ASSESSING THE ECOLOGICAL ROLES OF NINE-BANDED ARMADILLOS (*DASYPUS NOVEMCINCTUS*) ON GEORGIA'S BARRIER ISLANDS

by

ZACHARY P. BUTLER

(Under the Direction of Seth J. Wenger)

ABSTRACT

The nine-banded armadillo (*Dasypus novemcinctus*) has become a species of local abundance in many southeastern habitats and is viewed as a nuisance and invasive by many land managers. My objective was to examine both negative and positive effects of armadillos on the Georgia coastal islands by 1) quantifying armadillo predation of sea turtle nests and comparing it to other predators; and 2) quantifying behavior and activity of armadillo burrow associates. I found that while armadillos do indeed predate sea turtle nests, they are not a major contributor to total egg loss across the coast. I recorded 33 armadillo burrow associates, including 26 species not previously reported in the literature and multiple species of conservation concern. This research provides a data-driven basis for management of armadillos and provides a template for objectively evaluating the ecosystem effects of other "invasive" species.

INDEX WORDS: nine-banded armadillo, *Dasypus novemcinctus*, loggerhead sea turtle, *Caretta caretta*, egg predation, predator management, camera trapping, burrow use, activity, maritime forest, beach complex, hispid cotton rat, *Sigmodon hispidus*, barrier islands, Georgia coast

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DEDICATION

I would first and foremost like to dedicate this work to John Spencer and the Spencer family. Without the support of the Spencer Fellowship I would not have gotten the opportunity to pursue a graduate degree, and for that I will be forever thankful. I am humbled and honored to be the 2nd Spencer Fellow and hope that his friends and family can be proud of the ecological work I've completed as part of this fellowship. I cannot begin to describe how grateful I am that this opportunity will continue to be available for future ecology students in the years to come.

I would also like to dedicate this work to parents, Larry & Gail. You both have always been supportive of my life decisions even though you may not have agreed with them. You both have visited multiple field sites and seen multiple study animals firsthand, excited to share those experiences with your son. It is this kind of support that keeps me going and strive to be a better ecologist, educator, and person. I look forward to sharing my next adventure with you when ever that may be.

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CHAPTER 1

INTRODUCTION

Defining Invasive Species

The study of non-native species has become increasingly popular over the past decade, but research has focused almost exclusively on negative ecological impacts of non-native species. The benefits of non-natives remain a field in need of further research as conservationists look to help protect and preserve threatened ecosystems around the globe. Non-native species are defined as species that have been introduced beyond their historically native range as a direct or indirect result of human action (Jeschke et al. 2014). This is generally considered to be synonymous with the term “exotic” species. Invasive species are a subset of non-native species “whose introduction causes or is likely to cause economic or environmental harm or harm to human health” (National Invasive Species Council).

Although these terms are sometimes used interchangeably in the literature, it is important to distinguish that invasive species are generally identified specifically by the negative impact associated with their presence. This distinction has significant ramifications for how a specific organism is viewed and managed. Once a species is classified as invasive, most of the research conducted is limited to the perceived negative impacts of that species, while potential beneficial effects often go unstudied (Sagoff 2005). However, research is beginning to show that some non-native species facilitate the native species with which they co-occur (Rodriguez 2006, Schlaepfer et al. 2011).

Positive roles of non-native species can include providing habitat, refugia, and food for native species; serving as catalysts for restoration; functioning as ecosystem engineers; and providing various ecosystem services (Schlaepfer et al. 2011). Examples include invasive tamarisk (*Tamarix spp.*) providing nest habitat for the south western willow flycatcher (*Empidonax traillii extimus*; Stromberg et al. 2009), invasive zebra mussels (*Dreissena polymorpha*) filtering water and controlling cyanobacteria (Elliot 2008), non-native birds dispersing native plants seed in Hawaii (Foster & Robinson 2007), and non-native African honey bees (*Apis mellifera*) pollinating native plants in fragmented forest landscapes in Australia and Brazil (Dick 2001, Gross 2001). These examples demonstrate the need to account for both negative and positive effects when determining whether a species should be classified as merely non-native or as an invasive in need of management.

Nine-banded Armadillo (*Daypus novemcinctus*) Ecology

The nine-banded armadillo (*Dasypus novemcinctus*) is one of the most distinct mammals in the United States and the only representative from the order Cingulata that is currently established in North America. This species has the largest distribution of any cingulate, with a range extending from Kansas, USA to Uruguay (Feijó et al. 2020). The animal's range has expanded over the last several decades through both natural extension and translocation by humans, resulting in abundant populations throughout the southeastern United States (Taulman & Robbins 2014). The species has been classified as invasive in Georgia and Florida despite limited quantitative evidence of harm to humans or ecosystems (Georgia Invasive Species Strategy 2009, Center for Invasive Species & Ecosystem Health).

Nine-banded armadillos are suspected of preying on native species, such as terrestrial reptiles and amphibians, marine turtle nests, and ground-nesting birds (Kalmbach 1943, Layne 1997, Engeman et al. 2003, Staller et al. 2005). These are most likely incidental prey items, however, as several studies have documented that armadillos are primarily insectivores (Whitaker et al. 2012, Loughry & McDonough 2013). While there is direct evidence of armadillos predating species of concern (Douglas & Winegarner 1977, Engeman et al. 2003, Staller et al. 2005), it is not clear that armadillos represent a major negative impact (Degroote et al. 2013). The lack of information about the direct predatory effects of armadillos on native species suggests the need for further research before we can confirm it as an invasive with serious biological consequences.

As non-natives, armadillos additionally provide an important yet overlooked ecological function, as their fossorial behavior creates habitat in the form of burrows. Burrowing species are considered among some of the most important ecosystem engineers as the construction of their burrows provides shelter (Jackson 1989, Steen et al. 2010, Kinlaw & Grasmueck 2012) and foraging opportunities (Desbiez & Kluyber 2013, White & Tuberville 2017) for commensals, modifies nutrient cycling (Wesche et al. 2007, Gharajehdaghipour et al. 2016), and increases habitat heterogeneity (Cebellos et al. 1999, Davidson 2012). While there have been multiple species documented using armadillo burrows (Loughry & McDonough 2013), there have been limited attempts to quantify the extent to which commensal species utilize these burrows and for what purpose or function. The most extensive study on the commensal use of armadillo burrows since Clark (1951) was conducted by Platt et al. (2003), who documented seven commensal species occupying burrows in northern Belize, where armadillos are considered native. I hypothesize that armadillo burrows are also used by native species in areas where they are considered invasive.

Commensal foraging by multiple bird species with nine-banded armadillos has also been documented (Levey 1999, Di Giacomo & Di Giacomo 2006, Schaefer & Fagan 2006), but it is unknown if their burrows provide additional foraging resources as well. Given that native species could become reliant on armadillo burrows for multiple functions, drastic reductions in armadillo populations through invasive species management could be unwarranted as it could have detrimental effects to native species as well. Further information is needed in order to truly assess what types of ecological functions armadillos and their burrow are providing as well as what species are benefiting from the resources they provide.

Using Game Cameras to Monitor Burrows

Recently there has been an increase in the number of studies using game cameras to document the use and importance of burrows constructed by various semi-fossorial species. Prominent species include gopher tortoises (*Gopherus polyphemus*; Hipps 2019), greater bilbies (*Macrotis lagotis*; Dawson 2019), Indian crested porcupines (*Hystrix indica*; Mukherjee et al. 2019), pangolin (Ingram 2019), and giant armadillos (*Priodontes maximus*; Aya-Cuero et al. 2017). Camera-traps are effective in the monitoring elusive species, are considered one of the least intrusive methods of monitoring wildlife, and in recent years, have become considerably less expensive compared to other survey methods (O'Connell et al., 2011). Game cameras have been shown to be successful in quantifying burrow occupancy, faunal associations, mutual tolerance, seasonal variation in animal assemblage, and agonistic interactions between species (Aya-Cuero et al. 2017, Dawson et al. 2019, Mukherjee et al. 2019, Kondo 2018). While camera traps have proven to be efficacious in sampling small mammals (De Bonidi et al. 2010, Di Cerbo & Biancardi 2013), birds (O’Brien & Kinnaird 2008, Seki 2010), and squamates (Welbourne et al. 2017), they have yet to be used in any fashion to document any relevant ecological information about nine-banded armadillos.

Field Site: Little St. Simons Island

Little St. Simons Island (LSSI) (Figure 3.1) is a privately owned, minimally developed coastal barrier island in Glynn County, Georgia, USA (31.299°N, -81.328°W). LSSI is one of fourteen barrier islands off the Georgia coast and borders the Atlantic Ocean to the east, the Altamaha River to the north, and the Hampton River to the south and west, with no land connection. LSSI is one of the more unique and relatively natural barrier islands on the coast of Georgia and is one of the most significant natural areas remaining on the southeastern Coastal Plain of the United States. The island has not experienced the extent of farming, timber harvesting, or development that most others have, and has recently been placed in conservation easement in perpetuity. Currently, LSSI is managed by an ecological team that is supported by an eco-tourism operation with only a 32-guest capacity which minimizes human impacts. Approximately, four hectares of land support staff and guests while the rest of the island remains untouched and is only accessed by naturalists who take guests on tours through a network of primitive roads and firebreaks. Nine-banded armadillos arrived at the island in 1980. The absences of hunters and large predators, limited vehicle traffic, and favorable habitat and climatic conditions were likely all conducive to armadillo survival and population growth on the island.

Study Objectives

For the barrier islands of coastal Georgia, the nine-banded armadillo is considered an invasive species of concern, however island managers are unsure of how best to manage this species because there has been limited investigation into its effects on barrier island ecosystems.

Effective management requires at least a basic understanding of armadillo natural history, including the species' ecological niche in coastal systems and the ecological benefits and costs to species of local, state, regional, or national priority. On barrier islands, and Little Saint Simons Island (LSSI) specifically, priority species include, but are not limited to, ground nesting birds, sea turtles, eastern diamondback rattlesnakes, eastern kingsnakes, island glass lizards, and other egg-laying species found in beach, dunes, maritime grasslands, and maritime forest habitats.

My first objective was to analyze historical data collected on sea turtle and shorebird nest predations from multiple barrier islands. Specifically, I was interested in comparing sea turtle nest predations by predator across the Georgia barrier islands since 2009, when sea turtle monitoring first began on Little St. Simons Island. I hypothesized that over time and across islands, predation of sea turtle nest by armadillos was minimal compared to that of other predators such as raccoons, coyotes, and ghost crabs. This is because armadillos are known to be primarily insectivores and are not known to primarily inhabit beach and dunes habitats.

My second research objective was to determine if armadillo burrows benefit ecological communities through habitat enhancement and refugia creation. I hypothesized that armadillos served as ecosystem engineers that provided habitat for several native species through the creation of underground burrows. More specifically, I predicted that armadillo burrows provided thermal and foraging refugia, especially in areas where no other burrowing animal was present. My results will provide biologists and land managers with additional knowledge to inform management decisions about whether removal of armadillos is necessary to protect native species, or whether it could have negative consequences on native commensals.

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CHAPTER 2

PREDATION OF LOGGERHEAD SEA TURTLE EGGS ACROSS GEORGIA'S BARRIER ISLANDS[1]

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[1] Butler, Z.P., S.J. Wenger, J. B. Pfaller, M. G. Dodd, B. L. Ondich, S. Coleman, J. L. Gaskin, N. Hickey, K. Kitchens-Hayes, R. K. Vance, and K. L. Williams. Submitted to *Global Ecology and Conservation*.

Abstract

Nesting beach management is a vital element of the population recovery efforts for the vulnerable loggerhead sea turtle (*Caretta caretta*) across the globe. In the southeast United Sates, turtle nests are threatened by numerous anthropogenic and natural threats, including predation of eggs by native and non-native predators. We analyzed loggerhead nest predation and other egg loss using an exceptional 10-year data set (2009-2018) that covered nesting beaches on 12 islands on the Georgia coast. Our objectives were to 1) determine which predators cause the greatest loss of loggerhead sea turtle eggs, 2) evaluate whether non-native species have a higher rate of predation than native species, and 3) compare predation rates to other major sources of egg loss across these islands. Our results show that under current strategies for nest management: 1) non-native feral hogs and native raccoons have the greatest impact as predators on sea turtle eggs; 2) non-native predators have caused significantly more egg loss across Georgia's coast than native species, but the impact varies greatly by species; and 3) losses to predation are similar in magnitude to post-management losses from tides and storms over the last decade. We recommend the continued use of multiple management techniques, including nest screening and targeted predator management, but caution that predator controls should be focused on those demonstrated to cause significant losses in order to prioritize conservation funding.

Introduction

Loggerhead sea turtles (*Caretta caretta*) are one of the most studied and intensively managed species of sea turtle although they are still listed as vulnerable by the International Union for Conservation of Nature (Rees et al. 2016, IUCN; Mazaris et al. 2017). While sea turtles spend much of their life in a marine environment, nesting females and their eggs face multiple threats in the terrestrial environment of their nesting beaches. Incubating eggs are vulnerable to climatic risks such as overheating, overcooling, and tidal inundation, but the most significant threat in many locations is nest predation (Miller et al. 2003, National Marine Fisheries Service and U.S. Fish and Wildlife Service [NMFS-USFWS] 2008). Nest predation risk is a function of nest location (Leighton et al. 2008) and the behavior and interactions of predators inhabiting a nesting beach (Barton and Roth 2008). Nests are a particularly attractive resource because predators can locate and successfully prey upon eggs with little energetic costs or risks, while deriving considerable nutritional benefits (Leighton et al. 2009). Based on studies to date, globally, the most important predators of sea turtle eggs are ghost crabs (*Ocypode* spp.) and small to mid-size mammals (feral dogs, coyotes, foxes, pigs, and raccoons; Engeman et al. 2014, O'Conner et al. 2017, Pheasey et al. 2018).

In the southeastern United States, five species of sea turtles are found, with loggerheads being the dominant nesting species (Ruckdeschel & Shoop 2006). The loggerhead has been listed as Threatened under the US Endangered Species Act (ESA) since 1978, and the recovery plan for the Northwest Atlantic population of loggerheads lists the control of nest predation as an objective for population recovery (Federal Register 1978, NMFS-USFWS 2008). Studies from the southeastern U.S. have shown that northern raccoons (*Procyon lotor*) can predate up to 96% of loggerhead nests on some beaches (Hopkins et al. 1978, Stancyk et al. 1980). More recently, non-native species such as feral hogs (*Sus scrofa*) have been shown to have similar predation rates to those of raccoons, with hogs destroying an estimated 70% of loggerhead nests on Ossabaw Island, Georgia in 1990 (Bain et al. 1997, NMFS-USFWS 2008). Predator control/removal has been shown to be effective in reducing target species, but there can be unanticipated consequences for a nesting beach's food web from removing predators that also prey on other predator species (Barton & Roth 2008, Engeman et al. 2010). In order to advance effective predator management techniques, resource managers need to know which predators are the greatest threats to loggerhead nests and target their management efforts accordingly.

Currently in the southeastern U.S., managers tend to target non-native species when controlling for predators, in part because removal of non-natives is consistent with other island management objectives. However, while some non-natives (e.g., hogs and coyotes, *Canis latrans*) are known to be major threats to eggs, evidence for others (e.g., armadillos, *Dasypus novemcinctus*) is unclear as their predation events are either anecdotal or seemingly minor (Drennen et al. 1989, Engeman et al. 2005). This is significant because the southeast is a hotspot for non-native species, specifically non-native mammals and reptiles (U.S. Congress 1993). The current establishment of multiple non-native predators in this region and the possibility of other non-native predator invasion (e.g., the tegu, *Salvator merianae*) calls for quantification of taxon-specific predation risk in order to efficiently direct management efforts.

We analyzed loggerhead nest predation and other egg loss patterns in a long-term data set (2009-2018) from the Georgia coast that included 12 nesting beaches with varying nesting activity, predator richness, and human development. We examined the spatial and temporal variation in egg predation, calculating mean egg loss per predation event and predation event frequency for each predator. Our objectives were to 1) determine which predators cause the greatest loss of loggerhead eggs under current management strategies; 2) evaluate whether non-native species have a higher rate of predation than native species; and 3) compare predation rates to other sources of egg loss under the current strategies for nest management in Georgia. Based on our results, we suggest management actions to enhance sea turtle nest protection and reduce egg losses from nest predation.

Methods

Study Area

Our study area encompasses 12 of the 14 primary barrier islands of Georgia, excluding only Wolf and Sea Island (Figure 1). These islands were excluded due to limited survey effort and restricted data accessibility, respectively. Nesting beach characteristics, nesting activity, and island management are highly variable for the islands studied (Table 1). Most of the islands are undeveloped and constitute some of the least disturbed environments along the Atlantic coast of the United States. Sea turtles utilize these islands for nesting during the months of May through October, with loggerheads being the predominant species, although leatherback, green, and Kemp's ridley sea turtles have also been documented (Ruckdeschel & Shoop 2006, Seaturtle.org Inc. 2018).

Sea turtle monitoring programs began from the 1950's to mid-1960's starting with Jekyll (1958), Little Cumberland (1964) and Blackbeard (1965) islands, with programs in place across most of the remaining islands by 1989 (Dodd & Mackinnon 2003, Ondich & Andrews 2013). Historically, feral hogs and raccoons have been the most significant predators across these islands, but a variety of taxa have been documented predating sea turtle nests (Dodd &

Mackinnon 2003) (Table 2). Invasive mammalian predators of concern include feral hogs, nine-banded armadillos, and coyotes, which have occurred on Georgia's barrier islands since approximately the 1500's, 1973, and 1989, respectively (Georgia Invasive Species Strategy 2009, Mayer & Brisbin 1991, Whitaker Jr. et al. 2012, Whitaker Jr. et al. 2015). An additional non-native predator that is not classified as invasive is the red fox (*Vulpes vulpes*), which arrived on Wassaw Island in 2011(J. B. Pfaller, pers. obs.). Additionally, 14 species of ants have been documented in nests across these islands, with the red imported fire ant (*Solenopsis invicta*) being the only invasive (Braman 2018). On most undeveloped islands, including Wassaw, Ossabaw, St. Catherine's, Blackbeard, Little St. Simons and Cumberland, raccoon populations have been actively managed through trapping and hunting (Dodd & Mackinnon 2003). Additionally, 42% of the nest protection projects on the Georgia coast have used trapping and hunting to reduce feral hog populations (NMFS-USFWS 2008). The predator removal programs for these islands have been developed with the objective to reduce the annual rate of mammalian predation to at or below 10% of nests within each recovery unit (NMFS-USFWS 2008; Fig.2B).

Beach Monitoring & Nest Management

Sea turtle monitoring on the Georgia coast is a collaborative effort with Georgia Department of Natural Resources (GADNR) coordinating a network of volunteers, researchers, and government employees that conduct nest protection and management activities on their respective beaches. This group is known collectively as the Georgia Sea Turtle Cooperative (GSTC; Dodd & Mackinnon 2003). Survey efforts on all the barrier islands included in this study were characterized as standard daily surveys conducted throughout the duration of Georgia's sea turtle nesting season (15 May–1 October) from 2009–2018. The majority of nests detected during nesting surveys were marked and protected by screens to reduce predation. Large mesh screens (1.22 x 1.22 m; 4.1 x 4.1 cm mesh; MasterNet MN-L77) designed to protect against raccoons were used on all nests, while secondary smaller mesh screens (60 x 60 cm; 1.5 x 1.5 cm mesh) were used for additional protection against ghost crabs or to reduce partial predation of nests by raccoons. All located nests had a single egg removed for an ongoing genetic tagging study on the Northern Recovery Unit (loggerheads originating from nesting beaches from Florida-Georgia border through southern Virginia; Shamblin et al. 2011, Shamblin & Nairn 2015). To reduce egg loss from tidal inundation, clutches deposited below the spring high tide line were relocated to new sites nearer to the primary dune within 12 hours of deposition.

Nests were monitored daily for the duration of incubation (55–70 days). Surveyors recorded attempted, partial, or complete predation of nests and identified predators based on tracks. The total number of eggs predated per event was estimated by counting eggshell fragments ≥ 50% intact as one egg. Tidal and storm losses were monitored and documented whenever a nest was washed out or disappeared after a storm. These losses were assumed to include the entirety of the nest. Nests were excavated on the fifth day succeeding the first sign of hatchling emergence, while nests without signs of hatching were excavated at 70 days after deposition. Finally, the total hatched eggs, unhatched eggs, live hatchlings, and dead hatchlings were recorded. Data for each egg loss event used in the analyses included the date laid, the beach name, nest number, date of egg loss, reason for egg loss, and number of days until egg loss.

Data Management & Analysis

We accessed all egg loss data from the Seaturtle.org centralized database management system. We organized “reason for egg loss” into eleven categories, including all documented predators (Table 2) and four non-predator categories (poaching, research, tide/storm, and other egg loss). “Other egg loss” included losses from beach scraping, broken eggs inside the nest, excessive sand accumulation, lost nests, root entanglement, shallow nests, and unknown reasons. “Research egg loss” included all eggs taken for ongoing genetic research as well as eggs damaged through nest probing and excavation.

For every clutch that was fully lost and for which the number of eggs was unknown, we assumed a clutch size of 110 eggs, representing the mean clutch size for relocated nests during the study period (N = 6,959; mean = 109.57; SE = 0.28). This is within the range of the mean clutch size (112.4) found for 19 populations of loggerhead sea turtle reported by Buskirk & Crowder (1994). In some cases, ghost crabs were identified as a cause of high egg loss in a single event, which is inconsistent with other studies (Barton & Roth 2008, Lucrezi & Schlacher 2014); we therefore capped egg loss at 20 for any single ghost crab predation event.

For each source of egg loss, we quantified the number of loss events, the number of nests affected, and the number of eggs lost. Using these data, we calculated threat frequency (proportion of eggs affected by a threat) and threat intensity (proportion of eggs within a nest lost to a threat) for each threat category. We assessed spatial and temporal variation in these metrics and compared egg loss patterns between non-predator and predator sources and between native, non-native and invasive predators. Native, non-native, and invasive species were differentiated using the Georgia Invasive Species Strategy List (2009) and the Georgia Department of Natural Resources’ species fact sheets (2016). Finally, mean and median egg survival times were calculated using the time in days between when the nest was laid and when it was predated. All analyses were carried out in Excel and R (Version 1.1.456 RStudio Team, 2016).

Results

A total of 19,158 loggerhead nests were reported from 2009-2018, with an average of approximately 1,916 (SE = 197.85) nests laid per year. The percentage of nests suffering egg losses (excluding research loss) ranged from 12.67% (2014) to 30.36% (2017) per year, with the number of nests suffering egg losses fluctuating with annual nest abundance; for example, 2016 had the highest number of nests laid (3,178) as well as the highest number of nests predated (460; Fig. 2A). Total egg loss over the course of the study was estimated at 194,261 eggs (Table 3).

The primary cause of egg loss was predation (45%), although tide/storm loss was nearly as high (41%), with all other threats (14%) being minimal in comparison (Table 3). Nest losses due to storms and tides were lower than nests predated every year except 2017, when 306 nests were washed away due to severe storm events (Fig.2A). Research losses were by far the most frequent reason for egg loss (17,234 events), but only accounted for 10% of all documented egg loss (Table 3).

Annual nest predation rates ranged from 7.16% (2014) to 19.18% (2009) with an average annual rate of 12.67% (SE = 0.98). Overall, the total mammalian predation of nests was found to be at or below 10% of all nests laid from 2009-2018, meeting the federal recovery plan objective (Fig. 2B). The majority of nest predation was caused by feral hogs and raccoons, with these predators accounting for a combined 79% of all egg predation occurring on the islands (Fig. 3). Other mammalian predators such as coyotes (7%), fox spp. (5%), and armadillos (2%) were responsible for considerably less egg predation, combining for only 14% of all predation (Fig. 3). Ghost crabs (5%) and other incidental predators (2%) made up the remaining 7% of egg predation (Fig. 3). Mean egg loss per predation event and predation frequency varied widely across predator species, with hogs (83 eggs/nest) and coyotes (56 eggs/nest) having the largest mean predation rates, and ghost carbs (1,400 events) and raccoons (906 events) having the greatest predation frequency (Fig. 4). The "other predator" category included unknown predators

(N=35) as well as predators with low predation frequency (< 20): birds (*Corvus* spp.), American minks (*Mustela vison*), Virginia opossums (*Didelphis virginiana*), river otters (*Lontra canadensis*), eastern kingsnakes (*Lampropeltis getula*), and ants (Formicidae) (N=27).

The total proportion of egg loss caused by four invasive predators was higher (53%) than that of eight native (42%) and the single non-native (4%) predators. The remaining egg loss was caused by unknown predators (1%; Fig. 3B). While multiple invasive predators were responsible for considerable egg loss, feral hogs contributed to 83% of the total egg loss caused by invasive species. Non-native red foxes contributed substantially more egg loss (3,615) than that of the native common gray fox (*Urocyon cinereoargenteus*; 559). Overall egg loss caused by feral hogs (38,130) was greater than that of all native predators combined (36,506).

Nest predation and other egg loss patterns varied by island, with larger undeveloped islands with higher nesting densities suffering greater egg loss than smaller developed islands with generally lower nesting densities (Table 1; Fig. 5). Egg loss patterns also varied greatly by year, with the greatest egg losses in 2017, due mainly to tides/storms (32,535) and hogs (14,897; Fig. 6). Total egg loss then sharply declined in 2018 (8,249) concurrent with the reduction in losses from tides/storms and hogs.

Discussion

Under current strategies for nest management, our results indicate that predation was the greatest cause of loggerhead egg loss over 10 years across 110 miles of barrier islands in Georgia, USA, although tidal/storm losses were nearly as large. Native raccoons and invasive feral hogs were the most destructive species, while other invasive species caused much lower egg losses. To our knowledge, this is the first study to compare nest predation across a broad range of species inhabiting a diverse barrier island complex, and the largest analysis of sea turtle nest predation globally. The majority of nest predation research has focused on individual predators (raccoons, hogs, foxes, mongoose), although a few have looked at multiple predators on individual nesting beaches (Barton & Roth 2008, Engeman et al. 2014, Nordberg et al. 2019), and a study at Canaveral National Seashore covered approximately 38km of beach across a 20-year (1989-2008) span (Welicky et al. 2012). By examining multiple predators at a broad spatial scale, our study provides a data-driven basis for targeting predator management programs at sea turtle nesting beaches.

Over the last decade, invasive predators have had a greater impact on sea turtle nests in Georgia than native and non-native species. The primary species responsible for this are feral hogs, which caused the greatest amount of egg loss of any predator, even though they only occurred on five of the twelve islands. These animals had by far the greatest mean egg loss out of any predator found in the study, usually destroying the entire nest during each predation event, as the plastic screens used to protect nests from predators are ineffective against hogs. Despite aggressive predator management efforts, hog predation was particularly high on St. Catherine's Island (SCI) during the 2016 and 2017 nesting seasons, resulting in an estimated total of 24,279 eggs lost. Before the start of the 2018 nesting season, however, SCI management employed the U.S. Department of Agriculture Wildlife Services to eradicate feral hogs on the island, resulting in a 100% decrease in hog predation. For several islands, feral hogs are targeted year-round as part of larger management objectives where complete removal or reduction goals are currently in place.

Invasive coyotes caused much lower egg loss than hogs, though they were the primary predator of nests on Cumberland Island, causing an estimated egg loss of 4,712 eggs from 77 nests. Coyotes are a particularly effective predator because of their ability to learn and adapt to new environments and challenges (Bekoff & Gese 2003), including learning to remove or dig under mesh screens (Eskew 2012). Furthermore, they frequently predate nests on the first night of oviposition, before nests are protected with screening material. However, the lethal control of coyotes on Cumberland Island with the combination of foothold traps, snares, and shooting has proven extremely effective, reducing coyote nest predations from 59 in 2015 to one, two, and zero nests in 2016, 2017, and 2018, respectively. Management efforts throughout the year for animals like coyotes is necessary to prevent damage issues during nesting season for sea turtles. The known capacity of coyotes, specifically, necessitates removal at optimum times of year (winter) to be successful. Delaying removal efforts for this species until predation events occur all but guarantees a beach will experience losses with the possibility of them being significantly prolonged.

The invasive nine-banded armadillo, while found to be a significant predator of sea turtle nests in Florida and South America (Drennen et al. 1989, Engeman et al. 2003, Gandu et al. 2013), does not seem to be a significant predator on the Georgia coast. Armadillo nest predation was less than ten nests a year across the islands studied, with one exception in 2015 when 24 nests were predated. Since armadillos are considered an invasive species on the Georgia coast, some island managers have argued for including them in predator removal programs, especially because they are capable of burrowing under nest screens (Gandu et al. 2013). However, our data do not support the inclusion of armadillos in predator removal programs on the coast currently.

The native predator that poses the greatest threat to sea turtle eggs throughout the sea turtle nesting habitat in the southeastern United States is the raccoon (Mroziak et al. 2000, Williams & Frick 2000, Dodd & Mackinnon 2003, Engeman et al. 2003). Our results indicate that raccoons are the most widespread mammalian predator on Georgia's coast, causing the loss > 1,000 eggs per year. However, this rate would be much higher without the combination of predator removal and nest protection that has been employed across the Georgia barrier islands in recent years. Studies have shown the effectiveness of raccoon removal on reducing sea turtle nest predation in the region (Ratnaswamy & Warren 1998, Engeman et al. 2003), although nest screening may be the most effective tool in reducing raccoon predation (Ratnaswamy et al. 1997, Yerli et al. 1997, Antworth et al. 2006, McElroy 2015, O'Connor et al. 2017). We recommend focusing efforts on screening rather than removal because raccoons are important members of island food webs and their removal can affect nutrient flow, seed dispersal, and other animal dynamics (Bouchard & Bjorndal 2000, Barton & Roth 2008). We agree with others that the ecological connectivity provided by raccoons be evaluated in order to ensure that sea turtle nest protection strategies do not impair other coastal ecosystem functions (Ratnaswamy & Warren 1998, Barton & Roth 2007).

Ghost crabs are the most frequent and likely the most abundant native predator across the barrier islands. Ghost crabs may also facilitate mammalian predation by causing nests to be more easily found by transmitting chemical cues to the beach surface from their burrows (Barton & Roth 2008). On the other hand, raccoon and fox presence are likely to be limiting factors for ghost crab abundance on nesting beaches. Previous research suggests that ghost crabs can have a stronger direct effect on sea turtle egg mortality than raccoons when the latter are being managed (Barton & Roth 2008). The conventional screening of nests is not an effective tool in preventing ghost crab egg predation, but the finer mesh screen used on islands where crabs are highly abundant provides better protection. It should also be noted that ghost crabs often occur and are reported as secondary scavengers after a mammalian predator has dug into a nest.

Fox predation was limited to two islands on the coast, with gray foxes causing predation on Jekyll and red foxes on Wassaw. While these fox species combined to predate more nests than coyotes, they were responsible for less overall egg loss and had a significantly lower mean egg predation rate. Although gray foxes are native to the Georgia coast and could provide similar ecosystem functions to those of raccoons as native meso-carnivore predators, red foxes are considered a non-native (though not invasive) species of potential concern as a nest predator (Statham et al. 2012). This possible threat is supported by our results which show red foxes predating over six times as many eggs as gray foxes.

Species predation rates varied by island with much lower predation on developed islands r compared to undeveloped islands. We attribute this to lower nesting densities on developed islands and greater effort devoted to protecting nests on those beaches. While raccoons are an abundant predator on developed islands, it is likely that increased beach activity and increased greater monitoring efforts have kept predation levels low. For these islands, nest screening and monitoring have been effective and sufficient management methods. Less developed islands may need to incorporate additional predator management methods, such as the removal of problem individuals or the targeted reduction or removal of invasive species, when supported by predation data. Our results support the eradication of hogs and coyotes on all islands, whereas raccoons and other native predators generally can be managed by eliminating problem individuals (Table 4).

Although our focus was on predation, our results also demonstrate the contribution of extreme tides and severe storms to egg loss. It’s notable that losses would have been much higher without nest relocation efforts. Our tidal losses are also likely underestimated, as they only included documented loss of nests and did not account for partial nest inundation that reduced hatching success but was not noted as tidal loss. Of the 760 nests that were destroyed by tides or storms during the monitoring period, 39% (295) were lost to Hurricane Irma in 2017. This illustrates the impact a severe storm surge can have in a single nesting season, and this type of seasonal damage to nesting beaches is well documented in the literature (Ross 2005, Fuentes et al. 2011, Lindborg et al. 2016). The population level impact of an individual storm, however, may be limited because only a portion of adult females reproduce each year, and reproducing females lay multiple clutches over the season (Miller 1997, Dewald & Pike 2014). However, increased frequency of severe storms accompanied by rising sea levels due to climate change may lead to much greater losses in the future (Pike et al. 2015).

It is important to acknowledge some limits of our study associated with nest monitoring survey methodologies. There is error associated with attribution of egg losses to a specific cause using field signs. Our survey methods also likely have a limited ability to detect the predation of sea turtle eggs by cryptic fossorial species like ants, ghost crabs, snakes, and small mammals. It is entirely possible that broken eggs found inside nests during the initial nest detection process are the result of predation events on individual eggs. However, current methods are likely the best available options for monitoring egg loss over such large spatial and temporal scales. Small-scale programs have used game cameras to monitor the frequency of predator visits, time of visits, and nest predator identification (Lei & Booth 2017b, Lei & Booth 2018), but this methodology would be too costly over the scale of multiple islands with high nesting densities (≥ 20 nests/km).

Conclusion

We found that although predation was the largest source of egg loss under the current strategies of nest management in Georgia, rates were below the target level of 10% established in the Northwest Atlantic Loggerhead Sea Turtle Recovery Plan. We consider this a success, and attribute it in large part to the effective use of monitoring, nest screening, and targeted predator removal. It should be noted however, that nest predation varies drastically by nesting beach, and predator management should be viewed on a case by case basis rather than following a standardized management plan. For example, the targeted removal of feral hogs is essential as this species causes the greatest egg loss per predation event and can quickly cause extensive losses if uncontrolled. However, the removal of other predators should target species and locations of concern and should be conducted with consideration for the potential interactions between predators resulting in indirect effects on sea turtle egg predation and other aspects of beach ecosystem function.

Globally, individual programs deal with the threat of nest predation by native and non-native predators in different ways. Use of mesh screens seems to be a universally effective option because screens can be made from a variety of materials, protect against a range of predators, are fast to deploy, and unlike metal screens do not pose a risk to the navigational abilities of hatchlings (Irwin et al. 2004, Lei & Booth 2017a, Pheasey et al. 2018, Korein et al. 2019, Nordberg et al. 2019). Other programs may instead choose to translocate eggs into outdoor hatcheries to protect nests. While this approach is extremely effective in reducing predation rates, there is controversy around the method because protected nests may experience modified sex ratios and decreased hatching success (Limpus et al. 1979, Mrosovksy & Yntema 1980, Sari & Kaska 2017). The use of hatcheries has been shown to be effective on small beaches experiencing high rates of nest loss from natural causes (Garcia et al. 2003, Abella et al. 2007), but on larger beaches with high nesting densities, this option is often not effective, feasible, or needed.

While egg predation is still a significant reason for egg loss across several beaches, sea turtle nest protection and management can be seen as a global sea turtle conservation success, as these efforts are thought to have contributed to the recent growth in nesting trends at many nesting sites (Chaloupka et al. 2008, Mazaris et al. 2017). Many threats affect sea turtles over a range of different life stages, with nesting beach protection generally only having implications for nesting females, their eggs, and hatchlings in the terrestrial environment. Making informed predator management decisions based on various predators' destructive capabilities will allow beach managers to direct conservation funding in an efficient way that could allow for more funding availability for other conservation needs that are not nesting beach related.

Table 2.1. Georgia islands listed from north to south with their various attributes. Total size includes the salt marsh and upland areas of the islands (Georgia Natural Heritage Program 1998). Nesting beach sizes were determined by using the maximum amount of beach surveyed for each island in 2018 (seaturtle.org). Beach Development categories were selected based on NOAA's Coastal Change Analysis Program (Office for Coastal Management 2019).

Island	**Total Size (ha)**	**Upland Size (ha)**	**Nesting Beach (km)**	**Beach Devt.**	**Avg. Nests/ Year**	**Ownership**	**Management**
Tybee (TI)	3,100	607	7.5	High	16	Private	Tybee Marine Science Center
Little Tybee (LTI)	6,505	243	1.6	Low	14	GADNR	GADNR Staff
Wassaw (WI)	10,050	1,012	10.8	Low	189	USFWS	Caretta Research Project
Ossabaw (OI)	25,000	4,775	17.1	Low	285	GADNR	GADNR Staff
St. Catherine's (SCI)	14,640	2,780	16.6	Low	181	Private	SCI Sea Turtle Program
Blackbeard (BI)	5,618	1,578	12.6	Low	277	USFWS	USFWS & Savannah Coastal Refuges
Sapelo (SI)	17,950	4,411	9.0	Low	121	GADNR	GANDR Staff
Little St. Simons (LSSI)	8,840	931	11.6	Low	112	Private	LSSI & GANDR Staff
St. Simons (SSI)	27,630	4,978	4.0	High	5	Public	SSI Sea Turtle Project
Jekyll (JI)	5,700	1,781	15.4	High	145	State of Georgia	Jekyll Island Authority Staff
Little Cumberland (LCI)	2,400	647	4.3	Low	70	Private	LCI Sea Turtle Project
Cumberland (CI)	23,000	6,111	27.5	Low	514	USNPS	Cumberland Island National Seashore Staff

*GADNR: Georgia Department of Natural Resources, USFWS: U.S. Fish & Wildlife Service, USNPS: U.S. National Parks Service.

Table 2.2. List of sea turtle nest/egg predators documented in the Northern Recovery Unit. Sources of Seaturtle.org were predation events that were found during this research. Species are listed by taxa type and their percentage of total egg loss found in this study (descending).

Mammals	**Status**	**Source**
Feral Hog (*Sus scrofa*)	Invasive	Anderson 1981
Northern Raccoon (*Procyon lotor*)	Native	Hopkins et al. 1978
Coyote (*Canis latrans*)	Invasive	Eskew 2012
Red Fox (*Vulpes vulpes*)	Non-native	Stancyk 1982
Nine-banded Armadillo (*Dasypus novemcinctus*)	Invasive	Drennen et al. 1989
Common Gray Fox (*Urocyon cinereoargenteus*)	Native	Stancyk 1982
Virginia Opossum (*Didelphis virginiana*)	Native	Woolard 2004
Northern River Otter (*Lontra canadensis*)	Native	Seaturtle.org 2010
American Mink (*Mustela vison*)	Native	Seaturtle.org 2018
Domestic Dog* (*Canis lupus familiaris*)	Non-native	Dodd 1988
Birds		
American Crow (*Corvus brachyrhynchos*)	Native	Anderson 1981
Fish Crow (*Corvus ossifragus*)	Native	Witherington 1986
Black Vulture* (*Coragyps atratus*)	Native	Stancyk 1982
Turkey Vulture* (*Cathartes aura*)	Native	Stancyk 1982
Reptiles		
Eastern Kingsnake (*Lampropeltis getula*)	Native	Seaturtle.org 2012
Scarlet Snake* (*Cemophora coccinea*)	Native	Butler et al. 2019
Yellow Rat Snake* (*Pantherophis alleghaniensis*)	Native	Williams & Frick 2001
Invertebrates		
Atlantic Ghost Crab (*Ocypode quadrata*)	Native	Hopkins et al. 1978
Ant spp. (Formicidae)	Native & Invasive	Braman 2018

***** Not documented in this study

Table 2.3. Summary statistics of all egg loss factors found from 12 of Georgia's barrier islands from 2009-2018. Survival time was calculated using the difference between the date the nest was laid and the date eggs were predated or lost. Mean & median egg survival times were not calculated for species that were combined into the "Other Predators".

Loss type	# of events	# of nests	# of eggs	Mean eggs/nest (std. error)	% total egg loss	Mean egg survival time (days)	Median survival time (days)
All Losses	21,800	17,889	194,261				
Non-Predator Losses							
Tide/Storm	766	760	79,747	104.1 (0.66)	**41.05%**	47.48 (± 0.07)	52
Research	17,234	16,867	18,744	1.1 (0.01)	9.65%	0.18 (± 0.02)	0
Other	617	602	5,175	8.4 (0.90)	2.66%	38.78 (± 0.48)	47
Poaching	38	38	3,428	90.2 (4.55)	1.76%	17.41 (± 0.41)	8
Total	**18,655**	**-**	**107,094**	**-**	**55.13%**	**-**	**-**
Predator Losses							
Feral Hog	461	428	38,130	82.7 (1.76)	**19.63%**	21.23 (± 0.12)	14
Raccoon	906	671	30,988	34.2 (1.17)	**15.95%**	16.69 (± 0.13)	3
Coyote	104	102	5,836	56.1 (3.36)	3.00%	4.67 (± 0.20)	0
Ghost Crab	1,400	1,006	4,707	3.4 (0.12)	2.42%	28.19 (± 0.37)	22
Red Fox	67	64	3,615	54.0 (5.89)	1.86%	30.51 (±0.39)	37
Armadillo	86	50	1,914	22.3 (2.33)	0.99%	37.49 (± 0.51)	37
Unknown Predator	35	28	1,094	31.3 (6.21)	0.56%	NA	NA
Gray Fox	59	47	559	9.5 (0.90)	0.29%	36.76 (± 0.63)	43
Opossum	5	2	110	22.0 (5.58)	0.06%	NA	NA
Ant spp.	12	12	72	6.0 (2.78)	0.04%	NA	NA
Bird spp.	4	4	69	17.3 (12.68)	0.04%	NA	NA
River Otter	2	2	49	24.5 (7.50)	0.03%	NA	NA
Kingsnake	3	3	17	5.7 (4.18)	0.01%	NA	NA
Mink	1	1	7	7.0	0.00%	NA	NA
Total	**3,145**	**-**	**87,167**	**-**	**44.87%**	**-**	**-**

Table 2.4. The top predator for every island and the suggested management prescription based on the predators' destructive capabilities and their total amount of egg loss caused on each island.

Island	Top Predator	Management Prescription
Tybee (TI)	Ghost Crab	NSM
Little Tybee (LTI)	Raccoon	NSM
Wassaw (WI)	Raccoon	NSM, RPI
Ossabaw (OI)	Feral Hog	NSM, TSR
St. Catherine's (SCI)	Feral Hog	NSM, TSR
Blackbeard (BI)	Feral Hog	NSM, TSR
Sapelo (SI)	Raccoon	NSM, RPI
Little St. Simons (LSSI)	Raccoon	NSM, RPI
St. Simons (SSI)	Ghost Crab	NSM
Jekyll (JI)	Raccoon	NSM, RPI
Little Cumberland (LCI)	Raccoon	NSM, RPI
Cumberland (CI)	Coyote	NSM, TSR

[*] NSM: Nest screening & monitoring, RPI: Removal of problem individuals, TSR: Targeted species removal

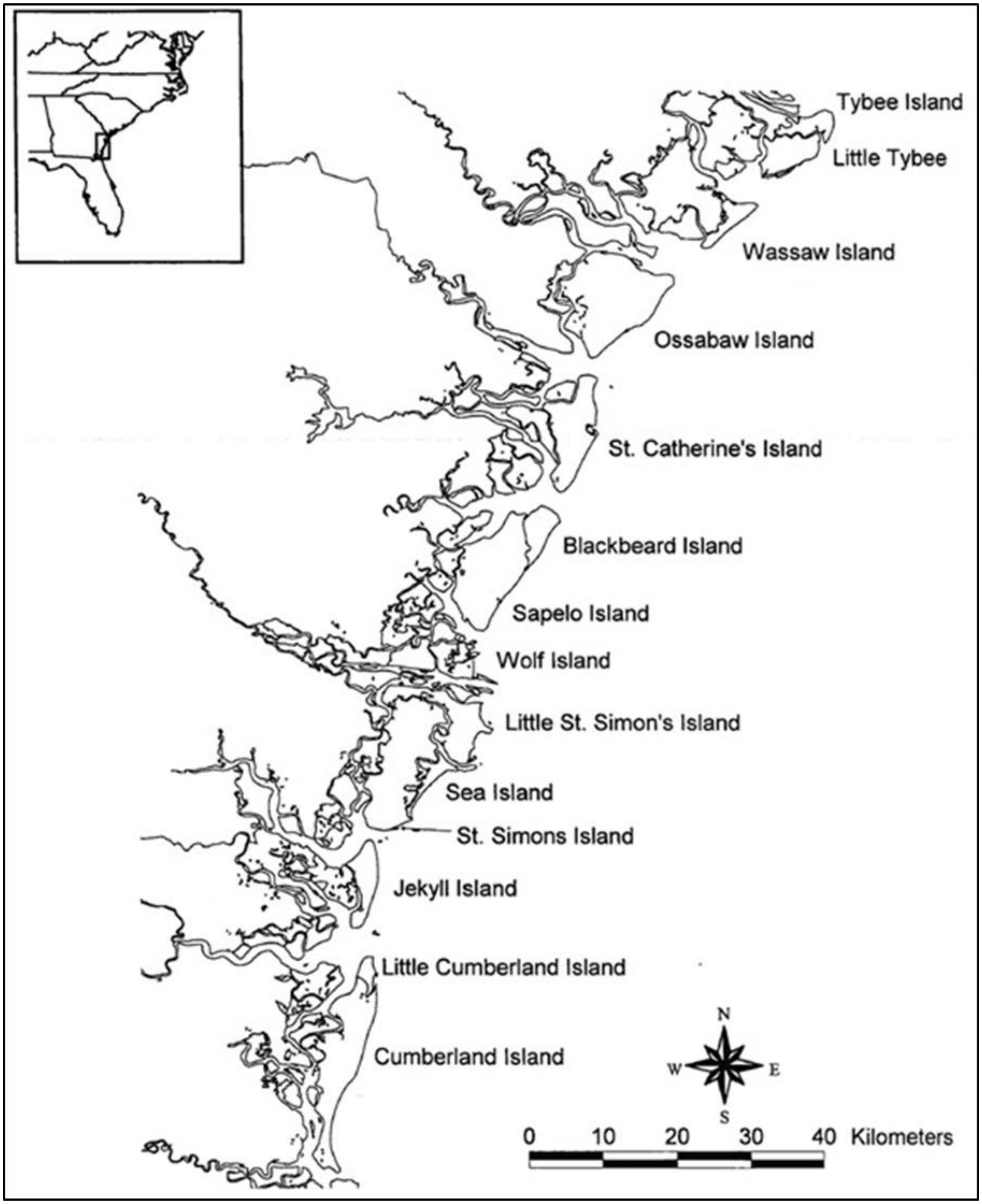

Figure 2.1. Map of the Georgia's coast and its barrier islands (Dodd & Mackinnon 2003). Wolf and Sea islands were not included in this study due to limited survey effort and restricted data accessibility, respectively.

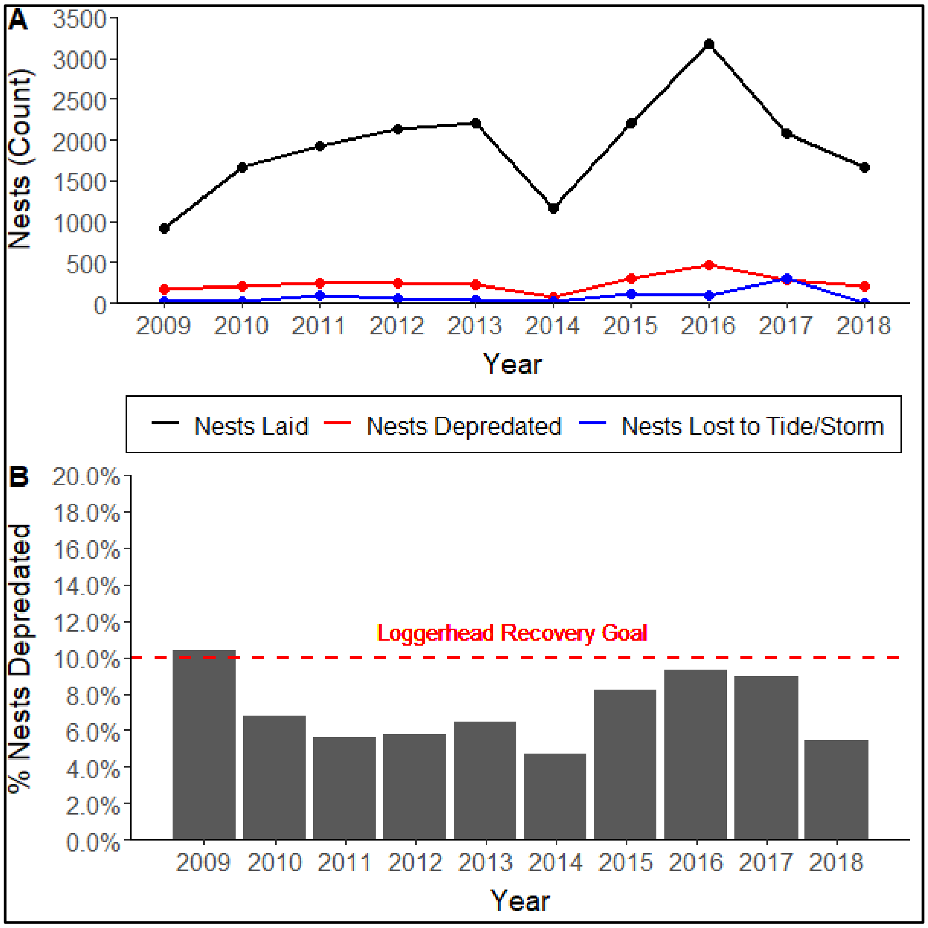

Figure 2.2. (A) The total number of sea turtle nests (black), total number of nests predated (red), and the number of nests lost to tides and storms (blue) across 12 of Georgia's barrier islands from 2009-2018. **(B)** The proportion of sea turtle nests predated by mammals. The red line represents the Northwest Atlantic Loggerhead Recovery Plan's objective of reducing the annual rate of mammalian predation to at or below 10% of nests within each recovery unit (NMFS-USFWS 2008). Both figures include fully and partially predated nests.

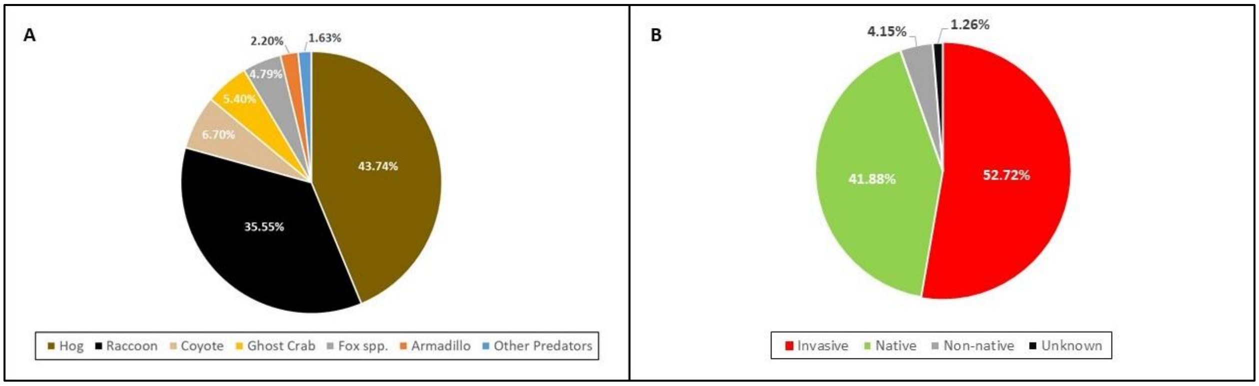

Figure 2.3. (A) The proportion of all loggerhead egg loss caused by predation on 12 barrier islands of the Georgia coast from 2009-2018. **(B)** The proportion of loggerhead egg loss from predation categorized by invasive predators (red), native predators (green), non-native predators (gray), and unknown predators (black).

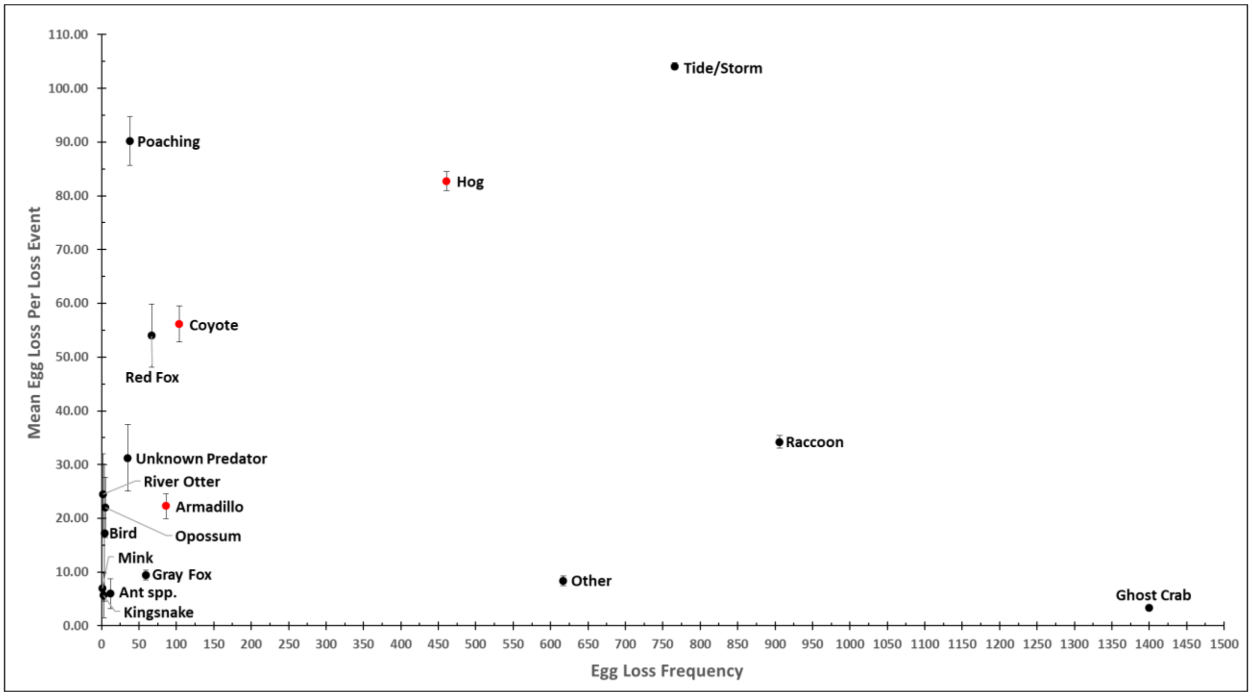

Figure 2.4. A comparison of the mean egg loss per predation event and predation frequency of multiple predators and other egg loss reasons found across 12 of Georgia's barrier islands from 2009-2018. Predators highlighted as red are considered Priority 1 invasive species of concern in Georgia (Georgia Invasive Species Strategy, 2009). Research egg loss is not shown (Frequency = 17,234, Mean Egg Loss =1.09 (± 0.01)). Error bars represent standard error. Species/factors in the upper right quadrant of the graph are the most destructive while species in the lower left are the least.

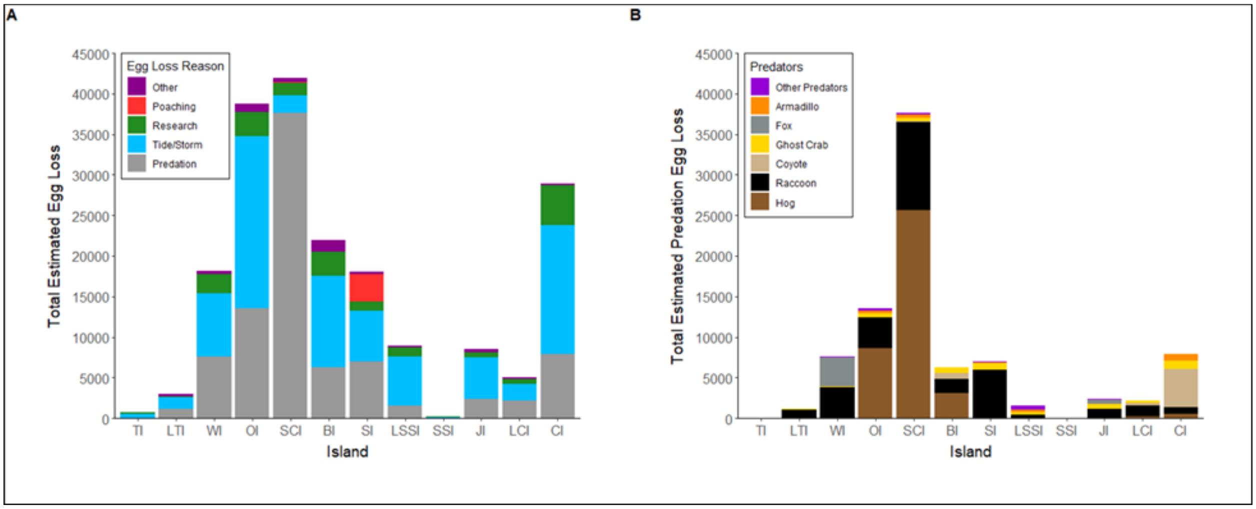

Figure 2.5. (A) Sources of loggerhead egg loss across 12 barrier islands of the Georgia coast from 2009-2018. **(B)** Predation egg loss by various predators across islands. Note that panel B constitutes a subset of panel A.

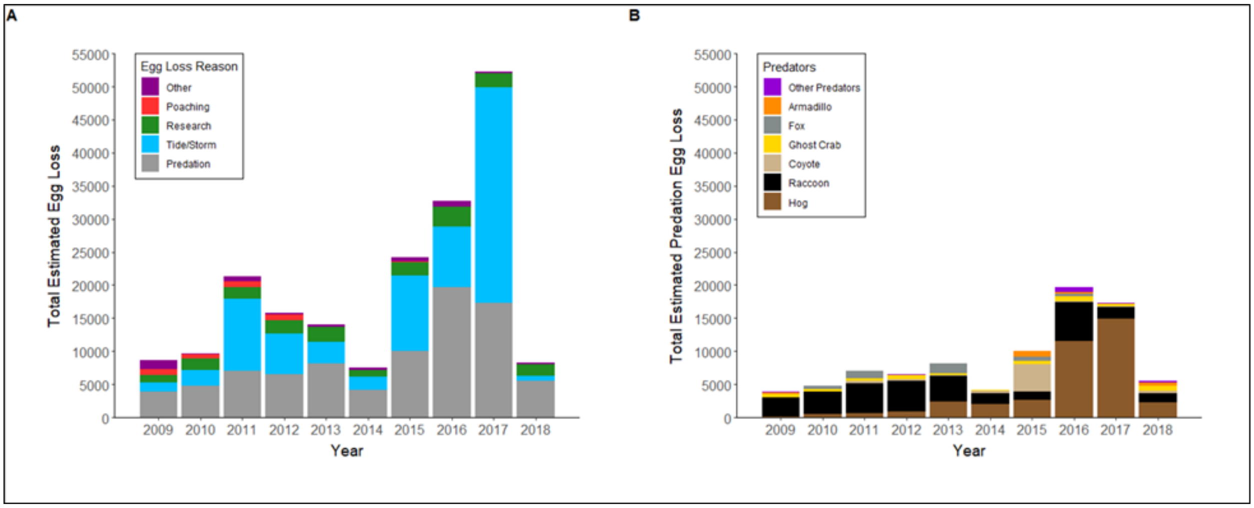

Figure 2.6. (A) The total estimated loggerhead egg loss by year across 12 barrier islands of the Georgia coast from 2009-2018. **(B)** Predation egg loss by various predators across years. Note that panel B constitutes a subset of panel A.

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CHAPTER 3

DOCUMENTING THE COMMENSAL BIODIVERSITY OF NINE-BANDED ARMADILLO BURROWS[2]

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[2] Butler, Z. P., S. J. Wenger, C. M. McDonough, V. Ezenwa, and S. Coleman. To be submitted to Journal of Mammalogy.

Abstract

Understanding how invasives species interact with native flora and fauna in their invaded environments is fundamental in determining if and how a species should be managed. Nine-banded armadillos are considered invasive throughout the southeast United States, although they also might provide important ecological functions as their fossorial behavior creates habitat in the form of burrows that provide refugia for other species. To determine if nine-banded armadillos are providing ecosystem services for native species on an invaded island, we used camera traps to identify the vertebrate species using burrows and document their behaviors on Little St. Simons Island, Georgia. Our objectives were to 1) quantify diversity of species using burrows and determine whether patterns differ between two major island habitat types (Maritime Forest, Dune Complex), 2) determine the types of associations occurring between commensal species and burrows and test whether these associations differ across taxa, and 3) compare overlap in activity patterns of burrow use between armadillos and burrow associates in order to investigate if there is co-occurrence or competition between species. Our results show that 1) 33 of 49 species documented were verified interacting with burrows in some way while mean species richness and species diversity did not vary across habitats. 2) Burrow behavior was significantly different across taxa with reptiles, armadillos, and mesopredators primarily engaging in burrow use, whereas shrews and birds were most frequently observed foraging at burrows. 3) Armadillos have high activity overlap with other common burrow associates. We believe this study highlights the potential importance of armadillo burrows as refugia structures across a barrier island landscape.

Introduction

Invasive species are considered a significant ecological and economic threat in the United States, with the federal government expending billions of dollars annually in control efforts (Pimental et al. 2005, Crafton & Angadjivand 2018). An invasive species is defined as "a species that is non-native to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health" (National Invasive Species Council). However, invasive species vary greatly in their potential to cause harm, and the perceived harm or benefit caused by an invasive organism can be influenced by changing values, acquisition of new information or evolving management goals (Beck et al. 2008). Previous research has shown that some invasives provide positive ecological functions by providing habitat, shelter, and food for native species (Schlaepfer et al. 2011). These and other possible beneficial effects often go unstudied, however, once a species is classified as invasive (Sagoff 2005). We argue that it is important to evaluate the possible beneficial roles of non-native species in order to make unbiased, data-driven decisions about their management.

In the US, the nine-banded armadillo (*Dasypus novemcinctus*) is an example of an understudied species that has been classified as invasive despite limited evidence of harm to humans or ecosystems (Chamberlain 1980, Hohbein & Mengak 2018, Rodrigues et al. 2019). The nine-banded armadillo is the only member of the family Dasypodidae currently established in the United States. It was originally recorded in the U.S. in 1849 and was thought to have naturally dispersed from Mexico with a range confined to the lower Rio Grande Valley (Audubon & Bachman 1854). A population in Florida was established by individuals released from a personal zoo in 1924, which was then augmented by the release of additional individuals in 1936 from a circus truck (Talmage & Buchanan 1954). In the decades since, the species range has expanded steadily, resulting in abundant populations throughout the southeastern U. S. (Taulman & Robbins 2014). Because the expansion appears to be partly natural and partly anthropogenic, there is disagreement about whether armadillos should be regarded as native or exotic, which sometimes confounds management efforts: is it a species to be protected or eliminated? (Loughry & McDonough 2013).

Armadillos provide important yet sometimes overlooked ecological functions, as their fossorial behavior creates habitat in the form of burrows that provide refugia for species of concern, such as eastern indigo snakes (*Drymarchon couperi*; Wilson & Poras 1983), eastern diamondback rattlesnakes (*Crotalus adamanteus*; Timmerman 1995), and Florida mice (*Podomys floridanus*; Layne & Jackson 1994). Burrow-creating organisms, such as tortoises, prairie dogs, and wombats, can be viewed as ecosystem engineers that provide ecological services for commensal species (Pike & Grosse 2006). For example, burrows can act as thermal refugia that allow species to avoid unfavorable or extreme environmental conditions (Walde et al. 2009, Pike & Mitchell 2013), and can provide shelter from predators (Layne & Jackson 1994, Waterman & Roth 2007) and fire (Friend 1993), as well as foraging sites (Desbiez & Kluyber 2013). Burrowing activity can also alter vegetation structure, promote sediment movement, and increase nutrient availability (Rodrigues et al. 2019). The removal of a burrowing species may cause negative impacts on species that rely on burrows created by other taxa (Desmond et al. 2000, Davidson et al., 2012, Dziadzio & Smith, 2016).

While studies have documented insects, reptiles, birds, and mammalian species occupying nine-banded armadillo burrows (Taber 1945, Clark 1951, Timmerman 1995, Zimmerman 1990, Platt et al. 2003), there has yet to be a long-term study documenting the frequency or type of burrow use by commensal species. In order to determine if nine-banded armadillos are providing ecosystem services for native species in a habitat to which they are not native, we deployed camera traps across two habitat types on a barrier island in Georgia, USA to identify the vertebrate species using burrows and document their behaviors. Our specific research objectives were to 1) quantify diversity of species using burrows and determine whether patterns differ between two major island habitat types (Maritime Forest, Dune Complex), 2) determine the types of associations occurring between commensal species and burrows and test whether these associations differ across taxa, and 3) compare overlap in activity patterns of burrow use between armadillos and burrow associates in order to investigate if there is co-occurrence or competition between species.

Methods

Study Site

Little St. Simons Island (LSSI) (Figure 2) is a privately owned, minimally developed coastal barrier island in Glynn County, Georgia, USA (31.299°N, -81.328°W). LSSI is one of fourteen barrier islands off the Georgia coast and borders the Atlantic Ocean to the east, the Altamaha River to the north, and the Hampton River to the south and west, with no land connection. Most of the island (~3,470 ha; 67%) consists of tidally influenced salt marshes dominated by smooth cordgrass (*Spartina alterniflora*), while upland habitats (~1,730 ha; 33%) include primary and secondary dune systems and maritime shrub communities dominated by wax myrtle (*Morella cerifera*), mixed pine-oak-palmetto forest, and mature maritime forests made up of live oak (*Quercus virginiana*) and laurel oak (*Quercus laurifolia*; Morse et al. 2009). Elevations on LSSI range from sea level to 9 m; however, most of the island is less than 3 m above mean sea level.

Armadillos, which were first recorded on the island in 1980, are the only burrowing medium-sized animals capable of creating elongated refugia. The absence of hunters, large predators, limited vehicle traffic, and favorable habitat and climatic conditions are likely all conducive to armadillo survival and population growth on the island.

The maritime live oak forest is the predominant climax community found across Georgia's barrier islands and resembles other hardwood habitats armadillos have been found in. Previous research from Cumberland island documented that the majority of armadillo burrow were found under saw palmettos (*Serena repens*) in the understory of these forests (Bond et al. 2000). The dune complex system (primary and secondary dunes interspersed by salt marsh), however, would be considered a novel habitat as it is only ~80 years old and has been formed by sediment accretion from the Altamaha River. To date armadillos have not been extensively studied in this type of habitat and any potential impacts of its burrowing nature are unknown.

Burrow Monitoring

We delineated one 40.5 ha (~ 1,300 x 300 m) plot within each habitat — maritime forest (MF) and dune complex (DC)— in which we conducted burrow surveys (Figure 1). Surveys were conducted semi-randomly through the plots, focusing on accessible areas where burrows were thought to be established. Each burrow was geo-referenced with a handheld GPS (Garmin eTrex 20x). We determined burrow lengths and initial occupancy with a burrow scope (cable hose with an attached camera; Environmental Management Systems), and a soft measuring tape. We measured burrow entrance heights and widths following McDonough et al. (2000) and determined burrow entrance orientation (aspect) using a standard compass. In each habitat we selected six initial burrows to monitor that were accessible, showed evidence of activity (based on initial occupancy check) and were at least 50cm in length (to differentiate from foraging digs). All burrows with camera traps were intended to be monitored throughout the yearlong study period, but in the case of burrow collapses, the camera was moved to the closest known active burrow. The number of recordings in each site varied per month because of camera malfunctions, tidal flooding, and user error. In total there were 4,004 days (DC = 1,908, MF = 2,096) of camera-trap effort at 29 burrow sites (DC = 17, MF = 12; Table 3). Five out the twelve originally selected burrows were monitored for the duration of the study while 24 were only observed for part of the year.

At each selected burrow we deployed a camera trap to capture images of commensal species. These camera traps monitored burrows from August 1st, 2018 to August 1st, 2019, with cameras checked every two weeks to ensure functionality, battery life, and storage capacity. We used Bushnell Nature View HD Max Model 119740 cameras, with close-focus lenses, capable of capturing images by sensing movement and heat. All parameter settings were standardized across cameras with each camera taking two pictures and a 10 second video each time it was triggered (Table 1). Because the IR flash was too bright at nighttime, producing white-out images, we placed yellow electrical tape over the IR flash to capture clear images at night. Our cameras were placed on stands constructed from a 45cm piece of 8.5x3.5cm wood with two 2.5cm holes drilled on each side. Two 19.05mm diameter PVC pipes, at a length of 100cm, were then placed firmly in each hole (Figure 2). This setup was designed to face the cameras straight down to maximize image quality, standardize the distance from where images were captured, and to gain an even profile of the commensal species that visited the burrow. When placing a camera directly above a burrow was infeasible due to vegetation, we placed them on the ground facing the burrow entrance outside of the burrow’s apron, approximately 100cm away from the burrow entrance (Figure 2). We downloaded camera trap photographs whenever a memory card reached over 500 pictures and saved files with the identity of the burrow and the date.

Image Processing

Four observers processed all images and videos and entered all corresponding metadata into an excel database by hand, which was then extensively quality checked by the lead author. We excluded all non-target pictures (i.e. pictures without wildlife) from the image processing. Images and videos from multiple triggers were combined to represent a singular behavioral event by an individual organism. A single behavioral event could include anywhere from a single image to hundreds. Individual behavioral events were distinguished by a behavioral change in a focal organism or period of inactivity greater than two minutes (i.e., if an organism was observed performing the same behavior twice in less than two minutes, it was counted as a single event, but if more than two minutes had elapsed, it was counted as two events). We identified species using fauna guides and consultation with experts. We assigned behaviors using the available pictures and video for each burrow interaction following an ethogram (Table 2) based on those used in other burrow behavioral studies (Aya-Cuero et al. 2017, Dziadzio & Smith 2016, White & Tuberville 2017). Our analysis focused on the most frequently observed behaviors as detailed in the ethogram. All other behaviors were rare and coded as “other”. For each behavioral “event”, we recorded burrow ID, species, date, time, temperature, duration of event, behavior, and image number. Taxa where classified into nine different categories: armadillos, birds, crustaceans, reptiles, mesopredators (*P. lotor* and *D. virginiana*), rodents, shrews, small mammals (*S. carolinensis* and *S. palustris*) and other (*D. dama* and unidentified animals).

Data Analysis

We quantified the total number of burrow behavioral events (an independent observation of an animal interacting with a burrow) based on taxonomic category, species, behavior and habitat. Species diversity for each burrow was calculated with the Shannon-Wiener diversity index using the “vegan” package (Oksanen et al. 2019) while species richness was determined as the number of species observed per individual burrow. All analyses were performed in program R (R Core Team 2019). Species relative abundance index (RAI) was calculated by species as the number of individual events divided by number of camera trap days multiplied by one hundred (O'Brien et al, 2003). We calculated species naïve occupancy as the proportion of sites that recorded at least one event by an individual species (Mackenzie et al. 2006). Mean species richness and species diversity were compared across habitats using the two-sample student’s t-test. Differences between taxa habitat use and behavior were compared using a chi-square tests.

To quantify the overlap between the burrow activity patterns of armadillos and other species of interest, we used the approach developed by Ridout and Linkie (2009). First, we estimated a species’ activity pattern using circular kernel density estimates which treat events as random samples from an underlying continuous distribution instead of grouping them into discrete time categories. The proportion of activity for each time period was then calculated by incorporating the areas under the activity curve for each respective period that corresponded to the probability of observing the animal during that time period. We then calculated the coefficient of overlap (Δ) between species, which varies from 0 (no overlap), to 1 (complete overlap) (Ridout & Linkie 2009). The package “camtrapR” (Niedballa et al. 2016) was used for all daily activity overlap estimates.

Results

A total of 4,497 events were recorded from 11,356 pictures and 3,907 videos with an effort of 4,004 trap nights. In total there were 49 species documented, not including unknown animals. We documented 22 species of birds, 12 species of reptiles, 13 species of mammals, and 3 species of crustaceans. Seventeen (35%) species were documented in both habitats while 20 (DC: 41%) and 12 (MF: 24%) species were unique to their respective habitat. Thirty-three species (67%) were documented interacting with burrows in some way, including 26 (53%) species not previously reported in the literature as associates of armadillo burrows. Hispid cotton rats (*Sigmodon hispidus*; 22%; RAI = 24.251), armadillos (19%; RAI = 21.528), and marsh rice rats (*Oryzomys palustris*; 12%; RAI = 13.462) were the three most common species documented, making up 53% of all event recordings. These animals also had the highest RAI values respectively. 11 species (22%; RAI = 0.025) were only documented once during the duration of the study. Armadillos (0.931), northern raccoons (*Procyon lotor*; 0.690), and *S. hispidus* (0.690) had the highest naïve occupancy rates while 16 species had a low occupancy rate of 0.034 (Table 5). Although mean species richness ($t_{27} = 1.18$, p = 0.25) and species diversity ($t_{27} = 1.48$, p = 0.15; Table 3) were not different across habitats, differences in taxa habitat use were statistically significant (X^2 (8, N = 4497) = 1757.799, P < 0.001; Fig 3.).

The most frequently observed behavior was "passing by" (N = 1669; 37%), while the least documented behavior was "vigilance" (N=72; 2%). The behavior that was documented across the most species was inspecting burrow (27 species); followed by foraging (23), burrow use (21), other (18), and investigating camera (13) (Table 5). Burrow behavior was significantly different across taxa (X^2 (48, N = 4497) = 1330.558, P < 0.001), with reptiles (50%), armadillos (34%), and mesopredators (24%) primarily engaging in burrow use, whereas small mammals (33%), rodents (33%) and crustaceans (18%) primary engaged in burrow inspection, and shrews (28%) and birds (20%) were most frequently observed foraging (Table 4).

Temporal armadillo activity patterns moderately differed between habitats ($\Delta_1 = 0.60$), with armadillos in the maritime forest being more diurnally active (Fig. 4). Armadillos also displayed relatively high (>0.75) species activity overlap with other mesocarnivores (*P. lotor*: $\Delta_1 = 0.86$, *D. Virginiana*: $\Delta_1 = 0.77$) present on the island (Fig. 5). Armadillos had moderate and high activity overlap with *S. hispidus* ($\Delta_1 = 0.56$) and *O. palustris* ($\Delta_1 = 0.73$) respectively (Fig. 6).

Discussion

This is the first long-term study to document and describe the commensal vertebrate use of nine-banded armadillo burrows using game cameras. We observed that on a barrier island to which they are considered invasive, armadillos provide not only refugia for native species, but possible foraging resources as well. While the most common commensal species were rodents, we also documented numerous records of passerine birds, mesopredators, and herpetofauna. The commensal usage of these burrows is comparable to, if not greater than, that of gopher tortoises (*Gopherus polyphemus*), which is considered a keystone species and ecosystem engineer (Lips 1991, Dziadzio & Smith 2016, White & Tuberville 2017, Hipps 2019). While the distribution of these two species overlaps, LSSI does not have tortoises or any other medium-sized burrowing species. Our study illustrates that armadillo burrows are clearly being used by native island taxa and provides novel information that can be used as a baseline for future evaluations of the frequency of vertebrate taxa use of armadillo burrows.

The most obvious benefit of armadillo burrows is the refugia they provide to other species. Armadillos are primary excavators that dig and use multiple burrows, switching among burrows throughout the year (Kinlaw 1999, Bond et al. 2000, Loughry & McDonough 2013). This means that there are possibly several burrows in any given habitat that are not being used by armadillos and are available as refugia for commensal species without the need for co-occupancy. We documented several species (raccoons, opossums, shrews, rattlesnakes, kingsnakes) using burrows as temporary dens, and although we could not ID these animals as individuals, we suspect some individual organism were using the dens for extended periods of time. It should be noted that although we did document any co-occupancy between any of the species recorded during this study, it is possible that armadillo burrows serve as openings/exits to smaller burrow systems used by other semi-fossorial species that allows for inter-specific coexistence (Kowalczyk et al. 2008, Mori et al. 2015, Mukherjee et al. 2019). While burrows are most likely to be used as refugia from extreme heat on a subtropical island like LSSI (Walde et al. 2009, Pike & Mitchell 2013), they have also been documented as overwintering and birthing sites for *C. adamanteus* (Means 2017). Additionally, we documented a diamondback terrapin (*Malaclemys terrapin*) nesting in an armadillo burrow during the pilot work for this study, which provides anecdotal evidence that burrows are used as nesting sites by native egg-laying species (Butler & Tweedy 2018). These documented interactions suggest that removal of this burrowing species could negatively affect populations of native island species (Fleming et al. 2014).

Foraging at the burrow apron and inside the burrow was primarily documented in passerine birds and rodents. Foraging activity at the burrows seemed to be related to the surrounding vegetation as several species appeared to target specific plants. *S. hispidus* were documented eating beach pennywort (*Hydeocotyle* spp.) on multiple occasions while yellow-rumped warblers (*Setophaga coronata*) were seen eating wax-myrtle (*Morella cerifera*) berries in the dune complex, and eastern gray squirrels eating southern live oak (*Quercus virginiana*) acorns in the maritime forest. Previous research on other burrowing species suggests that increased foraging resource (i.e. insects, seeds, legumes, fruit) availability could be due to increased nutrient deposition facilitated by the burrow organism (White &Tuberville 2017, Fafard et al. 2020). It is also worth noting that armadillos often create foliage nests within their burrows, and these may provide important microhabitat for invertebrates, which then in turn could attract insectivorous birds and mammals (Clark 1951, Eisenberg & Kinlaw 1999).

Several species were recorded as having “other” interactions with burrows, and it is our belief that several of these interactions could be ecologically significant. Other behaviors of interest included nest building (armadillos, shrew spp., *D. virginiana*, & *O. palustris*), dust bathing (Carolina wren - *Thryothorus ludovicianus*), basking (*L. getula* & *C. adamanteus*), and courtship (armadillos & *L. getula*). We believe that nest building by commensal species at armadillo burrows supports the idea that native species can and will take over these burrows as their own for substantial periods of time. Documented behaviors such as dust bathing, basking and courtship help illustrate that the uses of these burrows can be species specific and serve a variety of purposes. While many of these observations were anecdotal, they are still indicators of native species use of armadillo burrows and are behaviors that could warrant further research.

Armadillo activity was greater in the maritime forest with only moderate activity time overlap with armadillos from the dune complex. Armadillos in the maritime forest had higher diurnal activity from approximately 11:00-18:00 compared to the nocturnal behavior of dune complex armadillos. These disparities are most likely explained by the much higher ground temperatures found in the dune complex habitat, where canopy cover is limited. While armadillo activity patterns from previous studies indicate that juveniles are much more diurnally active compared to adults (McDonough & Loughry 1997), most of the individuals observed in the maritime forest appeared to be adults. Habitat fragmentation has also been shown to increase diurnal activity in armadillos (Norris et al. 2010), but this also seems to be an unlikely cause given the island is minimally developed. Seasonal activity shifts in armadillos have been documented and it is thought that air temperature and cloud cover are driving factors (McDonough & Loughry 1997, Green et al. 2016). All this information suggests that armadillos are flexible in the timing of their activity patterns, and these patterns can vary across season as well as habitat depending on ambient environmental conditions.

There was high activity overlap between armadillos, *P. lotor* and *D. virginiana*, indicating coexistence with sympatric mesocarnivores (Almeida Jácomo 2004, Zhao 2020). Armadillos are most likely capturing distinct prey species, because they are primarily insectivores (Whitaker et al. 2012, Loughry & McDonough 2013), whereas raccoons and opossums are both omnivorous with diets including plant material as well as carrion and diverse animal prey (Harman & Stains 1979, Gardner 1982). The primary commensal rodents (*S. hispidus* & *O. palustris*) also had moderate to high activity overlap with armadillos, but these species are primarily herbivorous and carnivorous respectively (Cameron & Eshelman 1996 & Sharp Jr. 1967). While one could argue that there could be direct foraging competition between armadillos, *P. lotor*, and *O. palustris*, we believe that the dune complex habitat in which they co-occur offers extensive prey resources for all three species in the form of fiddler crabs (*Uca* spp.). Although armadillos have not been directly observed utilizing fiddler crabs as a food resource, it is possible they comprise part of armadillos' diets on these island systems. Overall, our activity analysis supports the idea of coexistence between this invasive species and several native ones based on differentiation in diet and possible resource partitioning.

While we believe this study is an important first step in documenting and understanding the commensal burrow ecology on nine-banded armadillos, it is not without limitations. First, we did not investigate what invertebrates (other than crustaceans) were using these burrows, which would have required a different set of methods. Secondly, we recommend that future studies documenting vertebrate commensal biodiversity of armadillo burrows make their studies taxa-specific, as different camera methodologies work better for some species than others. For instance, we recommend the use of video to document the commensal use of burrows by birds and rodents as they are often moving too fast to obtain clear photos. Conversely, picture documentation is effective to document burrow use by small- to medium-sized mammals. While detection biases for this study were unknown, we suspect increased imperfect detection for herpetofauna species specifically due to their ectothermic nature (Meek et al. 2012). Lastly, and most importantly, we suggest using control (non-burrow) camera locations in future studies in order to quantify the influence of armadillos and their burrows on commensal species assemblage and usage.

Conclusions

Although our results only represent a single year of burrow monitoring, they demonstrate several unappreciated interactions between nine-banded armadillos and native island species. While the significance of these interactions remains unknown, we believe this study highlights the potential importance of armadillo burrows as refugia structures across a barrier island landscape. We also believe that nine-banded armadillos should be considered alongside the gopher tortoise as a burrowing ecosystem engineer across the coastal plain, rather than an invasive species in need of management. *C. adamateus* and *L. getula* are considered apex predators on the island and are thought to have decreasing populations throughout the southeast (Means 2017, Godley et al. 2017). Because these species of island conservation concern were documented using burrows, we suggest island managers proceed with caution when considering removal of armadillos. We would also argue that conservation funding that includes the removal of armadillos would be better used on other coastal invasive species like feral hogs (*Sus scrofa*), which are voracious predators of sea turtle eggs (Butler et al. in review) and have been documented to decrease native island biodiversity (Barrios-Garcia & Ballari 2012, Nogueira-Filho et al. 2009).

Table 3.1. Standardized game camera parameters that were used throughout the study. Details camera setting with a brief explanation for why each selection was used.

Parameter	Setting	Explanation
Mode	Hybrid (Camera & Video)	Allowed for easy observation of behaviors
Image Size	8m pixel	Highest photo quality for species identification
Image Format	Full Screen	Easier to view entire organism
Capture Number	Two Images	Allowed for behavior prediction before video started
Video Length	10 Seconds	Allowed sufficient time to monitor species behavior
LED Control	Low	The lowest, setting, and tape over LED lens prevented white-out videos at night
Interval	Two Seconds	Allowed for continuous documentation of species behavior
Sensor Level	Low	Prevented excessive photos from shade and vegetation movement
NV Shutter	High	Produced clearest night photos

Table 3.2. Ethogram used for focal behavior observations of various species while interacting with nine-banded armadillo burrows.

Behavior	Description
Burrow Use	Entering, exiting, or inside the burrow
Foraging	Looking for food, eating, drinking
Inspects Burrow	Looks at, sniffs at, or orients towards burrow
Investigating Camera	Any examination of the camera or stand apparatus
Passing By	Movement past the burrow with no interaction
Vigilance	Animal is alert, attentive standing or sitting
Other	Any behavior that deviates from the previously defined behaviors

Table 3.3. Study parameters and burrow characteristics for the maritime forest and dune complex habitats on Little St. Simons Island, GA. USA. Values in parentheses represent standard error unless noted otherwise.

Parameter	Dune Complex	Maritime Forest
Camera trapping days	1908	2096
Burrows Monitored	17	12
Mean trap days per Burrow	174.67 (23.68)	112.23 (34.99)
Mean Burrow Spp. Richness[a]	12.00 (1.74)	9.17 (1.41)
Mean Burrow Spp. Diversity[a]	1.71 (0.12)	1.43 (0.15)
Species Documented	37 (20)[b]	29 (12)[b]
Mean Burrow Length	101.41(11.88)	115.17 (11.83)
Mean Burrow Height	17.12 (0.44)	17.08 (0.89)
Mean Burrow Width	19.00 (0.58)	23.17 (1.40)

[a] Species Richness (*t* (27) = 1.18, p = 0.25) and Species Diversity (*t* (27) = 1.48, p = 0.15) were not significantly different across habitats.

[b] Value represents the number of species found only in that habitat

Table 3.4. Comparison of various taxa primary burrow behavior and passing-by behavior. Percentages represent the proportion of behavior compared to the total count.

Taxa	N	Primary Behavior	Passing By
Armadillo	862	Burrow Use (34.34%)	32.83%
Birds	778	Foraging (20.31%)	48.20%
Crustacean	53	Inspects Burrow (18.87%)	47.17%
Reptile	226	Burrow Use (50.44%)	23.89%
Mesopredator	410	Burrow Use (24.15%)	33.41%
Other	49	Investigating Camera (14.29%)	69.39%
Rodent	1852	Inspect Burrow (31.91%)	35.04%
Shrew	187	Foraging (27.81%)	42.25%
Small Mammal	80	Inspects Burrow (32.50%)	41.25%

[*] Burrow behavior was significantly different across taxa (X^2 (48, N = 4497) = 1330.558, P < 0.001).

Table 3.5. Documented species list with total counts (N), relative abundance index (RAI), naïve occupancy (NO), behavior proportions: Burrow Use (BU), Foraging (F), Inspects Burrow (IB), Investigating Camera (IC), Other (O), Passing By (PB), and Vigilance (V), and habitat detected (Dune Complex: Maritime Forest).

	Species	**Common Name**	**F**	**RAI**	**NO**	**BU**	**F**	**IB**	**IC**	**O**	**PB**	**V**	**Habitat**
Mammalia	*Sigmodon hispidus*	Hispid Cotton Rat	971	24.251	0.690	9%	24%	31%	0%	0%	33%	2%	888:83
	Dasypus novemcinctus	Nine-banded Armadillo	862	21.528	0.931	34%	10%	20%	1%	2%	33%	0%	288:574
	Oryzomys palustris	Marsh Rice Rat[a]	539	13.462	0.414	25%	14%	31%	1%	1%	28%	1%	522:17
	Procyon lotor	Northern Raccoon[a]	228	5.694	0.690	17%	3%	22%	22%	3%	33%	0%	59:169
	Mouse spp.	Mouse spp.	190	4.745	0.310	8%	5%	58%	0%	0%	29%	0%	DC
	Shrew spp.	Shrew spp.[a]	187	4.670	0.138	26%	28%	3%	0%	1%	42%	0%	MF
	Didelphis virginiana	Virginia Opossum	182	4.545	0.621	33%	1%	23%	7%	2%	34%	1%	38:144
	Sylvilagus palustris	Marsh Rabbit[a]	61	1.523	0.483	0%	10%	43%	11%	0%	36%	0%	45:16
	Sciurus carolinensis	Eastern Gray Squirrel[a]	19	0.475	0.103	0%	42%	0%	0%	0%	58%	0%	MF
	Rattus Rattus	Roof Rat[a]	9	0.225	0.103	33%	0%	44%	0%	0%	22%	0%	7:2
	Dama dama	Fallow Deer[a]	4	0.100	0.034	0%	75%	0%	0%	25%	0%	0%	MF
	Rattus norvegicus	Norway Rat[b]	2	0.050	0.034	0%	0%	0%	0%	0%	100%	0%	MF
Aves	*Thryothorus ludovicianus*	Carolina Wren[a]	222	5.544	0.655	3%	18%	18%	1%	14%	40%	6%	18:204
	Setophaga coronata	Yellow-rumped Warbler[a]	129	3.222	0.138	0%	23%	0%	4%	0%	67%	5%	127:2
	Dumetella carolinensis	Gray Catbird[a]	94	2.348	0.241	0%	20%	5%	22%	20%	27%	5%	54:40
	Troglodytes aedon	House Wren[a]	81	2.023	0.276	0%	20%	38%	2%	5%	33%	1%	DC
	Toxostoma rufum	Brown Thrasher[a]	79	1.973	0.241	0%	16%	10%	1%	0%	70%	3%	DC
	Pipilo erythrophthalmus	Eastern Towhee[a]	64	1.598	0.276	0%	34%	9%	3%	2%	45%	6%	DC
	Geothlypis trichas	Common Yellowthroat[a]	27	0.674	0.241	0%	22%	26%	7%	7%	33%	4%	26:1
	Melospiza melodia	Song Sparrow[a]	15	0.375	0.103	0%	53%	13%	0%	7%	27%	0%	DC
	Cardinalis cardinalis	Northern Cardinal[a]	12	0.300	0.103	0%	8%	8%	0%	0%	83%	0%	4:8
	Seiurus aurocapilla	Ovenbird[b]	9	0.225	0.138	0%	0%	0%	0%	0%	100%	0%	2:7
	Agelaius phoeniceus	Red-winged Blackbird[b]	7	0.175	0.103	0%	0%	0%	0%	14%	86%	0%	DC
	Zenaida macroura	Mourning Dove[b]	2	0.050	0.034	0%	0%	0%	0%	0%	100%	0%	DC
	Passerculus sandwichensis	Savannah Sparrow[a]	2	0.050	0.069	0%	100%	0%	0%	0%	0%	0%	DC

	Setophaga palmarum	Palm Warbler[b]	2	0.050	0.069	0%	0%	0%	100%	0%	0%	0%	DC
	Archilochus colubris	Ruby-throated Hummingbird[b]	1	0.025	0.034	0%	0%	100%	0%	0%	0%	0%	MF
	Rallus crepitans	Clapper Rail[b]	1	0.025	0.034	0%	0%	0%	0%	0%	100%	0%	DC
	Setophaga caerulescens	Black-throated Blue Warbler[b]	1	0.025	0.034	0%	0%	0%	0%	0%	100%	0%	DC
	Quiscalus major	Boat-tailed Grackle[b]	1	0.025	0.034	0%	0%	0%	0%	0%	100%	0%	DC
	Cistothorus platensis	Sedge Wren[b]	1	0.025	0.034	0%	0%	100%	0%	0%	0%	0%	DC
	Setophaga ruticilla	American Redstart[b]	1	0.025	0.034	0%	0%	0%	0%	100%	0%	0%	DC
	Catharus guttatus	Hermit Thrush[b]	1	0.025	0.034	0%	0%	0%	0%	0%	0%	100%	MF
	Turdus migratorius	American Robin[b]	1	0.025	0.034	0%	0%	0%	0%	100%	0%	0%	MF
Reptilia	*Crotalus adamanteus*	Eastern Diamond-back Rattlesnake	77	0.050	0.448	40%	0%	34%	0%	6%	16%	4%	67:10
	Coluber constrictor	Black Racer[a]	46	1.224	0.345	37%	2%	30%	0%	0%	30%	0%	43:3
	Lampropeltis getula	Kingsnake	26	1.149	0.172	73%	0%	8%	0%	15%	4%	0%	25:1
	Coluber flagellum	Coachwhip[a]	10	0.649	0.034	100%	0%	0%	0%	0%	0%	0%	DC
	Thamnophis sirtalis	Gartersnake[a]	4	0.100	0.138	25%	0%	0%	0%	0%	75%	0%	MF
	Pantherophis alleghaniensis	Yellow Ratsnake[a]	3	0.075	0.103	100%	0%	0%	0%	0%	0%	0%	MF
	Agkistrodon conanti	Florida Cottonmouth[a]	1	0.025	0.034	100%	0%	0%	0%	0%	0%	0%	MF
	Plestiodon spp.	Skink spp.[a]	50	1.249	0.241	57%	0%	2%	0%	0%	41%	0%	MF
	Aspidoscelis sexlineata	Eastern Six-lined Racerunner[b]	4	0.250	0.138	0%	0%	25%	0%	0%	75%	0%	3:1
	Anolis carolinensis	Green Anole[a]	3	0.100	0.034	67%	0%	33%	0%	0%	0%	0%	DC
	Ophisaurus ventralis	Eastern Glass Lizard[b]	1	0.075	0.034	0%	0%	0%	0%	0%	100%	0%	MF
	Malaclemys terrapin	Diamondback Terrapin	1	0.025	0.034	100%	0%	0%	0%	0%	0%	0%	DC
Malacostraca	*Ocypode quadrata*	Atlantic Ghost Crab[a]	29	0.724	0.172	14%	24%	28%	0%	0%	28%	7%	DC
	Uca pugnax	Sand Fiddler Crab[b]	19	0.475	0.103	0%	0%	0%	0%	0%	84%	16%	DC
	Armases cinereum	Wharf Crab[a]	5	0.125	0.069	0%	40%	40%	0%	0%	20%	0%	DC
Unidentified	Unidentified	Rodent spp.	141	3.521	0.448	0%	0%	4%	16%	4%	76%	0%	137:4
	Unknown Animal	Unknown Animal	45	1.124	0.241	0%	4%	0%	8%	4%	81%	4%	28:17
	Unknown Bird	Bird spp.	26	0.649	0.517	3%	3%	9%	6%	1%	79%	0%	26:0

[a] Species recorded for the first time as a nine-banded armadillo burrow associate.

[b] Species only observed and not considered a commensal or burrow associate.

Figure 3.1. Map of Little St. Simons Island. Habitats studied include the Maritime Live Oak Forest (Blue) and the Dune Complex (Yellow).

Figure 3.2. Example of the two types of camera setups used during study. (A) Setup with camera above burrow, (B) Setup with camera across from burrow. Cameras set up across from the burrow have increased risk of being blocked or covered by excavated soil.

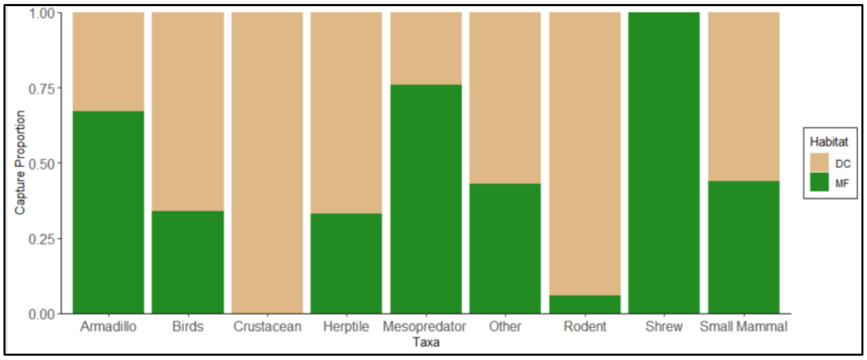

Figure 3.3. Comparison of taxa capture proportions in the dune complex and maritime forest. Differences between taxon habitat use were statistically significant (X^2 (8, N = 4497) = 1757.799, P < 0.001).

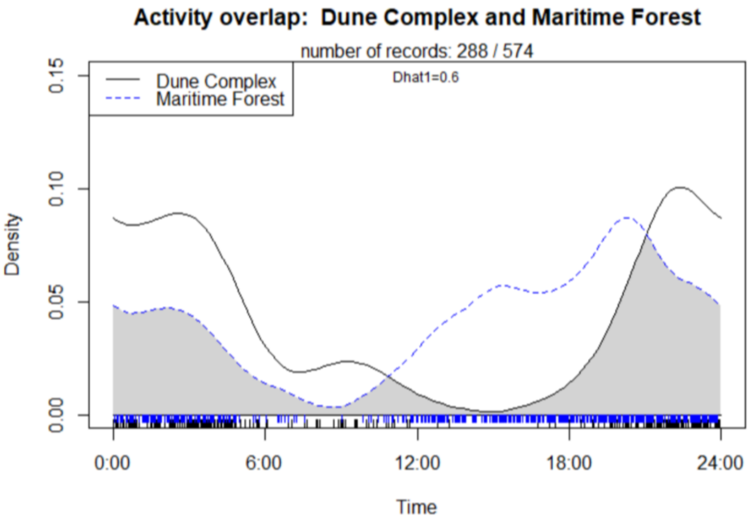

Figure 3.4. Coefficient of activity overlap between nine-banded armadillos in the dune complex (N = 288) and maritime forest (N =574) habitats on LSSI. Overlap is Dhat1 value which is represented by shaded area. Time is in military time.

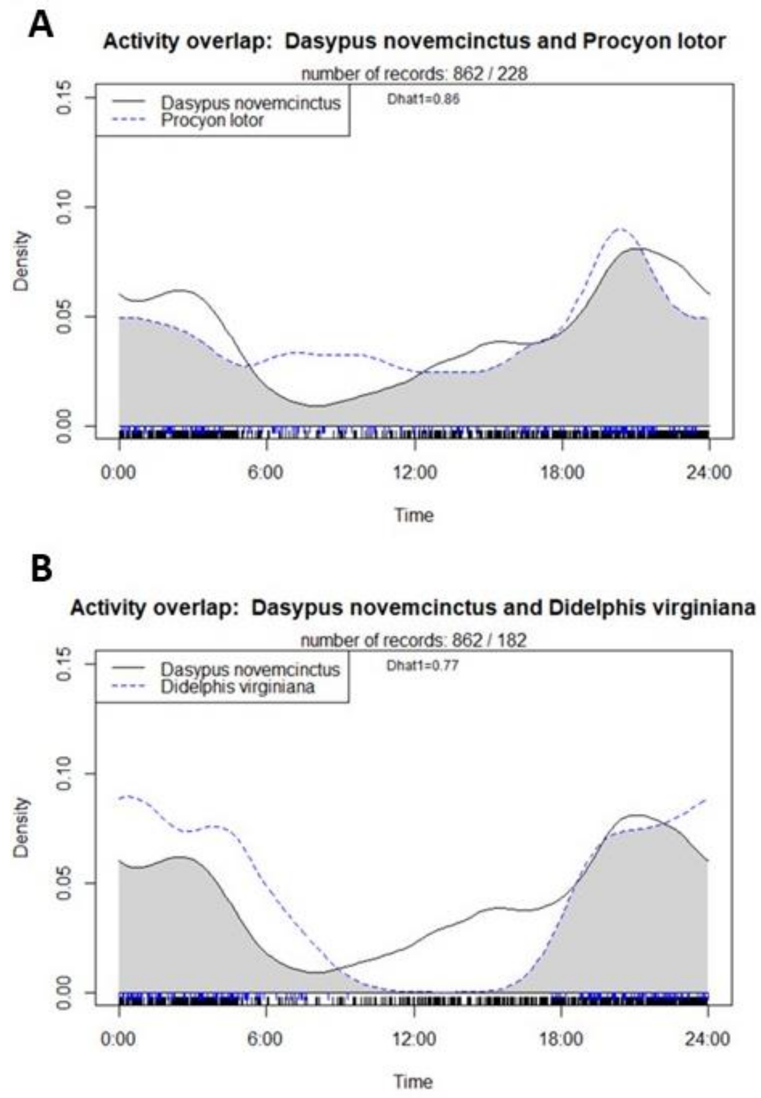

Figure 3.5. (A) Coefficient of activity overlap between nine-banded armadillos (*Daypus novemcinctus*; N = 862), northern raccoons (*Procyon lotor*; N = 228), and (B) Virginia opossums (*Didelphis virginiana*; N = 182) at burrows on LSSI. Overlap coefficient is Dhat1 value which is represented by shaded area. Time is in military time.

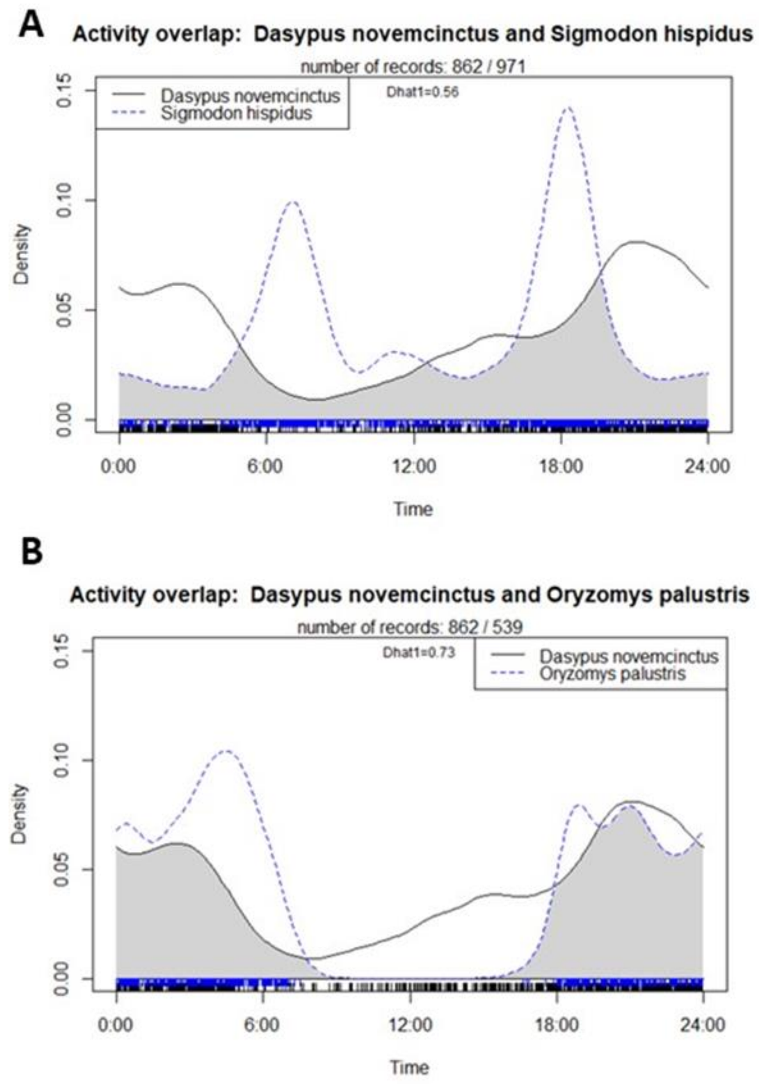

Figure 3.6. Coefficient of activity overlap between nine-banded armadillos (*Dasypus novemcinctus*; N = 862), hispid cotton rats (*Sigmodon hispidus*; N= 971), and marsh rice rats (*Oryzomys palustris*; N = 539) at burrows on LSSI. Overlap coefficient is Dhat1 value which is represented by shaded area. Time is in military time.

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CHAPTER 4

GENERAL CONCLUSIONS & RECOMMENDATIONS

Managers and decision makers have a professional and an ethical responsibility to understand an organism's natural history and the importance of its ecological niche before applying habitat or population interventions. Prior to this study, the essential question of whether we should actively manage armadillo populations could not be answered based on our depauperate understanding of the species' ecological interactions. Understanding the extent of armadillo foraging and burrow ecology helps to elucidate the interactions this species has with native taxa and if it is truly in need of management on barrier island ecosystems.

I found over the last decade that armadillos have not caused dramatic depredation rates of loggerhead sea turtle nests across Georgia's barrier islands compared to other native and non-native predators. Because armadillos are considered an invasive species on the Georgia coast, some island managers have argued for including them in predator removal programs, especially because they are capable of burrowing under nest screens. However, my data do not support the inclusion of armadillos in large scale removal programs on the coast. I suggest island managers focus their time, effort, and funds into managing disparate invasive predators like feral hogs and coyotes. However, the removal of individual problem armadillos seems to be effective and is encouraged in limiting nest depredations. The objective of the Georgia Sea Turtle Cooperative to keep sea turtle nest depredation below 10% annually has been met, and it seems that the <1% total egg loss cause by armadillos is a tolerable amount.

I found that passerine birds, rodents, mesopredators and snakes use armadillo burrows as refugia and foraging grounds. While the burrows are used as long-term dens by some species, others are using them as temporary shelter. Birds and small mammals use burrows as foraging grounds, which indicates that there could be an indirect boost of resources offered by these burrows. Due to these documented benefits, I believe that nine-banded armadillos should be considered a burrowing ecosystem engineer rather than an invasive species in need of management for the islands. I advise island managers to proceed with caution when contemplating management for this specie as changes in the availability of these burrow resources could have a negative impact on the species that have grown accustomed to using them. Further documentation of commensal invertebrates as well as species-focused research is needed in order to further understand how commensal species may be benefiting from these structures. Research directly comparing armadillo and gopher tortoise burrow use is also needed to determine if armadillos are having similar positive effects as this well-known keystone species.

The nine-banded armadillo is, in my opinion, highly misunderstood and unfairly maligned in the southeast. The species may in fact provide benefits besides ecosystem engineering. Armadillos could contribute to ecosystem services like nutrient cycling, seed dispersal, and pest control, although there is a need for research on the links between these ecosystem functions and services. I argue that if we are going to continue to classify this species as invasive, we also need to conduct more research into the actual economic cost of armadillos in novel ecosystems such as urban areas. A comprehensive ecosystem services approach to the role of armadillos could reveal that this species is much more valuable than we imagined.