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2019

Feral swine harming insular sea turtle reproduction: The origin, impacts, behavior and elimination of an invasive species

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Engeman, Richard M.; Byrd, Robert W.; Dozier, Jamie; McAlister, Mark A.; Edens, James O.; Kierepka, Elizabeth M.; Smyser, Timothy J.; and Myers, Noel, "Feral swine harming insular sea turtle reproduction: The origin, impacts, behavior and elimination of an invasive species" (2019). *USDA National Wildlife Research Center - Staff Publications*. 2260.
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Acta Oecologica 99 (2019) 103442

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Feral swine harming insular sea turtle reproduction: The origin, impacts, behavior and elimination of an invasive species

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ARTICLE INFO

Keywords:
Endangered species
Invasive species
Island eradication
Loggerhead turtle
North island
South Carolina
Wild pig
Wild boar

ABSTRACT

Feral swine are among the world's most destructive invasive species wherever they are found, with translocations figuring prominently in their range expansions. In contrast, sea turtles are beloved species that are listed as threatened or endangered throughout the world and are the focus of intense conservation efforts. Nest predation by feral swine severely harms sea turtle reproduction in many locations around the world. Here we quantify and economically assess feral swine nest predation at North Island, South Carolina, an important loggerhead sea turtle nesting beach. Feral swine depredation of North Island sea turtle nests was first detected in 2005, with annual nest monitoring initiated in 2010 documenting nearly total losses to feral swine in 2010 and 2011. The cumulative valuation of annual losses for North Island from 2010 to 2016 ranged as high as $1,166,500. To improve nesting success, an integrated approach for eliminating feral swine was implemented in 2010 and greatly intensified in 2013 by adding federal experts. Removal efforts were challenging due to the island's remoteness and impenetrable habitats, weather, hazards in accessing the island, and wariness of the animals, especially as their population diminished. Removal of the final 11 swine required efforts from 2014 to 2016. Nest predation was highly variable and provided another example of the significance of conditioning by feral swine to sea turtle nests on the consequent severity of nest predation. Even the final individual inflicted heavy losses before his removal. Genetic analyses of feral swine removed from North Island and the adjacent mainland revealed that the island's population did not originate from the nearby mainland, meaning they were (illegally) introduced to the island.

1. Introduction

The severity of threat posed to native biodiversity by invasive species is exceeded only by human-caused habitat destruction (Parker et al., 1999; Wilcove et al., 1998). In fact, invasive species have played a role in the listing of 42% of the species protected by the USA's Endangered Species Act (Stein and Flack, 1996). Notably, alien predator species tend to be more dangerous than native predators to prey populations (Salo et al., 2007), which is especially concerning because many endangered species worldwide are threatened by predation (Hecht and Nickerson, 1999). In particular, feral swine (*Sus scrofa*) are especially injurious invasive animals that imperil and hinder the recovery of many threatened and endangered wildlife species around the world and also have been implicated in a variety of wildlife extinctions (e.g., Doherty et al., 2016; Seward et al., 2004; USDA, 2016b).

Feral swine are among the world's most destructive invasive species wherever they are found, and, as such, the species has well-earned its inclusion as one of the 100 "World's Worst" invaders by the IUCN Invasive Species Specialist Group (Lowe et al., 2004). This species is globally infamous for damaging native plant species, animal species, habitats, and ecosystem processes, as well as archaeological sites (Choquenot et al., 1996; Engeman et al., 2007, 2013a, 2017; Seward et al., 2004; Singer et al., 1984; USDA, 1999; 2015, 2016a). Rapid range expansion in the USA over the past 30 years has been driven in part by natural population growth, with feral swine possessing the greatest reproductive potential of all large wild mammals in North America and possibly the world (Bieber and Ruf, 2005; West et al., 2009). In addition to their reproductive potential, range expansion occurs when new

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https://doi.org/10.1016/j.actao.2019.103442
Received 12 December 2018; Received in revised form 3 June 2019; Accepted 18 June 2019

populations establish through illegal translocation and release of feral swine (e.g., Tabak et al., 2017; Hernandez et al., 2018; USDA, 2015; Waithman et al., 1999).

One globally widespread conflict between feral swine and imperiled native biota arises from their harmful impacts on sea turtle reproduction through nest predation (e.g., Bhaskar, 1985; Nel, 2012; Richardson, 1990; Stancyk, 1995; Suganuma, 2005; Whytlaw et al., 2013; Zahl, 1973). Sea turtles, in contrast to feral swine, are beloved species that are listed as threatened or endangered throughout the world and are the focus of intense conservation efforts. As on other continents, sea turtle nesting beaches in the southeastern USA can suffer extensive losses of nests to feral swine (Engeman et al., 2010, 2016; NMFS & USFWS, 2008), although published assessments on the extent of nest predation losses to feral swine and corresponding benefits from swine removal at beaches in the USA are limited (Engeman et al., 2016). All sea turtle species are federally protected in the USA under the Endangered Species Act of 1973 as threatened or endangered (U.S. Fish and Wildlife Service, 1994), making successful reproduction of vital importance for recovery and ultimate delisting of the species.

Here, we quantify and economically assess losses from feral swine nest predation at North Island, South Carolina, an important loggerhead sea turtle (*Caretta caretta*) nesting beach. We also describe the challenges in detecting, locating, and removing feral swine from this relatively pristine island during a multiyear, interagency cooperative effort to fully eliminate them from the island. We also examine the role of conditioning by feral swine to sea turtle nests on the consequent severity of nest predation. Finally, we examine the role of feral swine translocation in creating the problem by presenting genetic evidence on how feral swine arrived on the island.

2. Methods

2.1. North Island

North Island is one of four islands comprising the Tom Yawkey Wildlife Center (Yawkey Center for short), Georgetown County, South Carolina, which is managed by the South Carolina Division of Natural Resources (SCDNR). North Island (33⁰15′02″ N, 079⁰11′20″ W) is an ~1800 ha sand island bordered on the north by North Inlet and south by Winyah Bay. North Island is designated as a barrier island wilderness area that can only be accessed by boat. Due to sometimes treacherous currents and wind patterns, the island often is logistically challenging (nearly impossible) to safely access. North Island's beach is 15 km long and comprises approximately 5% of sea turtle nesting in South Carolina. The island's habitats include beaches, marsh, managed wetlands, upland pine forests, and maritime forests. This island has the largest sand dunes in South Carolina, resulting in a sharply undulating topography over much of the island. Moreover, much of the island is heavily forested, primarily with live oaks (*Quercus virginiana*). The dense vegetation conspired with the island's topography to make traversing the interior extremely difficult. The beach has been geographically stable for several hundred years (Wright, 2002) and has a dune field 100 m wide in some places. The beach provides valuable nesting habitat for loggerhead sea turtles, with an occasional green sea turtle nest (*Chelonia mydas*) being deposited in some years.

Feral swine depredation of sea turtle nests was first observed on North Island in 2005. However, these observations provided little precision as to when feral swine first arrived on the island as it may take feral swine several years of conditioning before they begin predating sea turtle nests (Engeman et al., 2016).

2.2. Turtle nest monitoring

The South Carolina Department of Natural Resources Marine Turtle Conservation Program is responsible for monitoring, managing, and protecting sea turtles in the state of South Carolina. Prior to 2010, nest surveys on North Island had not been conducted systematically due to the difficulty in reaching the nesting beach. In 2010 a 26 nest subset of all nests present was monitored as part of a pilot study. In the years thereafter, systematic surveys of all nests were conducted. Rather, the beach was monitored three times per week for nest deposition starting the first week in May and continuing until October 1. Two people would arrive by boat just after sunrise and travel the entire front beach on an all-terrain vehicle (ATV). Crawls from previous nights were observed and potential nest locations were probed to search for an egg chamber. Nests were numbered, marked with a small colored flag, and a GPS location recorded so they could be monitored for signs of predation or hatching at each visit.

Fig. 1. A feral swine on North Island, South Carolina in the act of predating a loggerhead sea turtle nest that had a predator guard installed. Despite the protective apparatus designed to deter mesopredators, the swine succeeded in destroying the eggs. (Photo courtesy R. Byrd).

During 2014, when a new nest was found, a 1 m × 1 m protective wire screen was fastened on top of the nest to help fend off mesopredators such as coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) while allowing sufficient room for hatchling turtles to emerge. However, cages and screens offer little protection against feral swine depredation (e.g., Engeman et al., 2016, Fig. 1), and nest screening was discontinued in 2015 and thereafter because feral swine conditioned to the screens for locating nests.

2.3. Estimating number and value of hatchlings lost to swine predation

2.3.1. Number of hatchlings lost

The number of hatchlings lost to feral swine predation each year can be estimated from data on the number of nests, average clutch size, emergence rate from successful nests, and predation rates by feral swine. These established calculations are summarized in the following equation (e.g., Engeman et al., 2003):

$$L = N \times P \times C \times E$$

where L = number of hatchlings predicted lost to predation each year, N = number of nests each year, P = predation rate by feral swine on nests each year, C = average clutch size each year, E = emergence rate each year (undamaged nests only). Note that N x P, above, estimates the number of nests damaged. However for circumstances where all nests are monitored for fate, the number damaged is observed rather than estimated from a sample allowing the equation to be rewritten simply as

$$L = D \times C \times E$$

where C and E are defined as above and D is the number of depredated nests. While the number of nests and the number predated each year were observed on North Island, the annual figures for mean clutch size and emergence rate for intact nests were obtained from monitoring data on nearby South Island, a readily accessible island where all nests were monitored and clutches measured each year.

2.3.2. Value of hatchlings lost

Conservation success is usually evaluated on the basis of resource improvement, but an economic perspective allows managers to fiscally assess the rewards for conservation actions (Engeman et al., 2002a, 2004a). The value of feral swine elimination from North Island required placing dollar values on the estimated numbers of hatchling sea turtles lost to predation each year. Among the practical and applied means for placing a societal value on a species are statutory civil financial penalties (Bodenchuk et al., 2002; Engeman et al., 2004), which have been successfully used for valuing a variety of rare species, game species, and other protected species (Bodenchuk et al., 2002; Engeman et al., 2002a, 2004; Sementelli et al., 2008; Shwiff et al., 2003, 2007; Smith et al., 2003, 2007).

Rare and endangered species are almost universally protected with civil penalties set forth legislatively, and more than likely, will have more than one value available from multiple enabling legislations (e.g., United States federal and individual state laws). In particular, there has been a successful history among various studies for using this approach to value sea turtle hatchlings lost to nest predation by various predator species in Florida (e.g., Engeman et al., 2002a, 2010, 2016, among others) and is the approach of choice here. The Florida studies applied a conservative monetary valuation of $USD100/hatchling (e.g., Engeman et al., 2002). The dilemma for the Florida studies was determining which of multiple applicable civil penalties (federal Endangered Species Act, Florida Statutes and Florida Administrative Code) to incorporate into valuing hatchling sea turtles. This was resolved by selecting the minimum civil penalty ($100) among the enabling legislations, thereby producing conservative analyses. We take the same approach for North Island, but South Carolina statutes differ from those of Florida (§ 50-15-30; § 50-15-80). While the same federal laws pertain, the South Carolina Statutes specify that unlawful take of endangered species “must be fined one thousand dollars.” Considering the well-established conservative precedent for sea turtle values in Florida, we decided to take a more conservative and comparable route and value South Carolina sea turtles no more than for Florida and maintained the $USD100/hatchling valuation.

2.4. Feral swine removal methods

Management activities to reduce nest depredation were specifically recommended in the revised U.S. recovery plan for the loggerhead turtle, recommending in particular that ecologically sound predator control programs be used to reduce the annual mammalian predation rate to < 10% of nests within each recovery unit (NMFS and USFWS, 2008). Feral swine depredation of sea turtle nests can be a particularly significant threat to egg/hatchling survivorship, especially because it often results in complete, or nearly complete, annihilation of the nests (e.g., Engeman et al., 2016).

Feral swine control on North Island was initially conducted by SCDNR/Yawkey Center staff, but was intensified in 2013 when a cooperative agreement between the Yawkey Center and the U.S. Department of Agriculture/Wildlife Services (WS), the Federal agency responsible for managing conflicts with wildlife (USDA/APHIS et al., 1997) was instituted to fully eliminate feral swine from the island. Initially, SCDNR staff maintained two traps on the island, baited with manually spread shelled corn, which was labor intensive due to requiring frequent monitoring of traps for captured swine and bait replenishment. WS staff built three additional traps, with all traps fitted (retrofitted in the cases of existing traps) with Jager Pro remote triggering systems that could be monitored and operated remotely. The traps were also equipped with automatic feeders to dispense bait at predetermined times and amounts. These technologies allowed trap monitoring from the mainland, thereby reducing the number of trips to the island.

Ten trail cameras besides those used for monitoring the five traps were placed on the island to locate swine, find potential trap sites, and track population trends. Cameras were checked and moved periodically to areas expected to have highest swine activity. Also, because tracking plots have proven very valuable for detecting feral swine and monitoring their population trends (e.g., Engeman et al., 2001, 2013b), we applied the method on North Island. Twenty plots were placed on potential pathways for feral swine travel such as game trails. Plots were cleared and smoothed and then “read” the following day for tracks. The process was repeated to acquire three consecutive days of observation. Plot measurements were the number of track intrusions into each plot each day (Engeman et al., 2001). These observations were intended to detect and indicate spatial distribution, as well as to index swine abundance (Engeman et al., 2001).

Efforts to remove feral swine are inexorably linked to methods to detect and locate them. As a population dwindles the low density of remaining individuals reduces the probability of detecting an animal and is exacerbated by the heightened wariness of surviving animals (e.g. Engeman et al., 2019). Besides trapping, a variety of other control methods were integrated for removing feral swine, including the use of aircraft, nighttime sharpshooting (including over simulated turtle nests), public hunts, and privately contracted hunters using dogs, with this latter method valuable for removing a large proportion of the final individuals. The methods to be applied during a particular year were selected based on which might be currently optimal for the dynamically changing circumstances over years.

In particular, aerial control from a helicopter, which requires a certified pilot and gunner and compliance with strict federal and state laws (USDA/APHIS, 2018), was applied in March 2013 in an attempt to accelerate removal of feral swine. Aerial control has been an efficient means to remove large numbers of feral swine in short periods of time in parts of the USA, especially in areas with high abundances (Bodenchuk, 2014; USDA/APHIS, 2018), but it is less efficient in complex landscapes and is best suited when foliage cover is minimal (Choquenot et al., 1996; USDA/APHIS, 2018), as in our late winter timeframe.

2.5. Genetic testing

2.5.1. Laboratory methods

Tissue samples were collected in 2014 and 2015 for genetic comparison between North Island (n = 6) and adjacent mainland (n = 53) populations. DNA was extracted from samples via Qiagen DNeasy blood and tissue kits (Qiagen Inc, Valencia, CA), and normalized to 20 ng/μL. DNA extracts were amplified at 16 microsatellite loci developed for domestic swine (FH1589, FH2148, S0002, S0090, Sw24, Sw240, Sw2021, Sw911, Sw936, Sw949; Rohrer et al., 1994, 1996; UMNp09, UMNp358, UMNp445; Krause et al., 2002; S0226; Zhang et al., 1995; S0228; Archibald et al., 1995; S0101; Ellegren et al., 1994). Polymerase chain reactions were conducted in 12 μL volumes with 20 ng of template DNA, 10× AmpliTaq Gold Buffer, 2.5 mM MgCl2 Buffer, 1× bovine serum albumin, 0.2 mM of each dNTP, 5 pmol of each primer, and 0.5 U Amplitaq Gold. A touchdown PCR protocol was used that consisted of an initial 5 min denaturation at 95 °C followed by 20 cycles of touchdown PCR (95 °C for 30 s, 65 °C for 30 s with a −0.5 °C drop each cycle, and extension at 72 °C for 30 s), then 20 cycles of standard denaturation (95 °C), annealing (55 °C), and extension (72 °C) for 30 s each, and concluded with a final extension at 72 °C for 5 min. Amplified products were analyzed on an ABI 3170 Genetic Analyzer, and alleles were scored in GeneMapper (Life Technologies, Grand Island, NY).

Quality control involved two steps. First, all rare alleles and 10 randomly selected individuals at each locus were re-amplified to check for genotyping errors. No mismatches were detected within any loci. Finally, the program MICROCHECKER (Van Oosterhout et al., 2004) was used to check for null alleles.

2.5.2. Structure analysis

Program STRUCTURE 2.4.2 (Pritchard et al., 2000) was used to investigate whether North Island individuals originated from the adjacent South Carolina mainland. If North Island was colonized by feral swine from the adjacent mainland, then they should be genetically similar (i.e., members of the same genetic cluster) to the mainland samples. STRUCTURE sorts individuals into genetic clusters (K) that minimizes deviations from random mating, and calculates the proportion of their ancestry that belongs to each cluster (q). Individuals were considered strongly assigned to a cluster if their $q > 0.80$. We tested $K = 1$ to 10 with 10 runs per K where each run consisted of 100,000 burn-in followed by 100,000 permutations.

The most likely K was selected based on the highest ΔK (Evanno et al., 2005), and then longer runs of 1,000,000 burn-in and 1,000,000 permutations at K, K + 1, and K-1 (10 runs per K) to calculate q for each individual. Program CLUMPP (Jakobsson and Rosenberg, 2007) was used to obtain an average q-value for each individual across the 10 runs. Individuals were then assigned to each putative cluster based on their q-values. Following assignment, the same procedure described above was performed again on each cluster iteratively until no more population substructure was found.

2.5.3. Genetic diversity and differentiation

Following the STRUCTURE analysis, genetic diversity and differentiation were examined to further assess whether the North Island feral swine originated from the nearby mainland. Genetic diversity metrics included observed and expected heterozygosities, allelic richness, and FIS, and were calculated for the mainland samples, North Island, and all inferred STRUCTURE clusters. Additionally, we evaluated the presence of private alleles among the North Island samples because, if the island was colonized from adjacent mainland South Carolina, then the island would not be expected to harbor unique genetic variation. We also quantified genetic differentiation (FST) between the mainland and North Island samples as well as between all inferred STRUCTURE clusters. All genetic diversity, differentiation metrics, and associated 95% confidence intervals for AR, FIS, and FST were calculated in the R package diveRsity (Keenan et al., 2013).

3. Results

3.1. Feral swine detection and removal

A barrier sand island presents the mental image of a fairly level, easy-to-traverse landscape. However, North Island's topography with its overlaying layer of nearly impenetrable habitat made the island interior very difficult to traverse by either ATV or foot. These physical characteristics coupled with the island's remoteness, weather, access hazards, and the wariness of the animals, especially as the population diminished, severely challenged the removal efforts. During 2011–2013, trapping was particularly successful at removing swine, (Table 1). Although stomach content analyses was not a research thrust, we conducted some opportunistic examinations of swine stomachs that unsurprisingly revealed sea turtle eggs among their contents (Fig. 2). Besides trapping, a variety of other methods were applied and integrated throughout the course of the removal process (Table 1), with methods applied according to which combination would most likely be effective for the circumstances at a particular time. Note in Table 1 that the different methods were not all applied in the same years and different methods resulted in much different takes of swine. We note that these data cannot provide a valid or useful general indication of relative efficacy. For example, from 2008 to 2013 trapping removed by far the most swine, but from 2013 to 2016 trapping removed no swine (Table 1). From 2014 to 2016, hunting with dogs was applied six times on the island and only resulted in the removal of 5 swine, but those 5 swine were nearly half of the 11 remaining on the island. Aerial hunting, which has a history of removing very many feral swine in a short period of time in many places (Bodenchuk, 2014; USDA/APHIS, 2018), was applied on North Island on March 4 and 5, 2013. On the first, day 1.5 h of searching by helicopter located 3 feral swine, only one of which was removed, but the 1.8 h helicopter flight the next day did not locate any swine. The dense oak canopy coupled with the wariness of the animals rendered detection difficult. By 2014 feral swine were generally difficult to locate. Trail cameras provided infrequent detections, but those that were obtained gave insight into where activity was occurring. No feral swine tracks were observed on the tracking plots at the first assessment occasion and we determined that this method did not fit well with our logistics and we did not use it thereafter. Three years, numerous visits to the island, and a host of methods were required to eliminate the final 11 animals (Table 1). While hunting with dogs removed almost half of these animals, the method also presented logistical challenges including transporting the dogs and hunters to and from the island, all during favorable water and weather conditions.

Table 1
The number of feral swine removed by method and year from North Island, South Carolina. The cumulative totals across methods should not be used to infer relative efficacy, because the combination methods used each year were those considered best suited for the general set of circumstances at that time.

Total Number of Feral Swine Removed by Method and Year

Year	Trapping	Public hunts	Sharp shooting	Hunting with dogs	Aerial hunting
2008	20	21	12		
2009	18	16	9		
2010	16	28	11		
2011	26	23	21		
2012	23	16	15		
2013	26	10	9		1
2014	0	2		4	
2015	0	1	2	1	
2016[a]	0	na	1[b]		
Totals	129	117	80	5	1

[a] Feral swine were eliminated from the island in 2016.
[b] This was the last feral swine on the island.

Fig. 2. Sea turtle eggs in the stomach of a feral swine removed from North Island, South Carolina. (Photo courtesy R. Byrd).

Contracting to bring dogs to the island created added expenses and this method was not always successful, as it was applied on the island 6 times resulting in the removal of 5 animals during 3 of the 6 occasions. The final swine were removed by sharpshooting, primarily at night, which added another layer of risk, discomfort, and logistical difficulties. The final individual was conditioned to predating sea turtle nests (see below) and was shot on the beach at night while attempting to predate a nest.

3.2. Sea turtle nest predation

The benefits of feral swine control, as well as the propensity of feral swine to condition to sea turtle nests were both evidenced in our data. A dramatic reduction in feral swine depredation on sea turtle nests was observed after the intensive trapping from 2011 to 2013. Prior to the intensified trapping, a short, two-week pilot survey in 2010 observed 25 of 26 sampled nests were destroyed by feral swine. In 2011, the first season when monitoring attempted to survey all nests and after trapping was initiated, 138 of 158 nests (87%) were destroyed by feral swine. This represents an estimated loss of 11,665 emerging hatchlings. Unfortunately, the new traps had been installed only shortly before nesting season making it impossible to remove more than just few feral swine prior to nesting season. However, in 2012 a dramatic reversal in nest predation was observed in this first full nesting season to be affected by the intensified trapping effort, as only 3 of 226 nests (1%) were destroyed by feral swine. The 2013 nesting season showed similar results with only 2 of 162 nests (1%) destroyed by feral swine (Table 2). These remarkable numbers were primarily attributable to the improved and intensified trapping on North Island.

In 2014 the feral swine nest predation rate dropped to zero, although up to 11 feral swine remained on the island (Tables 1 and 2). Even among the few remaining feral swine, animals acclimated to feeding on a bountiful, nutritious food source likely would have continued to do so in 2014, yet no nests were predated by swine. However, the importance of feral swine conditioning to sea turtle nests as a food source was seen in 2015 when at most only 5 swine remained on the island but over a third (75 nests) of the 222 nests were depredated by this small handful of feral swine (Tables 1 and 2). This represented an estimated loss of 4532 emerging hatchlings. Further, only s single boar remained on the island by 2016, yet this animal was obviously conditioned to predating nests and accounted for the destruction of eight nests and estimated losses of 605 emerging hatchlings (Tables 1 and 2). In fact, he was shot on the beach while attempting to predate a nest and had previously been lured to and consumed in a single night 10 simulated nests holding chicken eggs. Without removing this animal, many more hatchlings likely would have been prevented from emerging and reaching the ocean. Thus, the reductions in nest predation to 0%–1% followed by spikes in nest predation in 2015 and 2016 despite a severely reduced swine population is strong reinforcement about the importance of conditioning by feral swine to sea turtle nests as an important factor affecting predation levels. Of course, there were no nests lost to swine predation in 2017 due to their elimination in 2016.

3.3. Genetic testing

3.3.1. Structure analysis

The overall STRUCTURE analysis suggested that the most likely number of genetic clusters (K) that minimize deviations from random mating was $K = 3$ ($\Delta K = 52.0503$, likelihood $= -1777.930$), but high ΔK values were also observed for $K = 4$ ($\Delta K = 50.148$, likelihood $= -1719.777$) and $K = 5$ ($\Delta K = 40.762$, likelihood $= -1690.765$). Secondary peaks commonly exist when there is further substructure, and in the iterative runs, one cluster was further subdivided into two clusters ($\Delta K = 25.174$, likelihood $= -950.411$). Therefore, the most likely K based on the iterative runs was $K = 4$. Regardless of value of K selected for the organization of samples into 3, 4, or 5 genetic clusters, the North Island samples were always strongly assigned to a distinct cluster (all $q > 0.950$). In contrast, STRUCTURE revealed admixture among all three mainland clusters consistent with gene flow among the mainland groups.

3.3.2. Genetic diversity and differentiation

Estimates of genetic diversity were similar across North Island, the total mainland, and the mainland inferred clusters, despite differing sample sizes. Allelic richness ranged from 2.57 to 3.13 alleles/locus, with no significant differences among sampling locations. Heterozygote excesses were found in two clusters (North Island and Mainland Cluster 1), but this result likely stemmed from highly polymorphic loci with multiple rare alleles. MICROCHECKER also did not suggest the presence of null alleles. North Island exhibited 7 private alleles across 4 loci, which indicated North Island harbored unique genetic variation not found on the adjacent mainland.

FST values between North Island and all mainland groups were the highest among all pair-wise comparisons, ranging from 0.138 to 0.164. Mainland clusters had significantly lower FST values than North Island comparisons (FST = 0.048–0.070) according to 95% confidence intervals, but were not significantly different from each other. The lowest FST value, however, corresponded to the third and fourth clusters detected in the iterative run in STRUCTURE.

Table 2

Sea turtle nesting results for North Island, South Carolina. All nests were by loggerhead turtles except a single green turtle nest was deposited in 2014, 2015, and 2017. Also shown are the estimated numbers of hatchlings lost to nest predation by feral swine. Estimation of number of hatchlings lost to feral swine nest predation required annual data on mean clutch size and mean hatchling emergence rates. These data were not observed on North Island, but were collected from extensively monitored nests on neighboring South Island and were used for the calculations. Only a sample of 26 nests were surveyed on North Island in 2010. Therefore, the number of nests in 2010 could not be included in the calculation of the mean number of nests over years. Similarly, the total observed number and value for nests predated would be higher if all nests had been monitored in 2010.

year	North Island nesting results			South Island nesting parameters		North Island	
	# sea turtle nests	# nests swine-predated	% nests swine predated	Mean clutch size	Mean % emergence	Est # hatchlings observed lost to predation	Value of lost hatchlings
2010	26	25	96%	116	76	2204	$220,400
2011	158	138	87%	107	79	11665	$1,166,500
2012	226	3	1%	110	70	231	$23,100
2013	162	2	1%	114	74	169	$16,900
2014	91	0	0%	105	24	0	$0.00
2015	222	75	34%	114	53	4532	$453,200
2016	216	8	4%	108	70	605	$60,500
2017	240	0	0%	116	65	0	$0.00
Mean	188			113	64	**Total** = 19406	**Total** = $1,940,600

4. Discussion

> "Give me a pig! He looks you in the eye and treats you as an equal."
> — Winston S. Churchill

Being equal to the task of eliminating feral swine from North Island was a formidable challenge. Sea turtle nesting beaches around the world, both insular and mainland, suffer nest depredation by swine (e.g., Stancyk, 1995; Whytlaw et al., 2013; Yılmaz et al., 2015; Zárate et al., 2013). This project demonstrated the value of eliminating feral swine to promote the conservation of endangered species and that it is possible even in the difficult logistical and environmental circumstances like those on North Island. Feral swine are destructive invasive animals that threaten endangered species on many islands worldwide, prompting a number of insular eradication efforts (e.g., Clout and Russell, 2006; Cruz et al., 2005; Donlan and Wilcox, 2008; Engeman et al., 2010, 2016; Kessler, 2002; Parkes et al., 2010; Pitman et al., 2005; Schuyler et al., 2002; Towns et al., 2009), with each circumstance having its own set of challenges to successfully achieve complete elimination of feral swine, including island size, topography, weather, habitats, and human interference. As with feral swine management in many places in the world, the commitment to carry our effort to completion in the face of the associated challenges was essential, as all benefits would be quickly lost if a breeding pair remained, and, as our results demonstrated, even one individual could inflict substantial losses. There were a variety of takeaway points from this project that are globally germane to managing feral swine impacts to threatened and endangered species.

4.1. Predator management

Predator management is a valuable strategy for protecting many endangered species (e.g., Engeman et al., 2009), and it may be especially valuable when rare species are threatened by invasive predators, as they are generally more harmful to prey populations than native predators (Salo et al., 2007). Clearly, elimination of an invasive species that heavily predates sea turtle nests also eliminates that source of predation. Moreover, a variety of studies have shown that reducing populations of nest predator species, both invasive and native, at nesting beaches can dramatically improve sea turtle nesting success (e.g., Engeman et al., 2003, 2005, 2010, 2012). Conversely, a sharp increase in predation can result from removal of such predation management efforts (Engeman et al., 2006). A wide variety of species, both native and invasive have been documented to predate sea turtle nets (e.g., Stancyk, 1995), but feral swine have the destructive capacity to supersede the impacts of sympatric nest predator species at US beaches (e.g., Engeman et al., 2016). Bearing in mind the destructive potential of feral swine and their high reproductive capacity, it would be wholly realistic to expect a high proportion, if not all, sea turtle nests to be lost in future years had swine removal efforts been discontinued and their elimination from North Island not achieved. There is no minimal population size for feral swine that ensures tolerable nest predation levels. Even one animal can produce severe consequences.

The elimination of feral swine from North Island not only eliminated their predatory impacts, but it also made it more possible to reduce the impacts from other predator species. Nest screens alerted feral swine to nest locations as opposed to deterring nest predation. Similarly, Engeman et al. (2016) found that the use of large nest cages effectively prevented raccoon predation of sea turtle nests, but in no way prevented feral swine from predating nests. Abandoning the use of nest screens on North Island potentially made access to sea turtle nests easier for the other predator species, if feral swine did not destroy the nest first. However, with elimination of feral swine from North Island, nest screens are again an option for use without concern that they would alert feral swine to the nests, thereby providing greater methodological flexibility for protecting sea turtle nests from raccoons and coyotes.

4.2. The role of conditioning

A behavioral context that is becoming more apparent as a determinant of the severity of feral swine nest predation is their conditioning to sea turtle nests as an exploitable food resource. This was first reported by Engeman et al. (2016) and appeared to play an important role in the severity of damage to North Island nests. Conditioning is an important management consideration for protecting sea turtle nests from feral swine predation. It is possible for sea turtle nesting to take place for extended periods, even several years, in the presence of feral swine with little or no damage occurring (Engeman et al., 2016). This could lead to complacency about the severity of threat feral swine actually pose, especially since implementation of feral swine control would be a management expenditure that might not appear urgent. As we've seen here and has been previously reported (Engeman et al., 2016), once feral learn of the ample food source available in sea turtle nests, nearly complete annihilation of all nests is a possibility. Thus, it would be prudent to address the potential for swine predation even if it has not yet been taking place.

4.3. Numerical losses and their value

The estimated numbers of hatchlings lost resulted in eye-opening numbers, even after greatly reducing the swine population. Placing those losses in an economic context can be very useful for managers and administrators to justify expenditures for removing feral swine. During the course of our study, 19,406 hatchlings were estimated lost to predation, worth an estimated $1,940,600. Had the eradication not taken place, the economic figures would probably have to account for close to 100% of hatchlings lost, based on rates of loss observed in 2010 prior to the initiation of feral swine control efforts. Also, the total loss figure includes 2,204 lost in 2010 from only a small sample of 26 monitored nests with all but one of those nests depredated. We can project what predation losses might truly have been in 2010 by assuming an average number of nests were deposited (188) and the same mean clutch size (113) and emergence rate (76%) as South Island in 2010. Then the 96% predation rate we observed for the sample would translate into estimated losses of 15,524 hatchlings that would be valued at $1,552,400.

The control costs (2011 through 2016) for removing feral swine from North Island totaled $189,880, a relatively small fraction (9.7%) of the $1,940,600 estimated for the observed nest losses to feral swine. However, this large discrepancy between control costs and the value of hatchling losses is not particularly enlightening, as it does not begin to illustrate the true value of the benefits from the control effort to eliminate feral swine from the island. As long as feral swine remain absent from North Island, control costs for feral swine will be $0, and since reinvasion is not likely to occur naturally, hundreds of thousands of dollars of annual benefits would be accrued in the absence of feral swine predation of sea turtle nests.

Funding is finite for the recovery and conservation of rare and endangered species and must be carefully applied to maximize the positive impact on the protected species. Biologists understand the impacts of reproductive losses. Administrators and government decision makers understand money and budgets. Placing numerical losses in an economic perspective can provide non-biologist administrators and government officials a context with which they can relate and thereby understand the urgency for providing the resources necessary to address the problem.

4.4. Translocation

Beginning with their initial introduction to North America by Hernando de Soto in 1539, feral swine range expansion and establishment of new populations has been facilitated through their (often illegal) translocation and release (e.g., Belden and Frankenberger, 1977; Hernandez et al., 2018; Mayer and Brisbin, 2008; Tabak et al., 2017; USDA, 2015; Waithman et al., 1999). Our genetic results were clear cut. The feral swine from North Island were genetically distinct from the feral swine on the nearby mainland, indicating that the population on North Island was unlikely to have been established through natural migration. Considering the difficulty and potential danger in crossing from the mainland to the island (even at low tide), it was not surprising to find no evidence of gene flow from either the adjacent mainland populations to the island or from the island to the mainland. So, how did feral swine from a more distant origin than the nearby mainland make the difficult journey to North Island? Probably the same way we did, by boat. Unauthorized translocation of feral swine is illegal in South Carolina, and a large majority of other states, yet translocation is a common means by which new feral swine populations have been established in the U.S. (e.g., Tabak et al., 2017; Hernandez et al., 2018; USDA, 2015; Waithman et al., 1999). Moreover, it is noteworthy that swine from the island had reasonable levels of genetic diversity despite isolation, thus implying more than just a few individuals were introduced at the time of colonization. In all probability, feral swine will be unlikely to reinvade North Island without (illegal) human introduction.

4.5. *Mitigating other sources of losses*

Considering a broader perspective, recent research has indicated that reducing predation to sea turtle and shorebird nests can help counter fisheries bycatch losses (Donlan and Wilcox, 2008; Wilcox and Donlan, 2007). The same logic would seem to apply for offsetting other sources of losses at sea, such as from oil spills. Notably, predator management of feral swine, whether controlling a mainland population at a nesting beach or eliminating feral swine from an island, is a straight-forward, conservation approach potentially allowing thousands more sea turtle hatchlings to enter the ocean each year in many parts of the world.

Acknowledgements

This research was supported by the intramural research program of the U.S. Department of Agriculture; South Carolina Department of Natural Resources; University of Georgia.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2019.103442.

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