	600.28	0.56	0.15	11	575.09	1.32
ϕ harvest intensity + season + sex	600.37	0.66	0.15	11	573.63	1.39
ϕ harvest intensity + sex + weight	601.25	1.54	0.09	12	573.22	2.16
ϕ harvest intensity + season + sex + age	601.26	1.55	0.09	12	573.23	2.17
ϕ season	601.66	1.95	0.08	9	579.31	2.65

^AAkaike's Information Criterion corrected for overdispersion and small sample size.

^BNumber of parameters.

^CLikelihood of the top-ranked model v. the competing model (e.g. the top model is 1.32 times more likely to be the model that best approximates truth than the second ranked model).

Table 2. Annual survival rates (s.e.) of juvenile female, adult female, juvenile male and adult male feral pigs at Fort Benning, Georgia, 2004–2006

Annual survival rates were estimated for the moderately harvested and heavily harvested populations by using averaging of models with and without harvest intensity effect

	Heavily harvested	Moderately harvested
Juvenile female	0.160 (0.042)	0.296 (0.035)
Adult female	0.205 (0.038)	0.354 (0.031)
Juvenile male	0.083 (0.045)	0.179 (0.042)
Adult male	0.113 (0.042)	0.227 (0.038)

(Gaillard *et al.* 2000) or a larger body size requiring higher food availability (Massei *et al.* 1997). The large home ranges of males (Saunders and McLeod 1999) may also make them more vulnerable to hunters. Because we estimated apparent survival (i.e. combined effects of survival and emigration), disproportionate emigration of males from our study areas could have biased our survival estimates for males. Juvenile males often disperse or emigrate from their natal area whereas females tend to remain (Greenwood 1980; Kaminski *et al.* 2005). If emigration of juvenile males from our study areas strongly influenced our estimates of apparent survival rates, we would expect survival between juvenile males and females to differ more than that between adult males and females with established home ranges. The negligible difference we observed between survival of juvenile males and females compared with that between adult males and females lends little support to the hypothesis that male emigration influenced our estimates of male survival rates.

Although we showed that lethal control is an effective method of reducing feral pig survival rates at Fort Benning, recruitment must also be considered when examining the effect of increased mortality on population growth. As we hypothesised, λ did not differ between the moderately and heavily harvested populations; per capita recruitment in the heavily harvested population was more than twice what we observed in the moderately harvested population, suggesting strong compensation. Because our estimates of recruitment combined reproduction with immigration, we could not discern whether compensation came from increased reproduction or increased immigration into the heavily harvested area. We found litter sizes did not differ between the heavily harvested and moderately harvested areas, but the number of litters produced annually by adult females differed by 22%, suggesting a compensatory reproductive response. We hypothesise, however, that this response was insufficient to compensate fully for differences in mortality we observed between the moderately harvested and heavily harvested populations and thus immigration is likely to have played a larger role in the population growth within the heavily harvested area.

Whereas lack of replication of treatments limits the generality of our inferences, our results support the conclusion that high-intensity harvest during a short period of time lowered survival rates on Fort Benning. Compensatory reproduction and immigration, however, ultimately resulted in little change in population growth. Stronger effects of lethal control than what we observed would require increasing the duration and intensity of lethal control and preventing the recolonisation by immigrants. Choquenot *et al.* (1997) and Choquenot (1998) successfully

reduced feral pig density through annual intensive short-term aerial shooting and documented a reduction in lamb predation (Choquenot *et al.* 1997). Other lethal control efforts have successfully reduced feral pig density by multiple intensive methods such as aerial shooting, poisoning and trapping over short periods of time (Saunders and Bryant 1988; Choquenot *et al.* 1990; Spencer *et al.* 2005). By comparison, our control effort, using traps and ground shooting, appears to be less effective than methods such as aerial shooting and poisoning, which can be used to remove many pigs in a short amount of time. However, if intensive efforts do not remain continuous or do not result in eradication, the density-dependent capacity of feral pig populations to grow rapidly through reproduction and immigration will result in quick recovery to pre-removal density (e.g. Saunders *et al.* 1990). Eradications of feral pigs have been successful only in demographically isolated locations where either removal was conducted over long periods of time, such as the 30-year removal on a Galapagos island (Cruz *et al.* 2005), or conducted within a very limited area, such as the 186 pigs removed on the 15-km² Lord Howe Island (Miller and Mullette 1985), or where the capacity of pigs to recolonise was limited through fencing (Hone and Atkinson 1983; Hone and Stone 1989; Katahira *et al.* 1993; Schuyler *et al.* 2002).

Methods proven effective at reducing densities of feral pigs are often unavailable to managers in the United States. For example, aerial shooting is expensive and unlikely to be effective where pigs inhabit heavily forested systems, and poisoning is likely to inflict unacceptable mortality on non-target species that also inhabit landscapes occupied by feral pigs (e.g. white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*)). Many managers in the United States must therefore rely on shooting and trapping to reduce pig densities. Low annual survival rates of feral pigs in the moderately harvested population on Fort Benning brought about by hunting meant that lowering survival rates further would be difficult to achieve by such removal techniques. Our lethal control effort produced only an average of one pig removed per day through trapping. Per-pig effort and cost of lethally removing individuals may thus be higher for populations with low survival than for those with high survival. Our research suggests that the most commonly used management techniques for controlling feral pig populations in the United States may have limited success for reducing pig densities or damage because density-dependent increases in reproduction and immigration can easily outpace typical rates of removal, especially when the managed area is not fenced off or large enough to provide a buffer to immigration. Further, effectiveness of these techniques is likely to diminish strongly as pig densities and survival are reduced to low levels, suggesting they are unlikely to result in eradication. Survival can be manipulated to reduce feral pig density and indirectly reduce their ecological and economical impacts (Choquenot 1998; Choquenot *et al.* 1999; Cowled *et al.* 2006); however, control efforts must be intensive and on-going to continue reducing the impacts caused by feral pigs.

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